Ecosystem services and disservices in small-scale tropical agriculture

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The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and other authors to this work has been explicity indicated in the Declaration section. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Declaration

The work contained in this thesis has involved collaborations with Tim Benton (TB), Luisa Carvalheiro(LC), Robert Copeland (RC), Felicty Edwards (FE), Lucas Garibaldi (LG), Mary Gikungu (MG), Jayne Macharia (JM), Darius Kimuzi (DK), Nathaniel Mkombola (NM), Joseph Mugambe (JM), Morris Mutua (MM), Benson Mwachala (BM), Peter Andrew Lombo Mwasi (PM), Claire Quinn (CQ), Steve Sait (SS), Gorm Shackelford (GB) and Claire Wordley (CW). Their contributions are listed below:

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Chapters 3 & 4: DK, NM, BM and PM assisted with data collection. RC, MG, JM, JM and MM identified insect specimens. CW and FE provided advice regarding the functional ecology analyses in Chapter 4.

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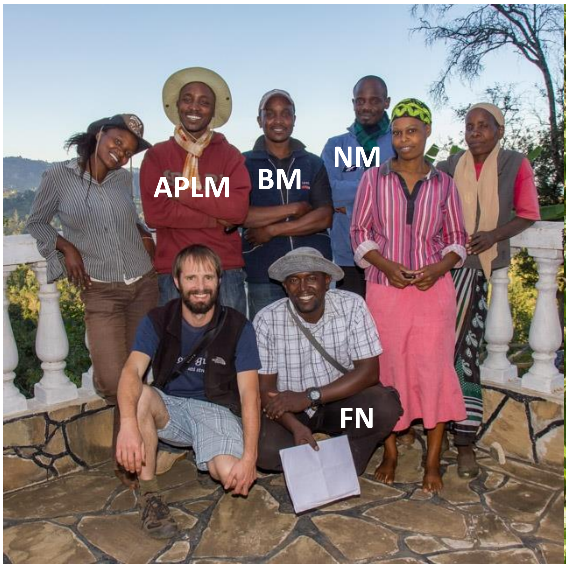

Abstract

Small-scale farmlands are dynamic systems crucial to the food-security and livelihoods of more than two billion people and there is political pressure in many developing nations to consolidate and expand small farms into larger units of management. This could have consequences for agro-ecosystem processes and the ecosystem services and disservices that regulate crop production. This thesis aims to highlight and address these issues in smallholder farming landscapes, which are poorly studied and represent significant knowledge gaps.

Research on pollination and biological control is biased towards large-scale systems, and biological control research shows a strong geographic bias to temperate developed nations, whilst pollination research is geographically more balanced. To have more impact on global issues of poverty and food-security, agricultural ecosystem service research needs to have a greater focus on small-scale farmed landscapes.

In a low-input, small-scale farmed area of Kenya, the response to land-use intensification of insect groups important to ecosystem services and disservices for crop production was examined. Small ecotone pollinators responded negatively to intensification, but larger bees did not. Natural enemies did not show a strong negative response to land-use intensification, which suggested that low pesticide application rates allowed cultural species to persist in croplands. The functional richness of Hymenoptera and Coleoptera was highest in the most intensified land-use context, which provides support for the intermediate landscape complexity hypothesis. Functional evenness and trait-environment associations showed that phytophagous traits increased with land-use intensification and could be linked to increased ecosystem disservice if crops are consumed.

Smallholder interviews showed that ecosystem disservices due to crop-raiding animals were a major problem and that attitudes to wildlife, elephants and protected areas became more negative with increasing proximity to large areas of wilderness. However, increasing the proportion of natural habitat in the vicinity of smallholdings moderated the negative effect of proximity to wilderness on attitudes towards protected areas. Thus, perceived ecosystem disservices may vary with land-sparing at different spatial scales (i.e., conserved habitat).

Whilst this thesis demonstrates that land-use intensification of early stage small-scale farming landscapes affects human perceptions and attitudes towards nature and the taxonomic and functional composition of cropland insect communities, direct quantification of the crop yield and economic consequences of this is sorely needed. Assessment of actual vs. perceived ecosystem disservices would also aid the conservation measures needed to make land-sparing work.

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Abbreviations

CIs	Confidence intervals
ES	Ecosystem service
FAO	Food and Agriculture Organisation of the United Nations
FDis	Functional dissimilarity
FDiv	Functional divergence
FEnt	Functional entropy
FEve	Functional evenness
Fide	Functional identity
FOri	Functional originality
FRic	Functional richness
FSpe	Functional specialisation
GOF	Goodness-of-fit
LSLM	Land sparing linking mechanism
MAM	Minimum adequate model
MST	Minimum spanning tree
PCA	Principal components analysis
PCOA	Principal coordinates analysis
RLQ	A double inertia analysis of two arrays (R and Q) with a link expressed by a contingency table (L)

Chapter 1. General introduction

1.1. Setting the scene: Consequences of increasing global land demand

Increases in global human population and per capita commodity consumption (Tilman et al. 2011; Alexandratos and Bruinsma 2012) are leading to increased demand for land (Lambin and Meyfroidt 2011; Fischer et al. 2014). In conjunction with global climate change (Schmidhuber and Tubiello 2007; Bajželj et al. 2014) this poses a serious threat to what remains of global biodiversity (Pereira et al. 2010; Newbold et al. 2014) and to the stability of future commodity production and food-security (Godfray et al. 2010; Foresight 2011). Sir John Beddington's 'perfect storm' describes a future scenario in 2030 that results in simultaneous global shortages of food, water and energy unless their availability can be substantially increased (30-50%) (Beddington 2009). Global agricultural productivity is also heavily reliant on phosphorous and as this is also predicted to reach peak production in 2030, new approaches of conserving or provisioning phosphorous in farmlands will be required (Cordell et al. 2009). In the last century global biodiversity has drastically diminished and continuing habitat loss and degradation, over-exploitation, disease, pollution, climate change, ocean acidification and spread of invasive species suggest the situation will only become worse (Butchart et al. 2010). Projections consistently indicate that biodiversity declines will continue throughout the 21st century (Pereira et al. 2010) and some studies postulate we are already in the midst of the Earth's sixth mass extinction event (Barnosky et al. 2011). In response contemporary science has provided many ideas and tools for mitigating increasing demands on global land resources and future scenarios of food insecurity that minimise biodiversity losses and/or erosion of agro-ecosystem functioning. These include the sustainable intensification of agriculture (Pretty 2008; Davies et al. 2009; Bommarco et al. 2013), trade-off analysis for the optimal spatial design of landscapes for biodiversity and commodity production (e.g., Licker et al. 2010; Fischer et al. 2014; Phalan et al. 2014), changing demand and diets (Bajželj et al. 2014), increasing commodity utilisation efficiency (Gustavsson et al. 2011; Bajželj et al. 2014), climate smart agriculture (Scherr et al. 2012; Campbell et al. 2014) and improving access to commodities (Brinkman et al. 2010; Foresight 2011). Using all these tools and theories, the mitigation of global land, food and biodiversity issues requires ambitious inter-disciplinary approaches at multiple socio-political, spatial and temporal levels. Ecology has a particularly strong role to play in the sustainable intensification of farmland via the ecosystem services framework (Daily 1997; Carpenter et al. 2009; Poppy et al. 2014) and spatial optimisation of the farmland landscape for commodity production, livelihoods, biodiversity and sustainability at multiple scales (Green et al. 2005).

1.2. Sustainable intensification and ecosystem services to increase commodity production with reduced environmental costs

Ecosystem services are benefits that humans derive from ecosystems or processes (Costanza et al. 1997) or conditions that lead to benefits for humans (Daily 1997) and, as such, the concept links ecology and society. Ecosystem services are broadly divided into four categories in the Millennium Ecosystem Assessment: 1) supporting services, such as nutrient cycling and soil formation; 2) provisioning services, such as food, fibre, fuel and water; 3) regulating services, such as crop pollination, pest control and water purification; and 4) cultural services, such as education, recreation and aesthetic value (MEA 2005; Bommarco et al. 2013). Biodiversity is crucial for many of the supporting and regulating ecosystem services from which provisioning ecosystem services are derived and therefore loss of biodiversity is a threat to the global production of commodities (Rands et al. 2010; Thompson et al. 2011; Macfadyen et al. 2012). In modern agro-ecosystems reductions in biodiversity and associated ecosystem services are compensated for through the use of external inputs of energy and agrochemicals. For example, inorganic fertilisers replace nutrient cycling and pesticides and herbicides are used to manage pests and weeds. However, concerns regarding the long-term sustainability of modern farming practises in terms of environmental degradation (e.g., soil exhaustion and eutrophication), the rising costs of inputs derived from finite resources (fossil fuels and phosphorous) and agro-biodiversity loss have led to the development of the sustainable intensification paradigm (Pretty 2008) which has received much publicity (Royal Society 2009; Foresight 2011; The Montpellier Panel 2013).

The key principals of sustainability, as presented in Pretty (2008), are to:

1) "integrate biological and ecological processes such as nutrient cycling, nitrogen fixation, soil regeneration, allelopathy, competition, predation and parasitism into commodity production processes;
2) minimize the use of those non-renewable inputs that cause harm to the environment or to the health of farmers and consumers;
3) make productive use of the knowledge and skills of farmers, thus improving their self-reliance and substituting human capital for costly external inputs; and
4) make productive use of people's collective capacities to work together to solve common agricultural and natural resource problems, such as for pest, watershed, irrigation, forest and credit management."

Of these principals 1) and 2) draw heavily on the discipline of ecology and are the basis of ecological intensification (Bommarco et al. 2013). By definition, "ecological intensification entails the environmentally friendly replacement of anthropogenic inputs and/or enhancement of crop productivity, by including regulating and supporting ecosystem services management in agricultural practices" (Bommarco et al. 2013). For ecological intensification to be effective the linkages between land-use at multiple spatial-scales and communities of ecosystem service-providing organisms needs to be understood, as does the flow, stability, yield contributions and management costs of the various services provided by these communities (Bommarco et al. 2013). Spatial scale is important as different components of biodiversity and the ecosystem processes they are linked to will respond to land-use or management change at different spatial scales, for example crop pollination may be managed by farmers at the scale of fields using floral manipulations or maintaining areas of natural habitat (Dicks et al. 2010), but the effectiveness of field-scale actions will depend on the wider landscape context (the landscape-moderated biodiversity versus ecosystem service management hypothesis, Tscharntke et al. 2012b). Further, some ecosystem services such as interception of rainfall by cloud forests will have a potential benefit to all people living along the watercourses that are fed by such forests, scaling up the size and number of forests feeding a catchment will increase the reliability of water supply (Postel and Thompson 2005) and water quality (Martínez et al. 2009) and therefore the spatial extent of downstream benefits (drinking water and water for irrigation). Scaling-up forest area will, in turn, benefit biodiveristy for species that are forest specialists with large minimum territory sizes or that are intolerant of edge effects and disturbance (Gibson et al. 2013; Rueda et al. 2013; Rybicki and Hanski 2013).

The concept of ecological intensification is somewhat focussed on modern conventional farmlands where there are already substantial anthropogenic inputs that can be substituted with ecosystem services (ecological replacement) or sub-optimal ecosystem services that can improved (ecological enhancement). In small-scale farming landscapes inputs and land-use intensity can be low (Steward et al. 2014) meaning that many ecosystem services may already be adequate (e.g., Kasina 2007; Hagen and Kraemer 2010) with little need for ecological replacement or enhancement. However, crop yield-gaps may still be high in such farming systems and there can be political drivers to not only increase yields per unit area of farmland using anthropogenic inputs (Tittonell et al. 2008; Dorward and Chirwa 2011), but to expand farmland area and consolidate management into larger units (Xinshe 2002; Min 2006; Huang et al. 2011). The conservation of existing ecosystem services as small-scale farming landscapes change ("ecological conservation") will be important if sustainable intensification objectives are to be realised, and should be considered along with ecological replacement or enhancement.

1.3. Small-scale farming

Small-scale farming (also referred to as smallholder farming in this document) is the backbone of global food security (Chappell and LaValle 2011; Horlings and Marsden 2011; Tscharntke et al. 2012a) and accounts for a substantial proportion of food production and GDP in many countries (Singh et al. 2002; Thapa 2009; Salami et al. 2010a; IFAD & UNEP 2013). Worldwide huge numbers of people are smallholders; estimates suggest there are 2.1-2.5 billion smallholders on 500 million farms and that these are mostly in developing nations (FAO 2010; IFAD & UNEP 2013) (Appendix B, Table B.2). Whereas small-scale farming is important in low or middle income nations where 37.7% of employed people work in agriculture, agricultural and small-scale farming is less prominent in high income nations where only 3.5% of employment is contributed by agriculture (World Bank 2014). Small-scale farming is also important in areas where the majority of projected human population growth by 2050 will occur and where food insecurity is currently rife (FAO 2013a; World Bank 2013, Appendix A Figure A.1, Appendix B Table B.2). Undernourishment is linked to poverty rather than global food production (Adams et al. 2004; Sachs et al. 2009) and as many poor live in rural areas, often with little access to productive farmlands, undernourishment and small farm sizes are associated (Tscharntke et al. 2012a). Not only are smallholders in lower income nations (as per World Bank categorisation) critical to addressing issues of global poverty and food security, they are also linked with biodiversity conservation. High rural population growth rates and marginalisation to low productivity lands means that smallholders are often at the frontline of human-wildlife conflict e.g., (Distefano 2005; Webber 2006; Linkie et al. 2007) and agricultural expansion into biodiversity rich natural habitats e.g., (Aldrich et al. 2006; Maeda et al. 2010b). To make matters worse, human population growth rates in the vicinity of protected areas can be double the rural average (probably due to international and national investment in protected areas) (Wittemyer et al. 2008) and this is associated with higher wildlife extinction rates within protected areas (Brashares et al. 2001). However, engaging communities to create effective local management of natural resources can, for example, reduce habitat loss in community forests compared to protected forests (Porter-Bolland et al. 2012).

Increasing commodity production in large-scale high-input agriculture typically relies on conventional methods. However such approaches are less relevant to lower-input small-scale farms of the poor where biodiversity and related ecological processes are more relied upon (Tscharntke et al. 2012a). Small farms are not necessarily less productive than large-scale farms growing monocultures and can be more productive in total output per area than larger farms, although with a much higher labour intensity (Cornia 1985; Rosset 2000; Singh et al. 2002; De Schutter 2008; Barrett et al. 2010; Horlings and Marsden 2011). When small farms are more productive than large farms the phenomenon is called the 'paradox of the scale' or the 'inverse farm size-productivity relationship' and it is attributed, in part, to the complexity of smaller farms and their resource intensive use of land (Kremen and Miles 2012). Complexity in farming systems has also been demonstrated to enhance resilience to environmental disturbance across multiple ecosystem services, an especially valuable trait in the face of global climate change (Lin 2011; Kremen and Miles 2012)

Promoting and developing sustainable intensification for the world's undernourished that live in developing countries, and in particular for those who live in smallholder households in the vicinity of natural habitats, will contribute to global food security, poverty reduction and biodiversity conservation (The Montpellier Panel 2013). Integrated policies are needed to enhance productivity and resilience in small-scale farmed landscapes via sustainable intensification and should include ecological intensification principals (Bommarco et al. 2013) or as Tscharntke et al. (2012) put it, "eco-efficient, environmentally friendly and sustainable techniques to typically manage highly diversified cropland, avoiding pesticide use as much as possible, integrating soil fertility strategies (combining organic and inorganic fertilisers) and intensifying production in combination with preservation of functional biodiversity". To be optimal sustainable intensification must consider trade-offs between biodiversity and production at multiple spatial scales, the complex linkages between production and demand and how to mitigate human-wildlife conflicts (linking mechanisms) (Fischer et al. 2014).

1.4. Land-sparing and the buffer zones of large natural habitats

Assuming increasing commodity production is part of a holistic strategy to address land-scarcity, food-insecurity and poverty for small-scale farmers, current agriculture could produce more food by increasing yields on existing farmland (intensification) and by expanding the area of land (extensification) under agricultural use (Tachibana et al. 2001; Green et al. 2005). Extensification will typically result in the conversion of natural habitats into farmlands with clear negative consequences for biodiversity (Green et al. 2005; Barnosky et al. 2011; Gibson et al. 2013; Newbold et al. 2014), unless abandoned and/or degraded agricultural areas can be rehabilitated (Pretty et al. 2011; Sawadogo 2011). As such, trade-off analyses for increased commodity production vs. biodiversity conservation consistently favour the intensification of current farmlands (usually with a penalty to the biodiversity found there) in the hope that this will reduce the pressure to convert natural areas elsewhere to agriculture (land-sparing) (land-sparing, e.g., Davey et al. 2010; Edwards et al. 2010; Waltert et al. 2011; Hulme et al. 2013). However, the reality of the situation is more complex due to social, political and economic factors, and trade-off frameworks such as land-sparing vs. lands-sharing have been considered to be largely intellectual because there are few reliable mechanisms that can guarantee producing food intensively in one-place can actually spare land elsewhere (DeFries and Rosenzweig 2010; but see Chandler et al. 2013; Phalan et al. 2014), demand is elastic, and landscapes are multifunctional producing more goods and services than just food (Fischer et al. 2014). For land-sparing to be effective stronger mechanisms linking increased commodity production in one area to biodiversity conservation in another are required. A recent trade-off analysis by Phalan et al. (2014) sought to identify global areas where closing crop yield-gaps as part of land-sparing strategies would have the highest and lowest impacts on biodiversity, but they strongly emphasise the need for robust mechanisms linking improvements in agricultural productivity to biodiversity conservation. Further practical and pragmatic improvements to the land-sparing trade-off framework are provided by Fischer et al. (2014).

Agricultural landscapes neighbouring natural habitats of conservation interest are obvious places where mechanisms linking land-sparing to biodiversity conservation are required. Such locations, called “buffer zones” from henceforth, can be hotspots of habitat loss and human wildlife conflict. Even if a natural habitat is protected by law, it is still affected by its’ surroundings, for example, the condition of protected areas correlates with environmental degredation and land-use trends in its’ buffer zone(Laurance et al. 2012). Large tracts of natural habitat are becoming threatened due to habitat conversion (Finlayson et al. 1999; Hoekstra et al. 2005; FAO 2011; Miettinen et al. 2011; Potapov et al. 2012; Coca-Castro et al. 2013) and they are the refuge for a large proportion of global biodiversity that cannot persist in agro-ecosystems, for example, natural habitat in biodiversity hotspots contains more than half of threatened terrestrial plants and mammals (Brooks et al. 2002), especially large charismatic animal species of high conservation and cultural values (Gaston and Blackburn 1995; Cardillo et al. 2005; Sergio et al. 2006; Thornton et al. 2012). Conversely, from a global perspective, species able to exist in human-modified landscapes because they can tolerate or adapt to a degree of disturbance are likely to be of lower conservation concern than those that cannot.

Discussion of conservation in large areas of natural habitat is often framed in the context of protected areas and the importance of non-protected natural habitats and human activities within their buffer zones (e.g., Naughton-Treves et al. 2005; Laurance et al. 2012). Negative environmental changes observed in protected areas mirror those observed in their buffer zones (Laurance et al. 2012) and the unplanned loss and fragmentation of natural habitat in buffer areas will reduce connectivity between protected areas (Sánchez-Azofeifa et al. 2003; Curran et al. 2004; DeFries et al. 2005; Naughton-Treves et al. 2005). To realise the full potential of the global protected area network, conservation and restoration of natural habitats in their buffer zones will be crucial and as such they are an ideal focus for mechanisms linking land-sparing to biodiversity conservation. A land-sparing strategy does not necessarily have to take place entirely within a buffer-zone and recently there has been considerable interest in the inclusion of “land-use teleconnections” into the land-sparing vs. land-sharing framework (Polasky et al. 2004; Fischer et al. 2014). This integrates trade and displacement dynamics (where trade and teleconnections allow for land-use in one area to affect and be affected by land-uses in other areas), making the framework more applicable to a connected world (Grau et al. 2013; Fischer et al. 2014). However, the agriculture-dependent livelihoods of those in the vicinity of protected areas should not be marginalised in favour of those where there is less biodiversity as this could be ultimately counter-productive for conservation in buffer-zones and land-sparing in general.

In brief summary of sections 1.1-1.3, the application of sustainable intensification and trade-off analyses to small-scale farming landscapes in the buffer zones of large natural areas could provide opportunities for enhanced biodiversity conservation, food security and livelihoods. However, as will be discussed in Section 1.6 there are land-use conflicts between wildlife and humans that may not easily or predictably be resolved.

1.5. Ecosystem services and spillover

As well being relevant to biodiversity conservation, the composition of land-uses within a landscape will, in part, determine the total landscape abundance of a species that are beneficial or detrimental to agricultural productivity (Gardiner et al. 2009b; Gardiner et al. 2010). How the configuration of landscape then moderates the spillover of these species between land-uses and the ecological processes they provide is a major research theme in ecosystem service science and landscape ecology (Tscharntke et al. 2012b), and is highly relevant to sustainable intensification of food production and the design of farming landscapes. Cross-habitat movements of species can occur between agricultural and non-agricultural land-uses and the configuration and composition of land-use classes within a landscape may therefore influence the agricultural ecosystem services and disservices provided by such organisms (Chaplin-Kramer et al. 2011; Fahrig et al. 2011; Kennedy et al. 2013). Species spilling into agriculture from other land-uses can pollinate crops, enhance or interfere with pest predation or parasitism, increase pest abundance, raid crops and change food-web structure (Webber et al. 2011; Tscharntke et al. 2012b). The spillover of species is moderated by the difference in resource availability and hostility (e.g., risk of mortaility due to pesticide application or mechanical disturbance such as ploughing) between the agricultural matrix and other habitats (Ricketts 2001; Cronin 2003; Perfecto and Vandermeer 2010; Hadley and Betts 2012). The spatiotemporal stability of resources in natural habitats is high compared to arable croplands (Landis et al. 2000; Bianchi et al. 2006) and this has implications for the directionality of resource differences between land-uses. For example, for most of a growing season a mass flowering crop will provide little floral resource and nearby natural habitats are likely to hold more floral resources than croplands, but for a short period of the year, when the crop is in flower distributions can be strongly reversed. Mass-flowering crops can have substantial pollination requirements (Klein et al. 2007) and if stable floral resources in non-crop habitats are not available to support pollinator populations outside of mass-flowering periods pollinator abundance may decline impacting crop pollination (Ricketts et al. 2008; Garibaldi et al. 2011). The nature of spillover will differ between species and some may persist entirely in the agricultural matrix, especially when disturbance is not intense and for soil fauna, and the spatial distribution of different functional groups of species can have important implications for ecosystem services (Tscharntke et al. 2005b).

Five patterns of spillover in agricultural landscapes (Figure 1.1) have been proposed by Duelli and Obrist (2003). Species that have a strong preference for non-crop habitats that rarely spillover into croplands are “stenotopic species” whereas species showing the opposite pattern, common in croplands and rare in non-crop land-uses, are “cultural species”. “Disperser” and “ecotone species” show highest densities in non-crop habitats or at the crop-non-crop interface then decline with distance into fields. Disperser or ecotone distributions are often shown by species that use different resources between crop and non-crop habitats such as pollinators foraging on within field floral resources to provision nests in non-crop habitats (Ricketts et al. 2008). Species that are evenly distributed across agro-ecological landscapes are “ubiquists”, which can result from a species having a long-distance passive dispersal strategy as observed for ballooning species (Halley et al. 1996).

Knowledge of the distributional responses of species to land-use change and the consequence of this for the ecosystem services they provide is relatively well studied for biological control and pollination (see Table 2.3 and Appendix A Table A.1). For pollination, tools have been created to model how crop-pollination varies between landscapes (e.g., the InVEST approach, Tallis et al. 2008; or ecological landscape modelling of pollination, Lonsdorf et al. 2009). However, the relevance of this knowledge to tropical small-scale farmed landscapes may be limited given their contrast to the intensive large-scale (mostly temperate) agricultural landscapes of developed nations. The distributional responses of ecosystem disservice providing species to land-use change is less well represented in research and synthesis. As such this thesis discusses small-scale farmed landscapes in terms of their global importance, contrasts to large-scale systems and regulating ecosystem service research biases (Chapter 2), empirically examines spill-over (Chapter 3) and community change (Chapter 4) for insect insect groups that relate to ecosystem services and disservices with land-use intensification in a small-scale farming landscape.

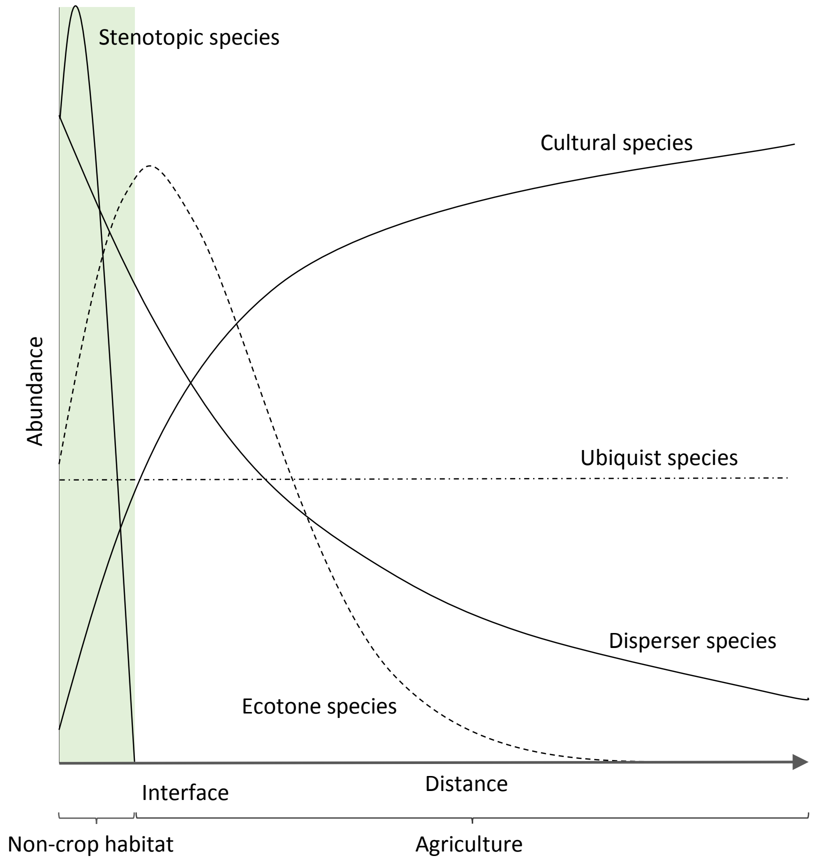


Figure 1.1 The five types of insect distribution pattern across the crop-non-crop interface. Stenotopic species are only found in non-crop habitats, cultural species prefer crops, dispersers colonise crops from non-crop habitats, ecotone species are typically found at the interface of crop and non-crop habitats and ubiquist species have no preference for either habitat (reproduced from Duelli & Obrist, 2003).

1.5.1. Land-use change and ecosystem services in sub-Saharan Africa

Intensification of global agriculture is likely to occur in areas such as sub-Saharan Africa where there are considerable crop yield-gaps and dietary undernourishment (25% of people) compared to the rest of the world (FAO/IIASA 2012; FAO 2014). Whilst current trends show improvements in diet and food production, sub-Saharan Africa will account for much of human population growth by 2050 (UN 2013) and this will lead to increasing demand for commodities and land. Africa is an important reservoir of global biodiversity (King 2011; McGinley 2011), but this is steep declining across the continent (Brashares et al. 2001; Brashares et al. 2004; Biggs et al. 2008; Craigie et al. 2010; Virani et al. 2011). Increasing demand for land and a growing human population will exacerbate matters. As such, improving food-security (and reducing poverty) and conserving biodiversity in sub-Saharan Africa is a global priority and sustainable intensification and trade-off analyses are pathways by which this can be realised with reduced costs to the environment and biodiversity (Green et al. 2005; Royal Society 2009; Pretty et al. 2011; Fischer et al. 2014). As discussed previously, sustainable intensification requires knowledge of ecosystem services and biodiversity so as to enhance or conserve them with land-use intensification for commodity production.

Data from East Africa suggest there can be considerable differences between tropical small-scale compared to temperate large-scale farming landscapes. Studies of landscape effects on pollination from Kakamega in Western Kenyan describe smallholder landscapes as consisting of numerous small farms (typically < 1 ha) growing a variety crops with a high proportion of hedgerows, field margins, gardens, homesteads, fallow lands, trees and bushes (Kasina, et al. 2009a, Kasina et al 2009b, Hagen and Kraemer 2010, Mailafiya et al. 2010, Mwangi et al. 2012). Studies from other Kenyan locations such as the Taita Hills (Clark and Pellika, 2007), Suam, Mtito Andei and Muhaka (Mailafiya et al. 2010) describe similar systems. The high complexity of East African small-scale farming landscapes indicates that the spatiotemporal stability of resources could be relatively high due to multi-cropping, non-crop land-uses and the fine grain of the landscape, and this may benefit ecosystem processes (Tilman 1996; Tilman et al. 2006). The diversity of landscape features and / or habitats within a landscape generates complexity and, in turn, this should increase species richness (for small animals such as insects) within agricultural areas relative to landscapes with more monotonic land-uses (e.g., large-scale agriculture or continuous forest, Tscharntke et al. 2012b). According to the intermediate landscape-complexity hypothesis (Tscharntke et al. 2012b) high local landscape complexity (see Appendix A Figure A.2) may mitigate the negative effects of landscape change at larger spatial scales (such as loss of large areas of natural habitat) on ecosystem services and service providing species. Therefore, the response of functionally important ecosystem service or disservice providing species in small-scale systems to commonly studied land-use scenarios, such as the conversion of natural habitat to agriculture may be different to that observed in large-scale systems. With the development of African nations, small-scale systems are likely to change (Collier and Dercon 2013). If these changes result in the consolidation of farms into larger areas of management then local landscape complexity could fall (see Appendix A Figure A.2) which may have negative consequences for resource stability and ecosystem processes (Tilman 1996; Tilman et al. 2006). Given the importance of understanding the interaction of land-use change at local and landscape scales (or indeed at any relevant spatial scales to a particular context or ecosystem service) more research needs to be conducted to allow estimation of thresholds beyond which negative effects of land-use change on beneficial ecosystem properties may occur and to understand how these may vary between biogeographical contexts.

Evidence for mitigation of the potential negative effects of large-scale land-use change on ecosystem service providing species due to local complexity in East Africa comes from studies of pollinators and pollination, but their findings are mixed. In farmlands surrounding Kakamega Forest, Kenya, one study found no effect of distance from forest habitat on bee species richness and suggested that farmland bee diversity might not depend on forest (Kasina 2007). A subsequent study in the same area found bee diversity, bee abundance and flower-visitor network size were greatest in farmland compared to forest or forest-edge, and suggested that resource rich structurally diverse farmland may subsidise plant-pollinator networks in natural habitats (Hagen and Kraemer 2010). However, despite bees being likely to use resources in the forest canopy (Roubik 1993; Nagamitsu and Inoue 1997; Ramalho 2004) the study did not sample bees or investigate floral networks above the forest understory and hence suffers from sampling bias. Pollinator abundance in pigeon pea (*Cajanus cajan*) fields in Kibwezi, Kenya, declined with increasing proximity to and abundance of semi-natural habitats (Otieno 2010). The same study also found that cropland bee abundance and species richness were predicted by habitat complexity, but not plant cover and species richness in semi-natural habitat. This suggests that land-use heterogeneity within croplands was more important for pollinators than the presence of non-crop habitats.

Other studies found a negative effect of land-use intensification on pollinators and/or pollination. In a coastal Kenyan forest (Arabuko-Sokoke) yields from cropland honey bee hives increased with proximity to forest, suggesting that the forests were supplementing agricultural resource availability (Sande et al. 2009). Aubergine (*Solanum melongena*) flower visitation rate significantly declined with distance from natural habitat in Nguruman, Kenya (Gemmill-Herren and Ochieng 2008). However, the study also found that pollinators foraged more in farmland than any other habitat and that bee abundance in farmland was highest in terms of abundance and richness. This was attributed to high spatio-temporal floral resource availability in the agricultural matrix. Hawkmoth abundance and visitation rates to papaya (*Carica papaya*) in Machakos District and Kerio Valley, Kenya, declined sharply with distance from natural habitat in small subsistence farms and sites with high levels of disturbance and poor farming practices showed reduced fruit set (although whether this was due to decreased matrix quality, soil quality or water availability is uncertain) (Martins and Johnson 2009). In Uganda, lowland coffee (*Coffea canephora*) yields from small-scale farms were positively correlated with the amount of natural habitat in the surrounding landscape, whereas distance to forest or wetland and cultivation intensity were negatively related to coffee yields and positively related to pollen limitation (Munyuli 2012). Finally, another study of Ugandan coffee production found that increasing the landscape proportion of cultivated land resulted in increased crop value but the biodiversity and carbon storage value of farmland both fell, especially when smallholder mixed-cropping systems were compared to large-scale plantation style agriculture (Renwick et al. 2014).

The contrasting findings of these studies highlight the need for more data from small-scales farmlands in tropical Africa that investigate land-use at multiple spatial-scales and incorporate resource availability.

1.6. Ecosystem disservices to agriculture

Whilst the ecosystem services framework and ecological intensification concept consider the substantial benefits that agriculture derives from biodiversity (e.g., Losey and Vaughan 2006; Gallai et al. 2009) biodiversity can also provide substantial costs to agriculture and livelihoods in the form of ecosystem disservices. Regulating ecosystem disservices that spillover into agricultural lands from natural habitats can include crop damaging animals (e.g., Naughton-Treves 1998; Avery et al. 2001; Madhusudan 2003; Webber 2006), predators of livestock (e.g., Kissui 2008; Gusset et al. 2009; Inskip and Zimmermann 2009; Suryawanshi et al. 2013) or the dispersal and colonisation of weeds that compete for crop resources (Oerke 2006). Animal ecosystem disservices to agriculture can be substantial. Estimated agricultural losses in the U.S. due to mammals and birds alone were valued at $944 million in 2002 (National Agricultural Statistics Service 2002). Between 2001-2003 animal pests were responsible for the loss of 375 million tons of production in six major global crops, reducing actual yields 7.9% for wheat, 15.1% for rice, 9.6% for maize, 10.9% for potatoes, 8.8% for soybeans and 12.3% for cotton (Oerke 2006). Economically significant bird damage has been well documented for cereals (reviewed by De Grazio 1978) and soft fruit crops (Tillman et al. 2000; Tracey and Saunders 2003)(De Grazio 1978; Boyce et al. 1999), and is estimated to cost Australian horticultural production $300 million annually (Tracey and Mary 2007).

Compared to those that focus on ecosystem service providing species relatively few studies have linked land-use change with ecosystem disservice providing species. Increasing proportions of natural habitat within a landscape or proximity to a natural feature have been positively associated with livestock predation rates (Michalski et al. 2006), crop damage by wild boar (Herrero et al. 2006)(Thurfjell et al. 2009), rodents (White et al. 1997; White et al. 1998; Eilers and Klein 2009a) and beetles (Zaller et al. 2008b), and pest (Thies et al. 2005) or weed (A.Kruess & T.Tscharntke unpubl. data in Tscharntke et al. 2005) colonisation rates. Regarding crop pest arthropods, abundances tend to have a negative rather than positive response to increasing semi-natural habitat (Veres et al. 2013) but no consistent response to landscape complexity (Chaplin-Kramer et al. 2011). Land-use simplification has been associated with increased crop raiding by deer and monkeys (Agetsuma 2007) and fragmentation of natural habitat has been shown to increase densities of deer in agricultural areas (Hewison et al. 2001). Agricultural expansion and loss of natural habitat increases human-baboon conflict (Hoffman and O'Riain 2012). Landscape resource availability has predicted crop damage by elephants (Chiyo et al. 2005), beetles and flies (Zaller et al. 2008a). Wilby and Thomas (2002) simulated patterns of pest emergence with agricultural intensification and suggested that endopterygote herbivores will become relatively more damaging pests with lower levels of land-use intensification than exopterygote herbivores because control of the latter is more resistant to loss of natural enemy species. They also suggested that exopterygote herbivores will become pests only after extreme reductions in natural enemy species richness (due to redundancy in natural enemy communities) and that concealed herbivores are more likely to emerge as pests at lower levels of land-use intensification than non-concelaed pests.

The importance of explicitly considering land-use change effects on ecosystem disservices becomes particularly apparent when considering large-spatial scales, such as those relevant to large mammals and protected areas for nature conservation. Proximity of agriculture to natural habitats can to lead human-wildlife conflict in buffer zones (Distefano 2005; Woodroffe et al. 2005b) which is both detrimental to both agriculture and biodiversity conservation. For example, large mammals of high conservation priority can spill out of protected areas into nearby agricultural areas, raiding crops (Naughton-Treves 1998; Osborn and Parker 2003; e.g., elephants, Chiyo et al. 2005; Wallace and Hill 2012; or primates, Hsiao et al. 2013) or predating livestock (e.g., lions, leopards and snow leopards, Holmern et al. 2007; Kissui 2008; Suryawanshi et al. 2013). The spillover of ecosystem disservices is a particularly important issue for the practical application of theory relating to the future design of farming landscapes. This is because the stakeholders of buffer zones may be particularly sensitive to ecosystem disservices that threaten livelihoods and safety perceiving greater threats than actually exist (Basili and Temple 1999; Webber 2006; Suryawanshi et al. 2013). However, there is evidence to suggest in some human communities that people can co-exist with large carnivores at a small spatial-scale and fine grain (Carter et al. 2012).

Generally, studies relating to land-use change and ecosystem services consider the top-down control of pests by predators or parasites as the regulating ecosystem service biological control. However, the pests themselves are rarely explicitly considered as ecosystem disservice providing species that negatively affect provisioning services. Pest damage is considered as limitation on crop production in the ecological intensification concept, thus ecosystem disservices are indirectly considered, but, ecosystem disservice providing species can also directly respond to land-use change and management interventions (and not just through top-down regulation via predation and parasitism). Therefore it seems conceptually inconsistent to consider crop damaging species as providing an ecosystem function that is somehow different to all other ecosystem functions and typically only considered in their interactions with other ecosystem service providing species. Therefore, where appropriate, ecosystem disservices are directly considered in this thesis.

1.7. Functional ecology

The functional diversity of a community is an important aspect of biodiversity in explaining the functioning and stability of an ecosystem (Díaz and Cabido 2001; Petchey et al. 2004; Mouchet et al. 2008; Villéger et al. 2008).The productivity (Hooper and Dukes 2004; Fargione et al. 2007; Griffin et al. 2009; Marquard et al. 2009) and resilience (Dukes 2001; but see Bellwood et al. 2003; Bellwood et al. 2004; Girvan et al. 2005; the recovery of an ecosystem process after perturbation, Tilman et al. 2006) of ecosystems is enhanced by functional diversity. There is also evidence that shows the functional identity of dominant species within a community, those species with the greatest proportional abundance within a community (as per the mass ratio hypothesis, Grime 1998), best predicts the processes relating to that community (Hillebrand et al. 2008; Mokany et al. 2008; Orwin et al. 2014). Therefore loss of functional diversity or shifts in functional identity in agroecosystems may negatively impact the provisioning of ecosystem services essential to commodity production and the associated replacement of lost ecosystem function with synthetic inputs incurs additional (potentially volatile) production expenses and may be unsustainable. Assessment of functional diversity can reveal when land-use change disproportionately affect particular functional traits or trait combinations, a phenomenon known as trait filtering, for example where habitat degradation or loss alters the balance of feeding behaviours within a community (Gray et al. 2007; Tscharntke et al. 2008).

A commonly used approach to assessment of functional diversity is to take a matrix containing values of representative functional traits for the species composing the community of interest to create a multidimensional functional space based on raw functional traits or synthetic traits constructed through ordination summarising multiple raw traits (Petchey and Gaston 2006; Villéger et al. 2008; Pakeman 2011; Naeem et al. 2012; Mouillot et al. 2013). A functional trait is a feature of an organism that links to its function (Lavorel et al. 1997) and thus functional traits will determine response to pressures and/or its influence on ecosystem processes and services (Harrington et al. 2010). Functional traits should suggest an organism's adaptations to the physical and biotic environment and the trade-offs between different functions within an organism, in animals these may include morphological, life history and behavioural traits that relate to habitat and resource use (Harrington et al. 2010). The multidimensional functional space created from specie's traits can be then used to quantify community changes with regards to environmental changes such as land-use change (Flynn et al. 2009; Edwards et al. 2014a), biotic pressure such as invasive species and direct human impacts such as pesticide use or harvesting of wild species (Mouillot et al. 2013). Determining the functional structure of a community then requires descriptions of the distribution of points (i.e., species or other taxonomic divisions) and their weights (i.e., biomass or abundances) in the multidimensional space using several indices that provide complementary information on different components of functional diversity (Mouillot et al. 2013). Using ordination to define the functional trait spaces has its drawbacks, such as risking the loss of information, since ordination axes will only capture a proportion of the variance in the data (Villéger et al. 2008). However constraints in data, such as categorical data or high numbers of traits compared to species number, commonly mean that ordination is often the only way forward. Complementary components of functional space or metrics used to describe functional diversity include functional richness, evenness, divergence and identity.

Functional richness (Figure 1.2) indicates the number of trait combinations present within a community and is calculated as the area or volume of functional space occupied by a community. Simply put, the convex hull volume method determines the most extreme points in multidimensional trait space, links them to build the convex hull and the calculates the volume inside (Villéger et al. 2008) (Cornwell et al. 2006). Reductions in functional richness mean that traits have been lost from a community. Functional richness does not consider the abundance of species and is therefore sensitive to the presence of rare but functionally distinctive species that may have relatively little effect on ecosystem processes (as per the biomass ratio hypothesis).

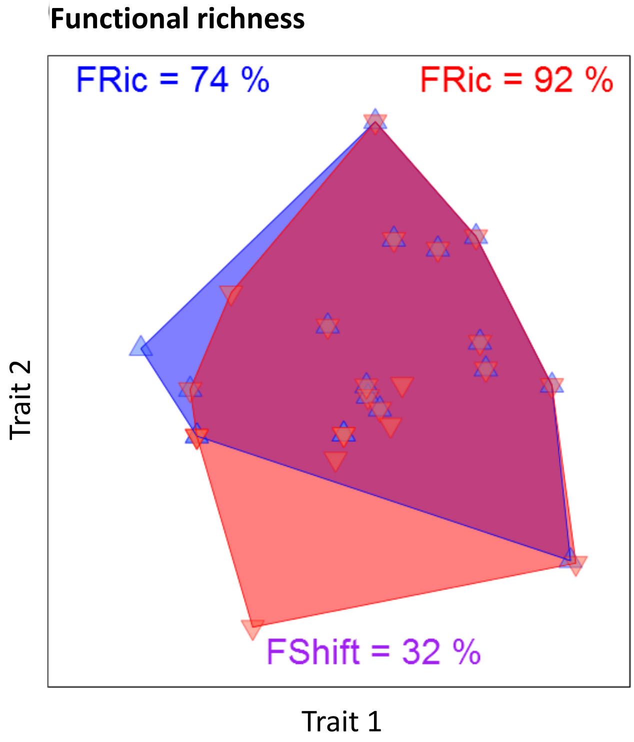


Figure 1.2 Illustration of how functional richness may change in multidimensional functional trait space before and after disturbance, e.g. land-use change leading to habitat loss and fragmentation. Species (triangles) are plotted in multidimensional functional space according to their trait values. To estimate functional richness convex hulls are drawn around the species representing the two different communities, the overall shift can be estimated using the percentage overlap between the two hulls. Here the functional space filled by only pre- or post- disturbance communities represents 28% of their combined volume and functional richness has increased with change. The large effect that a single species can have on the volume of functional space occupied (regardless of abundance) is demonstrated by the point with the lowest value for Trait 2. This figure and the accompanying text are adapted from Mouillot et al. (2013) and Villéger et al. (2008).

Functional evenness (Figure 1.3) reflects the change in the regularity of abundance distribution in functional trait space (Mason et al. 2005) or “the regularity with which the functional spaces is filled by species, weighted by their abundance” (Villéger et al. 2008). Functional evenness falls if abundance becomes less evenly shared between species or if the variability of functional distance between species increases. Changes in dominant traits are reflected by species evenness (Hillebrand et al. 2008; Mokany et al. 2008) and the effects of these on ecosystem function have been shown by manipulations of model grassland communities where functional evenness consistently enhanced ecosystem system functioning (Orwin et al. 2014). Evenness is considered to be complementary to dominance in that it reflects the distribution of traits within a community and the two negatively correlate, if a community is dominated by a species with particular traits then dominance is high but evenness low (Hillebrand et al. 2008). Functional evenness is derived using the minimum spanning tree (MST) that links all points contained with multidimensional trait space using the minimum distance (i.e., summed branch lengths) and the regularity of branch lengths and evenness in species abundances. These are calculated by 1) dividing each branch l of the MST by the sum of the relative abundances linked by the branch to give weighted evenness EW_l, 2) dividing EW_l by the sum of EW values for the entire MST to obtain partial weighted evenness PEW_l) subtracting $1/(S-1)$, where S is the number of species, from the numerator and denominator of the final functional eveness index equation:

$$FEve = \frac{\sum_{l=1}^{S-1} min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1-\frac{1}{S-1}}$$ (Villéger et al. 2008).

This gives a measure of functional evenness that is not biased by species richness, accounts for abundance and is constrained between 0 and 1.

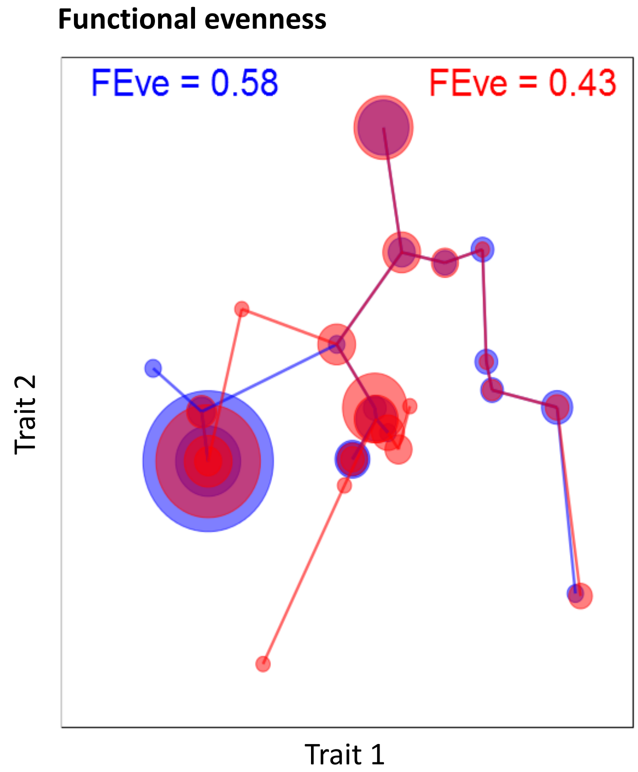


Figure 1.3 Illustration of how functional evenness may change in multidimensional functional trait space before and after disturbance, e.g. land-use change leading to habitat loss and fragmentation. Species (circles) are plotted in multidimensional functional spaces according to their trait values, the diameter of circles is proportional to species abundance. A minimum spanning tree (MST) links points in each community, and functional evenness measures the regularity of points along this tree and the regularity in their abundances, in this example functional evenness decreases after disturbance. This figure and the accompanying text are adapted from Mouillot et al. (2013) and Villéger et al. (2008).

Functional divergence (Figure 1.4) reflects how abundance is spread within the volume of functional traits space occupied by a community independent of the volume of functional space occupied and the evenness of abundance distribution within that volume (Villéger et al. 2008). Alternatively it is defined as “the proportion of the total abundance that is supported by the species with the most extreme functional traits"(Mouillot et al. 2013) or as the probability that two random individuals with the community will have different trait values (Leps et al. 2006; Pavoine et al. 2009).

Functional divergence

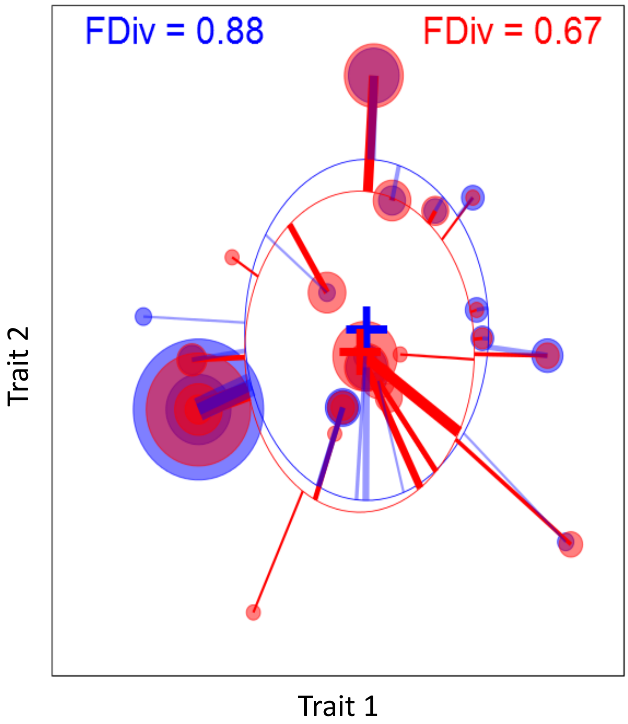


Figure 1.4 Illustration of how functional divergence may change in multidimensional functional trait space before and after disturbance, e.g. land-use change leading to habitat loss and fragmentation. Species (circles) are plotted in multidimensional functional spaces according to their trait values, the diameter of circles is proportional to species abundance. Functional divergence shows changes in the proportion of the total abundance supported by the species with most extreme functional traits. Crosses indicate the center of gravity for each community, the large unfilled circles are the mean distance to the centre of gravity for each community and deviation of the distance from the mean for each species are shown by coloured lines, whose width corresponds to the species' abundance, between species location in functional space and the mean distance to the centre of gravity for the community. The more species with high abundances diverge from the mean then the higher the functional divergence, in this case functional divergence falls after disturbance. This figure and the accompanying text are adapted from Mouillot et al. (2013) and Villéger et al. (2008).

The method proposed by Villéger et al. (2008) 1) calculates the coordinates of the centre of gravity of the V species that form the vertices of the convex hull boundary, 2) calculates for each of the S species within the community the Euclidean distance to the centre of gravity dG_i, 3) takes the mean distance of the S species to centre of gravity $\overline{dG}$ (which is calculated from species coordinates in trait space and is not weighted by abundance), 4) calculates the sum of abundance-weighted deviances Δd and the absolute abundance-weighted deviances $\Delta|d|$ for distances from the centre of gravity across species, 5) brings these calculations together to give the functional divergence index in the form:

$$FDiv = \frac{\Delta d + \overline{dG}}{\Delta |d| + \overline{dG}}$$

Functional divergence nears 0 when highly abundant species are much closer to the centre of gravity compared to rare species and increases as highly abundant species move further from the center of gravity compared to rare species.

Functional identity

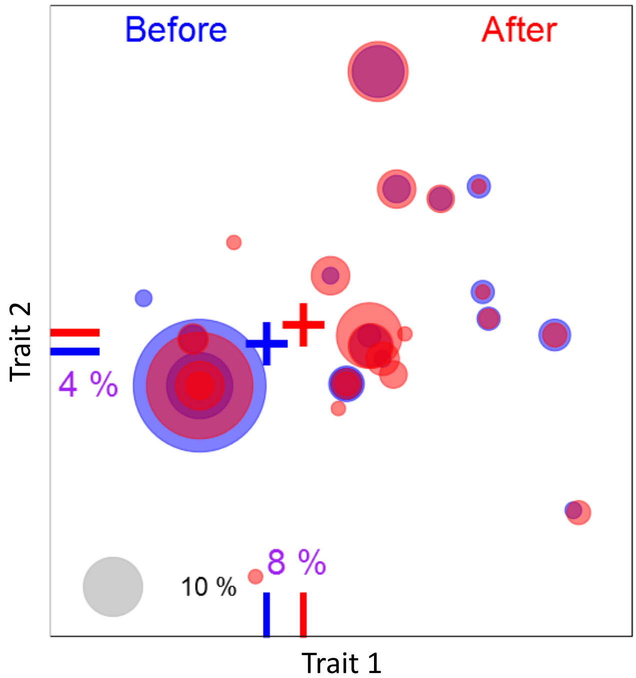


Figure 1.5 Illustration of how functional identitiy may change in multidimensional functional trait space before and after disturbance, e.g. land-use change leading to habitat loss and fragmentation. Species (circle) are plotted in multidimensional functional spaces according to their trait values, the diameter of circles is proportional to species abundance. Changes in species abundances can alter the functional identity (mean values of traits as crosses) of species communities (i.e., abundance-weighted average value for each trait) shown on each trait axis by the separation of the two coloured bars. This figure and the accompanying text are adapted from Mouillot et al. (2013) and Villéger et al. (2008).

Functional identity (Figure 1.5) is the mean trait scores of a community weighted by abundance (Garnier et al. 2004). If land-use change, for example, changes species abundances then this can change the functional identity of community. Changes in functional identity, where traits are linked to divergent ecosystem functions (e.g., a trait that separates species providing a potential ecosystem service, e.g., pollination or biological control, from those providing a potential disservice, e.g. herbivory of crops), could, suggest changes in the balance between various ecosystem services or disservices with an agro-ecosystem. Changes in the identity of dominant species can change the functional identity of a community and this can affect ecosystem function (Hillebrand et al. 2008; Mokany et al. 2008). Again, manipulations of model grassland communities have shown that the identity of dominant species can be crucial for ecosystem system functioning (Orwin et al. 2014).

For additional technical details of the functional diversity components summarised here see Mouillot et al. (2013) and Villéger et al. (2008), also a short summary of some additional functional components is included in Chapter 4.2.6.

Comparing functional diversity between communities with different species richness and regional species pools can be achieved by contrasting observed values relative to those expected from random communities derived using matrix swap randomisation that maintains the species richness of communities and the frequency of occurrence within randomised matrices (Manly 1995; Villéger et al. 2008). This is necessary because species functional traits within different communities will determine the range of functional-diversity values possible.

The use of the functional diversity, rather than just taxonomic diversity, for investigating land-use change in agro-ecosystem is relatively new. However, several studies have already found evidence for trait filtering with increasing land-use intensity (Tscharntke et al. 2008; Flynn et al. 2009; Edwards et al. 2013; Edwards et al. 2014a) suggesting that land-use intensification can lower the functional diversity of communities beyond changes in species richness alone, potentially affecting provisioning of ecosystem services or disservices. This confirms that understanding the implications of land-use change in small-scale farmlands requires consideration of functional diversity.

1.8. Thesis outline

There is a considerable amount of information regarding the effects of land-use change on agricultural ecosystem processes and the species that provide them, particularly in temperate, intensively farmed landscapes. However, despite the importance of small-scale farming to global food security and issues of poverty and biodiversity, there are surprisingly few studies whose narrative focusses on the description and conservation of such processes in small-scale contexts and accordingly this thesis attempts to address this knowledge gap.

Additionally, even though small-scale farmers in the buffer zones of large tropical protected areas are decision makers at the front-line of conservation and food-security issues, few, if any, attempts have been made in this context to conduct empirical research that links ecosystem disservices, such as human-wildlife conflict, to the land-sparing land-sharing framework, this study is one of the first to do. By exploring the attitudes and perceptions of a major group of buffer zone stakeholders in relation to natural habitat and wildlife at different spatial scales, this study approaches the land-sparing framework from a direction that is rooted in its practical application that will complement theoretical predictions regarding how best to optimise landscapes for ecosystem services and biodiversity conservation.

The study area, in rural Kenya, falls entirely within the buffer zone of a large national park for biodiversity conservation, Tsavo, and has potential for agricultural intensification due to large crop yield-gaps. Crop yield-gaps, habitat connectivity with an important protected area, populations of free-ranging large mammals (e.g., elephants and baboons) and rapid loss of natural habitat coupled with poverty, human-wildlife conflict and food-insecurity mean that the area is a prime candidate for sustainable intensification, including landscape management for ecosystem services. The area can be considered a hotspot of conservation conflict where the conservation of natural habitat is important for biodiversity conservation but there is also a strong need to improve commodity production and utilisation to improve livelihoods and meet the demands of a growing population.

The key questions addressed in this thesis are:

Is there evidence for geographical and farming system bias in ecosystem service research? Small-scale farming is central to issues of global food-security, poverty and demographic change but does contemporary ecosystem service research reflect this? Chapter 2 discusses the importance of small-scale farming, estimates global coverage of small-scale farming based upon FAO global census data and then assesses synthetic literature regarding pollination and biological control for geographical and farming-system biases.

How does the numerical abundance and spillover of important groups of ecosystem service or disservice providing species with cropland change along a land-use intensification gradient in low-input small-scale farmed landscapes? Small-scale farming landscapes are more heterogenous and complex at smaller spatials scales than large-scale farming landscapes, this may stabilise resource availability for species important to ecosystem processes providing enhanced ecosystem function.Many countries have land-use consolidation policies to intensify agricultural production in small-scale systems, but the ecological consequences of this are little known and answering this question helps to fill that knowledge gap. Therefore, Chapter 3 investigates the effect of land-use change on hymenopteran and coleopteran groups in a low-input tropical small-scale farming landscape using regression modelling and with particular reference to spillover.

How does the functional diversity of important agricultural insect groups change with land-use intensification in low-input small-scale landscapes? Functional diversity can reveal trends in the species traits that are linked to ecosystem processes which can differ substantially from taxonomic trends in species richness or diversity, this can have important implications for ecosystem functioning in farmlands and suggest what problems or benefits land-use intensification may create. Especially little is known from small-scale farming landscapes therefore Chapter 4, using recently developed analytical methods, examines the functional diversity of Coleoptera and Hymenoptera along the same land-use gradient as per Chapter 3.

How does landscape structure at different spatial scales influence stakeholder perceptions of ecosystem services, ecosystem disservices and attitudes towards nature, what are the implications for sustainable intensification? Ecosystem disservices (especially human-wildlife conflict) are poorly intergrated into studies of land-use intensification effects on agro-ecosystem processes, yet these may be greatest in the buffer zones of protected areas where trade-off analyses of commodity production vs. biodiversity conservation are likely to suggest that natural habitats should be conserved. As such, Chapter 5 assesses how small-scale farmers' perceptions of ecosystem services, ecosystem disservices and attitudes towards different facets of nature are affected by land-use intensification at two spatial scales with relevance to local wildlife habitat and a large protected area.

Chapter 2. Pollination and biological control research: are we neglecting two billion smallholders?

2.1. Introduction

Global food insecurity is receiving increasing attention from researchers and policy makers (De Schutter 2008; Bruinsma 2009; Royal Society 2009; Godfray et al. 2010; Foresight 2011). An increasing human population and rising demand for more varied, high-quality diets is placing pressure on agro-ecosystems and biodiversity across the globe (Royal Society 2009; Godfray et al. 2010; Foresight 2011). To prevent widespread food insecurity arising from the expected increase in human population size, predictions suggest that agricultural land will need to increase crop production by 60% or more by 2050 (Alexandratos and Bruinsma 2012). There are around 870 million hungry people today, nearly all of whom (98%) live in developing countries and half of them are from smallholder households (Dobie and Yuksel 2005; FAO 2013a). As we currently produce enough calories to feed the world (FAO 2013a; FAO 2013b) yet still have hunger, producing additional food in food secure areas will not solve global food insecurity alone (De Schutter 2008). Furthermore, the long-term sustainability of the industrial intensification of agriculture (high inputs, low crop and landscape diversity) has been questioned (Millennium Ecosystem Assessment 2005; Pretty 2008). Where industrial agriculture exists it is often associated with soil degradation and even desertification in arid regions (Royal Society 2009), thus in future we may suffer declining production in some currently productive areas. On-going industrial intensification of agriculture, typically in developing nations, is linked to negative social and economic impacts, including poverty and loss of local food security (Bacon et al. 2012; Kremen and Miles 2012). Sustainable intensification, the pursuit of higher or more sustainable yields with fewer negative consequences for the environment (Foresight 2011), is the conceptual solution to reducing global food insecurity and meeting future food demands, and it includes the management of ecosystem services (ecological intensification) (De Schutter 2008; Royal Society 2009; Foresight 2011). In this review, we examine how much ecosystem service research is derived from developing nations, tropical climates and smallholder farming landscapes, where local food security is at stake.

2.1.1. Smallholder-farmed landscapes

Agriculture, in general (Table 2.1), and smallholder farming is a major source of food production and income in many countries (Singh et al. 2002; Salami et al. 2010a) and for the global rural population in general. Global estimates suggest there are 2.1-2.5 billion people involved in farming smallholdings and 500 million smallholdings, mostly in developing nations

(FAO 2010; IFAD & UNEP 2013) (Appendix B, Table B.2). The majority of the population growth forecast for 2050 will occur in sub-Saharan Africa and South Asia (World Bank 2013) (Appendix A, Figure A.1), where food insecurity is currently rife and more than a third of agricultural land is composed of smallholdings (FAO 2013a) (Appendix B, Table B.2). Thus, ensuring that sustainable intensification can benefit the world's undernourished that live in developing countries, and in particular for those who live in smallholder households would contribute to both global food security and poverty reduction (The Montpellier Panel 2013).

Table 2.1 Significance of developing nations (as classified by the World Bank as low to upper-middle income) to global population and agriculture statistics (for regional information see Appendix A Figure A.1).

Measure	World	Developing Nations	All Other Nations
Agricultural land (million km^2)*	48	74%	26%
Cereal production (million metric tons)*	2587	71%	29%
Land under cereal production (million km^2)*	7.0	80%	20%
Population (million)*	6974	84%	16%
Agricultural population (million)*	2598	98%	2%
Yield-gap (percentage difference between actual and potential crop yields in high input systems)**	57%	63%	38%
Agricultural population using holdings <2 ha (million)***	2,147	99%	1%
Smallholdings<2ha as percentage of global agricultural area***	16%	15%	1%

* 2011 (FAO 2013b; World Bank 2013). **2000 (FAO/IIASA 2012). *** Values estimated using data from World Census of Agriculture 2000 (FAO 2010; FAO 2013b) (Appendix B Table B.2)

There is no single definition of a smallholding, but the common understanding is that the unit of land management is small. Several reports arbitrarily use a definition of two hectares or less (Singh et al. 2002; Salami et al. 2010a; IFAD 2011) but larger holdings (e.g. three to five hectares) will still create very complex landscapes compared to large-scale farming. Smallholder-farmed landscapes are therefore greatly sub-divided and potentially have high diversity of crops at relatively small spatial scales (Figure 2.1A). The higher potential for small-scale intermixing of crop and non-crop habitats (due to landscape configuration not composition) means that in a smallholder-farmed landscape the average distance of a crop-plant to a "natural" area that could enhance ecosystem service delivery can be much shorter than in a large-scale farming landscape. As smallholder-farmed landscapes can be highly heterogeneous within and between landscapes (Figure 2.1) there is a variety of such landscapes that could be described as smallholder. For example, they can be commercial or subsistence, polycultural or monocultural, and with high or low input (Appendix A, Figure A.2). Smallholdings can merge together to form an extensive area of contiguous agriculture or they can be isolated patches surrounded by other land-uses or natural habitats.

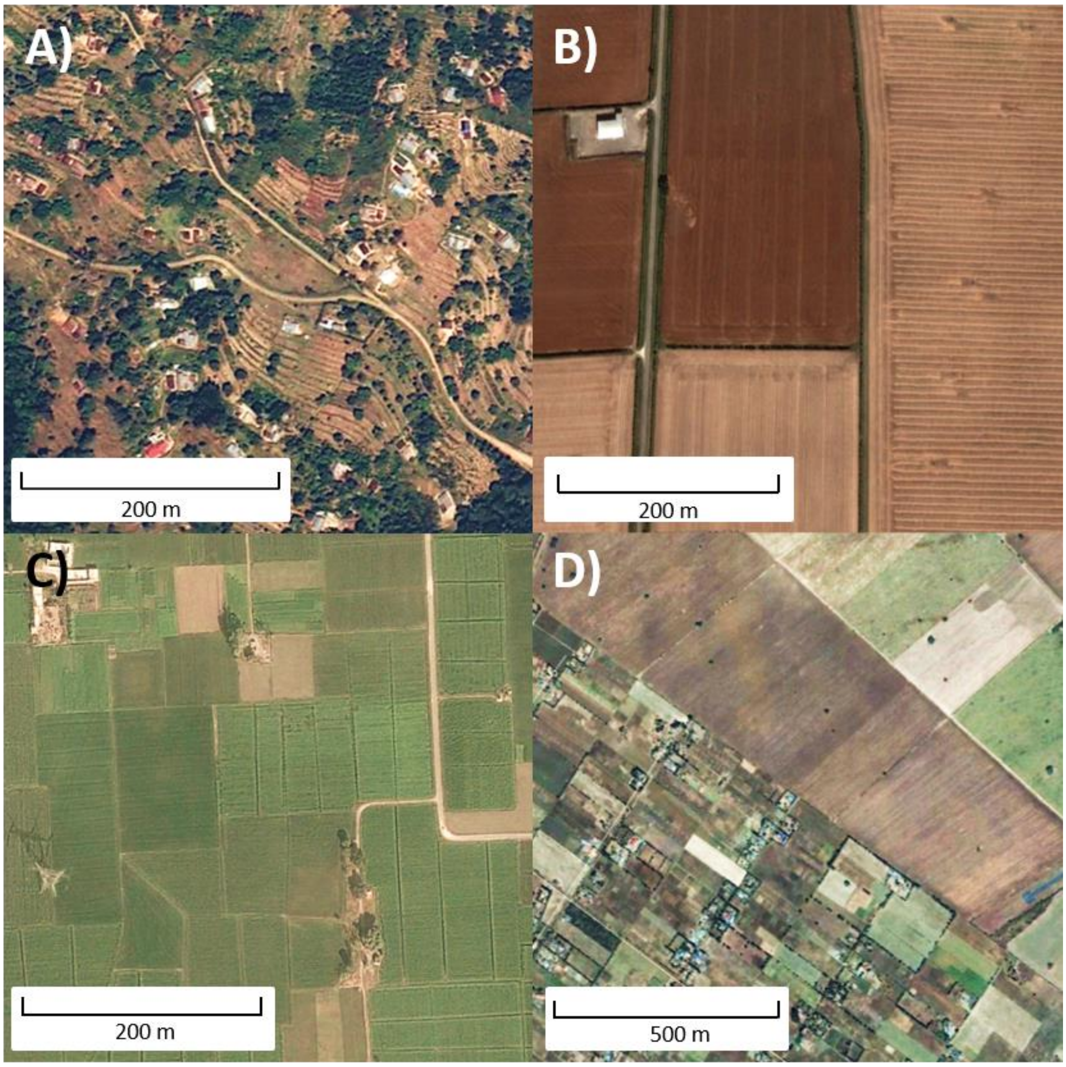


Figure 2.1 Examples of farming landscapes. A) Locally complex upland smallholdings, Taita, Kenya; B) Large-scale commercial farming, Norfolk, UK; C) Locally simple lowland smallholdings, Punjab, India; D) Dualistic farming with smallholdings and large-scale commercial farming, Nakuru, Kenya.

2.1.2. **Ecological intensification and the regulating ecosystem services of pollination and biological control**

The landscape provides a range of natural resources that are valuable to people. In analogy with economics, natural “capital” (such as soils and forests) provides ecosystem services (ES) as flows (or interest) of value. These include food, forage, fibre and fuel in the case of forests, and nutrients, water and carbon storage in the case of soils. ES are broadly separable into four categories: provisioning services (food, fuel, water), regulating services (carbon storage regulates climate, plant cover regulates flood risk), supporting services (soil microbes support nutrient cycles and aid food production) and cultural services (e.g., recreational, spiritual and educational values of a landscape). Pollination of crops and pest control, by natural enemies of crop pests, are regulating ecosystem services that contribute to food production. The notion of enhancing ES to increase crop yield (rather than using pesticides, fertilisers or other intensive agricultural practices) is known as “ecological intensification” (Bommarco et al. 2013). It is well-established that insufficient pollination and biological control services can limit crop production when other factors such as soil nutrients and water are sufficient (Bommarco et al. 2013). Evidence is now emerging to support the theory that pollination and biological control respond to similar drivers such as floral resources and landscape structure (Pontin et al. 2006; Krewenka et al. 2011; Shackelford et al. 2013) and it is therefore logical to consider them together.

Recent quantitative reviews (e.g, Ricketts et al. 2008; Williams et al. 2010; Chaplin-Kramer et al. 2011; Veres et al. 2013) have investigated factors that affect pollination and biological control services or providing species, such as the influence of landscape complexity and management practices, and have shown that variability in ES provision is likely to be context dependent (Winfree and Kremen 2009; Diekotter et al. 2010; Tscharntke et al. 2011; Veres et al. 2013). For example, the diversity of both pollinators and natural enemies seems to be higher in complex agro-ecosystems, and that pollination services are generally stronger and more stable on farms near natural habitats (Diekotter et al. 2010; Garibaldi et al. 2011). The results of quantitative reviews have a key role to play in synthesising the evidence and parameterising models that can predict ES provisioning (such as InVEST, see Kareiva et al. 2011), and therefore they contribute to the design of sustainable farming landscapes and the policy interventions that bring them about. The extent to which the body of the work synthesised in such reviews can suggest management interventions across a range of agricultural systems clearly depends on the range and representativeness of the studies included. Geographical biases have recently been demonstrated in reviews relevant to pollination ecology suggesting our understanding of pollination is poor in developing regions such as sub-Saharan Africa (Archer et al. 2014). We build on these findings, with regards to food security, by focussing on regulating ES research relevant to crop productivity and by evaluation of the farming landscape where data were collected, particularly with regard to smallholdings. This study specifically asks if the constituent studies of recent reviews relevant to agricultural pollination and biological control adequately represent farming landscapes (smallholder-farmed *vs*. large-scale farming), global biomes, regions (as defined by the World Bank), and national income statuses.

2.2. Methods

In May 2013, a Web of Science topic search for “[landscape OR disturbance OR diversity OR crop yield OR fruit set OR food production] AND [pollinat* OR natural enem* OR biological control OR CBC OR pest control] AND [meta-analysis OR review]” (Year > 2005) was used to find recent quantitative reviews relevant to crop pollination and biological control (note CBC means conservation biological control). Reviews were excluded (Appendix A, Table A.1) if they had were relevant only to specific crops, did not use meta-analysis or quantify/model a trend or pattern, or used few agricultural studies (less than 50%) . Any additional reviews relevant to pollination and biological control referenced in selected reviews were also included in the screening process. The agricultural studies used in each review (Appendix A, Table A.2) were selected for further analysis (n = 190). We excluded studies with no focus on crops (n=63) (for example, those conducted in natural habitats), no field component (those conducted in labs or greenhouses), or those conducted in plantation forests. The selected reviews and the studies therein did not necessarily consider ES impacts on crop yields directly. Often it was the response of ES providers that was the focus of a study, with no or limited quantification of impacts on food production. However, some reviews did link ES providers to yield, such as Garibaldi *et al.* (2013) which linked wild pollinators to fruit-set. Thus, when “pollination” reviews or studies are referred to, these are relevant to pollination, but they did not necessarily directly quantify it, and might instead have focused on the abundance and diversity of pollinators. The same is true for “biological control” reviews or studies, which did not necessarily directly estimate pest suppression, but might instead have used proxies such as natural enemy abundance and diversity.

Table 2.2 Criteria used to classify farming landscape. Farming landscapes were classified by the % of a studies’ landscape composed of different sized fields (arable and permanent cropland). These criteria were suitable for all the studies used in our selected reviews, but they do not encompass all combinations of field size.

	Field Size		
Farming Landscape	**≤ 3 ha**	**≥ 5 ha**	**≥ 10 ha**
Smallholder	≥ 33%	≤ 33%	-
Dualistic	≥ 33%	-	≥ 33%
Large-scale	-	≤ 33%	≥ 33%

Studies were manually assigned to a farming landscape (smallholder or large-scale; Table 2.2) based on descriptions in the publication, satellite imagery from BingMaps and GoogleMaps and, in some cases, direct correspondence from authors. It is possible that some landscapes may have changed since the date of fieldwork in a study, but no discordance between author descriptions and satellite imagery was found. It should be noted that the relative (%) composition detailed in Table 2.2 classifies landscapes from land that is under temporary arable agriculture and (or) permanent cropland. These comprise crops that are sown or planted once and crops that are not replanted after each harvest, such as cocoa, coffee and rubber (but not timber).

From an ES perspective it was considered that a 2 ha maximum field size (as often used in UNEP or FAO reports) was too small to define smallholder-farmed landscapes because areas with many fields of 3 ha still have high local and landscape complexity. Therefore a 3 ha maximum field size was used to give conservative results (given the *apriori* assumption that smallholdings will be underrepresented) that slightly over-estimated the number of studies from smallholder-farmed landscapes (considering our expected values are derived from (FAO 2010) using a maximum field size of 2 ha). Landscapes with ≥33% of (arable and permanent) cropland areas composed of fields <3 ha and <33% of cropland areas composed of fields >5 ha were considered to be smallholder-farmed landscapes. Landscapes with ≥33% of cropland areas composed of fields <3 ha and ≥33% of cropland areas composed of fields >10 ha were considered to be dualistic landscapes. To provide a sufficient contrast to smallholder or dualistic landscapes, large-scale landscapes were defined as having ≤33% of cropland areas composed of fields <5 ha and ≥33% of cropland areas composed of fields >10 ha. If a landscape had large areas under a single management, but small field sizes, such as a large-scale commercial orchard subdivided into small sub-units, these were classified as large-scale. Author descriptions of the farming system were particularly important in the characterisation of orchard and plantation systems which were more difficult to define from satellite imagery. If it was unclear whether a field was pasture or cropland then it was considered cropland.

Many studies defined their location as a single spatial point and in these cases the landscape was considered to be an area within a 1 km radius of the point. If the location of a study was defined as a general area (e.g., “West of Göttingen, Germany”), the study landscape was estimated from the dominant farming system for that area. Where study sites gave high resolution spatial references for multiple sites, the landscape was defined from all the sites. If multiple landscapes types were present, the study was included in multiple landscape categories.

To assess economic and biogeographic biases studies were classified according to national income and global region as per World Bank Databank 2011 data (World Bank 2013), and climate using ArcMap v10.0 (ESRI 2011) and The Nature Conservancy’s terrestrial global ecoregions map (The Nature Conservancy 2009). To generate expected values for studies by World Bank income group, World Bank region (including all national incomes and not just developing nations), and biome, it was assumed that the number of studies in a category would be proportional to the area of cropland contained in that category. FAOSTAT (FAO 2013b) was used to calculate 2011 cropland area (combined area of arable and permanent croplands) for World Bank income groups and regions. Cropland area per biome was extracted from the GlobCover2009 landcover map (ESA & UCLouvain 2009) using TNC's terrestrial ecoregions map (The Nature Conservancy 2009) in ArcMap V10.0 (ESRI 2011). Where crop cover for a pixel was defined by a range, the central value of that range was used. As figures were unavailable to describe the proportion of smallholding area that was cropland, expected values for global and regional areas of smallholder farming (large-scale vs. smallholder only) were generated by assuming that the number of studies in a category would be proportional to the area of agriculture contained in a category. Expected values for the number of studies from different farming landscapes were estimated using the World Census of Agriculture 2000 (FAO 2010) in conjunction with 2011 FAO national estimates of agricultural area and agricultural population (Appendix B, Table B.2). It should be noted that FAO census data were collected over the period 1995-2005 and for many countries data were deficient or the structural nature of agriculture was poorly assessed (Appendix B, Table B.1). This is an issue that will hopefully be addressed in future censuses and research. Chi-square or exact multinomial goodness-of-fit tests were used to compare observed against expected proportions. Exact multinomial tests used MonteCarlo simulations with one billion trials to generate significance values. Statistical analyses were performed in R 3.0.1 (R Development Core Team 2014).

2.3. Results

We analysed seven quantitative reviews (Table 2.3) relevant to crop pollination and four relevant to biological control containing a total of 190 studies (Appendix A, Table A.2).

Table 2.3 Quantitative reviews and meta-analyses of pollination and biological control selected for this review

	Author	Theme	Total Studies *	Agricultural Studies
Pollination	Ricketts et al. (2008)	Distance to natural habitat	22	22
	Winfree et al. (2009)	Disturbance	50	27
	Williams et al. (2010)	Disturbance	21	11
	Garibaldi et al. (2011)	Isolation from natural habitat	29	29
	Garibaldi et al. (2013)	Crop pollination by insects	43	43
	Kennedy et al. (2013)	Local and landscape effects	34	34
	Shackelford et al. (2013)	Local and landscape complexity	19	19
	Unique studies (n)		**115**	**88**
Biological Control	Letourneau et al. (2009)	Natural enemy diversity	63	30
	Chaplin-Kramer et al. (2011) **	Landscape complexity	45	44
	Veres et al. (2011)	Landscape complexity	25	24
	Shackelford et al. (2013)	Local and landscape complexity	28	28
	Unique studies (n)		**138**	**102**

* The number of studies presented may differ with those presented by a review as some combined studies from different years at the same location into single entries. These were spilt for the purposes of this review. Other QRs spilt single studies into multiple entries when more than one crop was investigated. Here they are considered as a single study

** 46 studies were used in this review but one PhD thesis (O'Rourke, 2010) was omitted due to lack of access.

2.3.1. **Farming landscape**

Overall, smallholder studies accounted for 12% (n = 22) of the pooled studies (7%, n = 7, of biological-control studies and 17%, n = 15, of pollination studies; Figure 2.2D). Both globally and in developing nations the expected proportion of smallholder studies was much higher than observed when considering agricultural population, but not for agricultural area (Figure 2.2D & Figure 2.3). For both services, there were far fewer smallholder studies than expected, given the size of the agricultural population in each farming landscape. Given the size of the agricultural area, in contrast to the agricultural population, biological control in smallholdings was insufficiently studied but there were approximately as many studies as expected for pollination.

Considering individual reviews (Appendix A Figure A.3, studies within a review, not the overall study pool), the mean ratio of large-scale to smallholder studies to for pollination was 5.4 (SD 4.5) and 18.3 (SD 8.4) for biological control. Most (10/11) reviews also differed significantly from expected values for farming landscape when considering agricultural population, but when considering global cropland area no significant differences were apparent.

When considering only smallholder studies, the regional distribution was uneven (based on agricultural area; Figure 2.3A). Most regions apart from 'Latin America and the Caribbean' had fewer than expected smallholder biological-control studies based on smallholder area or population. Smallholder pollination studies exceeded expectations based on area for 'East Asia and the Pacific' and 'Latin America and the Caribbean' but were lacking for 'sub-Saharan Africa'. Nearly all regions were deficient for smallholder pollination studies when considering agricultural population, again with the exception of 'Latin America and the Caribbean'.

2.3.2. **Regions**

Pooling the constituent studies of the quantitative reviews showed that 86% (n = 88) of the biological-control studies and 55% (n = 45) of the pollination studies came from Western Europe and North America (Figure 2.4& Figure 2.2A). Both percentages were significantly higher than expected compared to the 34% of global cropland contained within the World Bank Regions that encompassed these areas (Figure 2.2A). There were no biological-control studies in Africa or continental Asia and fewer pollination studies than expected given that these regions contain approximately half of global cropland with an agricultural population of approximately 2 billion (World Bank 2013). For information on the importance of a region to various global statistics (e.g., crop production, population, biodiversity, etc.) see Appendix A Figure A.1.

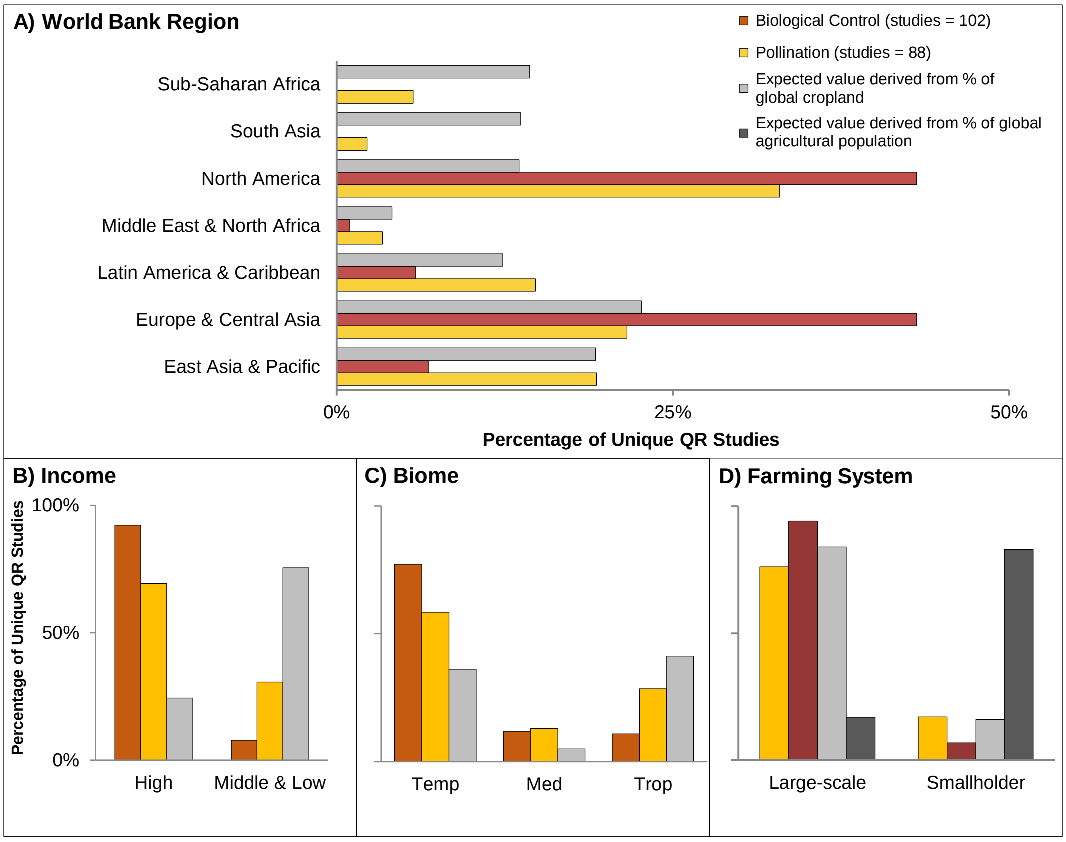
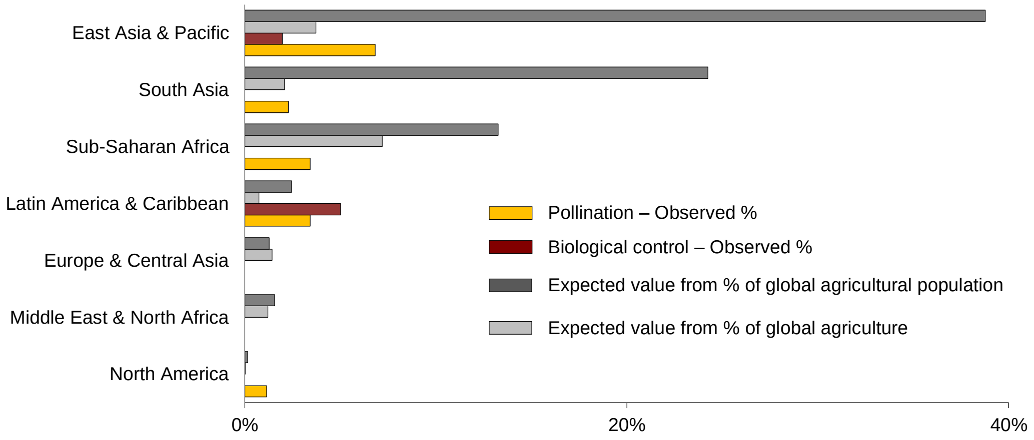


Figure 2.2 Analyses of pooled studies for biases in region, income group, biome and farming landscape. Unique pollination and biological control studies (relevant to agriculture) pooled from all quantitative reviews, are compared by percentage for World Bank regions (A), World Bank income groups (B), biomes (C) and farming landscapes (D). In C) Trop = tropical and sub-tropical; Temp = temperate; Med = Mediterranean. Expected values for each factor level were derived from the percentage of the total area of global cropland (A & B) (FAO 2013b); the percentage of the total area of global cropland (C) (ESA & UCLouvain 2009; The Nature Conservancy 2009); and the percentage of global agricultural area (D) (FAO 2010; World Bank 2013) or the % of global agricultural population in each farming landscape. A) **Region** Pollination (Poll):$\chi^2 = 37.9$, P<0.001; Biocontrol (BioC): P<0.001 (Exact Multinomial Test). B) **Income** Poll: $\chi^2 = 95.8$; P<0.001; BioC: $\chi^2 = 253.0$, P<0.001. C) **Biome** Poll: $\chi^2 = 18.3$, P<0.001; BioC: $\chi^2 = 78.1$, P<0.001. D) **Farming System** % Global Agriculture: Poll: P=0.541, $\chi^2 = 0.4$; BioC: P=0.014, $\chi^2 = 6.09$; % Global Agricultural Population: Poll: P<0.001, $\chi^2 = 237.5$; BioC: P<0.001, $\chi^2 = 412.4$ (Note α for tests in D is 0.025 due to a Bonferonni correction for multiple testing).


A) Smallholder studies per World Bank region

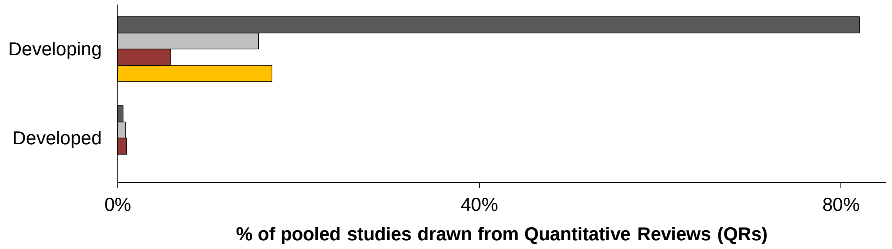

B) Smallholder studies per development class

Figure 2.3 Pollination and biological control studies from smallholder farming landscapes as a % of all unique pooled studies for each service are compared by A) World Bank regions and B) development class. Expected values for A and B were derived from (FAO 2010; FAO 2013b) and were generated by multiplying the global % of agricultural land/agricultural population for a region/development class by the within factor % that was estimated to be smallholder.

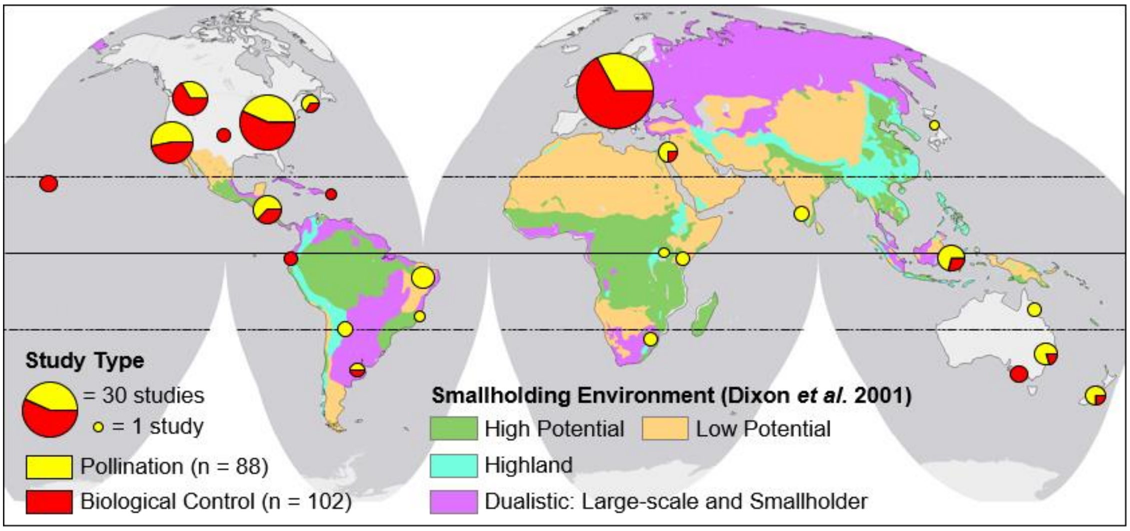


Figure 2.4 Distribution of pollination and biological control studies relevant to food production used in quantitative reviews. Smallholding Environment (coloured areas) is a broad classification of smallholding type (see Dixon et al. 2001 for definitions) for countries that are not defined as OECD-high income nations (greyed areas) by the World Bank. These colours state the likely type of smallholding to be found if present and do not reflect the presence/absence or importance of smallholding in an area. High potential environments (in terms of crop yield) are a combination of irrigated farming systems, wetland rice based farming systems, and rainfed farming systems in humid areas of high resource potential. Low potential environments are those of low current productivity or potential because of extreme aridity or cold. Highland environments are steep and highland areas.

2.3.3. Biome (climate)

With respect to the area of global cropland, the temperate region contributed double the expected number of pooled studies (77%, n = 78, for biological control and 58%, n =45, for pollination; Figure 2.2C). The number of biological control studies was a quarter of that expected (11%, n = 11) and, whilst higher, the number of pollination studies was also less than expected (27%, n = 22). Mediterranean studies were more numerous than expected from cropland area for both pollination and biological control. Individual reviews on pollination contained studies with the expected proportions (given cropland area) for temperate and tropical biomes, whereas the coverage within three biological-control reviews was significantly and strongly biased towards temperate biomes (Appendix A Figure A.3). The remaining biological control review by Letourneau et al. (2009) was also significantly skewed to temperate studies, but much less so, and it did explicitly compare tropical and temperate studies. Overall, nine studies were from biomes that were of low productivity (cold or dry) or small in extent: seven were from deserts and xeric bushlands and two were from boreal and taiga, a further study was from the montane grasslands and shrublands biome.

2.3.4. Income (development)

Studies from developed regions accounted for 82% (n = 155) of pooled studies (92%, n = 94, of biological control and 69%, n = 61, of pollination studies; Figure 2.2B). The number of pooled pollination studies from developing countries was approximately equal to expectations based on cropland area (Figure 2.3B) although with varied geographic distribution (Figure 2.3A). However, biological control (pooled) was insufficiently studied in developing countries (Figure 2.3B). On an individual basis most reviews (10 out of 11) also had significantly fewer studies than expected from developing regions (Appendix A Figure A.3).

2.4. Discussion

2.4.1. Food security and sustainable intensification

Agricultural growth is particularly effective in improving food security, especially in low income areas (McGuire 2013), and sustainable intensification is a pathway for realising this (Pretty 2008; Royal Society 2009; The Montpellier Panel 2013). Sustainable intensification includes enhancing or conserving ecosystem services for the role they can play in maintaining and increasing crop production. This aspect of sustainable intensification is known as “ecological intensification” (Bommarco et al. 2013). Ecological intensification is as important in the developing world as it is in the developed world. Whilst most of our understanding of some ecosystem services — exemplified here by pollination and biological control — comes from the temperate and developed world, the bulk of the world's agricultural land, production and human population can be found in the developing world. In addition, the diversity of farming systems in the developing world is greater than the more uniform large-scale and typically intensive agriculture in the developed world. Sustainable intensification of developing world agriculture must include the billions of farmers that are smallholders (McGuire 2013; The Montpellier Panel 2013) for whom management guidance for ecological intensification must also work (Dobie and Yuksel 2005). However, it is shown here that there are significant farming-landscape, regional, climatic and economic biases in the evidence base underpinning the likely contribution of regulating ecosystem services to sustainable intensification via quantitative review.

2.4.2. **Farming landscape**

Only 12% of pooled studies came from smallholder-farmed landscapes as most quantitative reviews were based on data from large-scale farming and typically used three or fewer studies from smallholder-farmed landscapes. The extent to which management interventions derived from research conducted in large-scale farms in developed regions such as the US and western Europe can be generalised to benefit food security in other regions is likely to be limited when there are significant contextual differences in farming system, climate (e.g., differences in extremes and modality of temperature and rainfall between temperate and tropical regions) and biogeography (e.g., differences in regional species pools).

Compared to large-scale farming landscapes smallholder-farmed landscapes are much more diverse in terms of local and landscape complexity, management intensity and the interactions between them (Appendix A Figure A.4). Smallholder landscapes, particularly in areas of subsistence farming, are likely to have a high richness and diversity of crop types, both spatially and temporally (IFAD & UNEP 2013). In smallholding areas typical of sub-Saharan Africa (Figure 2.1A & D), dwellings and associated livestock, trees, gardens, paths and boundary features generate local complexity, but this is much reduced in large-scale systems. Also, smallholder landscapes typically will not reach the levels of management intensity that occur in large-scale farms, simply because of the use of manual rather than mechanised labour. If research efforts are concentrated in large-scale systems then it is unlikely the gradients of farmland landscape, complexity and management intensity and their relationship with ecosystem service providers and function are being fully explored.

As well as differences between smallholder and large-scale farmed landscapes, there are clearly cultural and contextual differences within the smallholder system (e.g., coffee agroforestry in humid South-East Asia vs. maize farming in semi-arid sub-Saharan Africa).

However, of the 22 smallholder studies in the quantitative reviews, 16 came from a single context - coffee systems. Coffee is a cash crop, a perennial crop, and a stimulant that has no calorific value. Thus, research in these coffee landscapes is of low relevance to landscapes of annual crops that are grown for local consumption and contribute to local food security. Therefore, both an increase in the proportion of smallholder research and also an increase in the diversity of research is needed. All two billion smallholders —two billion decision makers — are unlikely to be served by the same research findings. Moreover, since our expectations of how much research should come from smallholder farmed landscapes were based on the number of smallholder farmers, the results were more significantly biased against smallholder farmed landscapes than they were when our expectations were based on the area of smallholder farmland. Although the area of smallholder farmland is more relevant to total global food production, it should be emphasized that the number of smallholders, who constitute a large proportion of the undernourished, would seem to be more relevant to local food security. Thus, the combination of diversity and food insecurity in smallholder systems means that research biases against these systems are all the more acute.

2.4.3. **Region**

We found that 55% of pollination and 86% of biological control studies came from North America and Western Europe. Regional biases such as these might pose a problem for generalising to other under-represented regions. The responses of different bee species to disturbance (Winfree et al. 2009; Cariveau et al. 2013) and the applicability of a generalised ES relationship (e.g., the relationship between flower visitation and distance from natural habitat) may depend upon the species present in a region. In some cases, functional groups of service-providing species may be absent or substantially different between regions (Archer et al. 2014). For example, bumblebees (*Bombus* spp.) are a well-studied genus of wild pollinator, for which management options have been developed in Europe and North America (Dicks et al. 2010), but they are absent from sub-Saharan Africa (Michener 2007). Furthermore, the balance between ecosystem services and disservices (services that reduce productivity or increase production costs, such as herbivory) flowing from a natural habitat to a nearby farmland may differ between regions. Quantitative reviews have often found that natural habitats benefit ecosystem services such as pollination in nearby farmland (for example, Garibaldi et al. 2011). However, the species that can move from natural habitats into croplands can fundamentally differ between regions. Proximity to a natural area in sub-Saharan African and South Asia can expose a farmer to crop-raiding elephants and primates that can reduce crop yields and create human-wildlife conflict. In contrast, in Europe and North America, regions to which research is biased, crop-raiding is a minor problem. When studying the net benefits of natural habitat in certain sub-Saharan African contexts, it could be that crop raiding (an ecosystem disservice) tends to outweigh the benefits of enhanced pollination and biological control services on farms near natural habitats. The consequences of crop raiding are likely to impact large landholders less than smallholders, as an individual smallholder can easily lose the majority of their harvest to an elephant or troupe of baboons. Although ecosystem disservices could strongly affect the design of sustainable farming landscapes (for example, crops that are unpalatable to primates might be used to buffer a habitat with many baboons and monkeys), they are poorly considered in the published literature (but see Zhang et al. 2007).

2.4.4. **Biome (climate)**

Two-thirds of pooled studies came from the temperate region despite tropical croplands occupying a larger area than temperate croplands. Obviously there are profound climatic differences between biomes that shape the assemblages of pollinators and invertebrate pests and their natural enemies. In general, the effects of climate and climate change on pollinators are much better understood than are effects on other groups of ecosystem service providers (Cock et al. 2013), and our analyses reflect this. We show individual quantitative reviews relevant to pollination tend to balance data from tropical and temperate regions whereas biological-control reviews were all significantly and often strongly biased to the temperate zone.

There can be major differences between tropical and temperate biomes in the spatial and temporal availability of resources important for ecosystem service providers in natural habitats (habitats that may enhance ES in nearby crops). For example, the plant community in aseasonal tropical lowland forests has a continuous pollination period throughout the year compared to just late spring and summer in northern temperate forests (Bawa 1990). Temperate forests also have higher mean flower longevity and a larger proportion of wind-pollinated plants than aseasonal tropical forests (Bawa 1990). As the functional significance (flowers providing nectar and pollen) of a forest to pollinators differs between and within biomes, this is likely to be the case for other habitats (including agricultural land), functions (e.g., nesting sites) and ecosystem service providers too. As such, interventions for ecological intensification that require manipulating or conserving natural areas in a farming landscape should carefully consider what climate the intervention was derived from and the implications of any functional differences in habitats between derived and target climates (see Cock et al. 2013).

2.4.5. Income (development)

It is not surprising that more than 80 % of studies were conducted in developed regions since funding for science is higher there. This may also reflect a publication bias in that researchers from developed nations may be more likely to publish their work in English-language peer-reviewed journals and a reviewer bias where studies are more likely to be cited when studies are in publications from high-income nations. The consequences of the overabundance of studies from temperate regions and large-scale landscapes (particularly the U.S. and Germany) were discussed above.

2.4.6. Insights from large-scale studies

Studies of ecosystem services from large-scale farming landscapes (typically temperate) provide insight into the aspects of an agro-ecosystem that should be conserved when a complex and/or low-intensity system is faced with intensification. For example, local management options are likely to have more positive effects on service providing insects in agricultural landscapes of intermediate complexity (Tscharntke et al. 2005a; Tscharntke et al. 2012b; Scheper et al. 2013), but less so in small-scale landscapes comprising many other habitats in addition to agricultural fields (Bengtsson et al. 2005; Winfree et al. 2009; Batáry et al. 2011; Kennedy et al. 2013). The interaction of local and landscape factors can be important for ES delivery as was the case for flower visitation and production in commercial South African sunflower fields where the enhancement of floral diversity within fields ameliorated the negative effects of isolation from natural habitat (Carvalheiro et al. 2011). Cultural species (dependent on crop habitats) of pollinators and natural enemies might be negatively affected by landscape complexity, whilst ecotone species and dispersers (dependent on non-crop habitats) might be positively affected (Shackelford et al. 2013).

The most recent reviews relevant to pollination should be commended for considering complexity at multiple spatial-scales. For example, Garibaldi et al. 2013 and Kennedy et al. 2013 stratify their study selections to incorporate a range of farming-landscapes for meta-analysis making it much easier to generalise their findings to multiple contexts. However, even in recent reviews, smallholding landscapes are not considered explicitly. As such, determining when generalisations can and cannot be applied to a type of smallholder landscapes across multiple regions (and thus climates) should be a priority for ES science.

2.5. Conclusions

Quantitative reviews are essential for modelling and predicting ES provisioning in the design of sustainable farming landscapes, for directing the policies required to adapt our current farming practices and advancing ecosystem service theory. However, the constituent studies of recent reviews relevant to agricultural biological control and, to a lesser extent, pollination were biased towards large-scale landscapes and/or global biomes (temperate), regions (North America and Western Europe) and national economic statuses (high-income, developed nations). Differences (spatial and temporal) in management intensity and local complexity between smallholder-farmed and large-scale farming landscapes may cause ecosystem service-providing insects to respond differently to disturbance and management interventions. The high local complexity of smallholder-farmed landscapes could promote beneficial species and consequently the ES they provide. In this scenario the conservation of ES whilst increasing crop production will be required (we might term this "ecological conservation") compared to large-scale landscapes where ES are diminished and their restoration or replacement is required (ecological intensification). Biogeographic differences between regions in terms of climate and service- and disservice-providing species pools may also present problems for the generalisation of findings and application of ecological intensification. Thus, generalisations from the quantitative reviews included here to smallholder-farmed landscapes and, for biological-control reviews, to tropical landscapes, should be made with caution, especially in regions where little research has been conducted.

More specifically, research bias in reviews affects their general application to informing about sustainable intensification. The large number of pollination and biological control studies from temperate large-scale farming landscapes suggests we are well placed to improve ES and trial ecological intensification there. However, lower data availability from other farming landscapes and/or climates, notably tropical (for biological control reviews) and smallholder, means it may be difficult to use current reviews to inform ecological intensification in such data-deficient regions. This problem is greatest in tropical regions with diverse farming landscapes and high agricultural populations such as South Asia and sub-Saharan African where smallholdings contribute more than a third of the agricultural area. Data deficiency for regions that contribute much of the world's population, crop production and hunger (e.g., South Asia, China, Russia and Africa) poses further problems to improving food security with ecological intensification (and ecological conservation).

Investing globally in smallholder research for multiple crops and finding more projects and publications from regions where there is little information (such as China, Russia, South Asia and Africa) is essential. This is especially the case for research relevant to biological control, which appears more biased than pollination-relevant research. To increase their global relevance, quantitative reviews investigating landscape or local effects on ES should consider the coverage of their datasets with regards to region, climate and farming landscape. Following on from this future empirical studies should target smallholder systems, with quantification of climate and complexity in time and at multiple spatial-scales. Classification of existing studies that do not present landscape information could also provide new data and this is becoming easier. Open-access satellite imagery (e.g., Landsat8 or GoogleEarth) and software (R, QGIS, GRASS) now enable *post-hoc* classification of farming landscapes, and detailed global datasets for biodiversity, food production and development are available from the IUCN, World Bank and FAO. International collaboration is needed to search for, translate (if necessary) and disseminate the ES datasets that no doubt exist in the developing world. We suggest that non-English language publications and agricultural institutions that may often be overlooked will be productive. Data regarding the cost of ecosystem disservices in agricultural areas near protected areas in South Asia or sub-Saharan Africa may already be available from social and developmental disciplines. If so, this should be integrated into current assessments of the net ES value of natural habitats.

Global datasets regarding the structure of farmland are incomplete and inconsistent. Therefore our estimates of smallholder area in some regions, such as sub-Saharan Africa, were based on limited data and it is hoped that the pending World Census of Agriculture 2010 will improve the situation. Furthermore, our classification of landscapes into broad structural categories was necessarily simplistic. From an ES perspective smallholding landscapes could better be defined using statistical measures of configuration (see Kennedy et al. 2013) and information regarding composition and management. An appropriate classification scheme for small-scale farming (perhaps building on Dixon et al. 2001) could be used as a guide to ecological intensification/conservation.

In the face of global climate change and food security, it is important to understand these issues for diverse environmental conditions and landscapes that fully represent the global farming constituency. Further investigation of the conditions that characterize smallholder-farmed landscapes would provide crucial information regarding the resilience of such landscapes to environmental disturbance across multiple ecosystem services.

Chapter 3. Land-use intensification effects on ecosystem service and disservice providing insects in a tropical smallholder landscape

3.1. Introduction

When harnessing ecosystem services for agricultural production, a process called ecological intensification, ecosystem services can be defined as the intermediate services that support a final service of crop yield (Bommarco et al. 2013). Ecological intensification manages (intermediate) ecosystem service providing species that contribute directly or indirectly to agricultural production (Bommarco et al. 2013), such as crop-pollinating bees, the natural enemies that consume crop pests or soil species that enhance nutrient cycling. Using ecological intensification to reduce crop yield-gaps, the difference between realised and potential yields, is a means of improving food security and production. This is highly relevant to small-scaled farmed landscapes in low-income nations where yield-gaps and food-insecurity are often high (FAO/IIASA 2012). Yields-gaps in small-scale farming landscapes have typically been reduced with conventional intensification (Briones and Felipe 2013) and/or the consolidation of landholdings into simplified landscapes of contiguous cropland (Huang et al. 2011). However, optimal levels of cost-effective production may not have been realised in these situations as conventional intensification can degrade ecosystem functioning (Singh 2000; Wood et al. 2000; Bennett et al. 2001; Zhengfeng 2008) leading to declining or stagnant crop yields despite technological advances or increased inputs (Foley et al. 2011). Loss of landscape resources, such as natural habitats that offer species that provide ecosystem service refugia from disturbance (Swinton et al. 2007; Coll 2009) or resources such as flowers providing nectar and pollen, can lead to sub-optimal yields (Halaj et al. 2000; Carvalheiro et al. 2011) and/or increased expenditure on substituting reduced services (e.g. , pesticides substituted for natural enemies, Pimentel 2005; Losey and Vaughan 2006). Additionally, conventional intensification leading to increased pesticide use can negatively impact beneficial ecosystem service providing insects (Desneux et al. 2007; Brittain et al. 2010; Potts et al. 2010; Brittain and Potts 2011). Landscapes in pre-intensification small-scale farmlands with large yield-gaps are often spatially and temporally complex (especially at local scales ,Steward et al. 2014) and research, derived mostly from large-scale farmlands, has shown that complexity can promote pollinators and natural enemies (Chaplin-Kramer et al. 2011; Shackelford et al. 2013). Given the high complexity of small-scale farming landscapes regulating ecosystem services for crop production may well be adequate (Tscharntke et al. 2012b). Increasing food-production efficiently in small-scale landscapes with yield-gaps will require conserving features that promote regulating ecosystems services whilst enhancing soil-nutrients and water availability (either conventionally or sustainably), further, given the strong policy drivers for consolidation and expansion of farmland in large countries such as China (Xinshe 2002; Niroula and Thapa 2005; Min 2006; Bledsoe et al. 2007; Huang et al. 2011; Ntirenganya 2012) it is important to understand how such features can be conserved as field size and landscape cropland area increase. This requires understanding of cross-habitat spillover of species between non-crop and crop habitats (reviewed by Blitzer et al. 2012; Tscharntke et al. 2012b), however, as discussed in Chapter 2, there is a need for more research into small-scale farming landscapes where we have a poor knowledge base for the costs and benefits of regulating ecosystem services and disservices and their interactions compared to large-scale farming systems (Steward et al. 2014, see also Chapter 2).This could hinder cost-effective (ecological) intensification of small-scale farming landscapes.

Spillover occurs when species move from one habitat type to another (this can be dispersal or foraging behaviour) and is implicit to many management options relevant to ecological intensification, such as providing or conserving non-crop floral resources in or adjacent to crops for pollinators and natural enemies (Pywell et al. 2006), and predicting where and when they will be most effective (e.g., the intermediate landscape-complexity hypothesis,Tscharntke et al. 2012b). In the context of small-scale farming landscapes it is important to understand how spillover will be affected by policies promoting landscape transformation as a means to produce more food, in particular how the spillover of agriculturally important taxa responds to the conversion of non-crop habitats to cropland and the consolidation of small fields into fewer larger fields growing a reduced number of crops. Reductions in community diversity, the overall abundance of beneficial insects and the ecosystem services they provideoccurs as distances to (or isolation from) natural habitats increases. For example, pollinator species richness, flower visitation, crop yield, and service stability all decline with increasing isolation from natural areas (a consequence of the expansion and consolidation of cropland) with effects occurring at spatial scales of kilometres to hundreds of meters depending on the species or group in question (Ricketts et al. 2008; Garibaldi et al. 2011). Crop-pest parasitism by parasitic natural enemies generally decreases with distance from field boundaries (Landis and Haas 1992; Baggen and Gurr 1998; Long et al. 1998; Thies and Tscharntke 1999; Jason et al. 2004; Bianchi et al. 2008) with effects seen at distances as small as tens of meters. Crop-pest predators in temperate regions, such as ground dwelling carabid beetles and some spiders, have been shown to hibernate in non-crop habitats going on to invade croplands in spring and penetrating up to several hundred meters from field margins (Coombes and Sothertons 1986; Booij et al. 1995). Reducing the length of the interface between crops and non-crop areas may reduce pest-control (Bianchi and Van der Werf 2003; but see Vollhardt et al. 2008; Perovic et al. 2010) and reducing the proportion of natural habitat within a landscape can reduce the overall landscape abundance of beneficial species that benefit from non-crop habitats which, in turn, results in reduced spillover into croplands (Schmidt and Tscharntke 2005). Reducing semi-natural habitat in the landscape can promote crop-pest populations (Veres et al. 2013), and decreasing landscape complexity can be detrimental to both pollinators (Shackelford et al. 2013) and natural enemies (Chaplin-Kramer et al. 2011; Shackelford et al. 2013) but does not necessarily affect pest abundances (Chaplin-Kramer et al. 2011). Kennedy *et al.* (2013) found that bee abundance and diversity were highest in diversified, organic agriculture in landscapes with resource rich surrounding land-cover. Non-crop habitats, however, may also be the source of ecosystem disservice providing species especially for small-scale farmers in the buffer zones of protected areas for nature conservation (Burgess 1981; Naughton-Treves 1998; White et al. 1998; Madhusudan 2003; Sitati et al. 2005).

Knowledge of how common ecosystem service or disservice providing species spillover from other habitats and into cropland (Figure 1.1, Duelli and Obrist 2003; Tscharntke et al. 2005b) will determine which management interventions are appropriate. Across the interface of cropland and non-crop habitats different species providing the same ecosystem service may have contrasting distribution patterns (Duelli and Obrist 2003; Tscharntke et al. 2005b) or have the same response pattern but at different spatial scales. Distribution patterns across the crop non-crop boundary include those of stenotopic species that are only found in non-crop habitats, cultural species that prefer crops, disperser species that colonise crops from non-crop habitats, ecotone species that are typically found at the interface of crop and non-crop habitats and ubiquist species that have no preference for either habitat (Duelli and Obrist 2003, see Chapter 1 Figure 1.1). For example Shackelford *et al.* (2013) found the compositional complexity of landscape had positive effects on spiders but results for predatory beetles and parasitoids were inconclusive, and Chaplin-Kramer *et al.* (2011) found specialist natural enemies tended to respond to landscape complexity at smaller scales than generalist natural enemies. As the response of different ecosystem service providing functional groups or taxa to landscape change is variable (e.g., Williams et al. 2010), in the context of ecological intensification it is important to consider the response of multiple agriculturally relevant taxa or functional groups when observing and predicting the effects landscape change. If a management intervention for one group of ecosystem service providing species benefits another, then its practical utility is improved creating a ‘win-win’ scenario (Power 2010).

Conversely if a management intervention for one beneficial species group or ecosystem service supresses another then a tradeoff may occur (Power 2010). Compatible responses to landscape and local complexity have been demonstrated for mobile arthropods providing biological control of crop pests and crop pollination (Shackelford et al. 2013), services that both provide substantial benefits to agriculture (Losey and Vaughan 2006; Fernandez-Cornejo et al. 2009; Gallai et al. 2009).

When planning for ecological intensification it is also important to remember that spillover is not always beneficial and can act as a source of ecosystem disservices such as pest-populations (Lavandero et al. 2006; Zhang et al. 2007; Eilers and Klein 2009b), disease (Despommier et al. 2006; Nugent 2011) or dangerous and/or crop-raiding mammals (Woodroffe et al. 2005a; Inskip and Zimmermann 2009). Economic losses in the United States due to wildlife damage were valued at $944 million in 2002 (National Agricultural Statistics Service 2002) and 2001-2003 global crop losses due to animal pests were estimated to be 5-19% for major cereals, 7-13% for potatoes, 3-16% for soybeans and 5-22% for cotton (Oerke 2006). In subsistence smallholder or commercial large-scale organic contexts where pesticide use may be relatively low, spillover of ecotone and disperser crop pests and their natural enemies might be of particular importance to crop productivity. This is also of particular relevance to fields of transgenic crops designed to reduce the need for pesticide use, such as Bt cotton, for which there is there is conflicting evidence regarding the build up vs. biological control of secondary crop pests (Wang et al. 2008; Lu et al. 2010; Lu et al. 2012). It is also relevant to interventions that promote natural enemies (e.g. floral resources or overwintering sites in different kinds of field margins) that could also benefit pests (Robertson 1993; White et al. 1997).

This study investigates the response of multiple groups of mobile insect pests, pollinators and natural enemies in a low-input small-scale landscape that is undergoing rapid transformation due to agricultural extensification (the conversion of non-crops habitats in to agricultural land) and consolidation (increasing area of contiguous cropland under the same management). For these groups similar and contrasting spillover responses and landscape distribution patterns are identified and discussed with relevance to land-use change in small-scale landscapes. The objectives of this study were three:

1. To determine how the spillover of different groups of agriculturally important insects into small-scale croplands is affected by local farmland extensification (the conversion of natural habitat to croplands) through observation of the abundance response of focal taxa to increasing distance from natural habitat at the field edge. For species groups with feeding and nesting traits suggesting that they could derive all essential resources from cropland cultural or disperser distribution patterns were expected. For groups with traits that suggested they required resources within both crop and non-crop habitats ecotone distributions were expected.

2. To determine the effect of large-scale farmland extensification (conversion of natural habitats to farmland) on the abundance of focal taxa whilst considering interactions with local farmland extensification. The abundance of cultural species was predicted to respond positively (or at least neutrally) to increasing farmland area and consolidation whereas abundances of ecotone and disperser species were predicted to decline.

3. To determine how cropland resource availability directly affects the abundance of focal taxa, their spillover and their abundance response to farmland extensification at local and landscape scales. It was expected that greater resource availability (e.g., floral resources for pollinators) in croplands would enhance spillover from non-crop habitats into fields for ecotone species.

3.2. Materials and methods

In summary, woody natural habitat in the study area (Figure 3.1) was mapped from satellite imagery and small and large fields (representing consolidation of fields) were selected from landscapes of high and low natural habitat (representing the conversion of natural habitat into cropland). To investigate spillover the abundance of blister beetles, ground beetles and darkling beetles (Coleoptera: Meloidae, Carabidae and Tenebrionidae) and hymenopteran pollinators, predators and parasitoids were assessed with increasing distance from field edge using pitfall and pan traps. To estimate field resource availability for flower visitors floral area was assessed using transects stratified between differing land-uses within fields and for epigeal beetles habitat structure at the trap was measure using quadrats.

3.2.1. **Study system**

The study landscape was located in lowland (<1100 m a.s.l.) areas of Taita-Taveta County of south-east Kenya approximately centered on the town of Mwatate (lat -3.503˚, long 38.364˚). The landscape was a mosaic of open dry woodland (*Acacia* spp. and *Commiphora* spp.) and rainfed, low-input, non-mechanised small-scale farming dominated by maize intercropped with dry beans or cowpeas. As agrochemical inputs (pesticides, herbicides and inorganic fertilisers) were very low to non-existent and tillage was manual (farmers used mattocks or a shallow ox plough) cropland hostility (to insects) from mechanical or chemical disturbance was low.

Agriculture is the dominant source of income for Kenyans employing 80% of the national labour force (World Bank 2013) and a rising population is increasing demand for agricultural land. Taita-Taveta County had an annual population growth rate of 1.6% between 1999-2009, the total population of the county in 2009 was c. 284,000 in c.17,000 km^2, 48% of whom were under 20 years old (National Council for Population and Development 2013). High population growth rates coupled with saturation of the farmland resource in the wetter highlands of the Taita Hills has resulted in rapid, unplanned, conversion of dry forest to croplands in lowland areas. Dry forest area in the Taita Hills and the surrounding lowlands is estimated to have shrunk 22% between 1987 and 2003 at an annual rate of approximately 1.5% and this recent deforestation has largely occurred in lowland areas (Maeda et al. 2010a). Simulations based on current rates of change predict lowland areas will be almost completely denuded of dry forest by 2030 (Maeda et al. 2010a), although there was still a substantial area remaining at the time of this study.

The dominant soil types within the study zone were rhodic ferralsols and chromic luvisols (Batjes and Gicheru 2004), these are clays or sandy loams with moderate fertility, low organic matter content and poor water retention capacity (Mbora 2002). Rainfall patterns in Taita are bimodal; with a long rainy season occurring from March to June, with a shorter rainy season in October to December (Pellikka et al. 2009). Rainfall increases with altitude with average annual totals for the lowlands 587 mm at 560 m (Voi) increasing to 1132 mm in the uplands at 1768 m (Mgange) (Pellikka et al. 2009). Rainfall is highly variable between years, from 1986 to 2003 the minimum annual rainfall was 200 mm in the lowlands and the maximum 2000 mm in the highlands (Pellikka et al. 2009).

3.2.2. **Natural habitat mapping**

The study zone was limited to lowland areas where dry forest and wooded grasslands (considered here to be non-agricultural areas with >20% cover of shrubs or trees) were the dominant natural habitats in the landscape. Landsat imagery was too coarse to provide spatial habitat information at a spatial-scale appropriate for agricultural insects, so woody habitat was mapped manually using QGIS 2.0 (QGIS Development Team 2013) and freely available high-resolution (c. 2 m pixel width) satellite images from the openlayers plugin. Imagery recorded during the dry seasons of 2010-2012 was used for mapping as this provided the greatest contrast between woody vegetation and agricultural areas. The minimum mapping unit was 25 m^2 and the final map was smoothed in ArcGIS 10.0 (ESRI 2011) using a PAEK algorithm with 10 m tolerance as this gave a good visual fit to satellite imagery. A total of 525 km^2 was mapped (Figure 3.1). The primary landuses of non-wooded areas were cropland, settlement, roads and pasture, of these cropland was dominant (>80% of non-wooded areas). From henceforth forest or woody natural habitat is referred to as “natural habitat” and all other areas as “agriculture”.

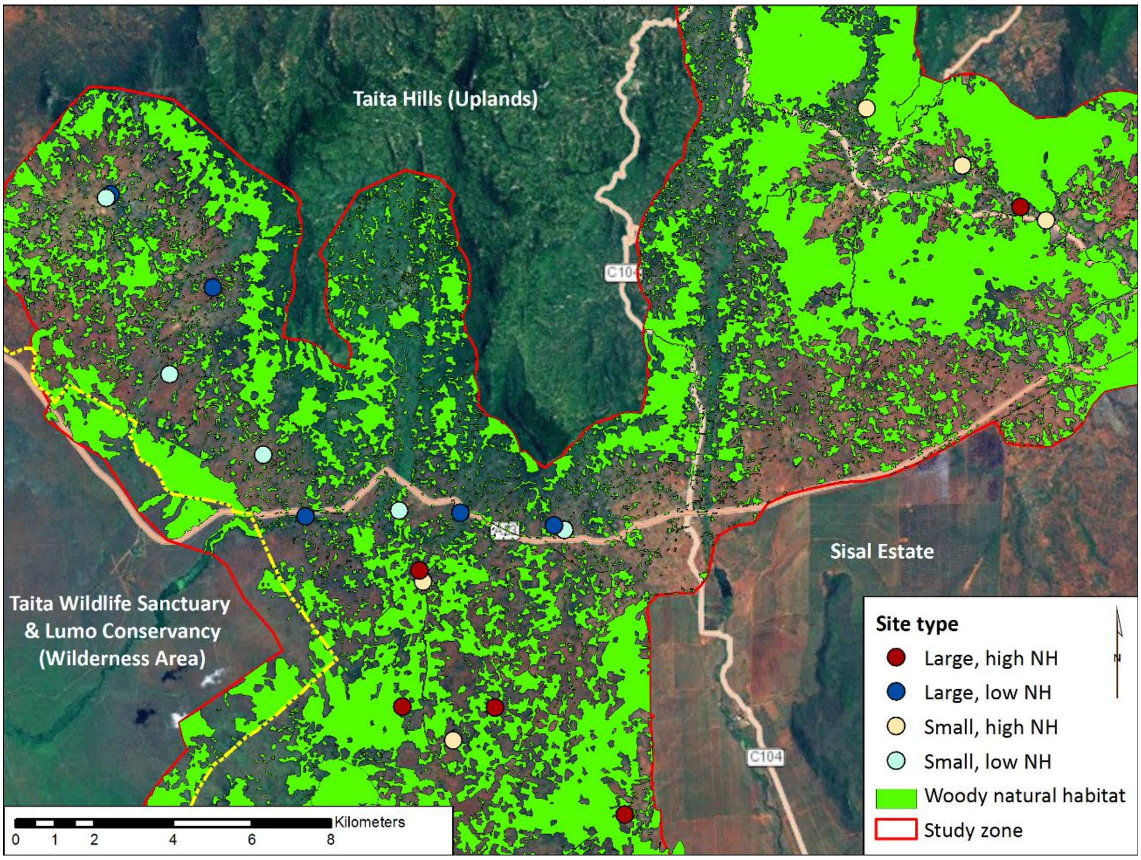


Figure 3.1 Study zone and sample site locations. The underlying basemap is a true colour landsat image.

Access to water is considered important for ecosystem service providing insects in arid environments (Zachariassen et al. 1987; Lovei and Sunderland 1996; Holland 2002; Martins 2004), so perennial or semi-perennial water features (streams and dams) were also mapped from satellite imagery in conjunction with the local knowledge of residents and ground truthing.

3.2.3. Analysis of landscape structure, study design and site selection

To determine the degree of agricultural extensification and loss of natural habitat across the entire study area, Patch Analyst 5.1 (Rempel et al. 2012) in ArcGIS 10.0 (ESRI 2011) was used to determine landscape fragmentation metrics within a radius of 1 km from points set in a 50 x 50 m fishnet grid clipped to agricultural areas. The 20% of points with the lowest proportion of natural habitat within 1 km and the 20% of points with the highest were selected and buffered to 100 m creating an area representing the extremes of landscape change. To improve standardisation between potential field sites, points within 1 km of large commercial sisal plantations and ranchlands, large settlements or protected areas were excluded, as were points above 1100 m a.s.l. or on slopes greater than 5°.Within the subset area landscape metrics were recalculated using the same procedure as before but for higher resolution 20 x 20 m fishnet point grid. Potential study landscapes were identified from this grid by selecting points within the upper 20% and lower 20% ranges for proportion of natural habitat and buffering them to a distance of 20 m. To investigate the effects of increasing distance from field edge (spillover) arable fields were mapped and the largest and smallest fields, defined as those differing in area by approximately an order of magnitude or more, were selected as potential study sites (Figure 3.2). To minimise correlations between boundary habitat and landscape potential study sites were limited to fields with boundaries comprising at 75% or more dry-forest or bushland that extended at least 5 m from the field edge (Figure 3.3).

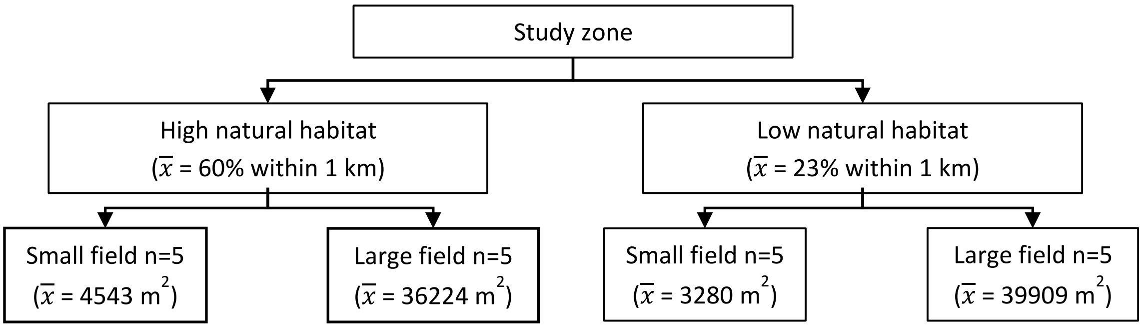


Figure 3.2 Study design with summary statistics for landscape and field size, see Table 3.2 for errors.

Figure 3.3 Examples the natural habitat cropland boundary in study fields.

Study fields were randomly selected from potential sites to give five large and five small fields in high and low natural habitat landscapes (Figure 3.2). Fields of the same size category were separated by a distance of approximately 2 km, this was assumed to give adequate spatial independence between study landscapes for the majority of ecosystem service providing insects (Steffan-Dewenter 2003; Kremen et al. 2004; Winfree et al. 2008; Chaplin-Kramer et al. 2011). Paired large and small sites were allowed within landscapes and at the 1 km scale the study contained 16 independent landscapes with four paired sites.

3.2.4. **Sampling methods**

Trapping was conducted between August 2012 to June 2013. Pan and pitfall traps shared fixed sampling points at the edge and centre of each field, the midpoint between these and at any 15m intervals from the edge that were not represented by midpoint or centre. The placement of the edge trap was random then the average distance between the remaining traps was maximised. Traps were only placed in cultivated areas where the nearest field boundary was dense woody habitat.

Triplicate pan-traps (12 cm diameter and 6 cm deep aluminium bowls with sloping sides) sampled mobile insects attracted to floral resources, the focal taxa for this study were bees, parasitoid Hymenoptera, predatory Hymenoptera and blister beetles (Coleoptera: Meloidae). Pan-trapping is the most efficient method of sampling bees in agricultural habitats (Westphal et al. 2008) and has also been used to study parasitic and predatory Hymenoptera (Bowie 1999; Christie and Hochuli 2009; Saunders and Luck 2013). Blister beetles were includedas they are potential pests of leguminous crops and were abundant in pan-traps (Durairaj and Ganapathy 2000; Otieno et al. 2011). To account for different colour preferences of hymenopteran species (Kirk 1984; Aguiar and Sharkov 1997; Toler et al. 2005; Campbell et al. 2007) pans were painted either fluorescent yellow (1005), sky blue (15) or white gloss enamel, blue and yellow pans were protected with clear varnish. Pans were repainted each sampling round. Pan-trap height was adjusted to ensure visibly was not obscured by local vegetation. Pans were filled with water mixed with a small amount of detergent to a depth of 2cm from the rim. Traps were set in the morning, mean (SD) 0905 hours ± 31 min and retrieved in the afternoon of the same day, mean (SD) 1557 hours ± 40 min, mean (SD) trap exposure was 6.88 ± 0.48 hours. Six rounds of pan-trapping were conducted during August, September and November in 2012, and in January / February, April and May / Jun in 2013. Pan-trapping was not carried out in strong winds or on rainy days and was repeated if the weather changed from favourable to unfavourable conditions during in the day. There were a total of 104 pan-traps, 66 in large fields (5-9 traps/field) and 38 in small fields (3-4 traps/field), spilt evenly between landscapes.

Pitfall traps (500 ml plastic cups, 94 mm in diameter and 135 mm deep) sampled epigeal beetles (Ekroos et al. 2010; Ikeda et al. 2010; Gilroy et al. 2014). The focal taxa in this study were ground beetles (Coleoptera: Carabidae) and darkling beetles (Coleoptera: Tenebrionidae); and these were chosen because they were abundant in traps and had relevance to crop production. Ground beetles are generally considered to be natural predators of crop pests (Holland 2002) and darkling beetles consume fresh or decaying vegetation with many species noted as significant crop pests (Allsopp 1980; Arnett and Michael 2002). Scarab beetles (Scarabidae) and blister beetles (Meloidae) were also evaluated but had strongly over-dispersed distributions (suggesting aggregative behaviour) that could not be dealt with by generalised models. Pitfalls were filled with water mixed with a small amount of detergent to a volume of 300 ml. To prevent birds scavenging trap contents and overflow from rain storms, and to reduce evaporation, pitfalls were covered with a 150 mm diameter white plastic plate raised 2.5 cm from the soil surface. Pitfalls were initially left in-situ for five days, however this was reduced to three days in subsequent trapping rounds. Pitfall trapping conducted in August and November in 2012, and in March and May / June in 2013. After discounting damaged traps, there were a total of 91 pitfall traps; in high natural habitat landscapes 28 in large and 19 in small fields, and in low natural habitat landscapes 16 in large and 18 in small fields.

For both trapping methods sites were stratified into groups that could be practically visited in a single day then the sampling order of sites was randomised each round. Sampling order was also randomised for the traps within sites. Collected specimens were temporarily stored in 70-99% ethanol until pinned for identification. If specimens were very small they were stored in sealed microtubes with 99% ethanol.

Taxonomic determinations for beetles > 04 mm in length were made to species by M.Mutua, and to genera and species/morpho-species for bees by M.Gikungu, J.Macharia and P.Steward, all using the reference collection at the National Museums of Kenya, Nairobi, Kenya, where bee and beetle specimens were deposited. Beetle specimens <0.4mm in length (365 / 3254 specimens, 11.2%) were not identified and are excluded from analyses. The identity of specimens of non-apiforme Hymenoptera was determined to family for parasitoid wasps and to genera for vespid or spheciforme wasps by R.Copeland at ICIPE, Nairobi, Kenya, and non-apiforme hymenopteran specimens were deposited at ICIPE.

Traits were attributed to taxa using the literature summarised in Appendix G and Appendix H.

3.2.5. Assessment of resource availability

Floral resources are considered an important indicator of cropland (and matrix quality) for the flower visiting insects attracted to pan-traps (e.g., Carvalheiro et al. 2011), and were estimated within study fields using transects.

To inform the location of floral transects within fields the following land-uses were mapped: fallow (cropland not cultivated for at least two season), very weedy areas (cropland not cultivated for the current season or if cultivated abandoned and non-crop vegetation dominant compared to crops), trees and shrubs (as defined in Di Gregorio 2005; scattered trees and shrubs within another landuse were considered part of that landuse) and croplands (areas growing crops or recently tilled bare ground). Small-scale variation in land-use within fields varied between seasons and was mapped twice after farmers had tilled and planted for the growing season. Mapping was conducted using a combination of field sketches cross-checked against GPS generated tracks and waypoints. The minimum mapping unit was 3 x 3 m, distinct areas smaller than this were marked as points.

Floral transects were conducted at the same time as insect sampling. Transects were randomly located with the constraints that they were separated by at least 15 m and did not cover more than one land-use. Transects were stratified between crop and non-crop habitats (within fields). Cropland received a 30 x 2 m transect plus one additional transect for every 10,000 m^2 of cropland area, up to a maximum of five transects. Non-crop transects were 20 x 2 m and were located in areas of fallow, recently abandoned crops/cultivation and trees or shrubs, if an area could not accommodate a 20 m transect then the longest dimension of that area was used. Impenetrable habitats were surveyed with perimeter transects extending 1m into the habitat. When a field contained one to five non-crop habitats each of these were allocated floral transects. If five to ten non-crop areas were present the two largest areas were allocated transects and then a further three transects were randomly allocated to the remaining areas. If 10 to 20 non-crops areas were present the four largest areas were allocated transects and then a further four transects were allocated to the remaining areas. A total of 530 transect surveys were completed, 242 in non-crop areas with the remainder in cropped areas.

All flowers within transects were counted (including grasses and sedges). Clusters of flowers in compound flowerheads or inflorescences were counted together unless individual flowers within a cluster were large (>10mm) in which case they were counted singly. Plants were photographed, described, sampled and pressed for later identification at the National Museums of Kenya, 97.8% of flowers recorded were identified to genera and 53.2% to species. Floral area of flowers was estimated using a combination of field measurements and reference to regional floras (Kew Royal Botanic Gardens 1952-2012; Kew Royal Botanic Gardens 1960-2013; Kew Royal Botanic Gardens 1993-2009). Floral area of compound flowers or inflorescences was the floral area of the floret multiplied by the mean number of open florets per inflorescence.

For each land-use class within a field floral diversity, calculated using Shannon's D, and floral area (cm^2 of flower per m^2) were estimated. Floral estimates at the field level were generated by combining scores for each land-use class within a field weighted according to the area of each class within the field. The floral area of *Datura stramonium* (which contributed 0.16% of all flowers recorded) was down-weighted (reduced) by 90% as its flowers are closed during in the day reducing their visible area and preventing access to nectar and pollen resources by day-flying species of Hymenoptera, it was not completely excluded as flowers may have still provided resources to flower-robbing species. Floral areas for species with wind-pollinated flowers (including species in the family Poaceae and some *Amaranthus* spp.) were down-weighted 50% as these plants only provided a single resource, pollen but not nectar. Wind pollinated species accounted for approximately 15% of the weighted floral area summed across all sites. Casual observations of large numbers of honey bees foraging on maize anthers indicated that grass pollen could provide an important resource to bees in this context.

Each sampling round, floral area was also assessed (as per transects) within a 1 m^2 quadrat centred on each trap. Within the same quadrat indicators of resource availability for epigeal beetles were also recorded, these were the percentage cover of vegetation, bare ground and leaf litter. Leaf litter is a potential source of cover for epigeal beetles and a potential source of food for detritivorous beetles (Robertson 1993) and living vegetation provides food for phytophagous beetles.

For coleoptera, predatory Hymenoptera and parasitoid Hymenoptera the measures of resource availability are proxies for resource availability prey and host densities, for example, would better predict resource availability (although to assess this would require resources beyond the means available to this thesis).

3.2.6. **Weather**

Hourly temperature records were estimated using data from naturally aspirated (open to the the air) DS1921G Thermochron iButtons (Maxim Integrated, San Jose, California). Temperature was separately averaged for the four eastern sites (Figure 3.1) and all others sites as the former were approximately 200 m lower in elevation and 2˚C warmer. Thermochrons were shaded by a 12 x 12 cm plyboard and positioned 15 cm from the ground in the centre of each field. Day time temperatures were derived from the period 0701-1700, corresponding to the hours of pan-trapping.

Rainfall was estimated using simple rain-gauges, consisting of a 23.2 cm diameter funnel and an 8 l collecting bucket dug into the centre of each field. Records from the University of Helsinki’s weather station at Mwatate were used to corroborate readings when available. Recent rainfall was considered to have a larger effect on trap catch than the annual estimate for a site hence rainfall as a predictor in models was the summed rainfall for a site for the 3 week windows prior to and including sampling dates.

Site coverage for both temperature and rainfall was variable due to repeated theft or damage, where data was missing it was substituted from the nearest spatial neighbour.

Temperature and rainfall values were scaled (values divided by the mean) and centred (mean subtracted from values) before use in analysis.

3.2.7. **Statistical analyses**

GLMMs in `glmmadmb` version 0.8.0 (Skaug et al. 2014) and R version 3.1.0 (R Development Core Team 2014) were used to assess the abundance response of species groups (as measured by summed trap-catch for all sampling rounds) to spillover (distance from edge of field), loss and fragmentation of natural habitat, and cropland resource availability. Table 3.1 details all predictors used in analyses and the subset of GLMM models they were included in. Some predictors were correlated (discussed subsequently) and, as such, were subset in models according to those for which there was an *a priori* reason to expect the greatest influence on the abundance response of focal taxa. To assess the importance of predictors that were not included in the global model, and to validate the choice of those that were chosen, ordination was used. Predictors were transformed using Principal Components Analysis (PCA) (rotation = varimax) into four ordination axes (always explaining ≥ 75% of variance between predictors). Henceforth, these models are referred to as “PCA” models. To account for spatial auto-correlation between landscapes and for traps within sites all models contained a fixed-slope random term for sites nested within landscape.

All combinations of landscape metric (edge density or proportion of natural habitat, for definitions see Table 3.1) and the spatial-scales at which they were calculated (buffers of field boundary scaled at 50 m, 100 m, 200 m and then at 200 m intervals until 2000 m) were tested in the global models. The nesting of sites within landscapes was adjusted for the spatial scale of landscape analysis. The metric and scale that gave the most predictive global model (lowest AIC) was selected for backwards stepwise model simplification. Model selection was based on Akaike’s Information Criterion (AIC) adjusted for small sample sizes relative to the number of parameters (Burnham and Anderson 2002). Model predictions were evaluated using the functions `glmer` or `glmer.nb` from the `lme4` library (Bates et al. 2014). Predictions were compared to observed data and if the match was poor, in particular for interactions, alternative model structures and further model simplification were investigated. Models were further evaluated by plotting residuals vs. fitted values, residuals vs. predictor variables, square-root-transformed fitted values vs. square-root-transformed observed values, Pearson residuals vs. square-root-transformed fitted values, raw residuals (observed vs. fitted values) vs. square-root-transformed fitted values, and by normal QQ-plots of residuals.

R^2 values are not directly provided for mixed models, and, the methods developed by Nakagawa and Schielzeth (2013) for obtaining marginal and conditional R^2 from mixed-models have not been implemented for negative binomial error distributions. Therefore the predictive power of the mixed models was assessed using a pseudo-R^2 value (in the following simply referred to as R^2) and calculated as the R^2 from a regression between predicted and observed values (Gabriel et al. 2010). The sensitivity of R^2 for each model variable was then estimated by ΔR^2 lost from the regressions between model predictions and observed values when the coefficients of each model variable (main effect and interaction) were set to zero whereas the other coefficients remained constant (Gabriel et al. 2010). Where the predictions of interacting terms in regression models are presented, one term was varied across the range of corresponding observed values whilst the other terms were fixed at high, moderate and low values derived from observed values (upper third, middle third and bottom third of values). Where observed values are plotted against predictions data was binned according to the same predictor quantiles as per the predictive plot. These datapoints can take any value within a quantile’s range. Plots of observed values do not show the influence of random effects and are intended to demonstrate general patterns in the data.

Table 3.1 Predictors used in GLMM analyses.

Predictor	**Unit / description**	**Pan traps**		**Pitfall Traps**	
		Main models	**PCA models**	**Main models**	**PCA models**
Day temperature[†,‡]	Mean temperature (˚C) for period 0700-1700 hours		Y		Y
Distance to edge	Distance from trap to edge of field (m)	Y	Y	Y	Y
Distance to water	Distance from trap to water source (km)	Y	Y	Y	Y
Edge density*	Edge density of natural habitat within a specified distance of field-edge (m / 100 m^2)	Y	Y	Y	Y
Fallow[§]	% of field fallow		Y	Y	Y
Field floral area[‡]	cm^2 flower area / m^2 field area	Y	Y		Y
Field floral diversity[‡]	Shannon's D		Y		
Leaf litter[‡]	% cover of leaf litter in 1 m^2 quadrat centred on trap			Y	Y
Natural habitat	% of natural habitat within a specified distance of field-edge	Y	Y	Y	Y
Rainfall [†,‡]	Summed rainfall for 3 week windows prior to and including sample date (cm)		Y		Y
Trap floral area[‡]	cm^2 flower area / m^2 field area		Y		
Vegetation cover[‡]	% cover of vegetation in 1 m^2 quadrat centred on trap				Y

* Included when edge density gave a global model with lower AIC than the global model using natural habitat, no global models included both these terms.

[†] Centered before including in analyses. [‡] Averaged across sampling rounds. [§] Averaged across two growing seasons.

To give a descriptive summary of the data bootstrapping was used to estimate dependent and predictor means and 95% CIs (resampling with 10000 replicates) between factorial combinations of small and large fields in low and high natural habitat landscapes. To give equal effort between factors only edge, midpoint and central traps were used to generate dependent estimates. Bootstrapping estimates do not take into account random effects or covariates (such as within-field resource availability) and cannot directly be compared to regression results.

Modelling potential flower visitor[1] response to local and landscape change

Models assessed the dependent variables of abundance of Hymenoptera, bees excluding stingless bees, stingless bees (species in the Tribe Meliponini), predatory Hymenoptera, parasitoid Hymenoptera and blister beetle abundance. Error distributions for models were negative binomial with variance equal to $\mu(1 + \mu/k)$. Global models contained fixed terms for $distance\ to\ edge \times\ landscape\ \times\ distance\ to\ water$ and $distance\ to\ edge\ \times\ landscape\ \times\ mean\ field\ floral\ area$, and a fixed-slope random term for sites nested within landscape (if landscape was considered at a scale where there was significant overlap). Field floral area, field floral diversity and trap floral area were significantly correlated (range of r values = 0.23 to 0.51, largest p-value = 0.021) and of these field floral area was retained in the starting model as it was considered the most biologically relevant to cropland resource availability for flower visitors. Field floral area was also significantly correlated with fallow land within fields (r=0.51, p < 0.01) and so the latter was excluded from the starting model.

The ordination axes used in global PCA models were derived from the predictors distance to water, landscape, fallow, rainfall, trap floral area, field floral area, field floral diversity and mean day temperature. Distance from edge was not strongly correlated with any other predictor hence was excluded from the PCA transformation. Global PCA models included three-way interactions between the PCA axis onto which landscape loaded most strongly, distance to edge and the remaining three PCA axes representing correlated aspects of resource availability (fallow land and floral resources), distance to water and climate (rainfall and day-time temperature).

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[1] Here, potential flower visitors are considered to be Hymenoptera and blister beetles caught in pan-traps.

Modelling epigeal beetle response to local and landscape change

Individual models assessed the dependent variables of ground beetle (Carabidae) and darkling beetle (Tenebrionidae) abundance, models had a negative binomial error distributions with variance equal to $\mu(1 + \mu/k)$.

Due to livestock damage missing data was an issue for 12 of 104 traps, eleven of which were in large fields and eight of which were from low natural habitat landscapes. Sensitivity of analyses to the missing data was investigated by comparing models where traps with missing data were coded with a random effect against models run with missing traps excluded and the results compared. In all cases there was good correspondence between models, and the results of the models excluding traps with missing data are presented.

Pitfall trap predictors differ to those used in pan trap models as ground level resource availability was considered to be of biological significance to cropland resource availability for beetles. Fallow was strongly correlated with field floral area ($r=0.52$, $p < 0.01$) therefore the latter was dropped from starting global models. Leaf litter and vegetation cover were also correlated ($r = 0.33$, $p < 0.01$) and the latter was dropped from starting global models.

Global models contained fixed terms for *landscape x distance to water*, *distance to edge x landscape x fallow* and *landscape x leaf litter x fallow*. Global PCA model ordinations contained the predictors distance to water, landscape, fallow, rainfall, leaf litter, vegetation cover, day temperature and floral area. Again, distance from edge was not strongly correlated with any other predictor hence was excluded from the PCA transformation. Models were structured as per the flower-visitor models.

3.3. Results

3.3.1. Descriptives

A total of 1657 Hymenoptera were caught in pan-traps, of these 25.8% were stingless bees, 29.8% were other bees, 16.2% were predatory and 28.2% were parasitoids. Stingless bees were dominated by the genus *Hypotrigona* (89.0%), and, of the other bees, *Macrogalea candida* was the most abundant taxon (46.9%) followed by species in the genus *Lasioglossum* (17.4%). Sand wasps or digger wasps (fossorial Crabronidae) accounted for 61.7% of predatory species, of these 48.8% were in the genus *Tachysphex*. Species in the superfamily Vespoidea contributed a further 38.3% of predators, these were typically spider wasps (Pompilidae, 49.5%) or potter wasps (Vespidae: Eumeninae, 39.8%). Parasitoids were represented by 28 families in 12 superfamilies. Chalcid wasps were most frequently caught (Chalcidoidea, 30.8%), followed by scelionid wasps (Scelionidae: Platygastroidea, 19.3%) then bethylid wasps (Bethylidae: Chrysidoidea, 14.6%). Blister beetles in the tribe Mylabrini were strongly attracted to pan traps as demonstrated by a total catch of 2033 individuals. *Coryna arussina* was the most frequently trapped species (52.7%) followed by a *Ceroctis sp.* (18.8%) then *Mylabris praestans* (16.0%).

Pit-fall traps caught a total of 1142 darkling beetles and 174 ground beetles. Darkling beetle catch was dominated by Pimeliinae (77.9%), in particular *Rhytinota gravidula* (41.2%) and *Zophosis anquisticostis/collaris* (22.8%), with *Gonocephalum simplex* (Tenebrioninae) also common (20.8%). Detailed summaries of trap catches are provided in Appendix C.

Bootstrapped means of summed catch per trap (referred to abundance from hereon) for factors of landscape vs. field size showed high variance. Bootstrapped values are intended to describe the data and highlight differences between sites, with subsequent regression models quantifying trends and relationships. Flower visitor 95% confidence intervals overlapped between all factors and species groups (Figure 3.4).

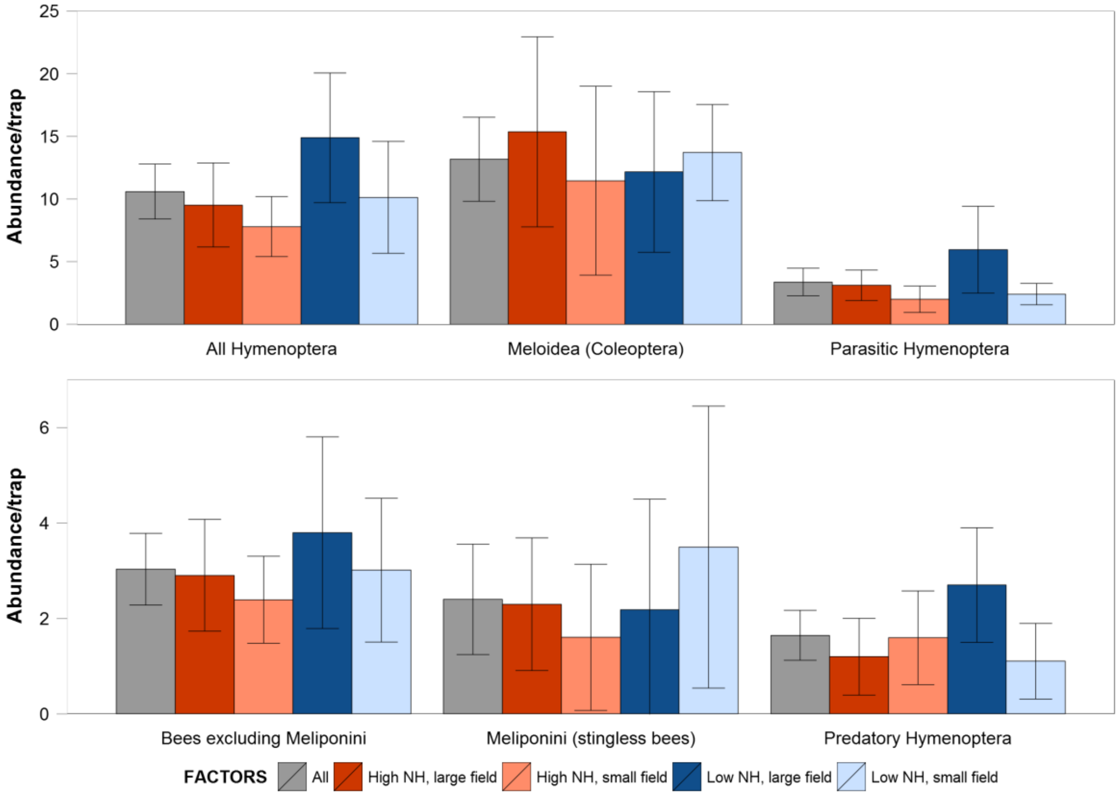


Figure 3.4 Flower visitor abundance bootstrapped means (10,000 replicates) with error bars for 95% confidence intervals from pan trapping. Abundance per trap was derived from the summed catch of six trapping rounds, using only edge, midpoint and centre traps.

Small fields in high natural habitat landscapes had significantly lower abundances (95% confidence intervals from bootstrapping did not overlap, Figure 3.5) for darkling and scarab beetles compared to all other factors, and for ground beetles compared to large. Blister beetles were significantly and substantially (approximately 4.5 times) more common in large fields in high natural habitat landscape.

Potential sources of variance for the bootstrapped abundances of focal taxa between study factors (Table 3.2) were distance to water (mean 1.3 km for large fields in low natural habitat landscapes and approximately 2.9 km for other sites), proportion of field fallow (approximately 20% in large fields and 40% in small fields, averaged over two growing seasons), field floral area (mean for small fields was approximately 5 cm^2 / m^2 compared to 2.5-4 5 cm^2 / m^2 in other sites) and, for pan-trapping only, recent rainfall (on average 2.6-2.7 cm in small fields in low natural habitat landscapes and large fields in high natural habitat landscapes, and 3.7-4.6 cm in other sites). These variables were considered as predictors in regression models.

The correlation within landscape metrics between the smallest and largest spatial scales of calculation (50 m, 2000 m) were $r = 0.25$ ($p = 0.012$) for edge density and $r = 0.511$ ($p < 0.0001$) for percentage of natural habitat. Correlations between edge density and natural habitat at the spatial scales of 50 m, 1000m and 2000 m were Pearson's r = -0.65, -0.97 and -0.94 respectively (all $p < 0.0001$). Therefore in regression models although the most predictive metric at the most predictive spatial scale was used to define the landscape independent variable for the abundance response of a particular taxa there was still likely to be an abundance response to other landscape metrics and spatial-scale.

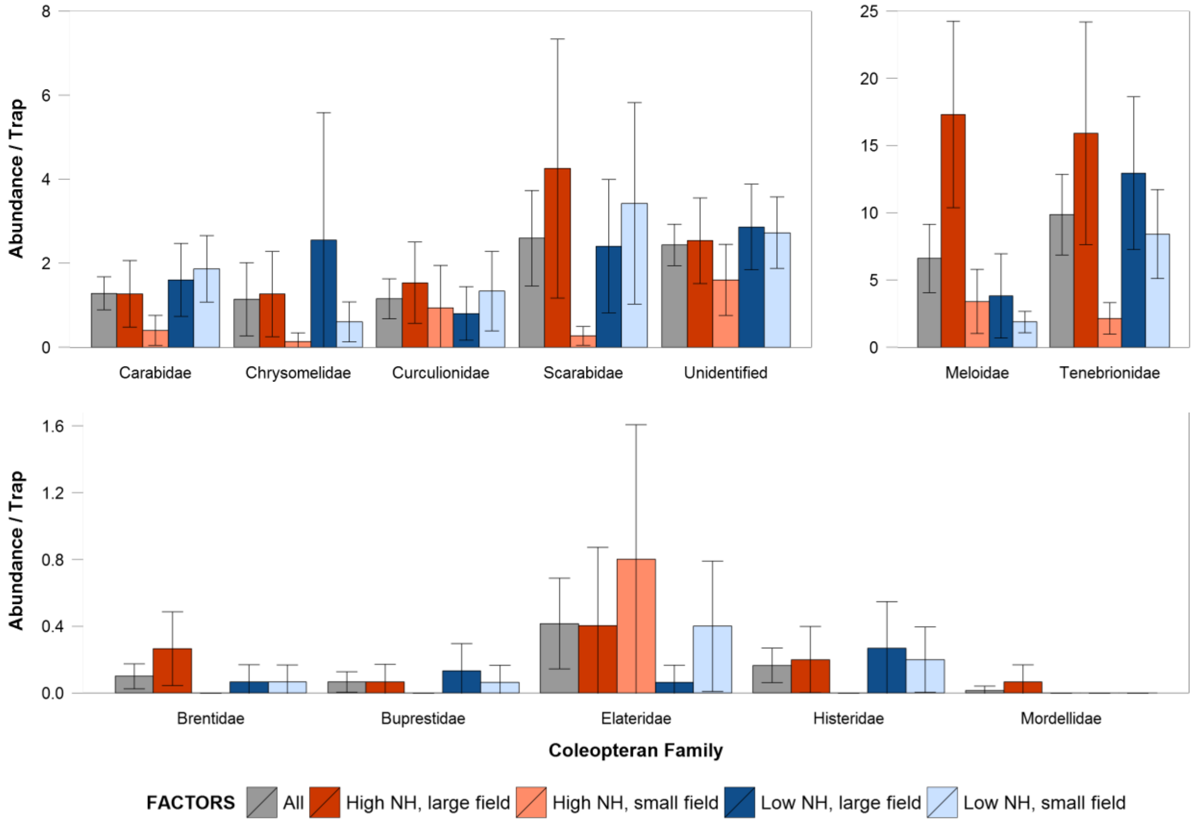


Figure 3.5 Epigeal beetle abundance bootstrapped means (10,000 replicates) with error bars for 95% confidence intervals. Abundance per trap was derived from the summed catch of four trapping rounds, using only edge, midpoint and centre traps.

Table 3.2 Summary statistics for local, landscape and climatic predictors of 20 sites surveyed during the period August 2012 – June 2013.

		Agricultural context									
Predictor	Sampling method	All sites (n=20)		Low natural habitat, large fields (n=5)		Low natural habitat, small fields (n=5)		High natural habitat, large fields (n=5)		High natural habitat, small fields (n=5)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Day temperature (˚C)*	Pit	28.9	0.16	28.5	0.26	28.6	0.18	29.2	0.38	29.4	0.15
Day temperature (˚C)*	Pan	29.3	0.29	28.5	0.11	29.0	0.56	30.8	0.55	28.7	0.15
Distance to water (km)[†]	Pan & Pit	2.5	0.41	1.3	0.78	3.0	0.91	2.9	0.75	2.9	0.87
Edge density within 1000 m (m / 100 m^2)	Pan & Pit	4.0	0.43	2.4	0.24	2.2	0.37	5.2	0.37	6.20	0.37
Fallow (%)*,[†]	Pit	29.1	4.56	22.2	5.46	43.8	8.61	17.3	2.27	33.5	11.19
Fallow (%)*,[†]	Pan	29.6	4.63	17.3	2.30	44.3	8.77	22.2	5.53	33.3	11.24
Field area (m^2)	Pan & Pit	20890	1233	39909	6308	3281	180	36224	4108	4545	324
Field floral area (cm^2 / m^2)*,[‡]	Pit	3.6	0.45	2.4	0.40	5.5	1.30	3.1	0.48	3.7	0.36
Field floral area (cm^2 / m^2)*,[‡]	Pan	3.7	0.41	2.8	0.32	5.0	0.94	3.0	0.75	4.2	0.54
Floral diversity (Shannon's D)*	Pan	0.9	0.06	0.8	0.09	1.0	0.15	0.8	0.11	0.9	0.10
Leaf litter (%)*,[†]	Pit	13.6	0.53	14.1	0.97	13.7	0.48	13.2	1.28	13.6	1.11
Natural habitat within 1000 m (%)	Pan & Pit	41.3	4.50	21.3	1.00	24.1	4.20	62.3	2.00	57.2	5.10
Night temperature (˚C)*	Pit	19.8	0.11	19.6	0.13	19.6	0.13	19.8	0.19	20.2	0.28
Rainfall (cm)*	Pit	4.0	0.21	4.6	0.48	4.2	0.31	3.7	0.39	3.7	0.28
Rainfall (cm)*	Pan	3.4	0.24	3.7	0.28	2.6	0.40	2.7	0.31	4.6	0.20
Vegetation cover (%)*,[†]	Pit	43.1	1.63	42.8	2.86	41.9	2.95	42.2	3.26	45.4	3.32
Vegetation cover (%)*,[†]	Pan	40.7	1.42	42.6	2.05	37.6	2.66	39.4	2.83	43.1	2.60

* Mean and standard error estimated by bootstrapping (replicates = 10,000). [†] Calculated from traps within sites rather than at site level (total n = 104, see Methods for n per context). [‡] Also referred to as simply 'floral area'.

3.3.2. Regression models: distance from field edge x landscape x resource availability

Unless stated otherwise discussion of models refers to untransformed minimum adequate models (MAMs, Table 3.3). Where estimates of abundance are given at high or low values of predictors these correspond to the predictor quantiles used to make predictive graphs and not the minimum or maximum of observed values. Where confidence intervals (CIs) are presented these include error from fixed and random terms.

Table 3.3 Summaries of GLMM minimum adequate models with untransformed predictor variables. ΔR^2 = Share in ΔR^2 relative to R^2 of fixed effects. R^2_{FE} = model R^2 fixed effect. $R^2_{\mathrm{FE+RE}}$: model R^2 fixed effect + random effect. Floral Area = field floral area. NH= proportion of natural habitat, ED = edge density, numbers following NH or ED refer to the spatial scale for calculation. If predictors were included in a significant interaction then only the interaction is presented. See Table 3.1 for descriptions of predictors. Note, as error distributions were negative binomial or Poisson, a log link was used in models.

		Flower visitors (pan trapping)				
Model	**Terms**	**Coefficient**	**Std. Error**	**p**	**Predictor**	**ΔR^2**
All Hymenoptera	Distance	-0.0066	0.0022	0.0026	Distance	53.7
	$(\text{Floral Area})^2$	0.0974	0.0275	0.0004	Floral Area	38.4
	$(\text{Floral Area})^3$	-0.0130	0.0037	0.0005	NH1000	10.7
	NH1000	-0.1023	0.0186	<0.0001		
	$(\text{NH1000})^2$	0.0011	0.0002	0.0026		
	R^2_{FE}: 0.39; $R^2_{\mathrm{FE+RE}}$: 0.49; AIC = 613.12					
Predatory Hymenoptera	Distance	-0.0107	0.0050	0.034	Distance	NA
	R^2_{FE}: 0.00 ; $R^2_{\mathrm{FE+RE}}$: 0.20; AIC = 327.8					
Blister beetles	ED1200 * Dist Water	-0.1134	0.0227	<0.0001	ED1200	19.6
	ED1200 * Distance * Floral Area	0.0034	0.0009	0.0002	Dist Water	37.7
	$(\text{Dist Water})^2$	-0.6822	0.1918	0.0004	Distance	15.9
	$(\text{Dist Water})^3$	0.0797	0.0259	0.0021	Floral Area	28.8
	R^2_{FE}: 0.60; $R^2_{\mathrm{FE+RE}}$: 0.69; AIC = 638.3					
Stingless bees	NH50 * Distance * Dist Water	-0.0007	3E-04	0.0122	NH50	30.2
	Distance * Floral Area	-0.0122	0.0044	0.0061	Distance	8.90
	$(\text{Dist Water})^2$	-2.4922	0.4986	<0.0001	Dist Water	30.6
	$(\text{Dist Water})^3$	0.3186	0.0680	<0.0001	Floral Area	30.3
	R^2_{FE}: 0.40; $R^2_{\mathrm{FE+RE}}$: 0.60; AIC = 393.0					
Bees (less stingless bees)	ED50 * Floral Area	-0.1251	0.0548	0.022	ED50	51.0
	$(\text{Floral Area})^2$	-0.0761	0.0450	0.091	Floral Area	49.0
	R^2_{FE}: 0.11; $R^2_{\mathrm{FE+RE}}$: 0.55; AIC = 446.7					
Parasitoid Hymenoptera†	NH100	-0.0195	0.0041	<0.0001	NH100	NA
	R^2_{FE}: 0.20; $R^2_{\mathrm{FE+RE}}$: 0.20; AIC = 409.4					
		Epigeal Coleoptera (pitfall trapping)				
Model	**Predictors:**	**Coefficient**	**Std. Error**	**p**	**Predictor**	**ΔR^2**
Darkling beetles	NH200 * Dist Water	0.019	0.005	0.0001	NH200	47.5
					Dist Water	52.5
	R^2_{FE}: 0.49; $R^2_{\mathrm{FE+RE}}$: 0.68; AIC = 565.9					
Ground beetles†	NH2000	-0.2101	0.4997	0.031	Dist Water	49.4
	Dist Water	0.1901	0.0777	0.018	NH2000	50.6
	R^2_{FE}: 0.10; $R^2_{\mathrm{FE+RE}}$: 0.10; AIC = 266.1					

†Random effects had a negligible influence on model fit and had very low variance components.

Table 3.4 GLMM summaries for minimum adequate models with PCA transformed predictor variables. PCA axes are shown within parentheses, codes refer to predictors that load ≥ 0.3 or ≤-0.3 onto an axis. DW = distance to water, T = temperature, F = % of field fallow, FA = field floral area, R = rainfall, FV = field floral area, field floral diversity and trap floral area, L = leaf litter and V = vegetation cover. PCA predictors are presented in order of loading strength and bold text indicates loading of ≥ 0.6 or ≤ 0.6. Distance was not transformed, but was scaled to units of 100 m. If predictors were included in a significant interaction then only the interaction is presented. For details of other table codes see Table 3.3**.** Note as error distributions were negative binomial or Poisson, a log link was used in models.

Flower visitors (pan trapping)

Model	Terms	Coefficient	Std. Error	p	Predictor	ΔR^2
All Hymenoptera	Distance	-0.7009	0.223	0.0017	Distance	13.5
	(**NH1000**/R/T)^2	0.1315	0.0639	0.0397	(**F**/**FA**)	9.5
	(**DW**/-**T**)	0.2521	0.0709	0.0004	(**NH1000**/R/T)	31.7
	(**F**/**FA**)^2	-0.0823	0.0386	0.033	(**DW**/-**T**)	45.3
	R^2_{FE}: 0.31; R^2_{FE+RE}: 0.47; AIC = 620.7					
Predatory Hymenoptera	Distance	-1.0650	0.5030	0.034	Distance	NA
	R^2_{FE}: 0.00 ; R^2_{FE+RE}: 0.20; AIC = 327.8					
Blister beetles	(**ED1200**) * Distance * (**F**/**FA**)	0.7936	0.36749	0.0308	(**ED1200**)	14.9
	(**DW**/-**T**)	-0.2224	0.0839	0.008	(**DW**/-**T**)	45.1
	(**FV**/**R**)	0.7157	0.0984	<0.0001	(**FV**/**R**)	10.9
					(**F**/**FA**)	16.9
	R^2_{FE}: 0.50; R^2_{FE+RE}: 0.68; AIC = 643.3				Distance	12.1
Stingless bees	(**NH50**/-TF) * Distance * (**R**/**FV**)	-1.834	6E-01	0.0032	(**NH50**/-TF)	10.9
	Distance * (-**T**/**DW**)	2.274	0.9100	0.0125	Distance	31.6
					(**T**/-**DW**)	40.5
					(**R**/**FV**)	17.0
	R^2_{FE}: 0.25; R^2_{FE+RE}: 0.71; AIC = 392.7					
Bees (less stingless bees)	(-**ED50**/**FV**/R) * Distance * (**F**/**FA**)	-2.0948	0.7981	0.0087	(-**ED50**/**FV**/R)	16.2
	(**DW**/-**T**)^2	1.0732	0.7405	0.1472	Distance	7.4
	(**DW**/-**T**)	0.0331	0.1052	0.0016	(**F**/**FA**)	14.3
	R^2_{FE}: 0.34; R^2_{FE+RE}: 0.56; AIC = 442.1				(**DW**/-**T**)	62.1
Parasitoid Hymenoptera†	(**NH100**) * Distance	-0.9665	0.3141	0.0021	(**NH100**)	45.0
	(**FV**/**R**) * Distance	0.8587	0.3265	0.0085	Distance	21.4
	(**F**/**FA**)	-0.2378	0.0866	0.006	(**F**/**FA**)	14.4
	(**FV**/**R**)^2	-0.2744	0.0813	0.0007	(**FV**/**R**)	19.2
	(**NH100**)^2	0.2302	0.0673	0.0006		
	R^2_{FE}: 0.33; R^2_{FE+RE}: 0.33; AIC = 399.6					

Epigeal Coleoptera (pitfall trapping)

Model	Predictors:	Coefficient	Std. Error	p	Predictor	ΔR^2
Darkling beetles	(**NH200**/R/T) * (**DW**/-**T**)	0.561	0.189	0.003	(**NH200**/R/R)	38.2
	R^2_{FE}: 0.69; R^2_{FE+RE}: 0.22; AIC = 570.9				(**DW**/-**T**)	61.8
Ground beetles†	(-**DW**/**T**/**NH2000**)	-0.4428	0.1513	0.0034	(-**DW**/**T**/**NH2000**)	32.8
	(**FA**/**F**)	-0.5334	0.1751	0.0023	(**FA**/**F**)	67.2
	(**FA**/**F**)^2	0.2521	0.0904	0.0053		
	R^2_{FE}: 0.21; R^2_{FE+RE}: 0.21; AIC = 263.9					

†Random effects had a negligible influence on model fit and had very low variance components.

3.3.3. Flower visitor (pan trapping) models

All Hymenoptera

Hymenoptera abundance showed a non-linear response to landscape change (Figure 3.6), which was best predicted as the percentage of natural habitat within 1000 m (Table 3.3). Predicted abundances were lowest when natural habitat was at intermediate values, declining by 50% or more at intermediate values. Conversely for resource availability, intermediate levels of floral resource were predicted to approximately double Hymenoptera abundance compared to very low or high levels, again in a non-linear relationship. Regarding spillover, Hymenoptera abundance significantly declined (p=0.003) with increasing distance from field-edge and ΔR^2 suggested distance was the most important predictor in the MAM (Table 3.3).

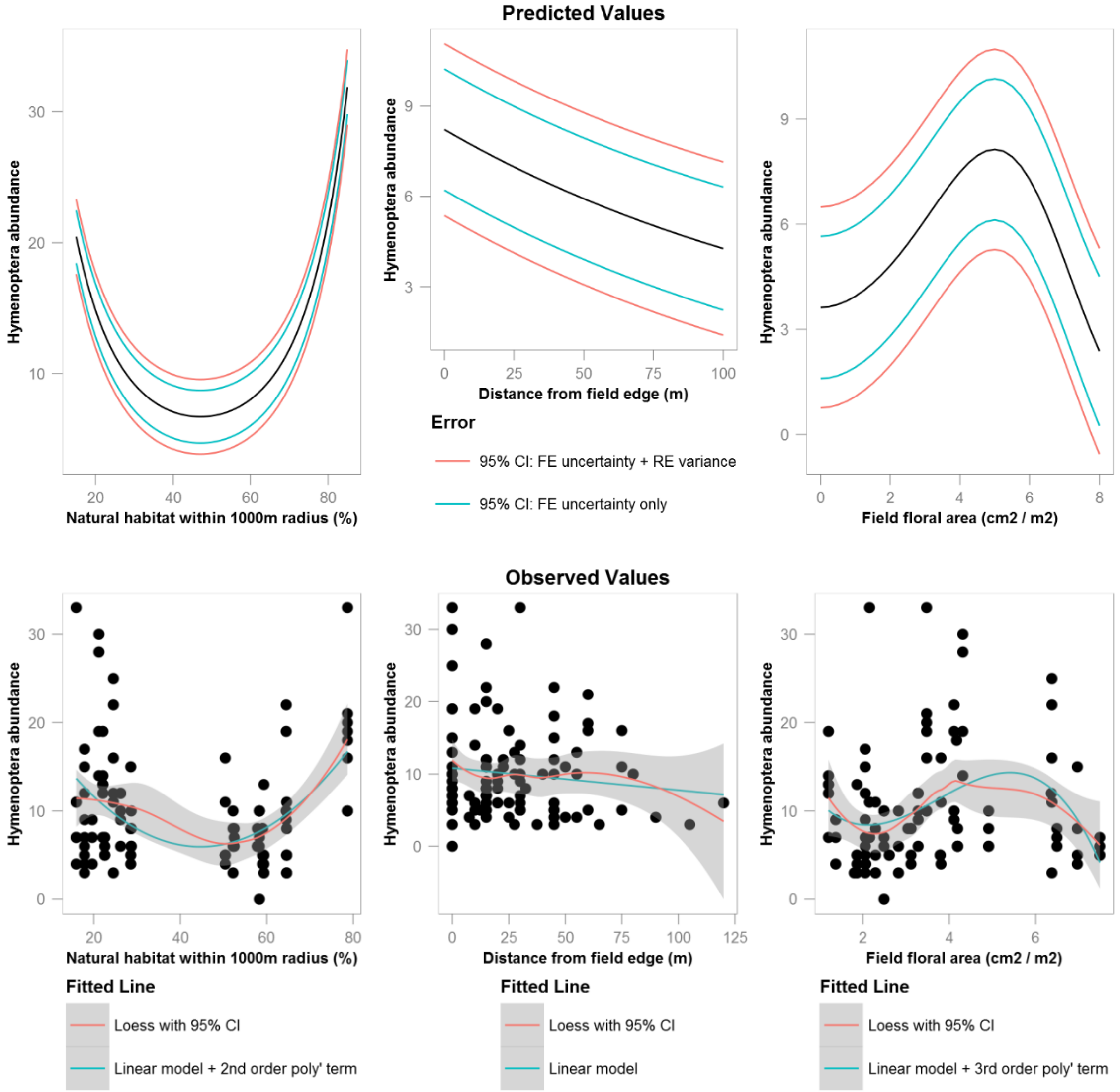


Figure 3.6 GLMM predicted and observed values of Hymemnoptera abundance (individuals trap^{-1}) when varying landscape, distance from field edge and resource availability (field floral area). When only fixed-terms were included in the model R^2 was 0.39 compared to 0.49 for the full model and there was good correspondence in model structure between untransformed and PCA models (**Table** 3.4), the former being most predictive. For further model details see Table 3.3. With natural habitat and floral area at intermediate values, predictions suggested a decline in Hymenoptera abundance from 8.22 individuals trap^{-1} (95% CIs 5.36 to 11.08) at the field edge to individuals 4.84 trap^{-1} (95% CIs 1.40 to 7.15) 100 m into a field, however there was substantial uncertainty for this estimate. Although the data suggest that there was a strong local effect of edge in this system it is likely that decay in abundance will attenuate beyond the range of distances available in the study zone (e.g., Ricketts et al. 2008). Extrapolation of distance beyond the range of observed values would give zero Hymenoptera at a distance of 1km from field-edge which is obviously unrealistic for cultural species (but is realistic for small ecotone species such as *Hypotrigona* stingless bees).

Stingless bees (Family: Apidae, Tribe: Meliponini)

Mean (SE) stingless bee abundance was 2.60 ± 0.383 individuals trap^{-1} and was best predicted using the percentage of natural habitat within 50 m of a field as the landscape metric within models. The MAM retained an interaction between landscape, distance to field-edge and distance to water (p = 0.012), and a two-way and interaction between distance to field-edge and floral area, it also included non-linear terms for distance to water (Table 3.3).

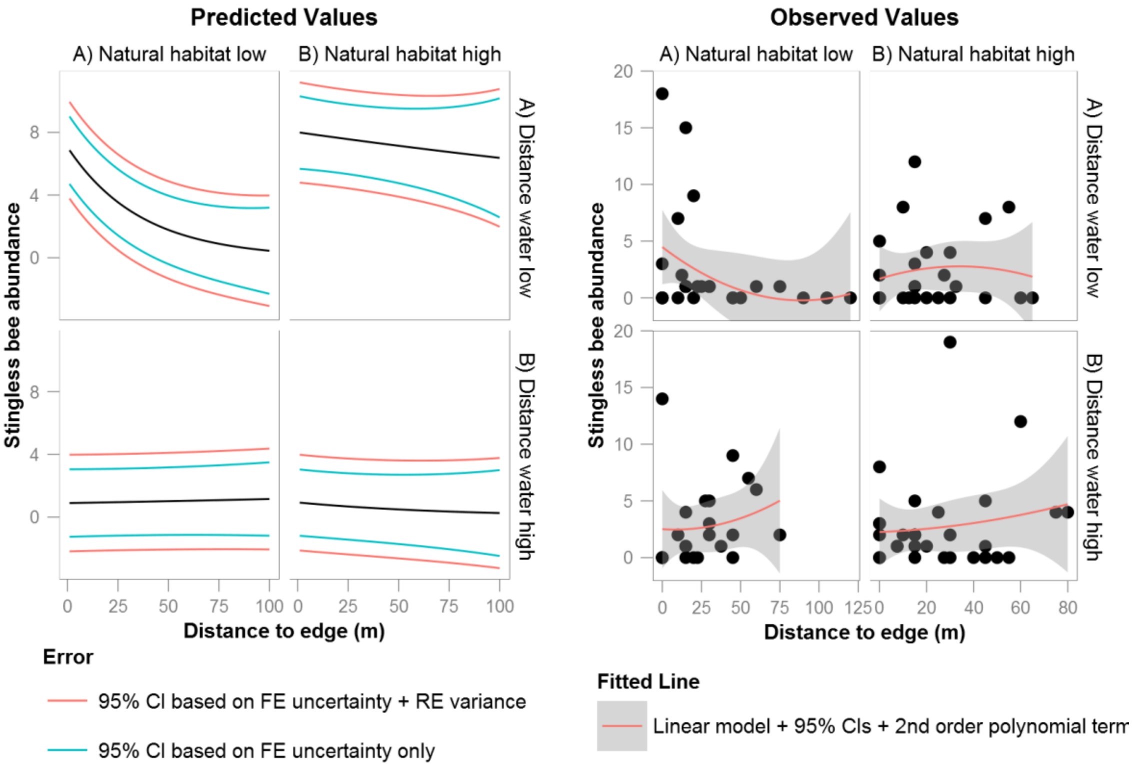


Figure 3.7 GLMM predicted and observed values of stingless bee abundance (individuals trap^{-1}) when varying distance to field-edge for high and low values of distance to water and landscape (percentage of natural habitat within 50m). Fixed terms only gave a R^2 of 0.40 which increased to 0.60 when random-effects were included and there was fair correspondence in model structure between untransformed and PCA models (Table 3.4). For further model details see Table 3.3

Regarding spillover, predicted stingless bee abundance was higher at the edge of fields closer to water (Figure 3.7), 7.05-8.01 individuals trap^{-1} (95% CIs 3.97 to 11.21), compared to those far from water with 0.89-0.94 individuals trap^{-1} (95% CIs -2.19 to 3.99). Distance only had a strong effect on stingless bee abundance when the landscape contained relatively little natural habitat and the field was near water, predicted abundance falling from 7.05 individuals trap^{-1} (95% CIS 3.97 to 10.14) at the field edge to 0.45 individuals trap^{-1} (95% CIs -3.08 to 3.97).

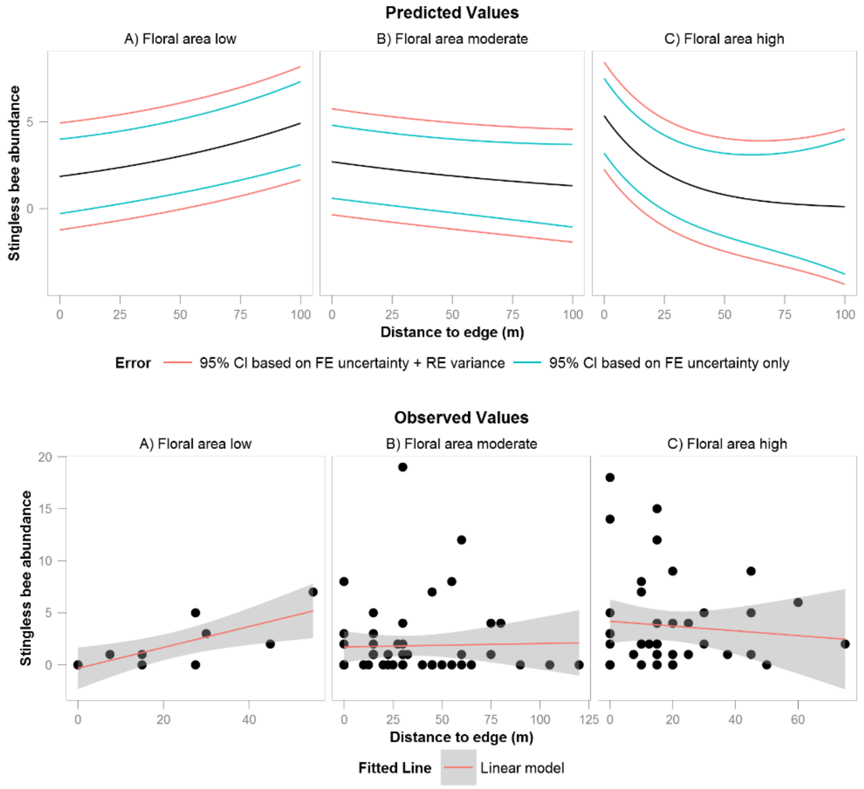


Figure 3.8 GLMM predicted and observed values of stingless bee abundance (individuals trap^{-1}) when varying distance to field-edge for high, moderate and low values of resource availability (field floral area). For further model details see Table 3.3 and Figure 3.7.

Regarding landscape, predictions suggested that stingless bee abundances were similar when local natural habitat was low and that increasing the percentage of natural habitat only had positive effect on abundance when distance to water was low (Figure 3.9). When near to water and to the field boundary, increasing local natural habitat within 50 m from 40% to 80% increased predicted stingless bee abundance from 4.46 individuals trap^{-1} (95% CIs 1.36 to 7.56) to 8.30 individuals trap^{-1} (95% CIs 5.11 to 11.49). This changed to 0.41

individuals trap^{-1} (95% CIs -2.85 to 3.67) and 9.15 individuals trap^{-1} (95% CIs 5.53 to 12.76) further from the field boundary.

The interaction of resource availability (floral area) and spillover (distance to field edge) (Figure 3.8) suggested that when floral area in the field was low stingless bees were more abundant further from the field edge and the opposite of this was true when floral area was high but with a faster rate of change.

ΔR^{2} values suggested that landscape (30.2), distance to water (30.6) and floral area (30.3) had a similar strength of effect on model predictions with distance to edge (8.9) being of less importance (Table 3.2).

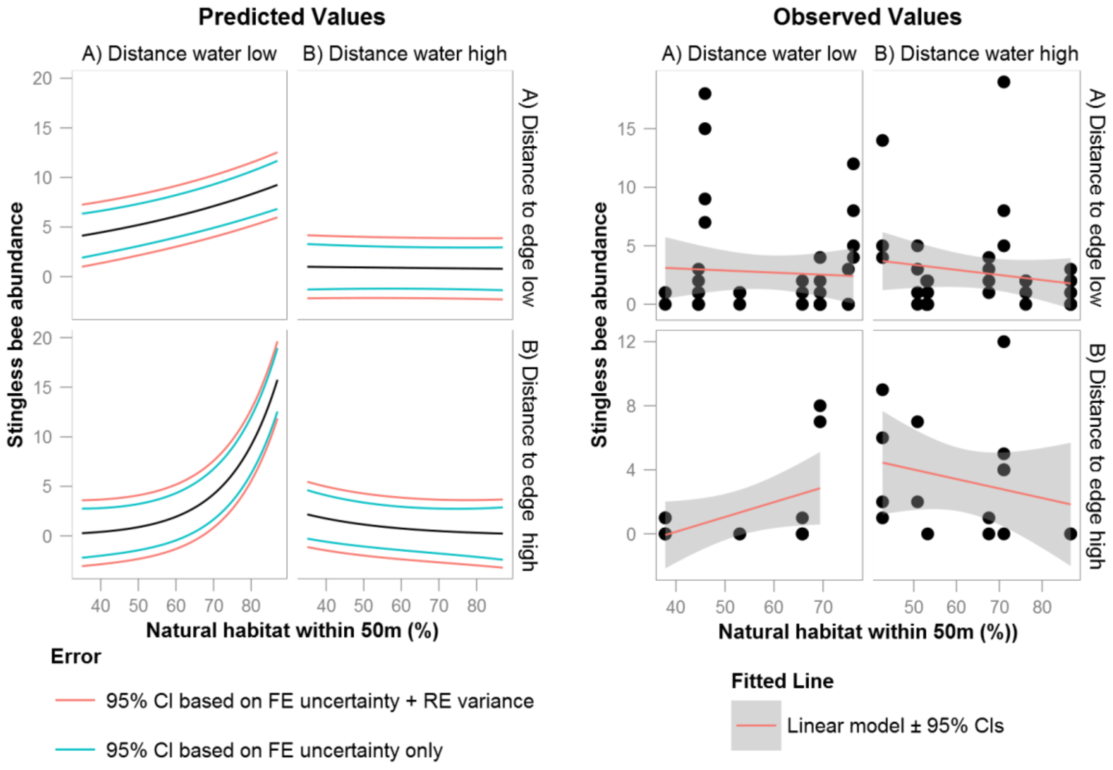


Figure 3.9 GLMM predicted and observed values of stingless bee abundance (individuals trap^{-1}) when varying landscape (proportion of natural habitat within 50m) for high and low values of distance to water and distance to field-edge. For model details see Table 3.3. For further model details see Table 3.3 and Figure 3.7.

Bees (excluding stingless bees)

Mean (SE) non-stingless bee abundance was 2.98 ± 0.233 individuals trap^{-1} and was best explained by landscape measured as the edge density (fragmentation) of natural habitat within 50m (Table 3.3). Resource availability and landscape had a significant interaction (p = 0.022), the predicted effect of edge density on abundance was weakly positive or neutral when floral area was low or moderate, and negative when floral area was high (Figure 3.8). Abundance fell from 5.74 individuals trap^{-1} (95% CIs 2.55 to 8.39), when floral area was low, to 1.78 individuals trap^{-1} (95% CIs 0.53 to 4.57) (Figure 3.10). Increasing floral area had a positive effect on abundance which weakened with increasing local fragmentation (Figure 3.11), when fragmentation was low the predicted effect of increasing floral area from low to high on abundance was an increase from 2.40 individuals trap^{-1} (95% CIs -0.47 to 5.29) to 3.91 individuals trap^{-1} (95% CIs 1.03 to 6.80).

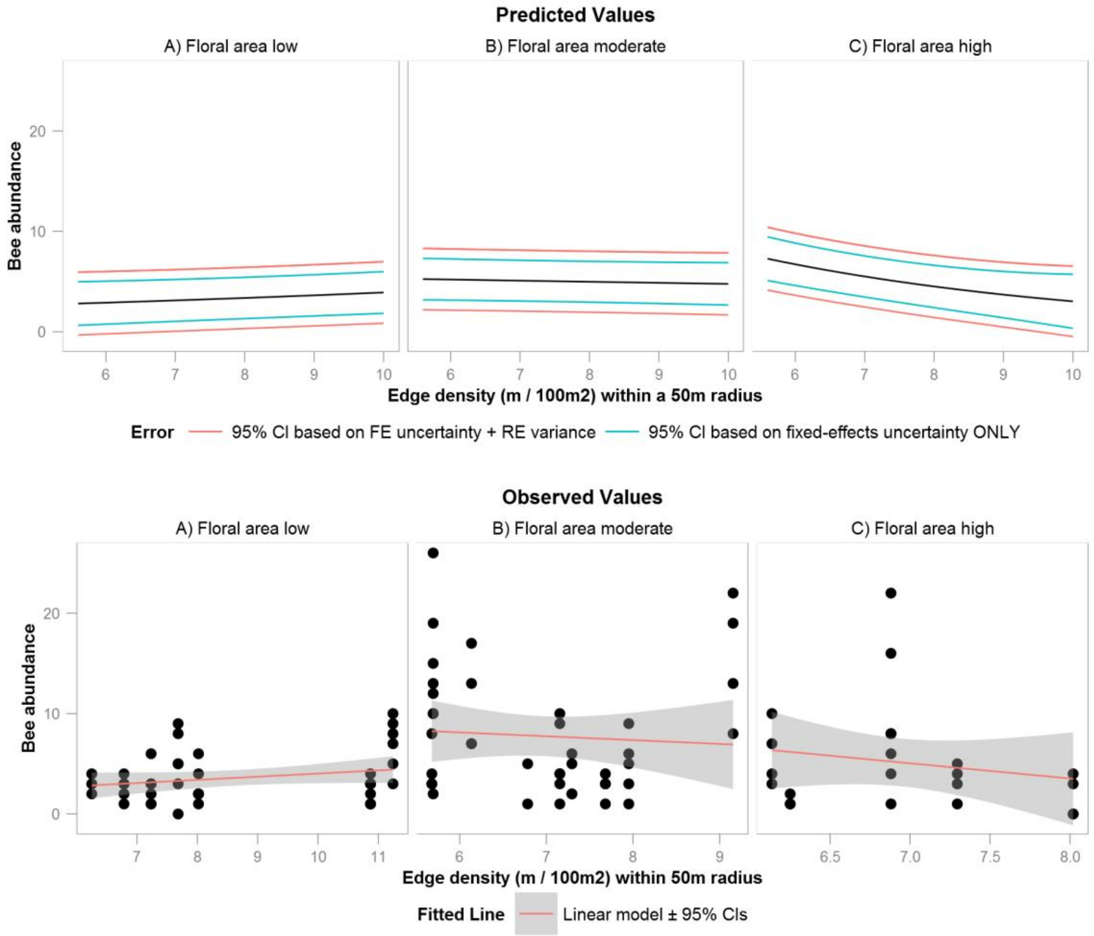


Figure 3.10 GLMM predicted and observed values of non-stingless bee abundance (individuals trap^{-1}) when varying landscape for high, moderate or low values of field floral area. Uncertainty around parameter estimates was relatively high and the untransformed model had a modest fixed effects R^2 of 0.11, R^2 increased to 0.55 when including random-effects suggesting site and landscape explained a significant amount variance within the data. For further model details see Table 3.3.

There was reasonable correspondence between the untransformed and PCA MAMs, however the latter was more predictive (fixed effects R^2 = 0.34) and complex suggesting a non-linear effect of distance to water and a three-way interaction of distance, landscape and resource availability. ΔR^2 values suggested that the PCA axis for proximity to water and temperature (ΔR^2 = 62.1%) was largely responsible for improving PCA model performance.

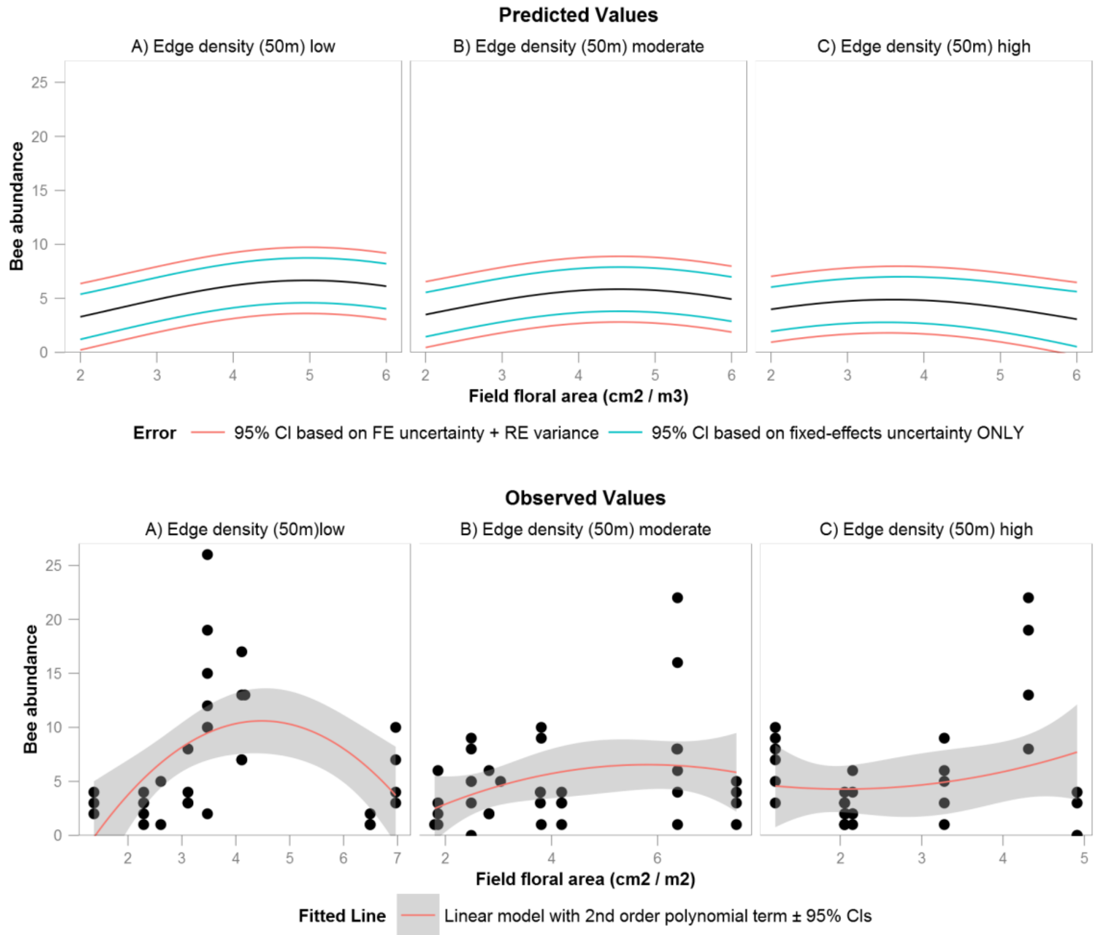


Figure 3.11 GLMM predicted and observed values of bee abundance (less stingless bees) when varying resource availability (field floral area) for high, moderate or low values of landscape fragmentation (edge density within 50m). For further model details see Table 3.3 and Figure 3.10.

Predatory Hymenoptera

Mean (SE) predatory Hymenoptera abundance was 1.31 ± 0.14 individuals trap^{-1} and best model predictions were from landscape measured as edge density of natural habitat (fragmentation) at a spatial scale of 1000m (Table 3.3). Only distance to edge was retained in the untransformed and PCA MAMs. Increasing distance had a negative effect on abundance (Figure 3.12) falling from 1.45 individuals trap^{-1} (CIs -1.57 to 4.48) at the field edge to 0.51 individuals trap^{-1} (95% CIs -2.62 to 3.64) at a distance of 100m. Although the direction of the effect of distance on abundance was statistically significant (p=0.034) there is considerable uncertainty for the strength of the effect as demonstrated by predictions (Figure 3.12 right panel). As with the effect of distance on overall Hymenoptera abundance the predicted decay of predatory Hymenoptera abundance is likely to give biologically unrealistic outcomes if extrapolated far beyond observed values.

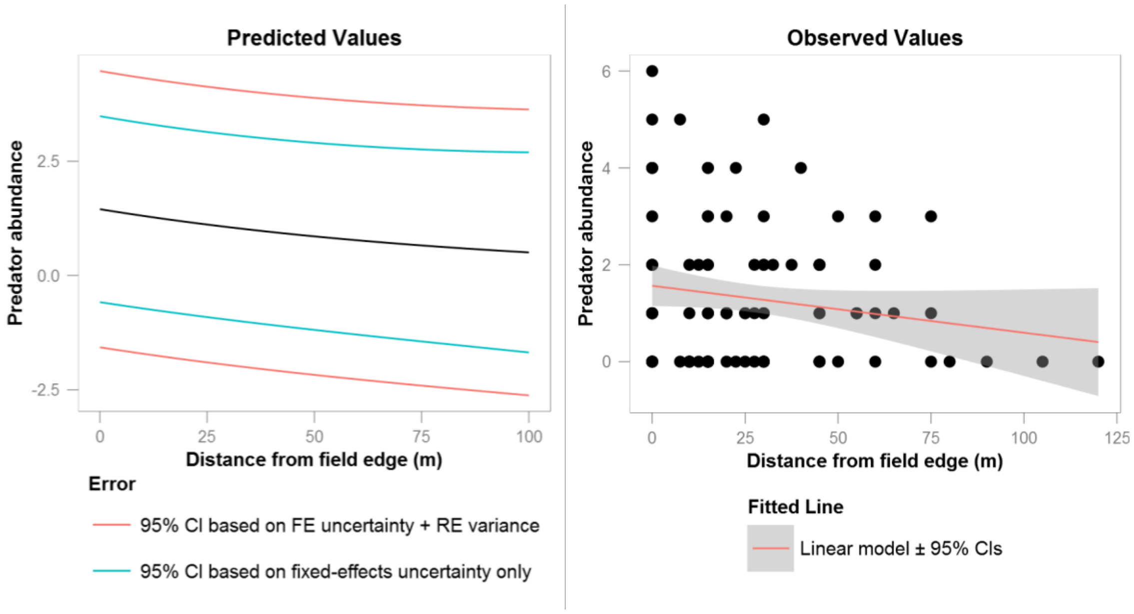


Figure 3.12 GLMM predicted and observed values of predatory Hymenoptera abundance (individuals trap^{-1}) with distance from field edge. The large uncertainty for predictions was likely due to variance in the response of abundance to distance between sites. Without a random-effect for site nested within landscape model R^2 dropped from 20.0 to 0.0. The effect of distance on abundance varied between sites with 15/20 sites showing a decline and 5/20 sites showing an increase, this variability in response between sites helps explain the importance of random terms in the predatory Hymenoptera model. For model details see Table 3.3.

Parasitoid Hymenoptera

Mean (SE) parasitoid Hymenoptera abundance was 2.79 ± 0.224 individuals trap^{-1} and best model predictions were from landscape measured as the proportion of natural habitat within 100 m of a field (Table 3.3). Only landscape was retained in the MAM which predicted a drop in abundance from 5.10 individuals trap^{-1} (95% CIS 2.26 to 7.94) at 20% to 1.58 individuals trap^{-1} (95% CIS -1.26 to 4.43) at 80% natural habitat within 100m (Figure 3.13). Fixed terms in the model gave a R^2 of 0.20 and there was poor correspondence in model structure between untransformed and PCA MAMs (Table 3.4), the latter being more complex and predictive. The PCA MAM had an R^2 of 0.33 and parasitoid abundance still had a strong negative response to landscape and landscape had more than double the ΔR^2 value (45.3) of any other predictor. In addition to landscape two PCA axes relating to resource availability and untransformed distance to field edge were retained in the PCA MAM and there were also two 2-way interactions between resource availabilityor landscape and distance to field edge (Appendix E). Predicted parasitoid abundance response was neutral or modestly positive to initial increases in resource availability (the PCA axis onto which loaded field and trap floral area, floral diversity, rainfall and fallow, with fallow loading negatively), but became negative at higher values. The predicted spillover response was an increase in abundance with greater distance from field edge when local natural habitat (within 100m) was low and a decrease when high, and was and abundance highest overall when natural habitat was low.

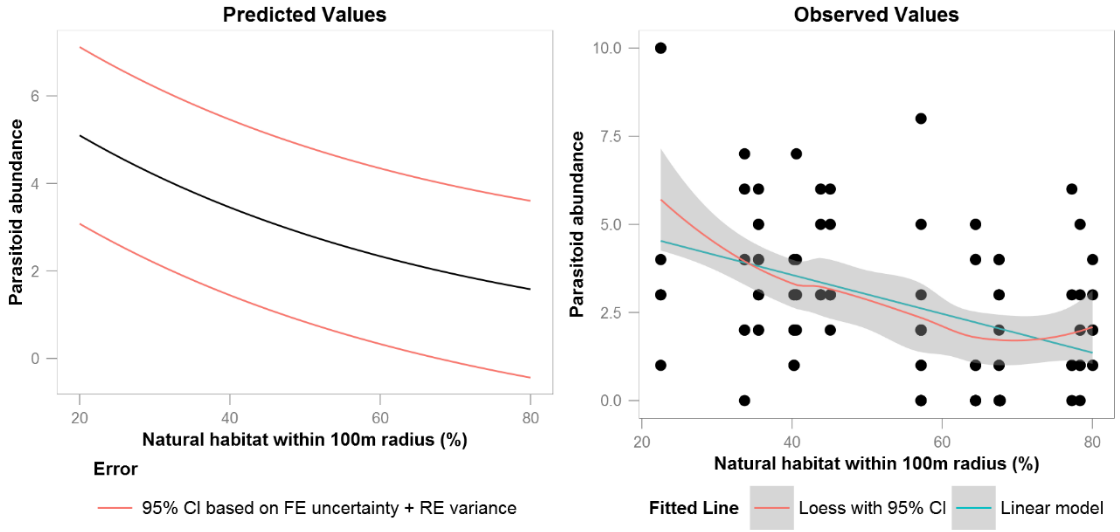


Figure 3.13 GLMM predicted and observed values of parasitoid Hymenoptera abundance with landscape change (percentage of natural habitat within 100m). Random effect variance was negligible in this model. Fixed terms in the model gave a R^2 of 0.20 and there was poor correspondence in model structure between untransformed and PCA models (Table 3.4). For further model details see Table 3.3.

Blister beetles (Order: Coleoptera, Family: Meloidae)

Mean (SE) blister beetle abundance was 12.40 ± 0.928 individuals trap^{-1} and best model predictions were given from landscape measured as edge density (fragmentation) of natural habitat (Table 3.1) within 1200 m of fields (Table 3.3).

Model selection retained the three-way interaction between landscape, distance to field edge and floral area and a two-way interaction between landscape and distance to water. The response of abundance to distance to water was non-linear.

Regarding spillover and landscape, predictions suggested a negative response of blister beetle abundance with increasing distance from field edge when fragmentation of natural habitat was low which became neutral when fragmentation was high and floral area low, and positive when both fragmentation and floral area were low (Figure 3.14). Predictions also suggested that increasing fragmentation, when floral area was low, had a strong negative effect on blister beetle abundance when distance to edge was low. At an edge density of 1 m 100 m^{-2} predicted abundance was 19.07 indiviuduals trap^{-1} (95% CIs 16.19 to 21.96) falling to 11.12 individuals trap^{-1} (95% CIs 8.20 to 14.04) when edge density was increased to 7 m 100 m^{-2}, but the effect was much weaker when distance to edge was higher (Figure 3.15). When floral area was high the predicted response to increasing fragmentation was strongly positive further from the field edge (but unrealistically so) and only weakly positive closer to the field edge.

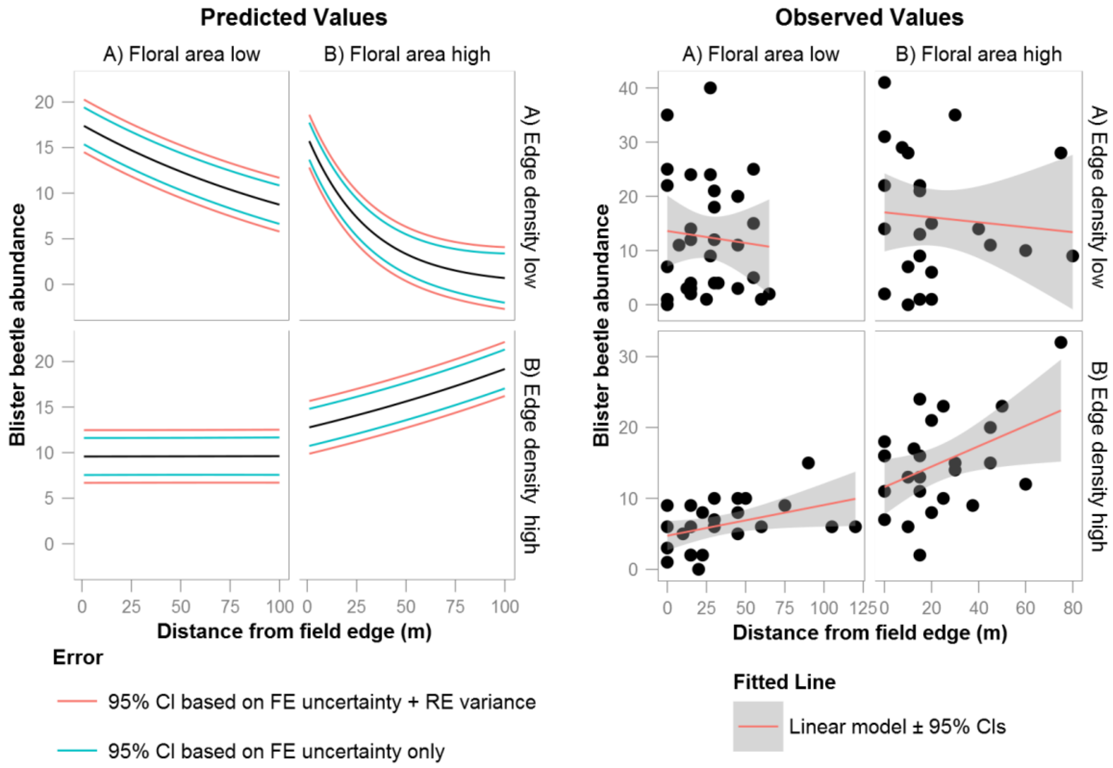


Figure 3.14 GLMM Predicted and observed values of blister beetle abundance (individuals trap^{-1}) when varying distance to field-edge for high and low values of floral area and landscape (edge density within 1200 m). For model details see Table 3.3. Model R^2 was high at 0.69 and without random-terms the fixed terms still strongly predicted observed values with an R^2 of 0.60. There was good correspondence in model structure and ΔR^2 values between untransformed and PCA models (Table 3.4).

Regarding resource availability, predictions suggested that increasing floral area had a positive effect on abundance when fragmentation of natural habitat was high (edge density) and a negative effect when low. The strongest effect of floral area was predicted when distance to field edge was high and fragmentation low (Figure 3.16), but the strength of abundance response of blister beetles appears exaggerated (compared to observed values) when the values of floral area and distance are both high (Figure 3.15). The predicted effect of increasing floral area from 1 to 7 cm^2 m^{-2} on blister abundance when distance to edge and fragmentation were low was a decline from 18.55 individuals trap^{-1} (95% CIs 15.11 to 22.99) to 9.99 individuals trap^{-1} (95% CIs 6.51 to 13.48), if fragmentation was high this changed to an increase with 8.43 individuals trap^{-1} (95% CIs 4.97 to 11.87) rising to 22.72 individuals trap^{-1} (95% CIs 19.07 to 26.38).

ΔR^2 values suggested that distance to water had the largest effect size (37.7) followed by floral area (28.8), landscape (19.6) then distance (15.9) (Table 3.2).

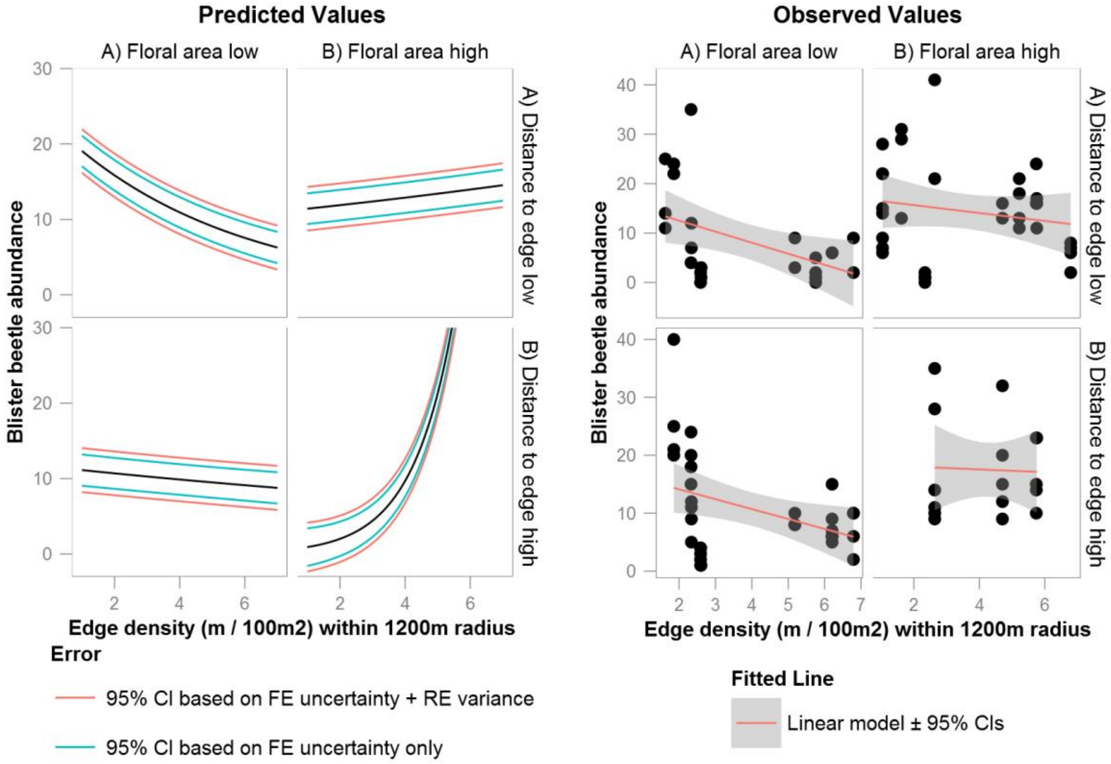


Figure 3.15 Observed and GLMM predicted values of blister beetle abundance (individuals trap^{-1}) when varying landscape (edge density within 1200m) for high and low values of distance to field edge and floral area. The predicted effect of landscape on abundance appears exaggerated when the values of floral area and distance were both high (predicted values were double the maximum abundance of blister beetles observed). However, the three-way interaction was retained as model predictions from the rest of parameter space appeared biologically realistic and the interaction was highly significant (p = 0.00016). For further model details see Table 3.3 and Figure 3.14.

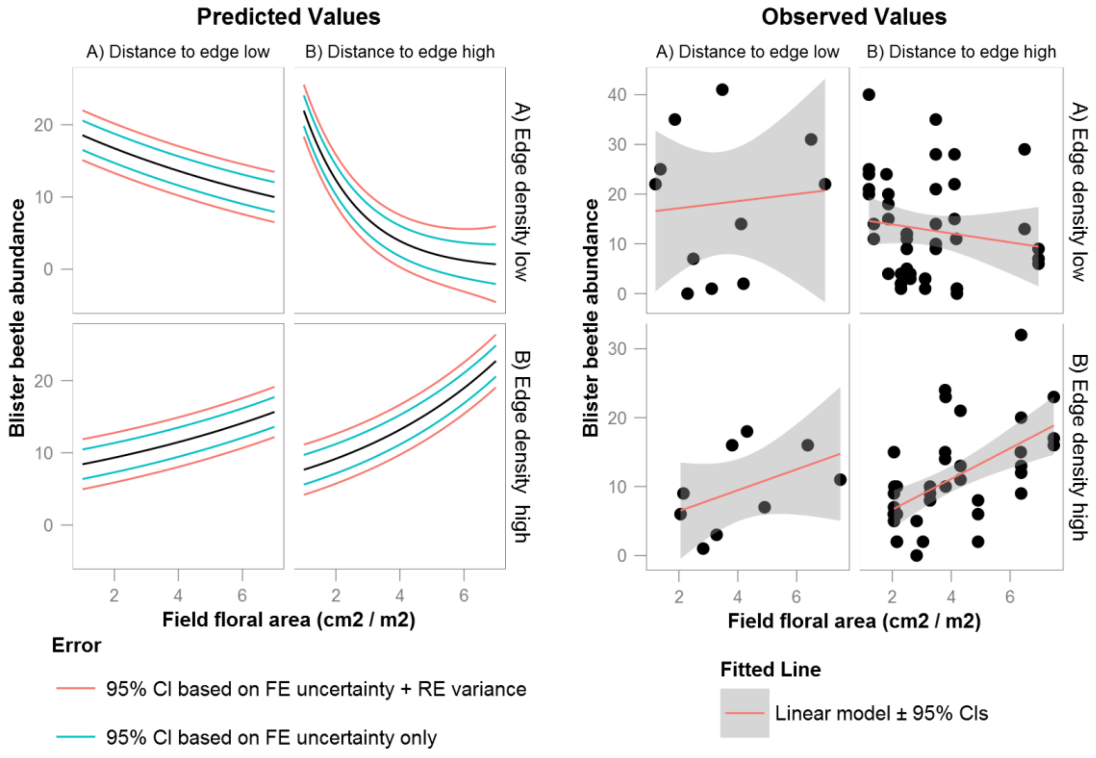


Figure 3.16 GLMM predicted and observed values of blister beetle abundance (individuals trap^{-1}) when varying floral area for high and low values of distance to field edge and landscape (edge density within 1200 m). For further model details see Table 3.3 and Figure 3.14.

3.3.4. Epigeal beetle (pitfall trapping) models

Darkling beetles (Family: Tenebrionidae)

Mean (SE) darkling beetle abundance was 10.86 ± 1.271 individuals trap^{-1} and best model predictions were given from landscape measured as the percentage of natural habitat within 200 m (Table 3.3).

Regarding landscape, at low distances to water darkling beetle abundance responded positively to loss of natural habitat (Figure 3.17), predicted abundance at 75% natural habitat was 0.91 individuals trap^{-1} (95% CIs -2.38 to 4.21) rising to 17.23 individuals trap^{-1} (95% CIs 14.04 to 20.42) at 15%. This relationship weakened at moderate distances and became negative at high distances where predicted abundance at 75% natural habitat was individuals 16.67 trap^{-1} (95% CIs 13.49 to 1.83) falling to 5.19 individuals trap^{-1} (95% CIs 1.99 to 8.39) at 15%. Changes in darkling beetle species composition associated with increasing distance from water may account for the different abundance responses to landscape. Across all sites less than 4 km from water total darkling beetle catch was dominated by three species, *Gonocephalum simplex* (33.6–39.4%), *Rhytinota gravidula* (22.6-30.6%) and *Zophosis anquisticostis/collaris* (21.8-25.3%). However in sites greater than 4 km from water *Gonocephalum simplex* was absent and *Rhytinota gravidula* contributed a much greater catch percentage (61.8%) This suggests *G.simplex* and *R.gravidula* had opposite responses to local landscape change (Appendix F Figure F.1).

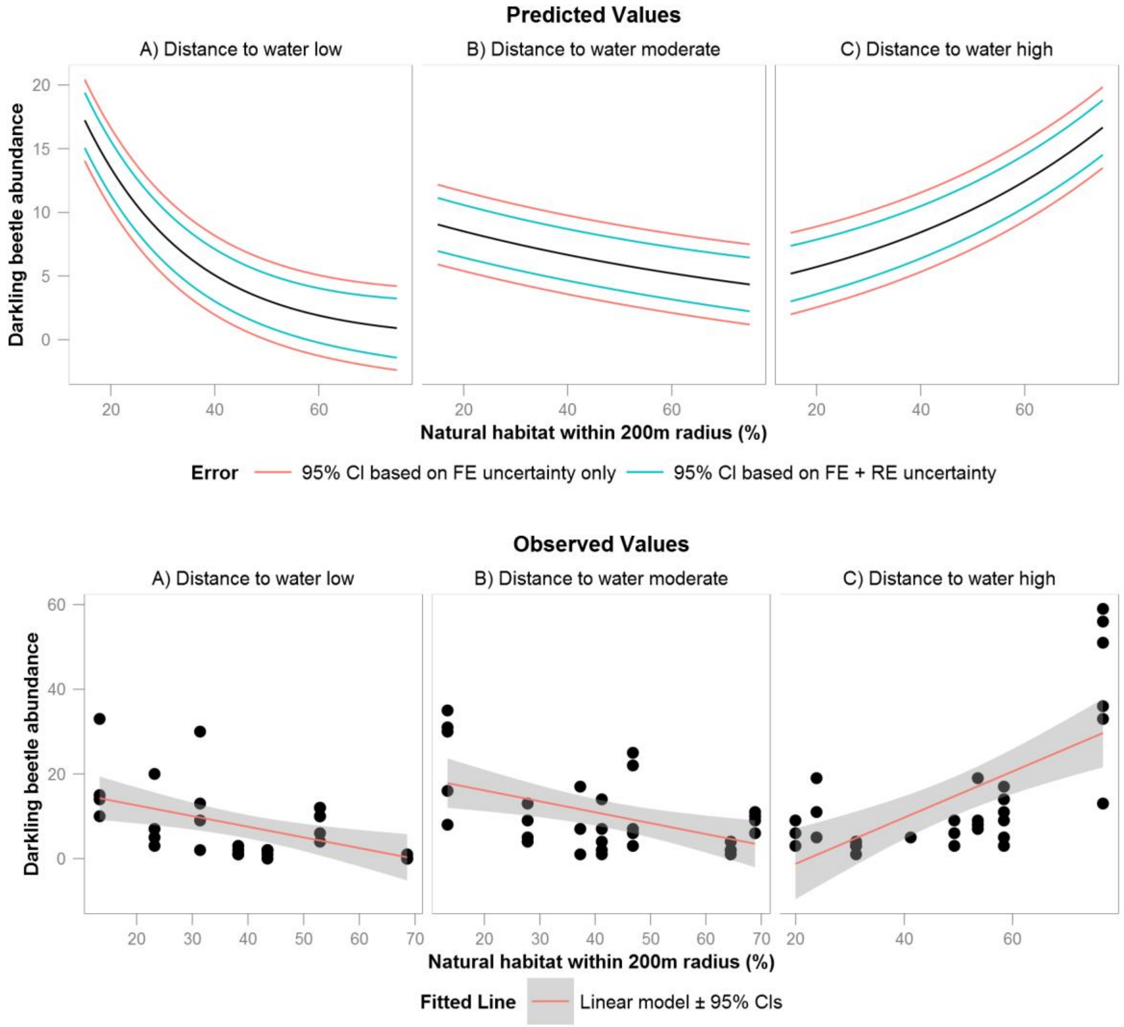


Figure 3.17 Observed and GLMM predicted values of darkling beetle abundance (individuals trap^{-1}) when varying landscape (proportion of natural habitat within 200m) for high, moderate and low values of distance to water. For model details see Table 3.3. Model R^2 was high at 0.68 dropping to 0.49 without random-terms, and ΔR^2 values suggested predictors were equally important. Correspondence of the untransformed and PCA models was good with the former being more predictive.

Ground beetles (Family: Carabidae)

Mean (SE) ground beetle abundance was 1.18 ± 0.161 individuals trap^{-1} and best model predictions were given from landscape measured as natural habitat within a 2000 m radius. Landscape and distance to water were the only predictor variables retained in MAMs (Table 3.3) and ΔR^2 values suggested they were equally important. Regarding landscape, ground beetle abundance responded negatively to increasing natural habitat (1.72 individuals trap^{-1} (95% CIs -2.04 to 5.47) at 25% natural habitat falling to 0.55 individuals trap^{-1} (95% CIs -3.49 to 4.60) at 70%. However error surrounding coefficient estimates was high therefore the strength of the effect was uncertain (Figure 3.18).

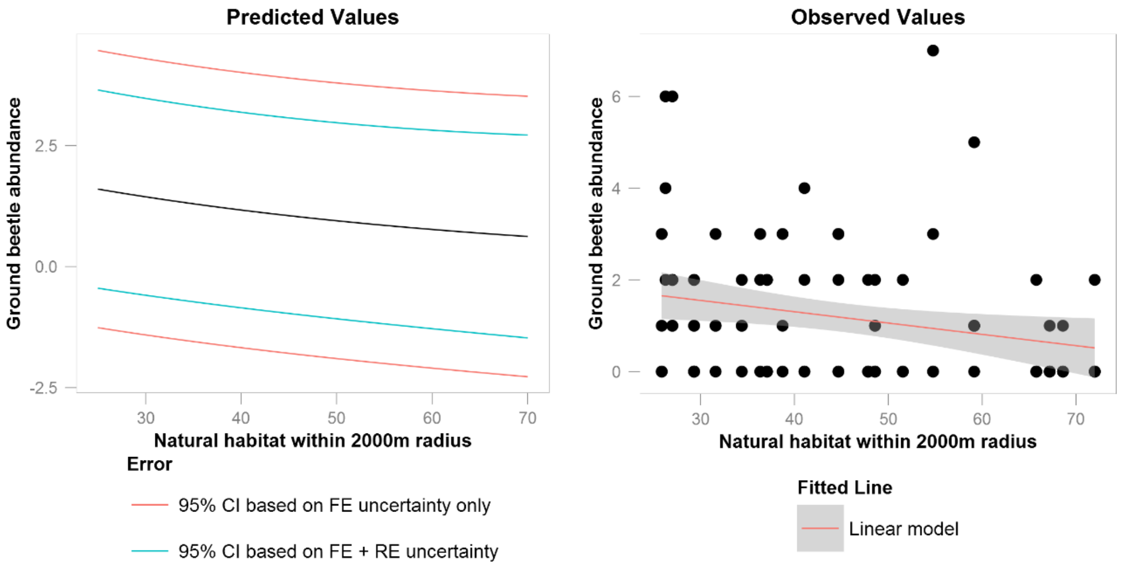


Figure 3.18 GLMM predicted and observed values of ground beetle abundance (individuals trap^{-1}) with landscape change (percentage of natural habitat within 2000m). The model had modest predictive power, $R^2 = 0.10$, and the removal of random-terms had a negligible effect. For further model details see Table 3.3. Values <0 in the predicted graph are biologically meaningless and are simply present to illustrate uncertainty in predictions.

The PCA MAM (Table 3.4) also contained a landscape term, but was more complex and predictive ($R^2 = 0.21$) than the untransformed model and included a non-linear term onto which floral area and fallow loaded. However the PCA MAM was difficult to interpret due to split loadings of predictors between PCA axes and poor correspondence to observed values, hence the model with untransformed predictors is preferred.

3.4. Discussion

This study provides one of the first multi-taxa assessments for how change in land-use at local and landscape scales affects the distribution of agriculturally important insect groups in a complex low-input small-scale system (see also Klein et al. 2002b; Otieno et al. 2011). Landscape scale agricultural extensification (from henceforth refered to as simply "agricultural extensification"), field enlargement and resource availability had significant effects on the abundance response of focal taxa (pollinator, predator and parasitoid Hymenoptera, and blister, darkling and ground beetles) within croplands, but, as expected, abundance responses to these predictors varied between groups for their direction, strength and interactions. Stingless bees, which are small pollinators, showed a strong negative response to the enlargement of field size and to agricultural extensification. Whereas, for natural enemies, hymenopteran predators showed a weak negative response to field enlargement but no response to agricultural extensification, ground beetles showed a positive response to agricultural extensification but no response to field enlargement, and hymenopteran parasitoid response to agricultural extensification varied with field enlargement. Pest species, darkling beetles and adult blister beetles, showed complex responses to agricultural extensification and field enlargement, discussed in detail below.

3.4.1. Spillover of agriculturally important taxa into croplands and the effect of field enlargement

An overall decline in Hymenoptera abundance with increasing distance from field edge, suggested ecotone or disperser species were spilling over from natural habitats into cropland and responding to land-use change at a relatively small spatial scale. However, the large variation in the effect of distance from field edge suggests variable responses between species and it was likely Hymenopteran species had diverse distribution patterns (Figure 1.1) and/or responded to land-use change at different spatial scales.

The decline in cropland stingless bee abundance observed within 100 m from field edge, when distance to water was low, is in-keeping with what is currently known regarding their ecology. Stingless bees are commonly ecotone species (Blanche et al. 2006; Chacoff and Aizen 2006; Munyuli et al. 2011; Munyuli 2012) that decline in croplands with increasing distance from natural habitat (Chacoff and Aizen 2006; Greenleaf et al. 2007; Munyuli 2012). *Hypotrigona* were the dominant stingless bee genera caught and given their small size they are only likely to forage at distances of 300-600 m from their colony (estimated using Greenleaf et al. 2007) hence effects of farmland extensification are seen at relatively small spatial-scales. As *Hypotrigona* accounted for 41.3% of all bee individuals trapped they are likely to be an important flower visitor and pollinator in croplands, especially close to water, and the extensification of croplands increasing the mean distance of crop plants to natural habitat could have substantial impacts on crop pollination by stingless bees (Heard 1999; Chacoff and Aizen 2006; Munyuli 2012; Garibaldi et al. 2013; Kiatoko et al. 2014). Provision of artificial nesting resources for *Hypotrigona* could be a feasible management option for ecological intensification of small-scale farmlands as these bees can be managed to produce honey and store pollen that can be harvestedthus providing additional benefits to small-scale farmers (Munyuli et al. 2011). Clearly, further study is required to establish the mechanism by which distance to water affects *Hypotrigona* stingless bee abundance and to determine if the provision of supplemental nesting resources can enhance cropland stingless bee abundance and crop pollination, especially in disturbed landscapes where local woody resources are used for cooking fuel and construction (Appendix L Figure L.8).

Non-stingless bees (primarily *Macrogalea spp.*) did not show a decline of abundance with increasing distance from field edge and it is probable that any effect of distance at the scales observed was too weak to detect (Ricketts et al. 2008) due to their larger size and foraging ranges relative to *Hypotrigona* stingless bees (Greenleaf et al. 2007; Pasquet et al. 2008), and/or many species were cultural and could persist in croplands. Given that *Macrogalea* construct their nests by tunnelling into soft, dead plant stems (Michener 1971; Michener 2007; Munyuli et al. 2011) it is likely that they were ecotone species. The second most commonly caught genus was *Lasioglossum* (Appendix C Table C.1) and these are soil nesting species (Munyuli et al. 2011) potentially making them cultural as they can nest within croplands. The constrasting responses of cultural and ecotone species could cancel one-another out suggesting another reason for a lack of an overall response of non-stingless bee abundance to increasing distance from field edge. Honey bees and carpenter bees were conspicuous in the study area but were poorly represented in pan-trap catches, these are ecotone taxa (Michener 2007) that can forage across large distances (Pasquet et al. 2008; Zurbuchen et al. 2010) and, as such, are also unlikely to show an abundance response to distance from edge at the scales observed in the study area. Isolation from natural habitat in this small-scale farming landscape did not reach levels at which change in the overall abundance of larger bees could be detected; this is in-keeping with other studies from East Africa (see Chapter 1.5.1) and suggests pollination by larger bees is unlikely to be impacted by moderate levels of landscape transformation.

Predatory Hymenoptera showed a decline in abundance with distance from field edge but perhaps for different reasons than stingless bees. The majority of predatory Hymenoptera caught had traits indicative of cultural and/or disperser species and nesting resources for these species can be found within croplands or human habitations; the sand wasps (Crabronidae) typically excavate nests in bare, sandy soil (Bohart and Menke 1976; Krombein and Pulawski 1986), spider wasps (Pompilidae) paralyse spiders which are concealed either in their own burrows or are dragged to a crack, crevice, excavated burrow or mud-nest made by the wasp (Goulet and Huber 1993; van Noort 2004-2014; Capinera 2008) and potter wasps (Vespidae: Eumeninae) either burrow in soil or wood, or construct exposed mud or paper nests (Goulet and Huber 1993; Tindo et al. 2002). Cultivation can destroy burrows so soil nesting species may require field margins and other no or low till areas to reproduce. Food resources for adult predatory wasps should have also been available in cropland habitats, these are typically nectar and pollen from flowers, honeydew from sap feeding insects, or larval prey items, where wasps puncture prey and drink fluids, a behaviour known as maxalation (Chilcutt and Cowan 1992). Although it appears most predatory Hymenopteran species caught could exist within croplands, the decline with distance from field edge suggests either some were using nesting sites outside of the field (in woody natural habitat or perhaps the untilled edges of fields, paths, yards or the mud brick walls of houses) or perhaps that cultural species were using natural habitat as a microclimatic refuge during the hottest parts of the day. The mean maximum shade temperature of study fields was 33.4 ˚C, and it was not uncommon for the maximum temperature to exceed 40˚C at some times of year. There is little information on the role of thermal refugia and beneficial insects, but Herrara the thermal biology of different hymenopteran and dipteran species does predict their irradiance-biased microhabitat selection. The decline with distance from edge could also have reflected a pattern in prey density. Regardless of the underlying mechanism proximity to field edge increased predatory Hymenoptera abundance and this could translate into enhanced predation of crop-pests, but it should be noted that wasp predation of spiders (Goulet and Huber 1993; van Noort 2004-2014) increases intraguild predation (Lang 2003; Prasad and Snyder 2004). Therefore the consequences of agricultural extensification for biological control will depend on the ratio of crop pests directly predated by wasps to crop pests that would have been controlled by the spiders predated by wasps (and the crop yield consequences of each).

Regarding parasitoid Hymenoptera, before discussing the effects of field enlargement, it should be noted that field floral area may not have been the best (and certainly not the only) predictor of cropland resource availability. The PCA MAM was more complex and predictive than the untransformed MAM retaining terms relating to spillover and resource availability whereas the untranformed MAM retained no term for the area of natural habitat in the surrounding landscape. As such the parasitoid PCA MAM is considered throughout the discussion and not the untransformed MAM. In Europe parasitoids are generally thought to be ecotone or disperser species dependent on natural habitats for floral nectar sources and favourable microclimate, and on crops for hosts (Dyer and Landis 1996; Siekmann et al. 2001; Scheid et al. 2011). In the complex landscapes of the small-scale farmed study area natural habitats may have provided important floral resources during dry seasons (Gemmill-Herren and Ochieng 2008) and thermal refugia. However, the relative importance of floral resources in natural habitats as compared to croplands within the study area may have been less than in Europe due to a lack of chemical and mechanical weed control resulting in relatively high cropland floral resource availability. As food sources for parasitoid larvae (host species) and adults (e.g., nectar) were both likely to have been present in study area croplands parasitoid species could have had distributions that reflected cultural species or well established dispersers. The very low levels of pesticide use in the study area also would favour cultural and disperser distributions of parasitoid species. Once a parasitoid colonises a field it can potentially persist across crop rotations without it or it's host being chemically eliminated.

The abundance of pan trapped parasitoid Hymenoptera was best modelled by a complex interaction between distance to edge (field enlargement), agricultural extensification and floral area. This interaction is not easily interpreted perhaps due to the high diversity of the group (28 families; Appendix C Table C.1) which had a wide range of different body sizes and host species. As most parasitoid species trapped were tiny, their foraging ranges were likely to be low (Corbett and Rosenheim 1996; Roland and Taylor 1997; Tscharntke et al. 2005b), however larger vespoid parasitoids such tiphiid and scoliid wasps were also trapped and these were likely to forage over larger distances. Tiny parasitoids, however, may passively get spread great distances by wind. With regard to field enlargement and agricultural extensification parasitoid abundance increased with distance from field edge when natural habitat was low but decreased when it was highest, and abundance was highest for all distances when natural habitat was low (PCA model, Appendix E). This could be interpreted as when natural habitat was high spillover of ecotone or disperser species into croplands was also high but overall parasitoid abundance in croplands was lower, perhaps indicating a lower abundance of cultural or established disperser species, therefore a decay in parasitoid abundance with increasing distance from field edge was detectable. Conversely in low natural habitat landscape ecotone and disperser spillover may have been lower and cultural or established disperser species were more abundant therefore the effect of any spillover could not be detected. The reasons for greater abundance of parasitoids further from the field edge in low natural habitat landscapes are unclear, it might suggest edge avoidance behaviour by parasitoids or hosts (Cronin 2009) due to increased predation risk (Puckett et al. 2009) or reduced host abundance (perhaps due to predation or lower crop plant density nearer to edges). Inferring the biological control consequences of changing cropland parasitoid distributions with agricultural extensification in small-scale farmed landscapes requires detailed knowledge of host-parasitoid and host-cropinteractions. Similar to the intra-guild competition caused by spider hunting predatory hymenoptera, parasitoids can parasitise beneficial as well as pest insects, including other parasitoids (hyper parasitism), predators and pollinators. Therefore generalisations relating to ecosystem services are perhaps inappropriate at this higher taxonomic level. Unfortunately, the ecology of sub-Saharan African parasitoid Hymenoptera is unknown for most species.

Blister beetle abundance had a complex response to field enlargement that was neutral to positive in landscapes of fragmented low natural habitat landscapes and negative in landscapes with more, less fragmented natural habitat (Figure 3.14). Depending on the location of larval food blister beetles could have been cultural, disperser or even ubiquist species (see Figure 1.1). A decline in abundance with distance from field edge in landscapes with abundant natural habitat suggests an ecotone or disperser distribution that became a more cultural distribution at higher levels of agricultural extensification. A possible explanations for this pattern could be that if cropland and natural habitats share a similar resource, such as nectar and pollen in flowers, represented by different species between habitats then blister beetles optimise their search strategy for food resources by preferentially foraging on the flower species present in the larger habitat (as they are more likely to encounter these). The potential for such a scenario would be enhanced if the floral resource value of natural habitat declines with increasing fragmentation and/or if floral species are substantially different between habitats. Studies of bumble bees in Europe suggest that transient dilution effects, reduced pollination or pollinator abundance in one habitat compared to another habitat rich in floral resources during a mass-flowering period, can occur in grasslands sharing landscapes with oilseed rape (*Brassica napus*) (Diekötter et al. 2010; Holzschuh et al. 2011). Although dilution influences the spatial distribution of bees within a landscape at a particular time, overall, the cover of mass flowering crops has been shown to increase bee densities in natural habitats (Westphal et al. 2003; Herrmann et al. 2007). Another explanation for blister beetle distributions could be that host distributions were also affected by landscape change, so as cropland increased in area grasshopper eggs would have had to become relatively more common in fields compared to natural habitat. Within the study area temporary grassy fallows within croplands were more common than grassy semi-natural areas, and sown grass strips in European agri-environment schemes have been shown to enhance grasshopper abundance (Marshall et al. 2006). Additionally grasshoppers have been shown to be more common in croplands compared to semi-natural grasslands (Wiegert 1965).

Regardless of the underlying mechanism, the model suggests the abundance and distribution of blister beetles within croplands depends on resource availability and the level of agricultural extensification within the vicinity of the field. This could have implications for the ecosystem disservice of crop damage, however this will depend on the ratio of crop damage prevented by larval blister beetle predation of grasshopper eggs to crop damage caused by adult blister beetles.

As expected for likely cultural species, darkling beetles and ground beetles showed no significant decline in abundance with increasing distance from field edge suggesting little spillover was occurring or that detectable declines in spillover were not occurring at the distances observed. The former of the preceding explanations is most likely as agricultural darkling beetles are typically cultural species (Watt 1974; Allsopp 1980; Robertson 1993) and their soil-dwelling larvae can do considerable damage to roots and seedlings of crops in semi-arid areas, whilst the surface dwelling adults may gnaw the stems of plants and eat leaves and buds (Butler 1949; Watt 1974; Allsopp 1980; Gu et al. 2007). Ground beetles are also often cultural or disperser species (Duelli et al. 1990; Booij et al. 1995), both adults and larvae are predatory, the former actively seeking prey or scavenging above the soil and the latter typically ambush prey from concealed burrows (Arnett et al. 2000; Holland 2002).

3.4.2. Effects of farmland extensification on agriculturally important insects

All but one focal taxa showed a significant abundance response to the loss and fragmentation of natural habitat due to agricultural extensification, and the spillover of blister beetles, stingless bees and parasitoid Hymenoptera differed depending on the level of agricultural extensification in the surrounding landscape.

Variation existed between focal taxa for the distance at which agricultural extensification in the surrounding landscape was most predictive of that group’s abundance. Distances were relatively small (local) for non-stingless bees (50 m), stingless bees (50 m), parasitoid Hymenoptera (100 m) and darkling beetles (200 m), and were greater for all Hymenoptera combined (1000 m), blister beetles (1200 m) and ground beetles (2000 m). Generalist predators are predicted to respond to landscape at larger spatial scales than more specialised natural enemies (Chaplin-Kramer et al. 2011) and this was reflected by ground beetles responding to landscape at a larger scale than parasitoid Hymenoptera. Landscape was not predictive of predatory Hymenoptera abundance. As non-stingless bee and blister beetle abundances were best predicted by fragmentation of natural habitat (edge density) this may suggest the length of the crop non-crop interface was more important to their abundance in croplands than the amount of natural habitat (which predicted the other focal taxa better). However as edge density (fragmentation) and proportion of natural habitat were inversely correlated a response to increasing fragmentation also reflects a response to loss of landscape natural habitat.

The abundance response of all Hymenoptera to agricultural extensification was non-linear, being lowest at intermediate values of natural habitat. This pattern is likely due to a combination of differing abundance responses from multiple species, for example there were groups of ecotone Hymenoptera species abundant when natural habitat was high (that declined quickly with habitat loss (stingless bees for instance) and other groups of cultural

Hymenoptera species that benefited from increased cropland area. This does not support an intermediate disturbance view of the impact of landscape structure on ecosystem services, at which intermediate levels of landscape complexity give the highest level of ecosystem service (Tscharntke et al. 2012b). However, the interaction of multiple taxa providing several ecosystem services could be obscuring the response of functional groups of species. The general response of Hymenoptera suggests that there will be winners and losers in small-scale farming landscapes when it comes the expansion of croplands, and that intermediate levels of disturbance (in this context) may not particularly benefit either ecotone or cultural species.

Stingless bee abundance was best modelled measuring landscape at a local scale (50 m) which reflects the low foraging range of the group (Greenleaf et al. 2007). Abundance responded negatively to agricultural extensification, but only when distance to water was low, and the effect was strongest when distance to edge was high suggesting spillover was reduced by agricultural extensification. It was likely that woody natural habitat close to water provided nesting sites for the *Hypotrigona* species that dominated stingless bee catch. *Hypotrigona* bees typically nest in small cavities in tree bark or tree cavities-(Eardley 2004; Michener 2007; Munyuli et al. 2011) and larger trees (such as *Ficus spp.*) could be found near semi-perennial water sources compared to trees in dry forest far from water, and these larger trees were likely to offer enhanced nesting opportunities. Access to water could have also been an important driver of stingless bee distribution and it could be that suitable nesting resources were present in natural habitats at any distance from water but population density was only high enough near water to allow detection of a response to habitat loss. These scenarios are not mutually exclusive and it could be that both access to large riparian trees and water itself were important predictors of stingless bee abundance. As stingless bees were relatively abundant the local clearance of natural habitat due to agricultural extensification near water sources is likely to have implications for crop pollination.

As with stingless bees the response of non-stingless bee abundance to agricultural extensification was best predicted at a local scale (50 m), this time with a significant interaction with floral area but not distance to water (Table 3.3, Figure 3.10). This was surprising as non-stingless bees had a larger predicted average foraging range than stingless bees (based on inter-tegular distance, Greenleaf et al. 2007) and were expected to respond at larger spatial scales to landscape, however previous studies have shown that body size does not consistently affect bee species response to environmental disturbance (Williams et al. 2010). Non-stingless bee abundance responded negatively to edge-density when floral area was high and neutrally or (weakly) positively when low. This interaction cannot be fully explained with the data available but may relate to floral resource density in natural habitats (for discussion of pollinators and floral density see Dauber et al. 2010; Essenberg 2012). If floral resource density was lower in fragmented natural habitat compared to consolidated natural habitat then, with increasing habitat loss, assuming a field had an intermediate floral resource density between the two types of natural habitat, it could be that bees switched from foraging in natural habitats to foraging in fields because the floral resource density of fields increased relative to natural habitat. If the floral resource density of fields was always higher than that of natural habitat then bees may have preferentially foraged in fields in all landscapes. As natural habitat dwindles and fragments with agricultural extensification overall bee numbers drop (natural habitat in this scenario has a complementary effect and provides some resource that the field does not, e.g a climatic refuge or nesting site). The transient dilution effects seen in bumble bees abundances due to differential resource availability between habitats in European landscapes (Diekötter et al. 2010; Holzschuh et al. 2011) may suggest that this scenario is possible. However, given that studies from European landscapes are conducted in a very different context to smallholder areas, where fields are very large monocultures of crops such as oil seed rape with resources being very transitory, such generalisation should be treated cautiously.

Hymenopteran predator abundance showed no significant response to agricultural extensification suggesting species were primarily cultural which is in keeping with the ecology of the species observed and previous studies (e.g., Klein et al. 2002a). Whilst observed levels of agricultural extensification in the study area posed no obvious threat to the abundance of predatory Hymenoptera in croplands, it likely that, as cultural species, increasing management intensity, e.g., use of agrochemicals and mechanical deep tillage, would have a negative impact**.**

Parasitoid Hymenoptera responded to natural habitat negatively (or agricultural extensification positively) at a small scale (100 m) reflecting the small size and low foraging ranges of most parasitoids caught (in agreement with previous studies e.g., Thomson and Hoffmann 2010), and suggesting that cropland was supplementing host and/or floral resources in the landscape. At the edge of fields agricultural extensification was predicted to decrease parasitoid abundance, however the effect was reversed as distance form edge increased. This perhaps suggests that ecotone and disperser parasitoids spilling into croplands benefit from nearby natural habitat and, as parasitoids (typically) have poor dispersal capabilities, declines in ecotone and disperser abundance with loss of natural habitat due to agricultural extensification were more pronounced nearer the edge of fields. As such, loss of natural habitat would have increased the relative abundance of cultural parasitoids, which were modelled as responding positively to increasing cropland area and being less abundant at field edges (as discussed for spillover and field enlargement). From an ecosystem services perspective it appears good news that cropland parasitoid abundance responds positively to agricultural extensification. However, the general consensus for semi-natural habitats in large-scale conventionally farmed landscapes is that their loss reduces ecotone and disperser natural enemy populations and this reduces pest suppression (Veres et al. 2013). If agricultural extensification continues until just a few percent of natural habitat remains declines in cropland parasitoids may eventually be observed in the study system. Yet, little is known regarding cultural parasitoid species in low-input small-scale systems, it could be possible that, with little pesticide use, the fine-scale landscape heterogeneity in space and time in these systems (discussed in Chapter 2.1.1) could support adequate biological control from parasitoids regardless of semi-natural habitat in the landscape. As with predatory hymenoptera increases in the management intensity of small-holder landscapes is likely to impact cultural species of parasitoid.

Blister beetle abundance was best predicted by agricultural extensifcation at a relatively large scale (1200 m), agreeing with studies of other flower visiting beetles (e.g., Zaller et al. 2008b), and responded negatively to the fragmentation of natural habitat when resource availability was low and positively (predicted) or neutrally (observed) when floral area was high. This suggests blister beetles distribution was ecotone or disperser because abundance fell within cropland as natural habitat was replaced by cropland, and that resource availability reduced the impact of habitat loss. The ecosystem service implications of this will depend on the on the ratio of crop damage prevented by larval predation of grasshopper eggs to crop damage caused by adults.

Darkling beetle abundance responded to agricultural extensification at a local scale (200 m) with an interaction with distance to water, this was due to the contrasting responses of three abundant species. Darkling beetle abundance strongly declined with loss of agricultural extensification at low or intermediate distances to water but increased when far from water. Far from water *Rhytinota gravidula* was abundant and *Gonocephalum simplex* was absent, but closer to water *G.simplex* became the most frequently caught species (Appendix F). A third species, *Zophosis anquisticotis/collaris* was abundant and present at all distances. As *G.simplex* responded positively to agricultural extensification it was probably a cultural species (or, if an ecotone or disperser, cropland supplemented landscape resources and any resource that natural habitat provided that was essential was not limiting). *R.gravidula*’s abundance response was the opposite, decreasing with agricultural extensification, suggesting an ecotone or disperser species. As *Z.anquisticotis/collaris* was common at all distances from water its response to agricultural extensification is unclear. Whether different responses between species were due to bottom-up effects such as resource availability or top-down effects such as predation or parasitism is unknown. As the individual responses of species to agricultural extensificatio within this major crop pest group (Allsopp 1980) was context dependent, future attempts to model darkling beetle abundance and ecosystem disservice with landscape change should consider the abundant taxa at a fine taxonomic resolution such as genus or family. Regarding ecosystem disservices, darkling beetle crop damage close to water may reduce with agricultural extensification, however, further from water the opposite may occur.

Ground beetle abundance responded positively to agricultural extensification and was best predicted when landscape was considered at a large spatial-scale (2000m), however model predictions had substantial error therefore the strength of the response was uncertain. The overall positive response to agricultural extensification was consistent with the distribution pattern of a cultural group. Being a relatively species rich group (see Appendix C) it is unsurprising that there was uncertainty surrounding the effect of landscape change as it is likely that some species responded more strongly than others and/or some species had an opposing response. Linking the effect of agricultural extensification to the biological control provided by ground beetles is difficult. A greater abundance of ground beetles in croplands could result in enhanced pest-control (see Kromp 1999) but could also reflect a bottom-up effect of greater resource availability of prey items, potential crop pests. Additionally, whilst most ground beetles are thought to be generalist predators (Lovei and Sunderland 1996; Kromp 1999; Holland 2002) some species of Harpaline ground beetles are omnivorous being primarily herbivorous at certain times of year (Ikeda et al. 2010), further as ground beetles will consume both beneficial and pest prey there is potential for intraguild interference (Lang 2003; Prasad and Snyder 2004) reducing the ecosystem services provided by other insect species.

3.4.3. Resource availability and interactions with spillover and landscape change

The effects of resource availability have already been discussed in interactions with spillover and landscape change, here they are discussed with the emphasis on resource availability. The abundances of most pan-trapped taxa showed significant responses to floral area often interacting with landscape or distance from field edge suggesting floral area was predictive of resource availability. However, as predatory Hymenoptera, darkling beetle and ground beetle abundance did not respond to the measures of resource availability used in this study it is likely that the resource requirements of these groups were poorly represented by them.

Overall Hymenoptera abundance had a non-linear response to floral area peaking at intermediate values. As with agricultural extensification this could suggest differing responses between functional groups or species. As floral area was correlated with fallow land the decline in abundance associated with high floral area may have been caused by cultural species responding negatively to a reduction in local cropland area. At low floral availability fields might have been less attractive to ecotone and disperser species and cultural species may have declined due to resource scarcity. At intermediate values floral area may have attracted ecotone or dispersers species into fields with minimal impacts from fallow on cultural species giving relatively high abundances for both groups and an overall peak in hymenopteran abundance. Floral availability may have also influenced host or prey density. In general this perhaps suggests that intermediate levels of cropland floral area will maximise Hymenoptera abundance in low-input small-scale farmed systems, however, as discussed below, the responses between groups providing contrasting services or disservices may differ.

Stingless bees responded to resource availabilityand there was an interaction with spillover predicting that increasing floral area increased abundance at the field edge and reduced abundance further into fields (Figure 3.8). This may suggest, that when high, floral resources were saturating the pollen and nectar requirements of stingless bee within a short distance from the edge of fields. At low floral abundances stingless bees would forage far into a field to meet their resource requirements giving a relatively dispersed distribution across the field. However, at high floral abundances resource requirements would be satisfied without travelling far into a field so stingless bee distributions are aggregated at the field edge. Although pollinator aggregations due to floral resources are often implied there appears to be no study that directly examines or supports this, although there are studies on isolation effects from floral resources (Ricketts et al. 2008; Garibaldi et al. 2011) and some on dilution (Diekötter et al. 2010; Holzschuh et al. 2011; Riedinger et al. 2014). With regards to crop pollination and ecological intensification this may suggest that stingless bees will be effective pollinators of mass flowering crops at relatively short distances from natural habitat, therefore, in a mixed cropping system, where stingless bees are important, pollinator dependent crops should be planted at the edge of fields with non-pollinator dependent crops such as cereals planted futher into fields.

Non-stingless bee abundance had a positive non-linear response to floral area (Figure 3.11). When agricultural extensification was low abundance initially increased with floral area then plateaued at intermediate values . This relationship weakened with agricultural extensification, possible explanations for this interaction were discussed the previous section (3.4.2).

Parasitoid abundance showed no response to floral area in the untransformed MAM, however in the PCA MAM two ordination axes relating to resource availability were retained. Parasitoid abundance intially had a neutral or modest positive response becoming negative with increasing values of the ordination axis loading field and trap floral area, floral diversity, rainfall and fallow (fallow loading negatively, Appendix E Figure E.2). As with the overall response of Hymenoptera to resource availability this perhaps suggested abundance initially increased due to ecotone and disperser species attracted by increased floral resources (Gurr et al. 2005; Géneau et al. 2012) then declined as cultural species responded negatively to an increasing proportion of fallow land. The interaction of floral area and distance was discussed previously. The response of individual parasitoid species will also have also depended on the density of potential hosts within fields (e.g., Martijn et al. 2010) which will also respond to floral variables and fallow. Relatively low levels of floral area appeared adequate for maintaining overall parasitoid abundance in study area with no benefit predicted from increasing floral resources within cropland. However, given the diversity of parasitoids trapped, the distribution pattern of individual parasitoid species or functional groups across the crop-non-crop interface will be important in predicting their response to resource availability.

Predatory Hymenoptera abundance had no significant response to floral area (Table 3.3). Adults of the species for the major families trapped can maxalate prey (reviewed by Chilcutt and Cowan 1992) or use honeydew produced by sap feeding insects (as shown for parasitoid Hymenoptera, Wäckers et al. 2008; Vollhardt et al. 2010) and may therefore be less reliant on floral resources than bees or parasitoid Hymenoptera.

Blister beetle abundance only responded positively to floral area when agricultural extensification was high with a negative responses predicted when low (however this appears exaggerated in the model predictions compared to observed values). This is an opposing response to that seen for non-stingless bees and may reflect the larval host requirements of blister beetles rather than adult resource requirements, but, without information regarding larval host availability (grasshopper eggs) in crop and natural habitats it is difficult to explain the observed patterns. Regardless of the explanation with agricultural extensification blister beetles positively responded to increasing floral area suggesting the pest potential of blister beetles to large areas of flowering crops will be higher in larger, consolidated areas of cropland. Although, for pollinators at least, a positive numerical response to increased flower density does not necessarily translate into a positive functional response (in this case of blister beetles this would be flower damage) (Klinkhamer et al. 1989; Jennersten and Nilsson 1993; Goulson et al. 1998; Feldman 2006).

3.4.4. **Conclusions**

In small-scale tropical agro-ecosystems the effects of field enlargement and agricultural extensification, resulting in the loss and fragmentation of natural habitat, on mobile ecosystem service and disservice providing species are unclear (Chapter 2, Steward et al. 2014) even though such systems support billions of people (IFAD & UNEP 2013) and are under pressure to intensify (Min 2006; Huang et al. 2011).

Bearing in mind that individual species may show a contrasting response to the aggregate response of their functional group, the general effect of continuing agricultural extensification within the study context on pollinators is likely to be negative. This is because of reduced spillover and landscape abundance of stingless bees. To maintain and enhance stingless bee pollination ecological intensification should aim to conserve natural habitat to minimise distances to natural habitat especially near water courses, the local response of stingless bees to landscape suggests that farm or community scale interventions could be well suited to this purpose.

The natural enemies associated with the biological control of crop pests (predatory and parasitoid Hymenoptera, and ground beetles) showed a mixed response to field enlargement and agricultural extensification and, whilst strong negative effects on natural enemy abundance were not observed in the complex small-scale farms of the study area, if continuing agricultural extensification and increasing field sizeleads to an extremely simplified farming landscape then declines may occur (Tscharntke et al. 2012b). However, relatively little is known regarding the potential pest control benefits of natural enemies in sub-Saharan Africa and more research is required. Given the diversity of natural enemies observed in this study the trophic webs of low-input small-scale landscapes may be large and complex and there is considerable potential for intra- and inter-guild interference between natural enemy species. The crop non-crop distributions and responses to landscape change in conjunction with the probable larval and adult feeding traits of natural enemies suggested that the majority of trapped specimens had cultural rather than ecotone or disperser distributions (although in more consolidated landscapes than observed here with larger distances from natural habitats distributions could become more ecotone). This is not suprising as pesticide use was minimal and therefore croplands were relatively benign to cultural insects. It can then be inferred that the natural enemies of undeveloped small-scaled farmlands may be particularly vulnerable to increased pesticide use if conventional agricultural intensification (rather than extensification) occurs. The detrimental effects of pesticide use on cultural species and the extent to which the local-complexity of small-scale landscapes can buffer this (particularly when non-crop habitats are rare), with particular relevance to the consequences of farmland consolidation, is an important topic for futher study.

Potential crop pests had complex responses to agricultural extensification. If darkling beetle abundance is considered a proxy for crop damage, ecosystem disservices from darkling beetles responded positively to agricultural extensification when close to water but negatively further away. It appeared that different species were responsible for the change, one with an ecotone/disperser distribution and one with a cultural distribution. As crop pests and pollinators both negatively responded agricultural extensificationclose to water there may well exist a trade-off between ecosystem services and disservices. The abundance of response of blister beetles was difficult to interpret in the absence of data regarding larval prey density but model predictions suggested that floral resources in landscapes dominated by cropland may have been more attractive to adult beetles, which can damage flowering crops. Therefore, depending on cropland floral resources, agricultural extensification could reduce pollination (fewer stingless bees) and increase crop damage. In this context management options for ecological intensification that manipulate cropland floral resouces could potentially attract crop pests as well as pollinators and natural enemies.

To accurately predict the consequences of change in small-scale farmed landscapes for all the groups considered here data are required for the ultimate provisioning ecosystem service of crop yield (Chaplin-Kramer et al. 2011). Also, for a more holistic appraisal of agriculturally important taxa, groups such as weevils, scarab beetles, lepidoptera, orthoptera, spiders, camel spiders, milipedes, centipedes, ants and flies should be considered.

The fieldwork for this chapter invested considerably more resources than required for just the insect sampling presented here attempting to assess crop pollination, pest damage and yield through manipulations of standardised crop plots. Attempts made in three different growing seasons failed to establish experimental plots with enough inter-site consistency due to 1) the unpredictability of rainfall, 2) untended domestic stock destroying plots, 3) elephants, baboons, vervet monkeys, antelope, gazelle and ground squirrels destroying plots, and 4) vandalism and theft of materials and crops.

The significant and sometimes contrasting abundance responses to agricultural extensification and field enlargementfor the different functional groups of mobile ecosystem service providing insects observed here demonstrates that predicting the ecosystem service consequences of landscape change in small-scale farming systems will be complicated. However, when taking into account the spatial-scale at which ecosystem services providers experienced their environment and how their resource requirements may have influenced their distribution between crop and natural habitats many of the patterns in abundance observed in this study could be related to current theory and synthesis. Whilst the theoretical tools and frameworks exist to predict and understand the agricultural distributions of ecosystem service providing species, the large diversity of beneficial and pest species and their interactions in these tropical small-scale farming landscapes highlights the need for information regarding species' basic ecology and biology to predict responses to agricultural extensification.

Chapter 4. Agricultural extensification and functional diversity in tropical smallholder agriculture

4.1. Introduction

To meet the demands of growing populations, changing diets and changing patterns of commodity consumption (Royal Society 2009; Godfray et al. 2010; Foresight 2011) there is a pressure for small-scale farming throughout the developing world to both expand and consolidate (Aldrich et al. 2006; Huang et al. 2011; Collier and Dercon 2013) which will result in land-use changes at multiple spatial scales. Small-scale farming (often referred to as smallholder farming) is the backbone of global food security (Chappell and LaValle 2011; Horlings and Marsden 2011; Tscharntke et al. 2012a) and accounts for a substantial proportion of food production and GDP in many countries (Singh et al. 2002; Thapa 2009; Salami et al. 2010a; IFAD & UNEP 2013). Land-use changes are likely to affect the ecosystem functioning of farming systems (Tscharntke et al. 2008) and understanding how communities of animals respond both functionally and numerically as small-scale farming evolves will be necessary if an optimal balance of ecosystem services and disservices is to be achieved. This is of particular relevance to the concept of ecological intensification where ecosystem services are optimised for sustainable food production (Bommarco et al. 2013). Whilst the supporting and regulating ecosystem services that are important for agricultural productivity have received a great deal of attention (e.g., pollination, Garibaldi et al. 2011; Garibaldi et al. 2013; Kennedy et al. 2013) (or ‘soil-based’ ecosystem services, Lavelle et al. 2006; Barrios 2007; Letourneau et al. 2009; Chaplin-Kramer et al. 2011; natural enemies and biological control , Veres et al. 2013), the same cannot be said of ecosystem disservices (but see, Zhang et al. 2007). This may reflect the fact that ecosystem disservices, such as damage to crops or disease transmission, are only a facet of regulating services that affect the provisioning of commodities and are indirectly considered in the biological control of crop-pests (i.e., crop damaging ecosystem disservice - biological control = ecosystem service). However it appears inconsistent, given that regulating ecosystem services and disservices can both respond to spatiotemporal land-use change (e.g., White et al. 1997; Michalski et al. 2006; Zaller et al. 2008b; Graham et al. 2010; Webber et al. 2011), that so much of regulating ecosystem service research focusses on land-use responses of beneficial rather than detrimental species.

Species with different feeding behaviours and diets can have different responses to land-use changes (Wilby et al. 2006) and the diversity of such traits can affect ecosystem services such as predation of crop pests (Snyder et al. 2006), crop pollination (Kremen et al. 2002; Albrecht et al. 2007) or disservices such as crop raiding by primates (Brashares et al.

2010). Land-use related changes in the diversity of feeding traits represented by a species community can have complex effects on ecosystem functioning by affecting parasitism of functionally important species (Tylianakis et al. 2006) or interference between feeding guilds (Snyder and Wise 1999; Lang 2003; Prasad and Snyder 2004). The process by which land-use changes disproportionally affect particular functional traits or trait combinations is known as trait filtering and examples of this include where habitat degradation or loss alters the balance of feeding behaviours within a community (Gray et al. 2007; Tscharntke et al. 2008) or causes the extinction of large bodied species (Larsen et al. 2005). Studies have traditionally used measures of taxonomic diversity (e.g., species richness) to assess the impact of land-use on biodiversity, however there is now a growing realisation of the importance of functional diversity. This is because taxonomic measures do not take into account how environmental filtering can alter the composition of life-histories or traits within community and therefore may be inappropriate indicators of structural change underestimating the true effects on biodiversity of land-use change (Cardinale et al. 2012; Mouillot et al. 2013; Edwards et al. 2014a). Functional diversity methods quantify the range of functional differences (traits) between the taxa that form a community thus linking species diversity to ecosystem processes through resource-use patterns (Tilman et al. 2001; Petchey and Gaston 2006). This can give insight in to the vulnerability or resilience of (agriculturally important) taxa and the ecosystem processes they regulate to land-use change or how well they may recover in response to environmental disturbance (Sekercioglu 2012).

Considering the relevance of a functional diversity approach to the inference of ecosystem services in agriculture (Tscharntke et al. 2008; de Bello et al. 2010; Sekercioglu 2012) relatively little is known regarding the impacts of land-use change on functional diversity in tropical agricultural landscapes (Edwards et al. 2014a), however some groups have received more attention than others such as dung beetles (Edwards et al. 2014a), trap-nesting Hymenoptera (Tscharntke et al. 2008; Williams et al. 2010) and birds (Tscharntke et al. 2008; Flynn et al. 2009; Sekercioglu 2012; Edwards et al. 2013). Most studies of functional diversity with relevance to agriculture discuss the topic by contrasts between different habitats or land-uses, such as forest vs. cropland. Discussion of change with specific relevance to gradients of agro-ecological intensification within cropland, that would illustrate the shape of functional relationships with land-use change and highlight thresholds, is uncommon (but see Flynn et al. 2009). Factorial comparisons of natural habitats to semi-natural then agricultural habitats indicate that functional diversity declines more strongly for birds than taxonomic measures suggest (Flynn et al. 2009), bee and dung beetle functional diversity declines (Tscharntke et al.

2008; Edwards et al. 2014a), and avian functional diversity and specialisation declines (Tscharntke et al. 2008; Sekercioglu 2012) or shows no trend (Edwards et al. 2013). In support of the intermediate landscape-complexity hypothesis, where intermediate levels of landscapes complexity promote diversity (Tscharntke et al. 2012b), the relative abundance of avian pollinators and seed dispersers is greatest in semi-natural habitats and community similarity for avians and Hymenoptera is highest in agriculture and highest in simplified compared to complex landscapes (Tscharntke et al. 2008).

Hymenoptera and Coleoptera are globally widespread insect orders that can strongly affect agricultural commodity production positively, such as pollination by bees (Garibaldi et al. 2013) or pest control by carabid beetles (Kromp 1999), or negatively, such as crop damage by eurytomid wasps (Nadel and Pena 1991; Hernández-Fuentes et al. 2010) or tenebrionoid beetles (Robertson 1993; Durairaj and Ganapathy 2000). Whilst a few studies have investigated land-use changes on functional diversity for specific families of Coleoptera (Vandewalle et al. 2010; Edwards et al. 2014a) or Hymenoptera (Tscharntke et al. 2008; Jha and Vandermeer 2010; Williams et al. 2010) no studies have looked at how overall hymenopteran or coleopteran functional diversity changes as small-scale agricultural landscapes expand, intensify or consolidate.

This study addresses a knowledge gap regarding how functional agro-biodiversity changes with land-use change in small-scale farming landscapes by investigating the effects of agricultural extensification at two spatial scales (field enlargement and proportion of agriculture/natural habitats in the landscape surrounding the field) on the functional and taxonomic diversity of Coleoptera and Hymenoptera. The study area falls within the buffer zone of Africa's largest national park, Tsavo, where current rates of agricultural expansion are high (Maeda et al. 2010a). In this novel context, the aims of this study are two-fold, first to test the hypothesis that agricultural intensification will lead to environmental trait filtering by selecting species more similar than expected by chance, leading to reduced functional diversity in extensified contexts. Second, it aims to investigate how particular functional traits are related to field size and landscape composition.

4.2. Materials and methods

This study analyses a subset of the data collected for Chapter 3, data were subset so as to standardise sampling effort between sites as required for the functional diversity metrics discussed subsequently.

4.2.1. **Study system**

The study landscape was located in lowland (<1100 m a.s.l.) areas of Taita-Taveta County of south-east Kenya approximately centered on the town of Mwatate (lat -3.503˚, long 38.364˚). Agriculture is the dominant source of income for Kenyans employing 80% of the national labour force (World Bank 2013) and a rising population is increasing demand for agricultural land. Taita-Taveta County had an annual population growth rate of 1.6% between 1999-2009, the total population of the county in 2009 was c. 284,000 in c.17,000 km^2, 48% of whom were under 20 years old (National Council for Population and Development 2013). High population growth rates coupled with saturation of the farmland resource in the wetter highlands of the Taita Hills has resulted in rapid, unplanned, conversion of dry forest to croplands in lowland areas. Overall loss of dry forest in the Taita Hills and surrounding lowlands between 1987 and 2003 was estimated at 22% giving an annual loss rate of 1.5% and losses were concentrated in lowland areas with little change in upland areas or hill slopes (Maeda et al. 2010a). Simulations based on current rates of change predict lowland areas will be almost completely denuded of dry forest by 2030 (Maeda et al. 2010a), although there was still a substantial area remaining at the time of this study.

The lowland landscape was a mosaic of open dry woodland (*Acacia spp.* and *Commiphora spp.*) and rainfed, low-input, largely unmechanised small-scale farming dominated by maize intercropped with dry beans or cowpeas. As agrochemical inputs (pesticides, herbicides and inorganic fertilisers) were very low to non-existent and tillage was manual (farmers used mattocks or a shallow ox plough) cropland hostility (to insects) from mechanical or chemical disturbance was low. As agrochemical inputs (pesticides, herbicides and inorganic fertilisers) were low and tillage was manual (farmers using mattocks or used a shallow plough driven by ox) negative impacts (matrix hostility) to insects from mechanical or chemical disturbance were minimal. The dominant soil types within the study zone were rhodic ferralsols and chromic luvisols (Batjes and Gicheru 2004), clays or sandy loams with moderate fertility, low organic matter content and poor water retention capacity (Mbora 2002). Rainfall patterns in Taita are bimodal; with a long rainy season occurring from March to June and a shorter rainy season in October to December (Pellikka et al. 2009). Rainfall increases with altitude with average annual totals for the lowlands 587 mm at 560 m (Voi) increasing to 1132 mm in the uplands at 1768 m (Mgange) (Pellikka et al. 2009). Rainfall is highly variable between years, from 1986 to 2003 the minimum annual rainfall was 200 mm in the lowlands and the maximum 2000 mm in the highlands (Pellikka et al. 2009). In line with annual averages a coarse estimate of rainfall from simple raingages for the study period (August 2012 to June 2013) gave approximately 610 ± 90 (SD) mm of rain at Mwatate.

4.2.2. **Natural habitat mapping**

The study zone was limited to lowland areas where dry forest and wooded grasslands (considered here to be non-agricultural areas with >20% cover of shrubs or trees) were the dominant natural habitats in the landscape. Landsat imagery was too coarse to provide spatial habitat information at a spatial-scale appropriate for agricultural insects, so woody habitat was mapped manually using QGIS 2.0 (QGIS Development Team 2013) and freely available high-resolution (c. 2 m pixel width) satellite images from the openlayers plugin. Imagery recorded during the dry seasons of 2010-2012 was used for mapping as this provided the greatest contrast between woody vegetation and agricultural areas. The minimum mapping unit was 25 m^2 and the final map was smoothed in ArcGIS 10.0 (ESRI 2011) using a PAEK algorithm with 10 m tolerance as this gave a good visual fit to satellite imagery. A total of 525 km^2 was mapped (Figure 3.1). The primary landuses of non-wooded areas were cropland, settlement, roads and pasture, of these cropland was dominant (>80% of non-wooded areas). From henceforth forest or woody natural habitat is referred to as “natural habitat” and all other areas as “agriculture”.

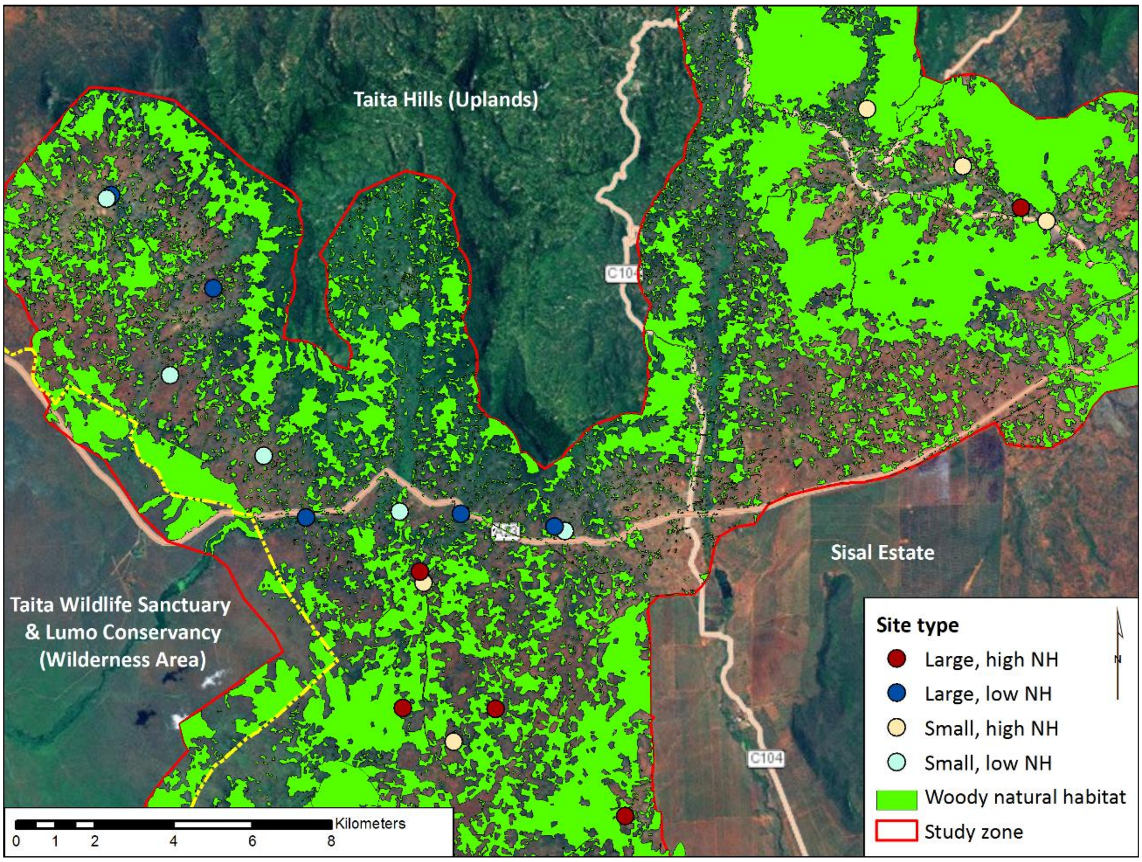


Figure 4.1 Study zone and sample site locations.

4.2.3. **Analysis of landscape structure, study design and site selection**

To determine the amount of agricultural extensification across the study area Patch Analyst 5.1 (Rempel et al. 2012) in ArcGIS 10.0 (ESRI 2011) was used to calculate landscape fragmentation metrics at a radius of 1 km for a point-grid spaced at 50 m and clipped to mapped agricultural areas. The 20% of points with the lowest proportion of natural habitat within 1 km and the 20% of points with the highest were selected and buffered to 100 m defining areas where agricultural extensification was high and low. To improve standardisation between potential field sites points within 1 km of a large commercial sisal plantation, ranchlands, large settlements or protected areas were excluded, as were points above 1100 m.a.s.l. or on slopes greater than 5˚. Landscape metrics were then recalculated for a higher resolution 20 m point grid clipped to the buffer. Potential study landscapes with high and low levels of agricultural extensification were identified from the new grid by buffering points with the 20% highest and lowest proportions of natural habitat to 20 m. Within this buffer, to investigate the effects of field enlargement arable fields were mapped and the largest and smallest fields (defined as those differing in area by approximately an order of magnitude or more) were shortlisted as potential study sites. To minimise correlations between boundary habitat and landscape, potential study fields were limited to those with boundaries comprising at least 75% or more dry-forest or bushland extending at least 5m from the field edge.

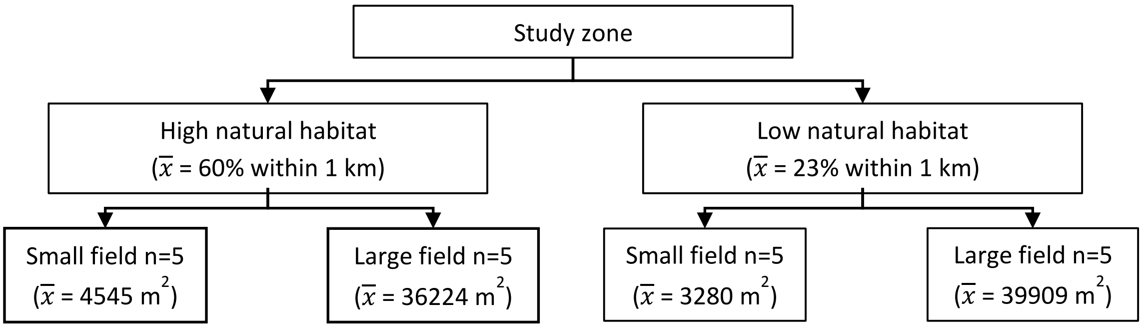


Figure 4.2 Study design with means for landscape and field size (agricultural context), see Chapter 3 Table 3.2 for errors.

Potential fields were randomly subset to give five large and five small fields in high and low natural habitat landscapes (Figure 4.2). Fields of the same size category were separated by a distance of approximately 2 km, this was assumed to give adequate spatial independence between study landscapes for the majority of ecosystem service providing insects (Steffan-Dewenter 2003; Kremen et al. 2004; Winfree et al. 2008; Chaplin-Kramer et al. 2011). Paired large and small sites were allowed within landscapes and at a separation distance of 2 km the study contained 16 independent landscapes and four paired sites.

4.2.4. **Sampling methods**

Trapping was conducted between August 2012 to June 2013. Pan and pitfall traps were placed at the same three fixed sampling points at the edge and centre of each field, the midpoint between these. The placement of the edge trap was random then average distance between the remaining traps was maximised with reference to the edge trap. Traps were only placed in cultivated areas where the nearest field boundary was dense woody habitat. There were a total of 60 traps, 15 in each agricultural context, in six sampling rounds for pan-traps and four sampling rounds for pitfall-traps. Species or family abundances are the summed catch of all traps across all sampling rounds (n = 20).

Triplicate pan-traps (12 cm diameter and 6 cm deep aluminium bowls with sloping sides) sampled mobile aerial insects attracted to floral resources, the focal taxa for this study were Hymenoptera. Pan-trapping is the most efficient method of sampling bees in agricultural habitats (Westphal et al. 2008) and has also been used to study parasitic and predatory Hymenoptera (Bowie 1999; Christie and Hochuli 2009; Saunders and Luck 2013). To account for different colour preferences of hymenopteran species (Kirk 1984; Aguiar and Sharkov 1997; Toler et al. 2005; Campbell et al. 2007) pans were (re)painted each sampling round either fluorescent yellow (1005), sky blue (15) or white gloss enamel. Blue and yellow pans were protected with clear varnish. Pan-trap height was adjusted to ensure visibly was not obscured by local vegetation. Pans were filled with water mixed with a small amount of detergent to a depth of 2 cm from the rim. Traps were set in the morning, mean (SD) 0905 hours ± 31 min and retrieved in the afternoon of the same day, mean (SD) 1557 hours ± 40 min, mean (SD) trap exposure was 6.88 ± 0.48 hours. Pan-trapping in 2012 was conducted during August, September and November, and in 2013 in January / February, April and May / Jun. Pan-trapping was not carried out in strong winds or on rainy days and was repeated if the weather changed from favourable to unfavourable conditions during in the day.

Pitfall traps (500 ml plastic cups, 94 mm in diameter and 135 mm deep) sampled epigeal Coeloptera (Ekroos et al. 2010; Ikeda et al. 2010; Gilroy et al. 2014). Pitfalls were filled with water mixed with a small amount of detergent to a volume of 300 ml. To prevent birds scavenging trap contents and overflow from rain storms, and to reduce evaporation, pitfalls were covered with a 150 mm diameter white plastic plate raised 2.5 cm from the soil surface. Pitfalls were initially left in-situ for five days, however this was reduced to three days in subsequent trapping rounds. Pitfall trapping conducted in 2012 was in August and November, and in 2013 in March and May/June.

For both trapping methods sites were stratified into groups that could be practically visited in a single day then the sampling order of sites was randomised each round. Sampling order was also randomised for the traps within sites. Collected specimens were temporarily stored in 70-99% ethanol until pinned for identification. If specimens were very small they were stored in sealed microtubes with 99% ethanol.

Taxonomic determinations for beetles > 04 mm in length were made to species by M.Mutua, and to genera and species/morpho-species for bees by M.Gikungu, J.Macharia and P.Steward, all using the reference collection at the National Museums of Kenya, Nairobi, Kenya, where bee and beetle specimens were deposited. Beetle specimens <0.4mm in length (365 / 3254 specimens, 11.2%) were not identified and are excluded from analyses. The identifity of specimens of non-apiforme Hymenoptera was determined to family for parasitoid wasps and to genera for vespid or spheciforme wasps by R.Copeland at ICIPE, Nairobi, Kenya, and non-apiforme hymenopteran specimens were deposited at ICIPE. Vernier calipers (± 0.05 mm accuracy) were used to measure total length (L, anterior median of head to posterior median of abdomen), thoracic width (T, widest span) and abdominal width (A, widest span) of beetles. Their ventral surface area was estimated using the formula $\left[\frac{2LA+LT}{3}\right]$ which weightsthe abdominal contribution to area higher than the thoracic contribution (adapted from Larsen et al. 2008), this was because the ventral area is nearly always larger than the thoracic area and the two can differ substantially in width.

4.2.5. **Functional trait matrix**

As data availability regarding the ecology and morphology of specimens was limited the functional trait matrices used here are relatively simple focussing on 1) the adult size, adult and larval feeding behaviour and larval location for Coleoptera species, and 2) larval feeding behaviour and larval diet for hymenopteran families. Traits were selected to be relevante to agricultural ecosystem services and, as such, indicate functional groups that share similar food resources which in turn relates to whether species are potentially beneficial (e.g. pollinators or natural enemies) or detrimental (e.g. crop pests). Whilst including additional morphological, behavioural and life-history traits would enhance the analysis by more accurately locating species in functional trait space, there was sufficient variability in the traits selected to clearly separate groups (Figure 4.5B and Figure 4.17B).

Pan-trapped Hymenoptera were analysed by families rather than species, reflecting the high diversity of specimens (37 families) and the impracticality and expense of identifying these to genera or species; it is likely that many species were unknown to science (R.Copeland, pers. comm.). Further, to analyse functional groups of Hymenoptera at a species or generic level more detailed knowledge of species ecology is required than is currently available or accessible, and at high taxonomic resolutions especially little is known regarding the functional ecology of most predatory and parasitoid Hymenoptera in sub-Saharan Africa. At the family level reasonably detailed descriptions of typical larval feeding behaviour and diet are available for Hymenoptera and traits were derived from the literature listed in Appendix H. As the ecology of species varies between species within families, in that not all species will share the same traits, traits were weighted according to their frequency of occurence within a family according to the information resources available (Appendix D Table D.2). A score of 1 indicated a strong association with a trait with the majority of species in a family demonstrating it, a score of 0.5 indicated a moderate association, but less than a majority of species demonstrating the trait, a score of 0.1 indicated the trait was demonstrated by just a few species within in the family (often considered to be atypical), and a score of zero indicated no association between family and trait.

The pit-fall trapped epigeal Coleoptera community (>0.4 mm in length) was considerably less diverse than the hymenopterans comprising 11 families and a greater taxonomic capacity existed for their identification. As such beetles were analysed at the species / morpho-species level. Detailed ecological information regarding many genera, and most species, was unavailable for most sub-Saharan African Coleoptera, therefore trait data was typically derived from a species' tribe or genera. When descriptions suggested that the species that form higher taxonomic groupings could possess divergent traits and no species-level data was available then a species was scored positive for all the possible traits it could possess (unless stated to be rare or unusual). Traits scores are listed in Appendix D Table D.1 and information sources are detailed in Appendix G.

The relatively simple trait matrices used and the low resolution of taxonomic detail available is likely to increase the degree of clustering between taxa than is perhaps biological accurate; this should be borne in mind when interpreting the results of this study. However, as it is the relative differences between agricultural contexts that is of interest, the trait matrices constructed in this study can still provide valid insights into functional change in this novel and challenging context, further simple feeding guild approaches have been used in studies that compare at functional diversity at higher taxonomic levels (such as order or class, see Tscharntke et al. 2008).

4.2.6. Statistical analyses

All analyses were conducted in `R` 3.1.0 (R Development Core Team 2014) unless stated otherwise. Note that while species or family abundance was used to calculate taxonomic and functional diversity metrics the values obtained from trapping methods are only indicators of the actual abundance or activity density of the groups in question and whilst the relationship between trap data and actual population densities is variable among taxa (e.g. for epigeal predatory beetles see Lang 2000) the standardised trapping methods used still allow direct comparisons between contexts indicating real patterns and trends.

Taxonomic metrics (richness, diversity, evenness and composition)

True individual-based rarefaction curves were used to compare species richness between agricultural contexts (Gotelli and Colwell 2001; Buddle et al. 2005) and confidence intervals were derived from multinomial models with 1000 randomisations using the EstimateS software v. 9.1.0 (Colwell 2013). Species diversity was calculated with the Shannon-Weiner index (note that this tends to be correlated with abundance) and species evenness with Pielou's evenness index using the `vegan` package (Oksanen et al. 2013). Change in species composition was assessed using a non-metric multidimensional scaling (NMDS) ordination in the `isoMDS` function within the `MASS` package (Venables and Ripley 2002) (Clarke and Warwick 2001) with a Bray-Curtis dissimilarity measure (Magurran 2009). Communities were standardised to the proportion of the total abundance of individuals at each site and a permutation multivariate analysis of variance using the `ADONIS` function in the `Vegan` package (Oksanen et al. 2013) with 10,000 permutations was used to test for significant differences (Edwards et al. 2014a) using a false discovery rate (FDR) correction for multi-testing in pairwise comparisons between agricultural contexts. Taxonomic metrics were calculated including singletons.

Measuring functional diversity

The `FDind` function (Villéger et al. 2008) was used to calculate four complementary measures of functional diversity: (1) functional richness (FRic), which calculates the volume of functional space that a group of taxa inhabit; (2) functional eveness (FEve), which quantifies how the abundances of taxa are spread across the inhabited functional space; (3) functional divergence (FDiv), which assesses the variations in taxa abundance with respect to the centre of functional space (known as the centre of gravity); and (4) functional specialisation (FSpe), which describes how functionally unique a community is relative to the regional pool. Pair-wise comparisons between agricultural contexts were conducted using linear models and least-squares means, with a FDR correction for multiple-testing, using the `lsmeans` function from the `lsmeans` package (Lenth 2014).

The `FSECchange` function (Mouillot et al. 2013) was used to assess change between paired contexts and figures illustrating functional change were constructed according to Mouillot *et al.* (2013). Functional change figures included the additional measures of functional diversity: (5) functional dispersion(FDis); which assesses the deviation of taxa trait values from the centre of functional space filled by the community; (6) functional identity (FIde), which shows how change in taxa abundance changes the mean trait value of species communities; (7) functional entropy (FEnt); which reflect the sum of pairwise functional distances between species (using Rao index); and (8) functional originality (FOri), which quantify how change in taxa abundance modify the functional redundancy between species. Traits were given equal weighting and transformed into synthetic coordinate axes using principal coordinate analysis (PcOA) (Villéger et al. 2008; Laliberté and Legendre 2010) and taxa were weighted by relative abundance in calculations of functional diversity measures. As traits were a mixture of binary, ordinal and continuous variables and to deal with correlations between them, traits were transformed into a distance matrix using a Gower distance measure then ordinated using PcOA. Two PCoA axes were used to calculate functional measures and the goodness-of-fit (GOF) statistic, an approximation of the proportion of variance explained by PcOA axes (Krzanowski 2000).The GOF of the regional trait space (excluding negative eigenvalues) was 51.6% for Coleoptera and 53.6% for Hymenoptera, and including additional axes did not substantially increase GOF. FSECchange metrics are limited to the context level and as such statistical significance is not available (this is generated at the site level) for the additional metrics.

As functional diversity measures can be skewed by, for example, rare taxa that have little functional relationship with agricultural habitats, but, by chance occasionally stray into them, singletons can artificially elevate functional diversity assessments, obscuring patterns between habitats (Barlow et al. 2006; Edwards et al. 2013). The effect of rare species on functional diversity metrics was explored by excluding any singletons (taxa with a single individual) for each agricultural contexts (Appendix J) and comparing results to the full dataset. Removing singletons only had a notable effect on FRic as the inclusion of rare species can greatly alter the volume of trait space occupied by a group of taxa and, unlike the other functional diversity metrics, it is not weighted by taxa abundance.

Observed and expected functional diversity within agricultural contexts

To determine whether agricultural contexts exhibited a more or less functionally complementary set of taxa, the observed level of functional diversity was compared to that of the regional pool for the four functional diversity components of FRic, FEve, FDiv and FSpe (Flynn et al. 2009). To do this the standardised effect size (SES) was calculated per site as $\left[\frac{(observed\ FD - mean\ expected\ FD\ )}{standard\ deviation\ of\ expected\ FD}\right]$ for 1000 iterations of expected values from random communities generated using an independent-swap algorithm (which maintains species frequency occurrence and richness) (Edwards et al. 2013) from the `randomizeMatrix` function in the package `picante` (Kembel et al. 2010). One-sample t-tests with $\mu = 0$ were used to determine whether the SES of each functional diversity metric was significantly different from zero.

Species composition and variation in functional traits

RLQ analysis (ade4 package, Chessel et al. 2004) was used to investigate how landscape characters (proportion of local natural habitat within 1 km and field area) may filter particular species (or family) traits. RLQ analysis uses three data matrices: R is $site \times environment$; L is $site \times species$; and Q is $species \times trait$ (Dolédec et al. 1996). Species abundances in L were converted to relative abundances and a centered chi-distance matrix (correspondence analysis) was created from it. Then an $R'LQ$ matrix was constructed by centering and standardising the columns of R and Q, taking the centre weighted average, where weights were row weights and species weights respectively, and the weighted standard deviation was calculated. Next, V was calculated as the product of $R'LQ$, the correlation matrix between the environmental traits and the species traits mediated by species abundances, and the cross-product matrix of V was calculated to give Z. Eigen decomposition of Z using the `eigen()` function gave species trait loadings as eigenvectors (plotted as arrows) and environmental trait scores as eigen values as per PCA (plotted as points) (Dolédec et al. 1996). The environmental variables used in RLQ analyses were derived from Chapter 3 where methods are detailed.

4.3. Results

Across all agricultural contexts 1401 individual epigeal Coleoptera (>0.4 mm length, from henceforth referred to as “Coleoptera” or “beetles”) of 84 species and 575 individual flower-visiting Hymenoptera (henceforth referred to as “Hymenoptera”) of 36 families were recorded, excluding singletons this fell to 1333 individuals of 55 species for Coleoptera and 496 individuals of 20 families for Hymenoptera.

4.3.1. Coleoptera

Taxonomic metrics (richness, diversity, evenness and composition)

Beetle catches were numerically dominated by tenebrionid (26.4 - 52.6%, Figure 4.3) and meloidid beetles (10.3 – 42.1%), both in the superfamily Tenebrionoidea. Scarabids (3.3 – 18.6%), curculionids (3.3 – 11.6%) and chrysomelids (1.7 – 10.3%) were commonly caught (Figure 4.3), but typically in lower numbers than tenebrionids and meloidids, beetles of other families were comparatively rare. Small fields in high natural habitat landscapes had lower Coleoptera abundance at both site ($P < 0.05$, Table 4.1) and context levels compared to all other contexts whereas large fields in high natural habitat landscapes accumulated the greatest number of individuals, but with considerable variability between sites (Figure 4.4, Table 4.1). Small fields in high natural habitat landscapes also had lower species richness at the context level compared to all other contexts, and, at the site level species richness and diversity were lower compared to large fields in high natural habitat landscapes and small fields in low natural habitat contexts ($P < 0.05$, Table 4.1). However, individual-based rarefaction curves (Figure 4.4) showed that the accumulation of individuals for small fields in high natural habitat landscapes and large fields in low natural habitat landscapes was insufficient to reach a relatively asymptotic level of species richness suggesting comparisons of species richness between contexts should be treated with caution. In the absence of singletons (Appendix J Figure J.2) all contexts reach relatively asymptotic levels of species richness (Table 4.1). Large fields in high natural habitat landscapes had significantly lower species evenness compared to small fields in low natural habitat landscapes (Table 4.1). Mean evenness was lowest in large fields in low natural habitat landscapes, but with relatively high variability between sites (Table 4.1).

Species composition did not significantly differ between contexts (Figure 4.5, Appendix I Table I.2).

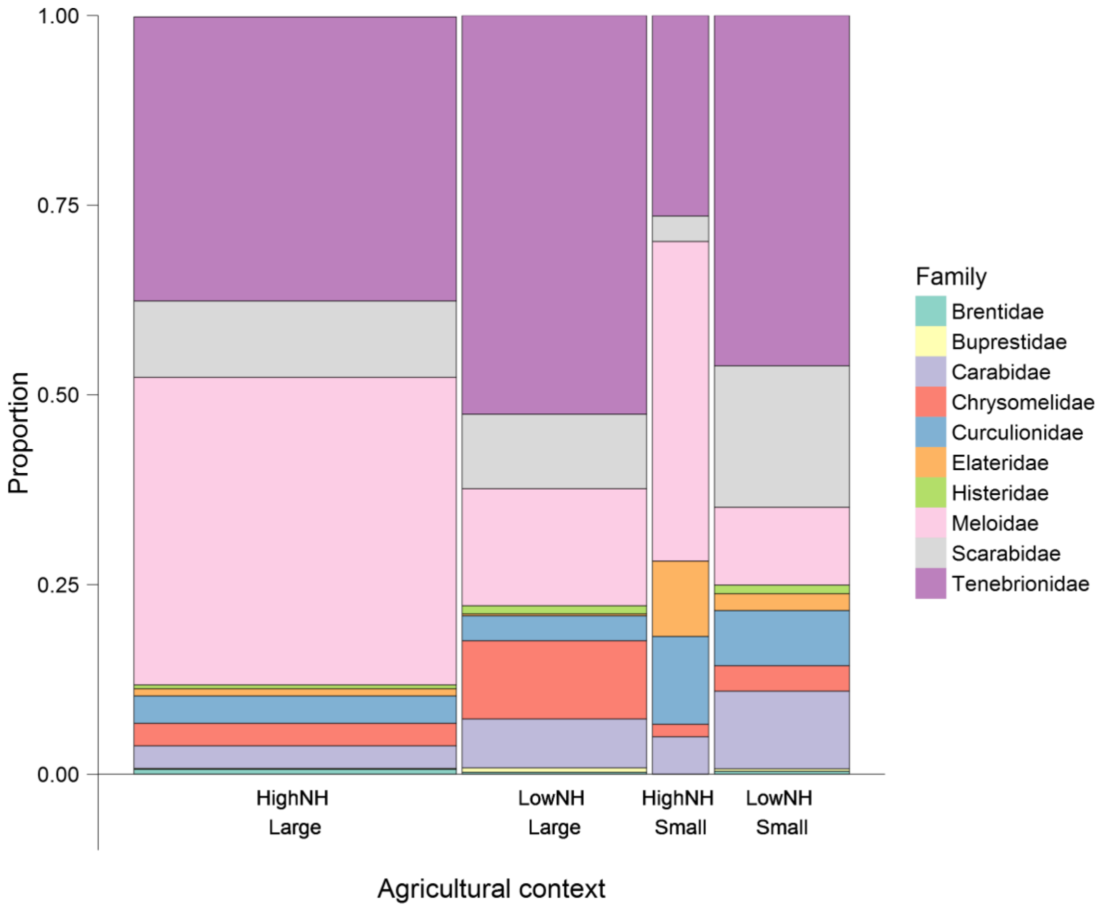


Figure 4.3 Proportional contribution of coleopteran families to the total catch from each agricultural context. Bar width is scaled to the total abundance of individuals caught in each context (see Table 4.1).

Table 4.1 Summary of taxonomic level coleopteran species metrics between agricultural contexts. At the context level richness confidence intervals are calculated using a multinomial model with 1000 randomisations. Diversity is measured using the Shannon index and evenness using Pielou's index. NH = natural habitat with 1000m, large and small refer to field area. Species richness metrics are presented with and without (NS) singletons.

Metric	**Agricultural context**			
	Large HighNH	**Large LowNH**	**Small HighNH**	**Small LowNH**
Context Level:				
Abundance	638	369	121	273
Species richness (SD)	52 ± 3.32	54 ± 4.64	30 ± 4.51	49 ± 2.57
Species richness 95% CIs	45.48 - 58.52	44.9 - 63.1	21.15 - 38.85	43.96 - 54.04
NS species richness (SD)	36 ± 0.50	30 ± 0.46	12 ± 0.30	32 ± 0.44
NS species richness 95% CIs	35.01 - 36.99	29.09 - 30.91	11.41 - 12.59	31.13 - 32.87
Species diversity	2.84	2.73	2.85	3.24
Species evenness	0.72	0.69	0.84	0.83
Site Level:				
Abundance (SD)	127.6 ± 57.16^{a}	73.80 ± 31.57^{a}	24.20 ± 17.09^{b}	54.60 ± 15.29^{a}
Species richness (SD)	22.00 ± 3.22^{a}	16.80 ± 7.62	8.60 ± 2.8^{b}	18.60 ± 3.72^{a}
NS species richness (SD)	19.00 ± 4.20^{a}	12.0 ± 4.43	5.40 ± 1.36^{b}	16.00 ± 2.76^{a}
Species diversity (SD)	2.31 ± 0.16^{a}	1.92 ± 0.93	1.71 ± 0.32^{b}	2.52 ± 0.29^{a}
Species evenness (SD)	0.75 ± 0.02^{a}	0.68 ± 0.26	0.82 ± 0.10	0.87 ± 0.05^{b}

Superscripts (^{a,b}) represent FDR corrected pairwise differences at $P \leq 0.05$.

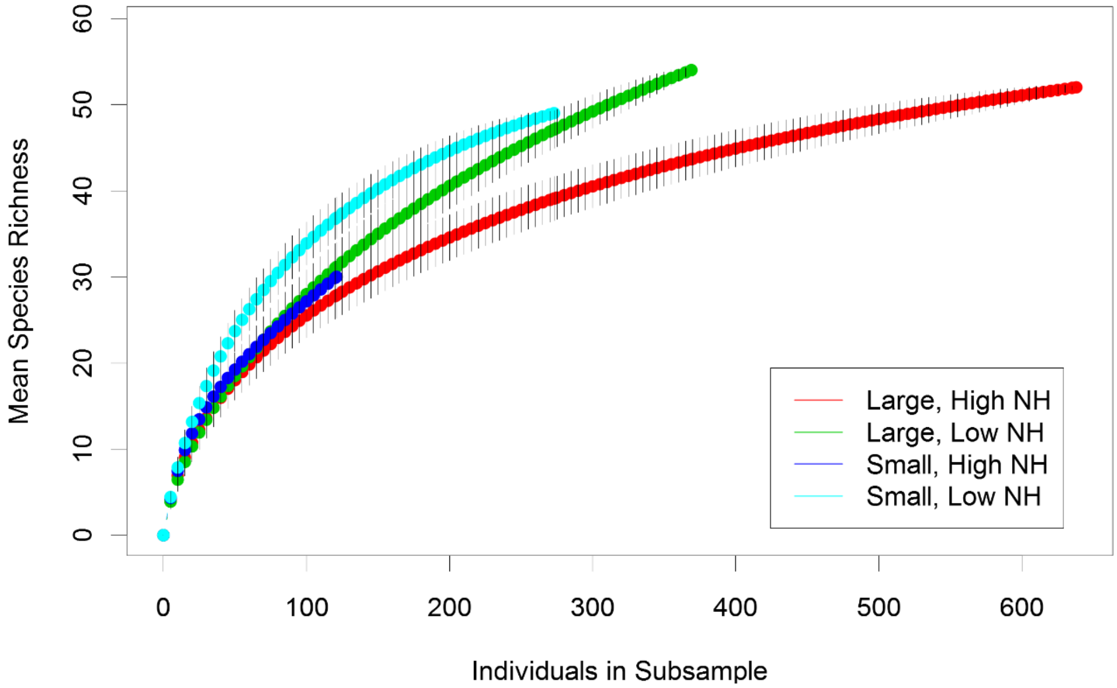


Figure 4.4 Observed Coleoptera species richness, calculated from sample-based rarefaction curves, shown between agricultural contexts. NH = natural habitat with 1000m, large and small refer to field area. Bars represent the standard error of iterations. Rarefaction with singleton species removed is presented in Appendix J Figure J.2.

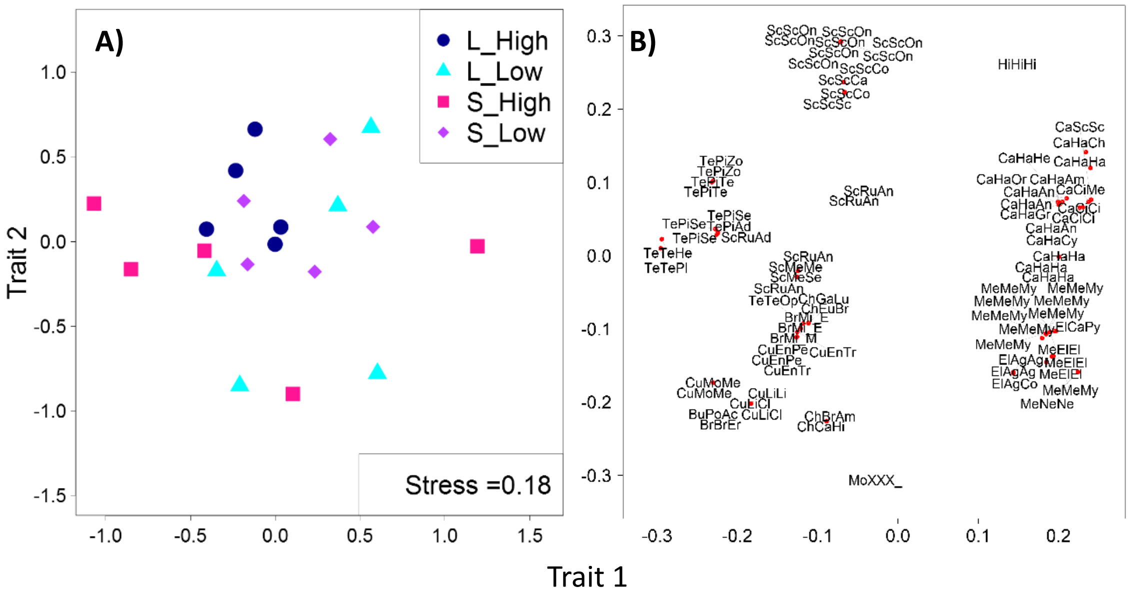


Figure 4.5 A) Non-metric multidimensional scaling (NMDS) ordination of Coleoptera community assemblages and B) Principal co-ordinates analysis (PcOA) on a Gower dissimilarity matrix of Coleoptera species functional traits. A) shows no significant differences between agricultural contexts (L = large field, S = small field, High & Low refer to local natural habitat within 1000 m of the fields). See Appendix I Table I.2 for statistical analysis. B) shows how species are distributed in functional traits space. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table C.1. Major families are Ca = Carabidae, Cu = Curculionidae, Me = Meloidae, Sc = Scarabidae and Te = Tenebrionidae. In both A) and B) the regional species pool is used.

Functional diversity metrics

Functional and divergence (FDiv) and specialisation (FSpe) did not differ between agricultural contexts (Figure 4.6., Figure 4.10dg, Figure 4.12-13dg, Table 4.2). Functional richness (FRic) was significantly lower in small fields in high natural habitat landscapes compared to all other contexts (Table 4.2, Figure 4.6, Figure 4.10b, Figure 4.12-13b) and removing singletons from the analysis increased the size of this effect (see Appendix J1 Figure J.9b, Figure J.11-12b). Before correcting for multiple testing functional evenness (FEve) was significantly lower for large fields in high compared to low natural landscapes (Figure 4.10c), however this became non-significant after a FDR correction was applied (Table 4.2). The frequencies of traits per context are illustrated in Appendix I Figure I.1.

Among all contexts FDiv and FSpe were not significantly different than expected from random community assemblages (Figure 4.7, Table 4.3). When singleton species were excluded from standardised effect-size calculations for FRic (this metric is not abundance weighted therefore singletons exert a disproportionately strong effect) small fields in high natural habitat landscapes had significantly lower functional richness than expected, whereas for small fields in low natural habitat landscapes it was significantly higher than expected (Table 4.3). FEve was significantly lower than expected for large fields in high natural habitat landscapes but other contexts showed no significant difference to a random community assemblage (Figure 4.7, Table 4.3).

Lower values of FRic demonstrated that small low natural habitat fields showed a reduced range of traits or trait combinations compared to other contexts. Lower values of FEve suggest abundances are less evenly shared between species (some species or traits are becoming more dominant) or variability of the distance between species in functional trait space is higher for large fields in high natural habitat contexts. No difference between contexts for FSpe and FDiv suggests that there was little change between the balance of specialists vs. generalists (FSpe) and that species abundances were distributed across functional space in a similar manner (FDiv).

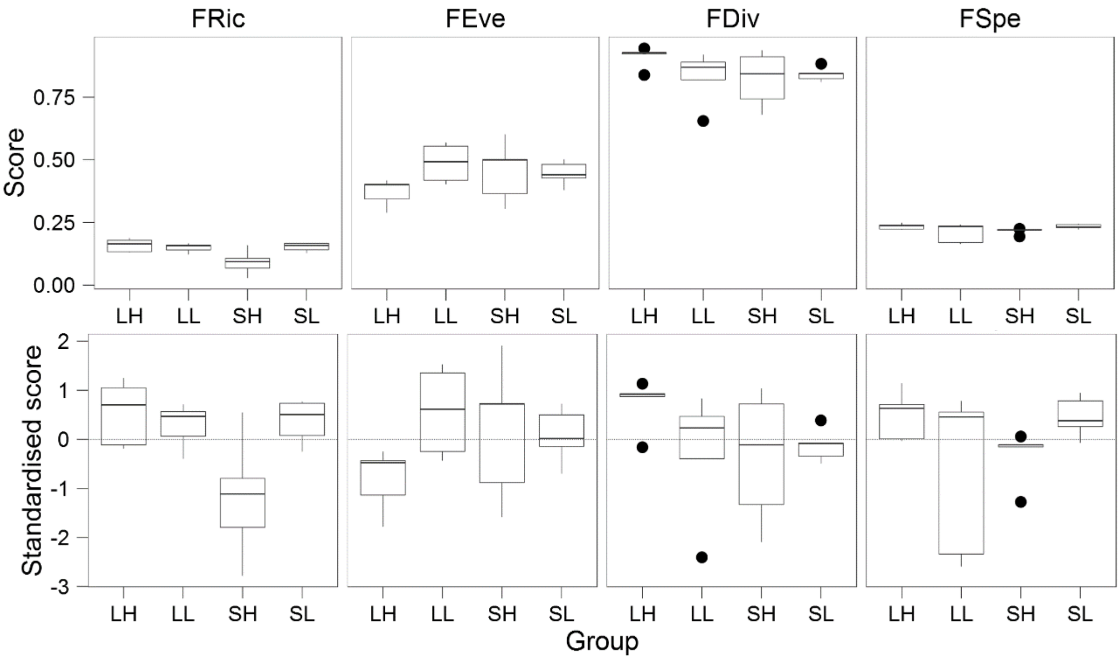


Figure 4.6 Boxplots for observed scores for Coleoptera functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LH = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SL = small field, low natural habitat). Top panels are raw scores and the lower panels are standardised (centred and scaled).

Table 4.2 Pairwise comparisons of observed functional metric scores for coleopteran species between agricultural contexts using two-tailed t-tests. A false discovery rate correction (FDR p) is applied for multiple testing with untransformed p-values also presented (p). Degrees of freedom in all cases was 9. High/Low = refers to local natural habitat and Large/Small = refers to field area. Functional metrics are FDiv = diversity, FEve = eveness, FRic = richness, FRic_NS = richness with the exclusion of singleton species, and FSpe = specialisation.

Contrasts	Metric	Estimate	t	p	FDR p
LargeHigh vs. LargeLow	FDiv	0.081	1.610	0.127	0.363
LargeHigh vs. SmallHigh	FDiv	0.089	1.772	0.095	0.363
LargeHigh vs. SmallLow	FDiv	0.070	1.397	0.182	0.363
LargeLow vs. SmallHigh	FDiv	0.008	0.161	0.874	0.874
LargeLow vs. SmallLow	FDiv	-0.011	-0.214	0.833	0.874
SmallHigh vs. SmallLow	FDiv	-0.019	-0.375	0.712	0.874
LargeHigh vs. LargeLow	FEve	-0.117	-2.336	**0.033**	0.197
LargeHigh vs. SmallHigh	FEve	-0.084	-1.683	0.112	0.299
LargeHigh vs. SmallLow	FEve	-0.076	-1.514	0.150	0.299
LargeLow vs. SmallHigh	FEve	0.033	0.653	0.523	0.628
LargeLow vs. SmallLow	FEve	0.041	0.822	0.423	0.628
SmallHigh vs. SmallLow	FEve	0.008	0.169	0.868	0.868
LargeHigh vs. LargeLow	FRic	0.010	0.529	0.604	0.864
LargeHigh vs. SmallHigh	FRic	0.068	3.567	**0.003**	**0.015**
LargeHigh vs. SmallLow	FRic	0.007	0.354	0.728	0.864
LargeLow vs. SmallHigh	FRic	0.058	3.038	**0.008**	**0.016**
LargeLow vs. SmallLow	FRic	-0.003	-0.175	0.864	0.864
SmallHigh vs. SmallLow	FRic	-0.061	-3.212	**0.005**	**0.016**

Contrasts	Metric	Estimate	t	p	FDR p
LargeHigh vs. LargeLow	FRic_NS	0.026	1.538	0.144	0.172
LargeHigh vs. SmallHigh	FRic_NS	0.098	5.774	**0.000**	**0.000**
LargeHigh vs. SmallLow	FRic_NS	0.000	-0.023	0.982	0.982
LargeLow vs. SmallHigh	FRic_NS	0.072	4.236	**0.001**	**0.001**
LargeLow vs. SmallLow	FRic_NS	-0.026	-1.561	0.138	0.172
SmallHigh vs. SmallLow	FRic_NS	-0.098	-5.797	**0.000**	**0.000**
LargeHigh vs. LargeLow	FSpe	0.026	1.880	0.079	0.260
LargeHigh vs. SmallHigh	FSpe	0.019	1.361	0.192	0.315
LargeHigh vs. SmallLow	FSpe	0.001	0.055	0.957	0.957
LargeLow vs. SmallHigh	FSpe	-0.007	-0.518	0.612	0.734
LargeLow vs. SmallLow	FSpe	-0.025	-1.825	0.087	0.260
SmallHigh vs. SmallLow	FSpe	-0.018	-1.307	0.210	0.315

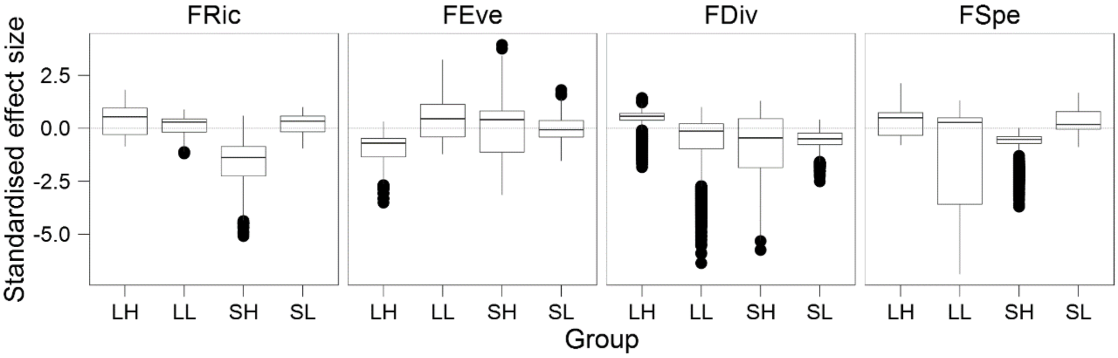


Figure 4.7 Boxplots of standardised effect size (SES) for Coleoptera functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). SES = (Observed - mean Expected) / SD Expected. SES is calculated from 1000 randomisations of the regional pool of species, where species frequency of occurrences and species richness are maintained. Values differing from zero indicate that the species pool of an agricultural context is different to that of the regional species pool.

Table 4.3 Observed and expected Coleoptera species functional metrics. Mean standardised effect (SES) of functional diversity metrics in each agricultural context calculated from 1000 randomisations (independent swap) of the regional species pool. One-sample t-tests with μ = 0 were used to determine if the SES of each metric was significantly different to zero. See Table 4.2 for abbreviations.

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FRic	0.145	0.038	0.159	0.373	0.634	-0.493	1.240	1.226	0.303
LargeLow	FRic			0.149	0.103	0.435	-0.483	0.690	0.533	0.625
SmallHigh	FRic			0.091	-1.446	1.205	-3.054	0.161	-2.483	0.069
SmallLow	FRic			0.152	0.193	0.428	-0.386	0.771	0.968	0.425
LargeHigh	FRic_ES	0.127	0.045	0.144	0.375	0.622	-0.476	1.226	1.254	0.294
LargeLow	FRic_ES			0.118	-0.216	0.751	-1.236	0.803	-0.563	0.613
SmallHigh	FRic_ES			0.046	-1.844	0.604	-2.538	-1.149	-7.335	**0.002**
SmallLow	FRic_ES			0.144	0.384	0.141	0.210	0.557	6.288	**0.006**
LargeHigh	FEve	0.452	0.091	0.370	-0.921	0.602	-1.685	-0.157	-3.378	**0.035**
LargeLow	FEve			0.487	0.416	0.821	-0.662	1.494	1.050	0.392
SmallHigh	FEve			0.455	0.042	1.253	-1.645	1.730	0.056	0.828
SmallLow	FEve			0.446	-0.055	0.526	-0.730	0.621	-0.259	0.613

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FDiv	0.881	0.081	0.912	0.382	0.521	-0.296	1.060	1.664	0.232
LargeLow	FDiv			0.831	-0.675	1.287	-2.368	1.018	-1.067	0.363
SmallHigh	FDiv			0.823	-0.781	1.345	-2.547	0.985	-1.190	0.314
SmallLow	FDiv			0.842	-0.535	0.426	-0.976	-0.093	-3.209	0.067
LargeHigh	FSpe	0.229	0.017	0.235	0.339	0.646	-0.537	1.216	1.081	0.357
LargeLow	FSpe			0.209	-1.245	2.169	-4.206	1.716	-1.166	0.310
SmallHigh	FSpe			0.216	-0.808	0.710	-1.758	0.142	-2.358	0.082
SmallLow	FSpe			0.234	0.293	0.531	-0.425	1.011	1.140	0.341

Species locations in PcOA functional trait space (labelled to subfamily) are presented to aid interpretation of the figures illustrating functional differences between contexts. Feeding behaviours, for Figures 4.8-4.12, were generally distributed in functional trait space as follows, trait 1 (x-axis) split larval predators (negative) from larval phytophages (positive) and trait 2 (y-axis) split adult predators, detritivores or scavengers (positive) from adult phytophages (negative). When comparing between small and large fields or high and low natural habitat landscapes only (Figure 4.16) species associations with trait 1 are flipped (Figure 4.5B). Interpretation is confirmed by the RLQ analysis in which axes 1 and 2 explained 75.1 and 17.1% of the total variation in environmental variables and in species functional traits, respectively (Figure 4.17). Axis 1 was explained by larval phytophages and larvae found in roots (positive), and larval parasitoids, larval predators and adult pollen and nectar feeders (negative). The proportion of natural habitat in a landscape was negatively associated with axis 1 (leaf-litter also co-loaded onto the same environmental PCA axis but positively) as were vegetation cover and distance to water. Axis 2 was explained by phytophagous adults (positive) and adult and larval detrivores or coprophages and adult scavengers (negative). Field size was positively associated with axis 2, field floral area and fallow negatively co-loaded onto the same environmental PCA axis (PCA axis entered as an environmental predictor in the RLQ analysis) with field size.

Regarding the additional functional diversity metrics generated by the FSECchange analyses (panels a, e ,f and h in Figure 4.10, Figure 4.12-14), there were no strong differences between contexts for functional dispersion (FDis), entropy (FEnt) and originality (FOri) (maximum differences were 5%, 0.04 and 2% respectively, Figure 4.10efh, Figure 4.12-13efh). This suggests that the dispersion of species abundances from the centre of their communities' functional trait spaces (FDis), the abundance weighted pairwise differences between species (FEnt) and the functional redundancy between species were not strongly affected by land-use intensification at the context level. Functional identity (FIde) for trait 1 showed a positive shift when small fields in high natural habitat landscapes were compared to other contexts (range

10 - 22%), in particular small-fields in low natural habitat landscapes. This reflects that the proportional abundance of tenebrionids (larval phytophages) was relatively low and elaterids (potential larval predators) and meloidids (larval predators) relatively high in small fields in high natural habitat landscapes compared to the other contexts (Figure 4.3). For the same comparison of contexts FIde shifts for trait 2 were also positive but less pronounced (range 3 – 9%). Again the greatest difference was observed between small fields in different landscapes contexts and this was due to the dissimilarities in the relative abundances of scarabids (scavengers or detritivores) vs. elaterids and meloidids, the former having higher relative abundance in low natural habitat landscapes with the remaining higher in high natural habitat landscapes (Figure 4.3). Differences between all functional change metrics for small vs. large fields were relatively low (Figure 4.14A), differences for FDiv (12% drop, Figure 4.14Bd) and FDis (5% drop, Figure 4.14Be) were greater when high vs. low natural habitat landscapes were compared but land-use change still did not appear to exert a particularly strong influence on functional diversity metrics in general. In large compared to small fields, a drop in FDiv suggests that less of the total abundance of the community was supported by the species with the most extreme functional traits, and a drop in FDis suggests that species abundances were less dispersed from the centre of the communities’ abundance-weighted functional trait space.

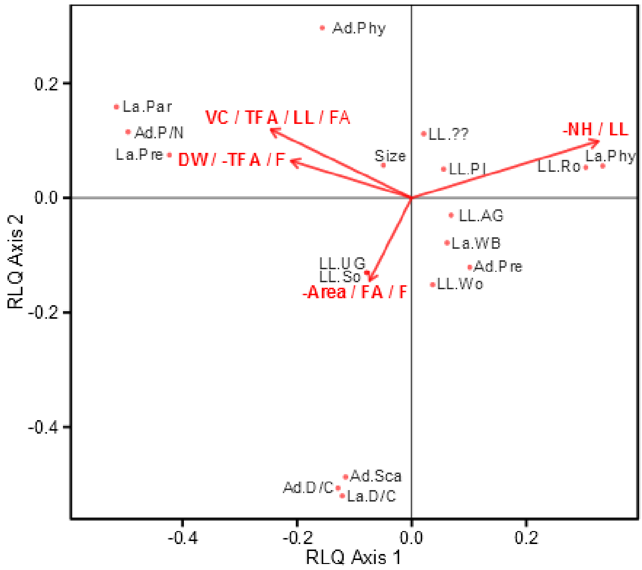


Figure 4.8 RLQ Biplot showing the relationship between Coleoptera functional traits (labelled points) generated from PcOA of a Gower dissimilarity matrix and PCA ordinated environmental variables (red arrows) for the regional species pool. Trait prefixes are Ad = Adult and La = larvae. Trait suffixes are D/C = detritivore and coprophage, Para = parasitic, Phy = phytophage, Pl = on or in plants (not roots or wood); P/N = pollen or nectar feeder, Pre = predator, Ro = associated with plant roots, Sca = scavenger, So = soil dwelling, WB = wood borer, Wo = associated with wood (either living or decomposing), UG = underground, ?? = location unknown. Environmental variables are VC = vegetation cover, TFA = trap floral area; LL = leaf litter; FA = floral area, DW = distance to water, F = fallow, Area = field area and NH = natural habitat within 1km. Environmental variables only loading >0.3 onto environmental PCA axes are shown, labels in bold indicated variables loading >0.5 and negative loadings are indicated with a minus. Axes 1 and 2 explain 75.1 and 17.1% of the total variation in in habitat type and in species functional traits, respectively.

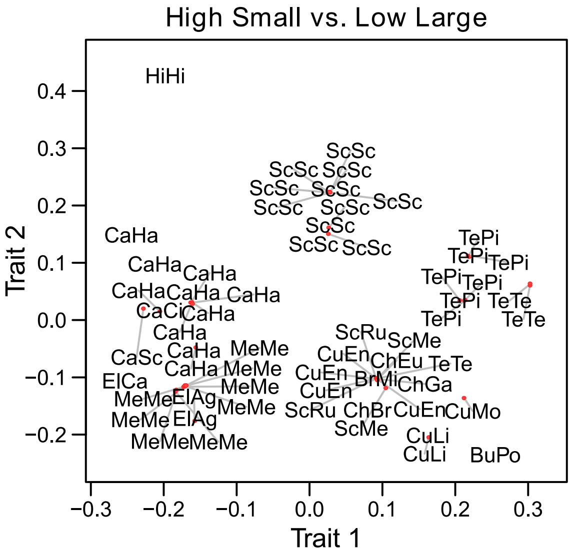


Figure 4.9 Principal co-ordinates analysis (PcOA) on a Gower dissimilarity matrix of Coleoptera species functional traits for the subset of the regional species pool represented by small fields in high natural habitat contexts and large fields in low natural habitat contexts. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table C.1. Major families are Ca = Carabidae, Cu = Curculionidae, Me = Meloidae, Sc = Scarabidae and Te = Tenebrionidae. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

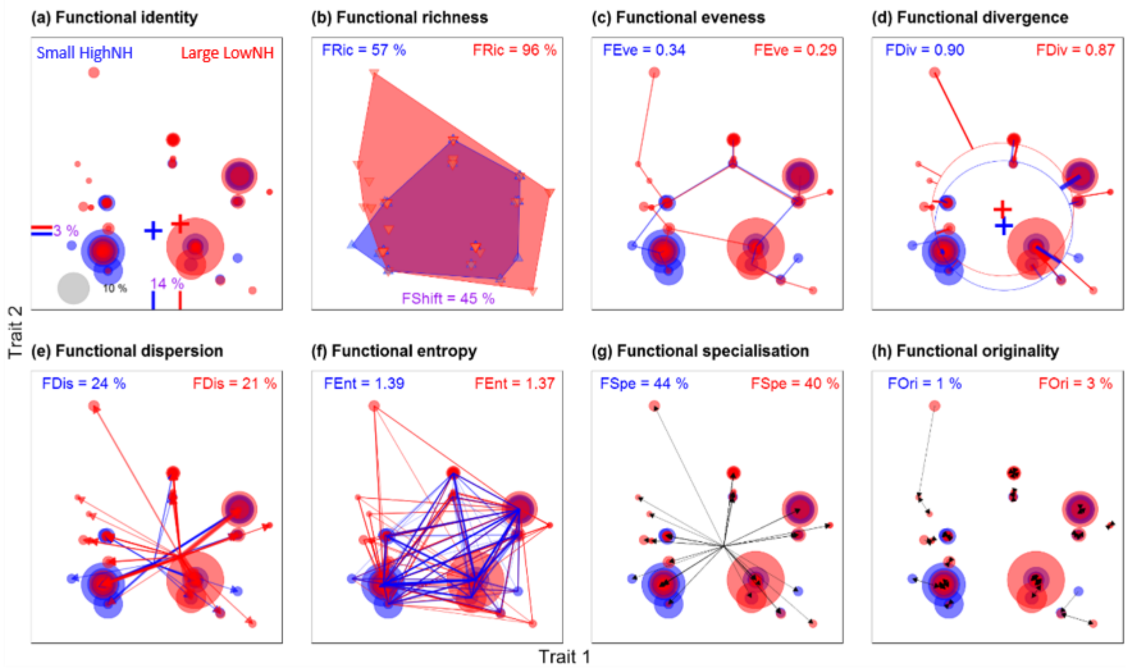


Figure 4.10 Changes in different components of the functional diversity of Coleoptera species communities between small fields with high local natural habitat (blue) vs. large fields with low local natural habitat (red). Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For subfamily locations in trait space see Figure 4.9. Note functional richness (b) is sensitive to rare species also see Appendix J Figure J.9 for the same analyses with singletons (rare species) removed.

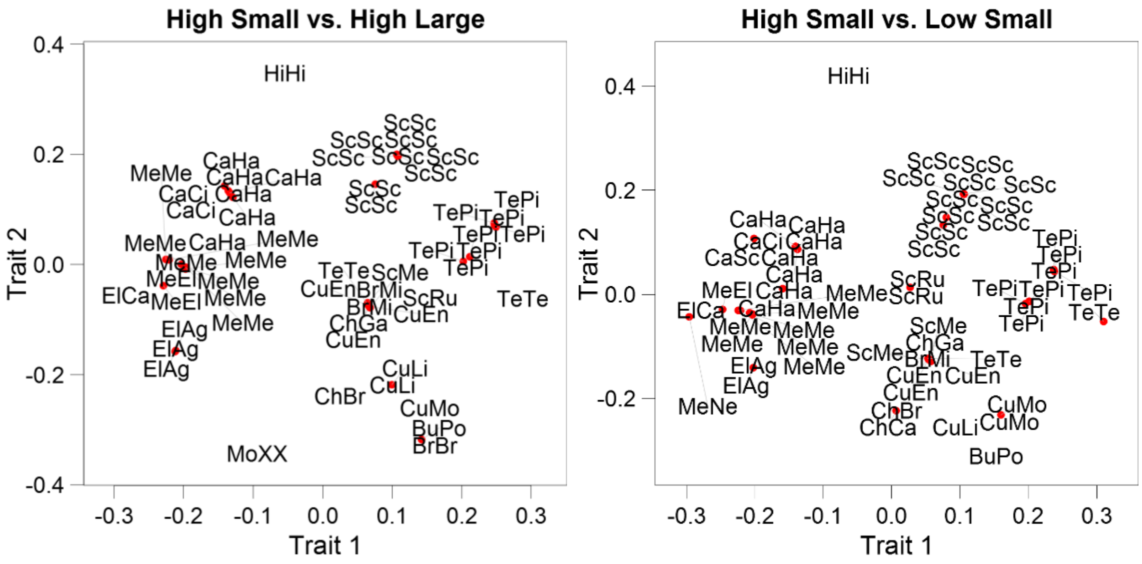


Figure 4.11 PcOA of Coleoptera species functional traits for the subset of the regional pool represented by the figure titles. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table C.1. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

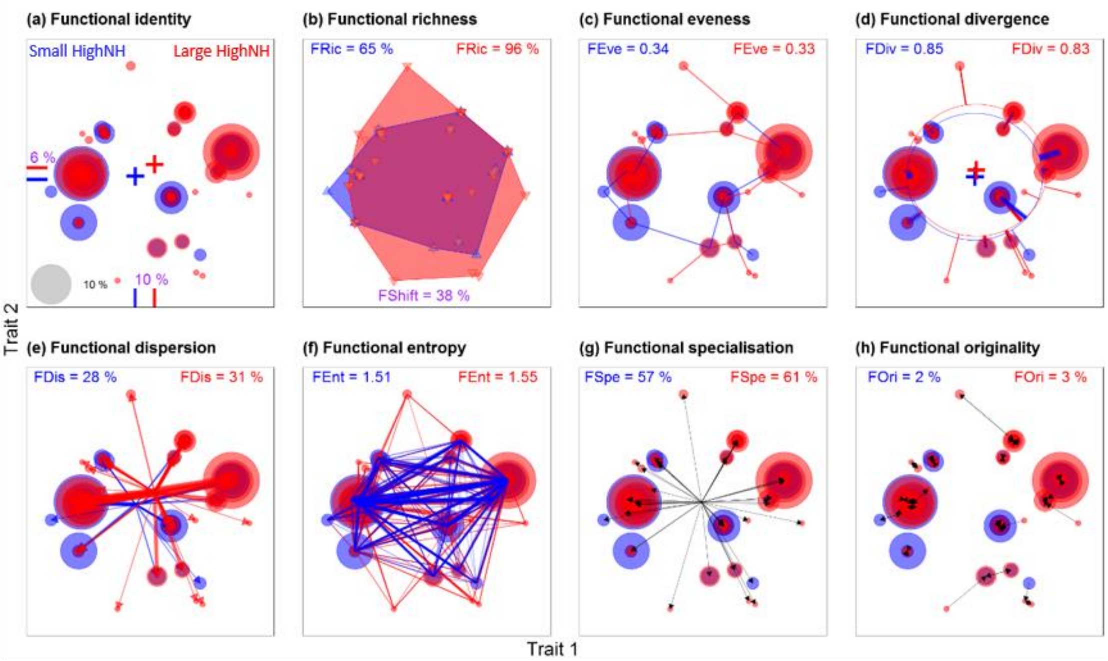


Figure 4.12 Changes in different components of the functional structure of Coleoptera species communities between the subset of species found in small (blue) and large (red) fields in high local natural habitat contexts. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure 4.11. Note functional richness (b) is sensitive to rare species also see Appendix J Figure J.10 for the same analyses with singletons (rare species) removed.

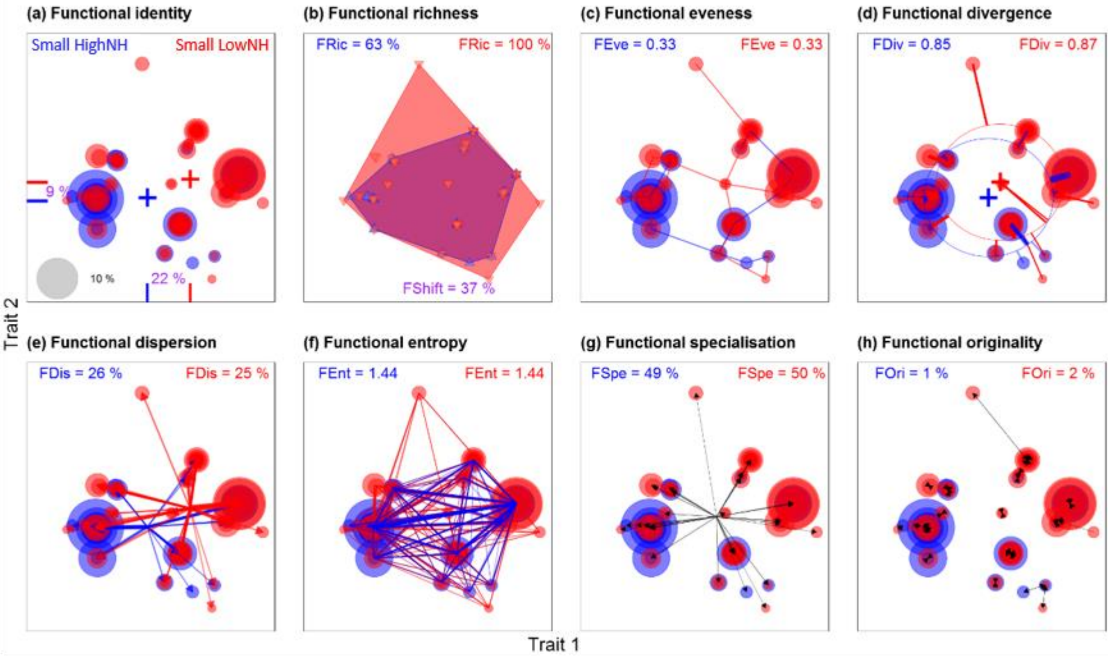
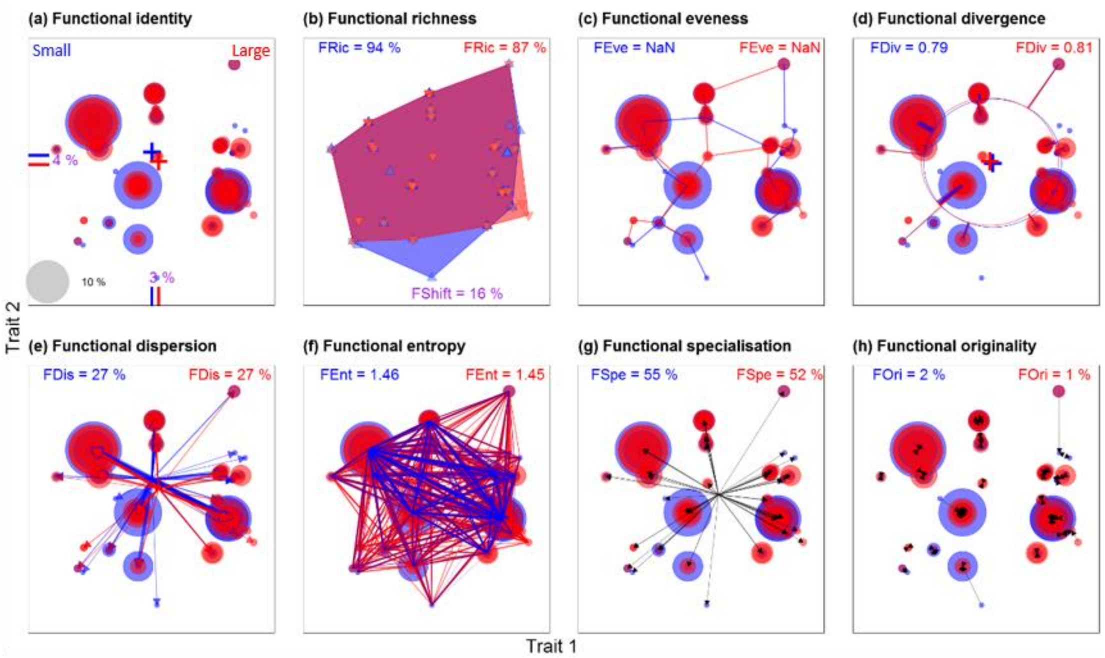


Figure 4.13 Changes in different components of the functional structure of Coleoptera species communities between the subset of species found in small fields in high (blue) and low (red) local natural habitat contexts. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure 4.11. Note functional richness (b) is sensitive to rare species also see Appendix J Figure J.11 for the same analyses with singletons (rare species) removed.

A) Small vs. Large



B) High vs. Low

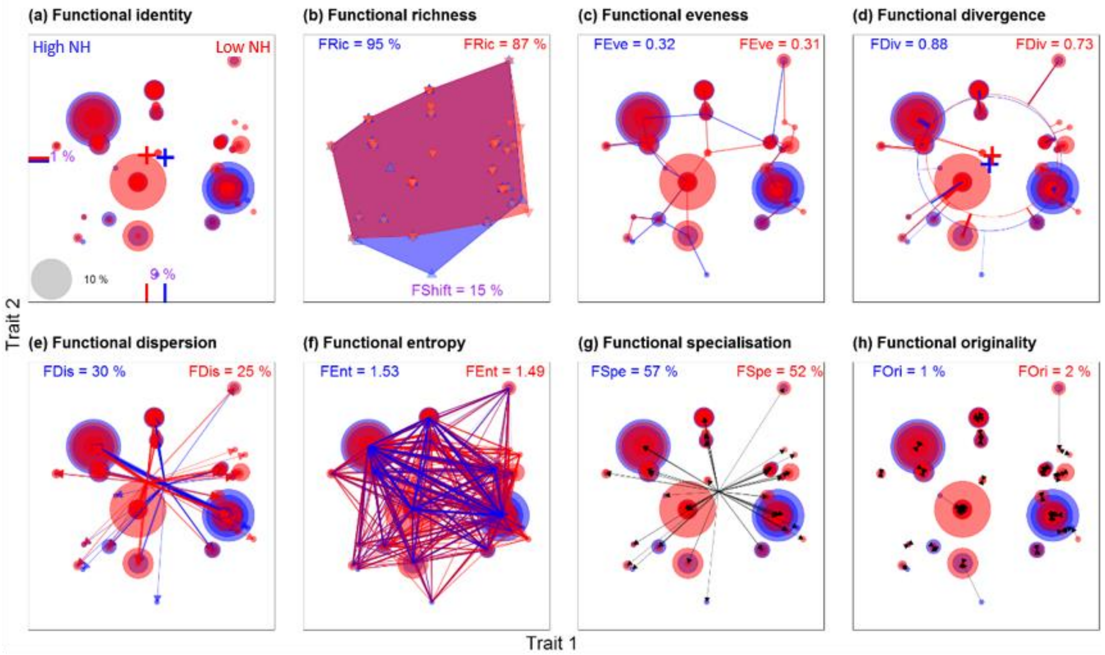


Figure 4.14 Changes in different components of the functional structure of Coleoptera species communities for A) small (blue) vs. large fields (red), and B) high (blue) vs. low (red) local natural habitat. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure 4.5B. Note functional richness (b) is sensitive to rare species also see Appendix J Figure J.12 for the same analyses with singletons (rare species) removed.

4.3.2. Hymenoptera

Taxonomic metrics (richness, diversity, evenness and composition)

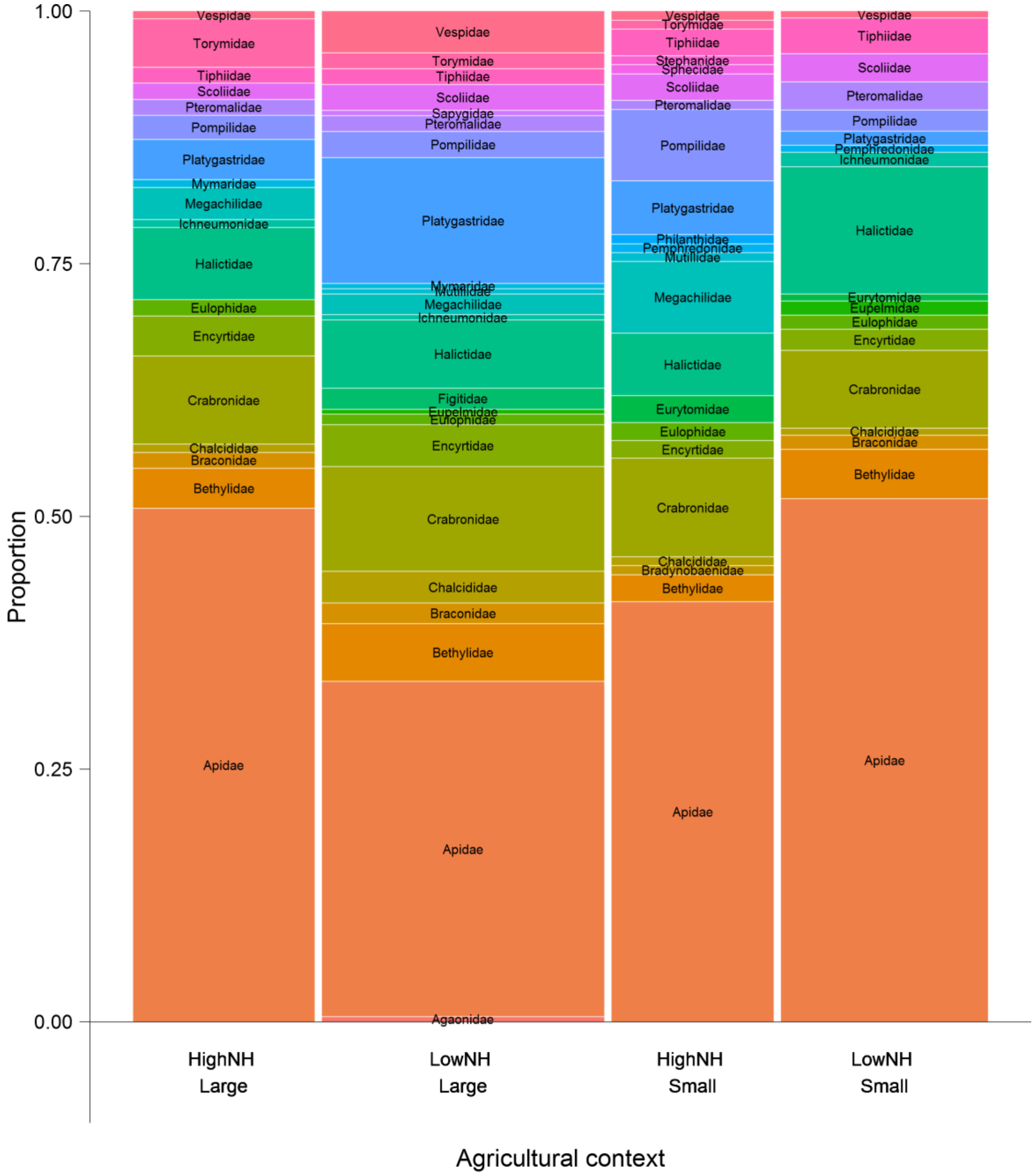


Figure 4.15 Proportional contribution of hymenopteran families to the total catch from each agricultural context. Bar width is scaled to the total abundance of individuals caught in each context (see Table 4.4).

Apidae were the most commonly trapped hymenopteran family (33.2 – 51.7%, Figure 4.15) with the remaining catch composed of a diverse mix of families. Relatively common individuals from families in the non-apidae catch component (Figure 4.15) included bethylids (2.7 - 5.7%), crabronids (7.7% - 10.4%), halictids (6.2 – 12.6%), megachilids (0 - 7.1%), platygastrids (1.4 – 12.4%) and pompilids (2.1 – 7.1%). At the context level, abundance was highest in large fields in low natural habitat landscapes and lowest in small fields in high natural habitat landscapes, however this difference was not significant at the site level (Table 4.4). At the site level family richness was significantly higher in large fields in low natural habitat landscapes compared to large fields in high natural habitat landscapes and small fields in low natural habitat landscapes (P<0.05, Table 4.4), but this was not significant at the context level (Table 4.4, Figure 4.16). Individual based rarefaction curves (Figure 4.16) suggested that family richness for all groups had not reached asymptotic levels and that large fields in low natural habitat landscape accumulated individuals more quickly than other habitats. As with coleoptera, metrics relating to taxonomic or functional richness should be interpreted bearing this in mind. The removal of singletons resulted in asymptotic levels of family richness being reached in all contexts (Appendix J Figure J.15) with large fields in low natural habitat contexts showing significantly higher family richness compared to all other contexts at the context level and to small fields in high and low natural habitat landscapes at the site level (Table 4.4). Also, when singletons were removed small fields in high natural habitat landscapes showed significantly lower family richness than all other contexts at the context level (Table 4.4) however only the contrast with large fields in low natural habitat landscapes was significant at the site level. When contrasted at the site level family diversity and evenness did not significantly differ between contexts (Table 4.4).

Family composition did not significantly differ between contexts (Figure 4.17A, Appendix I Table I.3).

Table 4.4 Summary of taxonomic level hymenopteran family metrics between agricultural contexts. At the context level richness confidence intervals are calculated using a multinomial model with 1000 randomisations. Diversity is measured using the Shannon index and evenness using Pielou's index. NH = natural habitat with 1000m, large and small refer to field area. Species richness metrics are presented with and without (NS) singletons.

Metric	**Agricultural context**			
	Large HighNH	**Large LowNH**	**Small HighNH**	**Small LowNH**
Agricultural Context Level:				
Abundance	126	193	113	143
Family richness (SD)	18 ± 1.21	23 ± 3.17	22 ± 3.41	18 ± 1.20
Family richness 95% CIs	15.63 - 20.37	16.78 - 29.22	15.31 - 28.69	15.63 - 20.36
NS family richness (SD)	13 ± 0.37	16 ± 0.42	11 ± 0.35	13 ± 0.49
NS family richness 95% CIs	12.27 - 13.73	15.18 - 16.82	10.31 - 11.69	12.03 - 13.97
Family diversity	1.92	2.34	2.21	1.83
Family evenness	0.68	0.76	0.73	0.65
Site Level:				
Abundance (SD)	25.20 ± 8.80	38.6 ± 10.31	22.6 ± 7.81	28.6 ± 16.28
Family richness (SD)	8.80 ± 2.71^{a}	12.60 ± 2.06^{b}	9.00 ± 2.83	8.00 ± 2.00^{a}
NS family richness (SD)	8.00 ± 2.28	11.40 ± 1.74^{b}	7.00 ± 2.00^{a}	7.20 ± 1.33^{a}
Family diversity (SD)	1.10 ± 0.65	1.57 ± 0.37	1.28 ± 0.35	1.20 ± 0.36
Family evenness (SD)	0.83 ± 0.19	0.89 ± 0.13	0.90 ± 0.10	0.83 ± 0.13

Superscripts (^{a,b}) represent FDR corrected pairwise differences at $P \leq 0.05$.

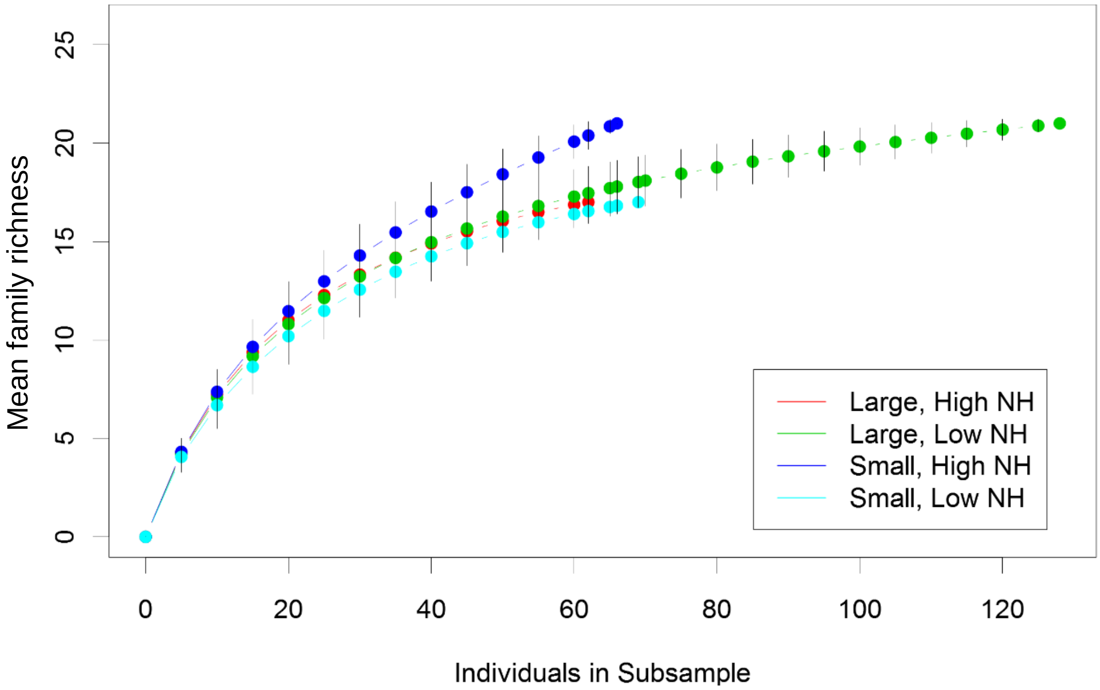


Figure 4.16 Observed Hymenoptera family richness calculated from sample-based rarefaction curves, shown between agricultural contexts. NH = natural habitat with 1000m, large and small refer to field area. Bars represent the standard error of iterations.

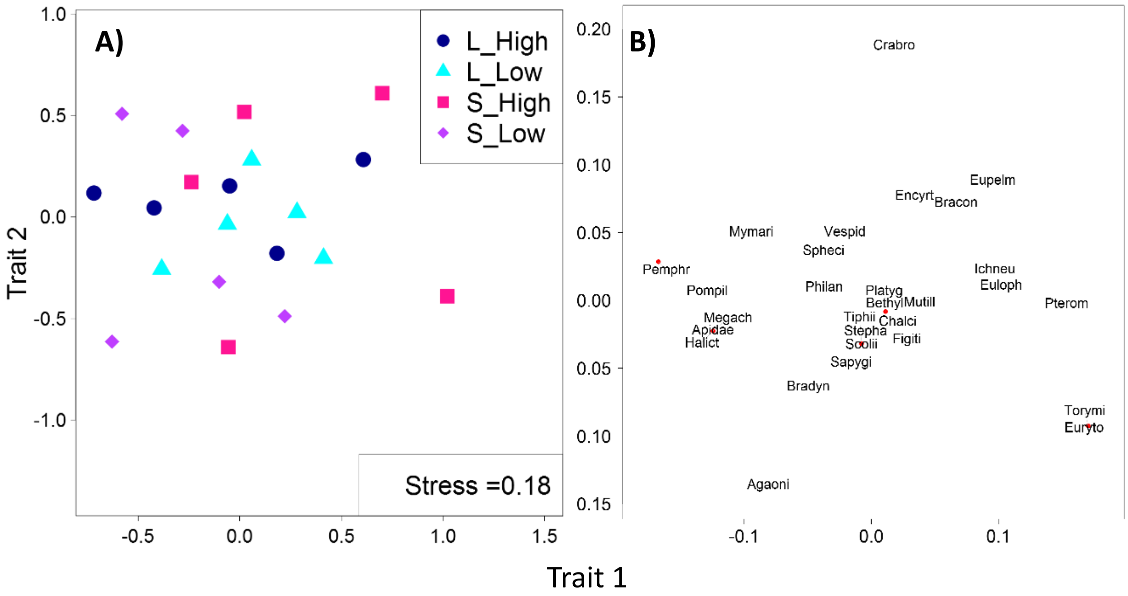


Figure 4.17 A) Non-metric multidimensional scaling (NMDS) ordination space of hymenopteran family community assemblages between agricultural contexts (L = large field, S = small field, High & Low refer to local natural habitat within 1000 m of the fields). See Appendix I Table I.3 for statistical analysis. B) Principal co-ordinates analysis (PcOA) on a gower dissimilarity matrix of Hymenoptera family functional traits for the regional pool. Abbreviations refer to the first six letters of each family, see Appendix C. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

Functional diversity metrics

Functional eveness (FEve), divergence (FDiv), richness (FRic) and specialisation (FSpe), did not differ between agricultural contexts (Figure 4.18, Figure 4.21edbg, Appendix I Table I.1). FEve, FDic and FSpe did not significantly differ from that expected from random community assemblages (P < 0.05, Table 4.5, Figure 4.19). FRic was significantly higher than expected in large fields in low natural habitat landscapes, but only when families were excluded from a context if represented by a single individual. Values for FRic did not differ from expectations in other contexts (P < 0.05, Table 4.5, Figure 4.19).

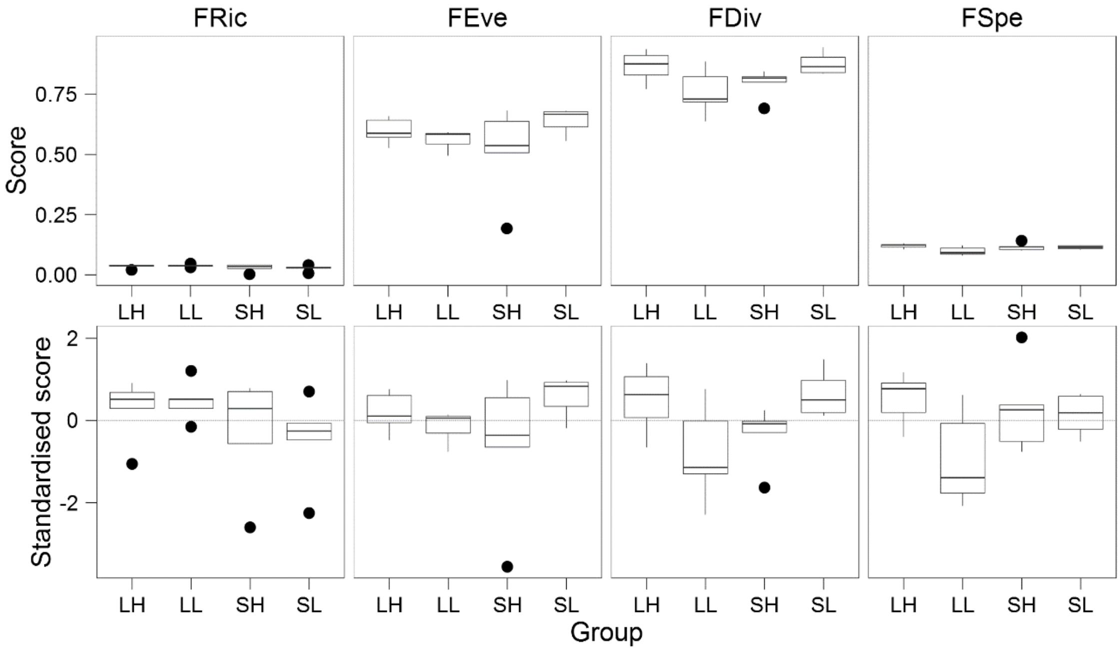


Figure 4.18 Observed scores for Hymenoptera family functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). Top panels are raw scores and the lower panels are standardised (centred and scaled).

Table 4.5 Observed and expected Coleoptera species functional metrics. Mean standardised effect (SES) of functional diversity metrics in each agricultural context calculated from 1000 randomisations (independent swap) of the regional species pool. One-sample t-tests with μ = 0 were used to determine if the SES of each metric was significantly different to zero. See Table 4.2 for abbreviations.

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FRic	0.032	0.011	0.036	0.304	0.722	-0.686	1.294	0.859	0.449
LargeLow	FRic			0.038	0.517	0.463	-0.111	1.145	2.296	0.090
SmallHigh	FRic			0.029	-0.258	1.306	-2.054	1.539	-0.395	0.715
SmallLow	FRic			0.027	-0.455	1.017	-1.851	0.940	-0.902	0.423
LargeHigh	FRic_NS	0.043	0.014	0.050	0.521	0.609	-0.313	1.356	1.749	0.163
LargeLow	FRic_NS			0.052	0.607	0.420	0.036	1.177	2.973	**0.045**
SmallHigh	FRic_NS			0.036	-0.487	1.248	-2.202	1.228	-0.781	0.482
SmallLow	FRic_NS			0.037	-0.444	0.936	-1.726	0.838	-0.952	0.402
LargeHigh	FEve	0.569	0.096	0.597	0.298	0.559	-0.432	1.029	1.166	0.367
LargeLow	FEve			0.560	-0.102	0.441	-0.659	0.455	-0.466	0.545
SmallHigh	FEve			0.511	-0.633	1.915	-3.217	1.951	-0.671	0.545
SmallLow	FEve			0.639	0.753	0.561	0.036	1.469	2.949	0.053
LargeHigh	FDiv	0.815	0.089	0.865	0.569	0.701	-0.381	1.518	1.677	0.179
LargeLow	FDiv			0.759	-0.653	1.023	-2.039	0.733	-1.299	0.271
SmallHigh	FDiv			0.795	-0.238	0.638	-1.099	0.623	-0.752	0.513
SmallLow	FDiv			0.877	0.711	0.502	0.043	1.379	2.976	0.045

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FSpe	0.111	0.015	0.120	0.610	0.591	-0.188	1.408	2.125	0.104
LargeLow	FSpe			0.098	-0.887	1.084	-2.362	0.588	-1.670	0.172
SmallHigh	FSpe			0.116	0.353	1.009	-1.028	1.735	0.711	0.520
SmallLow	FSpe			0.114	0.212	0.470	-0.426	0.851	0.926	0.424

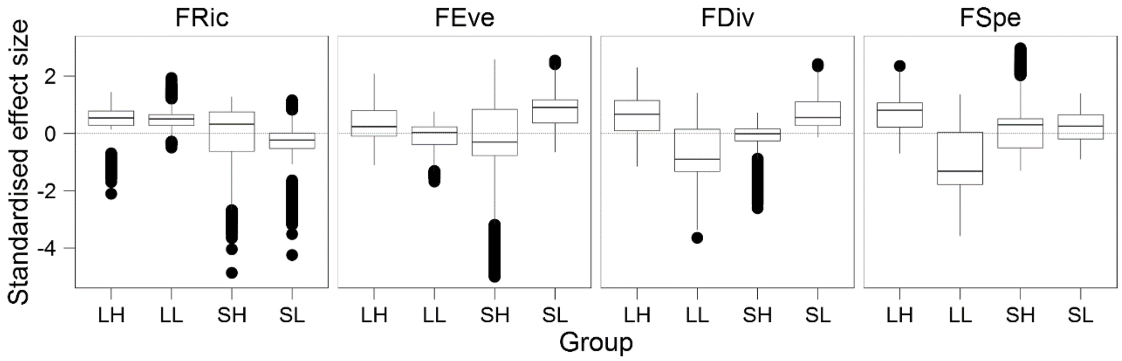


Figure 4.19 Standardised effect size (SES) for Hymenoptera family functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). SES = (Observed – mean Expected) / SD Expected. SES is calculated from 1000 randomisations of the regional pool of species, where species frequency of occurrences and species richness are maintained. Values differing from zero indicate that the species pool of an agricultural context is different to that of the regional species pool.

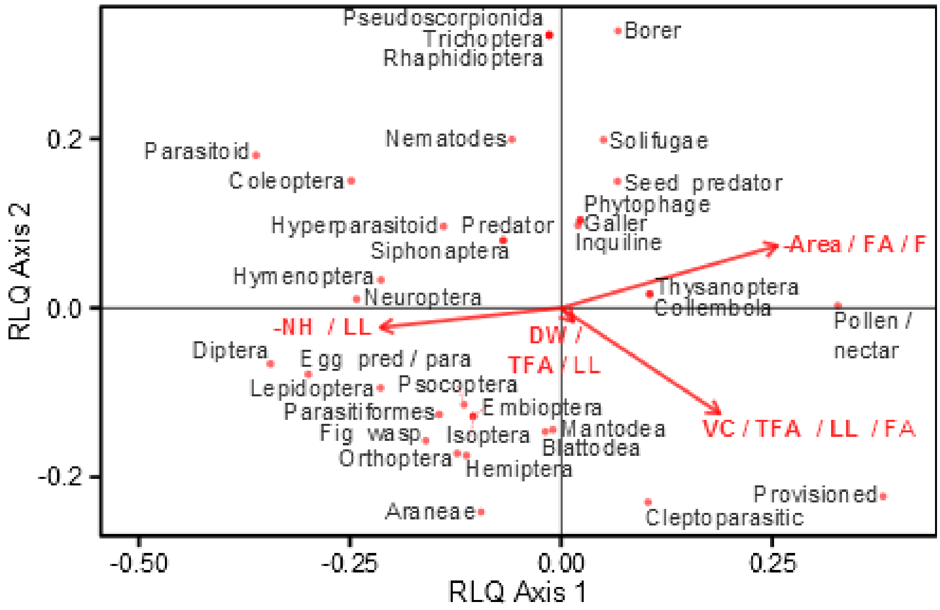
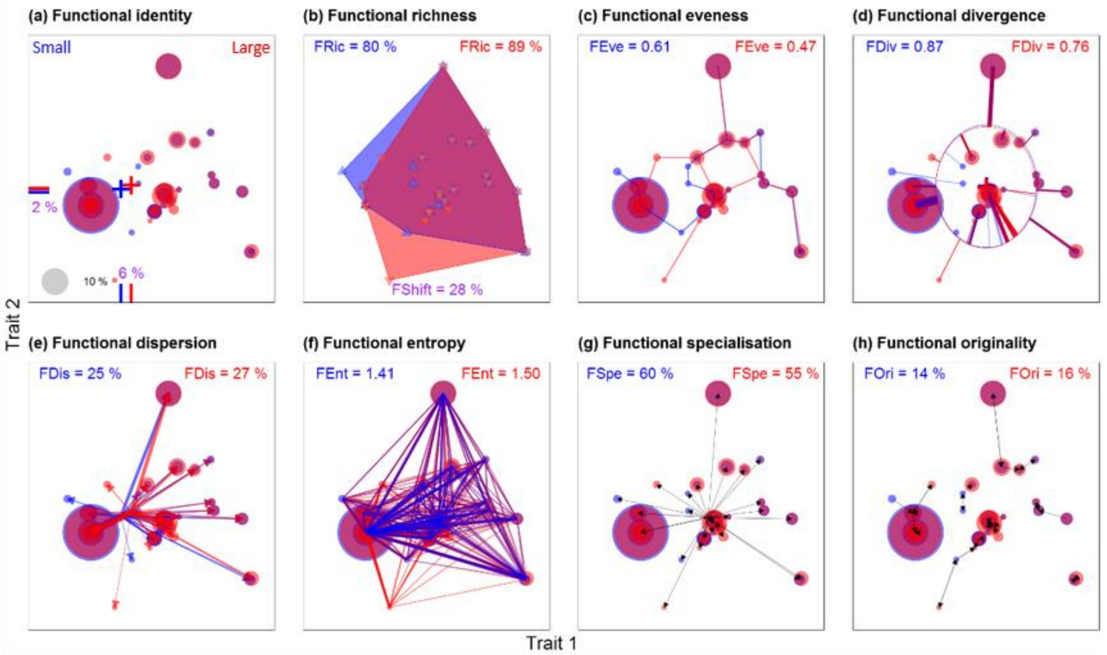


Figure 4.20 RLQ Biplot showing the relationship between Hymenoptera family functional traits (labelled points) generated from PcOA of a gower dissimilarity matrix and PCA ordinated environmental variables (red arrows) for the regional pool. NH = local natural habitat within 1 km, FA = floral area. Environmental variables abbreviations are VC = vegetation cover, TFA = trap floral area; LL = leaf litter; FA = floral area, DW = distance to water, F = fallow, Area = field area and NH = natural habitat within 1km. Environmental variables only loading >0.3 onto environmental PCA axes are shown, labels in bold indicated variables loading >0.5 and negative loadings are indicated with a minus. Axes 1 and 2 explain 75.1 and 17.1% of the total variation in in habitat type and in species functional traits, respectively.

A) Small vs. Large



B) High vs. Low

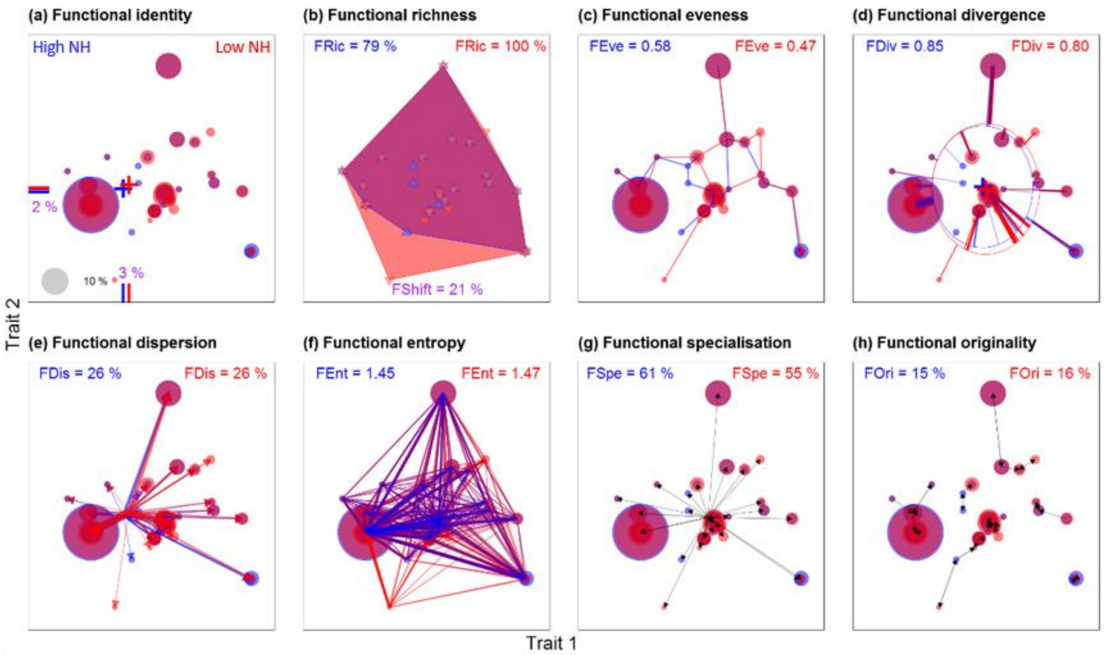


Figure 4.21 Changes in different components of the functional structure of hymenopteran family communities for A) small (blue) vs. large fields (red), and B) high (blue) vs. low (red) local natural habitat. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure 4.17B. Note functional richness (b) is sensitive to rare species also see Appendix J Figure J.20 for the same analyses with singletons (rare species) removed.

As contrasts revealed little difference between the four agricultural contexts (Table 4.4, Table 4.5) FSECchange functional change illustrations are only presented for large vs. small fields and high vs. low natural habitat landscapes (Figure 4.21). Family locations in PcOA functional trait space are presented in Figure 4.17B to aid interpretation of the functional change figures and an RLQ biplot (Figure 4.20) shows the association of traits with environmental variables, note that when comparing PcOA and RLQ plots the loadings between the two are reversed on both axes. Trait 1 (Figure 4.17B) separated families that provisioned larvae with pollen and nectar, and/or provision larvae in general (e.g., Apidae and Pomilidae) from families with parasitoid larvae and trait 2 separated the predatory crabronid wasps from potentially phytophagous parasitoid families (Torymid and Eurotomidae) and fig wasps (Agaonidae). The RLQ analysis (Figure 4.20) showed provisioning of pollen and nectar was associated with small fields (this environmental PCA axis also co-loads field floral area and fallow) and high natural habitat landscapes (this environmental PCA axis also co-loads leaf litter), and that parasitoids, hyperparasitoids, egg predators or egg parasitoids were associated with low-natural habitat landscapes and larger fields. Vegetation cover, trap floral area, leaf litter and field floral area were positively associated with larval provisioning and cleptoparastic larvae and negatively associated with parasitoid, hyperparasitoid and predatory larvae. Seed predators, phytophages and gallers, ecosystem disservices providers, had little correspondence to the proportion of natural habitat in the landscape and a rather weak correspondence with smaller field sizes.

With regard to the FSECchange generated functional change metrics differences between small and large fields (Figure 4.21A) appeared relatively minor for FDis, FEnt, FIde, FOri, FSpe and FRic (see Appendix J Figure J.20Ab for FRic with singletons removed) and there was a modest drop (14%) in FEve (Figure 4.21Ac) and FDiv (11%, Figure 4.21Ad) from small to large fields. Between landscapes FEve (Figure 4.21Bc) showed a modest decline (11%) between high and low natural habitat landscapes, and other metrics showed relatively minor changes (when considering the FRic metric with singletons removed, see Appendix J Figure J.20Bb). A decline in FEve with intensification would suggest abundances are less evenly shared between families or variability of the distance between families in functional trait space is higher. A decline in FDiv suggests that less of the total abundance of the community was supported by the species with the most extreme functional traits.

4.4. Discussion

Small-scale farmlands in the developing world account for a large proportion of agricultural commodity production and provide livelihoods and employment to billions are under-pressure to expand and consolidate (Aldrich et al. 2006; Huang et al. 2011; Collier and Dercon 2013) with poorly understood consequences for ecosystem functioning. This study is one of the first to assess how the functional diversity of agricultural arthropods linked to the regulation of crop production (Coleoptera and Hymenoptera) is affected by the extensification of small-scale agriculture.

Coleopteran species communities were not compositionally distinct between the land-use contexts that reflected the extremes of intensification present in the small-scale farmland of the study area. There was limited evidence for trait filtering (the process by which land-use changes disproportionally affect particular functional traits or trait combinations) and not in the direction hypothesised. Functional richness was lower than expected by chance in the least extensified context and lower compared to more extensified contexts. This suggests that species that are functionally distinct (but not particularly abundant) were added to the beetle community with land-use extensification, such as cicindeline and most harpaline carabids (predators), brentidids (phytophages), ruteline scarabids (phytophages), scarabine scarabids in the tribes Canthonini and Coprini (dung beetles), histerids (scavengers/predators) and pimeliinine tenebrionids in the tribe Sepidiini (phytophages). Functional evenness can be considered complementary to trait dominance (discussed in more detail subsequently) and reduced evenness suggests that trait abundance is becoming dominated by fewer traits (Hillebrand et al. 2008). Functional evenness was lower than expected in large fields in high natural habitat contexts and this is probably because community functioning was more skewed towards a subset of abundant species, in particular meloidids and tenebrionids, compared to a random community drawn from the regional pool. Meloidids and tenebrionids are potential crop pests as they are usually phytophagous in at least one life stage (Keleĭnikova 1963; Allsopp 1979; Gahukar 1991; Durairaj and Ganapathy 2000; Lebesa et al. 2012), therefore this data suggests that increasing land-use intensity promotes traits relating to phytophagy (also suggested by RLQ analysis). However, other components of functional change, such as functional specialisation and divergence showed little response to agricultural extensification suggesting that the balance of specialists vs. generalist species and the total abundance supported by the species with the most extreme functional traits changed little. Measures of taxonomic diversity reflected those of functional diversity; species richness was lowest in small fields in high-nautral habitat contexts and there was little evidence that taxonomic abundance, richness or diversity differed between the higher agricultural extensification contexts. There were substantial differences in overall coleopteran abundance between contexts, being lowest in low agricultural extensification contexts, which could have implications for the magnitude of ecosystem services and disservices, such as predation of crop pests or herbivory of crops, delivered by beetle communities to commodity production. Even if the ratio of functional traits remains the same with land-use extensification, increasing the abundance of Coleoptera should increase the magnitude of the ecosystem processes these functional traits relate to (Grime 1998).

Within this farmining system it is likely that increasing land-use extensification enhanced habitat heterogeneity and diversity and as the land-use extensification gradient was relatively short the most intensified landscapes were still locally complex landscapes that supported a greater functional and taxonomic richness of coleopteran species compared to unextensified landscapes dominated by a single land-use/class (dry forest). This interpretation is consistent with the intermediate landscape-complexity hypothesis (Tscharntke et al. 2005a; Tscharntke et al. 2012b) which suggests that structurally complex landscapes containing a substantial proportion of non-crop habitat (>20%) will have high levels of biodiversity and associated ecosystem functioning. The most extensified contexts in the study still had relatively high proportions of natural habitat (mean 23%) suggesting that land-use extensification is yet to result in the simplified landscapes that will reduce landscape heterogeneity and cause declines in functional and taxonomic diversity. This reflects patterns observed for vertebrates (reviewed in Tews et al. 2004), dung beetles (Lassau et al. 2005, but see inconclusive findings in Nichols et al., 2007) and beetle communities in West Africa (Dagobert et al. 2008).

RLQ analysis has previously been used to link species functional traits to increasing levels of habitat modification (logging and conversion to oil palm) for dry Dipterocarp forest in Indonesia (Edwards et al. 2013), plants in temperate Scottish crofting systems (Pakeman 2011) and carabid beetles across Scotland (Ribera et al. 2001), here a similar analysis reveals functional trait and environmental associations between coleopteran communities assocatiated with different levels of land-use intensification in small-scale agriculture. The potentially crop-damaging trait of root feeding phytophagous larvae (e.g., Murphy et al. 2010; Abney and Kennedy 2011; Brill et al. 2013; Takei et al. 2014) was favoured by low natural habitat landscapes whilst the potentially beneficial traits of larval parasitoid and larval predator (e.g., Eilers and Klein 2009b; Gardiner et al. 2009a; Mailafiya et al. 2010; Scheid et al. 2011) were associated with high-natural habitat landscapes. Adult pollen and nectar feeders were also positively associated with high natural habitat landscapes, but this trait may not be particularly beneficial to agriculture as it is also associated with adult phytophages that may consume the reproductive parts of flowers (e.g., meloidid beetles, Gahukar 1991; Durairaj and Ganapathy 2000; Lebesa et al. 2012). Traits associated with high natural habitat landscapes were also positively associated with increasing field vegetation cover and fallow land, indicative of field management intensity, and distance from water. Larger field sizes were positively associated with potentially crop damaging adult phytophages (ecosystem disservice) whereas smaller fields (with field floral area and fallow) were linked to adult and larval traits relevant to nutrient cycling (e.g., detrivory, coprophagy and scavenging, ecosystem service). The RLQ analysis suggests that the balance of functional traits represented in the coleopteran community could shift towards traits representative of disservices with increasing agricultural extensification, this is consistent with the negative shifts with land-use intensification observed for arthropod-predator-prey ratios in small-scale systems in Central Sulawesi, Indonesia (Klein et al. 2002b).

There was limited evidence for trait filtering in Hymenoptera, community composition and function between land-use contexts appeared relatively similar with little difference between functional metrics. Only functional richness was higher than expected in large fields in low natural habitat landscapes, again supporting the view that agricultural extensification created complex landscapes that enhanced diversity as per the intermediate landscape disturbance hypothesis (Tscharntke et al. 2012b). However, at the context level, functional evenness, specialisation and divergence were lower in large fields, and functional evenness and specialistation lower in low natural habitat landscapes. This perhaps indicates that community functional structure was influenced by land-use change, but a more powerful study along a longer land-use gradient with higher taxonomic resolution will be needed to clarify this. Taxonomic metrics largely reflected functional metrics with abundance, family evenness, family diversity and community composition varying little between contexts. Measures of taxonomic diversity showed that landscapes with low levels of agricultural extensification had lower family richness than other contexts at the context level, but only compared to the most extensified context (large fields in low natural habitat landscapes) at the site level. These findings tentatively corroborate the few other studies of Hymenoptera along land-use intensification gradients in small-scales farmed landscapes. For example, large overlaps between hymenopteran communities have been shown in Ecuador for a gradient incorporating natural areas and both small-scale and large-scale farming (Tylianakis et al. 2005), neutral or positive effects of land-use intensification on Hymenoptera were seen in agroforestry landscapes in Indonesia (Klein et al. 2002a) and no effect of distance from forest was observed on bee species richness in Kenya (Kasina et al. 2007). Bee abundance and species richness were predicted by habitat complexity in Kenya (Otieno 2010) and changes in ecosystem functioning regarding pollination and land-use change were not observed in small-scale landscapes in coffee-production in India (Boreux et al. 2013) but were observed in Uganda (Munyuli 2012).

Trait-environment associations (RLQ analysis) indicated that larval provisioning of pollen and nectar (i.e., bees that are probable crop pollinators) was positively associated with less agriculturally extensified landscapes, whilst larval parasitoids, hyperparasitoids and egg predators (potential natural enemies that regulate crop pests and contribute towards biological control) were positively associated with extensified landscapes. Similar results to these come from a study of trap-nesting Hymenoptera in Ecuadorian small-scale farming landscapes where the abundance and diversity of parasitoids increased with land-use intensification (Tylianakis et al. 2006), this study also found that parasitoid diversity was positively correlated with rates of parasitism (ecosystem functioning). Here, as no significant differences existed between contexts for functional eveness or divergence at the site level, there was no strong effect of agricultural extensification on (abundance weighted) functional community structure. However, as the RLQ analysis hints that parasitoid traits may be favoured by land-use change and, at the context level, functional evenness, divergence and originality show declines, further study within this farming system along a longer land-use extensification/intensification gradient with greater taxonomic resolution is warranted.

In general, more research is required to determine how the response of parasitoids directly relates to land-use changes in small-scale farming systems (see Appendix A Figure A.2), such as consolidation (increasing areas under the same management leading to reduced landscape heterogeneity in time and space), extensification (increasing landscape proportion of agricultural land-use at multiple spatial scales) and increasing management intensity (e.g., pesticide, herbicide and fertiliser use and mechanisation). To accurately assess the relationship between parasitoid, or any natural enemy, diversity and natural pest control the response of parasitized species to land-use change and subsequent bottom-up effects on their parasitoids should be considered (Wilby and Thomas 2002). For example, parasitism of the armyworm *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), an agricultural pest, by braconid wasps did not respond to landscape structure in temperate large-scale farming landscapes but instead a trend of increasing of parasitoid richness and diversity was found with increasing host density (Costamagna et al. 2004). In the context of this study phytophagous Coleoptera were positively associated with land-use intensification and total abundance was highest in intensified contexts (although this was not significant at the site level), therefore coleopteran parasitoid communities could have been responding to changes in their host community. The ecology of agro-biodiversity is poorly known for most sub-Saharan African species, yet basic biological insights can help to outline the structure of ecosystem processes and give more accurate predictions for the effect of land-use change on the delivery of ecosystem services (Wilby and Thomas 2002), recommendations for closing this knowledge gap can be found in Chapter 6 (general discussion).

When interpreting functional diversity and its implications for ecosystem processes it is important to consider that some species could exert a stronger effect on ecosystem processes relevant to the agricultural system in question than others. Changes in dominant traits are reflected by species evenness and the identity of dominant species (Hillebrand et al. 2008; Mokany et al. 2008) and the effects of these on ecosystem function have been shown by manipulations of model grassland communities where the functional evenness and identity of dominant species consistently enhanced ecosystem system functioning (Orwin et al. 2014). Evenness is considered to be complementary to dominance in that it reflects the distribution of traits within a community and the two negatively correlate, if a community is dominated by a species with particular traits then dominance is high but evenness low (Hillebrand et al. 2008). Here, there was evidence for increasing dominance in Coleoptera communities in the highest land-use intensification context, in that phytophagous traits were becoming relatively more abundant. Another means of considering dominance in functional trait analysis is to use body size or biomass rather than species abundance to measure the relative contribution of species or functional traits to the community and ecosystem processes because biomass is directly related to the amount of energy and resources assimilated within a species (Grime 1998; Villéger et al. 2008). It should be noted that allometric scaling means that animal size or biomass is unlikely to relate to energy or resource accumulation in a linear fashion. For example larger dung beetles burying a greater volume of dung than smaller beetles have a greater impact on nutrient cycling (Andresen 2002; Slade et al. 2007). Further, studies of dung beetles have shown abundance and biomass can respond very differently to disturbance and that the impacts of habitat modification may be more clearly reflected by biomass than abundance (Vulinec 2000; Scheffler and Scheffer 2005). Species biomass should be considered complementary to abundance and using both will provide further insight into how communities are affected by landscape change (Villéger et al. 2008). Size or mass is not a perfect substitute for the efficacy (or rate) of a species regarding a functional trait relevant to a particular ecosystem process in particular for keystone predators (Clemente et al. 2010; Eisenberg 2010) or ecosystem engineers (de Visser et al. 2013) whose abundance or biomass does not necessarily reflect the strong impact they have on ecosystem functioning and community structure. Therefore whilst a functional diversity approach to assessment of community change can describe how functional traits vary between contexts, it may not always be possible to accurately predict the ecosystem service consequences of this without detailed information regarding the ecology of species within the community.

As mentioned previously, expanding the gradient of agricultural extensification and consolidation to include much larger fields in simplified and/or cleared landscapes than available in this study area will provide greater insight into the consequences of land-use change for agriculturally important taxa. Pre-existing global datasets from agricultural contexts, including small-scale farming, with accompanying spatial landscape data appropriate for this purpose are available for bees (see Kennedy et al. 2013), but, as yet, such datasets have not been compiled for other important groups that provide ecosystem services or disservices. Whilst data regarding the general sampling of overall coleopteran communities in tropical agricultural contexts are rare (but see Dagobert et al. 2008) there appears to be a substantial body of global data for dung beetle communities in the literature (see review by Nichols et al. 2007), some including small-scale contexts in Africa (e.g., Tind Nielsen 2007). Carabids are also relatively well studied (e.g., Ekroos et al. 2010; Gardiner et al. 2010; Woodcock et al. 2010) with some studies from small-scale farmed tropical landscapes (e.g., Magagula 2003). Compiling agricultural dung beetle and carabid community datasets and trait databases for review will be an important step forward towards explicit modelling of the response of these groups to extensification and consolidation in small-scale farming, however more information is required on the ecosystem service role of taxa before changes in community composition can be translated into ecosystem service values relative to crop production (for example using the InVEST modelling approach, Tallis et al. 2008).

Conclusions

In summary this study provides new data on the functional impacts of agricultural extensification on Coleoptera and Hymnenoptera of small-scale tropical agricultural systems. Within coleopteran communities there was evidence for agricultural extensification increasing the dominance of phytophagous traits which may suggest that ecosystem disservice due to herbivory could increase as small-scale farms consolidate and natural habitat is lost from the landscape. Increasing functional richness with agricultural extensification for both Coleopteran (species) and Hymenoptera (families) supported the intermediate landscape-complexity hypothesis (Tscharntke et al. 2012b) in that agricultural extensification, at the levels present in this system, resulted in more complex landscapes that promoted functional and taxonomic diversity. However, given the knowledge gaps for the ecology of sub-Saharan African agro-biodiversity, it is difficult to confidently infer the ecosystem process consequence of functional change and what this means for ecosystem services and disservices without further research to directly quantify the relationships between land-use change, functional trait communities and ecosystem process.

Chapter 5. Smallholder perceptions of ecosystem services and disservices and attitudes towards nature in the buffer zone of an African wilderness

5.1. Introduction

Agricultural extensification (often in conjunction with deforestation) is one of the biggest threats to natural habitats (Barbier 2004; Naughton-Treves et al. 2005; Pacheco 2006; Buys 2007) and by definition it will typically occur at the interface of natural areas and agriculture. Agricultural extensification that causes the fragmentation and isolation of natural habitats, and in particular within the buffer zones of protected areas, is of particular concern for the long-term viability of the global protected area network (Laurance et al. 2012). In large areas of sub-Saharan Africa and South Asia where farms are small-scale (see Appendix B Table B.2) and farmers are poor (IFAD & UNEP 2013) there is considerable potential for developing mechanisms (interventions or programmes) to link land-sparing (Green et al. 2005) to conservation in buffer zones (Phalan et al. 2014). Such 'land-sparing linking mechanisms' (LSLMs) may have to realise multiple goals of reducing poverty, land-scarcity and food insecurity for human residents (Tscharntke et al. 2012a) whilst encouraging the conservation and restoration of natural areas in buffer zones. Buffer zones present a particular challenge for conservation as there is often considerable potential for ecosystem disservices from large animals using natural habitats in buffer zones (Distefano 2005; Woodroffe et al. 2005a). Surprisingly, given the importance of protected areas and buffer zones to biodiversity conservation, ecosystem disservices are rarely considered explicitly in empirical work relating to land-sparing and land-sharing, yet it is a common topic in conservation research in the form of human-wildlife conflict (e.g., Nyhus and Tilson 2004; Woodroffe et al. 2005b; Treves et al. 2006). Further, ecosystem disservices are also an issue for high-income large-scale farming nations, agricultural crop losses in the US due to mammals and birds caused were estimated at $944 million in 2002 (National Agricultural Statistics Service 2002) and birds are estimated to cost Australian horticultural production $300 million annually (Tracey and Mary 2007).

The behaviours, attitudes and perceptions of farmers in buffer zones towards biodiversity and their relationship with natural habitats will be important for the selection and design of appropriate LSLMs to conserve natural habitats. For example, If stakeholders perceive a significant risk, accurately so or exaggerated, from LSLMs designed to promote biodiversity then they will be more reluctant to support them (Riley and Decker 2000; Holmern et al. 2007; Gangaas et al. 2013) or may engage in retaliatory activities (Kissui 2008; Gusset et al. 2009). Buffer zones are hotspots for human wildlife conflict especially in low-income countries where dense human populations are in close vicinity to natural habitats and agriculture is essential to rural livelihoods (Distefano 2005; Gusset et al. 2009). The charismatic species that attract tourist revenue, receive substantial conservation funding and occupy protected areas and their associated non-protected natural habitats within buffer zones, such as primates, elephants and predators can inflict costs on local human communities (Madhusudan 2003; Chiyo et al. 2005; Inskip and Zimmermann 2009; Wallace and Hill 2012; Suryawanshi et al. 2013). This can foster negative attitudes towards reserves and wildlife in residents and undermine conservation efforts (Distefano 2005; Kissui 2008). Achieving sustainable use of resources in protected areas and their buffers is an additional challenge that LSLMs will need to address as low-income small-scale farmers often rely on natural habitats for resources such as fuel-wood and fodder and may view these as compensation for production losses and other damage from wild animals (Sekhar 1998). Whilst, in the short to medium-term LSLMs in buffer zones are required to mitigate human-wildlife conflicts and to reduce pressure on natural resources, in the longer-term the sustainability of conservation via land-sparing will rely on a combination of approaches such as education and awareness programmes, landscape planning and incentives to encourage human migration away from buffer zones and reduce population growth.

Despite small-scale farmers in the buffer zones of large tropical protected areas being decision makers at the front-line of conservation and food-security issues, few, if any, attempts have been made in this context to conduct empirical research that links ecosystem disservices, such as human-wildlife conflict, to the land-sparing vs. land-sharing or similar trade-off frameworks; this study is one of the first to do. By exploring the attitudes and perceptions of a major group of buffer zone stakeholders in relation to natural habitat and wildlife at different spatial scales, this study approaches the land-sparing framework from a direction that is rooted in its practical application that will complement theoretical predictions regarding how best to optimise landscapes for ecosystem services and biodiversity conservation. This chapter attempts to do so in manner in-keeping with spatial trade-off analyses for the optimisation of ecosystem services and biodiversity with changing agricultural land-use intensity (e.g., Edwards et al. 2014b; Gilroy et al. 2014; Lee et al. 2014) and with relevance to the paradigm of sustainable and ecological intensification (e.g., Bommarco et al. 2013). Here, questionnaire based interviews are used to investigate the perceptions and attitudes with regards to nature of low-income small-scales farmers living the buffer zone of a large protected African wilderness. Farmer perceptions of crop damage (ecosystem disservices) and their attitudes to wildlife, local wildlife habitat and protected areas are assessed between different landscape contexts for agricultural extensification. Two spatial scales of natural habitat are examined, 1) local natural habitat in the immediate context of a farm, and 2) natural habitat at a wider scale as measured by distance to a wilderness area.

It is hypothesised that proximity to local and large wilderness areas is positively associated with increasing spillover of ecosystem disservice providing wildlife (e.g., causing crop damage or livestock predation, White et al. 1997; Michalski et al. 2006; Linkie et al. 2007; Warren et al. 2007; Thurfjell et al. 2009) leading to the expectation that increasing local wildlife habitat and proximity to wilderness areas will have a significant negative effect on perceptions of crop damage and attitudes, and that perceptions of crop damage would also have a significant effect on attitudes (Allendorf et al. 2006). The implication of this is that the conservation of local wildlife habitat in buffer zones could become more difficult near to protected areas where it is most important, and thus LSLMs would need to consider how multiple spatial scales of landscape context influences a stakeholder's relationship with their environment. Understanding the relationship between small-scale farmers and the natural habitats and biodiversity they support and its spatial correlates will inform the design and selection of mechanisms to link land-sparing to conservation.

5.2. Methods

5.2.1. Study system

The 525 km^2 study area was located in the semi-arid small-scale farmlands of lowland Taita, Kenya (Figure 5.1), the largest town in this area, Mwatate, was approximately central (lat -3.503˚, long 38.364˚). Across the study area poverty is acute (Mwanyumba et al. 2010) and agricultural production is small-scale, low-input and mostly for direct consumption by the farming household. The study area was bounded by the Taita Hills to the north (an altitude of 1200 m was the cut off), the Taita Wildlife Sanctuary to the west, the commercial Teita Sisal Plantation (>120 km^2) to the south-east and stretched as far as the Voi River and its tributaries to the east. The wider Taita area (including the Taita Hills and Voi) is almost completely surrounded by Africa's largest national park, Tsavo, and can be considered within the Taita-Tsavo buffer zone. Tsavo is a 22812 km^2 protected area home to 46 % of Kenya's 26,000 African elephants (*Loxodonta africana*) (if including the wider Tsavo ecsoystem, AfESG and AsESG 2013). Elephants have traditionally foraged, sought water and migrated through the Taita lowlands and the continuing expansion of agricultural activities into natural habitats has created a flashpoint for human-wildlife conflict (Ngure 1993; Smith and Kasiki 1999; McKnight 2004). The study area landscape is a mosaic of small fields and open dry woodland (*Acacia spp.* and *Commiphora spp.*), the ratio of these varying from landscapes being dominated by large consolidated areas of dry woodland to landscapes dominated by agriculture where forest has been reduced to scattered fragments (see Figure 5.3). Especially in the East near the Taita Wildlife Sanctuary connectivity exists between protected areas for nature conservation and substantial blocks of natural habitat into which farmland has recently expanded. High population growth rates (National Council for Population and Development, 2013) coupled with insufficent farmland to meet demand in the wetter highlands of the Taita Hills has resulted in rapid, unplanned, expansion of agriculture into dry forest wilderness areas that form part of the Tsavo ecosystem (Maeda et al. 2010a). Although there was still a substantial area of dry forest remaining at the time of this study, losses are ongoing and simulations based on current rates of change predict lowland landscapes could be almost completely denuded of dry forest by 2030 (Maeda et al. 2010a).

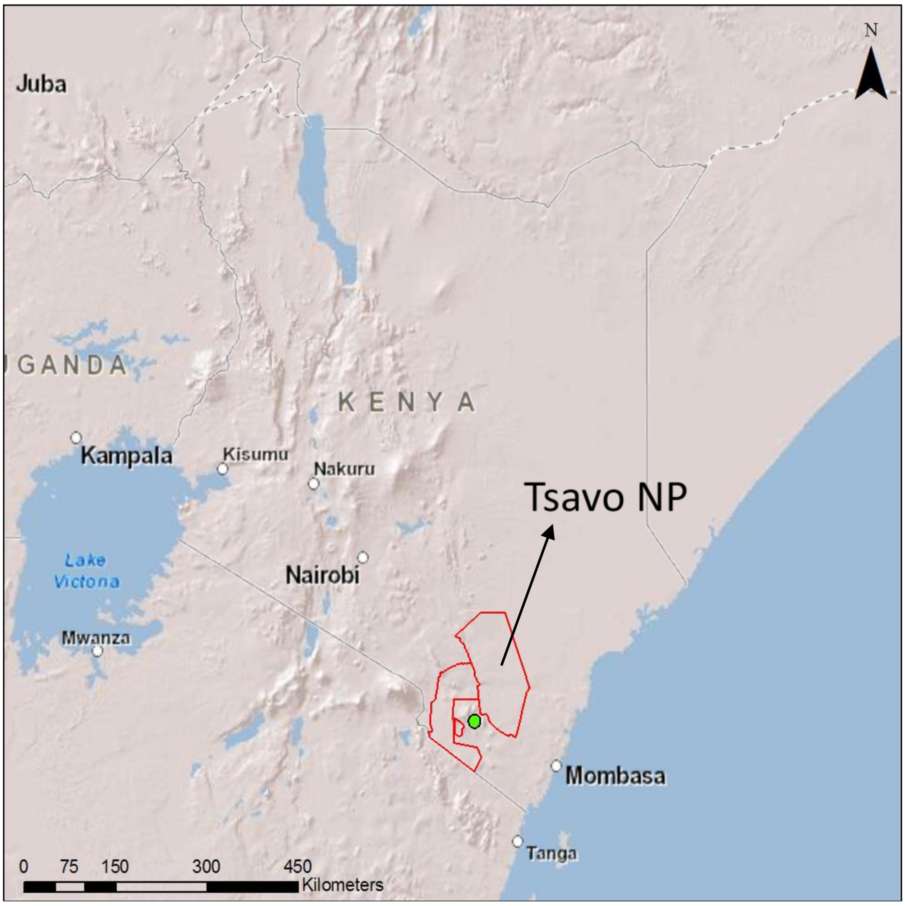


Figure 5.1 The regional context of the study area. A protected area for nature conservation, Tsavo National Park (red boundary) and associated private conservancies almost completely encircle the lowland farmers of the Taita community (green polygon = study area).

Large mammals, such as elephants and lions, could freely access large patches of natural habitat and croplands within the study area from the west and south-west, but their access was restricted from other directions; to the north access was blocked by the steep slopes and heavily populated Dabiba massif, to the south it was blocked by the Teita Sisal Plantation and to the East electric fences associated with the Mombasa-Nairobi highway and Voi presented a barrier to movements. Smaller mammals such as primates were ubiquitous in patches of remnant dry forest throughout the study area.

5.2.2. **Mapping and site selection**

In order to select interview locations with different local and large-scale landscapes wildlife habitats were mapped within the study area and interview locations assigned to four combinations (Figure 5.2) of distance from wilderness area (near <1 km and far >10km) and local wildlife habitat with 1000 m (low < 25% and high > 60%).

Woody habitat, protected areas and areas of savannah/ranch-land adjoining protected areas were considered as wildlife-habitat and from hereon are referred to as “wildlife habitat”. The primary land-uses of non-wooded areas were cropland, small settlements, roads and small pastures not associated with the large ranches beyond the south-west of the study area. Of these land-uses cropland was dominant and from hereon they are referred to in combination as “agriculture”. Ranch lands and savannah occupied a small part of the south-western study area and were very similar in habitat structure to protected areas, therefore were considered to present little barrier to the movement to animal fauna and were likely to support populations of some potential crop raiding taxa (such as yellow baboons *Papio cynocephalus*).

Woody habitat and grasslands less than 1200 m.a.s.l. were digitised manually (Figure 5.3) using QGIS 2.0 and high-resolution (c. 2 m pixel width) satellite imagery freely available using the openlayers plug-in (QGIS Development Team 2013). Imagery recorded during the dry seasons of 2010-2012 was used for mapping as this provided the greatest contrast between natural vegetation and agricultural areas. The minimum mapping unit was 25 m^{2} and the final map was smoothed in ArcGIS 10.0 (ESRI 2011), a PAEK algorithm with 10 m tolerance gave a good visual fit to satellite imagery. A total of 525 km^{2} was mapped (Figure 5.3).

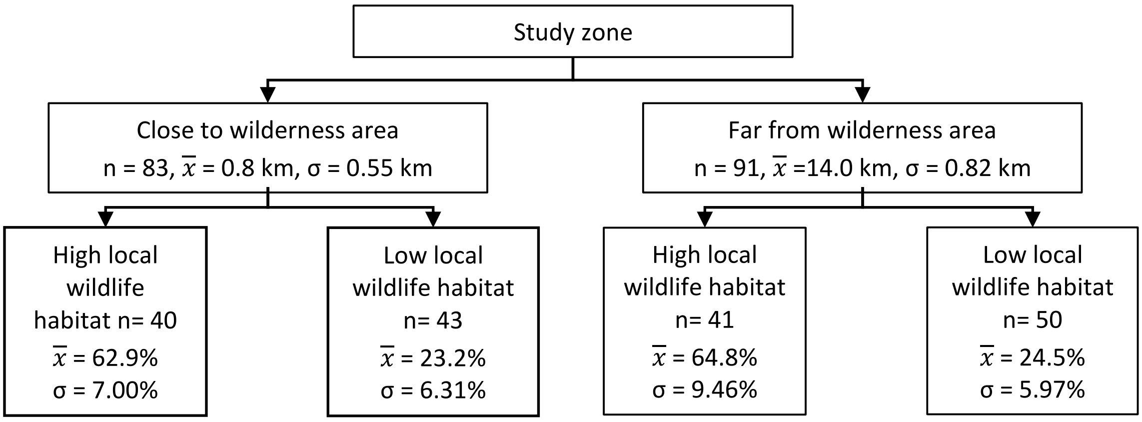


Figure 5.2 Summary statistics between study design factors and number of interviews (n) conducted in each. Local wildlife habitat was calculated for a radius of 1000 m from the interview area.

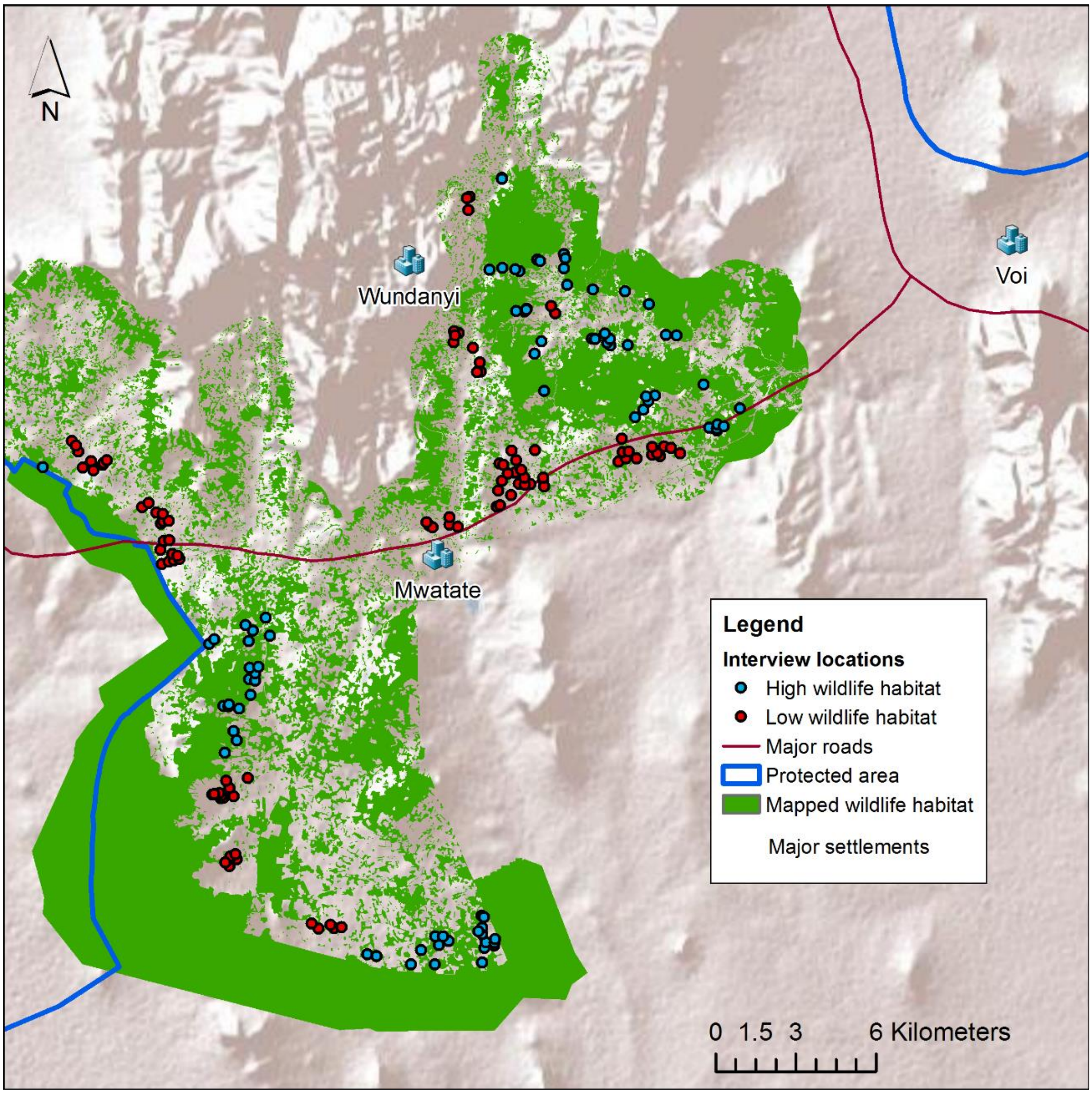


Figure 5.3 Distribution of interview locations within the study area (n = 174). Wildlife habitat % is calculated for the landscape within 1 km of each point. Wilderness areas include non-protected areas of natural habitats or semi-natural habitats such as ranchlands contiguous with protected areas and separated by corridors of no less than 500 m width.

To define landscapes that were and were not strongly associated with expansive natural areas at large spatial scales the frontier between landscapes of natural wilderness and landscapes of agro-ecosystems was taken as the boundary of the unfragmented Tsavo ecosystem. This was derived by taking the boundary of protected areas from the World Database of Protected Areas (IUCN and UNEP 2014) and expanding them to include contiguous areas of dry forest, savannah or unfenced ranch bordering the protected areas with the requirements that they were uninhabited, uncultivated and connected to the protected area by corridors of at least 500 m width.

Regarding site selection, to maximise the effect size of distance from wilderness on farmer attitudes and perceptions croplands within 1 km and greater than 10 km away from wilderness areas were selected, with altitude limited 1200 m a.s.l. or less (Figure 5.3). Within these distance restrictions the proportion of local wildlife habitat within 1 km of croplands was estimated for a point grid spaced at 150 m clipped to agricultural areas using ArcGIS 10.0 (ESRI 2011).

Points (interview locations) were then subset for croplands with less than 25% and greater than 60% wildlife habitat within 1 km and then grouped into clusters using convex hulls with a maximum separation distance of 350 m, this gave four combinations of local landscape and distance to wilderness area. Seventy points were selected for each landscape-distance combination. Points were randomly selected from each cluster according the proportion of points that cluster contributed to the landscape-distance combination total. Using freely available satellite imagery in QGIS (QGIS Development Team 2013) selected points were moved to the nearest dwelling or shelter, but if no houses were nearby the point was left at its original location in the expectation that farmers would be found labouring in the fields.

5.2.3. **Interviews**

Data were collected between July to October 2013 and sampling was carried out at the household level on the basis that this constitutes the basic unit of shared economic production and resource utilisation within the study area, aligning with studies in similar contexts (e.g, Gillingham and Lee 1999). Respondents were informed that their identity would remain anonymous, their details would not be shared with anyone and the data was for research purposes only, and they were given the option to decline participation and opt out of the interview at any time. Only farmers with landholdings that were at least partially given over to crop production were considered as potential respondents. Where a land-holding was unoccupied, had no cropland or the farmer was away the next closest farm was visited and so on until a farmer was found. If respondent could not be found within 45 minutes of searching the point was abandoned.

Interviews were conducted in Swahili by two field staff of the same ethnicity as the large majority of respondents. The survey questionnaire (Appendix J) contained a mixture of 51 open and fixed-response Likert scale questions which covered: 1) respondent's background (age, gender, ethnicity and education); 2) farm size , activities and income; 3) perceptions of crop damage and crop damaging animals; and 4) attitudes to wildlife, local natural habitat (dry forest and bushland) and protected areas. Respondents were usually the elder of the household and were balanced between males (48.8%) and females (51.2%) with mean (SD) age 46.0 ± 14.89 years. Participation rates were high, > 95%, as farmers were disposed to discuss the problems they faced in day-to-day to life. It was not possible to conduct double-blind interviews as the interviewers were aware of the location of a respondent and their socio-economic status, but the rationale of the study was not explained to the interviewers to reduce any expectation effects. However, the interviewees were unaware of any groupings and can be considered blind.

Interviewer was a significant term in the regression analyses for several attitude indices (Table 5.6) suggesting that inter-rater reliability was an issue, however interviewers were given similar numbers of sites in each study factor so the effect should have be standardised between factors.

5.2.4. Statistical analyses

Construction of attitude indices

Attitude indices (e.g. Goddard et al. 2013) were designed as a relative measure to allow comparisons between respondents for their attitudes to wildlife, local wildlife habitat (referred to as dry forest or bushland in interviews), protected areas for nature, elephants and all of thse combined. Indices were constructed from interview data as per Table 5.1. Where respondents failed to answer > 2 questions for the overall attitude index and > 1 for all other indices their responses were excluded from data analysis. Where missing values were present below the threshold for exclusion, missing values were imputed based on response to other questions in same index (after Luck et al. 2011). If data were missing from a predictor or a component of the attitude index for an interviewee, that interviewee was omitted. People that were unaware of the existence of protected areas (21% of all respondents) explain the drop in respondents for the overall and protected area indices compared to other indices (Table 5.5). Suprisingly, there was little difference in knowledge of protected areas between respondents near and far from wilderness areas (79.5% and 79.1% respectively).

Answers to fixed-response attitudinal Likert questions were scored +2, +1, 0, -1 and -2 for strongly positive, positive, neutral, negative and strongly negative answers. The number of beneficial wildlife and benefits reported from dry forest (local wildlife habitat) and protected areas were added to indices and problems for the same subtracted. Respondents attitude towards elephants was incorporated into indices as 1) their suggested actions for elephants in the area (scored as: cull all = -4, cull > 50% = -3, cull < 50% = -2, fence or translocate = -1, take no action or drill boreholes = 0); 2) their opinion of elephant numbers (scored as: too many = -1, no opinion = 0, enough = +1, too few = +2); and 3) they reported elephants as problem animals damaging crops or in general (scored 0 if not reported and -1 otherwise, elephants were never reported as beneficial wildlife). Crop-protection measures were classified into non-destructive practises that do not harm wild animals but act as deterrents (scored as 0, methods included guarding, guard dog, scarecrows, fencing, no action, call wildlife services, burning dung or plastic, and early harvesting) and destructive methods that kill or harm wild animals (scored as -1, methods included poison and trapping), the summed score being added to the attitude index. It is suspected that destructive practises were under-reported due to the illegality of their nature. In the overall attitude index the positive benefits of dry forest were modified by their potential to be destructive; extractive practises that could clearly lead to habitat loss or degradation or loss of wildlife scored -1 (extraction of timber for cooking, construction and charcoal burning, and the hunting of meat), extractive practises with lower impact scored 0 (grazing of livestock and collection of traditional medicines and compost) and benefits that no or little potential negative impact were scored as +1 (shelter, fresh air, promotes rainfall, prevents erosion, wildlife (not for consumption) and bees and other beneficial insects).

Table 5.1 Components of attitudinal indices are indicated with a "X". The scoring for each component question or question set is described in the main text of section 5.2.4 with interview questions found in Appendix K.

Component	Questions	Attitude indices				
		Overall	**Wildlife**	**Local wildlife habitat**	**Protected areas**	**Elephant**
Wildlife attitude	18-19	X	X			
Bushland attitude	22-24	X		X		
Protected area attitude	27-32	X			X	
Beneficial wildlife	20	X	X			
Problem wildlife	21	X	X			
Bushland benefits	25	X		X		
Bushland problems	26	X		X		
Protected area benefits	33	X			X	
Protected area problems	34	X			X	
Elephant actions	38	X				X
Elephant numbers	37	X				X
Crop protection methods	16	X	X			
Impact of bushland-use	25	X				
Elephants reported as a problem or damaging crops	14,21					X

Measurement of predictor variables

In addition to landscape predictors, socio-economic covariates including wealth indicators, age, education and gender (e.g., Hill 1998; Gillingham and Lee 1999; Linkie et al. 2007; Suryawanshi et al. 2013) were considered likely to explain some of the variance in perceptions or attitude between farms (Table 5.2). Perception of animal crop damage was analysed as response variables in its own right and used as a predictor in altitudinal models. If respondents did not provide information regarding any one predictor used in modelling their data was excluded from analyses.

The relative value of livestock between farms was estimated as the combined summed weight of each stock multiplied by the ratio of the per kg value of each stock to the most expensive stock. The weight of livestock was conservatively estimated at 50% of the average weight of well-tended commercial stock (Biovision Foundation 2014) because reported figures included immature stock and stock were generally thin and undernourished. Cattle were taken to be the East African zebu breed, goats the East African goat, sheep the Persian blackhead and chicken as light breeds. Values per kg meat were taken from January 2012 end market figures in Nairobi (Farmer and Mbwika 2012), ducks were taken to be equivalent to chicken.

Table 5.2 Predictors used in regression analyses, all but local wildlife habitat, gender and recorder were PCA transformed. Codes PX refer to proximity to and DI to distance from. To the left Code W the radius (m) at which local wildlife habitat was calculated is noted in models (e.g., W250). Age and education were always strongly correlated and are given the combined code of AE.

Predictor	Unit	Code	Description
Distance to wilderness area	km	PX_1 / DI_1	Euclidean distance between an interview location and natural habitat contiguous with a protected area
Distance to protected area	km	PX_2 / DI_2	Euclidean distance between an interview location and the formal boundary of a protected area
Local wildlife habitat	Prop.	W	Percentage of wildlife habitat (e.g., dry forest, bushland or wilderness area) within a specified radius of the study location
Monthly income	KES	IN	Household income from selling crops, animal products or labouring
Land owned or rented	acres	LA	Size of household's landholding
Livestock value index	KES	LS	Relative value of household's livestock*
Age	years	AE	Age of respondent
Education	years		Years in education (including vocational training)
Crop losses due to drought	Prop.	DR	Perceived crop losses due to drought for the two most recent growing seasons
Crop damage due to animals	Prop.	CD	Perceived crop losses due to animals for the two most recent growing seasons
Gender	factor	G	Male or female
Recorder	factor	R	Two different interviewers

Regression modelling of attitude indices and crop damage

Collinearity in explanatory variables was assessed using variance inflation factors (VIF) with a threshold of VIF = 3 (Zuur et al. 2007). This suggested most were correlated, as such all predictors apart from local wildlife habitat, gender and recorder were transformed into PCA axes using a varimax rotation. PCA axes with Eigen values >1 were kept and included in regression models, loadings vary between analyses according to the identity of respondents included. See Appendix M for details of PCA loadings and correlations between raw predictors.

Respondents' perceptions of crop damage by animals were at a coarse resolution (e.g., a little, a quarter, half, most, all) and as such responses were coded into high, moderate and low perceived crop damage and analysed using ordinal regression. Where perception of crop damage was used as a predictor in models it had been converted into a proportional score (a little = 0.1, a quarter = 0.25, half = 0.5, most = 0.75, all = 1) averaged across the two most recent growing seasons prior to ordination.

Global models were built around the *a prori* assumption that local wildlife habitat and distance to protected/wilderness area would have significant effect on attitudes and perceptions of crop damage, that perceptions of crop damage would also have a significant effect on attitudes and that the strongly negatively correlated covariates of age and education would also influence attitudes and perceptions with higher levels of education having a positive effect (e.g., Infield 1988; Fiallo and Jacobson 1995; Kideghesho et al. 2007; Røskaft et al. 2007). Global regression models for attitude contained interactions for local wildlife *habitat * distance to protected/wilderness area * perception of animal crop damage* and *local wildlife habitat * distance to protected/wilderness area * age/education*; the PCA axes onto which these predictors loaded most strongly were substituted for these terms (see Appendix M for full model details). The global regression model for crop damage used the same interactions without perception of animal crop damage and included additional terms for presence or absence of common crop damaging animals (elephants, livestock, primates and birds). The scale at which local wildlife habitat was most predictive (250, 500, 750 and 1000 m radii) and whether distance to wilderness or protected area was most predictive were tested in global models and the scale and distance giving the lowest AICc score selected for model simplification. In attitudinal analyses both raw and centred-scaled indices were tested in global models, again AICc score determined which was selected for model simplification.

Model selection and model averaging based on AICc were conducted using the `dredge` function from the `MuMIn` package (Barton 2011). Averaged models were derived from the 95% confidence set (the set of models containing the best model within a given level of confidence, Hansen et al. 2011) of the full dredged model set and models are presented in full in Appendix M. Regression bootstrapping using the `boot` function from the package `boot` (Davison and Hinkley 1997; Canty and Ripley 2014) was used to assess the sensitivity of the most predictive model (lowest AICc) to the underlying data. Results from the most predictive models are presented and to be considered meaningful predictors had to be statically significant ($p<0.05$) in averaged and bootstrapped models.

For the maximal and most predictive models homogeneity assumptions were investigated by plotting of the standardised residuals versus fitted values and the standardised residuals versus each explanatory variable. To investigate spatial-autocorrelation maximal generalised least squares models were fitted with different correlation structures and compared a null model with no correlation structure using AIC and ANOVA to test if there was any improvement in fit (Zuur et al. 2009). Additionally bubbleplots and semi-variograms were used to visually inspect spatial-autocorrelation.

For models analysing attitude predictions were visualised using partial plots that showed the relationship between the response and the explanatory variable while controlling for the effect of other explanatory variables in the model. Cohen's f^2 was used to compare effect-sizes between models and between regressors within a model (Cohen 1988) using adjusted R^2 values for linear regression and pseudo-R^2 for ordinal regression. Pseudo-R^2 values for ordinal regression were derived using the `pR2` function in the `pscl` package (Jackman et al. 2012) or calculated as McFadden's pseudo-R^2. Where an interaction was present the effect size for an individual predictor was calculated removing all terms containing that predictor.

Additional statistical tests

The effect of local landscape and distance to wilderness for answers to individual questions (Table 5.3, Table 5.4, Table 5.7 and Appendix L) were tested using chi-squared analyses or, if values < 5 were present, exact multinomial tests with monte-carlo simulations using 1,000,000 replicates using the `EMT` package (Menzel 2013). Questions relevant to attitudinal indices are presented in the results section and the answers to additional questions are presented in Appendix L.

Bootstrapping (1000 replicates) was used to assess the significance of differences in the ratios of perceived benefits and costs from wildlife, local wildlife habitat and protected areas between landscape combinations (Table 5.8).

Ordinal regression with a logit link function (Williams 2006), using the `polr` function in the `MASS` package (Venables and Ripley 2002), examined the effect that the presence of common pest taxa, and landscape and socio-economic factors had on perceptions of crop damage (Figure 5.4).

Regression analyses for reporting of individual crop damaging taxa and number of taxa damaging crops (when asked specifically regarding crop damage or in general) are presented in Appendix N with accompanying methods.

5.3. Results

Whilst local wildlife habitat was included as an independent variable in models and, as such, is easily interpreted, distance from / proximity to protected areas or wilderness consistently loaded onto multiple PCA ordination axes with other predictors and its interpretation is more complex. Farmers in close proximity to wilderness areas tended to have larger fields, more livestock and had spent less time in education, however, whilst crop damage often loaded with proximity they were not significantly correlated in the raw data(Appendix M Table M.1).

5.3.1. Perceptions of animal crop damage

Animals were perceived to be the second largest cause of recent crop losses, after drought, with 59.8% and 35.2% of respondents reporting moderate or high crop loss respectively (a quarter or more crop loss, Table 5.3). Comparatively, drought was perceived to cause moderate to high crop losses for 75% of respondents. Almost two thirds (63%) of respondents reported primates as damaging crops (Table 5.4) and two major crop raiding primate species were present in the study area, these were yellow baboons (*Papio cynocephalus*) and vervet monkeys (*Chlorocebus pygerythrus*).

Table 5.3 Farmer perceptions of crop losses due to animals, drought and disease. Responses were coded into categories as follows: High = all or more than half of crops lost, Medium = approximately half or more than a quarter of crops lost, Low = a quarter or less of crops damaged, or no damage. The Bonferroni corrected p-value for statistical significance in chi-squared test is p<0.025.

			Response (%)			Test		
Question	**Grouping**	**n**	**High**	**Medium**	**Low**	**χ^2**	**df**	**p**
15. For all your crops how much loss before harvest did animals cause in the most recent growing season?	Far	75	14.7	41.3	44.0			
	Near	67	25.4	38.8	35.8	2.7	2	0.259
	High	67	20.9	41.8	37.3			
	Low	75	18.7	38.7	42.7	0.4	2	0.807
	Overall	142	19.7	40.1	40.1			
12. How much of your crops were lost due to drought in the most recent growing season?	Far	75	61.3	20.0	18.7			
	Near	67	49.3	19.4	31.3	3.2	2	0.198
	High	67	59.7	20.9	19.4			
	Low	75	52.0	18.7	29.3	1.9	2	0.39
	Overall	142	55.6	19.7	24.6			
13. How much of your crops were lost due to disease before harvest in the most recent growing season?	Far	75	24.0	13.3	62.7			
	Near	67	19.4	13.4	67.2	0.5	2	0.797
	High	67	23.9	13.4	62.7			
	Low	75	20.0	13.3	66.7	0.3	2	0.848
	Overall	142	21.8	13.4	64.8			

Ordinal regression modelling of perceived crop damage showed distance from wilderness and local wildlife habitat had no significant effect on perceptions of animal crop loss (Appendix M Table M.2). The model was weakly predictive with low pseudo-R^2 values ranging from 0.034 (Macfadden's) to 0.078 (Cragg and Uhler's) and a small effect-sized based on the former of f^2 = 0.04. Whether or not a respondent had reported primates damaging crops was the only significant term retained in the model (income was also significant in the best AICc model but not the averaged model) and the presence of primates had the, initially counterintuitive, effect of reducing respondents' perception of crop damage (Figure 5.5). Damage was caused by primates taking maize cobs, eating cowpeas or common bean leaves and associated trampling of crop plants. Examination of crop protection methods in the presence and absence of primates (Figure 5.5) revealed that, when primates were present respondents were significantly more likely to invest in guarding (92% vs. 67%), guard dogs (53% vs. 20%) and scarecrows (32% vs. 15%), and to take a prevention action in general (95% vs. 74%). Increased effort in crop protection when primates were present may explain why perceived losses were lower compared to when they were absent. When comparing between spatial contexts (Appendix L Figure L.1 Table L.2) for the five most commonly used crop protection methods (including doing nothing) there were no significant differences between respondents near and far from wilderness areas, but respondents in high compared to low local wildlife habitat landscapes were significantly more likely to guard crops (96% vs. 71%).

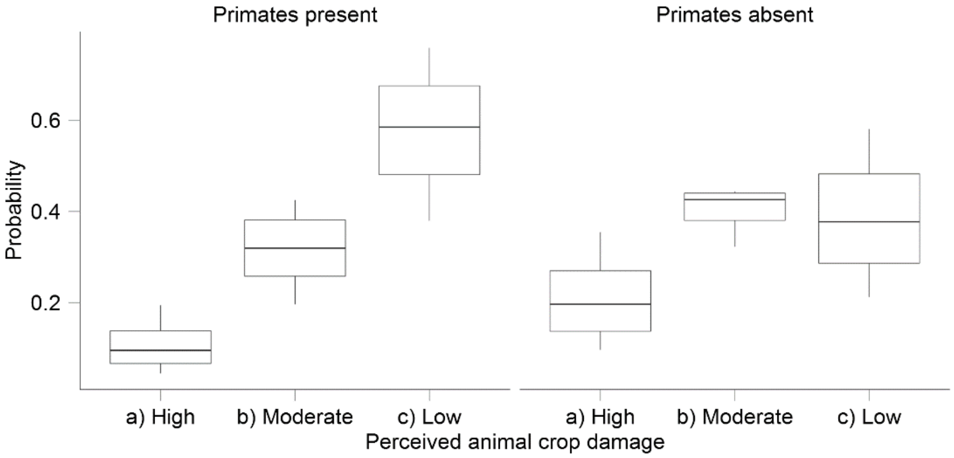


Figure 5.4 Ordinal regression results for respondents' perceptions of animal crop damage. Boxplots correspond to predicted variance in probability due to respondents' income (based on the spread of observed values within the data). Observed proportions for high, moderate, and low values of crop damage were 0.14, 0.37, 0.47 in the presence of primates and 0.28, 0.43, 0.30 in their absence. Model details are presented in Appendix M Table M.2 the effect of income is not fully explored here as it was not significant in the averaged model, however it is presented in Appendix M Figure M.1.

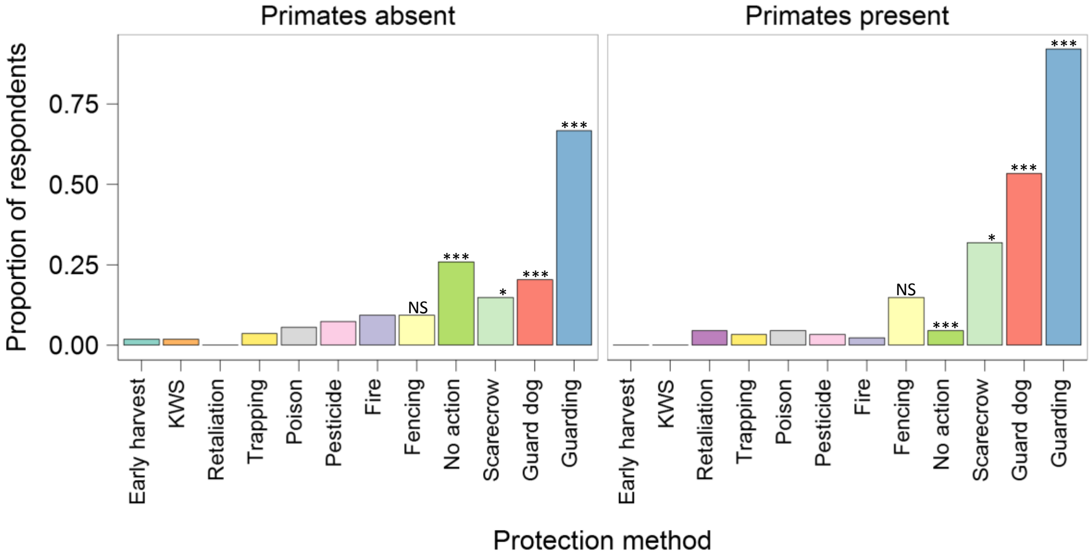


Figure 5.5 Types of crop protection used by respondents in response to animals damaging their crops (Q16, Appendix J), for those reporting primates damaging their crops (present, n = 88) and those not (absent, n = 54). Chi-squared significance is presented (NS $p > 0.05$, * $p < 0.5$, ** $p < 0.01$, *** $p < 0.01$) for the five most commonly used methods (df = 1, from left to right χ^2 = 0.5, 12.0, 4.3, 13.8 and 13.2).

Regarding perceptions of the individual taxa raiding crops rather than total perceived animal crop damage, respondents were significantly more likely to perceive primates damaging crops in low wildlife habitat landscapes compared to high and if they were far from wilderness areas compared to close (Table 5.4), the age and education of respondents were also important (see regression analyses in Appendix N). Other than primates, respondents far from wilderness were also significantly more likely to report squirrels, rats, moles and birds damaging crops (Table 5.4 and Appendix N). Conversely respondents in close proximity to wilderness were more significant likely to report elephants as crop damaging animals than those far away (92% vs. 3%), and when asked about problem animals in general the same was true for lions (24% vs. 0%, Appendix N). Regarding local wildlife habitat, when low, in addition to primates, respondents were significantly more likely to report errant livestock and wild pigs damaging crops than when high and vice versa for birds and rabbits or hares (Table 5.4).

Table 5.4 Percentage of respondents reporting crop damaging taxa in different spatial contexts (see Q14 Appendix J). Df =1 for chi-squared tests, where χ^2 = N/A exact multinomial tests are used to estimate significance, p is two-tailed, n = 147 and respondents unaware of protected areas are included. See Appendix N for regression models for commonly reported crop damaging and problem taxa.

Crop damaging species	**Overall % reporting**	**Local Wildlife Habitat**		**χ^2**	**p**	**Distance to wilderness**		**χ^2**	**p**
		Low (%)	**High (%)**			**Far (%)**	**Near (%)**		
Elephants	0.45	0.47	0.44	0.07	0.789	**0.03**	**0.92**	**N/A**	**<0.001**
Birds	0.33	**0.24**	**0.41**	**3.94**	**0.047**	0.40	0.25	3.06	0.080
Domestic animals	0.50	**0.67**	**0.35**	**14.34**	**<0.001**	0.52	0.48	0.11	0.742
Insects	0.14	0.11	0.17	0.46	0.499	0.19	0.08	2.84	0.092
Primate	0.63	**0.79**	**0.49**	**12.83**	**<0.001**	**0.78**	**0.46**	**14.32**	**<0.001**
Dik dik	0.25	0.17	0.32	3.61	0.057	0.19	0.31	2.03	0.154
Antelope	0.03	0.03	0.04	N/A	1.000	0.03	0.04	N/A	0.676
Mongoose	0.07	0.07	0.08	N/A	1.000	0.13	0.01	N/A	0.012
Squirrel	0.16	0.11	0.21	1.62	0.203	**0.25**	**0.07**	**7.21**	**0.007**
Hare/rabbit	0.05	**0.00**	**0.10**	**N/A**	**0.009**	0.01	0.10	N/A	0.033
Wild pig	0.07	**0.13**	**0.01**	**N/A**	**0.009**	0.05	0.08	N/A	0.536
Rat	0.26	0.27	0.24	0.04	0.843	**0.38**	**0.13**	**10.81**	**0.001**
Tortoise	0.02	0.01	0.03	N/A	1.000	0.03	0.01	N/A	1.000
Mole	0.04	0.04	0.04	N/A	1.000	**0.08**	**0.00**	**N/A**	**0.032**

5.3.2. **Attitudes towards nature**

Local wildlife habitat influenced respondents’ attitudes towards local wildlife habitat and protected areas (Table 5.5, Table 5.6). Interpretation of the effect of perceptions of crop damage and distance to wilderness or protected area on attitudes is somewhat complicated as the two predictors typically loaded onto the same PCA axis, with the former loading more strongly, Table 5.6). PCA axes strongly loading (> 0.5) proximity/distance to wilderness/protected area were significant in the overall, wildlife, protected area and elephant attitude indices. As predicted overall attitude to nature responded negatively to the PCA axis for perception of animal crop damage (loading 0.88) and proximity to wilderness (loading 0.56) with a moderate effect-size (f^2 = 0.12; Table 5.6, Figure 5.6). Overall attitude to nature also weakly positively responded (f^2 = 0.06) to perception of crops lost to drought (loading 0.98) and distance to wilderness (loading 0.24). It is likely that all three predictors that loaded onto the significant ordination axes were important, the direction of the effects was as expected but due to collinearity estimating the effect size of crop losses vs. proximity is not possible.

Table 5.5 Summary of effort and score per attitude index (number of interviews) per spatial context. Effort was lower overall for protected area indices as many farmers were unaware of protected areas, especially those living far away from them. Standardised scores were centred and scaled.

	Number of interviews				**Mean (SD) score**				**Mean (SD) score standardised**			
Attitude index	**Near**		**Far**		**Near**		**Far**		**Near**		**Far**	
	High	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**
Overall	22	32	28	30	-10.77 (5.15)	-10.28 (8.35)	-4.07 (6.68)	-5.70 (8.11)	-2.18 (3.75)	-1.68 (5.59)	1.84 (5.01)	1.57 (6.06)
Wildlife	32	35	35	40	-4.00 (2.18)	-4.09 (2.43)	-3.83 (2.32)	-3.00 (2.22)	-0.26 (2.07)	-0.37 (2.54)	-0.18 (2.11)	0.67 (2.39)
Local wildlife habitat	35	36	35	41	1.23 (2.84)	0.58 (2.98)	1.17 (3.44)	0.15 (3.18)	0.35 (1.91)	-0.19 (1.78)	0.37 (2.27)	-0.52 (1.78)
Protected area	24	33	28	33	-2.79 (2.99)	-3.09 (5.14)	1.54 (3.66)	-0.24 (3.83)	-0.72 (1.43)	-0.96 (2.49)	1.18 (1.79)	0.43 (2.03)
Elephant	33	35	31	32	-3.82 (1.13)	-3.51 (1.40)	-1.97 (1.72)	-1.88 (1.56)	-1.47 (1.16)	-1.15 (1.53)	1.39 (2.04)	1.42 (1.84)

Table 5.6 Summaries of regression models for farmer attitude indices. Significant terms from models are presented, terms were only considered significant if p < 0.05 in averaged models. For each term the effect size (Cohen's f^2) is presented with the direction of the effect in parentheses and the p-values of the term for the most predictive regression model vs. the averaged model. * p < 0.05, ** p<0.01, *** p<0.001. Where terms were PCA axes the predictors loading >0.2 are presented with the loading strength in parentheses, see Table 5.2 for abbreviations. Interactions are denoted by ":" and effect sizes and significance are given for the interaction then for individual terms in parentheses. † denotes indices that were scaled and centred.

Attitude Index	**Overall**†	**Wildlife**	**Local wildlife habitat**†	**Protected areas**†	**Elephants**
Model R^2 / Cohen's f^2	0.26 / 0.30	0.26 / 0.35	0.04 / 0.04	0.25 / 0.33	0.39 / 0.64
Terms / df	3 / 108	4 / 137	2 / 144	6 / 111	6 / 124
Term 1	Recorder	Recorder	W250	CD (0.89) PX$_1$(0.51) : W1000	Recorder
Cohen's f^2 & p-values	0.14 ***/***	0.20 ***/***	0.02 (+ve) */*	0.04 (0.21:0.06) */* (***/***:ns/ns)	0.21 ***/***
Term 2	CD (0.88) PX$_1$ (0.56)	LS (0.94) LA (0.47) MI (0.29)		DR (0.96) DI$_1$ (0.31)	LS (0.82) LA (0.73) PX$_1$ (0.69)
Cohen's f^2 & p-values	0.12 (-ve) ***/**	0.08 (+ve) ***/**		0.07 (+ve) **/**	0.18 (-ve) ***/***
Term 3	DR (0.98) DI$_1$ (0.24)	PX$_2$ (0.91) LA (0.54) IN (0.36)		AE (-0.79, 0.86)* LA (0.30)	DR (0.95) DI$_1$ (0.27)
Cohen's f^2 & p-values	0.06 (+ve) **/**	0.03 (-ve) */*		0.04 (-ve) */	0.09 (+ve) ***/***
Term 4					CD (0.93) PX$_1$ (0.39)
Cohen's f^2 & p-values					0.08 (-ve) **/**

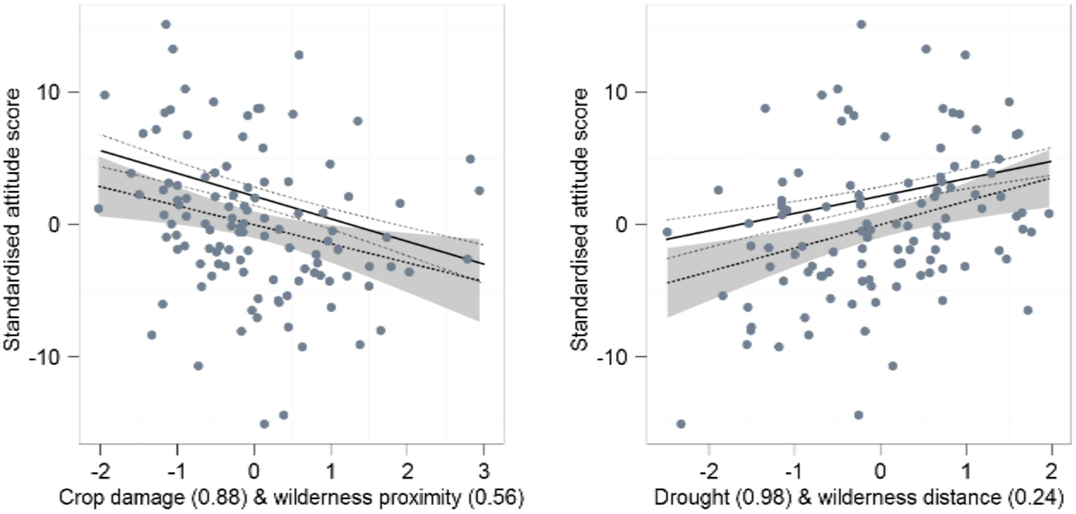


Figure 5.6 Overall attitude to nature shows a negative response to crop damage/proximity to wilderness and a positive response to drought/distance from wilderness. All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{observed}$. Predicted score (±SE) is given by the solid line with dashed CIs. Predictors are PCA transformed and loadings are given in parentheses.

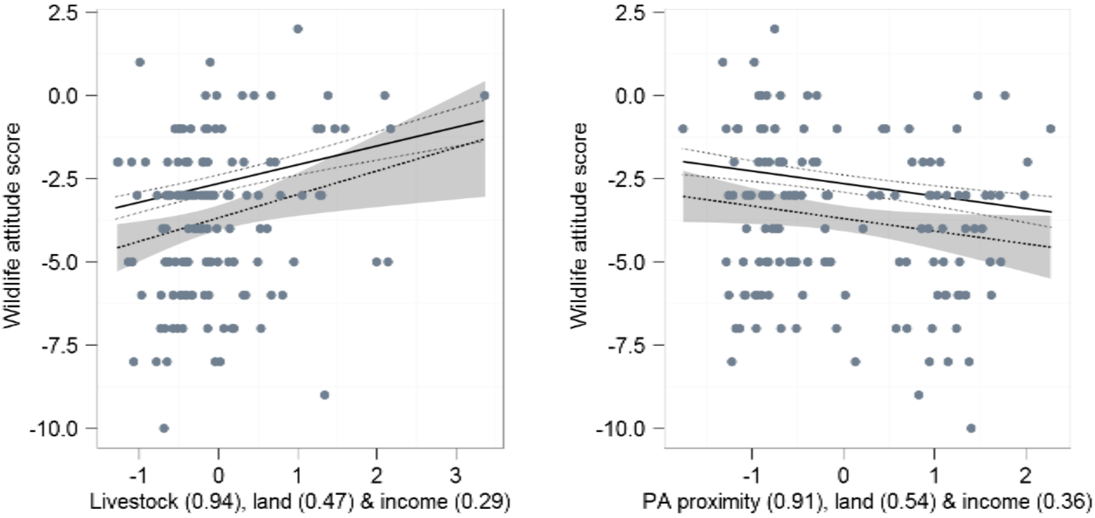


Figure 5.7 Attitude to wildlife shows a positive response to livestock value index/land owned or rented/monthly income and a negative response to proximity to protected area/land owned or rented/monthly income. All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{observed}$. Predicted score (±SE) is given by the solid line with dashed CIs. Predictors are PCA transformed and loadings are given in parentheses. PA = protected area.

Attitude to wildlife responded positively to the PCA axis for wealth (f^2 = 0.08; livestock value index, land owned or rented, and monthly income; Table 5.6, Figure 5.7) and negatively, but with a smaller effect-size, to proximity to protected area and wealth (f^2 = 0.03; proximity loading 0.91, land owned or rented 0.54, and monthly income 0.36). Agreement between paired Likert questions was high with 87% of respondents agreeing that wildlife was a problem for farming and 83% disagreeing it was beneficial (Table 5.7). Respondents perceived more problems than benefits from wildlife and the ratio of benefits to problems was significantly higher closer to wilderness areas (Table 5.8). Eleven percent of respondents reported using lethal crop protection methods such as the poisoning or trapping of problem animals (Figure 5.5).

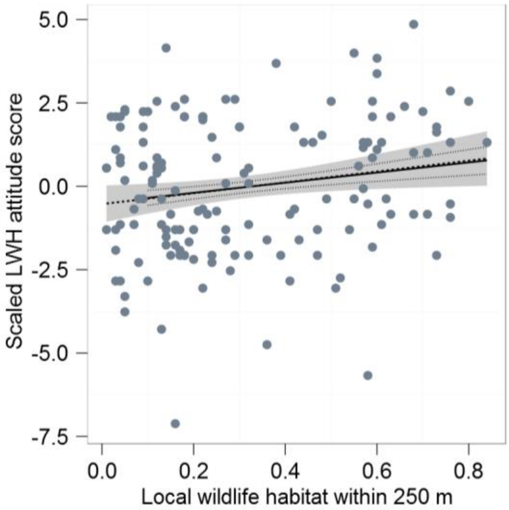


Figure 5.8 Attitude to local wildlife habitat improves with increasing local wildlife habitat within 250 m of a respondents location. All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{\ observed}$. Predicted score (±SE) is given by the solid line with dashed CIs.

Attitude to local wildlife habitat responded positively to the proportion of wildlife habitat in the respondent's local landscape (Figure 5.8) and was best predicted at the smallest scale assessed (250 m). However, the model was only weakly predictive (R^2 = 0.04) and no other terms were significant (Table 5.6). Of all the attitude indices the average response of respondents was only consistently positive for local wildlife habitat (Table 5.5) and this was driven by a perception, on average, of double the number benefits to problems from local wildlife habitat (Table 5.8). Benefits derived from local wildlife habitat were typically consumptive, 89% of respondents gathered fuel for cooking, 41% gathered construction timber from it and 12% made charcoal (Appendix L Figure L.8). The majority of respondents, 89%, perceived crop raiding animals as a problem from local wildlife habitat (Appendix L Figure L.9). The responses to fixed answer Likert questions about local wildlife habitat suggested that more respondents thought that bushland was a problem than a benefit with 62% agreeing it was a problem and 15% not, 38% agreeing it was beneficial and 41% not, and 45% of respondents agreeing it was important and 37% not (in all cases the remainder answered neutrally). Significantly fewer respondents in high local wildlife habitat landscapes (at 1000 m) agreed that local wildlife habitat was a problem that those in low local wildlife landscapes (54% vs. 69%).

Attitudes to protected areas were significantly influenced by the PCA axis for perceived animal crop damage (loading = 0.89) and proximity to wilderness (loading = 0.51), and local wildlife habitat (within 1000 m) which interacted (Table 5.6). Attitude to protected areas became more negative with increasing perceived crop damage when local wildlife habitat was low, but this effect attenuated becoming neutral when local wildlife habitat was high (Figure 5.9). Mirroring this, increasing the proportion of local wildlife habitat had a positive effect on protected area attitude, but the effect was only notable when perceived animal crop damage was high. Animal crop damage/proximity to wilderness appeared to be the more influential of the two interacting predictors as when it was excluded from the model the effect was larger (f^2 = 0.21) than when local wildlife habitat was excluded (f^2 = 0.06); the effect size of the interaction was moderate (f^2 = 0.15). Attitude to protected areas responded positively to the PCA axis for drought (loading 0.96) and distance to wilderness (loading 0.31), and negatively to the PCA axis for age (loading 0.84), years in education (loading -0.79) and land (loading 0.30), although effect sizes were smaller than for the interaction term (f^2 = 0.07 and 0.04 respectively; Figure 5.10 and Table 5.6).

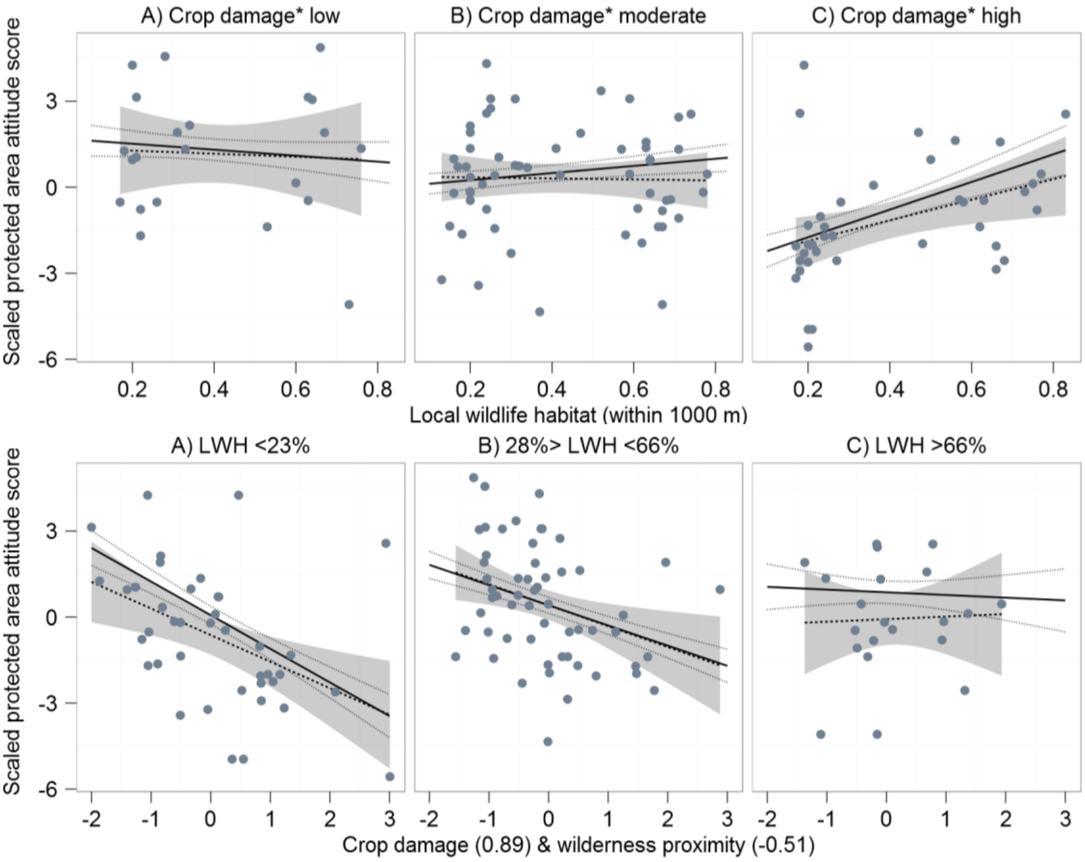


Figure 5.9 Attitude to protected areas for the interacting terms of perceived animal crop damage/proximity to wilderness and local wildlife habitat within 1000 m of the interview location. All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{observed}$. Predicted score (±SE) is given by the solid line with dashed CIs. Predictors are PCA transformed and loadings are given in parentheses. LWH = local wildlife habitat within 1000m. *PCA axis for crop damage and proximity to wilderness.

Respondents perceived fewer benefits than problems from protected areas (bootstrapped 95% CIs for their ratio was 0.58-0.80; Table 5.8), with respondents near to wilderness areas perceiving a significantly higher ratio of benefits to problems than those far away.

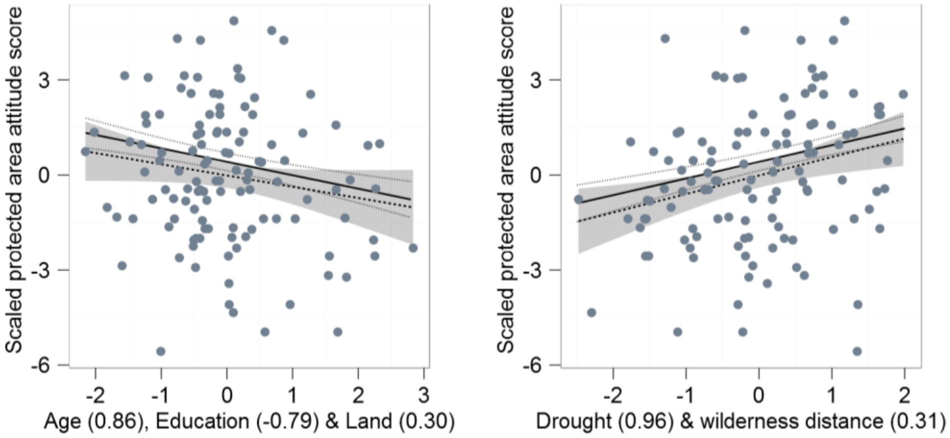


Figure 5.10 Attitude to protected areas for nature conservation declined with increasing respondent age and land owned or rented and decreasing years in education, and improved with increasing crop losses due to drought and distance from protected area. All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{\ observed}$. Predicted score (±SE) is given by the solid line with dashed CIs. Predictors are PCA transformed and loadings are given in parentheses. LWH = local wildlife habitat within 1000m. *PCA axis for crop damage and proximity to wilderness.

In general, personally and regarding their community, respondents near to wilderness areas were more likely to perceive protected areas for nature as more problematic than those far-away. Answers to fixed response Likert questions (Table 5.7) revealed that more respondents agreed protected areas were generally bad than disagreed (21% vs.46%) and responses were significantly more negative near to than far from wilderness areas (32% vs. 10% agreeing). When asked at a personal level a different pattern was observed and fewer respondents agreed that protected areas for nature benefitted them compared to those that disagreed (19% vs. 54%) and responses were significantly more positive far from wilderness areas than close (24% vs. 14% agreeing). At a personal level slightly more respondents agreed protected areas were a problem compared to those disagreeing (39% vs. 30%) and responses were significantly more negative close to wilderness areas than far (53% vs. 27%). When asked regarding their community only 14% of respondents agreed protected areas for nature were beneficial whereas 74% disagreed. Responses were more balanced when regarding protected areas as a problem to the community (36% agreeing vs. 31% disagreeing), but were significantly more negative close to wilderness areas than far (53% vs. 19% agreeing). However, when asked in general more respondents agreed that protected areas for nature were good than disagreed (64% vs.19%) and responses were significantly more positive in high than low local wildlife areas (80% vs. 53% agreeing).

Attitude to elephants negatively responded to increasing values of the PCA axis for livestock value (loading = 0.82), land owned/rented (loading = 0.73) and proximity to wilderness area (loading = 0.69), with a moderate effect-size (f^2 = 0.18, Figure 5.11). Higher values of the PCA axis for perceived crop losses to drought and distance to wilderness resulted in significantly more positive attitudes to elephants, but with a small effect size (f^2 = 0.09). Whereas higher values of the PCA axis for perceived animal crop damage and proximity gave significantly more negative attitudes, again with a small effect size (f^2 = 0.08).

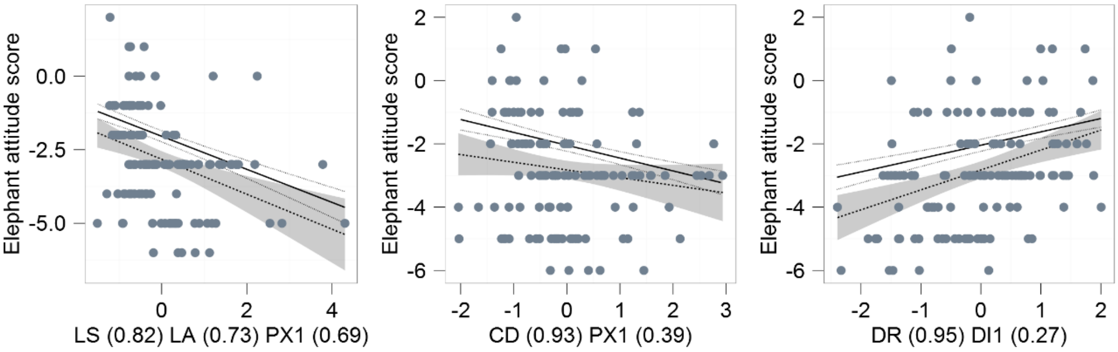


Figure 5.11 Attitude to elephants declined with increasing livestock value index (LS)/land owned or rented (LA)/proximity to wilderness area (PX1) and perceived crop damage (CD)/proximity to wilderness area, and improved with increasing perceived crop losses due to drought (DR)/distance from wilderness area (DI1). All predictors other than the x-axis are held constant at their mean. Data points are observed values. The dashed line with shaded CIs (95%) is a linear regression of $x_{observed} \sim y_{observed}$. Predicted score (±SE) is given by the solid line with dashed CIs. Predictors are PCA transformed and loadings are given in parentheses.

Overall 81% of respondents thought elephants numbers were too high, and respondents near to wilderness areas were significantly more likely to state there were too many elephants (97%) compared to those far away (64%). Lethal control of elephants (culling) was desired by 27% of respondents (Appendix L Table L.4) compared to 79% wanting non-lethal control measures that would prevent conflict by excluding elephants from non-protected wildlife areas (such as fences or translocating elephants elsewhere). Only 8% of respondents suggested no action regarding elephants was required or measures to improve coexistence (such as the construction of boreholes in protected areas to keep elephants from seeking agricultural and residential water sources). As discussed previously elephants were far more likely to be reported damaging crops near to wilderness areas (Table 5.4).

Table 5.7 Farmer responses to Likert questions regarding wildlife, local natural habitat and protected areas (see Appendix J for questions). The Bonferroni corrected p-value for statistical significance in chi-squared test is p<0.025. Responses were originally recorded on a five point scale but have been reduced to three groups to aid interpretation here. Statistical significance is highlighted in bold.

Question			**Response (%)**			**Test**		
	Grouping	**n**	**Agree**	**Neutral**	**Disagree**	**χ^2**	**df**	**p**
18. Some wildlife is beneficial to farming.	Far	81	14.3	7.7	78.0			
	Near	91	4.9	6.2	88.9	4.5	2	0.103
	High	80	13.8	8.8	77.5			
	Low	92	6.5	5.4	88.0	3.5	2	0.173
	Overall	172	9.9	7.0	83.1			
19. Some wildlife is a problem for farming.	Far	90	90.0	7.8	2.2			
	Near	80	82.5	7.5	10.0	4.6	2	0.099
	High	79	87.3	6.3	6.3			
	Low	91	85.7	8.8	5.5	0.4	2	0.819
	Overall	170	86.5	7.6	5.9			
22. Bushland and forest is important.	Far	91	40.7	18.7	40.7			
	Near	83	49.4	18.1	32.5	1.5	2	0.466
	High	81	45.7	23.5	30.9			
	Low	93	44.1	14.0	41.9	3.6	2	0.167
	Overall	174	44.8	18.4	36.8			
23. Having bushland or forest near or around the shamba is a problem for my farming.	Far	90	64.4	18.9	16.7			
	Near	75	58.7	28.0	13.3	2.0	2	0.369
	High	**78**	**53.8**	**33.3**	**12.8**			
	Low	**87**	**69.0**	**13.8**	**17.2**	**8.9**	**2**	**<0.001**
	Overall	165	61.8	23.0	15.2			
24. Having bushland or forest near or around the shamba (farm) is beneficial to my farming.	Far	89	34.8	23.6	41.6			
	Near	79	40.5	19.0	40.5	0.8	2	0.675
	High	78	35.9	24.4	39.7			
	Low	90	38.9	18.9	42.2	0.7	2	0.689
	Overall	168	37.5	21.4	41.1			
27. Protected areas for nature are a good thing.	Far	73	71.2	15.1	13.7			
	Near	66	56.1	18.2	25.8	4.0	2	0.132
	High	**59**	**79.7**	**8.5**	**11.9**			
	Low	**80**	**52.5**	**22.5**	**25.0**	**11.0**	**2**	**0.004**
	Overall	139	64.0	16.5	19.4			
28. Protected areas for nature are a bad thing.	**Far**	**70**	**10.0**	**27.1**	**62.9**			
	Near	**66**	**31.8**	**39.4**	**28.8**	**17.9**	**2**	**<0.001**
	High	59	13.6	28.8	57.6			
	Low	77	26.0	36.4	37.7	6.0	2	0.051
	Overall	136	20.6	33.1	46.3			
29. Protected areas for nature are beneficial to me.	**Far**	**71**	**23.9**	**38.0**	**38.0**			
	Near	**66**	**13.6**	**15.2**	**71.2**	**15.5**	**2**	**<0.001**
	High	59	18.6	30.5	50.8			
	Low	78	19.2	24.4	56.4	0.7	2	0.716
	Overall	137	19.0	27.0	54.0			
30. Protected areas for nature are a problem for me.	**Far**	**71**	**26.8**	**33.8**	**39.4**			
	Near	**66**	**53.0**	**27.3**	**19.7**	**10.9**	**2**	**0.004**
	High	58	36.2	32.8	31.0			
	Low	79	41.8	29.1	29.1	0.4	2	0.799
	Overall	137	39.4	30.7	29.9			
31. Protected areas for nature benefit my community.	Far	67	16.4	11.9	71.6			
	Near	66	12.1	10.6	77.3	0.6	2	0.732
	High	58	19.0	10.3	70.7			
	Low	75	10.7	12.0	77.3	1.9	2	0.396
	Overall	133	14.3	11.3	74.4			
32. Protected areas for nature create problems for my community.	**Far**	**68**	**19.1**	**42.6**	**38.2**			
	Near	**66**	**53.0**	**22.7**	**24.2**	**16.893**	**2**	**<0.001**
	High	59	37.3	25.4	37.3			
	Low	75	34.7	38.7	26.7	3.016	2	0.221
	Overall	134	35.8	32.8	31.3			

Table 5.8 Benefits and problems associated with wildlife, local wildlife habitat around farms and protected areas. Statistical significance occurs between groups when their bootstrapped 95% confidence intervals do not overlap.

	Grouping	**n**	**Mean (SE) number**		**Ratio of benefits to problems**	
			Benefits	**Problems**	**Mean**	**Bootstrapped 95% CIs**
Wildlife	Far	83	0.43 ± 0.08	2.43 ± 0.12	0.18	0.12 - 0.25
	Near	91	0.87 ± 0.09	2.30 ± 0.12	0.38	0.30 - 0.47
	High	93	0.78 ± 0.09	2.33 ± 0.13	0.34	0.25 - 0.43
	Low	81	0.52 ± 0.08	2.40 ± 0.12	0.22	0.15 - 0.29
	Overall	174	0.66 ± 0.06	2.36 ± 0.09	0.28	0.23 - 0.34
Local wildlife habitat	Far	83	2.18 ± 0.13	1.05 ± 0.05	2.08	1.80 - 2.41
	Near	91	2.22 ± 0.14	1.05 ± 0.06	2.11	1.79 - 2.47
	High	93	2.02 ± 0.12	1.13 ± 0.06	1.79	1.52 - 2.06
	Low	81	2.41 ± 0.15	0.96 ± 0.05	2.23	2.15 - 2.93
	Overall	174	2.20 ± 0.10	1.05 ± 0.04	2.1	1.87 - 2.35
Protected area	Far	66	1.30 ± 0.13	2.41 ± 0.12	0.54	0.44 - 0.66
	Near	71	1.52 ± 0.14	1.73 ± 0.14	0.88	0.69 - 1.11
	High	79	1.22 ± 0.13	2.04 ± 0.14	0.60	0.47 - 0.76
	Low	58	1.69 ± 0.13	2.09 ± 0.14	0.81	0.66 - 0.99
	Overall	137	1.42 ± 0.10	2.06 ± 0.10	0.69	0.58 - 0.80

5.4. Discussion

The low-income small-scale farmers living within the buffer zone of a large sub-Saharan African wilderness area did perceive substantial ecosystem disservices in the form of crop losses due to animals. However, against predictions perceptions of animal crop damage were not significantly influenced by distance to wilderness (a very large area of land spared for biodiversity) or the amount of local wildlife habitat within the vicinity of their farms (usually unprotected dry forest vulnerable to agricultural conversion). The reporting of primates damaging crops was the only significant predictor of respondents' perceptions of crop damage. Whilst many other human-wildlife conflict studies from tropical small-scale systems have also found land-use change or spillover of primates into croplands to be a perceived and actual issue for the residents of buffer zones (Naughton-Treves 1998; Hill 2004; Warren et al. 2007; Hoffman and O'Riain 2012; Wallace and Hill 2012), this study counter-intuitively found when primates were present perceived crop losses due to animals were actually lower. This was most likely explained by differences in crop protection against animals in the presence or absence of primates. Farmers were five times more likely not to protect their crops at all when they thought primates were not damaging their crops, and when primates were present farmers were significantly more likely to protect crops by human or canine guarding or by using scarecrows. Guarding against primates has been found to be a particularly effective method of reducing primate crop damage in a similar Ugandan context, however it does present a significant opportunity cost to a household due to the labour required (Webber

2006). Regarding land-sparing linking mechanisms (LSLMs) required to make large-scale trades-off in commodity production and biodiversity conservation work (Phalan et al. 2014) this suggests that conservation initiatives that enhance the efficacy of farmers' current primate crop protection methods (see Hockings and Humle 2009), especially in terms of labour reduction, to mitigate crop-raiding primates will be well received and could lead to decreased perception of animal crop damage. Less positively, it may also suggest that when farmers perceive less threat of primate crop raiding then they invest less resources into crop protection and exposing them to increased risk of crop damage by non-primate species in turn this could modify their perception of wildlife crop damage. Perceptions of animal crop damage were significant predictors in several attitude indices however the interpretation of this is complicated by co-loading with proximity to protected areas, although the former typically loaded more than twice as strongly than the latter. Notably, perceived animal crop damage/proximity to wilderness area did not significantly influence attitudes to local wildlife habitat but did for protected areas, attitudes that will be discussed in more detail shortly.

Whilst perceptions of animal crop damage and crop protection methods did not significantly change with distance from wilderness, the reporting of particular groups of animals damaging crops did. Birds, primates, squirrels and rats were reported significantly more frequently at greater distances. This could reflect actual animal distribution patterns, perhaps driven by meso-predator release due to loss of predators with degradation of natural habitats (Brashares et al. 2010; Ruscoe et al. 2011) and distance from wilderness (Holmern et al. 2007; Gusset et al. 2009), or changes in the abundance of species that favour or avoid open agricultural landscapes. Alternatively it could reflect a tendency of farmers to focus on elephant damage when elephants are present and to perceive more damage from other animals when elephants are not a problem. Perceptions of risk are skewed towards more "visible" species (i.e., large animals Hill 2004) and, in pastoral trans-Himalayan systems, perception of livestock depredation by wolves was better explained by wolf abundance rather than actual wolf depredation rates (Suryawanshi et al. 2013). This phenomenon has implications for conservation management, for example mitigating human-elephant conflict could unexpectedly enhance perceived conflict with other species or restoration of disturbed habitats (e.g. improving connectivity for elephants or lions) could alter the spillover of crop raiding animals. To establish the underlying mechanisms of respondents' behaviours, attitudes and perceptions further study is required to quantify actual levels of crop damage, frequency of crop raiding events and the distribution and density of perceived pest species.

Crop damage by domestic stock was an issue in the interpretation of animal crop damage, changes in density of livestock with landscape could explain why local wildlife habitat did not have an effect on perceptions of animal crop damage. Crop damage by livestock has been shown to be an important driver of crop losses in a similar Ugandan context increasing with distance from forest edge as damage by wildlife falls (Webber 2006), and more generally in the buffers of other African protected areas (Gillingham and Lee 1999; Warren et al. 2007). Farmers were typically uncertain as how much crop damage livestock had caused compared to wild animals so only "animal" damage was assessed. More detailed questioning or advanced interview techniques could perhaps improve the situation but field data on actual livestock vs. wild animal crop raiding is preferred. Respondents in this study did report livestock as damaging crops almost twice as frequently in low compared to high wildlife habitat landscapes with no difference between reporting near and far to wilderness areas. This suggests that perceptions of livestock crop raiding changed with landscape composition, rather than distance from protected area per se (Webber 2006). In this context increasing agricultural area also increased human population densities, therefore changing perceptions of livestock raiding could reflect increased livestock density and therefore demand for livestock fodder and grazing land (Mishra et al. 2004), social factors (Dickman 2010), or changes in farming practise, such as large communal fields with shared management and diffuse boundaries that are more difficult to defend against wandering livestock.

Overall farmer attitude to nature (attitudes to local wildlife habitat, wildlife in general, protected areas and elephants combined) was significantly reduced by increasing perceived crop losses due to animal damage and proximity to wilderness, and increased by perception of crops losses due to drought and to a lesser degree distance from wilderness. Whilst perceived crop losses and proximity to wilderness loaded onto the same ordination axis, the direction of effects on attitudes matches *a priori* expectations and it is likely that both were having a significant negative effect on attitudes. These findings provide some support for the assumption that attitudes would be more negative closer to wilderness areas (e.g., Sarker and Røskaft 2011) due to increased perception of ecosystem disservices (De Boer and Baquttee 1998) such as animal crop damage or livestock predation (e.g., Allendorf et al. 2006; Webber 2006; Holmern et al. 2007; Linkie et al. 2007; Røskaft et al. 2007; Gusset et al. 2009). Comparison of the sub-indices of attitude suggested that a strong negative response of attitude towards elephants with increasing proximity to wilderness was likely to be driving this trend. However, as discussed subsequently, animal crop damage did not significantly influence attitudes towards wildlife per se and the ratio of benefits to problems perceived from protected areas was significantly higher closer to rather than far from protected areas. Also the strong co-loading of perceived animal crop damage and proximity onto the same PCA ordination axis was not well supported in the analysis for perceived animal crop damage, discussed previously, which suggested that perceived animal crop-damage was not significantly affected by proximity to wilderness, or by the fact that the untransformed values did not significantly differ between near and far locations. Thus it cannot be reliably inferred from the ordination that perceptions of crop damage were significantly higher closer to wilderness areas, as was expected, but it does suggest that there could be an underlying trend requiring more statistical power to unambiguously detect. The mechanism for perception of crop losses due to drought affecting attitude is unclear, clearly crops lost to drought cannot then be lost to animals and perceptions of animal loss could thus be diluted, and this could in turn affect attitudes to nature. However, as perceptions of crop losses due to animals were not significantly influenced by perceived crop losses due to drought there does not appear to be a strong argument for this explanation.

There was evidence that attitudes towards elephants consistently responded negatively to ordination axes that loaded proximity to wilderness. Although proximity always co-loaded with other factors, given that farmers were 30 times more likely to report elephants damaging crops near to wilderness areas than far and more commonly stated elephants numbers were too high, it is reasonable to assume that proximity was having a strong effect on elephant attitudes rather than just the co-loading predictors. These patterns are consistent with the general findings of studies of elephant movements and/or crop-raiding. Raiding into crops by elephants from large areas of natural habitat, occurred at a mean distance of 1.54 km in Kenya (Graham et al. 2010) and within 6 km for Asian elephants (*Elephas maximus indicus*) in South India (Gubbi 2012), although some African elephant individuals can show a preference for small-scale farming compared to natural habitats penetrating deeper into them (Graham et al. 2009). A strong negative response in attitude to elephants is also in-keeping with perceptions of risk being skewed towards large or visible species (Hill 2004). Bearing in mind co-loading with proximity/distance to wilderness, increasing perceived animal crop losses made attitudes towards elephants more negative and increasing perceived drought crop losses made attitudes more positive. Regardless of the exact mechanism, at distances of greater than 10 km from wilderness area residents of the Taita-Tsavo buffer zone no-longer considered elephants to be a problem species at a personal level and had more a positive attitude towards them than people living much closer to the wilderness. Local landscape structure appeared to have little effect on attitudes to elephants overall or when considering responses to individual questions, this contrasts with actual data on elephant crop raiding from Laikipia district, Kenya which suggested that aggregated smallholdings should suffer less conflict with elephants (Graham et al. 2010). It could be that elephants are behaving differently in the Taita-Tsavo buffer zone or that perceptions of crop raiding animals poorly reflect actual risk (Hill 2004; Webber 2006). High resolution spatiotemporal data for elephant movements and crop raiding in the study area is required to investigate potential mismatches between farmer perceptions or attitudes and reality. If elephants or other functionally similar large animals are present within wilderness areas of importance for land-sparing then LSLMs should focus on mitigating human conflicts with these species within the immediate vicinity (< 6km) of the boundaries between agriculture and wilderness, taking into account landscape features such as rivers, waterholes, corridors or traditional migration routes (Hoare 2000; Douglas-Hamilton et al. 2005; Galanti et al. 2006) that could provide exceptions to this general rule. Fortunately, there is a wealth of information with regards to the mitigation of human-elephant conflict (for example see Osborn and Parker 2003; Jackson et al. 2008; King et al. 2009; Graham et al. 2010; King et al. 2011; Webber et al. 2011), given the recent upsurge in elephant poaching (Wittemyer et al. 2014) and continental declines in large mammals (Craigie et al. 2010; Maisels et al. 2013) the need for effective conservation has never been greater.

Against expectations, there was no evidence that proximity to a wilderness area affected attitudes towards local wildlife habitat (dry forest), however farmer attitude to local wildlife habitat was positively influenced by the amount of wildlife habitat in the vicinity of their land and this response was strongest when considering dry forest within the immediate vicinity of their landholding (within 250 m). A weak effect size of the amount of local wildlife habitat on attitudes towards could mean that there is a trade-off between costs and benefits perceived from it, and that other factors need to be taken into consideration, such as length of residency (Gillingham and Lee 1999) or social parameters (Dickman 2010). In general farmers stated more tangible benefits than costs from dry forest and this could explain the positive effect that the amount of local wildlife habitat had on attitudes towards it. Previous research has shown that the attitudes of nearby residents towards protected areas are more positive if they are permitted to extract resources or experience direct benefits (Infield 1988; Fiallo and Jacobson 1995; Maikhuri et al. 2001). A study from Burma found that access to extraction benefits meant people were five times more likely to have a positive view of protected areas (Allendorf et al. 2006). This study suggests the same is true of local wildlife habitats but with a considerably less pronounced effect-size than reported by Allendorf et al. (2006). Protected areas within this study area were off-limits to nearby communities and resource extraction prohibited and accordingly respondents perceived fewer benefits than problems from protected areas (in contrast to accessible local wildlife habitats) and few thought protected areas benefitted them at a personal level. Benefits from local wildlife habitat related to consumptive uses, such as the provision of fuel wood, timber and charcoal, and the grazing of livestock, uses that may be unsustainable (Ektvedt 2011; Alkemade et al. 2013; Brown et al. 2013; Al-Amin 2014) and encourage further agricultural expansion (Hartter et al. 2011). With regards to LSLMs this generally suggests that interventions to conserve natural habitats will need to consider their current utility to poor smallholders and that preventing extractive uses is likely to negatively impact attitudes and, speculatively, substituting resources provisioned by natural habitats could reduce the perceived value of natural habitats.

Perceptions of animal crop damage and proximity to protected areas had a strong negative effect on attitudes towards protected areas when local wildlife habitat was low, but had little effect when local wildlife habitat was high. In other words, increasing amounts of local wildlife habitat appeared to moderate the negative effects on attitudes to protected areas from increasing perceived animal crop damage and, to a lesser degree, proximity to wilderness area. It is possible that enhanced access to or provision of resources from local wildlife habitat, when it was abundant in the vicinity of a farm, was seen to compensate for crop damage from animals from protected areas. This would be in keeping with studies, as discussed previously, that found access to extractive benefits from protected areas enhanced attitudes towards them (Infield 1988; Fiallo and Jacobson 1995; Maikhuri et al. 2001; Allendorf et al. 2006). Attitude to protected areas also positively responded to increasing perception of crop losses due to drought (co-loading, to a lesser degree, with distance from wilderness); as discussed for overall attitudes towards nature, the mechanism for this is unclear but could relate to attribution of blame for crop-losses. Older and less educated farmers had a more negative opinion of protected areas than younger farmers who tended to have at least received primary education (median 6 years). Education has been demonstrated to be an important driver of perceptions and attitudes in a range of human-wildlife conflict studies (Infield 1988; Fiallo and Jacobson 1995; Allendorf et al. 2006; Holmern et al. 2007; Kideghesho et al. 2007; Røskaft et al. 2007; Suryawanshi et al. 2014) and it is interesting that education and age only had a significant effect on attitudes towards protected areas and not wildlife, local wildlife habitat or elephants. Examination of responses to individual questions showed that at a personal or community scale farmers perceived few benefits from protected areas and more problems, the situation being worse closer to wilderness areas, in keeping with predictions. However when asked in general more than double the number of respondents reported protected areas were good rather than bad and the benefits reported from protected areas suggest that there was a good awareness of the regional and national economic benefit of the parks and their role in conserving Kenya's natural heritage. Regarding LSLMs, this again suggests that extractive resource use at a local scale within buffer-zones is important for conservation attitudes, this time for land-sparing at a large-spatial scale and not just within the vicinity of a smallholder's land, and that investment in education may improve perceptions and attitudes towards conservation at large scales but less so at local scales.

Finally, attitudes towards wildlife, in contrast to attitudes towards local wildlife habitats, were negative and a significant majority of farmers stated that wild animals were a problem for farming and that crop-raiding animals came from local wildlife habitat. Increasing proximity to a protected area (and to a lesser extent land ownership and income) significantly lowered attitudes to wildlife, this was likely linked to an increased conflict with elephants and lions which were reported as problem animals far more frequently closer to protected areas than further away. Studies of predators have found that people who experience material losses by having large carnivores nearby express more negative attitudes towards them (Holmern et al. 2007; Røskaft et al. 2007). Although other studies suggest attitudes to be more related to cultural or social factors than material losses (Heinen 1993; Gangaas et al. 2013) and synthetic review has shown that subsistence farmers compared to commercial farmers have a lower probability of being positive towards carnivores irrespective of material losses (Kansky et al. 2014). The mechanism by which increasing proximity affects attitude to wildlife here is unclear as perceptions of crop damage (material losses) did not significantly influence attitude towards wildlife perhaps suggesting that cultural or social factors may be more important. Farmers with more livestock, typically having larger land-holdings and higher incomes too, had a more positive attitude towards wildlife, perhaps suggesting crop raiding animals, elephants in particular, presented less risk to their livelihoods. Graham et al.'s (2009) study of elephant movements in another Kenyan small-scale farming landscape including ranches and reserves found that the more smallholder land within an elephant's range, the more it was utilised and the higher the degree of conflict. Therefore it could be possible, in this study's location, that elephant behaviour differs between landowners that primarily invest in livestock vs. those that are primarily rely on arable farming. In general, indicators of prosperity are associated with improved attitudes towards wildlife including carnivores (indicators were farm production and employment, Suryawanshi et al. 2014), protected areas (employment outside of farming, Allendorf et al. 2006) or conservation in general (general affluence, Infield 1988). With regards to LSLMs in buffer-zones this suggests, as for the elephant attitude index, that the need to mitigate human-wildlife conflict increases with proximity to protected areas. A potential avenue for future trade-off analyses for biodiversity conservation vs. commodity production and the needs of buffer-zone stakeholders would be to examine how landscapes of consolidated livestock holdings, as an alternative to landscapes of small-scale crop production, could change attitudes and perhaps reduce conflict. However, a drastic land-use shift from small-scale arable to consolidated pastoral production would result in complex and multi-faceted trade-offs and cannot be justified on the analysis presented here (e.g., there was no evidence to suggest that a pastoral income from consolidated land would improve attitudes towards natural habitats at local or large scales, or elephants) or from information currently available in scientific literature. Increasing livestock densities could result in increased competition between wild and domestic animals for resources and over-grazing could lead to the degradation of natural habitats (Mishra et al. 2004). Further, conversion from arable to meat and dairy productions may be a relatively unsustainable means of producing calories and commodities from existing farmlands potentially increasing demand for land (Steinfeld et al. 2006; Virani et al. 2011; Herrero et al. 2013). Whilst land-use consolidation is a controversial issue, it is already a trajectory that is politically desired and promoted in many countries, such as China (Min 2006; Huang et al. 2011) and Rwanda (Bledsoe et al. 2007; Ntirenganya 2012), and is typically the path that agricultural development in high-income nations has taken as labour productivity increases (Rackham 1986; Vitikainen 2014). It is pragmatic to assume that, given changes in economic opportunities (Lambin et al. 2001), this too could be the fate of small-scales farms in many buffer zones, thus predicting the consequences of consolidation and associated social and demographic change on commodity production, human-wildlife conflict and biodiversity will be important.

5.4.1. **Conclusions**

In summary the linking-mechanisms required to make land-sparing work (LSLMs) need to ensure the conservation or restoration of natural habitats (spared land) and the wildlife they support. This will depend on understanding of how stakeholder attitudes, perceptions and behaviours change, and how ecosystem services and ecosystem disservices operate across different spatial scales and social, economic and biogeographic contexts. The farmer interviews conducted in this study provide evidence that attitudes to natural habitats and biodiversity are affected by the scale at which land-sparing is considered and the isolation of a respondent from large-scale spared areas (wilderness) in particular. The proportion of local wildlife habitat in the landscape positively affected attitudes towards local wildlife habitat and moderated the negative effect that perceived animal crop damage (and proximity to wilderness) had on attitudes towards protected areas. Proximity to wilderness (in combination with perceived animal crop damage) had a negative effect on attitudes overall and to wildlife, protected areas and elephants specifically, but not local wildlife habitats. This may have been due to trade-offs between ecosystem services and disservices operating at different spatial scales. Land-sparing at a large scale (wilderness or protected areas) conserves or restores habitats that in turn support large animals that compete for land with buffer zone residents at the edges of the reserves, reflecting the negative effect of proximity on attitudes and the increased reporting of lion and elephants as problem animals. Protected areas were off-limits to buffer-zone residents, and thus were perceived to provide few personal benefits compared to the costs and risks associated with large mammals; however it should be noted that this study is not advocating resource extraction from protected areas as a solution to human wildlife conflict. Respondents did, however, perceive benefits from large areas of spared land at a regional and national scale and thought protected areas were a good thing in general. Unlike for protected areas, farmers stated more benefits than problems from local wildlife habitats and extractive resource use may explain its positive effect on attitudes towards natural areas at local and large scales. Attitudes towards local natural habitats were more positive than for the wildlife associated with them, therefore the conservation of wildlife may require different LSLMs than for the habitat that supports it and LSLMs for wildlife may be more controversial to stakeholders and difficult to implement.

The observed spatial effects of land-use change on perceptions and attitudes of smallholder stakeholders within the Taita-Tsavo buffer zone highlights the priority areas and species for ecosystem disservices (human-wildlife conflict) that LSLMs will need to consider within a common farming context important for biodiversity conservation. Crucially, such interview-based approaches allow limited resources to be effectively targeted at an early stage and help elucidate the key issues and concerns for a majority of stakeholders. Unexpected results where attitudes and perceptions do not closely match *a priori* assumptions may suggest mismatches between perceptions and reality or incorrect assumptions; in such cases the underlying mechanisms defining perceptions and attitudes require more detailed study. Given the effort that will be required to facilitate LSLMs, and the complexity of real-world situations compared to intellectual frameworks, a strong evidence base is required to justify interventions. Whilst the findings presented here highlight the point that human perceptions and attitudes of ecosystem disservices and conservation issues vary with the scale and context of land-sparing, they will need to be integrated within a wider body of evidence to inform

LSLMs. Although evidence regarding ecosystem disservices already exists from studies of human-wildlife conflict in social, development and conservation disciplines, more data is required for their effects on stakeholder decision-making and trade-offs with ecosystem services and other factors, especially in a form that can be used to predict how they scale spatially.

Chapter 6. General Discussion

Billions of people, largely in rural developing areas, rely on small-scale farming for their income and food security (IFAD & UNEP 2013). Rising global population and changing diets are increasing global land scarcity and commodity prices (Lambin and Meyfroidt 2011; Tilman et al. 2011; Alexandratos and Bruinsma 2012); to meet this demand part of the solution entails improving agricultural productivity in small-scale farming landscapes where there are crop-yield-gaps (Bindraban et al. 2000; Licker et al. 2010). Small-scale systems are typically dynamic (van Wijk et al. 2009) with land-use and management responding to local and global drivers of change (Serneels and Lambin 2001) including demographic trends such as human population growth and rural to urban migation or economic drivers such as commodity prices. As such, rapid changes will occur and are already happening in small-scale farming systems resulting in agricultural abandonment, consolidation, expansion and/or management intensification (Xinshe 2002; Min 2006; Bledsoe et al. 2007; Lambin and Meyfroidt 2011; Collier and Dercon 2013).

With the increase of both global land scarcity and commodity demand it is inevitable that the rate of change in small-scale faming systems is only likely to increase (Collier and Dercon 2013). With land-use change comes trade-offs, such as increasing agricultural area or management intensity to raise yields vs. loss of ecosystem services and biodiversity; there is now considerable interest in how to best optimise trade-offs in land-use at multiple spatial scales to sustainably optimise commodity production, biodiversity and livelihoods or social capital (Fischer et al. 2014; Phalan et al. 2014). The development of the sustainable intensification paradigm (Pretty 2008), which includes the concept of ecological intensification (optimising ecosystem services)(Bommarco et al. 2013), the profusion of ecosystem service research in agro-ecosystems and the body of literature regarding the land-sharing land-sparing debate reflects the global need to address current and future land-scarcity and commodity demand whilst making agriculture more sustainable (with regards to inputs, long-term viability and biodiversity).

With a focus on regulating ecosystem services and disservices in tropical small-scale farming landscapes, this thesis aimed to address the relevance of such literature to land-use change in small-scale farming systems, highlight the importance of ecosystem disservices and human-wildlife conflict regarding biodiversity conservation, and to provide new data regarding the response of agriculturally important insect taxa to land-use change in a novel context.

Chapter 2 revealed that there were no quantitative reviews of regulating ecosystem services with specific relevance to land-use change in small-scale farming systems highlighting a considerable knowledge gap for sustainable/ecological intensification and trade-off analyses for ecosystem services vs. other goods or services such landscapes provide. There was evidence that the data used to populate quantitative reviews regarding regulating ecosystem service research into pollination and biological control were strongly biased towards large-scale farming systems, although Kennedy et al. (2013) did consider local landscape structure in their analysis of local and landscape effects on wild bee pollinators. Individual reviews of biological control were significantly and strongly biased towards data from large-scale farming in temperate regions. In contrast pollination reviews included more smallholder studies and were more balanced between climatic regions. It was also found that the majority of smallholder studies included in quantitative reviews (72%) were related to coffee, a crop that is distinct in its structure and management from the herbaceous annuals that provide most of our global calories and a crop that is a stimulant of no direct relevance to food security. Thus, even when data from small-scale systems was included in reviews it was often unrepresentative of the most important crops for food security. More balance in future ecosystem services research or synthesis by a greater consideration of a diverse range of smallholder-farmed landscapes in Africa and continental Asia will help to reduce these knowledge gaps. Of particular importance to both regions will be the resilience of ecosystem services and disservices in small-scale farming systems to climate change and how this is affected by land-use intensification (Cooper et al. 2008). Whilst rural populations are generally increasing in these regions, for economic development to ultimately succeed it is thought that increases in agricultural labour productivity will lead to large-scale emigration from rural areas (Collier and Dercon 2013). Rural-urban migration has occurred in developed nations (Allen 2009), is occurring in countries such as China (Zhang et al. 2007) and is likely to occur with future development in others (Collier and Dercon 2013). Framing current trends in rural land-use change with urban migration in terms of its effect on ecosystem services will help trade-off analyses to determine how best to conserve landscape features important to sustainable crop production as farmlands intensify.

The consequence of land-use intensification can be investigated by comparing landscape at different stages along development pathways. For example, Chapter 3 demonstrated that field enlargement and agricultural extensification in low-input small-scale farming landscapes in semi-arid Kenya had a negative impact on stingless bee abundance within croplands. As stingless bees are important crop pollinators this could have impacts regarding the ecosystem service of crop pollination and ultimately the provisioning of crop yields. Land-use extensification, at the relatively low levels observed in the study area, had no negative effect on larger, non-stingless bee abundance. This was not surprising as larger bee species typically have greater foraging ranges than smaller ones and are therefore less vulnerable to land-use change at smaller spatial scales (Greenleaf et al. 2007). The responses of predators and parasitoids (potential natural enemies and biological control agents) to land-use extensification were more mixed. Ground beetles responded positively as natural habitat was replaced by cropland and predatory Hymenoptera weakly declined; neither showed a response to field enlargement (distance from field edge). Parasitoid Hymenoptera abundance increased as natural habitat was replaced by cropland especially as distance to field edge increased. This perhaps suggests that many natural enemies were cultural species that benefited from landscapes increasingly dominated by agriculture and reflects minimal to no pesticide use in study fields. Tenebrionid beetles, which are potential ecosystem disservice providing crop pests (Allsopp 1980), responded positively to the conversion of natural habitat to cropland close to water, but negatively further away with the identity of the dominant tenebrionid species changing. As tenebrionids and stingless bees both negatively respond to the loss of natural habitat close to water, there may well exist a trade-off between ecosystem services and disservices as small-scale farming landscapes extensify. Whilst these patterns appear largely consistent with contemporary theory regarding landscape effects on ecosystem service providing species, the response of stingless bees, for example, to land-use change even in a complex low-input landscape demonstrates the importance of geographic context. Stingless bees are absent from temperate climates and therefore conclusions drawn from temperate studies applied to tropical climates may underestimate the effect of land-use change on pollinators.

Applying a functional diversity approach examining flower-visiting Hymenoptera and epigeal Coleoptera communities (Chapter 4) suggested that agricultural extensification in low-input small-scale farming landscapes increased the dominance of phytophagous traits in turn suggesting that ecosystem disservice due to herbivory could increase. Increasing functional trait richness with agricultural extensification, for both Hymenoptera and Coleoptera, provided support for the intermediate land-use hypothesis (Tscharntke et al. 2012b). Unextensified landscapes were relatively simple and dominated by dry forest, whereas extensified landscapes were more heterogeneous and contained a mixture of complex small-scale farmland and remnants of dry forest; the heterogeneity in the latter increases complementation (Dunning et al. 1992) where the needs of many species that move between multiple habitats to complete their life-cycles are met (Kremen et al. 2007; Kremen et al. 2008). For Chapters 3 and 4, linking changes in functional diversity, species abundance or dominance to crop-yields is required for accurately predicting the ecosystem service or disservice consequences of land-use change, and knowledge gaps regarding the basic ecology and biology of agricultural insects in sub-Saharan Africa need to be addressed. Yield effects of different functional groups can be assessed in-situ using manipulations to exclude (e.g., Freitas and Paxton 1996; Perfecto et al. 2004; Borkhataria et al. 2006; Priston 2009) or enhance (e.g., Vaissiare et al. 2011) particular functional groups. Direct observations, pollen analysis or trap nests (Tscharntke et al. 1998; Dafni et al. 2005) can be used to determine trophic interactions between some species and advances in DNA sequencing such as DNA-barcoding (Valentini et al. 2009b) allow the identification, for example, of insect gut contents to infer trophic connections within a community (discussed subsequently).

Information regarding land-use change effects on ecosystem services and disservices (Chapters 3 and 4) can be used to predict trade-offs between commodity production, multiple ecosystem services and biodiversity conservation, which are essential to the design of future farming landscapes optimised for sustainable commodity production in small-scale farming (and other properties). Trade-offs can occur at different spatial scales (Fischer et al. 2014) and this is especially important in biodiversity conservation where large continuous habitats must be spared from agricultural conversion for conservation of certain species, such as large mammals, that cannot persist in agricultural landscapes. Whereas land-sparing (as refined by Fischer et al. 2014) for ecosystem services may occur at smaller scales, e.g., relevant to the foraging ranges of pollinators, land-sparing to optimise the trade-offs between biodiversity and increasing commodity production at large-spatial scales requires the conservation of large intact areas of non-protected natural habitats, in particular, within the buffer zones of protected areas (e.g., Laurance et al. 2012). This in turn requires interventions to restore natural habitats and to prevent their degradation or conversion to farmland by buffer-zone stakeholders, which are typically smallholders in developing tropical nations (Wittemyer et al. 2008). Ecosystem disservices from large or abundant animals (which is synonymous with human-wildlife conflict) can be particularly severe within buffer zones (Distefano 2005). As such, understanding the spatial correlates of the attitudes and perceptions of buffer-zone stakeholders to wildlife and natural habitats will be essential for the successful planning of conservation for land-sparing (land sparing linking-mechanism, LSLMs).

In the buffer zone of the Tsavo ecosystem, Kenya, where large mammals include African elephants, lions and yellow baboons, this study found that proximity to a wilderness area (a large-area of spared land) negatively affected smallholder attitudes towards protected areas, wildlife in general and elephants in particular. However, proximity to wilderness did not affect attitudes towards local wildlife habitat (dry forest), which was likely explained by the benefits that local wildlife habitat provided such as fuel wood and timber, or grazing and browse for livestock. Although smallholders perceived benefits, they still considered crop-raiding by wildlife from nearby habitats to be a major ecosystem disservice from it. This suggests that whilst smallholders may be receptive to the conservation of dry forest on the basis that they can extract important resources from it, conserving the wildlife that uses the dry forest may be more difficult and different LSLMs may be required for habitats and the (mobile) fauna they support. Interestingly, the presence of a high proportion of local wildlife habitat within the vicinity of a smallholder's field appeared to moderate the negative effect that perceived crop-raiding by wildlife had on attitudes towards protected areas. This suggests that the extractive benefits of local natural habitats compensate for the problems associated with protected areas.

Perceptions of ecosystem disservices (crop damage) responded differently from attitudes, and were predicted only by the presence / absence of primates damaging crops, and not landscape. Surprisingly, the presence of primates reduced perceptions of crop damage. This was likely due to farmers investing more effort in crop protection when primates were present which, in the form of human crop guarding, presents a significant opportunity cost to smallholders. There was also evidence that, whilst perceptions of crop damage did not change, perceptions of the species damaging crops did, with elephants being a significant problem close to protected areas and smaller animals such as birds, squirrels and rats being more frequently reported damaging crops further away. There are studies suggesting that perceptions of wildlife risk are skewed towards "visible" species, which appear abundant or are large in size (Hill 2004; Suryawanshi et al. 2013), and it may be that smallholders' perception of risk from smaller animals was reduced in the presence of elephants. If there is substantial mismatch between perceived and actual risk, and this varies according to the abundance and visibility of crop damaging animals, this will have implications for LSLMs. For example, if elephant-human conflict is mitigated through fencing this may not improve perceptions of ecosystem disservices if the perceived risk of crop damage by the next largest or most abundant species increases as a consequence. Alternatively, perceptions could reflect real patterns relating to spill-over or meso-predator release. To enable a better understanding of the underlying drivers of smallholders' perceptions, and their attitudes towards nature in general further study is required to establish actual crop damage, frequency of crop raiding events and the distribution and density of perceived pest species (including domestic or feral stock). A substantial amount of unexplained variance in models suggested that social and cultural factors, little considered here, had a substantial role to play in shaping respondents' views and future attitudinal studies should aim to incorporate these.

Generally, whilst the data chapters in this thesis examined an agricultural system with universally low management intensity, quantifying the consequences of increasing management intensity (e.g., pesticide, herbicide and fertiliser use, and mechanisation) and the concomitant changes in resources will also be of importance (Eycott et al. 2010; Perfecto and Vandermeer 2010; Hadley and Betts 2012) for understanding how the potential land-use trajectories of small-scale farming (e.g., conventional vs. sustainable intensification, conservation or loss of natural habitats or landscape features, different degrees of human population growth and urban migration etc.) will affect agro-ecosystem functioning. For example, if local spatial complexity in small-scale farming landscapes compensates for large-scale conversion of non-crop habitats to agricultural uses, then what is the threshold at which loss of local complexity due to consolidation reduces different regulating ecosystem services and which components of complexity have the largest effect when removed or lost? The land-use intensification gradient available to work with in the study landscape was relatively short and further studies should seek to extend this gradient to better capture how subsistence small-scale farming can develop. This requires incorporating landscapes with a greater range of rural population densities and developmental levels (in particular relating to rural-urban migration), to capture variance in landscape and local heterogeneity, and management intensity. If working in the same location as the data chapters presented here, then large-scale commercial farms exist in a similar climatic envelope at Ziwani (70 km west) and south of Emali (200 km north-west). Dualistic landscapes (see Figure 2.1), where large and small-scale farming exist in close proximity, also offer opportunities to study the effect of local heterogeneity on ecosystem processes whilst controlling for edaphic and climatic factors. Whilst much research has been conducted, disentangling the effects of spatial and temporal changes in land-use complexity and structure, and management intensity at multiple spatial scales remain a key challenge for ecologists, especially in small-scale systems. Finally, it is important to consider the interdisciplinary expertise required to address issues of poverty, food-security and biodiversity conservation; for example, a focus on closing yield-gaps might improve food production but without improvements in labour productivity there may be little effect on development and poverty for smallholders (Schreinemachers 2005).

Other future directions

Other future directions from this research including expanding the diversity of agricultural insects considered in analysis. Whilst winged flower-visiting Hymenoptera and epigeal

Coleoptera are proven to provide important ecosystem functions in agricultural contexts, there are numerous other groups of animals such as ants (Folgarait 1998; Jetter et al. 2002; Philpott et al. 2004), lizards (Spiller and Schoener 1988), birds (Basili and Temple 1999; Tillman et al. 2000; Mols and Visser 2002; Hooks et al. 2003; Tracey and Saunders 2003; Sekercioglu 2012; Railsback and Johnson 2014), spiders (Riechert and Lockley 1984; Sunderland and Samu 2000; Kobayashi et al. 2011), solifuges, flies (White et al. 1995; Aluja et al. 1997; Cooper et al. 2011; Joseph and Martinez 2014), lacewings (van Lenteren et al. 1997; Jacometti et al. 2010), mantises, mammals (White et al. 1997; Naughton-Treves 1998; Putman and Moore 1998; Ruscoe et al. 2011), Hemiptera (Arnó et al. 2010; Naranjo et al. 2011; Huang et al. 2014), Orthoptera (Lomer et al. 2001), Gastropoda (Barker 2002; Glen et al. 2002), cockroaches and termites (Mitchell 2002; Sekamatte et al. 2003; Sileshi et al. 2005), millipedes (Snyder and Hendrix 2008), moths and butterflies (Kfir et al. 2002; Midega et al. 2005) and scorpions, that were abundant in semi-arid small-scale agriculture which could play a role in provisioning ecosystem services or disservices. Many of the epigeal species of these groups were abundant in pitfall traps (in particular millipedes, spiders, cockroaches and solifuges). Flies (Diptera) were numerically more common in pan-trap samples than Hymenoptera so relatively little extra effort would be required to gather specimens of these, but other groups would require more specific methods of sampling. Any of these groups could enhance or reduce crop yields and/or interact with other species that are functionally important to agricultural production. Accurately predicting land-use effects on crop yield via ecosystem services will first require knowledge of which are the most important taxa (functional dominance and identity). Working from the crop backwards would be a logical way of narrowing the search for functionally important taxa. Methods could be tailored to focus on particular crops through observations and direct searches; this would ensure that all the species considered in analysis have a direct trophic link to the crop plant and are therefore very likely to provide an ecosystem service or disservice, changes in taxonomic and functional diversity in the crop-specific communities could be analysed using the methods in Chapters 3 and 4. Working directly with crops would also facilitate the direct estimation of the ecosystem service values of species; once functionally important taxa are identified, these can be manipulated to assess their interactions and their ultimate effects on crop yield.

Soil or root dwelling (hypogeal) larvae of pest communities can cause significant crop losses (Murphy et al. 2010; Abney and Kennedy 2011); these could be accurately sampled using a simple technique of washing soil cores or roots with salty water and collecting the hypogeal larvae and pupae that float to the surface of the water (Ladell 1936), or by taking soil cores and using Tullgren style funnels to extract soil organisms (e.g. Macfadyen 1961).

As discussed, a major constraint on understanding or predicting how landscape and land-use change might affect ecosystem services in tropical contexts is a lack taxonomic and ecological knowledge for many species. Metabarcoding technology can characterise the species composition of mass samples and offers a promising approach to issues of taxonomic expertise or knowledge; it is also considered to be a more taxonomically comprehensive method of species identification than standard methods (Valentini et al. 2009b; Ji et al. 2013; Gibson et al. 2014). Additionally, it is far faster than standard methods; time-savings meant that even pilot biodiversity metabarcoding projects, such as that of Ji et al. (2013), were at least as cost-effective as standard methods. If meta-barcoding is adopted as a standard procedure over time, costs should be reduced even further. Such technology would be ideal for the identification of difficult groups such as the larvae or pupae of soil dwelling arthropods (which are little known for most African insects), micro-Hymenoptera and, in general, for the very diverse arthropod communities sampled in semi-arid small-scale farmlands. The time or cost savings that metabarcoding technology offers to functional diversity projects are less impressive when considering that, whilst the technology offers a means for easily establishing the presence or absence of species, it cannot provide information on biomass or abundance, and, as such, these data must still be gathered manually through the painstaking sorting, counting and measurement of trap catches. Perhaps the most exciting prospect offered by metabarcoding technology is the ability to identify the gut contents of animals and therefore the species interactions needed to build trophic webs (e.g., Soininen et al. 2009; Valentini et al. 2009a; Rougerie et al. 2011; García-Robledo et al. 2013). Metabarcoding can also be used to determine the prey content of animal diets from faeces (e.g., Deagle et al. 2010; Stech et al. 2011; Zeale et al. 2011); this could provide valuable unbiased data regarding the diets of herbivorous or carnivorous species of mammal implicated in human-wildlife conflict in the buffer zones of protected areas. Whilst diet can be determined using metabarcoding, standard methods are still required to establish most other species traits regarding morphology, life-history or behaviour.

Small-scale farming systems are dynamic, changing landscapes; at their beginning, natural habitats must be converted to small fields, and with economic development these may become intensive large-scale farms. Understanding how best to conserve or enhance ecosystem processes in these systems as they change is essential for sustainable intensification. However, the balance of research effort into this appears to be biased towards the end of the intensification process rather than the beginning. Whilst this thesis has demonstrated taxonomic and functional changes with land-use change in early stage small-scale farming landscapes, more information is needed, especially at the interface between agriculture and natural areas of importance for wildlife conservation. The expansion of small-scale farms (and agriculture in general) in such areas is detrimental to biodiversity conservation, and these can be considered priority landscape for land-sparing. The choice and success of conservation measures for land-sparing will depend on smallholder attitudes to biodiversity and this can be context dependent (e.g., presence and identity of large mammal species) and vary with landscape structure at different spatial scales. To increase their chances of being successfully implemented, hypothetical landscapes to optimise trade-offs between biodiversity conservation, ecosystem services and commodity production should take into account stakeholder attitudes and preferences, especially regarding ecosystem disservices.

Chapter 7. References

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Appendix A (Chapter 2) Supplemental materials

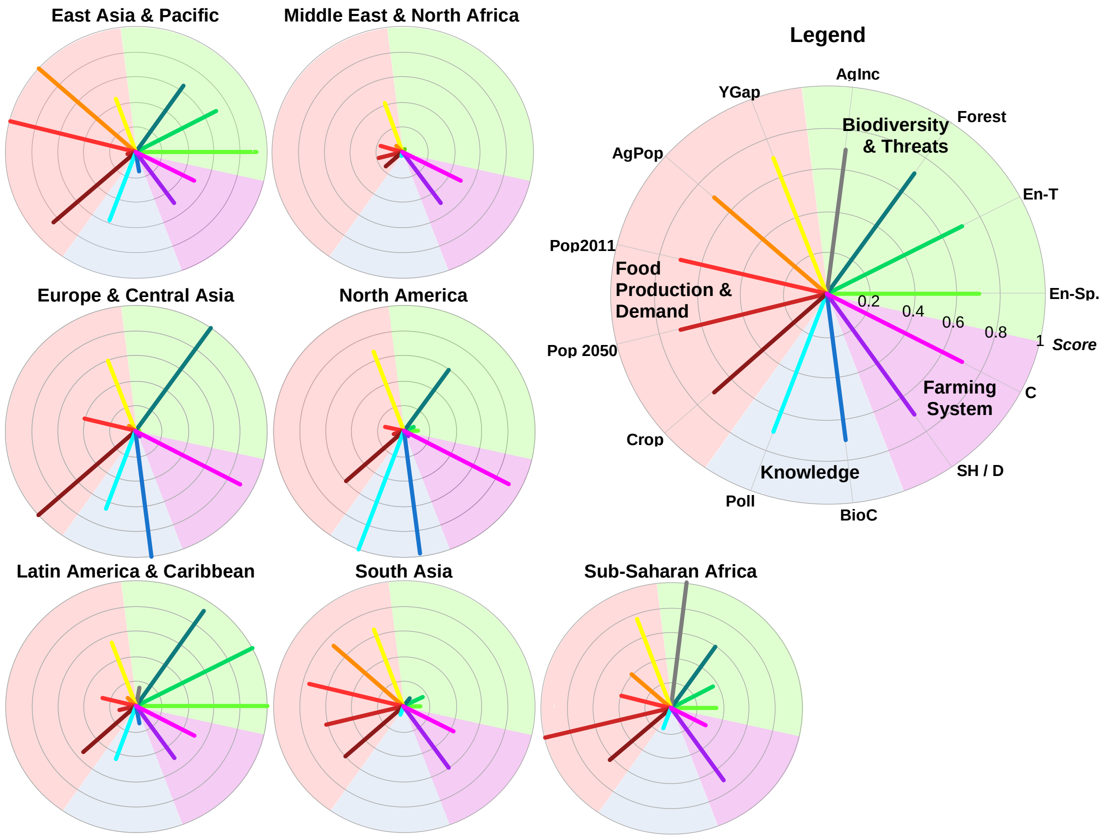
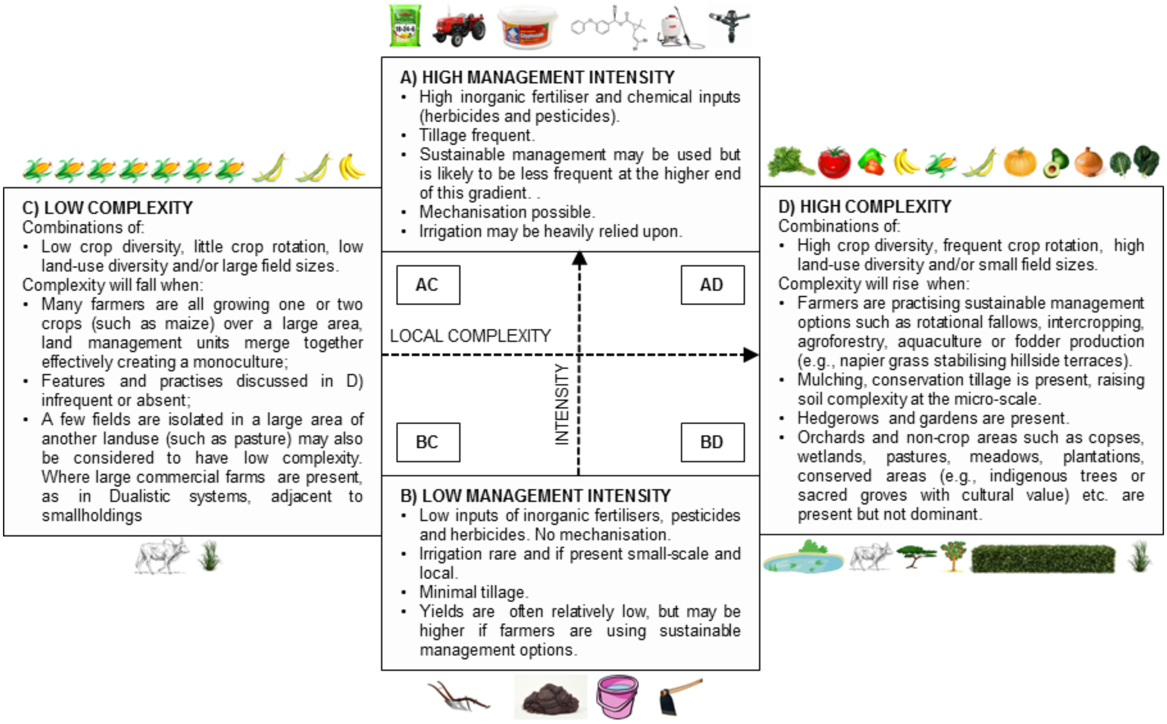


Figure A.1 Relative significance of agricultural, human population and biodiversity indicators between World Bank Regions. Each factor (represented by a coloured line) is scored by dividing the regional value by the highest value recorded for that factor (maximum score is therefore 1), with the exception of yield-gap which is the actual percentage for each region. Factor values were derived as follows: *Biodiversity and threats* (green sector): **AgInc** = increase in agricultural area for 2001-2011 (FAO 2013b); **Forest** = area of forested land (FAO 2013b); **En-T** = threatened endemic species (IUCN 2012), En-Sp = endemic species (IUCN 2012). *Food production and demand* (red sector): **YGap** = percentage gap between actual and potential production (FAO/IIASA 2012); **AgPop** = agricultural population (World Bank 2013); **Pop2011** = total population (World Bank 2013); **Pop2050** = predicted 2050 population increase (World Bank 2013); **Crop** = area of global cropland (FAO 2013b). *Knowledge* (blue sector) was derived from the numbers of studies contributing to quantitative reviews (Figure 2.2): **Poll** = studies relevant to pollination; **BioC** = studies relevant to biological control. *Farming System* (purple sector) bars represent a qualititative estimation of importance to production and livelihoods based on reports (Singh et al. 2002; Salami et al. 2010b) and the informed opinion of the authors: **SH/D** = smallholder and dualistic farms and landscapes, **C** = large-scalefarms.



A) HIGH MANAGEMENT INTENSITY

- High inorganic fertiliser and chemical inputs (herbicides and pesticides).
- Tillage frequent.
- Sustainable management may be used but is likely to be less frequent at the higher end of this gradient. .
- Mechanisation possible.
- Irrigation may be heavily relied upon.

C) LOW COMPLEXITY

Combinations of:

- Low crop diversity, little crop rotation, low land-use diversity and/or large field sizes.

Complexity will fall when:

- Many farmers are all growing one or two crops (such as maize) over a large area, land management units merge together effectively creating a monoculture;
- Features and practises discussed in D) infrequent or absent;
- A few fields are isolated in a large area of another landuse (such as pasture) may also be considered to have low complexity. Where large commercial farms are present, as in Dualistic systems, adjacent to smallholdings

D) HIGH COMPLEXITY

Combinations of:

- High crop diversity, frequent crop rotation, high land-use diversity and/or small field sizes.

Complexity will rise when:

- Farmers are practising sustainable management options such as rotational fallows, intercropping, agroforestry, aquaculture or fodder production (e.g., napier grass stabilising hillside terraces).
- Mulching, conservation tillage is present, raising soil complexity at the micro-scale.
- Hedgerows and gardens are present.
- Orchards and non-crop areas such as copses, wetlands, pastures, meadows, plantations, conserved areas (e.g., indigenous trees or sacred groves with cultural value) etc. are present but not dominant.

B) LOW MANAGEMENT INTENSITY

- Low inputs of inorganic fertilisers, pesticides and herbicides. No mechanisation.
- Irrigation rare and if present small-scale and local.
- Minimal tillage.
- Yields are often relatively low, but may be higher if farmers are using sustainable management options.

Figure A.2 Smallholding land-use scenarios. Complexity is a combination of spatio-temporal compositional and configurational heterogeneity (see Fahrig et al. 2011). Intensity refers to management intensity including factors such as chemical and inorganic fertiliser inputs, irrigation and mechanisation, lower intensity need not lead to lower yields when sustainable management options are used. Scenarios: AD is high intensity and high local complexity; AC is high intensity and low local complexity (1.8 Figure 2.1C); BD is low intensity and high local complexity (1.8 Figure 2.1A); and BC: low intensity and low local complexity. Due to 'conventional' agricultural intensification it is probable that of global farms more will fall in the region between AC to BD than AD to BC.

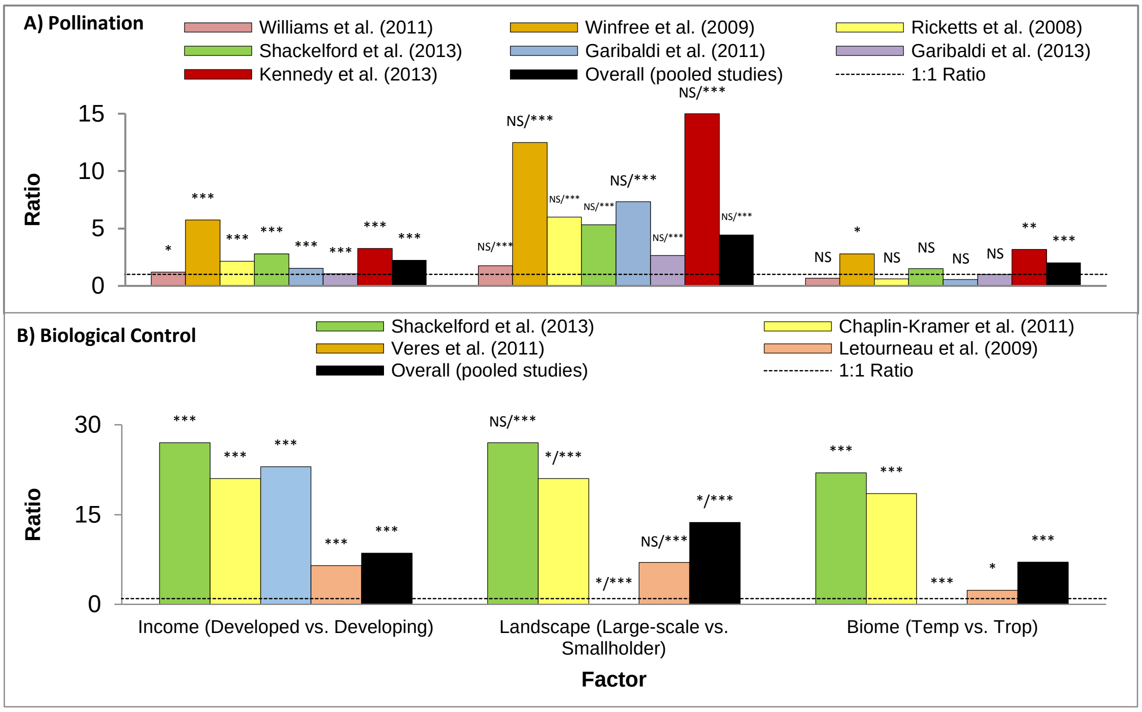


Figure A.3 Study ratios for individual quantitative reviews. For each quantitative review included in the analyses the ratio of studies (relevant to agriculture) is shown for: 1) Income, high-income nations vs. low- and middle-income nations (derived from; World Bank categories); 2) Landscape, large-scale vs. smallholder landscapes; and 3) Biome, temperate regions vs. tropical regions. There were zero smallholder or tropical studies contributing to Veres et al. (2011). Chi-squared (or Exact Multinomial Test when values <5 present) significance values were calculated in R 3.0 and are presented by: NS = P>0.05; * = P≤0.05; ** = P <0.01; and *** = P<0.001. Tests compared observed values with expected values which were derived from: 1) (Income) Estimates of % 2012 global arable and permanent cropland (FAO 2013b); 2) (Landscape) Estimate of total farming system area (IFAD & UNEP 2013) converted into a % of 2012 global arable and permanent cropland area (FAO 2013b) (left value) and estimate of % of global number farms that were in each class (IFAD & UNEP 2013) (right value); and 3) (Biome) % of global cropland (ESA & UCLouvain 2009).

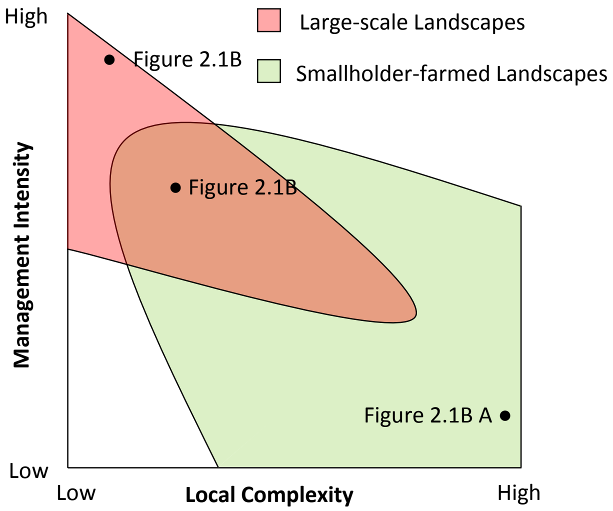


Figure A.4 Interaction of local complexity and management intensity between farming landscapes. Here theoretical large-scale farming landscapes (green) are compared to smallholder farming landscapes (red). Points suggest the location of the farming systems shown in Figure 2.1 within this space. There is overlap between farming systems, but there is a greater diversity of smallholder-farmed landscapes hence they occupy a much greater area than large-scale landscapes. Configurational heterogeneity (geometry) limits both farming types for local complexity. A relatively small maximum field size for smallholder landscapes puts a lower limit on local complexity and vice-versa for large-scale farms. Limits for both axes are hypothetical and will vary with context.

Table A.1 Excluded quantitative reviews.

Year	Lead Author	Summary	Type	Ecosystem Services Provider	Reason for Exclusion
2013	Nicholls	Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review	Review	Pollinators	Narrative
2012	Montero-Castano	Impact of landscape alteration and invasions on pollinators, a meta-analysis	Meta-analysis	Pollinators	Scope was natural habitat only
2012	Hadley	The effects of landscape fragmentation on pollination dynamics absence of evidence not evidence of absence	Review	Pollinators	Not focused on crops, narrative
2012	Tooker	Genotypically diverse cultivar mixtures for insect pest management and increased crop yields	Review	Natural enemies & pests	Narrative
2012	Davila	Ecosystem services of pollinator diversity: a review of the relationship with pollen limitation of plant reproduction	Review	Pollinators	Non-crop focussed
2012	Kremen	Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalities, and Trade-Offs	Review	Multiple ES	Although details of effect, significance of effect and strength of evidence presented the discussion is narrative. Results of keyword searches not presented in supplemental materials.
2012	Winqvist	Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account	Review	N/A	Narrative review. Covers multiple taxonomic groups some of which contain sub-taxa that can have contrasting functions in an agro-ecosystem (e.g. breeding birds).

Year	Lead Author	Summary	Type	Ecosystem Services Provider	Reason for Exclusion
2012	Ratnadass	Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review	Review	Natural enemies & pests	Only a small part of the review relates to natural enemies of crop pests and it is a narrative review.
2012	Blitzer	Spillover of functionally important species between managed and natural habitats	Review	Multiple ES	Neither quantitative review (in the sense of modelling/demonstrating a trend or pattern) nor meta-analysis. Highlights research biases through counting papers.
2011	Garrett	Effects of farming system and fertilisers on pests and natural enemies	Meta-analysis	Natural enemies & pests	Meta-analysis studies not presented in article nor provided in supplementary materials (supporting materials not available)
2011	Batary	Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis	Meta-analysis	Mulitple groups including pollinators	Part of this meta-analysis did focus on pollinators. However it was unclear as to which of the studies collected for the primary analyses of species richness and abundance contributed to the pollinator sub-analyses. Of 114 entries for abundance analysis, 105 were from Europe or North America, 5 from Argentina and 4 from Indonesia. For richeness of 109 entries, 99 were from Europe or North America, 5 from Argentina, 4 from Indonesia and 1 from Columbia.
2011	Prieto-Benítez	Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis	Meta-analysis	Spiders	Laregely non-agricultural studies, approximately 60% of studies were from forest or rangeland.
2011	Winfree	Native Pollinators in Anthropogenic Habitats	Meta-analysis	Pollinators	Largely non-agricultural studies, only 33% of studies involved land-use change to agriculture.
2011	Letourneau	Does plant diversity benefit agroecosystems? A synthetic review	Meta-analysis	Plants	Focus on herbivore response not natural-enemies.
2010	Simon	Biodiversity and pest management in orchard systems	Review	Natural enemies & pests	Narrative review

Year	Lead Author	Summary	Type	Ecosystem Services Provider	Reason for Exclusion
2010	Jonsson	Habitat manipulation to mitigate the impacts of invasive arthropod pests	Review	Natural enemies & pests	Narrative review
2010	Potts	Global pollinator declines: trends, impacts and drivers	Review	Pollinators	Narrative review
2010	Decourtye	Landscape enhancement of floral resources for honey bees in agro-ecosystems	Review	Pollinators	Narrative and focussed on Europe and USA
2010	Rusch	Biological control of insect pests in agroecosystems: effects of crop management, farming systems and semi-natural habitats at the landscape scale	Review	Natural enemies & pests	Narrative review
2008	Fielder	Maximizing ecosystem services from conservation biological control: The role of habitat management	Review	Natural enemies & pests	Largely narrative with some descriptives reported
2008	Attwood	Do arthropod assemblages display globally consistent responses to intensified agricultural land-use and management?	Meta-analysis	Various Taxa	Meta-analyses considered predators, decomposers and herbivores however it was unclear as to precisely which studies contained taxa that were considered predators (e.g. studies that listed taxa as 'various' or 'coleoptera' categories).
2008	Poveda	Diversification practices: their effect on pest regulation and production	Review	Natural enemies & pests	No meta-analysis or quantification of a trend or pattern.
2008	Jonsson	Recent advances in conservation biological control of arthropods by arthropods	Review	Natural enemies & pests	Narrative review
2008	Hajjar	The utility of crop genetic diversity in maintaining ecosystem services	Review	Multiple ES	Narrative review

Year	Lead Author	Summary	Type	Ecosystem Services Provider	Reason for Exclusion
2007	Klein	Importance of pollinators in changing landscapes for world crops	Review	Pollinators	Focus is on crop dependence on pollination rather than ES itself
2006	Bianchi	Pest regulation in agricultural landscapes; landscape composition, biodiversity and natural pest control.	Review	Natural enemies & pests	Largely narrative with some descriptives reported
2005	Bengtsson	The effects of organic agriculture on biodiversity and abundance a meta-analysis	Meta-analysis	General biodiversity	Focus too broad, considered all species of animal not just ES providers.
2005	Landis	Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes	Review	Natural enemies & pests	Narrative review

Table A.2 Studies relative to agriculture included in analyses. The "$" column refers to the World Bank Income status for the country or countries a study was conducted in: H = High Income; UM = Upper Middle Income; LM = Lower Middle Income; and L = Low Income. High income nations were considered to be developed economies and all other nations developing economies. The "ES" column refers to the ecosystem service a study was relevant to.

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Acheampong & Stark (2004)	Washington State, USA	North America	H	Brocolli	Large-scale	Temperate	47°11'N	122°17'W	Biological Control
Ameixa & Kindlmann (2008)	Czech Republic	Europe & Central Asia	H	Wheat	Large-scale	Temperate	48°59'N	14°29'E	Biological Control
Anjum-Zubair et al. (2010)	Switzerland	Europe & Central Asia	H	Wheat	Large-scale	Temperate	47°03'N	7°27'E	Biological Control
Arthur et al. (2010)	New South Wales, Australia	East Asia & Pacific	H	Oil-seed Rape	Large-scale	Temperate	34°26'S	148°43'E	Pollination
Bailey et al. (2010)	Switzerland	Europe & Central Asia	H	Apple	Large-scale	Temperate	47°27'N	8°51'E	Biological Control
Bandano (2011)	Mexico	Latin America & Caribbean	UM	Coffee (Highland)	Smallholder	Tropical	19°20'N	96°56'W	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Benjamin (unpub.)	New Jersey, USA	North America	H	Blueberry (Highbush)	Large-scale	Temperate	NoData	NoData	Pollination
Bianchi et al. (2005)	Netherlands	Europe & Central Asia	H	Brussel Sprouts	Large-scale	Temperate	52°08'N	5°20'E	Biological Control
Bianchi et al. (2008)	Netherlands	Europe & Central Asia	H	Brussel Sprouts	Large-scale	Temperate	52°08'N	5°20'E	Biological Control
Blanche & Cunningham (2005)	Queensland, Australia	East Asia & Pacific	H	Atemoya	Large-scale	Tropical	17°07'S	145°30'E	Pollination
Blanche et al. (2006)	Queensland, Australia	East Asia & Pacific	H	Macadamia and longan	Large-scale	Tropical	17°07'S	145°30'E	Pollination
Boccaccio &Petacchi (2009)	Italy	Europe & Central Asia	H	Olive	Large-scale	Mediterranean	43°43'N	10°24'E	Biological Control
Bogdanski (2005)	Brazil	Latin America & Caribbean	UM	Passion fruit	Dualistic	Desert & Xeric	9°27'S	40°30'W	Pollination
Boiteau et al. (2008)	New Brunswick, Canada	North America	H	Potato	Large-scale	Temperate	46°17'N	66°07'W	Biological Control
Bommarco et al. (2012), Rundlöf & Bommarco (unpub.)	Sweden	Europe & Central Asia	H	Red Clover	Large-scale	Temperate	60°08'N	18°39'E	Pollination
Bommarco, Marini &Vassiere (2012)	Sweden	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	59°49'N	17°39'E	Pollination
Boreux (2012)	Kodagu, India	South Asia	LM	Coffee (Lowland)	Smallholder	Tropical	12°19'N	75°52'E	Pollination
Borkhataria et al. (2006)	Puerto Rico	Latin America & Caribbean	H	Coffee	Smallholder	Tropical	18°18'N	66°33'W	Biological Control
Brewer et al. (2008)	Wyoming, Colorado & Nebraska, USA	North America	H	Wheat	Large-scale	Temperate	41°°01' N	104°04'W	Biological Control
Brittain et al. (2010)	Italy	Europe & Central Asia	H	Grape	Large-scale	Temperate	45°39'N	12°26'E	Pollination
Büchi (2002)	Switzerland	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	47°42'N	8°29'E	Biological Control
Bukovinszky et al. (2008)	Netherlands	Europe & Central Asia	H	Brussel Sprouts	Large-scale	Temperate	51°57'N	5°38'E	Biological Control
Cardinale et al. (2003)	Wisconsin, USA	North America	H	Alfalfa	Large-scale	Temperate	43°18'N	89°21'W	Biological Control
Cardinale et al. (2006)	Wisconsin, USA	North America	H	Alfalfa	Large-scale	Temperate	43°18'N	89°21'W	Biological Control

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Cariveau (unpub.)	New Jersey, USA	North America	H	Cranberry	Large-scale	Temperate	40°01'N	74°47'W	Pollination
Carré et al. (2009)	France, Germany, Poland, England, Sweden	Europe & Central Asia	H	Field Bean	Large-scale	Temperate	43°52'N	4°31'E	Pollination
Carré et al. (2009); Steffan-Dewenter et al. (unpub.)	Germany	Europe & Central Asia	H	Strawberry	Large-scale	Temperate	51°33'N	9°56'E	Pollination
Carvalheiro et al. (2010)	South Africa	Sub-Saharan Africa	UM	Mango	Large-scale	Tropical	24°31'S	30°44'E	Pollination
Carvalheiro et al. (2011)	South Africa	Sub-Saharan Africa	UM	Sunflower	Large-scale	Montane	27°57'S	28°32'E	Pollination
Chacoff & Aizen (2006)	Argentina	Latin America & Caribbean	UM	Grapefruit	Large-scale	Tropical	23°08'S	64°20'W	Pollination
Chacoff (2008)	Argentina	Latin America & Caribbean	UM	Grapefruit	Large-scale	Tropical	23°09'S	64°22'W	Pollination
Chang & Eigenbrode (2004)	Idaho, USA	North America	H	Pea	Large-scale	Temperate	46°43'N	116°57'W	Biological Control
Chaplin-Kramer (2010)	California, USA	North America	H	Cabbage	Large-scale	Mediterranean	35°08'N	120°36'W	Biological Control
Cisneros & Rosenheim (1997)	California, USA	North America	H	Cotton	Large-scale	Mediterranean	35°30'N	119°16'W	Biological Control
Clough et al. (2005)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	50°95'N	8°28'E	Biological Control
Clough et al. (2007)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	50°95'N	8°28'E	Biological Control
Clough et al. (2007)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°12'N	9°02'E	Pollination
Colfer et al. (2003)	California, USA	North America	H	Cotton	Large-scale	Mediterranean	35°30'N	119°16'W	Biological Control
Costamagna et al. (2007)	Michigan, USA	North America	H	Soybean	Large-scale	Temperate	42°36'N	84°23'W	Biological Control
Costamagna et al. (2008)	Michigan, USA	North America	H	Soybean	Large-scale	Temperate	42°26'N	85°22'W	Biological Control
den Belder et al. (2002)	Netherlands	Europe & Central Asia	H	Leek	Large-scale	Temperate	51°22'N	5°54'E	Biological Control
Drapela et al. (2008)	Austria	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	48°04'N	16°57'E	Biological Control

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Eilers & Klein (2009)	California, USA	North America	H	Almond	Large-scale	Mediterranean	38°50'N	122°05'W	Biological Control
Ekroos et al. (2010)	Finland	Europe & Central Asia	H	Cereals	Large-scale	Temperate	61°23'N	25°21'E	Biological Control
Fabre et al. (2005)	France	Europe & Central Asia	H	Wheat, Barley, Oats	Large-scale	Temperate	49°01'N	1°38'E	Biological Control
Finke & Snyder (2008)	Washington State, USA	North America	H	Radish	Large-scale	Temperate	46°48'N	119°03'W	Biological Control
Forehand et al. (2006)	North Carlolina, USA	North America	H	Tomato	Large-scale	Temperate	35°23'N	78°02'W	Biological Control
Frank et al. (2007)	New Zealand	East Asia & Pacific	H	Grape	Large-scale	Temperate	43°39'S	172°28'E	Biological Control
Freier et al. (2007)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	52°05'N N	12°33'E	Biological Control
Frietas (unpub.)	Brazil, Ceará	Latin America & Caribbean	UM	Annato	Smallholder	Desert & Xeric	3°39'S	38°51'W	Pollination
Frietas (unpub.)	Brazil, Ceará	Latin America & Caribbean	UM	Cotton	Smallholder	Desert & Xeric	4°43'S	39°11'W	Pollination
Frietas (unpub.)	Brazil, Ceará	Latin America & Caribbean	UM	Acerola	Large-scale	Desert & Xeric	3°53'S	41°05'W	Pollination
Gaines (unpub.)	Wisconsin, USA	North America	H	Cranberry	Large-scale	Temperate	44°09'N	90°20'W	Pollination
Gardiner et al. (2009a)	Iowa, Michigan, Minnesota, Wisconsin, USA	North America	H	Soybean	Large-scale	Temperate	44°44'N	91°12'W	Biological Control
Gardiner et al. (2009b)	Iowa, Michigan, Minnesota, Wisconsin, USA	North America	H	Soybean	Large-scale	Temperate	44°44'N	91°12'W	Biological Control
Gardiner et al. (2010)	Iowa, Michigan, Minnesota, Wisconsin, USA	North America	H	Soybean	Large-scale	Temperate	44°44'N	91°12'W	Biological Control
Gemmill-Herren&Ochieng (2008)	Kenya	Sub-Saharan Africa	L	Aubergine	Smallholder	Tropical	1°45'S	36°02'E	Pollination
Greenleaf & Kremen (2006a)	California, USA	North America	H	Tomato	Large-scale	Mediterranean	38°32'N	121°°52' W	Pollination
Greenleaf & Kremen (2006b)	California, USA	North America	H	Sunflower	Large-scale	Mediterranean	38°32'N	121°°52' W	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Greenleaf (unpub.)	California, USA	North America	H	Sunflower	Large-scale	Mediterranean	38°32'N	121°°52'W	Pollination
Grilli & Bruno (2007)	Argentina	Latin America & Caribbean	UM	Maize	Large-scale	Temperate	33°28'S	62°09'W	Biological Control
Haenke et al. (2009)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°54'N	9°93'E	Biological Control
Hajek et al. (2007)	New York State, USA	North America	H	Soybean	Large-scale	Temperate	42°50'N	76°41'W	Biological Control
Heard & Exley (1994)	Eastern, Australia	East Asia & Pacific	H	Macadamia	Large-scale	Temperate	29°01'S	146°32'E	Pollination
Holland & Fahrig (2000)	Ottowa, Canada	North America	H	Alfalfa	Large-scale	Temperate	45°15'N	75°47'W	Biological Control
Holzschuh et al. (2007)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°11'N	9°21'E	Pollination
Holzschuh et al. (2012)	Germany	Europe & Central Asia	H	Cherry	Large-scale	Temperate	51°20'N	9°51'E	Pollination
Hooks et al. (2003)	Hawaii, USA	North America	H	Brocolli	Large-scale	Tropical	21°32'N	158°16'W	Biological Control
Howlett (2009)	New Zealand	East Asia & Pacific	H	Onion	Large-scale	Temperate	42°04'S	173°23'E	Pollination
Isaacs & Kirk (2010)	Michigan, USA	North America	H	Blueberry	Large-scale	Temperate	42°36'N	86°05'W	Pollination
Javorek (unpub.)	Canada	North America	H	Blueberry	Large-scale	Temperate	46°22'N	63°25'W	Pollination
Jha&Vandermeer (2010)	Mexico	North America	UM	Coffee	Smallholder	Tropical	15°10'N°	92°20'W	Pollination
Jonsen&Fahrig (1997)	Canada	North America	H	Alfalfa	Large-scale	Temperate	45°15'N	75°47'W	Biological Control
Julier&Roulston (2009)	Northern Virginia & Maryland, USA	North America	H	Pumpkin	Large-scale	Temperate	38°36'N	78°29'W	Pollination
Kevan (1975)	Canada	North America	H	Blueberry	Large-scale	Temperate	45°36'N	65°37'W	Pollination
Kim et al. (2006)	California, USA	North America	H	Sunflower	Large-scale	Mediterranean	38°41'N	121°58'W	Pollination
Klein (2009)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee	Smallholder	Tropical	1°24'S	120°20'E	Pollination
Klein et al. (2002)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee & Cocoa	Smallholder	Tropical	1°24'S	120°20'E	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Klein et al. (2003a)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee	Smallholder	Tropical	1°24'S	120°20'E	Pollination
Klein et al. (2003b)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee	Smallholder	Tropical	1°24'S	120°20'E	Pollination
Klein et al. (2006)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee Agroforestry	Smallholder	Tropical	1°24'S	120°20'E	Biological Control
Klein et al. (2006)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee	Smallholder	Tropical	1°24'S	120°20'E	Pollination
Klein et al. (2012)	California, USA	North America	H	Almond	Large-scale	Mediterranean	38°50'N	122°05'W	Pollination
Klug et al. (2003)	Germany	Europe & Central Asia	H	Spinach	Large-scale	Temperate	50°43'N	7°43'E	Biological Control
Kremen (unpub. a)	California, USA	North America	H	Almond	Large-scale	Mediterranean	38°52'N	122°04'W	Pollination
Kremen (unpub. b)	California, USA	North America	H	Muskmelon	Large-scale	Mediterranean	38°52'N	122°04'W	Pollination
Kremen et al. (2002)	California, USA	North America	H	Watermelon	Large-scale	Mediterranean	38°44'N	121°56'W	Pollination
Kremen et al. (2004)	California, USA	North America	H	Watermelon	Large-scale	Mediterranean	38°44'N	121°56'W	Pollination
Krishnan (2012)	Kodagu, India	South Asia	LM	Coffee (Lowland)	Smallholder	Tropical	12°08'S	76°01'E	Pollination
Kriz et al. (2006)	NoData, USA	North America	H	Alfalfa	Large-scale	Temperate	NoData	NoData	Biological Control
Kruess (2003)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Lee &Heimpel (2005)	Minnesota, USA	North America	H	Cabbage	Large-scale	Temperate	44°43'N	93°06'W	Biological Control
Letourneau & Goldstein (2001)	California, USA	North America	H	Tomato	Large-scale	Mediterranean	38°35'N	121°45'W	Biological Control
Losey & Denno (1998)	Maryland, USA	North America	H	Alfalfa	Large-scale	Temperate	39°01'N	76°49'W	Biological Control
MacKenzie & Eickwort (1996)	New York State, USA	North America	H	Blueberry	Large-scale	Temperate	42°50'N	77°00'W	Pollination
Mand at al. (2002)	Estonia	Europe & Central Asia	H	Various	Large-scale	Temperate	58°16'N	25°10'E	Pollination
Mandelik (unpub.)	Israel	Middle East & North Africa	H	Almond, Sunflower, Watermelon	Dualistic	Desert & Xeric	31°30'N	34°54'E	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Mandelik (unpub.)	Israel	Middle East & North Africa	H	Watermelon	Dualistic	Desert & Xeric	31°30'N	34°54'E	Pollination
Mandelik (unpub.)	Israel	Middle East & North Africa	H	Sunflower	Dualistic	Desert & Xeric	31°30'N	34°54'E	Pollination
Mayfield (2005)	Costa Rica	Latin America & Caribbean	UM	Oil Palm	Large-scale	Tropical	8°37'N	83°06'W	Pollination
Mayfield (unpub.)	New South Wales, Australia	East Asia & Pacific	H	Macadamia	Large-scale	Temperate	28°44'S	153°27'E	Pollination
Menalled et al. (2003)	Michigan, USA	North America	H	Maize	Large-scale	Temperate	42°26'N	84°29'W	Biological Control
Meyerhöfer et al. (2008)	Germany	Europe & Central Asia	H	Spinach	Large-scale	Temperate	51°51'N	6°52'W	Biological Control
Miliczky & Horton (2005)	Washington State & Oregon, USA	North America	H	Apple & Pear	Large-scale	Temperate	45°54'N	119°31'W	Biological Control
Morandin & Winston (2006)	Canada	North America	H	Oil-seed Rape	Large-scale	Boreal & Taiga	58°00'N	116°0'W	Pollination
Morandin & Winston (2005)	Canada	North America	H	Oil-seed Rape	Large-scale	Boreal & Taiga	58°00'N	116°0'W	Pollination
Morandin et al. (2007)	Canada	North America	H	Oil-seed Rape	Large-scale	Temperate	49°43'N	122°49'W	Pollination
Motzke (unpub.)	Sulawesi, Indonesia	East Asia & Pacific	LM	Cucumber	Smallholder	Tropical	1°24'S	120°19'E	Pollination
Munyuli (2012)	Uganda	Sub-Saharan Africa	L	Coffee (Lowland)	Smallholder	Tropical	0°20'N	32°56'E	Pollination
Nash et al. (2008)	Western Victoria, Australia	East Asia & Pacific	H	Cereals	Large-scale	Temperate	38°04'S	142°20'E	Biological Control
Neame& Elle (unpub.)	Canada	North America	H	Squash	Large-scale	Temperate	49°26'N	120°06'W	Pollination
Noma et al. (2010)	Iowa, Michigan, Minnesota, Wisconsin, USA	North America	H	Soybean	Large-scale	Temperate	44°44'N	91°12'W	Biological Control
Oberg et al. (2008)	Germany	Europe & Central Asia	H	Barley	Large-scale	Temperate	50°41'N	9°08'E	Biological Control
Östman (2002)	Sweden	Europe & Central Asia	H	Barley	Large-scale	Temperate	59°51'N	17°41'E	Biological Control
Östman et al. (2001)	Sweden	Europe & Central Asia	H	Barley	Large-scale	Temperate	59°51'N	17°41'E	Biological Control
Otieno et al. (unpub.)	Kenya	Sub-Saharan Africa	L	Cowpea	Smallholder	Tropical	2°25'S	34°58'E	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Park & Danforth (unpub.)	New York State, USA	North America	H	Apple	Large-scale	Temperate	42°45'N	76°49'W	Pollination
Pease & Zalom (2010)	California, USA	North America	H	Tomato	Large-scale	Mediterranean	38°30'N	121°26'W	Biological Control
Perfecto et al. (2004)	Mexico	North America	UM	Coffee	Large-scale	Tropical	15°10'N	92°20'W	Biological Control
Perovic et al. (2010)	New South Wales, Australia	East Asia & Pacific	H	Cotton	Large-scale	Temperate	31°00'S	148°00'E	Biological Control
Petersen (unpub.)	New York, USA	North America	H	Pumpkin	Large-scale	Temperate	NoData	NoData	Pollination
Pluess et al. (2010)	Israel	Middle East & North Africa	H	Wheat	Large-scale	Desert & Xeric	31°14'N	34°45'E	Biological Control
Potts (unpub.)	UK	Europe & Central Asia	H	Field bean	Large-scale	Temperate	51°23'N	0°59'W	Pollination
Prache et al. (unpub.)	New South Wales, Australia	East Asia & Pacific	H	Oil-seed Rape	Large-scale	Temperate	34°43'S	147°43'E	Pollination
Prasad & Snyder (2006)	Washington State, USA	North America	H	Mixed veg - inc.Brocolli and Cauliflower	Large-scale	Temperate	48°26'N	122°23'W	Biological Control
Prasifka et al. (2004)	Texas, USA	North America	H	Cotton	Large-scale	Temperate	31°45'N	98°38'W	Biological Control
Purtauf et al. (2005a)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°06'N	9°21'E	Biological Control
Purtauf et al. (2005b)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Rader (2009)	New Zealand	East Asia & Pacific	H	Turnip Rape	Large-scale	Temperate	43°45'S	171°09'E	Pollination
Rader (2012)	New Zealand	East Asia & Pacific	H	Turnip Rape	Large-scale	Temperate	44°25'S	170°32'E	Pollination
Ramos (2008)	Costa Rica	Latin America & Caribbean	UM	Coffee	Smallholder	Tropical	9°48'N	83°36'W	Biological Control
Ricci et al. (2009)	France	Europe & Central Asia	H	Pears & Apples	Large-scale	Mediterranean	43°49'N	4°54'E	Biological Control
Ricketts (2004)	Costa Rica	Latin America & Caribbean	UM	Coffee	Large-scale	Tropical	9°22'N	83°42'W	Pollination
Ricketts et al. (2004)	Costa Rica	Latin America & Caribbean	UM	Coffee	Large-scale	Tropical	9°22'N	83°42'W	Pollination

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Ricketts et al.?(2006)	New Zealand	East Asia & Pacific	H	Kiwifruit	Large-scale	Temperate	NoData	NoData	Pollination
Roschewitz et al. (2005)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Rosenheim (2001)	California, USA	North America	H	Cotton	Large-scale	Mediterranean	35°30'N	119°16'W	Biological Control
Rosenheim et al. (1993)	California, USA	North America	H	Cotton	Large-scale	Temperate	36°10'N	118°20'W	Biological Control
Rosenheim et al. (2004a)	Hawaii, USA	North America	H	Papaya	Large-scale	Tropical	21°32'N	158°16'W	Biological Control
Rosenheim et al. (2004b)	Hawaii, USA	North America	H	Papaya	Large-scale	Tropical	21°32'N	158°16'W	Biological Control
Rundlof et al. (2008)	Sweden	Europe & Central Asia	H	Cereal crops	Large-scale	Temperate	55°48'N	13°22'E	Pollination
Sáez et al. (2012)	Argentina	Latin America & Caribbean	UM	Sunflower	Large-scale	Temperate	37°50'S	58°15'W	Pollination
Saska et al. (2007)	Netherlands	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°58'N	5°40'E	Biological Control
Schmidt & Tscharntke (2005)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Schmidt et al. (2005)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Schmidt et al. (2008)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°06'N	9°21'E	Biological Control
Schmidt-Entling&Dobeli (2009)	Switzerland	Europe & Central Asia	H	Wheat	Large-scale	Temperate	47°06'N	7°30'E	Biological Control
Schüepp (unpub.)	Switzerland	Europe & Central Asia	H	Cherry	Large-scale	Temperate	47°2'N	7°25'E	Pollination
Sepp et al. (2004)	Estonia	Europe & Central Asia	H	Legumes & Unspecified Arable	Large-scale& Dualistic	Temperate	58°13'N	25°10'E	Pollination
Shuler et al. (2005)	Virginia, Maryland, West Virginia, USA	North America	H	Pumpkin	Large-scale	Temperate	39°00'N	77°49'W	Pollination
Snyder & Ives (2003)	Wisconsin, USA	North America	H	Alfalfa	Large-scale	Temperate	43°18'N	89°21'W	Biological Control

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Snyder & Wise (2001)	Kentucky, USA	North America	H	Cucumber & Squash	Large-scale	Temperate	38°08'N	84°30'W	Biological Control
Snyder et al. (2006)	Washington State, USA	North America	H	Collards	Large-scale	Temperate	46°48'N	119°03'W	Biological Control
Snyder et al. (2008)	Washington State, USA	North America	H	Collards	Large-scale	Temperate	46°48'N	119°03'W	Biological Control
Sousa (2010)	Brazil	Latin America & Caribbean	UM	Mango	Dualistic	Tropical	9°14'S	40°17'W	Pollination
Steffan-Dewenter & Leschke (2003)	Germany	Europe & Central Asia	H	Apple, Sweet Cherry, Plum, Pear, Sour Cherry	Large-scale	Temperate	51°32'N	9°55'E	Pollination
Steffan-Dewenter & Tscharntke (1999)	Germany	Europe & Central Asia	H	Radish	Large-scale	Temperate	52°02'N	9°50'E	Pollination
Steffan-Dewenter (2002)	Germany	Europe & Central Asia	H	Cereals	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Steffan-Dewenter (2002)	Germany	Europe & Central Asia	H	Cereal crops	Large-scale	Temperate	51°30'N	9°54'E	Pollination
Steffan-Dewenter (2003)	Germany	Europe & Central Asia	H	Apple, Sweet Cherry, Plum, Pear, Sour Cherry	Large-scale	Temperate	51°32'N	9°55'E	Pollination
Steffan-Dewenter et al (2001)	Germany	Europe & Central Asia	H	Cereal crops	Large-scale	Temperate	51°30'N	9°54'E	Pollination
Straub & Snyder (2006)	Washington State, USA	North America	H	Potato	Large-scale	Temperate	46°48'N	119°03'W	Biological Control
Straub & Snyder (2008)	Washington State, USA	North America	H	Potato & Cabbage	Large-scale	Temperate	46°48'N	119°03'W	Biological Control
Taki et al. (2010)	Japan	East Asia & Pacific	H	Buckwheat	Large-scale	Temperate	39°36'N	140°27'E	Pollination
Thies&Tscharntke (1999)	Germany	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	52°41'N	10°24'E	Biological Control
Thies et al. (2003)	Germany	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Thies et al. (2005)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control

Author	Country	World Bank Region	$	Crop	Landscape	Climate / Biome	Lat.	Long.	Ecosystem Service
Thies et al. (2008)	Germany	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	52°41'N	10°24'E	Biological Control
Thomson & Hoffmann (2010)	South Australia, Australia	East Asia & Pacific	H	Grape	Large-scale	Mediterranean	36.03'S	139°53'E	Biological Control
Thomson et al. (2010)	South Australia, Australia	East Asia & Pacific	H	Grape	Large-scale	Mediterranean	36.03'S	139°53'E	Biological Control
Tuell et al. (2009)	Michigan, USA	North America	H	Blueberry	Large-scale	Temperate	42°35'N	86°06'W	Pollination
Tylianakis et al. (2006)	Ecuador	Latin America & Caribbean	UM	Rice/Coffee	Large-scale& Smallholder	Tropical	1°26'S	80°28'W	Biological Control
Tylianakis et al. (2008a)	Ecuador	Latin America & Caribbean	UM	Rice/Coffee	Large-scale& Smallholder	Tropical	1°26'S	80°28'W	Biological Control
Tylianakis et al. (2008b)	Central Sulawesi, Indonesia	East Asia & Pacific	LM	Coffee	Smallholder	Tropical	1°24'S	120°20'E	Biological Control
van Helden et al. (2006)	France	Europe & Central Asia	H	Grapes	Large-scale	Mediterranean	45°55'N	00°09'W	Biological Control
Varchola & Dunn (2001)	Iowa, USA	North America	H	Maize	Large-scale	Temperate	40°51'N	93°19'W	Biological Control
Veres and Szalkai (2006)	Hungary	Europe & Central Asia	H	Maize	NoData	Temperate	NoData	NoData	Biological Control
Viana & Silva (unpub.)	Brazil	Latin America & Caribbean	UM	Passion fruit	Dualistic	Desert & Xeric	9°27'S	40°30'W	Pollination
Vollhardt et al. (2008)	Germany	Europe & Central Asia	H	Wheat	Large-scale	Temperate	51°33'N	9°56'E	Biological Control
Weibull et al. (2003)	Sweden	Europe & Central Asia	H	Cereals, Leys, Semi-natural pasture	Large-scale	Temperate	59°43'N	16°47'E	Biological Control
Werling & Gratton (2008)	Wisconsin, USA	North America	H	Potato	Large-scale	Temperate	44°03'N	89°32'W	Biological Control
Westphal et al. (2003)	Germany	Europe & Central Asia	H	Various	Large-scale	Temperate	51°30'N	9°54'E	Pollination
Wiethoff et al. (2004)	Germany	Europe & Central Asia	H	Cucumber	Large-scale	Temperate	52°14'N	9°48'E	Biological Control
Williams (unpub.)	California, USA	North America	H	Watermelon	Large-scale	Mediterranean	38°42'N	121°57'W	Pollination
Winfree et al. (2008)	New Jersey & Pennsylvania, USA	North America	H	Cantaloupe	Large-scale	Temperate	40°15'N	74°53'W	Pollination

Author	**Country**	**World Bank Region**	**$**	**Crop**	**Landscape**	**Climate / Biome**	**Lat.**	**Long.**	**Ecosystem Service**
Winfree et al.?(2007b)	New Jersey & Pennsylvania, USA	North America	H	Watermelon	Large-scale	Temperate	40°15'N	74°53'W	Pollination
Wyckhuys & O'Neil (2007)	Honduras	Latin America & Caribbean	L M	Maize	Smallholder	Tropical	14°03'N	86°52'W	Biological Control
Zaller et al. (2008a)	Austria	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	48°04'N	16°57'E	Biological Control
Zaller et al. (2008b)	Austria	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	48°04'N	16°57'E	Biological Control
Zaller et al. (2009)	Austria	Europe & Central Asia	H	Oil-seed Rape	Large-scale	Temperate	48°04'N	16°57'E	Biological Control

Appendix B (Chapter 2) World Census of Agriculture 2000 farm area and population coverage and estimates

For each nation reporting in the WCA2000 land holding number and total area were classified according to holdings <2 ha and > 2 ha. Where national statistics were reported in area intervals that did not match our criteria values were proportionally divided between our size criteria. Where nations reported values for area but not number of smallholdings, the total area for each land holding size class was divided by the middle value of the size class range to estimate the number of holdings. We acknowledge the relationship between number of holdings and size is non-linear and that the linear method we have used will slightly underestimate the number of holdings in a class. Where nations reported values for the number of land holdings but not the total area for the size class the number of land holdings was multiplied by the middle value of the size class range to estimate total area. Again in reality the relationship is non-linear and we acknowledge that this method will slightly over-estimate the total area for a size class.

Total holding size was used to record landholding areas, some nations reported agricultural landholding area and total landholding area but the latter was reported far more frequently than the former hence its selection.

Total agricultural area for a nation was taken to be the summed area of the landholding size classes.

It should be noted that are methodological differences between nations in how their censuses were conducted, in particular the area and/or unit economic productivity used to define the minimum threshold for landholding inclusion in a census. We suspect there may be some underrepresentation of smallholdings in developed compared to developing nations, for example the USA presents a suspiciously low number of small landholdings, however we think this is a minor issue and reflects the small contribution smallholdings make to developed nations. Reporting for some developing nations appears unrealistic, for example Indonesia reports no landholdings > 3 ha in size. There also appeared to be discrepancies between the number of landholdings and total size class area for some nations, for example Norway reports 16,720 landholdings of 5 - 10 ha, theoretically this can give a maximum total size of 167,200 ha yet the census reports 1 312 629 ha. Although question marks are present for some of the WCA 2000 they are relatively infrequent and should not undermine the estimates drawn from the Large-scale dataset.

National income classifications were taken from the WorldBank Databank. Overseas territories and dependences (which are not included in the WorldBank Databank) were independently listed if included in the WCA2000, the national income status for these were derived from GDP as reported in the CIA FactBook classified as per WorldBank criteria.

Table B.1 shows that overall coverage of WCA2000 for global agricultural area was 46% with notably reduced coverage for low income nations, sub-Saharan Africa and Europe and central Asia (Russia did not report).

To generate estimated values of agricultural population for holdings <2 ha and >2 ha (Table B.2) for nations that did not report in WCA2000 the FAO estimate of 2011 agricultural population for that nation was multiplied by the proportions of agricultural holdings (number of holdings) <2 ha and > 2 ha for that nations income group (Table B.2). If a nation had reported for holding number per size class in WCA2000 the proportional values for the number of holdings <2 ha and >2 ha for that nation were multiplied by the agricultural population to give the estimate.

WCA2000 reporting nations were used to generate proportion estimates for each size class (Table B.2) per national income group. Do to the issues with national standardisation, coercion of data into different structures and some potential errors in national reporting, we urge that estimates generated from our analysis are taken as approximations. To our knowledge this analysis is the only published (peer-reviewed) estimate of smallholder area and population with a global perspective and with transparent reporting of methods. However since this analysis was conducted an NGO called GRAIN has also conducted a global analysis of small-scale farming, however this is not peer-reviewed and the uses a variable definition of small-scale farming between nations that makes comparisons difficult. See http://www.grain.org/article/entries/4929-hungry-for-land-small-farmers-feed-the-world-with-less-than-a-quarter-of-all-farmland.

Table B.1 Census coverage, smallholding (defined as holding <2 ha in area) area and smallholding number from World Census of Agriculture 2010. In this table nations which did not provide statistics or summarise data by holding size or number do not contribute to values.

Region	Census Coverage		Holding Area (Agricultural Area, million ha)				Number of Holdings (million)			
	Cropland	Agricultural Area	Area < 2ha	Area > 2ha	% Area < 2ha	% Area > 2ha	Holdings < 2ha	Holdings > 2ha	% Holdings < 2ha	% > Holdings 2ha
High income: nonOECD	14%	1%	0.2	1.3	15%	85%	0.4	0.2	67%	33%
High income: OECD	70%	54%	4.7	563.5	1%	99%	4.6	8.2	36%	64%
High income (Developed)	69%	45%	4.9	564.7	1%	99%	5	8.4	37%	63%
<High income (Developing)	55%	46%	152.4	810.5	16%	84%	360.7	58.2	86%	14%
Low income	31%	28%	14.1	16	47%	53%	17.7	5.3	77%	23%
Lower middle income	67%	53%	92.8	158.5	37%	63%	145.1	33.3	81%	19%
Upper middle income	52%	46%	45.5	636.1	7%	93%	198	19.6	91%	9%
East Asia & Pacific	76%	54%	64.6	131.4	33%	67%	0.4	15.2	2%	98%
Europe & Central Asia	37%	27%	7.7	213.3	3%	97%	8.2	9.5	47%	53%
Latin America & Caribbean	53%	54%	3.5	481.7	1%	99%	2.8	7	29%	71%
Middle East & North Africa	75%	43%	4.6	41.6	9%	90%	7.3	4.6	61%	39%
North America	77%	87%	0.1	379.6	0.04%	99.96%	0.1	2	4%	96%
South Asia	91%	81%	66.9	115.6	37%	63%	105	24.9	81%	19%
Sub-Saharan Africa	18%	19%	9.9	12.1	45%	55%	13.3	3.4	80%	20%
Global	58%	46%	157.4	1375.2	10%	90%	365.7	66.6	85%	15%

Table B.2 Estimated regional values for the total area of smallholder farmland (< 2 ha) and the smallholder agricultural population. Note areas for holding area should be interpreted as the area of both arable and pastoral agriculture. In this table values were estimated for nations which did not provide statistics or summarise data by holding size or number.

Region	Holding Area (Agricultural Area, million ha)				Agricultural Population (million)			
	%Area < 2 ha	%Area > 2 ha	Area < 2 ha	Area > 2 ha	% AgPop< 2 ha	% AgPop> 2 ha	AgPop< 2ha	AgPop> 2ha
East Asia & Pacific	15%	85%	115.1	641.7	92%	8%	1012.5	89.3
Europe & Central Asia	9%	91%	69.7	735	62%	38%	45	27.1
Latin America & Caribbean	5%	95%	41.1	811.1	63%	37%	66.2	39.4
Middle East & North Africa	16%	84%	40.7	221.2	64%	36%	48	27.2
North America	0%	100%	0.7	441.7	8%	92%	0.4	5.2
South Asia	39%	61%	90.1	142.5	79%	21%	629.7	163.7
Sub-Saharan Africa	34%	66%	305.7	589.3	78%	22%	344.6	99.1
High income: nonOECD	15%	85%	32.2	183.1	67%	33%	5.1	2.5
High income: OECD	1%	99%	8.9	1062.8	33%	67%	10	20.7
High income (Developed)	3%	97%	41.2	1246	39%	61%	15.1	23.2
<High income (Developing)	21%	79%	622.1	2336.8	83%	17%	2131.5	428
Low income	45%	55%	224.1	275.8	76%	24%	392.3	125.4
Lower middle income	37%	63%	285.6	489	80%	20%	818	210.1
Upper middle income	7%	93%	112.4	1571.9	91%	9%	921.1	92.5
Global	16%	84%	663.3	3582.7	83%	17%	2146.5	451.1

Appendix C (Chapters 3-4) Total catch from all valid traps

Table C.1 Total pan trap catches: Hymenoptera and blister beetles (Coleoptera: Meloidae)

Superfamily	Family	Subfamily	Tribe	Genus	Count	
Apoidea	Apidae	Anthophorinae	Anthophorini	Amegilla	5	
Apoidea	Apidae	Apinae	Apini	Apis	12	
Apoidea	Apidae	Apinae	Eucerini	Tetralonia	23	
Apoidea	Apidae	Apinae	Meliponini	Hypotrigona	380	
Apoidea	Apidae	Apinae	Meliponini	Plebeina	39	
Apoidea	Apidae	Apinae	Meliponini	Other	8	
Apoidea	*Apidae*	*Apinae Total*				*462*
Apoidea	Apidae	Nomadinae	Ammobatini	Pasites	1	
Apoidea	Apidae	Xylocopinae	Allodapini	Braunsapis	4	
Apoidea	Apidae	Xylocopinae	Allodapini	Macrogalea	231	
Apoidea	Apidae	Xylocopinae	Ceratinini	Ceratina	31	
Apoidea	Apidae	Xylocopinae	Xylocopini	Xylocopa	3	
Apoidea	*Apidae*	*Xylocopinae Total*				*269*
Apoidea	***Apidae Total***					***737***
Apoidea	Crabronidae	Bembicinae	Bembicini	Stizina	2	
Apoidea	Crabronidae	Crabroninae	Crabronini	Dasyproctus	4	
Apoidea	Crabronidae	Crabroninae	Other		2	
Apoidea	Crabronidae	Crabroninae	Larrini	Gastrosericus	1	
Apoidea	Crabronidae	Crabroninae	Larrini	Liris	28	
Apoidea	Crabronidae	Crabroninae	Larrini	Tachysphex	80	
Apoidea	Crabronidae	Crabroninae	Larrini	Tachytes	1	
Apoidea	Crabronidae	Crabroninae	Miscophini	Solierella	2	
Apoidea	Crabronidae	Crabroninae	Trypoxylonini	Trypoxylon	30	
Apoidea	Crabronidae	Crabroninae	Trypoxylonini	Pison	16	
Apoidea	*Crabronidae*	Crabroninae *Total*				*164*
Apoidea	***Crabronidae Total***					***166***
Apoidea	Halictidae	Halictinae	Halictini	Lasioglossum	86	
Apoidea	Halictidae	Halictinae	Halictini	Seladonia	14	
Apoidea	Halictidae	Halictinae	Halictini	Thrinchostoma	1	
Apoidea	Halictidae	Nomiinae		Lipotriches	13	
Apoidea	Halictidae	Nomiinae		Nomia (Leuconomia)	1	
Apoidea	Halictidae	Nomiinae		Pseudapis	2	
Apoidea	Halictidae	Nomioidinae		Nomioides	1	
Apoidea	Halictidae	Rophitinae		Systropha	7	
Apoidea	***Halictidae Total***					***125***
Apoidea	Megachilidae	Megachilinae	Megachilini	Megachile	37	
Apoidea	Megachilidae	Megachilinae	Osmiini	Heriades	4	
Apoidea	***Megachilidae Total***					***41***
Apoidea	Melittidae	Meganomiinae		Pseudophilanthus	3	
Apoidea	***Melittidae Total***					***3***
Apoidea	Pemphredonidae	Pemphredoninae			2	
Apoidea	***Pemphredonidae Total***					***2***
Apoidea	Philanthidae	Cercerinae			1	
Apoidea	Philanthidae	Philanthinae			1	
Apoidea	***Philanthidae Total***					***2***
Apoidea	Sphecidae	Ammophilinae			1	
Apoidea	***Sphecidae Total***					***1***
Apoidea	Spheciformes	Other			3	
Apoidea	Other				11	
Apoidea Total						***1089***
Ceraphronoidea	**Ceraphronidae**				**3**	
Chalcidoidea	Agaonidae				1	
Chalcidoidea	Chalcididae	Chalcidinae		Brachymeria	1	
Chalcidoidea	Chalcididae	Dirhininae		Dirhinus	1	
Chalcidoidea	Chalcididae	Haltichellinae			15	
Chalcidoidea	Chalcididae	Other			1	
Chalcidoidea	***Chalcididae Total***					***18***
Chalcidoidea	***Encyrtidae***				***31***	
Chalcidoidea	***Eulophidae***				***21***	
Chalcidoidea	***Eupelmidae***				***13***	
Chalcidoidea	***Eurytomidae***				***7***	
Chalcidoidea	***Mymaridae***				***2***	
Chalcidoidea	***Perilampidae***				***3***	
Chalcidoidea	Pteromalidae	Pteromalinae			1	
Chalcidoidea	Pteromalidae	Spalangiinae			1	
Chalcidoidea	Pteromalidae	Other			21	
Chalcidoidea	***Pteromalidae Total***					*23*
Chalcidoidea	***Torymidae***				***25***	
Chalcidoidea Total						***144***
Chrysidoidea	***Bethylidae***				***68***	
Chrysidoidea	Chrysididae	Chrysidinae	Chrysidini		5	
Chrysidoidea	Chrysididae	Chrysidinae	Elampini		1	
Chrysidoidea	***Chrysididae Total***					***6***

Superfamily	**Family**	**Subfamily**	**Tribe**	**Genus**	**Count**	
Chrysidoidea	***Dryinidae***				***2***	
Chrysidoidea Total						***76***
Cynipoidea	Figitidae	Aspicerinae	Aspicerini	Anacharoides	2	
Cynipoidea	Figitidae	Eucoilinae			6	
Cynipoidea	Figitidae	Eucoilinae		Stentorceps	2	
Cynipoidea	***Figitidae Total***					***10***
Cynipoidea Total						***10***
Evanioidea	***Evaniidae***				***8***	
Evanioidea Total						***8***
Ichneumonoidea	Braconidae	Cheloninae			3	
Ichneumonoidea	Braconidae	Other			13	
Ichneumonoidea	***Braconidae Total***					***16***
Ichneumonoidea	***Ichneumonidae***				***9***	
Ichneumonoidea Total						***25***
Platygastroidea	***Platygastridae***				***3***	
Platygastroidea	***Scelionidae***				***90***	
Platygastroidea Total						***93***
Proctotrupoidea	***Diapriidae***				***1***	
Proctotrupoidea Total						***1***
Stephanoidea	***Stephanidae***				***1***	
Stephanoidea Total						***1***
Tenthredinoidea	***Tenthredinidae***				***4***	
Tenthredinoidea Total						***4***
Vespoidea	***Bradynobaenidae***				***3***	
Vespoidea	***Mutillidae***				***8***	
Vespoidea	***Pompilidae***				***51***	
Vespoidea	***Sapygidae***				***1***	
Vespoidea	***Scoliidae***				***41***	
Vespoidea	Tiphiidae	Anthoboscinae			21	
Vespoidea	Tiphiidae	Myzininae			3	
Vespoidea	Tiphiidae	Tiphiinae			5	
Vespoidea	Tiphiidae	Other			2	
Vespoidea	***Tiphiidae Total***					***31***
Vespoidea	Vespidae	Eumeninae	Ropalidiini	Belongaster	3	
Vespoidea	Vespidae	Eumeninae	Other		41	
Vespoidea	***Vespidae Total***					***44***
Vespoidea Total						***179***
Damaged/Missing					22	
Grand Total					**1657**	

Superfamily	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**	**Count**
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Actenodia	unimaculata	2
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Ceroctis	sp1	383
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	apicicornis	20
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	arussina	1072
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	chevrolati	3
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	parenthesis	144
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Mylabris	aperta	326
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Mylabris	praestans	83
Grand Total						**2033**

Table C.2 Total pitfall trap catches: Coleoptera

Superfamily	**Family**	**Subfamily**	**Tribe**	**Genus**	**species**	**Count**	
Buprestoidea	Buprestidae	Polycestinae	Acmaeoderini	Acmaeodera	sp1	5	
Buprestoidea Total							**5**
Caraboidea	Carabidae	Brachininae	Brachinini	Styphlomerus	sp1	1	
Caraboidea	Carabidae	Brachininae	Crepidogastrini	Crepidogaster	bioculata	8	
Caraboidea	Carabidae	Brachininae	Crepidogastrini	Crepidogaster	hubenthali	2	
Caraboidea	Carabidae	Brachininae	Crepidogastrini	Crepidogaster	sp1	2	
Caraboidea	*Carabidae*	*Brachininae Total*					*13*
Caraboidea	Carabidae	Cicindelinae	Megacephalini	Megacephala	regalis	10	
Caraboidea	Carabidae	Cicindelinae	Cicindelini	Cicindela	brevicollis	1	
Caraboidea	Carabidae	Cicindelinae	Cicindelini	Dromica	schaumi	1	
Caraboidea	Carabidae	Cicindelinae	Cicindelini	Elliptica	kenyana	3	
Caraboidea	*Carabidae*	*Cicindelinae Total*					*15*
Caraboidea	Carabidae	Harpalinae	Anthiini	Cypholoba	spathulata	18	
Caraboidea	Carabidae	Harpalinae	Anthiini	Cypholoba	tenuicollis	7	
Caraboidea	Carabidae	Harpalinae	Anthiini	Cypholoba	tetrastigma	4	
Caraboidea	Carabidae	Harpalinae	Anthiini	Cypholoba	trilunata	6	
Caraboidea	Carabidae	Harpalinae	Anthiini	Thermophilum	hexasticum	1	
Caraboidea	Carabidae	Harpalinae	Chlaeniini	Chlaenius	laetoides	2	
Caraboidea	Carabidae	Harpalinae	Chlaeniini	Chlaenius	xanthomerus	1	
Caraboidea	Carabidae	Harpalinae	Cyclosomini	Tetragonoderus	bilunatus	16	

Superfamily	**Family**	**Subfamily**	**Tribe**	**Genus**	**species**	**Count**
Caraboidea	Carabidae	Harpalinae	Graphipterini	Graphipterus	interlineatus	4
Caraboidea	Carabidae	Harpalinae	Harpalini	Axinotoma	punctulata	2
Caraboidea	Carabidae	Harpalinae	Harpalini	Harpalus	asemus	10
Caraboidea	Carabidae	Harpalinae	Harpalini	Ooidius	ephippium	1
Caraboidea	Carabidae	Harpalinae	Harpalini	Platymetopus	tesselatus	1
Caraboidea	Carabidae	Harpalinae	Harpalini	Parophonus	escheri	2
Caraboidea	Carabidae	Harpalinae	Harpalini	Parophonus	sp1	1
Caraboidea	Carabidae	Harpalinae	Helluonini	Triaenogenius	sculpturatus	6
Caraboidea	Carabidae	Harpalinae	Platynini	Agonum	sp1	1
Caraboidea	*Carabidae*	*Harpalinae Total*				*83*
Caraboidea	Carabidae	Harpalinae / Orthogoniinae	Amorphomerini	Amorphomerus	opacus	35
Caraboidea	Carabidae	Harpalinae / Orthogoniinae	Orthogoniini	Orthogonius	coracinus	10
Caraboidea	*Carabidae*	*Harpalinae / Orthogoniinae Total*				*45*
Caraboidea	Carabidae	Scaritinae	Scaritini	Scarites	molussus	18
Caraboidea	***Carabidae Total***					***174***
Caraboidea Total						**174**
Chrysomeloidea	Chrysomelidae	Bruchinae	Amblycerini	Spermophagus	cicatricosus	94
Chrysomeloidea	Chrysomelidae	Cassidinae	Hispini	Dactylispa	sp1	1
Chrysomeloidea	Chrysomelidae	Chrysomelinae	Chrysomelini	Colaspidema	discoidale	3
Chrysomeloidea	Chrysomelidae	Eumolpinae	Brominiini	Scelodonta	spinipes	4
Chrysomeloidea	Chrysomelidae	Galerucinae	Luperini	Exsosoma	kohlschutteri	18
Chrysomeloidea	***Chrysomelidae Total***					***120***
Chrysomeloidea Total						**120**
Cleroidea	Melyridae	Melyrinae		Melyris	sp1	1
Cleroidea Total						**1**
Curculionoidea	Brentidae	Brentinae	Eremoxenini	Perisymmorphocerus	compactus	1
Curculionoidea	Brentidae	Microcerinae		Episus	spinosus	1
Curculionoidea	Brentidae	Microcerinae		Episus	tuberosus	1
Curculionoidea	Brentidae	Microcerinae		Microcerus	spiniger	6
Curculionoidea	***Brentidae Total***					***10***
Curculionoidea	Curculionidae	Brachycerinae	Brachycerini	Brachycerus	hofmanni	1
Curculionoidea	Curculionidae	Entiminae	Peritelini	Systates	sp1	1
Curculionoidea	Curculionidae	Entiminae	Peritelini	Diaecoderus	sp1	6
Curculionoidea	Curculionidae	Entiminae	Tanymecini	Polyclaeis	maculata	2
Curculionoidea	*Curculionidae*	*Entiminae Total*				*10*
Curculionoidea	Curculionidae	Lixinae	Cleonini	Calodemas	biguttatum	1
Curculionoidea	Curculionidae	Lixinae	Cleonini	Pycnodactylus	tibialis	27
Curculionoidea	Curculionidae	Lixinae	Lixini	Neocleonus	mitis	8
Curculionoidea	*Curculionidae*	*Lixinae Total*				*36*
Curculionoidea	Curculionidae	Microcerinae		Microcerus	abiventer	3
Curculionoidea	Curculionidae	Molytinae	Mecysolobini	Alcidodes	leucogrammus	1
Curculionoidea	Curculionidae	Molytinae	Mecysolobini	Microcerus	annuliger	2
Curculionoidea	*Curculionidae*	*Molytinae Total*				*6*
Curculionoidea	Curculionidae	Entiminae	Tropiphorini	Spartecerus	guasonicus	51
Curculionoidea	Curculionidae	Entiminae	Tropiphorini	Spartecerus	sp1	30
Curculionoidea	*Curculionidae*	*Entiminae Total*				*81*
Curculionoidea	***Curculionidae Total***					***133***
Curculionoidea Total						**143**
Elateroidea	Elateridae	Agrypninae	Agrypnini	Tylotarsus	sp1	2
Elateroidea	Elateridae	Agrypninae	Agrypnini	Adelocera	kinangopa	32
Elateroidea	Elateridae	Agrypninae	Agrypnini	Adelocera	occiidentalis	5
Elateroidea	Elateridae	Agrypninae	Agrypnini	Adelocera	tumidipennis	17
Elateroidea	Elateridae	Agrypninae	Conoderini	Heteroderes	flavonotatus	3
Elateroidea	*Elateridae*	*Agrypninae Total*				*59*
Elateroidea	Elateridae	Cardiophorinae	Pyrophorinae incertae sedia	Cardiophorus	sp1	2
Elateroidea	Elateroidea Total					61
Histeroidea	Histeridae	Histerinae	Histerini	Hister	sp1	28
Histeroidea Total						**28**
Scarabaeoidea	Hybosoridae	Hybosorinae		Phaeochrous	beccarii	1
Hybosoridae Total						***1***
Scarabaeoidea	Scarabaeidae	Melolonthinae	Melolonthini	Apogonia	sp1	1
Scarabaeoidea	Scarabaeidae	Melolonthinae	Melolonthini	Brachylepis	elephas	8
Scarabaeoidea	Scarabaeidae	Melolonthinae	Melolonthini	Schizonycha	sp1	1
Scarabaeoidea	Scarabaeidae	Melolonthinae	Sericini	Sphaerotrochalus	bohmi	18
Scarabaeoidea	Scarabaeidae	Melolonthinae	Sericini	Trochalus	sp1	2
Scarabaeoidea	*Scarabaeidae*	*Melolonthinae Total*				*30*
Scarabaeoidea	Scarabaeidae	Rutelinae	Adoretini	Adoretus	flavovittatus	1
Scarabaeoidea	Scarabaeidae	Rutelinae	Anomalini	Anomala	ancilla	2
Scarabaeoidea	Scarabaeidae	Rutelinae	Anomalini	Anomala	bottae	3
Scarabaeoidea	Scarabaeidae	Rutelinae	Anomalini	Anomala	sp1	1
Scarabaeoidea	Scarabaeidae	Rutelinae	Anomalini	Nothophanus	sp1	3

Superfamily	Family	Subfamily	Tribe	Genus	species	Count	
Scarabaeoidea	Scarabaeidae	Rutelinae	Anomalini	Nothophanus	sp2	3	
Scarabaeoidea	*Scarabaeidae*	*Rutelinae Total*					*13*
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Canthonini	Anachalcos	convexus	7	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Canthonini	Gyronotus	fimetarius	1	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Coprini	Catharsius	opacus	24	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Coprini	Catharsius	stulmanni	7	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	atrofasciatus	49	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	bellus	7	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	laceratus	3	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	proteus	61	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	quadrimaculata	49	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	simoni	30	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	sinuosicollis	3	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	sp 1	1	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	variegatus	19	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Onthophagini	Onthophagus	vinctus	21	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Scarabaeini	Scarabaeus	ebenus	21	
Scarabaeoidea	Scarabaeidae	Scarabaeinae	Sisyphini	Sisyphus	caffer	3	
Scarabaeoidea	*Scarabaeidae*	*Scarabaeinae Total*					*306*
Scarabaeoidea	***Scarabaeidae Total***						***349***
Scarabaeoidea Total							**350**
Tenebrionoidea	Meloidae	Eleticinae	Eleticini	Eletica	sp1	1	
Tenebrionoidea	Meloidae	Eleticinae	Eleticini	Eletica	sp2	1	
Tenebrionoidea	Meloidae	Eleticinae	Eleticini	Eletica	sp3	2	
Tenebrionoidea	Meloidae	Eleticinae	Eleticini	Eletica	sp4	4	
Tenebrionoidea	*Meloidae*	*Eleticinae Total*					*8*
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Actenodia	unimaculata	8	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Ceroctis	sp1	338	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	apicicornis	51	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	arussina	231	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	chevrolati	95	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Coryna	parenthesis	53	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Mylabris	aperta	45	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Mylabris	praestans	8	
Tenebrionoidea	Meloidae	Meloinae	Mylabrini	Mylabris	tristigma	3	
Tenebrionoidea	*Meloidae*	*Meloinae Total*					*832*
Tenebrionoidea	Meloidae	Nemognathinae	Nemognathini	Zonitodema	caerulans	1	
Tenebrionoidea	***Meloidae Total***						***841***
Tenebrionoidea	Mordellidae					1	
Tenebrionoidea	***Mordellidae Total***						***1***
Tenebrionoidea	Tenebrionidae	Cossyphinae	Cossyphini	Endustomus	sp1	1	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Adelostomini	Pogonobasis	costa	11	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Sepidiini	Psammodes	catenatus	26	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Sepidiini	Psammodes	manifestus	5	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Sepidiini	Sepidium	muscosum	50	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Tentyriini	Rhytinota	gravidula	470	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Tentyriini	Rhytinota	sp1	11	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Zophosini	Zophosis	anqusticostis / collaris*	260	
Tenebrionoidea	Tenebrionidae	Pimeliinae	Zophosini	Zophosis	sulcata	57	
Tenebrionoidea	*Tenebrionidae*	*Pimeliinae Total*					*890*
Tenebrionoidea	Tenebrionidae	Stenochiinae	Stenochiini	Praogena	marginata	2	
Tenebrionoidea	Tenebrionidae	Tenebrioninae	Helopini	Micrantereus	femoratus	2	
Tenebrionoidea	Tenebrionidae	Tenebrioninae	Opatrini	Anomalipus	heraldicus	1	
Tenebrionoidea	Tenebrionidae	Tenebrioninae	Opatrini	Gonocephalum	simplex	237	
Tenebrionoidea	Tenebrionidae	Tenebrioninae	Platynotini	Quadrideres	sp1	7	
Tenebrionoidea	*Tenebrionidae*	*Tenebrioninae Total*					*249*
Tenebrionoidea	Tenebrionidae	Unknown				2	
Tenebrionoidea	***Tenebrionidae Total***						***1142***
Tenebrionoidea	Zopheridae	Colydiinae				1	
Tenebrionoidea	***Zopheridae Total***						***1***
Tenebrionoidea Total							**3127**
Unidentified						23	
Beetles <0.4 mm						365	
Grand Total						**3254**	

* Species pair, unknown whether specimens are one of the species or a mixture of both.

Appendix D (Chapters 3-4) Functional trait tables

Table D.1 Coleoptera species functional traits table. See Appendix G for reference materials. Species codes can be cross-referenced to the first two letters of Family, Subfamily, Tribe, Genera and Species for each species as per Appendix C Table C.1, an "X" indicates that the classification was unknown.

Species Code	Size (cm^2)	Adult feeding behaviour					Larval feeding behaviour					Larval location						
		Phytophage	Pollen or nectar	Scavenger	Predator	Detrivore or coprophage	Predator	Phytophage	Wood boring	Detritivore / coprophage	Parasite	Unknown	Soil	Roots	Under-ground	Above-ground	Wood	Plants
BrBrErPe_com	0.066	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1
BrMi_Ep_spi	0.273	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
BrMi_Ep_tub	0.507	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
BrMi_Mi_spi	1.777	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
BuPoAcAc_sp1	0.163	1	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0
CaHaHaPa_esc	0.328	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaHaHaPa_sp1	0.161	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaBrBrSt_sp1	0.126	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaBrCrCr_bio	0.614	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaBrCrCr_hub	0.378	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaBrCrCr_sp1	0.138	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
CaCiCiCi_bre	0.336	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaCiCiDr_sch	0.324	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaCiCiEl_ken	0.655	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaCiMeMe_reg	2.481	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAmAm_opa	1.103	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAnCy_spa	2.103	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAnCy_ten	0.503	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAnCy_tet	1.191	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAnCy_tri	1.615	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaAnTh_hex	4.625	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaChCh_lae	1.005	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaChCh_xan	0.571	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaCyTe_bil	0.171	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaGrGr_int	0.450	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaHaAx_pun	0.394	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0

Species Code	Size (cm^2)	Adult feeding behaviour					Larval feeding behaviour					Larval location						
		Phytophage	Pollen or nectar	Scavenger	Predator	Detrivore or coprophage	Predator	Phytophage	Wood boring	Detritivore / coprophage	Parasite	Unknown	Soil	Roots	Under-ground	Above-ground	Wood	Plants
CaHaHaHa_ase	0.191	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaHaOo_eph	0.469	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaHaPl_tes	0.194	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaHeTr_scu	1.377	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaOrOr_cor	1.100	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaHaPlAg_sp1	0.596	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0
CaScScSc_mol	3.198	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
ChBrAmSp_cic	0.113	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
ChCaHiDa_sp1	0.072	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
ChChChCo_dis	0.137	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
ChEuBrSc_spi	0.083	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ChGaLuEx_koh	0.137	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuBrBrBr_hof	2.141	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuEnPeDi_sp1	0.323	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuEnPeSy_sp1	0.185	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuEnTaPo_mac	0.866	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuEnTrSp_gua	0.387	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuEnTrSp_sp1	0.266	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuLiClCa_big	0.535	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1
CuLiClPy_tib	0.679	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1
CuLiLiNe_mit	1.251	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1
CuMi_Mi_abi	0.770	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
CuMoMeAl_leu	0.271	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1
CuMoMeMi_ann	0.488	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1
ElAgAgAd_kin	0.173	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0
ElAgAgAd_occ	0.406	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0
ElAgAgAd_tum	0.073	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0
ElAgAgTy_sp1	0.535	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0
ElAgCoHe_fla	0.225	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0
ElCaPyCa_sp1	0.457	0	1	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0
HiHiHiHi_sp1	0.428	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0

Species Code	**Size (cm^2)**	**Adult feeding behaviour**					**Larval feeding behaviour**					**Larval location**						
		Phytophage	**Pollen or nectar**	**Scavenger**	**Predator**	**Detrivore or coprophage**	**Predator**	**Phytophage**	**Wood boring**	**Detritivore / coprophage**	**Parasite**	**Unknown**	**Soil**	**Roots**	**Under-ground**	**Above-ground**	**Wood**	**Plants**
HyHy_Ph_bec	0.537	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	0
MeElElEl_sp1	1.241	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
MeElElEl_sp2	1.035	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
MeElElEl_sp3	1.128	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
MeElElEl_sp4	1.416	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
MeMe_Me_sp1	0.101	1	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0
MeMeMyAc_uni	0.196	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyCe_sp1	1.029	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyCo_api	0.350	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyCo_aru	0.447	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyCo_che	0.193	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyCo_par	0.370	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyMy_ape	2.465	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyMy_pra	2.790	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeMeMyMy_tri	1.466	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
MeNeNeZo_cae	0.243	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
MoXXX_sp1	0.077	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1
ScScCaGy_fim	1.233	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
ScMeMeAp_sp1	0.277	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScMeMeBr_ele	3.547	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScMeMeSc_sp1	0.435	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScMeSeSp_boh	0.165	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScMeSeTr_sp1	0.305	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScRuAdAd_fla	0.318	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0
ScRuAnAn_anc	0.970	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScRuAnAn_bot	0.725	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScRuAnAn_sp1	0.572	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
ScRuAnNo_sp1	0.308	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
ScRuAnNo_sp2	0.422	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
ScScCaAn_con	3.540	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScCoCa_opa	1.197	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0

Species Code	Size (cm^2)	Adult feeding behaviour					Larval feeding behaviour					Larval location						
		Phytophage	Pollen or nectar	Scavenger	Predator	Detrivore or coprophage	Predator	Phytophage	Wood boring	Detritivore / coprophage	Parasite	Unknown	Soil	Roots	Under-ground	Above-ground	Wood	Plants
ScScCoCa_stu	3.113	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_atr	0.139	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_bel	0.285	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_lac	0.335	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_pro	0.363	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_qua	0.132	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_sim	0.124	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_sin	0.561	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_sp_	0.166	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_var	0.106	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScOnOn_vin	0.293	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScScSc_ebe	1.645	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
ScScSiSi_caf	0.231	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
TeCoCoEn_sp1	1.002	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0
TePiAdPo_cos	0.259	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiSePs_cat	2.222	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiSePs_man	2.280	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiSeSe_mus	1.093	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiTeRh_gra	0.341	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiTeRh_sp1	0.458	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiZoZo_anq	0.226	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TePiZoZo_sul	0.659	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TeStStPr_mar	0.472	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0
TeTeHeMi_fem	1.222	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0
TeTeOpAn_her	3.695	0	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0
TeTeOpGo_sim	0.537	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
TeTePlQu_sp1	0.485	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0
ZoCoXX_sp1	0.086	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0

Table D.2 Hymenopteran family functional traits table. See Appendix H for reference materials. Family codes can be cross-referenced to the first four letters of Family Appendix C Table C.2. Larval feeding behaviours: Gall =galler; Fig = fig wasp; Seed = seed predator or granivore; Bore = stalk, stem, twig, flower, etc. borer; Mine = leaf miner or similar; Prov = provisioned by adult; Pred = predatory; Egg = egg predator or parasitoid; Inq = inquiline; Para = parasitoid; Hyp = hyperparasitoid and clep = cleptoparasite. Larval diet: P/N = pollen or nectar; Phyt = phytophage; Ara = Araneae; Bla = Blattodea; Cole = Coleoptera; Coll = Collembola; Dip = Diptera; Emi = Embioptera; Hem = Hemiptera; Hym = Hymenoptera; Iso = Isoptera; Lep = Lepidoptera; Man = Mantodea; Neu = Neuroptera; Nem = Nematoda; Ort = Orthoptera; Par = Parasitiformes; Pse = Pseudoscorpionida; Pso = Psocoptera; Pha = Rhaphidioptera; Sip = Siphonaptera; Sol = Solifugae; Thy = Thysanoptera; Tri = Trichoptera. A score of 1 indicates a strong association with a trait with a majority of species in the family demonstrating it, a score of 0.5 indicates a moderate association with many species, but less than a majority, in the family demonstrating it, a score of 0.1 indicates the trait is demonstrated by just a few species within in a family which are considered to be somewhat atypical, and a score of zero indicates no association with the trait.

Family	Larval feeding behaviour													Larval diet (parasitoid hosts, provisioned items, etc.)																							
	Gall	Fig	Seed	Bore	Mine	Leaf	Prov	Pred	Egg	Inq	Para	Hyp	Clep	P/N	Phyt	Ara	Bla	Cole	Coll	Dip	Emi	Hem	Hym	Iso	Lep	Man	Neu	Nem	Ort	Par	Pse	Pso	Pha	Sip	Sol	Thy	Tri
Crab	0	0	0	0	0	0	1	0	0	0	0	0	0.1	0	0	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Apid	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pemp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Cera	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Agao	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eury	1	0	1	1	0	0	0	0	0.1	0.5	1	0.1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tory	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0.1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Peri	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0.5	0	0.5	0	0	0	0	0	0	0	0
Ency	0	0	0	0	0	0	0	0	0	0	1	0.5	0	0	0	0.5	0	0.5	0	0.5	0	1	0.5	0	0.5	0	0.5	0	0.5	0.5	0	0	0	0	0	0	0
Myma	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0.5	0	0	0	1	0	0	0	0	0	0	0.5	0	0	0.5	0	0	0	0	0
Chal	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0.1	0	1	0	0	0.1	0	1	0	0.1	0	0	0	0	0	0	0	0	0	0
Eulo	0	0	0	0	0	0	0	0	0	0	1	0.5	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Eupe	0	0	0	0	0	0	0	0	0.1	0	1	1	0	0	0	0.1	0	1	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Pter	0	0	0	0	0	0	0	0.5	0.5	0.5	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Beth	0	0	0	0	0	0	0.5	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Dryi	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Figi	0	0	0	0	0	0	0	0	0	0	1	0.5	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Brac	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0.5	0.5	0.5	0.5	0.5	1	0	0	0	0.5	0	0	0.5	0	0	0	0	0
Ichn	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.5	0	1	0	0.5	0	0	1	0	1	0	0	0	0	0	0.5	0	0.5	0	0	0	0.5
Plat	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0.5	0	0.5	0	1	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Step	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tent	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Family	Larval feeding behaviour													Larval diet (parasitoid hosts, provisioned items, etc.)																							
	Gall	Fig	Seed	Bore	Mine	Leaf	Prov	Pred	Egg	Inq	Para	Hyp	Clep	P/N	Phyt	Ara	Bla	Cole	Coll	Dip	Emi	Hem	Hym	Iso	Lep	Man	Neu	Nem	Ort	Par	Pse	Pso	Pha	Sip	Sol	Thy	Tri
Pomp	0	0	0	0	0	0	1	0	0	0	0	0	0.5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sapy	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brad	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tiph	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hali	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mega	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meli	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phil	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphe	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0.5	0	0	0	0	0	0	0	0
Chry	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Evan	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muti	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.5	0.5	0	0.5	0	0	1	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0
Scol	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vesp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.5	0	1	0	0	0	0.5	0	0	0	0	0	0	0	0

Appendix E (Chapter 3) Regression model predictions and observed data for parasitoid Hymenoptera using PCA transformed predictors

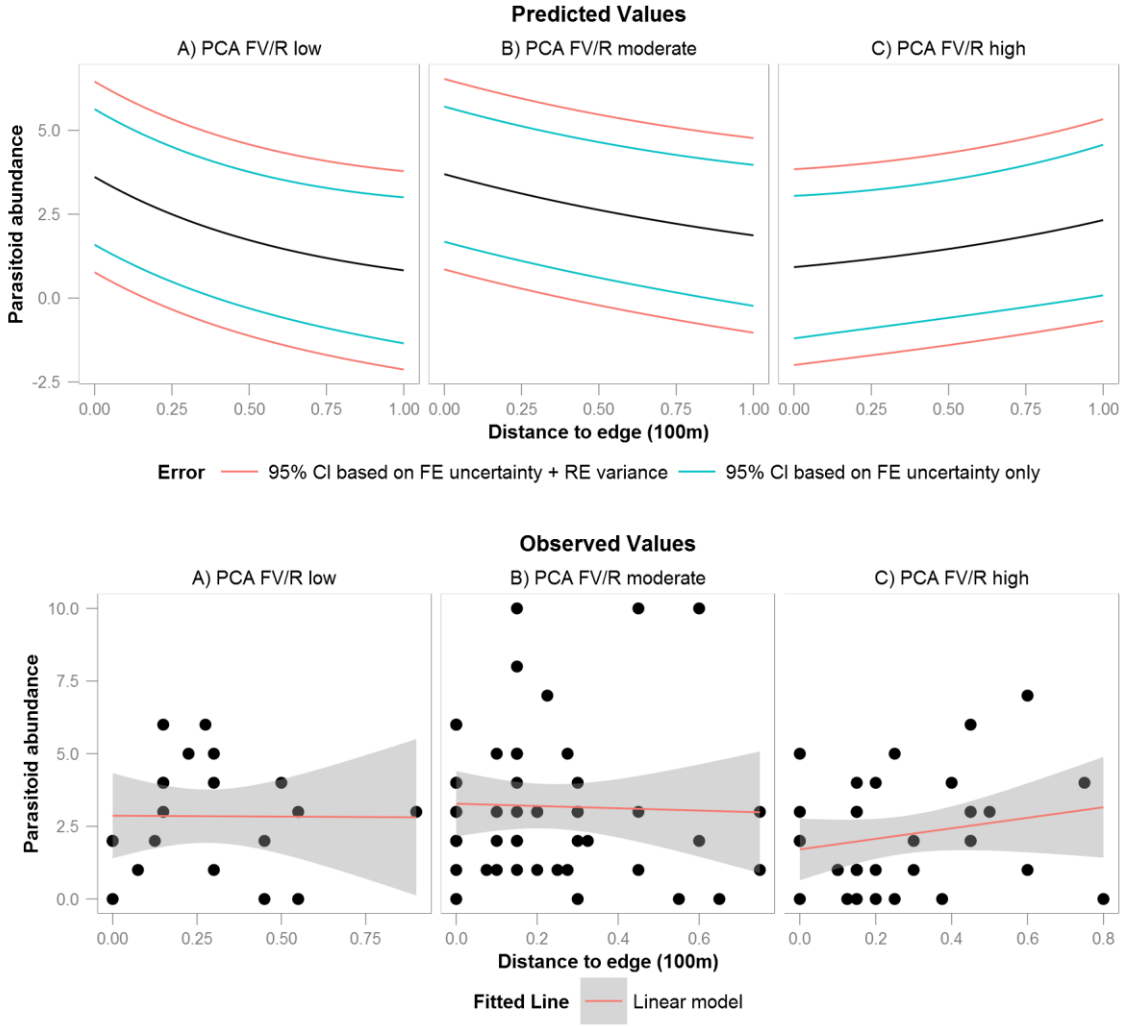


Figure E.1 Observed and GLMM predicted values of parasitoid Hymenoptera abundance when varying distance to edge for high, moderate or low values of matrix quality. PCA FV/R low refers to the PCA axis onto which field and trap floral area, floral diversity and rainfall loaded. For model details see Table 3.4**.**

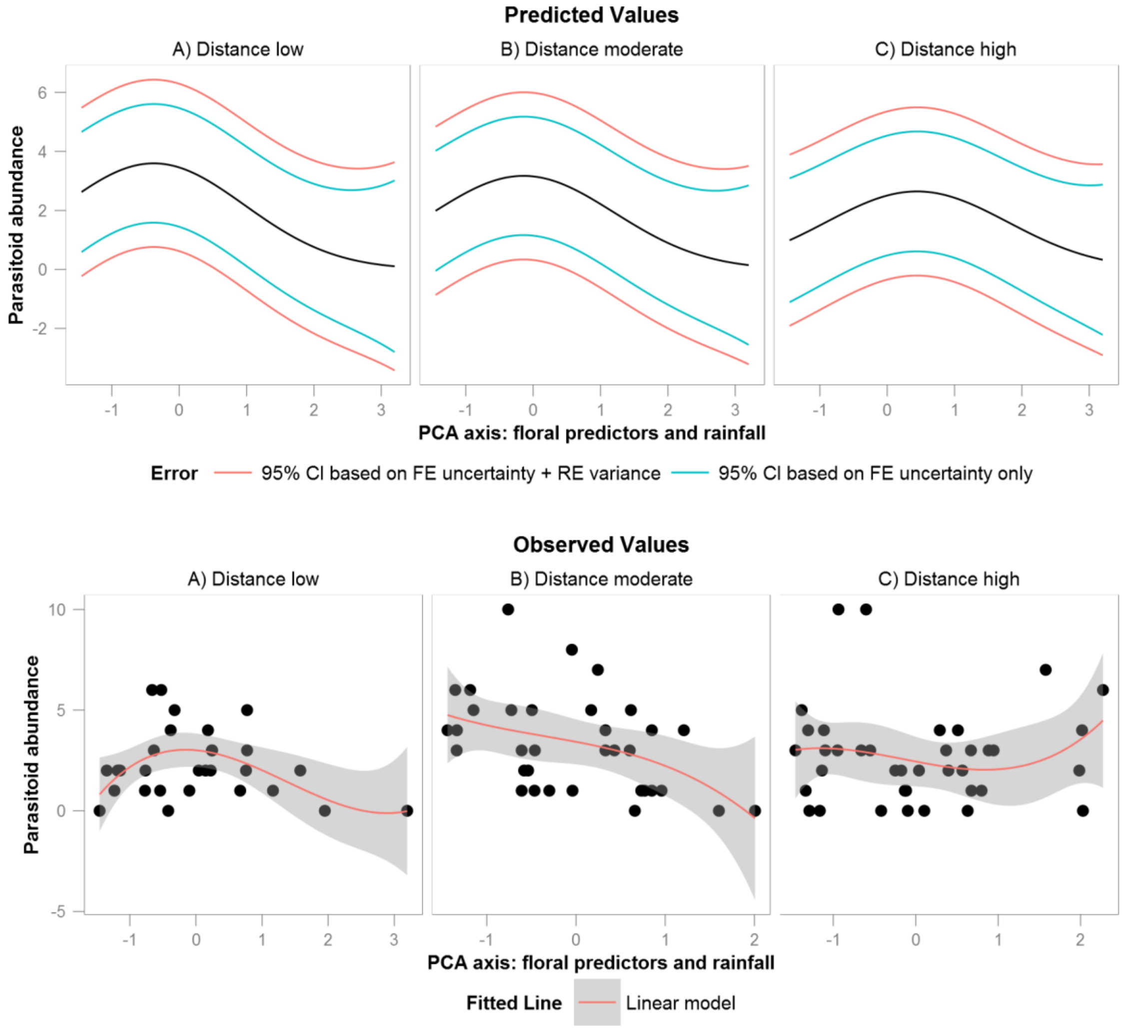


Figure E.2 Observed and GLMM predicted values of parasitoid Hymenoptera abundance when varying the PCA axis onto which field and trap floral area, floral diversity and rainfall loaded onto, for high, moderate or low values of distance to field edge. For model details see Table 3.4**.**

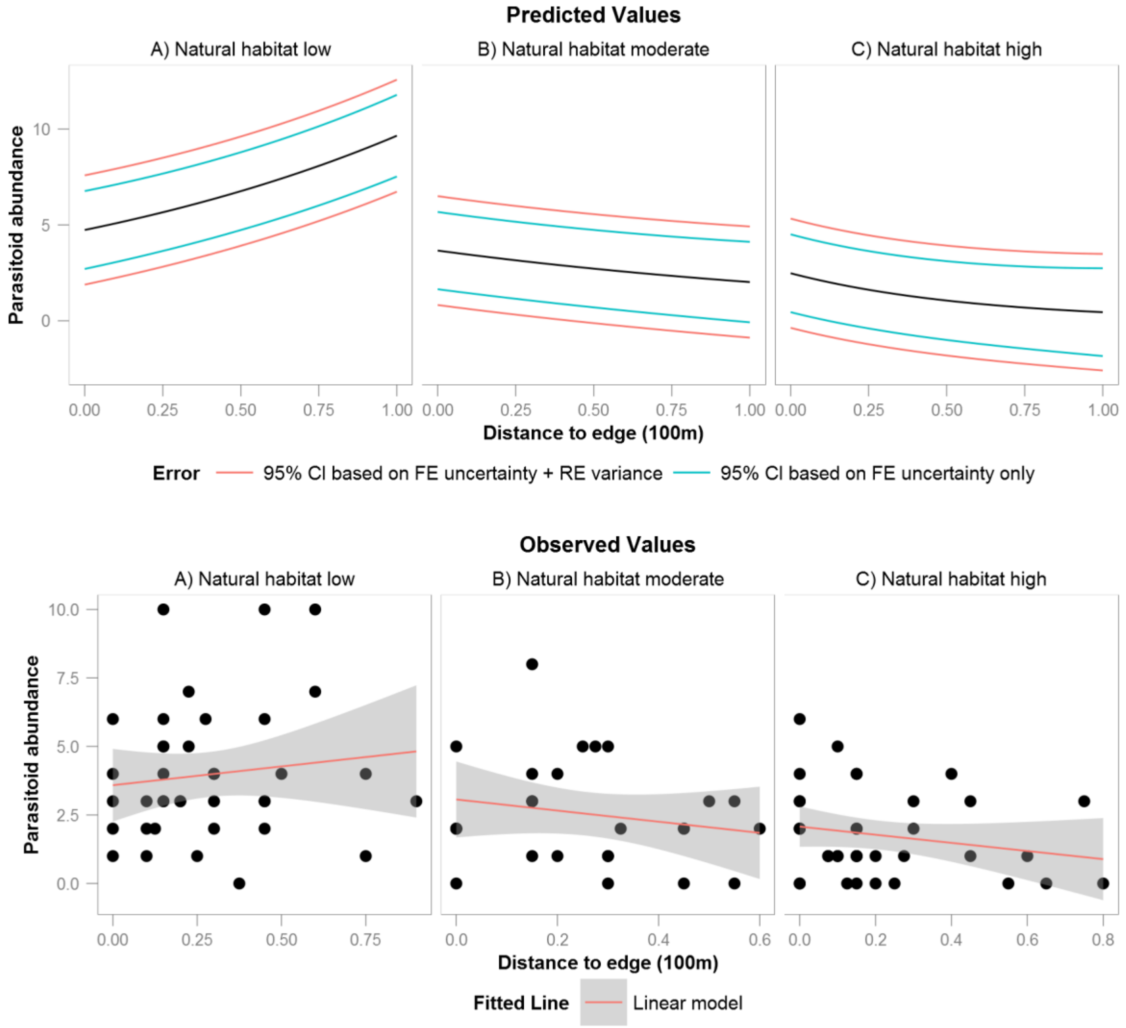


Figure E.3 Observed and GLMM predicted values for parasitoid Hymenoptera abundance when varying distance to edge for high, moderate or low values of the PCA axis onto which landscape (natural habitat within 100 m) loaded most strongly. For model details see Table 3.4**.**

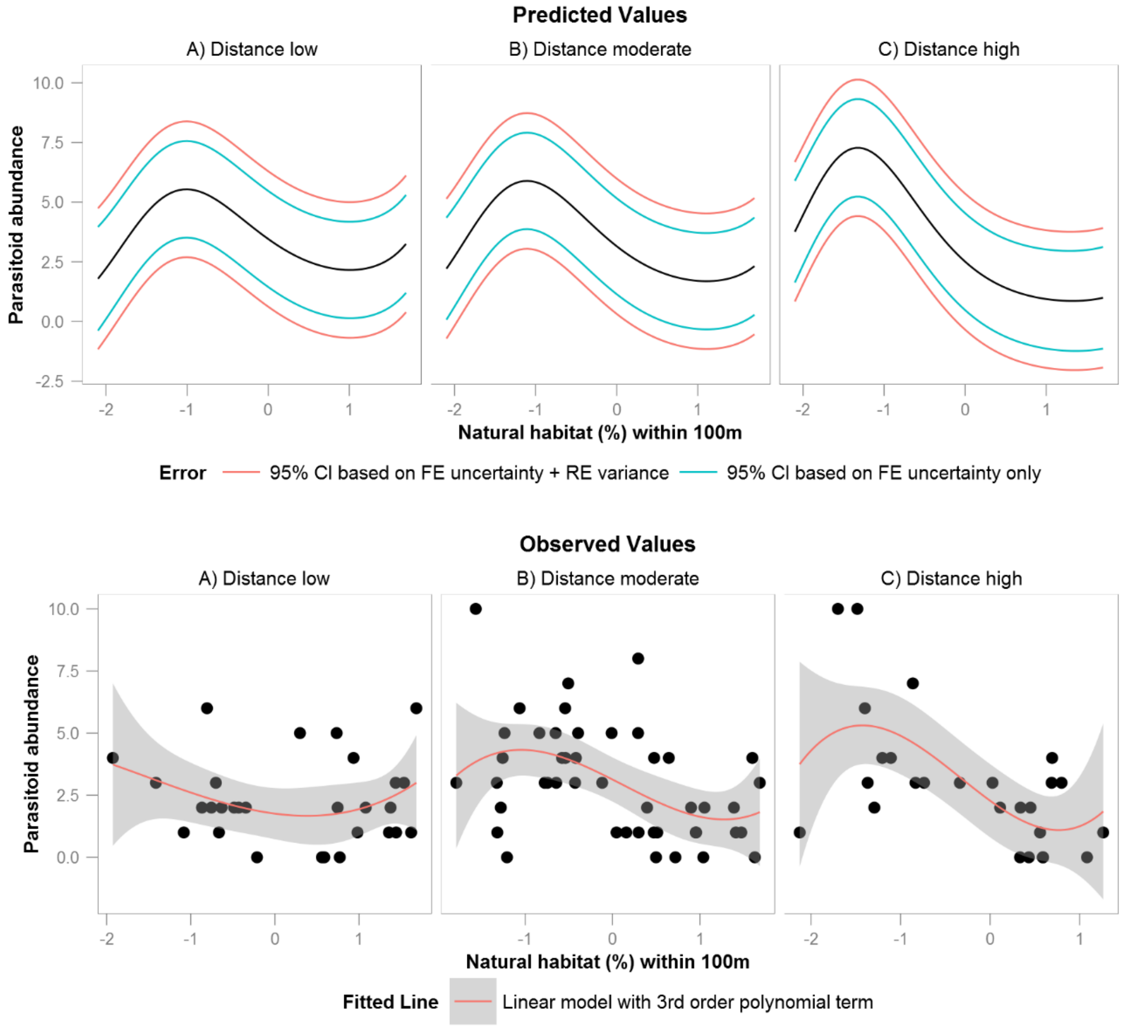


Figure E.4 Observed and GLMM predicted values for parasitoid Hymenoptera abundance when varying the PCA axis onto which landscape (natural habitat within 100 m) loaded most strongly, for high, moderate or low values of distance to edge. For model details see Table 3.4**.**

Appendix F (Chapter 3) Change in relative abundance of three major darkling beetle species at different distances to a (semi-) perennial water source

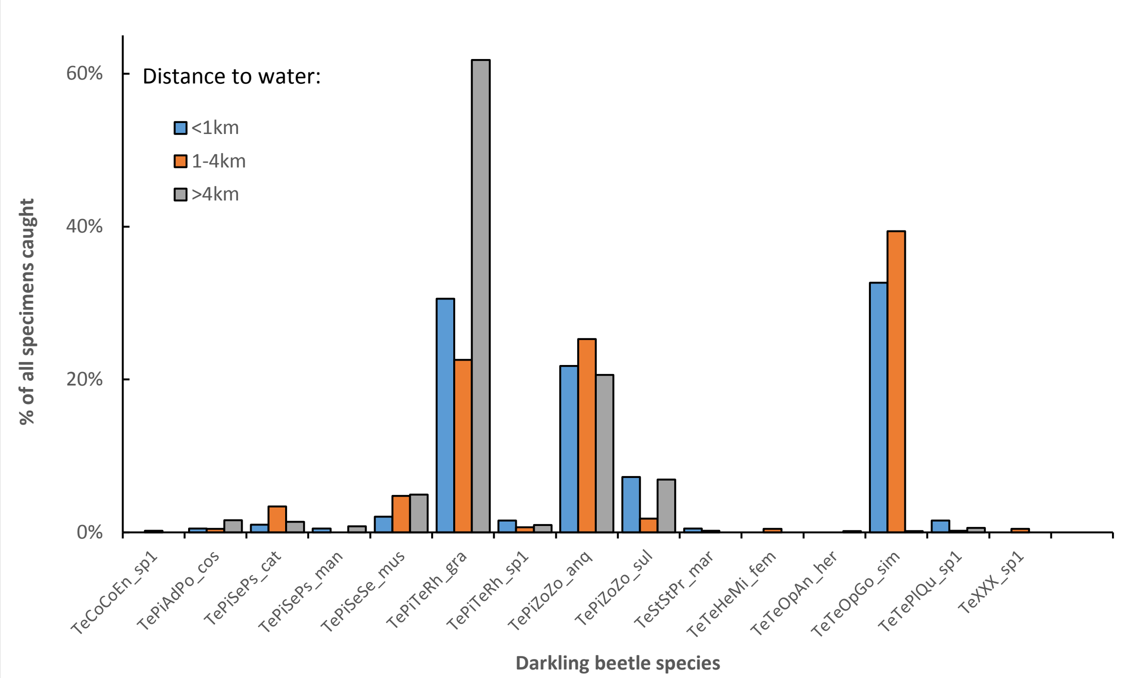


Figure F.1 Darkling beetle species composition at three distance from water intervals, percentages were derived from summing all trap catches within a distance interval. Species codes are a concatenation of the first 2 letters of each taxonomic rank from family to genus and the first 3 letters of the species separated with an underscore, see Appendix C Table C.2.

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Appendix I (Chapter 4) Supplemental materials

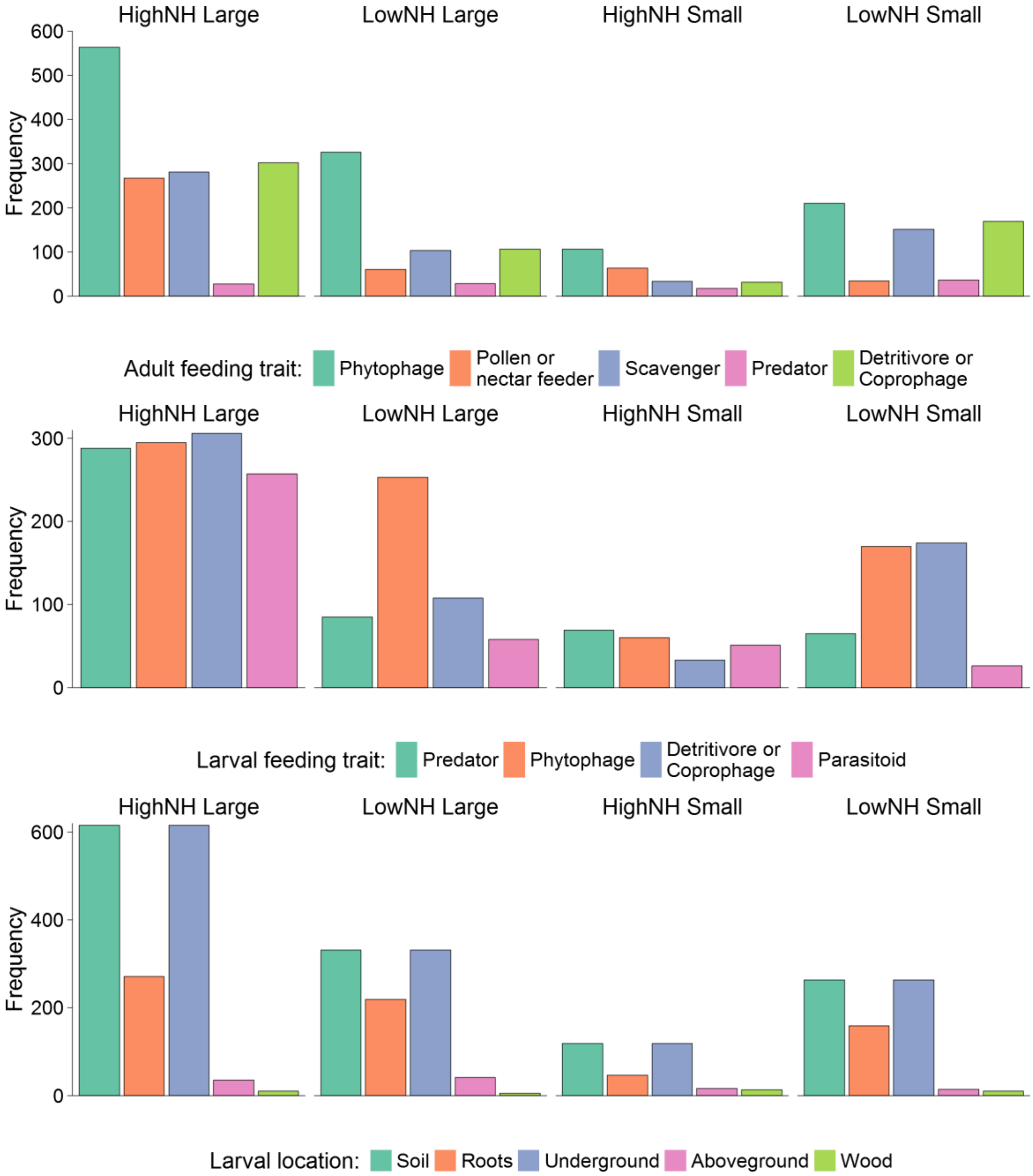


Figure I.1 Coleopteran species trait frequencies between agricultural contexts, note that traits are not mutually exclusive and a species can be positive for more than one trait in each group. For total abundances see Chapter 4 Table 4.1.

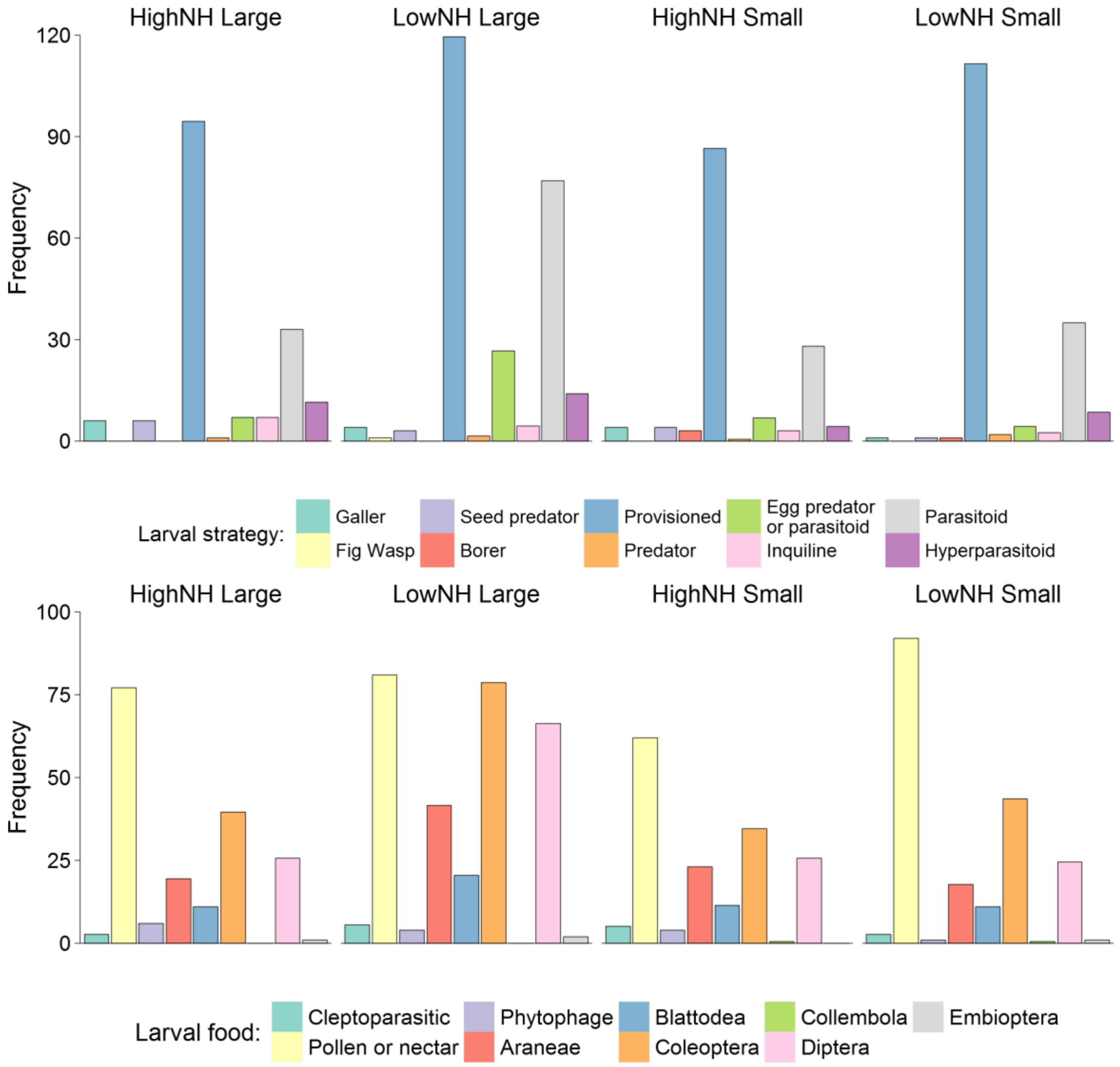


Figure I.2 Hymenopteran family weighted trait frequencies (see Chapter 4.2.5 for explanation of weightings) between agricultural contexts, note that traits are not mutually exclusive and a species can be positive for more than one trait in each group. For total abundances see Chapter 4 Table 4.1. Singletons are excluded.

Table I.1 Pairwise comparisons of observed functional metric scores for hymenopteran families between agricultural contexts using two-tailed t-tests, a false discovery rate corrected (FDR p) is applied to correct for multiple testing, untransformed p-values are also present (p). Degrees of freedom in all cases was 9. High/Low = refers to local natural habitat and Large/Small = refers to field area. Functional metrics are FDiv = diversity, FEve = eveness, FRic = richness, FRic_NS = richness with the exclusion of singleton species and FSpe = specialisation.

Contrasts	**Metric**	**Estimate**	**t**	**p**	**FDR p**
HighLarge vs. LowLarge	FDiv	0.106	2.396	0.029	0.087
HighLarge vs. HighSmall	FDiv	0.070	1.582	0.133	0.200
HighLarge vs. LowSmall	FDiv	-0.012	-0.280	0.783	0.783
LowLarge vs. HighSmall	FDiv	-0.036	-0.814	0.428	0.513
LowLarge vs. LowSmall	FDiv	-0.118	-2.676	0.017	0.087
HighSmall vs. LowSmall	FDiv	-0.082	-1.862	0.081	0.162
HighLarge vs. LowLarge	FEve	0.037	0.554	0.587	0.587
HighLarge vs. HighSmall	FEve	0.086	1.290	0.215	0.508
HighLarge vs. LowSmall	FEve	-0.042	-0.629	0.538	0.587
LowLarge vs. HighSmall	FEve	0.049	0.736	0.473	0.587
LowLarge vs. LowSmall	FEve	-0.079	-1.184	0.254	0.508
HighSmall vs. LowSmall	FEve	-0.128	-1.919	0.073	0.438
HighLarge vs. LowLarge	FRic	-0.002	-0.327	0.748	0.765
HighLarge vs. HighSmall	FRic	0.006	0.862	0.402	0.602
HighLarge vs. LowSmall	FRic	0.009	1.165	0.261	0.522
LowLarge vs. HighSmall	FRic	0.009	1.188	0.252	0.522
LowLarge vs. LowSmall	FRic	0.011	1.492	0.155	0.522
HighSmall vs. LowSmall	FRic	0.002	0.303	0.765	0.765
HighLarge vs. LowLarge	FRic_NS	-0.001	-0.142	0.889	0.944
HighLarge vs. HighSmall	FRic_NS	0.010	1.672	0.114	0.194
HighLarge vs. LowSmall	FRic_NS	0.010	1.600	0.129	0.194
LowLarge vs. HighSmall	FRic_NS	0.011	1.813	0.089	0.194
LowLarge vs. LowSmall	FRic_NS	0.011	1.742	0.101	0.194
HighSmall vs. LowSmall	FRic_NS	0.000	-0.071	0.944	0.944
HighLarge vs. LowLarge	FSpe	0.022	2.597	0.019	0.117
HighLarge vs. HighSmall	FSpe	0.004	0.445	0.662	0.794
HighLarge vs. LowSmall	FSpe	0.006	0.690	0.500	0.750
LowLarge vs. HighSmall	FSpe	-0.018	-2.151	0.047	0.141
LowLarge vs. LowSmall	FSpe	-0.016	-1.907	0.075	0.149
HighSmall vs. LowSmall	FSpe	0.002	0.244	0.810	0.810

Table I.2 Pair-wise comparisons of change in Coleoptera species composition, determined from relative abundances in NMDS ordination, between agricultural contexts. Permutation multivariate analysis of variance (ADONIS) was used to test for significant differences between communities with 9999 permutations. P-values were corrected for multiple testing using false discovery rate (FDR p) and degrees of freedom were 5.

Compare	Against	F	p	FDR p
HighLarge	LowLarge	-1.970	0.578	0.727
HighLarge	SmallHigh	-3.795	0.579	0.727
HighLarge	SmallLow	-1.157	0.643	0.727
LowLarge	SmallHigh	447.212	0.035	0.212
LowLarge	SmallLow	-1.339	0.727	0.727
SmallHigh	SmallLow	32.425	0.194	0.581

Table I.3 Pair-wise comparisons of change in hymenopteran family composition, determined from relative abundances in NMDS ordination, between agricultural contexts. Permutation multivariate analysis of variance (ADONIS) was used to test for significant differences between communities with 9999 permutations. P-values were corrected for multiple testing using false discovery rate (FDR p) and degrees of freedom were 5.

Compare	Against	F	p	FDR p
HighLarge	LowLarge	3.535	0.425	0.637
HighLarge	SmallHigh	6.169	0.146	0.579
HighLarge	SmallLow	-0.888	0.659	0.659
LowLarge	SmallHigh	22.186	0.315	0.629
LowLarge	SmallLow	-0.589	0.633	0.659
SmallHigh	SmallLow	36.510	0.193	0.579

Appendix J (Chapter 4) Functional diversity and taxonomic metric with singletons excluded.

J.1 Coleoptera

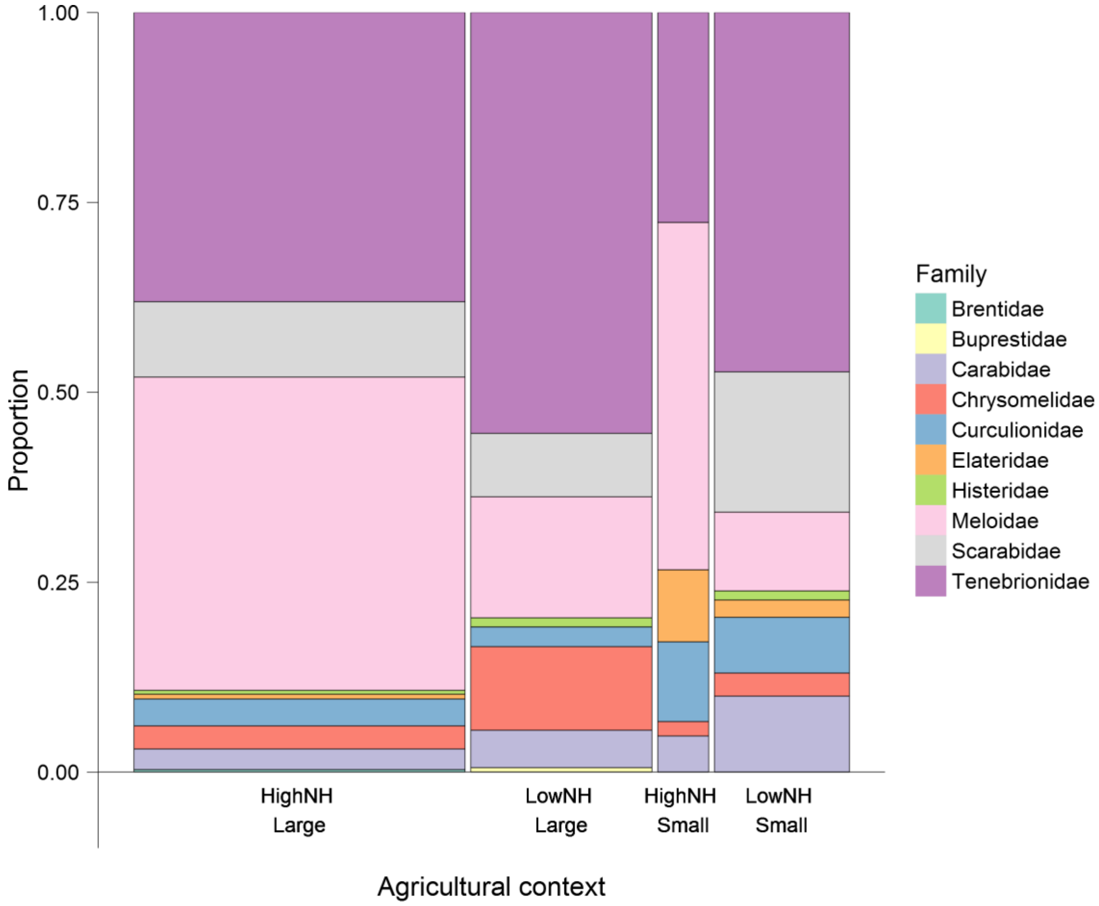


Figure J.1 Proportional contribution of coleopteran families to the total catch from each agricultural context, bar width is scaled to the total abundance of individuals caught in each context.

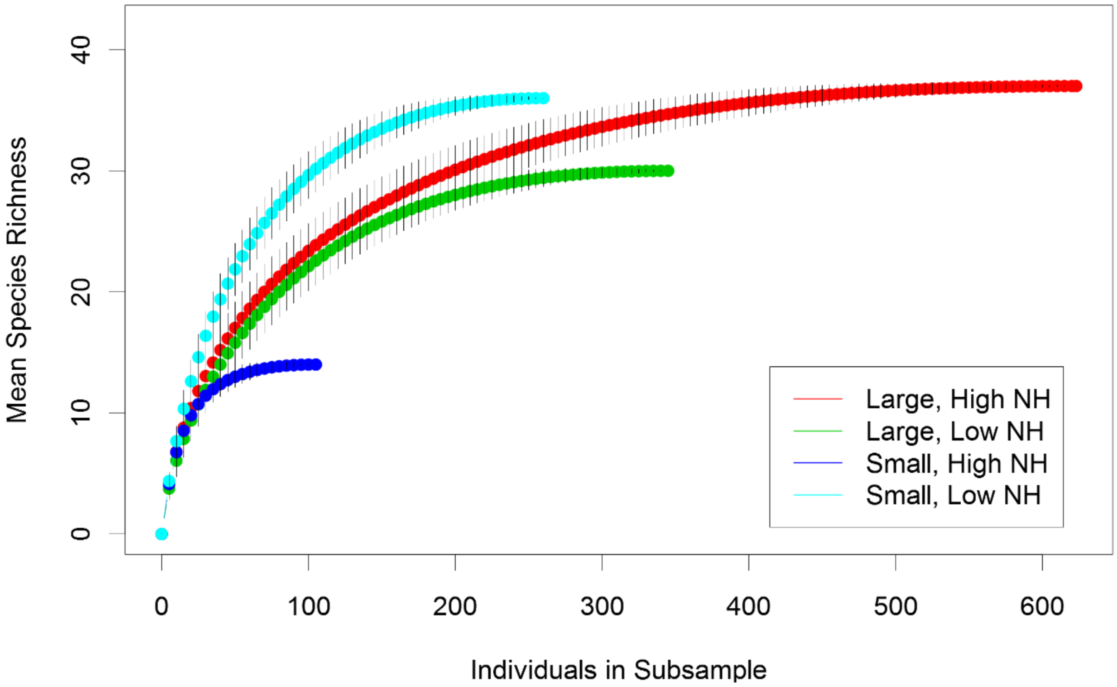


Figure J.2 Observed Coleoptera species richness, calculated from sample-based rarefaction curves, shown between agricultural contexts. NH = natural habitat with 1000m, large and small refer to field area. Bars represent the standard error of iterations.

Table J.1 Pair-wise comparisons of change in Coleoptera species composition, determined from relative abundances in NMDS ordination, between agricultural contexts. Permutation multivariate analysis of variance (ADONIS) was used to test for significant differences between communities with 9999 permutations. P-values were corrected for multiple testing using false discovery rate (FDR p) and degrees of freedom were 5.

Compare	Against	F	p	FDR p
HighLarge	LowLarge	85.239	0.047	0.094
HighLarge	SmallHigh	112.058	0.032	0.094
HighLarge	SmallLow	6.644	0.122	0.146
LowLarge	SmallHigh	90.865	0.210	0.210
LowLarge	SmallLow	130.516	0.017	0.094
SmallHigh	SmallLow	107.884	0.101	0.146

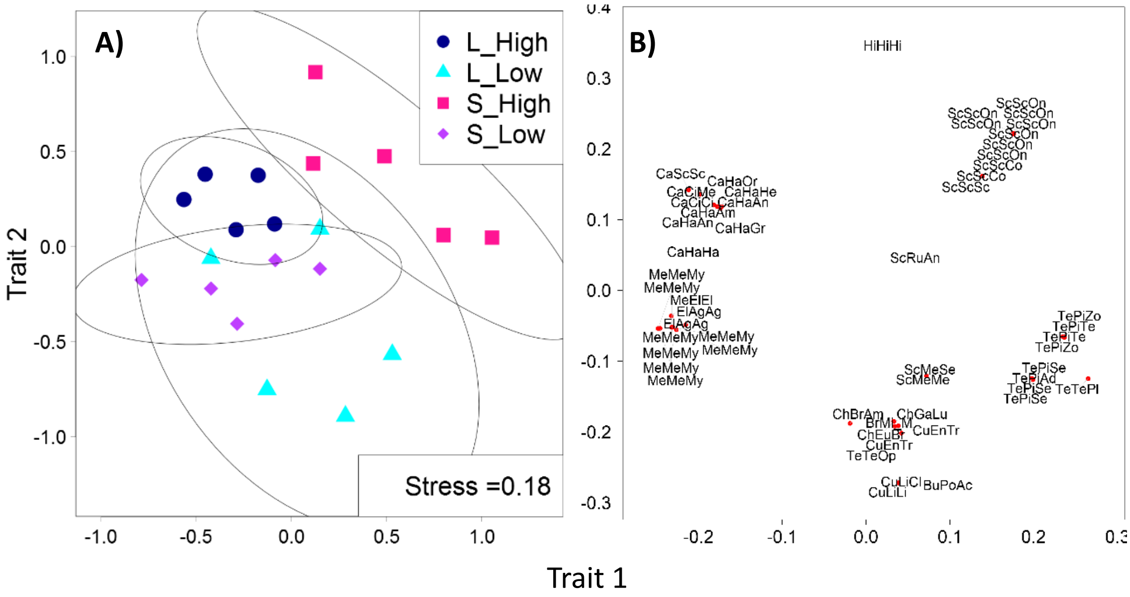


Figure J.3 A) Non-metric multidimensional scaling (NMDS) ordination space of Coleoptera community assemblages between agricultural contexts (L = large field, S = small field, High & Low refer to local natural habitat within 1000 m of the fields). See Table O.1 for statistical analysis. B) Principal co-ordinates analysis (PcOA) on a gower dissimilarity matrix of Coleoptera species functional traits. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table D.1. Major families are Ca = Carabidae, Cu = Curculionidae, Me = Meloidae, Sc = Scarabidae and Te = Tenebrionidae. In both instances the regional species pool is used.

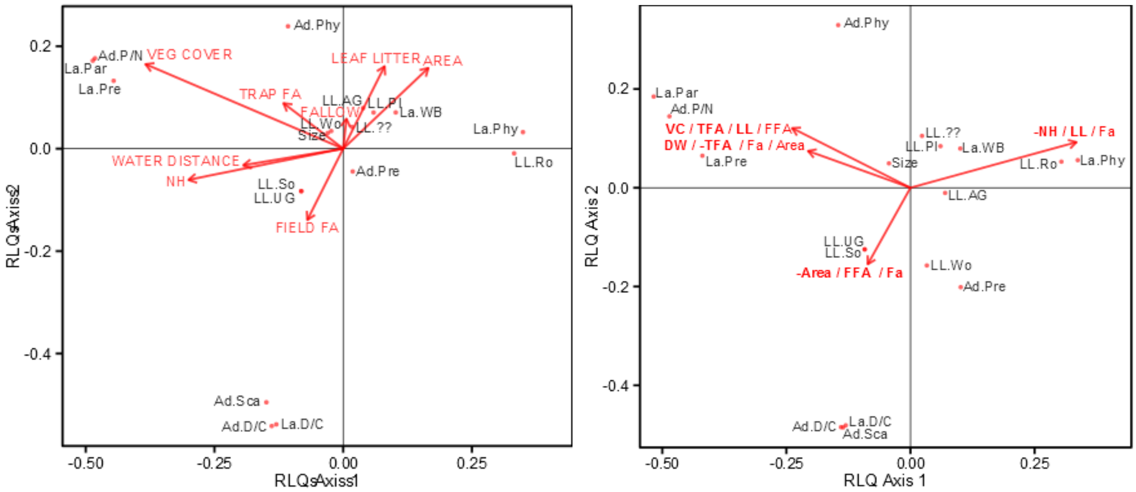


Figure J.4 RLQ Biplot showing the relationship between Coleoptera functional traits labelled points) generated from PcOA of a gower dissimilarity matrix and agricultural context for the regional species pool (red arrows). Prefixes are NH = local natural habitat, LL = larval location and La = larvae. Sufixes are Ad = Adult, D/C = detritivore and coprophage, Para = parasitic, Phy = phytophage, Pl = on or in plants (not roots or wood); P/N = pollen or nectar feeder, Pre = predator, Ro = associated with plant roots, Sca = scavenger, So = soil dwelling, WB = wood borer, Wo = associated with wood (either living or decomposing), UG = underground, ?? = location unknown.

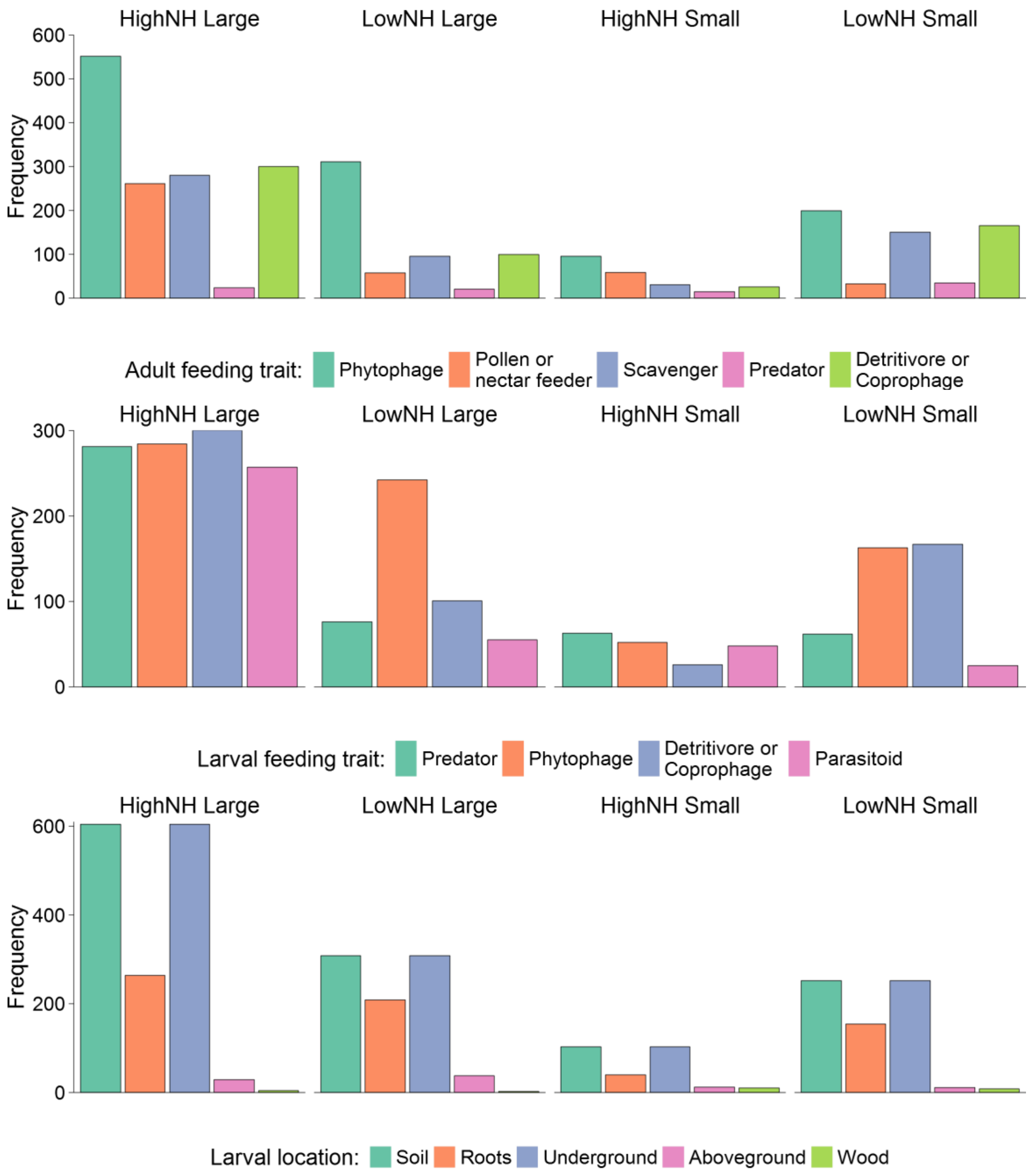


Figure J.5 Coleopteran species trait frequencies between agricultural contexts, note that traits are not mutually exclusive and a species can be positive for more than one trait in each group.

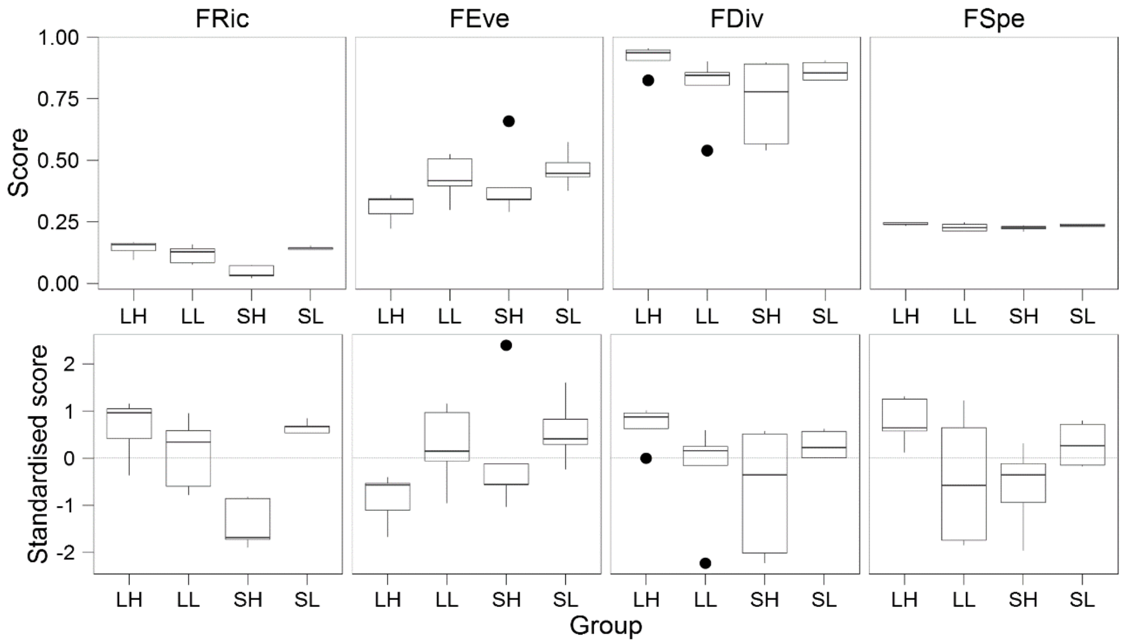


Figure J.6 Observed scores for Coleoptera functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). Top panels are raw scores and the lower panels are standardised (centred and scaled).

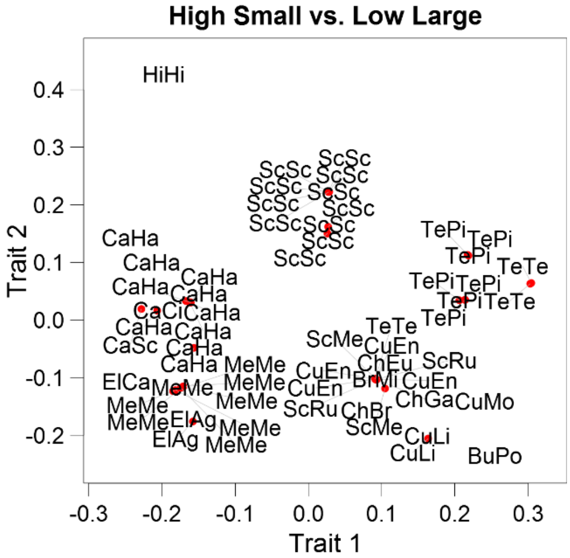


Figure J.7 Principal co-ordinates analysis (PcOA) on a Gower dissimilarity matrix of Coleoptera species functional traits for the subset of the regional pool represented by small fields in high natural habitat contexts and large fields in low natural habitat contexts. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table D.1. Major families are Ca = Carabidae, Cu = Curculionidae, Me = Meloidae, Sc = Scarabidae and Te = Tenebrionidae. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

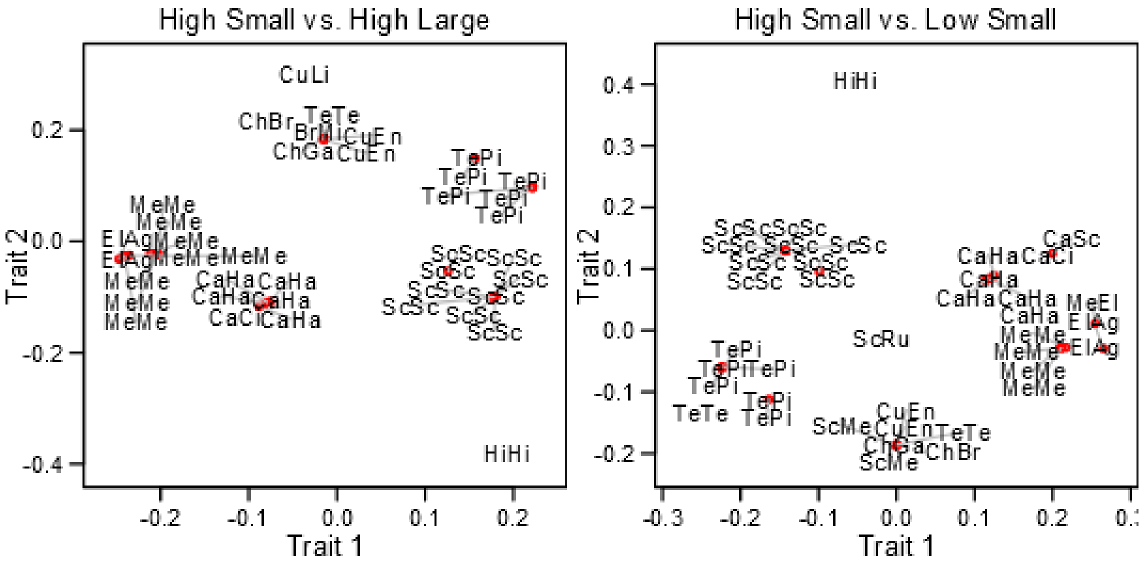


Figure J.8 PcOA of Coleoptera species functional traits for the subset of the regional pool represented by the figure titles. Abbreviations refer to the first two letters of family, subfamily and tribe for the species listed in Appendix C Table D.1. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

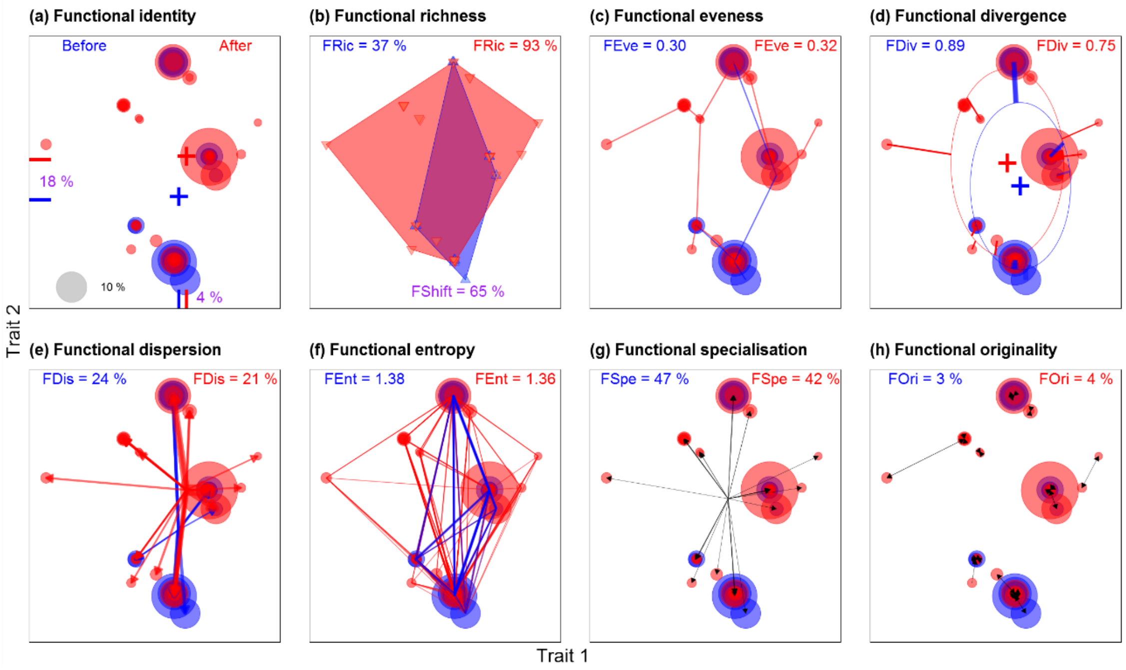


Figure J.9 Changes in different components of the functional structure of Coleoptera species communities for small fields with high local natural habitat (blue) vs. large fields with low local natural habitat (red). Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure J.7.

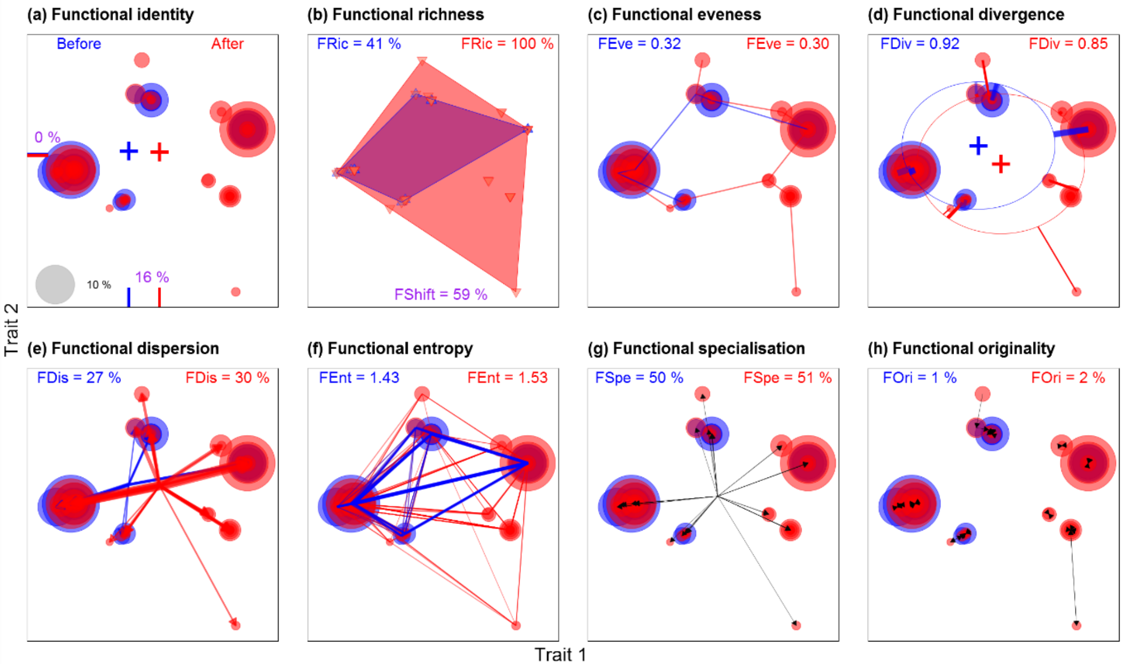


Figure J.10 Changes in different components of the functional structure of Coleoptera species communities between the subset of species found in small (blue) and large (red) fields in high local natural habitat contexts. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure J.8.

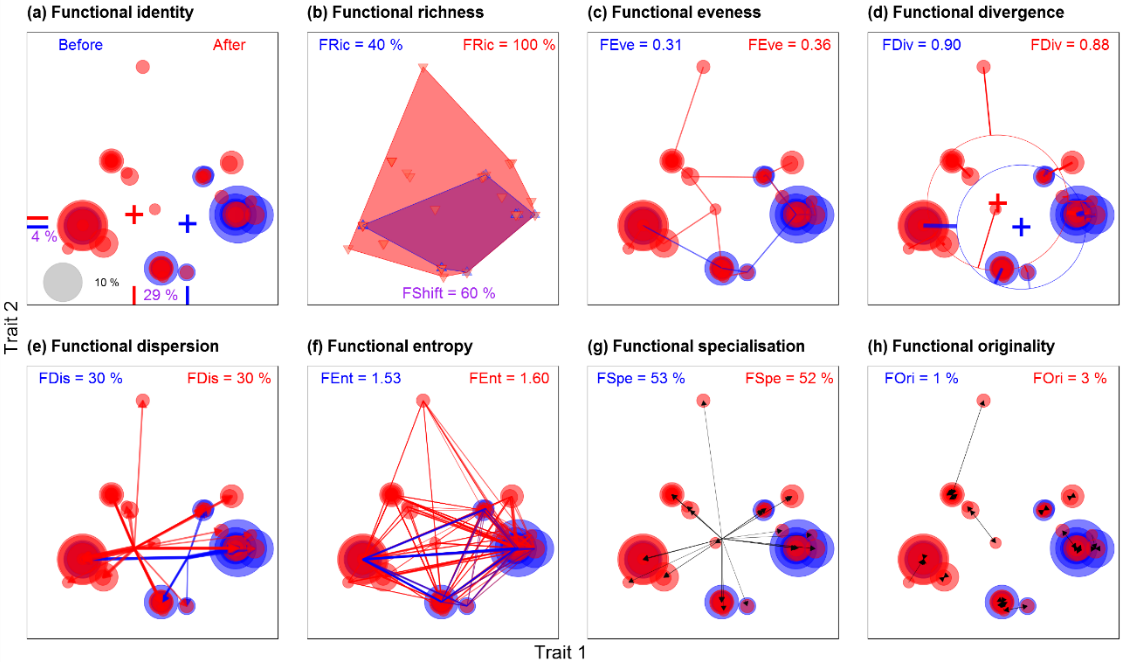
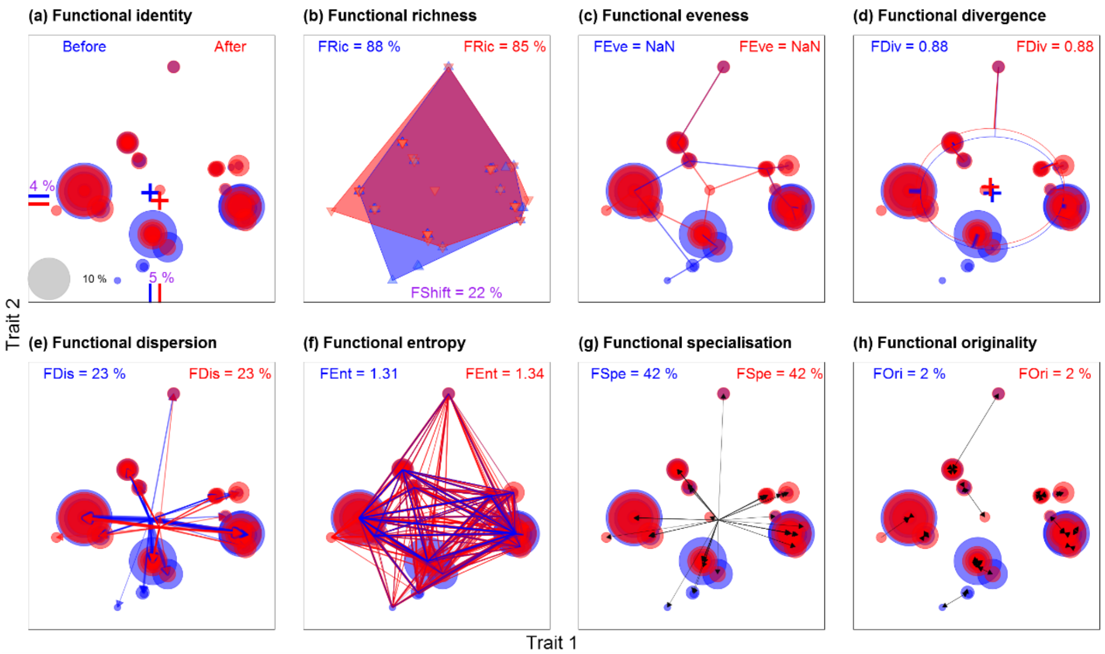
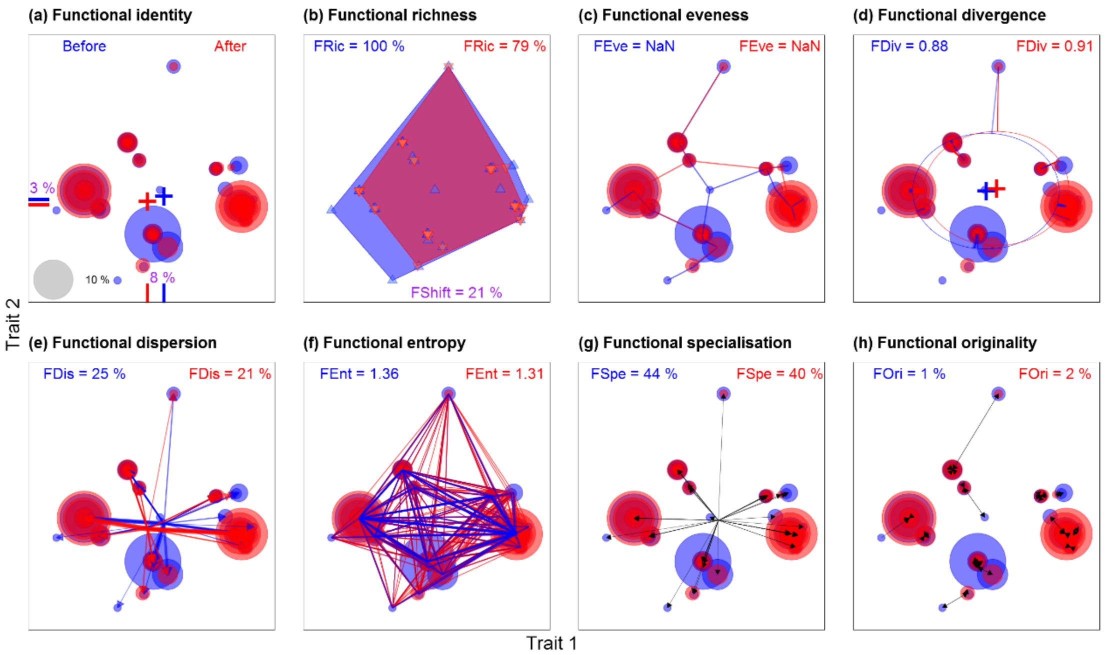


Figure J.11 Changes in different components of the functional structure of Coleoptera species communities between the subset of species found in small fields in high (blue) and low (red) local natural habitat contexts. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure J.8.



A) Small vs. Large



B) High vs. Low

Figure J.12 Changes in different components of the functional structure of Coleoptera species communities for A) small (blue) vs. large fields (red), and B) high (blue) vs. low (red) local natural habitat. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure J.3B.

Table J.2 Pairwise comparisons of observed functional metric scores for coleopteran species between agricultural contexts using two-tailed t-tests, a false discovery rate corrected (FDR p) is applied to correct for multiple testing, untransformed p-values are also present (p). Degrees of freedom in all cases was 9. High/Low = refers to local natural habitat and Large/Small = refers to field area. Functional metrics are FDiv = diversity, FEve = eveness, FRic = richness and FSpe = specialisation. Nbsp = family richness.

Contrasts	Metric	Estimate	t	p	FDR p
LargeHigh vs. LargeLow	FDiv	0.124	1.679	0.113	0.225
LargeHigh vs. SmallHigh	FDiv	0.178	2.416	0.028	0.168
LargeHigh vs. SmallLow	FDiv	0.052	0.704	0.492	0.492
LargeLow vs. SmallHigh	FDiv	0.054	0.737	0.472	0.492
LargeLow vs. SmallLow	FDiv	-0.072	-0.976	0.344	0.492
SmallHigh vs. SmallLow	FDiv	-0.126	-1.712	0.106	0.225
LargeHigh vs. LargeLow	FEve	-0.119	-1.920	0.073	0.219
LargeHigh vs. SmallHigh	FEve	-0.094	-1.526	0.147	0.293
LargeHigh vs. SmallLow	FEve	-0.154	-2.486	0.024	0.146
LargeLow vs. SmallHigh	FEve	0.024	0.394	0.699	0.699
LargeLow vs. SmallLow	FEve	-0.035	-0.567	0.579	0.694
SmallHigh vs. SmallLow	FEve	-0.059	-0.961	0.351	0.526
LargeHigh vs. LargeLow	FSpe	0.014	2.212	0.042	0.126
LargeHigh vs. SmallHigh	FSpe	0.016	2.483	0.024	0.126
LargeHigh vs. SmallLow	FSpe	0.006	0.872	0.396	0.475
LargeLow vs. SmallHigh	FSpe	0.002	0.272	0.789	0.789
LargeLow vs. SmallLow	FSpe	-0.009	-1.339	0.199	0.299
SmallHigh vs. SmallLow	FSpe	-0.010	-1.611	0.127	0.253
LargeHigh vs. LargeLow	Nbsp	7.000	2.899	0.010	**0.021**
LargeHigh vs. SmallHigh	Nbsp	13.600	5.633	0.000	**0.000**
LargeHigh vs. SmallLow	Nbsp	3.000	1.242	0.232	0.232
LargeLow vs. SmallHigh	Nbsp	6.600	2.733	0.015	**0.022**
LargeLow vs. SmallLow	Nbsp	-4.000	-1.657	0.117	0.140
SmallHigh vs. SmallLow	Nbsp	-10.600	-4.390	0.000	**0.001**

Table J.3 Observed and expected Coleoptera species functional metrics. Mean standardised effect (SES) of functional diversity metrics in each agricultural context calculated from 1000 randomisations (independent swap) of the regional species pool. One-sample t-tests with μ = 0 were used to determine if the SES of each metric was significantly different to zero. See Table 4.2 for abbreviations.

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FRic	0.127	0.045	0.144	0.375	0.622	-0.476	1.226	1.254	0.294
LargeLow	FRic			0.118	-0.216	0.751	-1.236	0.803	-0.563	0.613
SmallHigh	FRic			0.046	-1.844	0.604	-2.538	-1.149	-7.335	**0.002**
SmallLow	FRic			0.144	0.384	0.141	0.210	0.557	6.288	**0.006**
LargeHigh	FEve	0.420	0.113	0.310	-1.018	0.562	-1.670	-0.366	-4.342	**0.017**
LargeLow	FEve			0.428	0.085	0.801	-0.968	1.137	0.219	0.688
SmallHigh	FEve			0.404	-0.141	1.259	-1.826	1.544	-0.236	0.763
SmallLow	FEve			0.464	0.411	0.663	-0.437	1.259	1.338	0.319
LargeHigh	FDiv	0.871	0.081	0.913	0.512	0.655	-0.344	1.368	1.759	0.206
LargeLow	FDiv			0.789	-1.098	1.765	-3.413	1.217	-1.280	0.282
SmallHigh	FDiv			0.735	-1.804	2.134	-4.580	0.972	-1.774	0.156
SmallLow	FDiv			0.861	-0.163	0.512	-0.771	0.446	-0.604	0.481
LargeHigh	FSpe	0.236	0.010	0.242	0.548	0.558	-0.186	1.281	2.071	0.125
LargeLow	FSpe			0.228	-0.914	1.490	-2.933	1.105	-1.257	0.282
SmallHigh	FSpe			0.226	-1.093	0.971	-2.384	0.198	-2.352	0.082
SmallLow	FSpe			0.236	-0.029	0.505	-0.700	0.643	-0.120	0.714

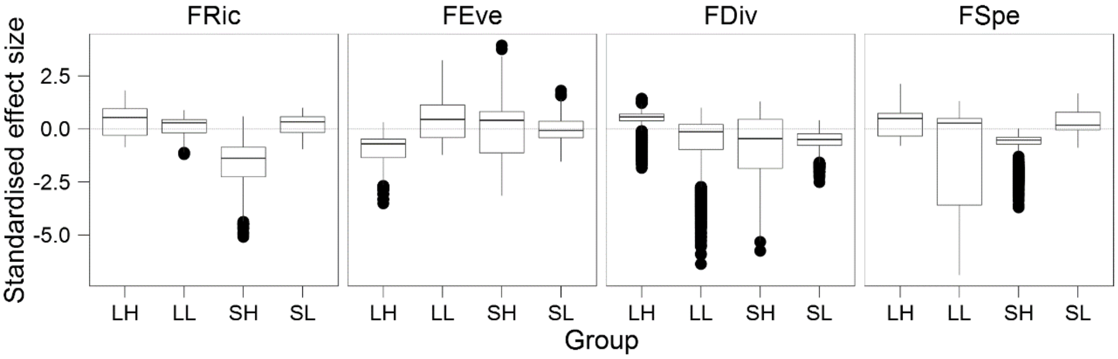


Figure J.13 Standardised effect size (SES) for Coleoptera functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). SES = (Observed – mean Expected) / SD Expected. SES is calculated from 1000 randomisations of the regional pool of species, where species frequency of occurrences and species richness are maintained. Values differing from zero indicate that the species pool of an agricultural context is different to that of the regional species pool.

J.2 Hymenoptera

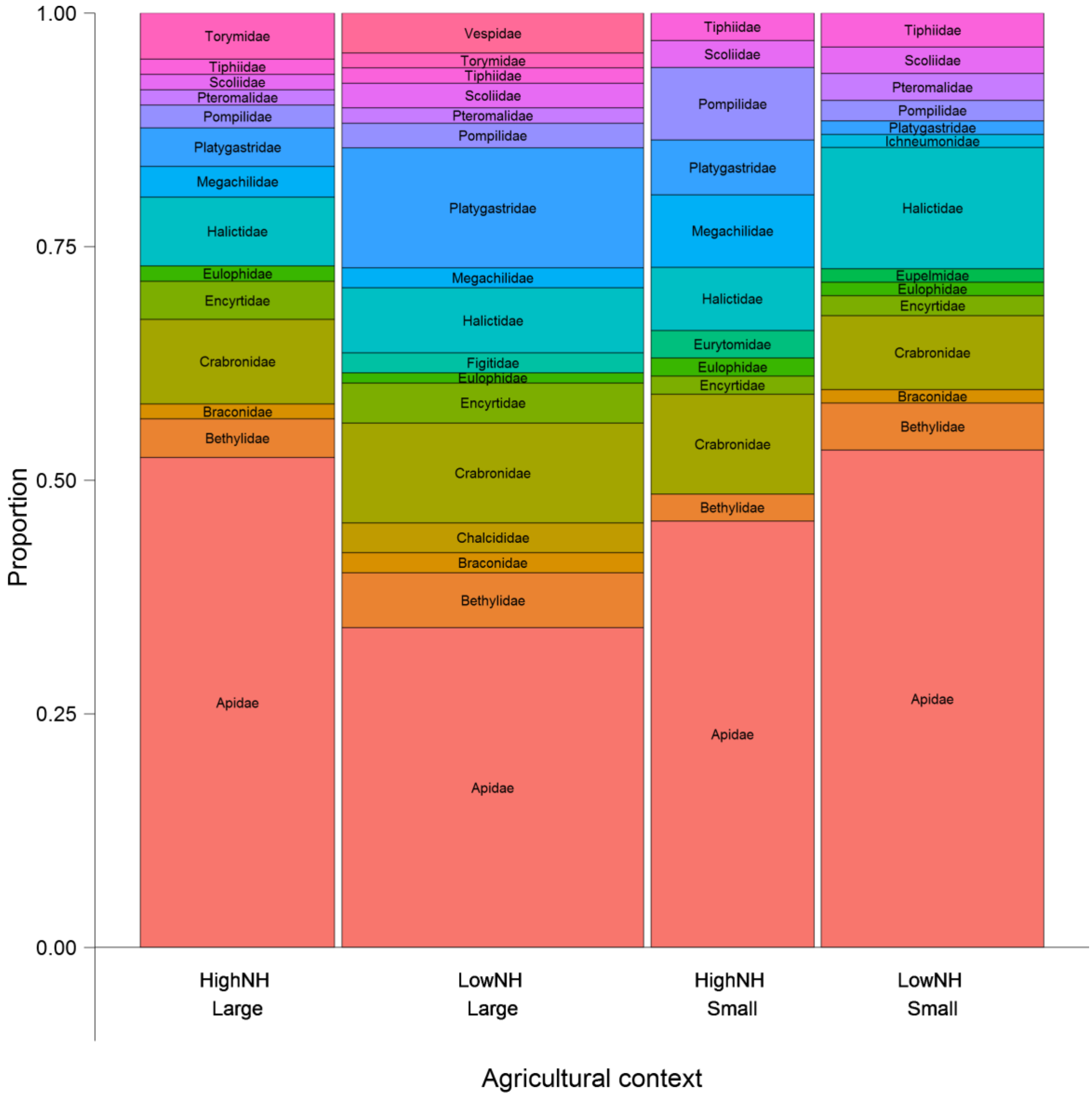


Figure J.14 Proportional contribution of hymenopteran families to the total catch from each agricultural context, bar width is scaled to the total abundance of individuals caught in each context.

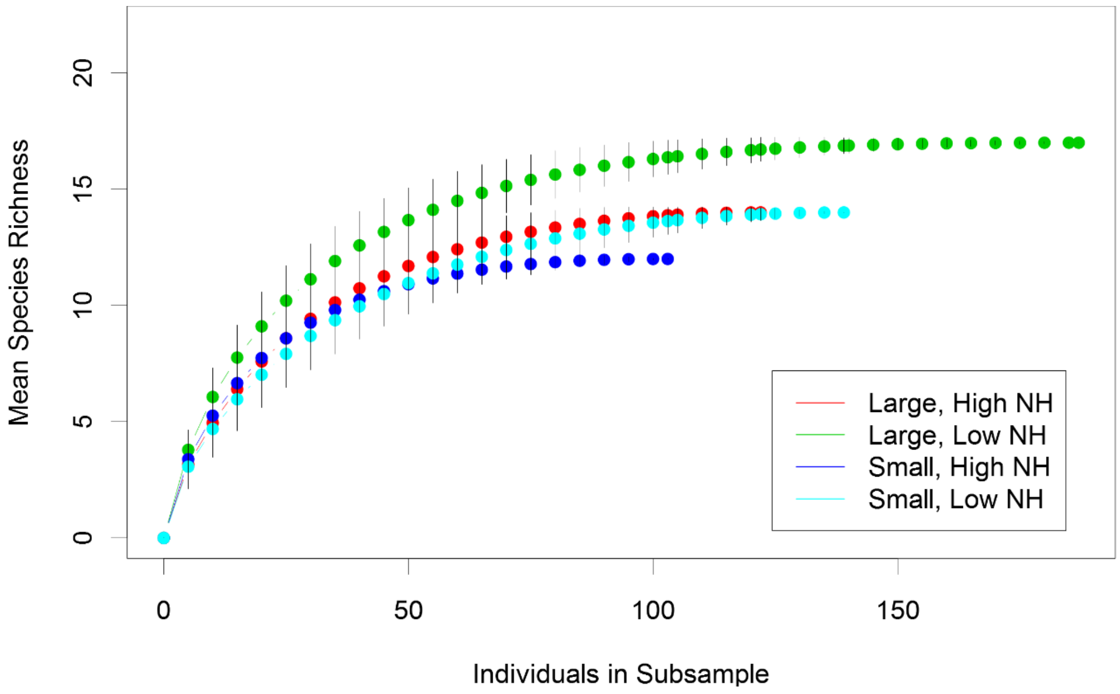


Figure J.15 Observed Hymenoptera family richness calculated from sample-based rarefaction curves, shown between agricultural contexts. NH = natural habitat with 1000m, large and small refer to field area. Bars represent the standard error of iterations.

Table J.4 Pair-wise comparisons of change in hymenopteran family composition, determined from relative abundances in NMDS ordination, between agricultural contexts. Permutation multivariate analysis of variance (ADONIS) was used to test for significant differences between communities with 9999 permutations. P-values were corrected for multiple testing using false discovery rate (FDR p) and degrees of freedom were 5.

Compare	**Against**	**F**	**p**	**FDR p**
HighLarge	LowLarge	-2.549	0.566	0.766
HighLarge	SmallHigh	-3.926	0.639	0.766
HighLarge	SmallLow	-3.959	0.938	0.938
LowLarge	SmallHigh	52.408	0.160	0.481
LowLarge	SmallLow	5564.769	0.140	0.481
SmallHigh	SmallLow	32.285	0.391	0.766

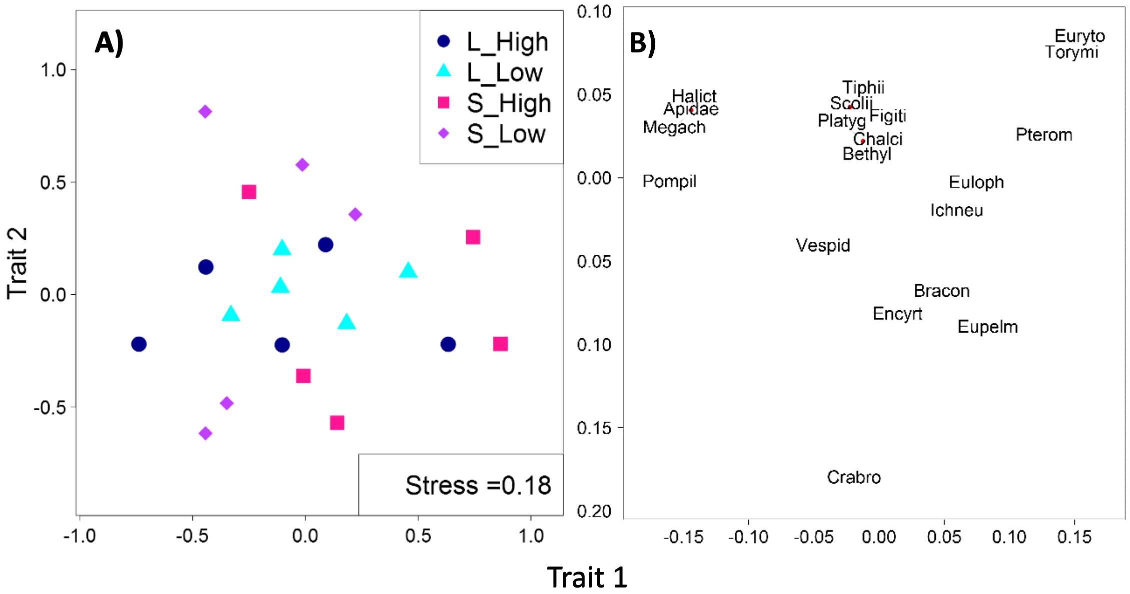


Figure J.16 A) Non-metric multidimensional scaling (NMDS) ordination space of Hymenoptera community assemblages between agricultural contexts (L = large field, S = small field, High & Low refer to local natural habitat within 1000 m of the fields). See Table J.4 for statistical analysis. B) Principal co-ordinates analysis (PcOA) on a gower dissimilarity matrix of Hymenoptera family functional traits for the regional pool. Abbreviations refer to the first six letters of each family, see Appendix C. Red points show the location of species sharing similar trait values, species codes are linked to their location with a grey line. Where a species code has no grey line it is accurately placed in functional trait spaced.

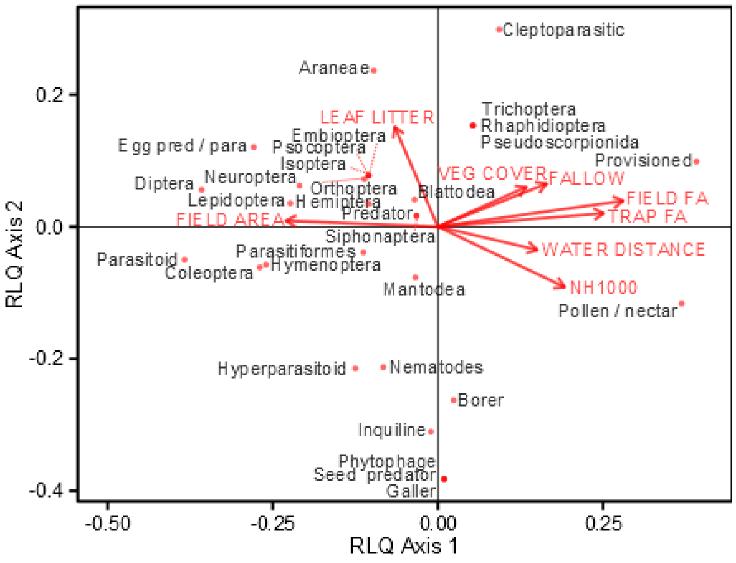


Figure J.17 RLQ Biplot showing the relationship between Hymenoptera family functional traits (labelled points) and agricultural context calculated for the regional pool. NH1000 = local natural habitat within 1 km, FA = floral area.

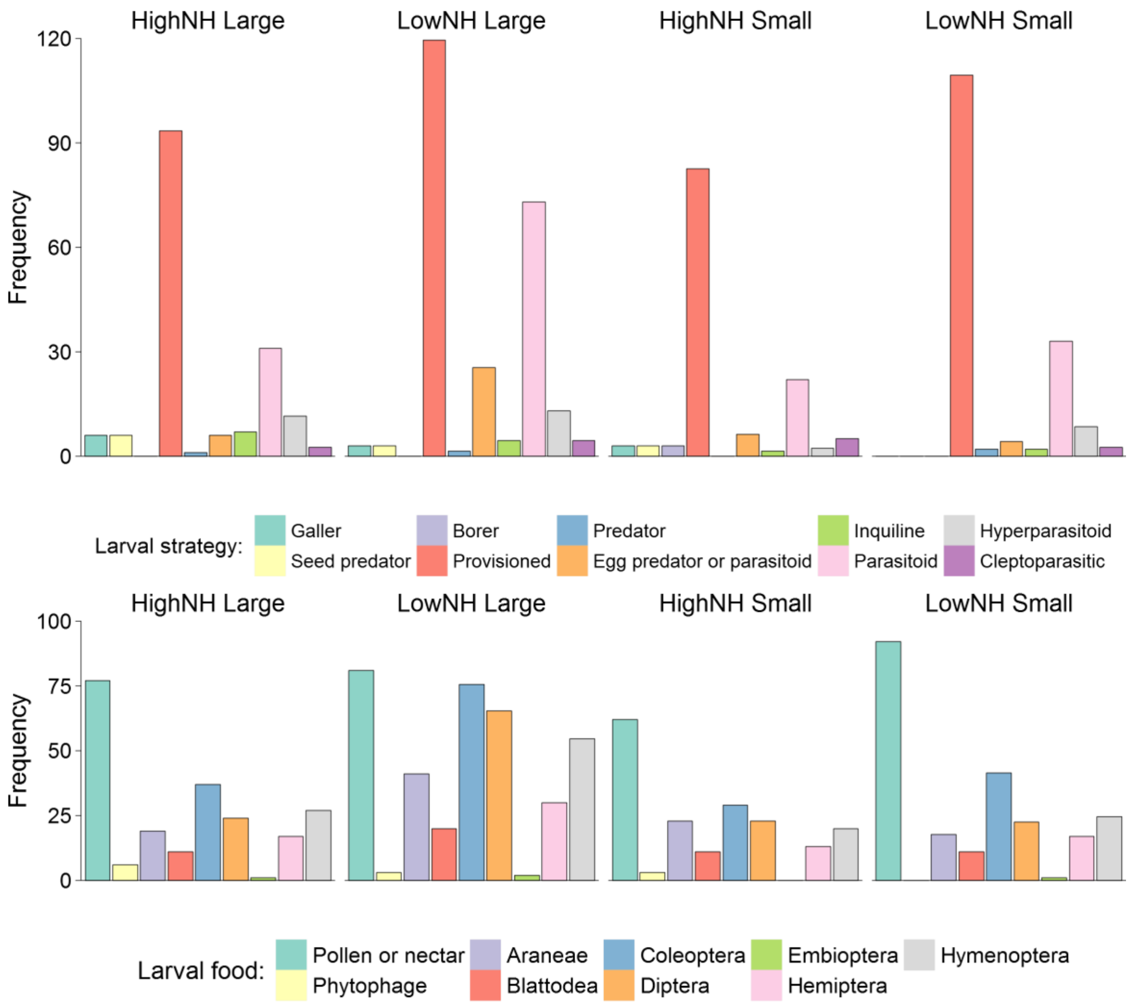


Figure J.18 Hymenopteran family weighted trait frequencies (see Chapter 4.2.5 for explanation of weightings) between agricultural contexts, note that traits are not mutually exclusive and a species can be positive for more than one trait in each group.

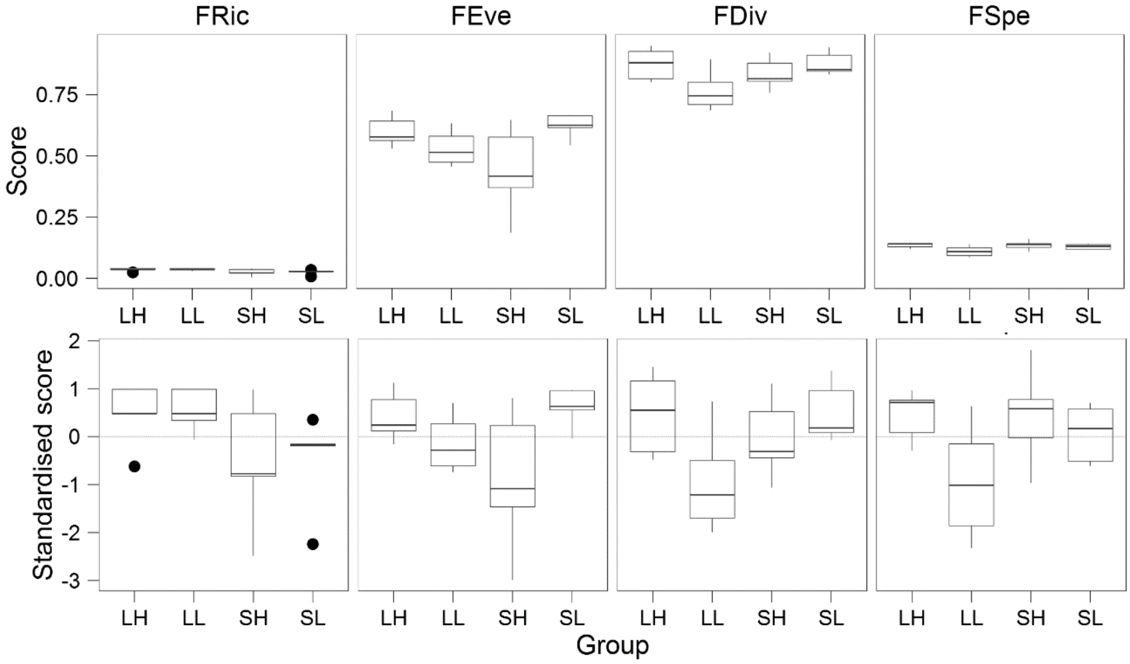
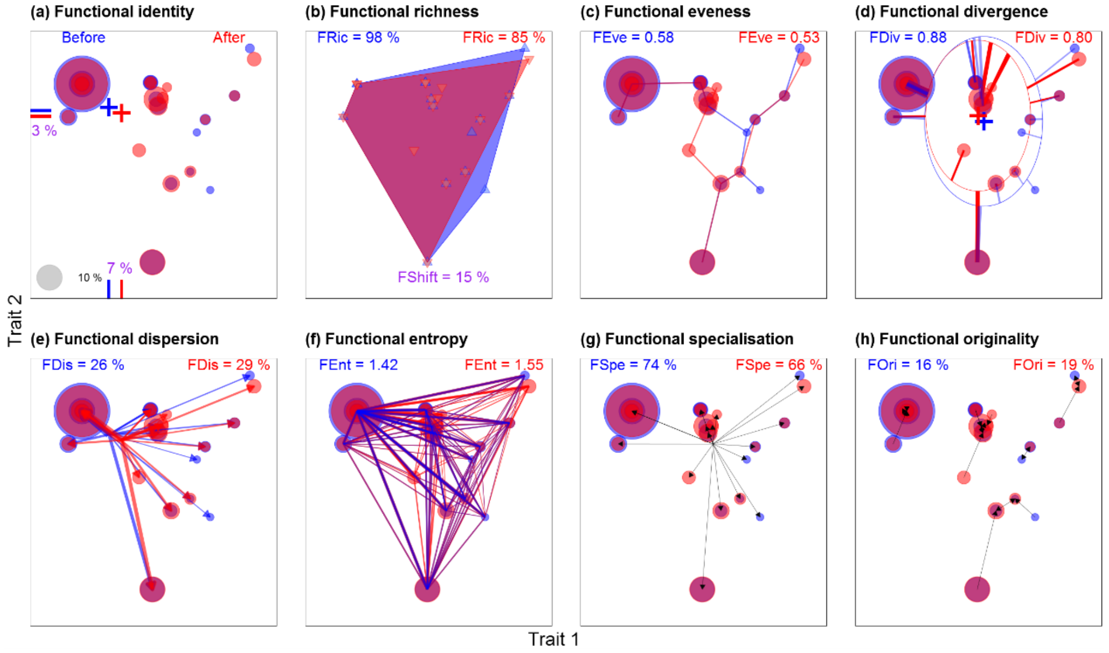


Figure J.19 Observed scores for Hymenoptera family functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). Top panels are raw scores and the lower panels are standardised (centred and scaled).

Table J.5 Pairwise comparisons of observed functional metric scores for hymenopteran families between agricultural contexts using two-tailed t-tests, a false discovery rate corrected (FDR p) is applied to correct for multiple testing, untransformed p-values are also present (p). Degrees of freedom in all cases was 9. High/Low = refers to local natural habitat and Large/Small = refers to field area. Functional metrics are FDiv = diversity, FEve = eveness and FSpe = specialisation. FRic is presented in Appendix J Table J.1 as FRic_NS.

Contrasts	Metric	Estimate	t	p	FDR p
HighLarge vs. LowLarge	FDiv	0.107	2.553	0.021	0.064
HighLarge vs. HighSmall	FDiv	0.039	0.926	0.368	0.442
HighLarge vs. LowSmall	FDiv	-0.002	-0.053	0.959	0.959
LowLarge vs. HighSmall	FDiv	-0.068	-1.627	0.123	0.247
LowLarge vs. LowSmall	FDiv	-0.109	-2.605	0.019	0.064
HighSmall vs. LowSmall	FDiv	-0.041	-0.978	0.342	0.442
HighLarge vs. LowLarge	FEve	0.067	1.004	0.330	0.396
HighLarge vs. HighSmall	FEve	0.160	2.393	0.029	0.088
HighLarge vs. LowSmall	FEve	-0.024	-0.356	0.727	0.727
LowLarge vs. HighSmall	FEve	0.093	1.389	0.184	0.289
LowLarge vs. LowSmall	FEve	-0.091	-1.359	0.193	0.289
HighSmall vs. LowSmall	FEve	-0.184	-2.749	0.014	0.086
HighLarge vs. LowLarge	FSpe	0.026	2.480	0.025	0.078
HighLarge vs. HighSmall	FSpe	0.000	0.027	0.979	0.979
HighLarge vs. LowSmall	FSpe	0.007	0.682	0.505	0.626
LowLarge vs. HighSmall	FSpe	-0.025	-2.453	0.026	0.078
LowLarge vs. LowSmall	FSpe	-0.019	-1.798	0.091	0.182
HighSmall vs. LowSmall	FSpe	0.007	0.655	0.522	0.626

A) Small vs. Large



B) High vs. Low

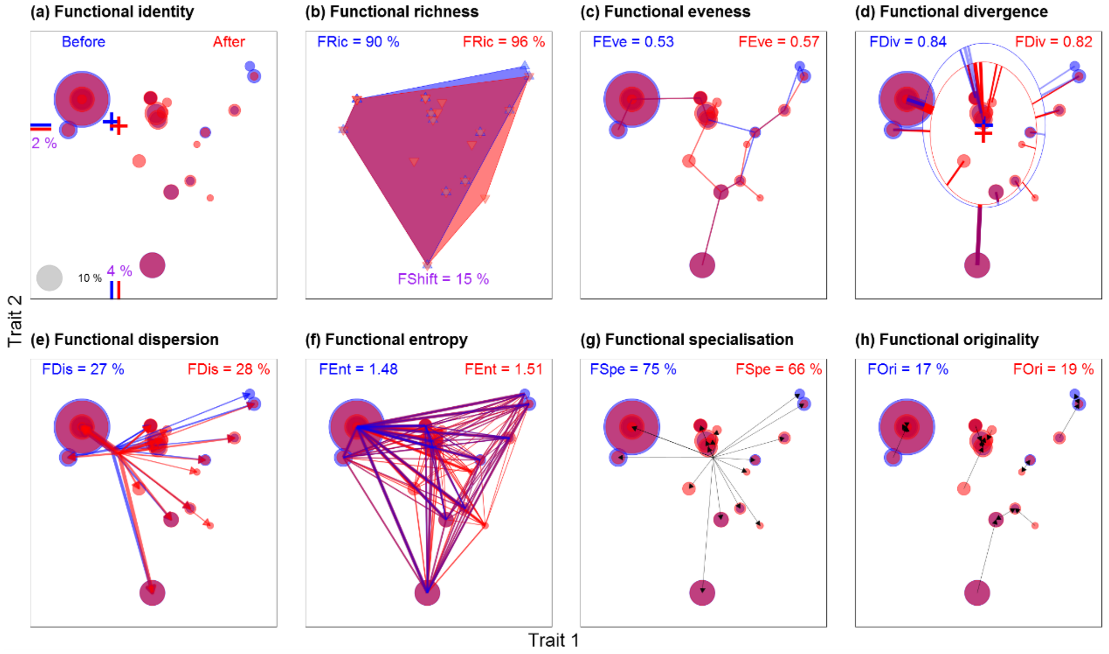


Figure J.20 Changes in different components of the functional structure of Hymenoptera family communities for A) small (blue) vs. large fields (red), and B) high (blue) vs. low (red) local natural habitat. Families (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are traits extracted principal coordinate analysis (PCoA). Circle sizes are proportional to species relative abundances in each agricultural context. For family locations in trait space see Figure J.16B.

Table J.6 Observed and expected Coleoptera species functional metrics. Mean standardised effect (SES) of functional diversity metrics in each agricultural context calculated from 1000 randomisations (independent swap) of the regional species pool. One-sample t-tests with μ = 0 were used to determine if the SES of each metric was significantly different to zero. See Table J.5 for abbreviations.

Group	Metric	Mean Expected	SD Expected	Mean Observed	Mean SES	SD SES	95% CI low	95% CI high	t	p
LargeHigh	FRic	0.043	0.014	0.050	0.521	0.609	-0.313	1.356	1.749	0.163
LargeLow	FRic			0.052	0.607	0.420	0.036	1.177	2.973	**0.045**
SmallHigh	FRic			0.036	-0.487	1.248	-2.202	1.228	-0.781	0.482
SmallLow	FRic			0.037	-0.444	0.936	-1.726	0.838	-0.952	0.402
LargeHigh	FEve	0.540	0.109	0.598	0.542	0.586	-0.228	1.312	1.979	0.143
LargeLow	FEve			0.535	-0.056	0.602	-0.853	0.740	-0.172	0.707
SmallHigh	FEve			0.439	-0.976	1.593	-3.116	1.164	-1.257	0.284
SmallLow	FEve			0.623	0.783	0.470	0.192	1.373	3.714	**0.026**
LargeHigh	FDiv	0.828	0.083	0.875	0.570	0.739	-0.429	1.570	1.598	0.197
LargeLow	FDiv			0.768	-0.744	0.938	-2.006	0.518	-1.626	0.187
SmallHigh	FDiv			0.836	0.094	0.726	-0.891	1.079	0.278	0.767
SmallLow	FDiv			0.877	0.598	0.543	-0.128	1.323	2.305	0.092
LargeHigh	FSpe	0.150	0.019	0.162	0.633	0.564	-0.130	1.396	2.311	0.085
LargeLow	FSpe			0.131	-0.991	1.285	-2.740	0.759	-1.569	0.193
SmallHigh	FSpe			0.161	0.615	1.082	-0.865	2.095	1.158	0.314
SmallLow	FSpe			0.153	0.187	0.642	-0.691	1.065	0.597	0.590

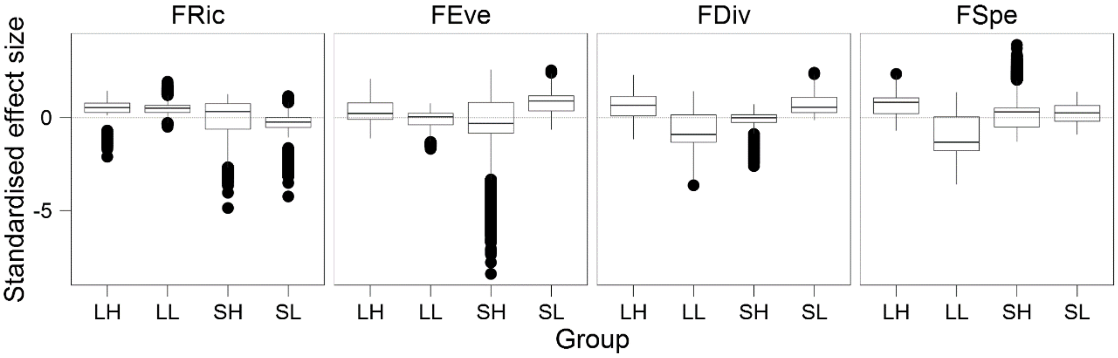


Figure J.21 Standardised effect size (SES) for Hymenoptera family functional richness (FRic), evenness (FEve), divergence (FDiv) and specialisation (FSpe) between agricultural contexts (LL = large field, high natural habitat; LL = large field, low natural habitat; SH = small field, high natural habitat; and SH = small field, low natural habitat). SES = (Observed – mean Expected) / SD Expected. SES is calculated from 1000 randomisations of the regional pool of species, where species frequency of occurrences and species richness are maintained. Values differing from zero indicate that the species pool of an agricultural is different to that of the regional species pool.

Appendix K (Chapter 5) Questionnaire

"This questionnaire will be used as part of a study at the University of Leeds, UK into farmer perceptions of the environment. This study is a one off and you may not hear from the researcher again. The questionnaire will be anonymous your details will not be shared with anyone. Please let the researcher know if you would prefer not to take part"

Section 1: Farm and farming

1. Is your home in this shamba? If not, where is it?
2. How many cows do you keep?
3. How many sheep do you keep?
4. How many goats do you keep?

5. How many ducks or chicken do you keep?
6. What is the size of the farm you own or rent?
7. What are your farming activities? Rank from highest to lowest importance.
8. What crops do you plant?
9. What was your household cash income from selling crops for the most recent growing season and the season before that:
10. What was your household cash income from selling livestock, eggs or milk for the most recent growing season and the season before that:
11. What was your household cash income from work outside of your farm (e.g. labouring for somebody else) for the most recent growing season and the season before that.

Section 2: Perception of Crop Damage.

For questions 12, 13 and 15 the question was asked openly and responses were coded into groups that typically represented the type of answer given by farmers.

12. How much of your crops were lost due to drought in the most recent growing season? What about the season before that?
    - *a. All your crops;*
    - *b. A lot of/ more than half*
    - *c. Half of your crops*
    - *d. A little bit of your crops/ a quarter*
    - *e. Nothing/ very little*
13. How much of your crops were lost due to disease before harvest in the most recent growing season? What about the season before that?
    - *a. All your crops;*
    - *b. A lot of/ more than half*
    - *c. Half of your crops*
    - *d. A little bit of your crops/ a quarter*
    - *e. Nothing/ very little*
14. Which animals, including insects and livestock, damaged your crops before harvest (standing in the field) for the two most recent growing seasons? List the animals in order of most to least damaging.
15. For all your crops how much loss before harvest did those animals cause in the most recent growing season? What about the season before that?
    - *a. All your crops;*
    - *b. A lot of/ more than half*
    - *c. Half of your crops*
    - *d. A little bit of your crops/ a quarter*
    - *e. Nothing/ very little*
16. How do you protect your crops from animal damage?

Section 3: Attitude towards wildlife and conservation habitat

A: Groups of wildlife

17. What would you like to do with or see happen to problem wildlife?

Do you strongly agree, strongly disagree, agree, disagree or neither agree nor disagree with following statements:

18. Some wildlife is beneficial to farming.
19. Some wildlife is a problem for farming.

20. What wildlife is beneficial to you and why? Rank in order from most to least beneficial.
21. Other than animals that damage crops, what wildlife is a problem to you and why? Rank in order from most to least problematic.

B: Habitat

Do you strongly agree, strongly disagree, agree, disagree or neither agree nor disagree with following statements:

22. Bushland and forest is important.
23. Having bushland or forest near or around the shamba is a problem for my farming.
24. Having bushland or forest near or around the shamba is beneficial to my farming.
25. Why is the bush or dry forest beneficial? Rank reasons in order of most to least importance
26. Why is the bush or dry forest a problem? Rank reasons in order of most to least importance

C: Protected Areas

Do you strongly agree, strongly disagree, agree, disagree or neither agree nor disagree with following statements:

Protected areas for nature include the Tsavo National Park, the Taita Wildlife Sanctuary and the Lumo Conservancy.

27. Protected areas for nature are a good thing.
28. Protected areas for nature are a bad thing.
29. Protected areas for nature are beneficial to me.
30. Protected areas for nature are a problem for me.
31. Protected areas for nature benefit my community.
32. Protected areas for nature create problems for my community.
33. If beneficial then why?
34. If a problem then why?
35. What should be done with problem animals from protected areas for nature?
36. How could protected areas for nature be improved or changed to benefit nearby communities more?
37. What are your thoughts on the number of elephants in protected areas for nature?
38. What would you like to do with or see happen to elephants in this area?
39. What is more important to the government: people or elephants? Why?

Section 4: Demographics

47. Age:
48. Gender:
49. Ethnicity:
50. Place:
    a. District:
    b. Location:
    c. Village:
51. Education:
    a. No schooling
    b. Vocational Training
    c. Primary (Class 1 - 8)
    d. Secondary (Form 1 – Form 4)
    e. College/University/Polytechnic

Appendix L (Chapter 5) Other interview responses

Table L.1 Farmer responses to Q17 and Q35, for Q17 interviewees unaware of protected areas were included but were excluded for Q35. Answers were coded as following: Neutral = fencing or translocation (no direct harm to wildlife but without coexistence); Positive = no actions needed, construct boreholes, improve security, dialogue and education (no harm to wildlife but potential for coexisitence); and Negative = retaliatory killing or culling (direct harm to wildlife). Interviewees were counted in a category if they gave one or more answers corresponding to that category.

Question			% Giving Answers		
	Grouping	n	Negative	Neutral	Positive
Q17. What would you like to do with or see happen to problem wildlife?	Far	77	24.7	63.6	18.2
	Near	71	5.6	97.2	8.5
	High	70	15.7	85.7	10.0
	Low	78	15.4	74.4	16.7
	Overall	148	15.5	79.7	13.5
Q35. What should be done with problem animals from protected areas for nature?	Far	57	5.3	96.5	31.6
	Near	53	7.5	94.3	24.5
	High	48	4.2	97.9	31.2
	Low	62	8.1	93.5	25.8
	Overall	110	6.4	95.5	28.2

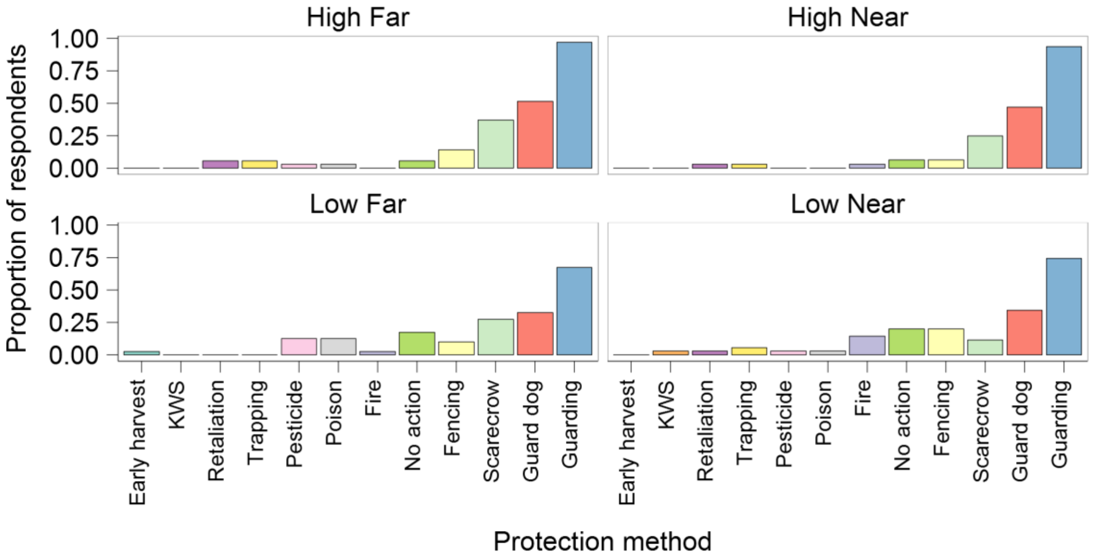
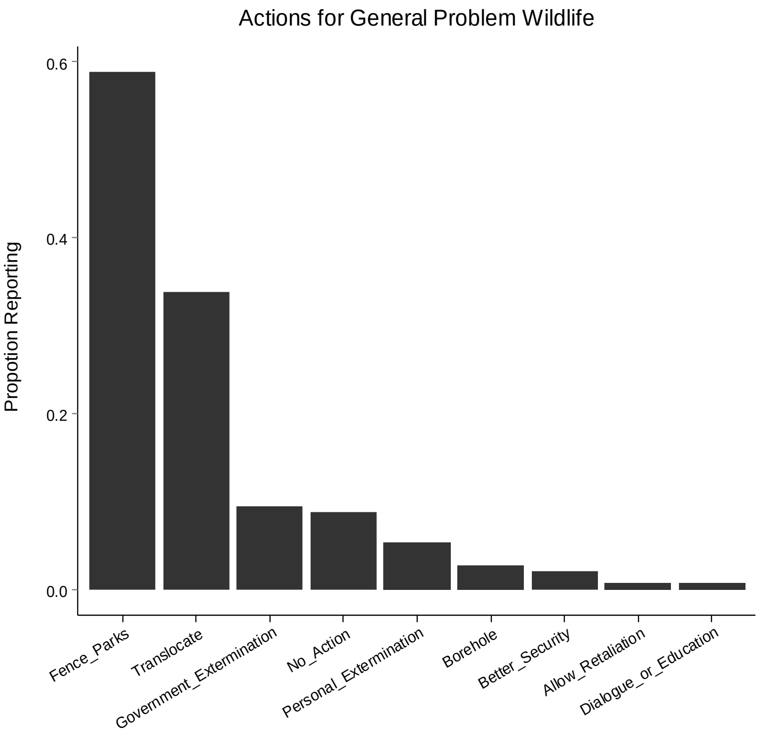


Figure L.1 Types of crop protection used by respondents in response to animals damaging their crops (Q16, Appendix J) in different spatial contexts. Statistical significance is presented in Table L.2, below. Interviewees unaware of protected areas were included.

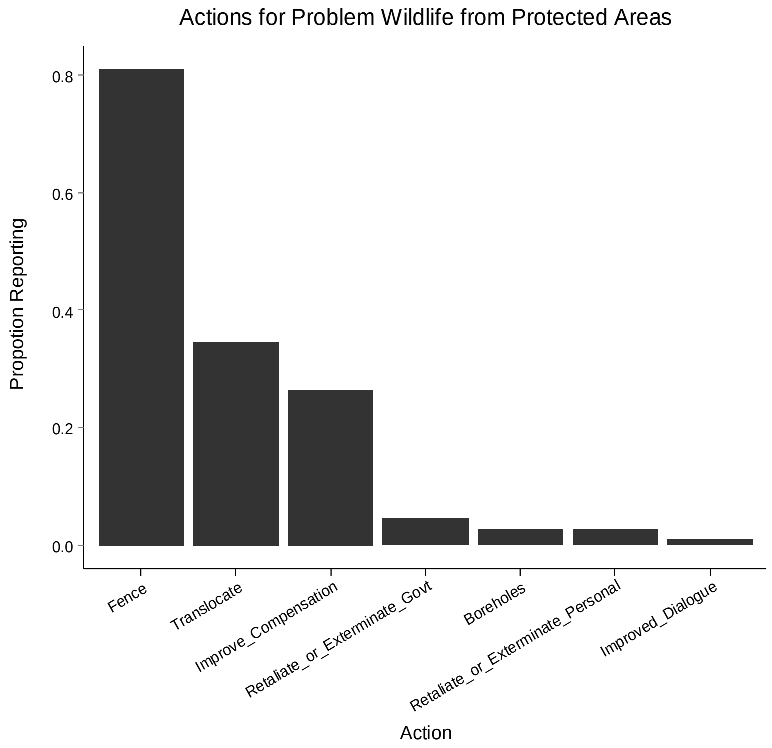
Table L.2 Types of crop protection used by respondents in response to animals damaging their crops (Q16, Appendix J) in different spatial contexts. Degrees of freedom for all tests = 1. Bonferonni corrected statistical significance = 0.025.

Protection method	Group	n	% using method	χ^2	p
Guarding	far	56	83.6		
	near	61	81.3	0.017	0.896
	high	64	95.5		
	low	**53**	**70.7**	**13.407**	**<0.001**
Guard dog	far	27	40.3		
	near	31	41.3	0.000	1.000
	high	33	49.3		
	low	25	33.3	3.082	0.079
Scarecrow	far	12	17.9		
	near	24	32.0	3.005	0.083
	high	21	31.3		
	low	15	20.0	1.844	0.174
No action	far	9	13.4		
	near	9	12.0	1.266	0.997
	high	4	6.0		
	low	**14**	**18.7**	**4.070**	0.044
Fencing	far	9	13.4		
	near	9	12.0	0.000	0.997
	high	7	10.4		
	low	11	14.7	0.252	0.616



Action suggested	No. reporting
Fence parks or wildlife habitats	86
Translocate animals	50
Government extermination	14
No action	13
Personal extermination	8
Boreholes	4
Better security	3
Improved dialogue or education	1
Allow retaliation	1

Figure L.2 Desired actions regarding problem wildlife reported by interviewees (see Q17 in Appendix J, interviewees unaware of protected areas were included, n = 147).



Action suggested	n	Prop.
Fence	89	0.8
Translocate	38	0.3
Improve compensation	29	0.26
Government extermination	5	0.0
Government extermination or retaliation	3	0.0
Boreholes	3	0.03
Improved dialogue with community	1	0.01

Figure L.3 Desired actions regarding problem wildlife from protected areas for nature reported by interviewees (see Q35 in Appendix J, interviewees unaware of protected areas were included, n = 110).

Table L.3 Farmer responses to Q37, interviewees unaware of protected areas were excluded.

Question	Grouping	n	Response (%)				p*
			Too many	Enough	Too few	No opinion	
Q37. What are your thoughts on the number of elephants in protected area for nature?	Far	63	63.5	6.3	6.3	23.8	<0.001
	Near	70	97.1	0.0	2.9	0.0	
	High	65	84.6	6.2	3.1	6.2	0.615
	Low	68	77.9	0.0	5.9	16.2	
	Overall	133	81.2	3.0	4.5	11.3	

* P-values calculated using exact multinomial test with monte-carlo simulation of 1,000,000 replicates. The Bonferroni corrected p-value for statistical significance is p<0.025.

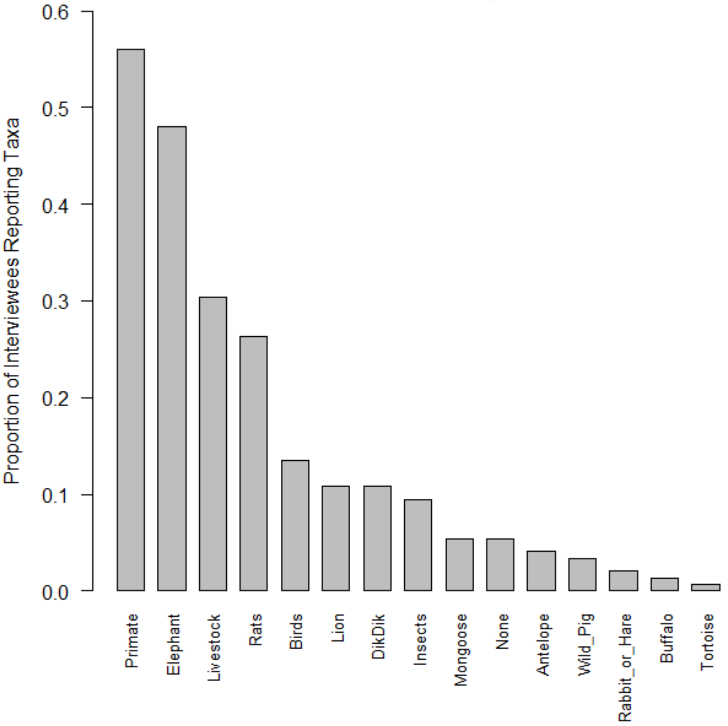
Table L.4 Farmer responses to Q38 (Appendix J), interviewees unaware of protected areas were included. Answers were coded as following: Neutral = fencing or translocation (no direct harm to wildlife but without coexistence); Positive = no actions needed, construct boreholes (no harm to wildlife but potential for coexistence); and Negative = culling (direct harm to wildlife). Interviewees were counted in a category if they gave one or more answers corresponding to that category.

Question	Grouping	n	% Giving Answers		
			Negative	Neutral	Positive
Q38. What would you like to do with or see happen to elephants in this area?	Far	69	21.7	71.0	14.5
	Near	69	31.9	87.0	2.9
	High	66	28.8	81.8	7.6
	Low	72	25.0	76.4	9.7
	Overall	138	26.8	79.0	8.7

Table L.5 Farmer responses to Q39 (Appendix J), interviewees unaware of protected areas were included.

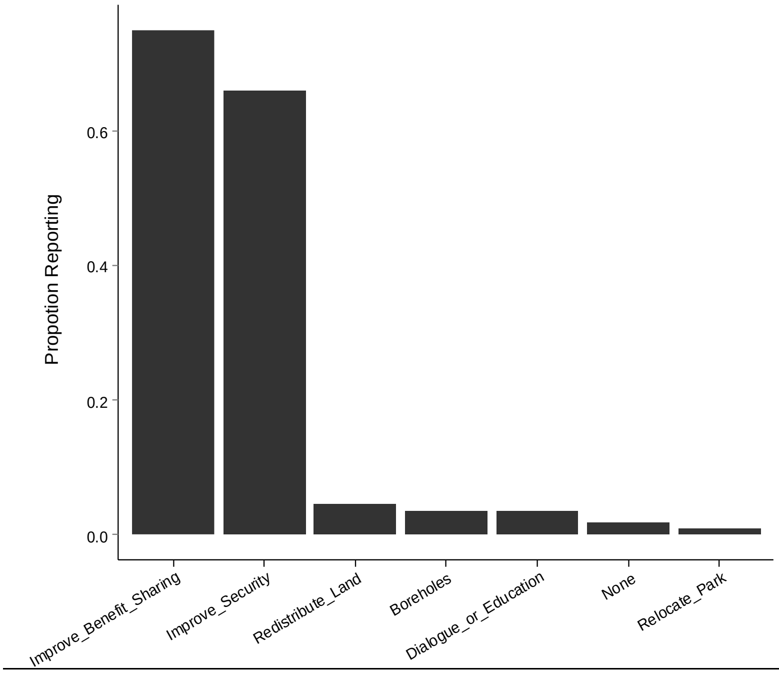
Question	Grouping	n	Response (%)				p*
			Elephant	Equal	No Opinion	People	
Q39. What is more important to the government: people or elephants?	Far	66	77.3	1.5	13.6	7.6	<0.001
	Near	71	95.8	1.4	1.4	1.4	
	High	66	84.8	0.0	9.1	6.1	0.384
	Low	71	88.7	2.8	5.6	2.8	
	Overall	137	86.9	1.5	7.3	4.4	

* P-values calculated using exact multinomial test with monte-carlo simulation of 1,000,000 replicates. The Bonferroni corrected p-value for statistical significance is p<0.025.



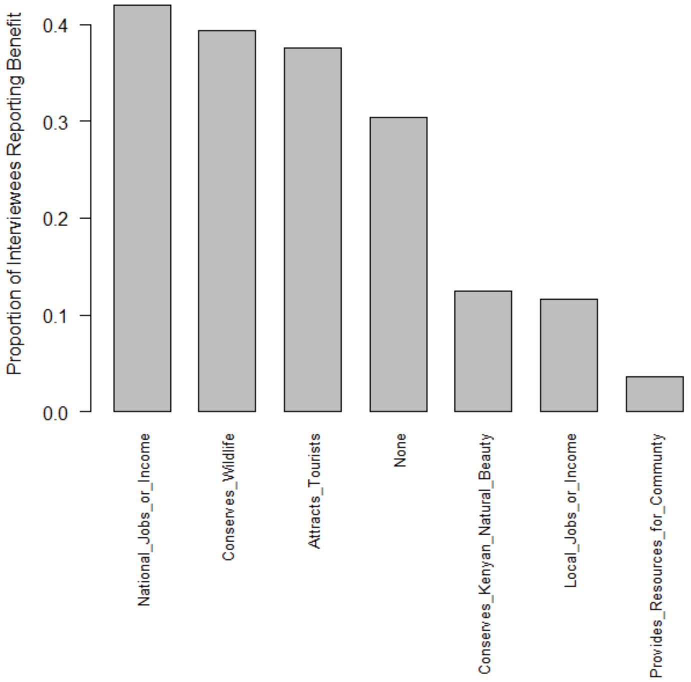
Taxa	n	Prop
Primate	83	0.56
Elephant	71	0.48
Livestock	45	0.30
Rats	39	0.26
Birds	20	0.14
Lion	16	0.11
DikDik	16	0.11
Insects	14	0.10
Mongoose	8	0.05
None	8	0.05
Antelope	6	0.04
Wild pig	5	0.03
Rabbit or hare	3	0.02
Buffalo	2	0.01
Tortoise	1	0.01

Figure L.4 General problem animals reported by interviewees (Q21 in Appendix J, n = 148, interviewees unaware of protected areas were included).



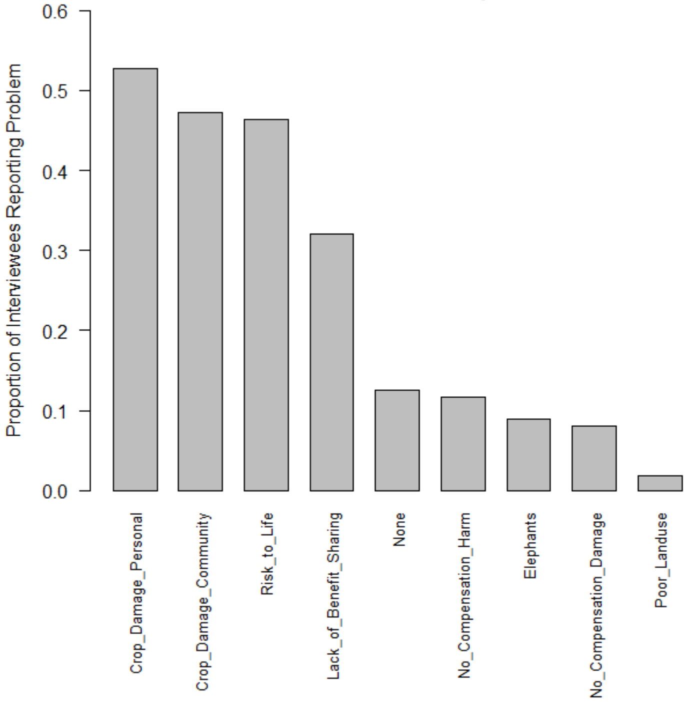
Suggested action	n	Prop
Improved benefit sharing	84	0.75
Improved security	74	0.66
Redistribution of land to local communities	5	0.05
Boreholes	4	0.04
Improved dialogue and education	4	0.04
None	2	0.02
Relocate park	1	0.01

Figure L.5 Desired actions regarding protected areas for nature reported by interviewees (see Q36 in Appendix J, interviewees unaware of protected areas were excluded, n = 112).



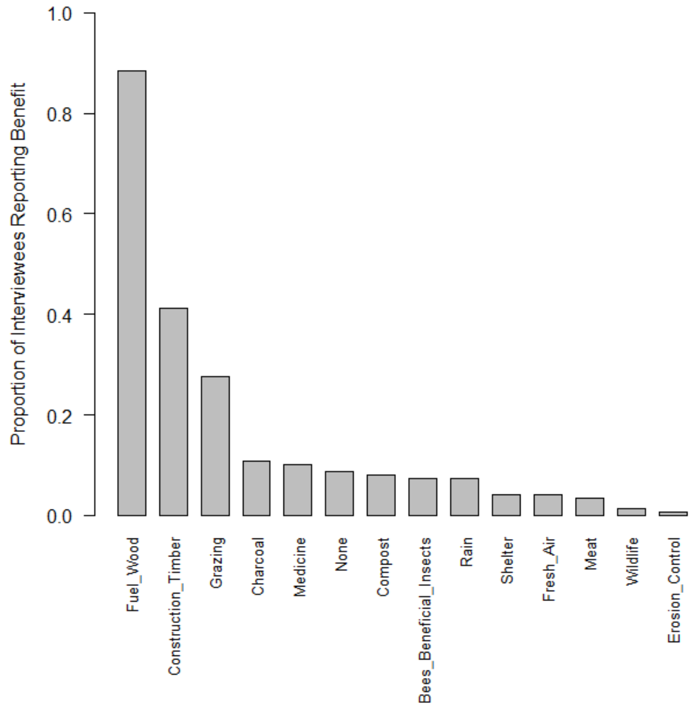
Benefit	n	Prop
Creates jobs or income at a national scale	47	0.42
Conserves wildlife	44	0.39
Attracts tourists	42	0.3
None	34	0.30
Conserves Kenya's natural beauty	14	0.13
Creates local jobs or income	13	0.12
Provides resources for nearby communities	4	0.04

Figure L.6 Benefits from protected areas for nature reported by interviewees (see Q33 in Appendix J, interviewees unaware of protected areas were included, n = 112).



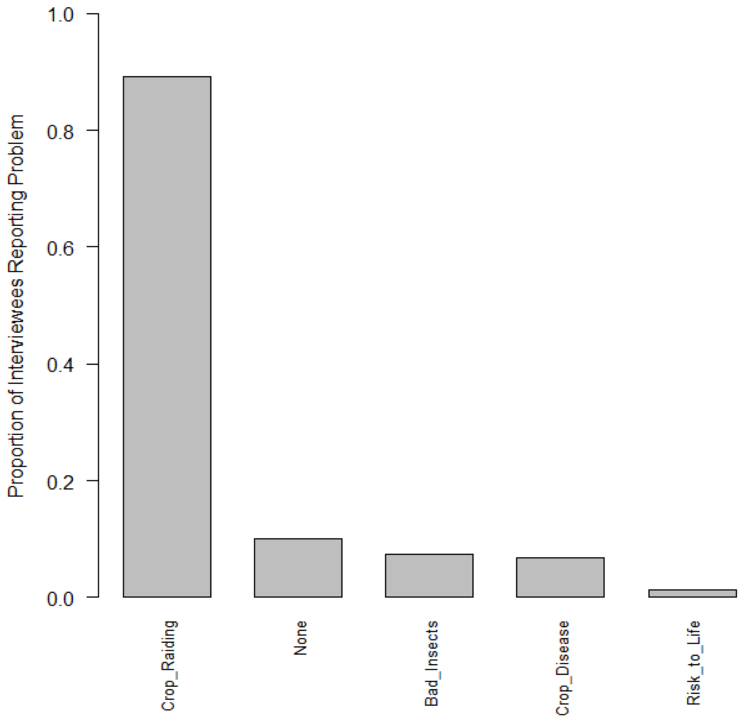
Problem	n	Prop
Damages my crops	59	0.52
Damages other people's crops	53	0.47
Risk to human life	52	0.46
Lack of benefit sharing	36	0.32
None	14	0.13
No compensation for injury	13	0.12
Elephants	10	0.09
No compensation damage	9	0.08
Poor use of land	2	0.02

Figure L.7 Problems due to protected areas for nature reported by interviewees (see Q34 in Appendix J, interviewees unaware of protected areas were included, n = 112).



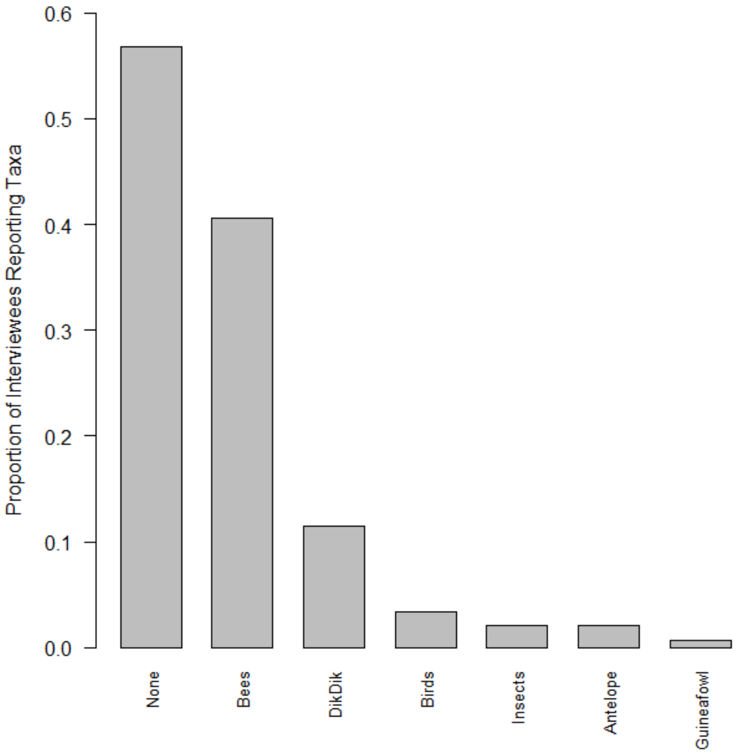
Benefit	n	Prop
Fuel wood	131	0.89
Construction timber	61	0.41
Grazing	41	0.29
Charcoal	16	0.12
Medicine	15	0.10
None	13	0.09
Compost	12	0.08
Bees and other beneficial insects	11	0.07
Rain	11	0.07
Shelter	6	0.04
Fresh air	6	0.04
Meat	5	0.03
Wildlife	2	0.01
Erosion control	1	0.01

Figure L.8 Benefits perceived from local natural habitat (bush and dry forest) in the vicinity of interviewees' farms (see Q25 in Appendix J, interviewees unaware of protected areas were included, n = 148).



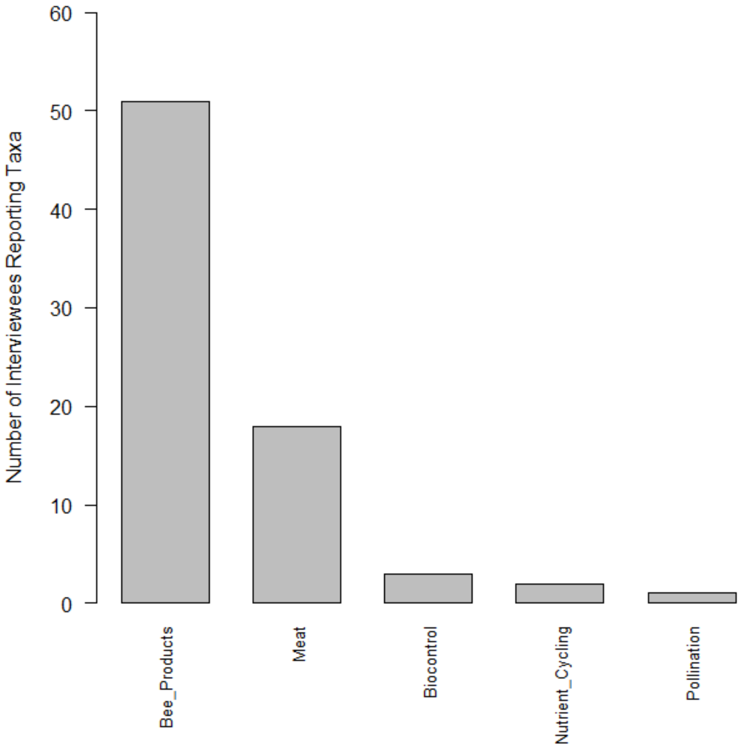
Problem	n	Prop
Crop raiding animals	132	0.89
None	15	0.10
Insect pests	11	0.07
Crop disease	10	0.07
Risk to human life	2	0.01

Figure L.9 Problems perceived from local natural habitat (bush and dry forest) in the vicinity of interviewees' farms (see Q26 in Appendix J, interviewees unaware of protected areas were included, n = 148).



Taxa	n	Prop
None	84	0.57
Bees	60	0.41
Dik dik	17	0.12
Birds	5	0.03
Insects	3	0.02
Antelope	3	0.02
Guineafowl	1	0.01

Figure L.10 Wildlife perceived as beneficial by interviewees (see Q20 in Appendix J, interviewees unaware of protected areas were included, n = 148).



Benefit	n
Bee products	51
Meat	18
Biological control of crop pests	3
Nutrient cycling	2
Crop pollination	1

Figure L.11 Benefits perceived from wildlife by interviewees (see Q20 in Appendix J, interviewees unaware of protected areas were included, n = 56).

Appendix M (Chapter 5) Regression model summaries for perceived crop losses and attitude indices

Table M.1 Relationships between predictors. In the lower half of the table Pearson's r correlations between continuous predictors with significance are presented (number + superscript significance notation, e.g., "0.19*"), where one predictor was ordinal/nomial and the other continuous ANOVA was used to test for differences between factors (significance is presented as "p="), where both predictors were ordinal/nominal in the case of gender vs. design factors chi-squared tested for differences. The study design factors distance to wilderness and proportion of local wildlife habitat were considered as factors, as these were controlled they are not compared in this table (but see Figure 5.2). The upper half of the table shows the mean difference in continuous predictors between ordinal/nominal factors (N = near to wilderness, vs. far, F = female, vs. male, and L = low local wildlife habitat, vs. high), where gender is compared between design factors the proportion of females is shown between categories (f/n = far/near), h/l = high/low). Abbreviations are as follows: Age = age of respondent; CropDam = perceived crop damage; Distance = distance to wilderness area (nominal, near/far); Drought = perceived crop losses due to drought; Education = number of years in education; Gender = sex of respondent (nominal, male/female); LOR = land owned or rented; LVI = livestock value index; MI = monthly income; % LWH = proportion of local wildlife habitat (ordinal, low/high); and prefix "log" = $\log_{10}$ transformed values.

	Age	CropDam	Distance	Drought	Education	Gender	LogLOR	LogLVI	LogMI	LOR	LVI	MI	%LWH
Age			N +1.6			F -2.9							L -2.0
CropDam	0.06^{NS}		N +0.05			F +0.04							L +0.00
Distance	p=0.5	p=0.16		N -0.06	N -1.418	F 0.55f/0.4n	N +0.68	N +0.64	N +1.28	N +5.66	N +333	N +939	
Drought	-0.03^{NS}	**0.19***	p=0.23			F +0.07							L -0.04
Education	**-0.39*****	-0.01^{NS}	**p = 0.02****	-0.08^{NS}		F -0.4							L +0.56
Gender	p = 0.22	p = 0.25	NS	p=0.13	p=0.555		F -0.25	F -0.05	F -1.42	F -2.6	F -141	F -1072	F 0.46h/0.49l
LogLOR	**0.28****	-0.00^{NS}	**p<0.001*****	-0.13^{NS}	-0.14^{NS}	**p=0.04***							L -0.06
LogLVI	0.01^{NS}	0.02^{NS}	p=0.09	-0.05^{NS}	0.02^{NS}	p=0.90	**0.33*****						L +0.66
LogMI	-0.06^{NS}	**-0.19***	p=09	**-0.23****	0.02^{NS}	p=0.09	**0.25****	**0.33*****					L +0.48
LOR	**0.19***	0.01^{NS}	**p=0.001****	0.17^{NS}	-0.03^{NS}	p = 0.15							L +0.87
LVI	0.08^{NS}	0.03^{NS}	**p=0.003****	-0.18^{NS}	-0.04^{NS}	p = 0.22				**0.71*****			L +147
MI	0.02^{NS}	-0.13^{NS}	p=0.14	**-0.19***	0.03^{NS}	p = 0.09				**0.37*****	**0.28****		L +1062
%LWH	p=0.39	p=0.94		p=0.38	p=0.37	NS	p=0.62	p=0.09	p=0.53	p=0.63	p=0.20	p=0.09	

Table M.2 Respondent's perceptions of crop damage (coded as high, moderate and low) analysed by ordinal regression. W1000 = proportion of wildlife habitat within 1000m of the interview location and primates, livestock, birds and elephants are factorial predictors indicating whether the respondent reported the group as a crop damaging taxa or not (Appendix J, Q14).

Term	Best model*			Averaged model						Bootstrapped best model					
	P	**coeff**	***f²***	**P**	**coeff**	**RI**	**coeff + shrinkage**	**95% CIS**		**Bias**	**original SE**	**Boot SE**	**coeff**	**BCA 95% CIs**	
high | moderate crop damage		-0.96		0.277	-1.09			-2.05	-0.13						
moderate | low crop damage		0.95		0.227	0.84			-0.12	1.80						
Primates (present)	0.013	0.82	0.02	0.026	0.77	0.69	0.53	-0.03	1.57	0.00	0.33	0.35	0.82	0.14	1.49
Income	0.034	0.35	0.02	0.087	0.35	0.75	0.26	0.00	0.69	0.02	0.16	0.18	0.35	0.06	0.69
Recorder				0.525	0.46	0.45	0.21	-0.22	1.14						
Drought				0.469	-0.27	0.51	-0.14	-0.62	0.09						
Gender (male)				0.598	0.38	0.38	0.14	-0.27	1.04						
Number of crop damaging taxa reported				0.708	-0.13	0.32	-0.04	-0.46	0.19						
Proximity_Land_Livestock				0.535	-0.26	0.48	-0.12	-0.68	0.17						
Age_Education_Land				0.681	-0.15	0.37	-0.05	-0.50	0.21						
Livestock (present)				0.614	0.39	0.37	0.14	-0.31	1.08						
Birds (present)				0.796	-0.22	0.28	-0.06	-1.00	0.57						
W1000				0.858	-0.31	0.31	-0.10	-2.14	1.52						
Elephants (present)				0.899	-0.12	0.28	-0.03	-1.05	0.82						
Proximity_Land_Livestock *W1000				0.906	0.56	0.04	0.02	-0.94	2.05						
Age_Education_Land * Proximity_Land_Livestock				0.980	0.02	0.04	0.00	-0.29	0.33						
Age_Education_Land*W1000				0.974	-0.17	0.02	0.00	-1.65	1.30						

* McFadden's pseudo r-squared = 0.034 , Maximum likelihood pseudo r-squared = 0.069,Cragg and Uhler's pseudo r-squared = 0.078, Cohen f^2 using McFadden's pR^2= 0.04

Table M.3 PCA loadings for perception of animal crop damage model predictors

Predictors:	Proximity_Land_Livestock	Age_Education_Land	Income	Drought
Livestock value index	0.681	-0.114	0.174	
Monthly income	0.132		0.955	
Land owned or rented	0.758	0.269	0.225	
Age		0.865		
Education	-0.145	-0.766		
Distance to wilderness area	-0.815		0.155	0.125
Crop losses to drought				0.988
Eigen value	1.748	1.429	1.034	1.003
Proportion variance	0.25	0.204	0.148	0.143
Cumulative variance	0.25	0.454	0.601	0.745

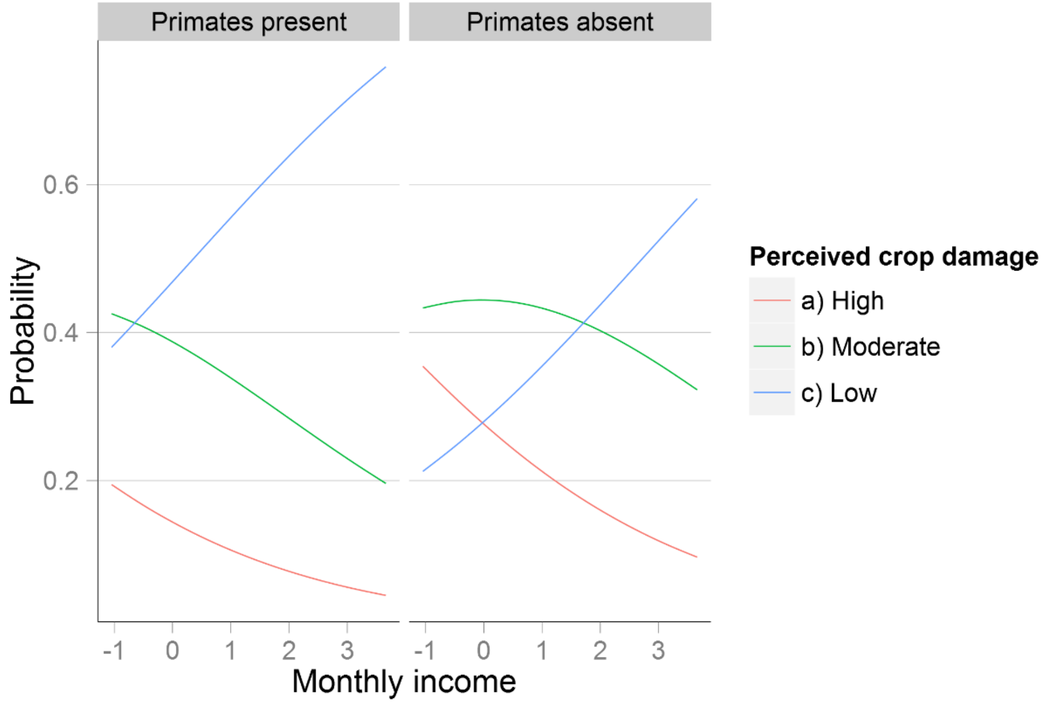


Figure M.1 Change in the relationship between farmer perceptions of crop damage due to animals and perceptions of crop losses to drought, for farmers reporting primates as crop pests compared to those not. Respondents with higher incomes perceived lower crop damage by animals and less animal crop damage was perceived when primates were present compared to absent, the latter is perhaps due to increased vigilance and investment in crop protection when primates were present (Figure 5.5). Monthly income is a PCA axis (see Table M.3) and model details can be found in Table N.1.

Table M.4 Overall attitude index (Table 5.1) analysed by linear regression. W1000 = proportion of wildlife habitat within 1000m of the interview location.

	Best model*			Averaged model						Bootstrapped best model							
Term	**P**	**coeff**	**f²**	**P**	**coeff**	**RI**	**coeff + shrinkage**	**95% CIS**		**Bias**	**original SE**	**Boot SE**	**coeff**	**Skew**	**Kurtosis**	**BCA 95% CIls**	
Intercept	0.003	2.14		0.083	1.72		1.72	-0.23	3.66	0.006		0.70	2.14	0.07	0.07	0.81	3.58
CropDamage_Proximity	2.65E-04	-1.72	0.121	0.002	-1.77	1.00	-1.77	-2.88	-0.65	-0.008		0.46	-1.71	-0.15	0.10	-2.68	-0.85
Drought_Distance	0.006	1.3	0.064	0.005	1.35	0.98	1.33	0.42	2.28	-0.010		0.46	1.30	0.02	0.05	0.47	2.26
RecorderNM	1.12E-04	-3.79	0.138	8.66E-05	-3.83	1.00	-3.83	-5.74	-1.92	-0.020		0.95	-3.80	-0.06	-0.02	-5.68	-2.00
GenderMale				0.235	1.10	0.40	0.44	-0.72	2.91								
Age_Education_Land				0.317	-0.82	0.53	-0.43	-2.44	0.79								
Livestock_Land_Proximity				0.586	0.25	0.26	0.06	-0.65	1.15								
W1000				0.573	1.22	0.41	0.50	-3.01	5.44								
Income_Land_Proximity				0.701	-0.18	0.24	-0.04	-1.10	0.74								
Age_Education_Land * W1000				0.165	2.90	0.12	0.34	-1.19	6.99								
Age_Education_Land * CropDamage_Proximity				0.638	0.26	0.12	0.03	-0.84	1.37								
CropDamage_Proximity * W1000				0.532	1.44	0.11	0.15	-3.08	5.97								

*Adjusted R^2 = 0.26, Cohen's f^2 = 0.30

Table M.5 PCA loadings for overall attitude model predictors

Predictors:	**Age_Education_Land**	**Livestock_Land_Proximity**	**Income_Land_Proximity**	**CropDamage_Proximity**	**Distance**
Livestock value index		0.94			
Monthly income			0.911	-0.12	
Land owned or rented	0.306	0.536	0.555	0.194	
Age	0.857				
Education	-0.79			-0.121	
Crop damage			-0.152	0.878	0.174
Distance to wilderness area	-0.181	-0.415	-0.35	-0.559	0.243
Crop losses to drought					0.974
Eigen value	1.493	1.357	1.292	1.159	1.052
Proportion variance	0.187	0.17	0.161	0.145	0.131
Cumulative variance	0.187	0.356	0.518	0.663	0.794

Table M.6 Elephant attitude index (Table 5.1) analysed by linear regression. W1000 = proportion of wildlife habitat within 1000m of the interview location.

Term	**Best model***			**Averaged model**						**Bootstrapped best model**							
	P	**coeff**	**f²**	**P**	**coeff**	**RI**	**coeff + shrinkage**	**95% CIS**		**Bias**	**original SE**	**Boot SE**	**coeff**	**Skew**	**Kurtosis**	**BCA 95% CIls**	
(Intercept)	0.000	-2.04		0.000	-1.98		-1.98	-2.50	-1.46	0.00	0.19	0.18	-2.05	0.07	-0.03	-2.38	-1.66
Age_Education_Land	0.057	0.23	0.021	0.139	0.21	0.8	0.17	-0.07	0.50	0.00	0.12	0.11	0.23	0.12	0.10	0.00	0.44
CropDamage_Proximity	0.001	-0.41	0.083	0.028	-0.36	1	-0.36	-0.68	-0.04	0.00	0.12	0.10	-0.41	-0.03	0.07	-0.61	-0.21
Drought_Distance	0.001	0.42	0.087	0.000	0.44	1	0.44	0.19	0.69	0.00	0.12	0.13	0.42	-0.10	0.03	0.16	0.67
Livestock_Land_Proximity	0.000004	-0.56	0.179	1.50E-06	-0.57	1	-0.57	-0.80	-0.34	-0.01	0.12	0.13	-0.56	-0.29	0.25	-0.81	-0.33
RecorderNM	0.000001	-1.31	0.205	1.50E-06	-1.26	1	-1.26	-1.78	-0.75	0.00	0.25	0.25	-1.31	-0.01	-0.06	-1.81	-0.83
Age_Education_Land*CropDamage_Proximity	0.097	-0.19	0.014	0.106	-0.19	0.45	-0.08	-0.41	0.04	-0.01	0.11	0.09	-0.20	-0.39	0.94	-0.38	-0.03
Income_Land				0.382	-0.49	0.28	-0.22	-1.60	0.61								
W1000				0.471	0.09	0.44	0.02	-0.15	0.32								
GenderMale				0.984	0.00	0.22	0.00	-0.48	0.47								
CropDamage_Proximity*W1000				0.430	-0.48	0.12	-0.06	-1.68	0.72								
Age_Education_Land*W1000				0.836	0.11	0.08	0.01	-0.94	1.16								

* Adjusted R-squared = 0.39, Cohen's f² = 0.64

Table M.4 PCA loadings for elephant attitude model predictors

Predictor	**Livestock_Land_Proximity**	**Age_Education_Land**	**CropDamage_Proximity**	**Drought_Distance**	**Livestock_Land_Proximity**
Livestock value index	0.823	-0.106	-0.153		
Monthly income	0.168				0.966
Land owned or rented	0.725	0.306			0.271
Age		0.882			
Education	-0.153	-0.771	-0.137	-0.14	
Crop damage			0.934	0.133	
Distance to wilderness area	-0.693		-0.394	0.272	
Crop losses to drought			0.117	0.951	
Eigen value	1.74	1.50	1.09	1.04	1.03
Proportion variance	0.22	0.19	0.14	0.13	0.13
Cumulative variance	0.22	0.41	0.54	0.67	0.80

Table M.7 Protected area attitude index (Table 5.1) analysed by linear regression. W1000 = proportion of wildlife habitat within 1000m of the interview location.

Term	Best model*			Averaged model						Bootstrapped best model							
	P	coeff	f²	P	coeff	RI	coeff + shrinkage	95% CIS		Bias	original SE	Boot SE	coeff	Skew	Kurtosis	BCA 95% CIls	
(Intercept)	0.613	-0.21		0.516	-0.29		-0.29	-1.16	0.58	0.00	0.41	0.42	-0.21	0.07	-0.07	-0.97	0.65
Age_Education_Land	0.018	-0.42	0.04	0.095	-0.56	0.93	-0.52	-1.22	0.10	0.00	0.18	0.16	-0.43	0.06	0.08	-0.72	-0.11
CropDamage_Proximity	0.0001	-1.54	0.21	0.006	-1.29	1.00	-1.29	-2.22	-0.37	-0.01	0.37	0.48	-1.55	0.10	-0.23	-2.37	-0.47
Drought_Distance	0.005	0.52	0.07	0.003	0.57	0.99	0.57	0.20	0.94	0.00	0.18	0.18	0.52	-0.02	0.10	0.17	0.87
RecorderNM	0.053	-0.74	0.03	0.085	-0.67	0.61	-0.41	-1.44	0.09	-0.02	0.38	0.37	-0.76	0.02	-0.02	-1.45	0.01
W1000	0.068	1.51	0.06	0.132	1.29	0.91	1.17	-0.39	2.96	0.02	0.82	0.82	1.54	0.00	0.08	-0.17	3.04
CropDamage_Proximity*W1000	0.021	2.04	0.04	0.031	1.95	0.74	1.44	0.18	3.72	-0.02	0.87	1.05	2.03	-0.07	0.01	-0.10	3.96
Livestock_Land_Proximity				0.15	-0.26	0.49	-0.13	-0.62	0.09								
Age_Education_Land*W1000				0.25	0.95	0.34	0.32	-0.66	2.56								
Age_Education_Land*CropDamage_Proximity				0.46	0.19	0.29	0.05	-0.31	0.68								
GenderMale				0.58	0.20	0.25	0.05	-0.51	0.92								
Income_Land				0.96	-0.01	0.21	0.00	-0.36	0.35								
Age_Education_Land*CropDamage_Proximity*W1000				0.80	-0.25	0.02	0.00	-2.18	1.68								

* Adjusted R-squared = 0.25, Cohen's f² = 0.33

Table M.8 PCA loadings for protected area attitude model predictors

Predictor	Livestock_Land_Proximity	Age_Education_Land	Income_Land	CropDamage_Proximity	Drought_Distance
Livestock value index	0.907				
Monthly income			0.938		
Land owned or rented	0.657	0.304	0.445	0.121	
Age		0.864			
Education		-0.794		0.135	
Crop damage			-0.12	0.893	0.168
Distance to wilderness area	-0.526	-0.138	-0.247	-0.506	0.312
Crop losses to drought				0.113	0.964
Eigen value	1.546	1.498	1.162	1.118	1.067
Proportion variance	0.193	0.187	0.145	0.14	0.133
Cumulative variance	0.193	0.381	0.526	0.665	0.799

Table M.9 Wildlife attitude index (Table 5.1) analysed by linear regression. W1000 = proportion of wildlife habitat within 1000m of the interview location.

Term	Best model*			Averaged model						Bootstrapped best model							
	P	coeff	f^2	P	coeff	RI	coeff + shrinkage	95% CIS		Bias	original SE	Boot SE	coeff	Skew	Kurtosis	BCA 95% CIls	
(Intercept)	0.000	-2.65		0.000	-2.50		-2.50	-3.27	-1.73	0.00	0.26	0.21	-2.64	-0.12	0.03	-3.09	-2.26
Drought	0.107	0.28	0.01	0.094	0.30	0.62	0.18	-0.05	0.64	0.00	0.17	0.18	0.28	-0.05	-0.12	-0.08	0.62
Proximity_Income	0.027	-0.37	0.03	0.027	-0.39	0.91	-0.32	-0.73	-0.04	-0.01	0.17	0.17	-0.39	-0.04	0.09	-0.70	-0.04
Livestock_Land	0.001	0.56	0.08	0.014	0.53	1.00	0.53	0.11	0.95	0.03	0.17	0.20	0.57	0.63	1.19	0.23	1.04
RecorderNM	0.0000004	-1.84	0.20	0.000	-1.96	1.00	-1.96	-2.68	-1.23	0.00	0.35	0.33	-1.84	0.08	0.05	-2.47	-1.17
negCropDamage_Income				0.230	0.59	0.61	0.36	-0.37	1.55								
W1000				0.549	-0.50	0.66	-0.30	-2.13	1.13								
negCropDamage_Income * W1000				0.034	-1.89	0.40	-0.68	-3.64	-0.14								
GenderMale				0.477	0.25	0.28	0.07	-0.44	0.95								
Age_Education_Land				0.997	0.00	0.34	0.00	-0.47	0.47								
Proximity_Land_Income * W1000				0.662	0.39	0.29	0.06	-1.37	2.15								
negCropDamage_Income * Proximity_Land_Income				0.958	-0.01	0.15	0.00	-0.45	0.43								
Age_Education_Land * Proximity_Land_Income				0.524	0.14	0.09	0.01	-0.30	0.59								
Age_Education_Land * W1000				0.509	0.52	0.06	0.03	-1.02	2.05								
negCropDamage_Income *Proximity_Land_Income * W1000				0.212	-1.18	0.01	-0.02	-3.03	0.672								

* Adjusted R-squared 0.26, Cohen's F^2 = 0.35

Table M.10 PCA loadings for wildlife attitude model predictors

Predictor	Age_Education_Land	Proximity_Income	Livestock_Land	negCropDamage_Income	Drought
Livestock value index			0.941		
Monthly income		0.36	0.292	0.577	
Land owned or rented	0.331	0.541	0.474	0.173	0.145
Age	0.854		-0.11	0.115	
Education	-0.777		-0.141	0.204	0.104
Crop damage		0.19	0.124	-0.85	
Distance to wilderness area		-0.907			0.104
Crop losses to drought					0.977
Eigen value	1.45	1.288	1.244	1.155	1.014
Proportion variance	0.181	0.161	0.155	0.144	0.127
Cumulative variance	0.181	0.342	0.498	0.642	0.769

Table M.11 Bushland attitude index (Table 5.1) analysed by linear regression. W1000 = proportion of wildlife habitat within 1000m of the interview location.

Term	Best model*			Averaged model						Bootstrapped best model							
	P	coeff	f²	P	coeff	RI	coeff + shrinkage	95% CIS		Bias	original SE	Boot SE	coeff	Skew	Kurtosis	BCA 95% CIs	
(Intercept)	0.08	-0.50		0.13	-0.54		-0.54	-1.24	0.16	0.00	0.28	0.27	-0.50	-0.06	0.02	-1.03	0.02
Income	0.08	-0.29	0.01	0.08	-0.30	0.63	-0.19	-0.63	0.04	0.01	0.17	0.20	-0.28	-0.11	0.03	-0.78	0.04
W250	0.04	1.52	0.02	0.02	1.66	0.88	1.46	0.21	3.11	0.00	0.72	0.68	1.52	-0.07	0.07	0.14	2.84
Land_Livestock_Proximity				0.26	0.25	0.55	0.14	-0.19	0.70								
GenderMale				0.35	0.32	0.34	0.11	-0.36	1.00								
Land_Livestock_Proximity * W250				0.23	-0.85	0.21	-0.18	-2.23	0.53								
Drought				0.58	-0.10	0.27	-0.03	-0.44	0.24								
CropDamage_Proximity				0.94	-0.02	0.32	-0.01	-0.44	0.41								
RecorderNM				0.99	0.01	0.24	0.00	-0.70	0.71								
Age_Education				0.94	-0.01	0.34	0.00	-0.40	0.37								
CropDamage_Proximity * W250				0.67	-0.35	0.07	-0.02	-1.96	1.26								
Age_Education * W250				0.80	-0.18	0.07	-0.01	-1.55	1.19								
Age_Education * Land_Livestock_Proximity				0.34	-0.17	0.07	-0.01	-0.52	0.18								
CropDamage_Proximity * Land_Livestock_Proximity				0.92	-0.02	0.04	0.00	-0.41	0.37								
Age_Education * Land_Livestock_Proximity * W250				0.35	-0.70	0.00	0.00	-2.15	0.76								
CropDamage_Proximity * Land_Livestock_Proximity * W250				0.41	-0.63	0.00	0.00	-2.12	0.86								

Adjusted R-squared 0.04, Cohen's F² = 0.04

Table M.12 PCA loadings for bushland attitude model predictors.

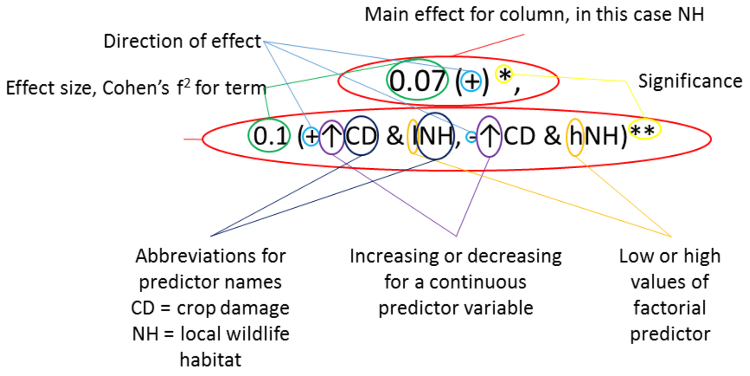
Predictor	Land_Livestock_Proximity	Age_Education	CropDamage_Proximity	Drought	Income
Livestock value index	0.777	-0.124			
Monthly income	0.11				0.981
Land owned or rented	0.781	0.272			0.218
Age		0.859	-0.158		
Education		-0.778	-0.215		
Crop damage			0.928	0.108	
Distance to wilderness area	-0.692		-0.381	0.232	
Crop losses to drought				0.974	
Eigen value	1.718	1.44	1.101	1.02	1.02
Proportion variance	0.215	0.18	0.138	0.128	0.127
Cumulative variance	0.215	0.395	0.532	0.66	0.787

Appendix N (Chapter 5) Summarised results of regression analyses regarding crop damage and wildlife reported damaging crops.

Table N.1 Modelling of respondent's reporting of the overall number of problem taxa and reporting of individual taxa as a problem (yes/no), when asked specifically regarding crops (Q14) or in general (Q21, see Appendix K for full questionnaire).Predictor variable abbreviations: P = presence of primates; D = perceived crop losses due to drought; CD = perceived crop damage due to animals; AE = respondent's age and education (these are strongly correlated); LA = land owned or rented; LI = livestock value index; R = recorder; IN = monthly income; PX = proximity to wilderness area; DI = distance from wilderness area; NH = local wildlife habitat (hNH -= high, lNH = low). Models: lm = linear regression with Gaussian error family, lm (o) = ordinal regression, glm = generalised linear regression with binomial error family. R^2 is adjusted and is presented for linear models, whereas D^2 (amount of deviance accounted for) is presented for ordinal regression and glm models (derived using ModEVA package's Dsquared function, Barbosa et al. 2013). All predictors apart from R and NH are PCA ordination axes. Where predictors are presented relating to spatial terms PX = land owned or rented / proximity to wilderness / livestock (loadings: 0.81, 0.74, 0.71), CD = perceived animal crop damage / proximity to wilderness / education (loadings: 0.93, 0.31,-0.26) and AE = age / education/ land owned or rented (0.85,-0.78, 0.26). Predictors not directly listed under spatial terms but significant in models as co-loading predictors in PCA in spatial terms and their interactions or as terms that did not interact with spatial terms at all are listed under other terms, only predictors loading > 0.2 onto PCA ordination axes are shown. Mean or percentage values for response variables are presented for each landscape combination (columns "near" and "far") and units are present in the response variable description. As this is a particularly complex table a graphical guide to interpretation is presented following it.

			Near		Far		Spatial terms: Cohen's F^2, direction of effect, significance			
Response variable	**Model**	**R^2 or D^2 / f^2**	**High NH (n= 34)**	**Low NH (n = 32)**	**High NH (n = 41)**	**Low NH (n =37)**	**Prop Wildlife Habitat**	**Distance to PA[‡]**	**Interaction**	**Other terms**
Q14. Number of taxa damaging crops (mean ± SD)[†]	lm (o)	0.04 / 0.04	2.9 ± 1.1	3.0 ± 1.2	3.3 ± 1.3	2.8 ± 1.3	*(+) ^{NS},* *0.1 (+↑CD & lNH,* *-↑CD & hNH)*****			D, IN
Q14. Number of taxa damaging crops (mean ± SD)[†]	lm	0.07 / 0.08	2.9 ± 1.1	3.0 ± 1.2	3.3 ± 1.3	2.8 ± 1.3	0.07 (+) *, 0.1 (+↑CD & lNH,			D, IN

Response variable	Model	R^2 or D^2 / f^2	Near		Far		Spatial terms: Cohen's F^2, direction of effect, significance			
			High NH (n= 34)	Low NH (n = 32)	High NH (n = 41)	Low NH (n =37)	Prop Wildlife Habitat	Distance to PA‡	Interaction	Other terms
							-↑CD & hNH)**			
Q14. Primates (% reporting taxa)	glm	0.34 / 0.52	56.3	34.2	97.1	60	0.27 (+) ***, 0.11 (+↑AE & lNH; -↑AE & hNH) ***	0.11 (+) ***		AE, CD, LA, LI, D
Q14. Elephants (% reporting taxa)	glm	0.59 / 1.45	90.6	91.4	2.9	2.5		1.3 (-) ***, 0.6 (++↑PX & lAE, -↑PX & hAE) ***		CD, LA, LI, AE, D
Q14. Livestock (% reporting taxa)	glm	0.14 / 0.16	65.6	31.4	68.6	35	0.08 (+) ***	0.03 (-↑PX & lCD, +↑PX & hCD) *		CD, LA, LI, R
Q14. Birds (% reporting taxa)	glm	0.09 / 0.10	21.9	28.6	28.6	50		0.02 (+) *		IN
Q14. Rats (% reporting taxa)	glm	0.25 / 0.34	6.3	20	48.6	27.5	0.03 (+↑CD & lNH, ±↑CD & hNH) **	0.1 (+) ***, 0.02 (-↑PX & lAE, --↑PX & hAE)*		CD, IN, R, LA, LI
Q14. Dik dik (% reporting taxa)	glm	0.03 / 0.03	18.8	40	14.3	25	0.02 (-) *			
Q14. Squirrel (% reporting taxa)	glm	0.08 / 0.09	3.1	11.4	20	27.5	0.02 (-) ^{NS}	0.07 (-) *, 0.06 (-↑PX & lAE, +↑PX & hAE) *		LA, LI, AE
Q21. No. of taxa reported as a problem in general (mean ± SD)†	lm (o)	0.14 / 0.17	2.1 ± 0.9	2.7 ± 1.3	2.7 ± 1.1	2.0 ± 1.2	*(-)* ^{NS}	(+)*	(+↑PX & lNH, -↑PX & hNH) ***	R, LA, IN
Q21. No of taxa reported as a problem in general (mean ± SD)†	lm	0.30 / 0.42	2.1 ± 0.9	2.7 ± 1.3	2.7 ± 1.1	2.0 ± 1.2				R
Q21. Primates (% reporting taxa)	glm	0.12 / 0.14	46.9	42.9	85.7	45	0.05 (+) **	0.03 (+) *		CD, LI, LA, R
Q21. Elephants (% reporting taxa)	glm	0.62 / 1.62	90.6	91.4	8.5	5		1.47 (-) ***		CD, IN, LA, LI, R
Q21. Livestock (% reporting taxa)	glm	0.21 / 0.26	28.1	17.1	51.4	20	*0.02 (+)* ^{NS}	0.05 (+) *		LA, LI, R
Q21. Birds (% reporting taxa)	glm	0.18 / 0.22	0	17.1	14.3	22.5	*0.08 (-)* ^{NS}	*0.03 (-)* ^{NS}	0.09 (±↑PX & lNH, -↑PX & hNH) *	IN
Q21. Rats (% reporting taxa)	glm	0.21 / 0.26	0	20	48.6	37.5	*0.01 (-)* ^{NS}	*0.00(+)* ^{NS}	0.02 (-↑PX * lNH, --↑PX * hNH) *	R, LA, LI
Q21. Dik Dik (% reporting taxa)	glm	0.09 / 0.09	6.25	17.1	5.7	12.5	*0.04 (-)* $^{NS(p = 0.056)}$			R
Q21. Lion (% reporting taxa)	glm	0.17 / 0.20	9.4	37.1	0	0	0.05 (±↑CD_PX & lNH, -↑CD_PX & hNH) *	0.05 (-) *		CD


Main effect for column, in this case NH
Direction of effect
Effect size, Cohen's f^2 for term
0.07 (+) *,
Significance
0.1 (+↑CD & lNH, -↑CD & hNH)**
Abbreviations for predictor names
CD = crop damage
NH = local wildlife habitat
Increasing or decreasing for a continuous predictor variable
Low or high values of factorial predictor

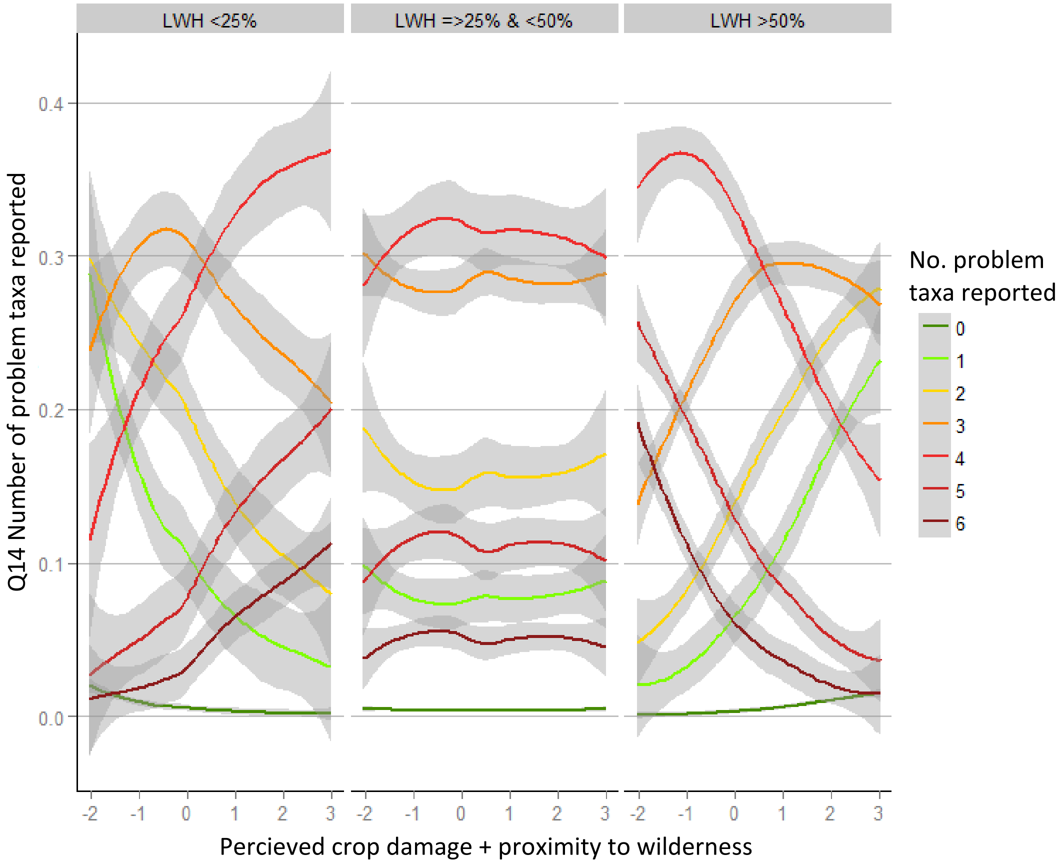


Figure N.1 Relationship between the perceived number of problem animals (taxa) and perceived crop damage caused by animals in three different landscape contexts (LWH = % of landscape that was local wildlife habitat within 1000 m of an interviewee's farm). See Table N.1 for model details (response = Q21. No. of taxa reported damaging crops, model = lm(o)). Crop damage + proximity to protected area was a PCA axis onto which crop losses due wildlife (as a proportion of all crops averaged across the two most recent growing seasons) loaded 0.934, distance to protected area, years in education and age also all loaded onto the same axis, but more weakly (-0.307, -0.255 and -0.181 respectively).

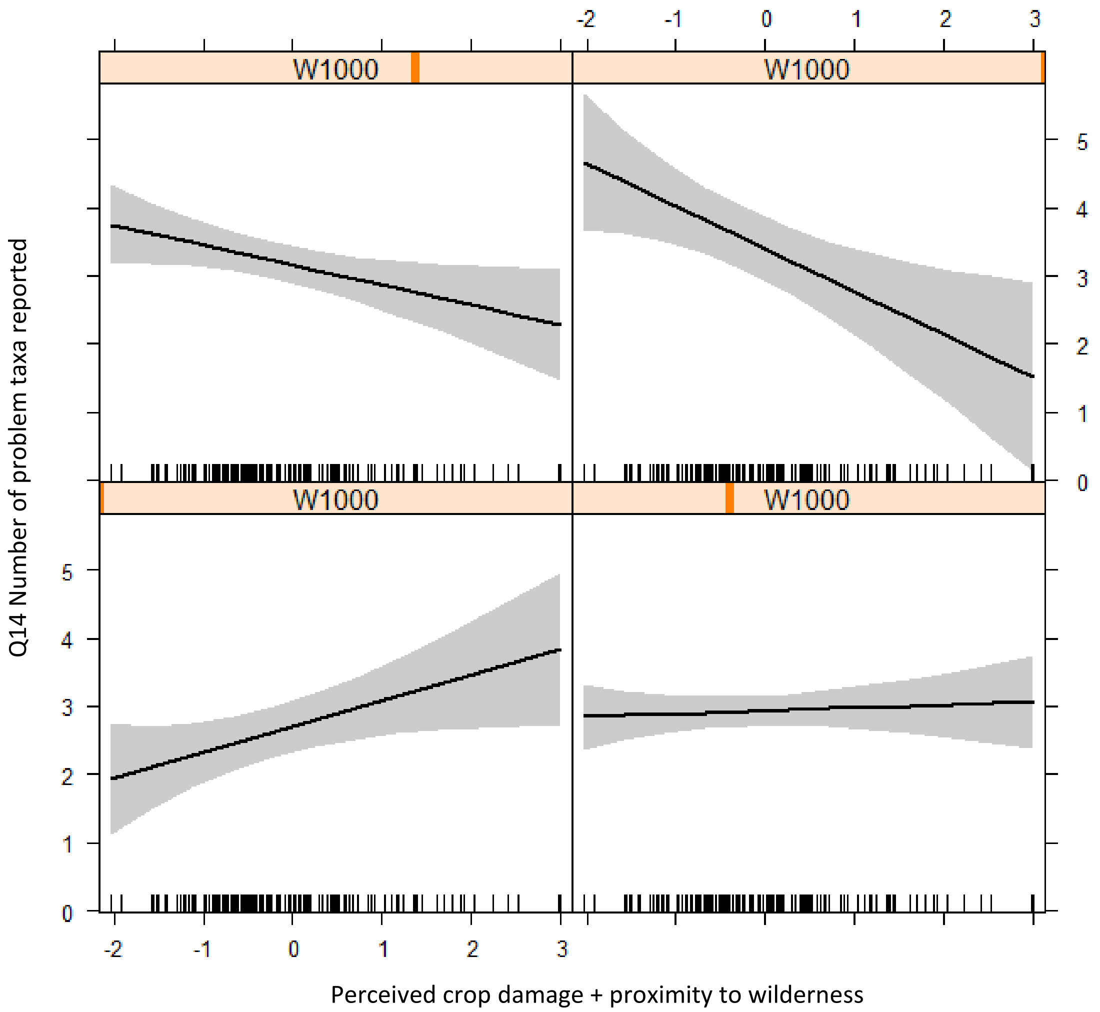


Figure N.2 Relationship between the perceived number of problem animals (Q14) and perceived crop damage caused by animals in three different landscape contexts (W1000 = % of landscape that was local wildlife habitat within 1000 m of an interviewee's farm, orange vertical bars indicates low values when on the left and high values when on the right). See Table N.1 for model details (response = Q14. No. of taxa reported damaging crops, model = lm). Crop damage + proximity to protected area was a PCA axis onto which crop losses due wildlife (as a proportion of all crops averaged across the two most recent growing seasons) loaded 0.934, distance to protected area, years in education and age also all loaded onto the same axis, but more weakly (-0.307, -0.255 and -0.181 respectively).