Biodiversity and Ecosystem Services: Pollination, Biological Control, and Nature Conservation in Agricultural Landscapes

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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 the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2 is based on a jointly-authored publication [Shackelford G., Steward, P. R., Benton, T. G., Kunin, W. E., Potts, S. G., Biesmeijer, J. C., Sait, S. M. (2013). Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews* 88(4):1002–1021]. The candidate designed the research, collected and analyzed the data, and wrote and revised the manuscript for this publication. Peter Steward contributed to data collection. The other authors supervised the research and gave feedback on the manuscript. A plural pronoun (“we”) is used in parts of this thesis, and this is not meant to suggest that the candidate (“I”) is not the author, but it is meant to acknowledge the feedback that others have given, or to prepare these parts of the thesis for jointly-authored submissions to scientific journals. All of Chapter 2 was written only by the candidate.

Chapter 3 is based on a jointly-authored manuscript [Shackelford G. E., Steward, P. R., German, R. N., Sait, S. M., Benton, T. G. (in press). Conservation planning in agricultural landscapes: hotspots of conflict between agriculture and nature. *Diversity and Distributions*]. The candidate designed the research, collected and analyzed the data, and wrote and revised the manuscript. The other authors gave feedback on the manuscript. In particular, Tim Benton suggested that hotspots for agricultural intensification could also be identified, as a counterpoint to the hotspots of conservation conflict that the candidate had suggested. The candidate then redesigned the conceptual framework, reanalyzed the data, and completely rewrote the manuscript. Three anonymous peer reviewers gave feedback on the manuscript. In particular, one of them suggested that hotspots of agricultural intensification should not be identified, because it implied that agricultural intensification could not or should not be stopped or questioned. The candidate again redesigned the conceptual framework, replaced hotspots for agricultural intensification with coldspots of conservation conflict, reanalyzed the data, and completely rewrote the manuscript. All of Chapter 3 was written only by the candidate.

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Abstract

Agriculture has done more damage to nature than any other human activity, and yet food production could need to be doubled by the middle of this century. As agricultural land is expanded and intensified, critical thresholds in the loss of natural habitats are crossed. This loss of non-crop habitats can have negative feedback on crop production, because it can cause a loss of “ecosystem services” that support and regulate crop production, such as the pollination of crops by bees and the biological control of crop pests by their natural enemies. Because of this connection between non-crop habitats and crop yields, there could be potential for habitat conservation to benefit both agriculture and nature. The research in this thesis focuses on pollinators and natural enemies, because these species constitute a vital connection between food production and biodiversity conservation. Could habitat management be used to conserve both pollinators and natural enemies in agricultural landscapes? Will the relationships between pollinators, natural enemies, and natural habitats change with climate change? Where should we prioritize the resolution of conflict between agriculture and nature, and how? This thesis addresses these questions through literature review and meta-analysis, geographic information systems (GIS) and hotspot analysis, field research on the distributions of trap-nesting bees and wasps on environmental gradients, and laboratory research on the development of bees and wasps at high temperatures. This thesis suggests that it might be possible to conserve communities of both pollinators and natural enemies, in general, by means of habitat management, but it might not be possible to conserve specific combinations of pollinators and natural enemies, which might have opposite responses to some forms of environmental change, such as global warming. This thesis also suggests that the resolution of conflict between agriculture and nature should be prioritized in sub-Saharan Africa, and it outlines a conceptual framework for systematic conservation planning in agricultural landscapes.

Table of contents

List of tables

List of figures

Biodiversity and ecosystem services: conservation of pollinators, natural enemies, and natural habitats in agricultural landscapes

Introduction to the thesis

Agriculture has done more damage to nature than any other human activity (Balmford *et al.*, 2012), and yet by 2050 we may need our agricultural landscapes to produce about twice as much food as they did in 2005 (Tilman *et al.*, 2011), which could have a massive impact on the environment (Tilman *et al.*, 2001; Gibbs *et al.*, 2010). From 2000 to 2050, the human population could grow by about 52%, from 6.1 to 9.3 billion (UN, 2011), and therefore we would need to produce about 52% more food in 2050 than we did in 2000, if per-person production and consumption did not also need to increase. However, about 15% of the population was undernourished in 2000, and it is hoped that by 2050 this will have decreased to about 4% worldwide, and per-person calorie consumption will have increased by about 16% in developing countries and 29% in sub-Saharan Africa (FAO, 2006; FAO *et al.*, 2012). Moreover, consumption of meat and dairy might also increase by about 39% and 28% per person, as incomes increase in developing countries (FAO, 2006; not including butter). Therefore, because of growth in the human population and growth in per-person consumption, we may need our agricultural landscapes to produce about 50–100% more food in 2050 than they did in 2005, not including crops produced for biofuel (Bruinsma, 2009; The Royal Society, 2009; Godfray *et al.*, 2010; Foresight, 2011; Tilman *et al.*, 2011). If agricultural production is doubled, how much more damage will be done to nature?

In 2010, when I began this research, I found it confusing that I was being funded by the Biotechnology and Biological Sciences Research Council (BBSRC) of the United Kingdom, which typically funds research on biomedicine, as opposed to being funded by the Natural Environment Research Council (NERC), which typically funds research on biodiversity. However, I then learned that the BBSRC also funds research on food security, and I had a good example in Tim Benton, who the BBSRC now funds as the UK Champion for Food Security, who is among the many supervisors of this research (see “Acknowledgments”), and who also works on biodiversity in agricultural landscapes (*e.g.*, Benton *et al.*, 2003). Thus, I began this research by looking for connections between biodiversity conservation and food production, through the lens of UK food policy.

In 2007, there was a sudden increase in the price of food—an increase which has been attributed to many causes, such as an increase in food commodity trading, supported by the Goldman Sachs Commodity Index, and an increase in biofuel production, supported by the European Biofuels Directive (Mueller *et al.*, 2011;

Tscharntke *et al.*, 2012). In turn, this increase in the price of food has been credited with the rise of a "new productionism" or "new productivism" in UK food policy: a renewal of interest in "feeding the world" by means of agricultural intensification (Marsden, 2010; Horlings & Marsden, 2011; Lang & Barling, 2012; Fish *et al.*, 2013). However, UK food policy is not now, nor has it always been, synonymous with productionism, and neither is this thesis.

The "old" productionism cropped up after World War II (Lang & Barling, 2012), but by the end of the Twentieth Century there was a massive surplus of food, and UK food policy began to pay farmers not to produce food, but to become stewards of the environment, by using agricultural land for biodiversity conservation, through "agri-environment schemes" (Kleijn & Sutherland, 2003). These schemes—such as maintaining "extensive" grassland with low levels of agrochemical inputs, as opposed to "intensive" grassland with high levels of agrochemical inputs—have been effective at conserving some species, in some areas, but not others (Kleijn *et al.*, 2004, 2006; Batáry *et al.*, 2011). However, in the aftermath of the 2007 increase in the price of food, and with the growing recognition that demand for food could as much as double, the new productionism in UK food policy cropped up and turned toward the "sustainable intensification" of agriculture, as a means of producing more food (*e.g.*, The Royal Society, 2009; Godfray *et al.*, 2010; Foresight, 2011; Pretty *et al.*, 2011; Tomlinson, 2013). Some farmers have seen this as a renewal of their "license to produce" (Fish *et al.*, 2013), and it remains to be seen whether or not the new productionism will cause farmers to turn away from agri-environment schemes, and what the impact on biodiversity will be.

As a counterpoint to the new productionism, it has been pointed out by both environmental and social scientists that—just as efforts are being made to mitigate the effects of increasing global temperatures on agriculture and the environment—efforts could and should be made to mitigate the effects of increasing global demand for food (Horlings & Marsden, 2011; Tscharntke *et al.*, 2012; Loos *et al.*, 2014). To be absolutely clear, nobody has suggested that hunger should not be ended worldwide, but an increase in demand for food and a decrease in undernourishment could both be met by either an increase in food production, or by a decrease in food waste and a decrease in demand for livestock feed and biofuel feedstock (Foley *et al.*, 2011; Bajzelj *et al.*, 2014), or else by some combination of the two (an increase in supply, a decrease in demand for inefficient supply, and a decrease in waste). In any case, an increase in food security will not result from an increase in food supply *per se*, but from an increase in the accessibility, affordability, and availability of food (Lang & Barling, 2012; Tscharntke *et al.*, 2012; Loos *et al.*, 2014). However, such a massive restructuring of the global food system might be more than we can muster in the time we have available to us. If it is, then there will probably need to be a massive increase in food production, and some of this increase will probably be justifiable, in terms of meeting development goals, such as hunger reduction (MEA, 2005). However, a compromise will need to be found between the benefits that such an increase in food production could confer on the global food system and the costs that it could impose on local and global agro-ecological systems ("agroecosystems").

The search for compromise between food production and other ecosystem services

Producing more food will probably be a harder "row to hoe" in 2050 than it was in 2005, for three reasons. Firstly, food production will increasingly come into competition with other demands on energy, land, and water, such as biofuel production and urban expansion (Fischer *et al.*, 2011). It is less efficient to use energy, land, and water to produce feed for dairy and meat animals (feed which needs to be metabolically converted by these animals into food for humans, at a loss of energy) than it is to use these resources to produce food for humans (Gerbens-Leenes *et al.*, 2002; Pimentel & Pimentel, 2003). Thus, the competition for these resources will get increasingly worse as demand for dairy and meat increases. Secondly, climate change will have increasingly severe impacts on crop yields. For example, by 2050, the yield of irrigated wheat may have decreased by 21–34% in developing countries (compared to the year 2000), as a result of climate change (Nelson *et al.*, 2009). Thirdly, across the world, critical thresholds in the loss of natural habitats will increasingly be crossed.

This third process takes takes place as agriculture is expanded and intensified (Gibbs *et al.*, 2010), and it potentially has negative feedback on food production, as the "ecosystem services" that support and regulate crop yields are lost (Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011). Ecosystem services, such as crop pollination and pest regulation, are functions of ecosystems that serve the needs of humans (Daily, 1997). This thesis focuses on crop pollination and pest regulation (specifically, the biological control of crop pests by their natural enemies), because these ecosystem services constitute a vital connection between food production and biodiversity conservation. About two thirds of crop species are pollinated by animals (Klein *et al.*, 2007), and about one third of crop production is lost to crop pests (Oerke, 2006). Each year, crop pollination and pest regulation are worth billions of dollars in the United States and hundreds of billions of dollars worldwide (Pimentel *et al.*, 1997; Losey & Vaughan, 2006). As natural habitats in agricultural landscapes are lost, crop-pollination and pest-regulation services are also lost, because pollinators and natural enemies depend on natural habitats (or "semi-natural" habitats or "non-crop" habitats) as sources of food and other resources (reviewed in Chapter 2). Critical thresholds in the loss of these habitats are being crossed, beyond which these natural inputs to crop production—ecosystem services—will increasingly have to be replaced, at outlandish costs, by artificial inputs, such as the hand pollination of fruit crops (Allsopp *et al.*, 2008).

The research in this thesis is part of a search for compromise between ecosystem services—compromise between food production and biodiversity conservation, and compromise between crop pollination and pest regulation. Finding a compromise between food production and biodiversity conservation has often been framed as a debate between “land sharing” (“extensive” agriculture that is wildlife-friendly) and “land sparing” (“intensive” agriculture that is less wildlife-friendly but also less extensive) as methods of growing the most food while doing the least damage to nature (Waggoner, 1995; Green *et al.*, 2005; Phalan *et al.*, 2011). In this debate, the intensification of agriculture is seen as potentially beneficial to nature, if it allows for the sparing of more land for nature (Ewers *et al.*, 2009). However, there has also been a debate about whether or not intensification can ever be sustainable (Loos *et al.*, 2014), and “sustainable intensification” has been called an oxymoron (Marsden, 2010). One way in which agricultural intensification could become more sustainable is in the form of “ecological” intensification—the “harnessing” of ecosystem services to increase crop yields (Bommarco *et al.*, 2013). In this thesis, crop pollination and pest regulation are seen as ecosystem services that could contribute to ecological intensification, and thereby they could contribute to the resolution of conflicts between food production and biodiversity conservation (Chapter 3).

In the Twentieth Century, increases in food production were brought about by both “intensive” agriculture (producing more food on the same amount of land) and “extensive” agriculture (producing more food on more land). About 1.77 billion tonnes of food and fodder crops were produced in 1961, and about 4.89 billion tonnes were produced in 2010 (FAO, 2012) [the above numbers, and those below, were based on data from the FAOSTAT database, which is maintained by the Food and Agriculture Organization of the United Nations (FAO, 2012), and data were used on food and fodder crops, but not fiber crops, for which FAOSTAT had data for the 50 years from 1961 to 2010, but data on cassava leaves, kiwi fruit, pome fruit, popcorn, and triticale were not included in this calculation, because records for these crops began after 1961, or ended before 2010]. Thus, in the fifty years from 1961 to 2010, the production of food and fodder crops increased by about 176%, but the land on which these crops were produced increased by only about 12% (FAO, 2012). In other words, the “intensification” of agriculture contributed much more to the increase in crop production than did the “extensification” of agriculture. It has been suggested that extensification could contribute about 10% of the increase in food production that could be needed by 2050 (assuming a productionist pathway to food security), whereas intensification could contribute about 90% (Bruinsma, 2009).

The intensification of agriculture in the Twentieth Century was unsustainable (Pimentel & Pimentel, 2008). It was based on “perverse” subsidies, unsustainable inputs (such as inorganic fertilizer, synthetic pesticide, and irrigation water), and unsustainable outputs (such as not having to pay for the “externalities” of food production, such as the pollution of air and water, and the loss of biodiversity) (Myers, 1998; Tilman *et al.*, 2002). In the Twentieth Century, the loss of natural habitat, as a result of agricultural expansion and intensification, was the leading cause of biodiversity loss worldwide, and it will probably continue to be the leading cause in the Twenty-First Century (Sala *et al.*, 2000;

Gibbs *et al.*, 2010; Balmford *et al.*, 2012), unless there are massive changes in the food production system. Therefore, it is imperative that agricultural intensification in the Twenty-First Century should be “sustainable” intensification—and that means an increase in yields, but it also means the conservation of agricultural inputs (such as fertilizer and water) and the conservation of biodiversity and ecosystem services (Pretty, 1997; The Royal Society, 2009; Foresight, 2011).

The sustainable intensification of agriculture in sub-Saharan Africa

Food production has become a global industry, and global food security is complicated by the exportation and importation of food, and also by the “grabbing” of agricultural land (in which one nation grows its own food on the agricultural land of another nation) (Lambin & Meyfroidt, 2011). Therefore, food policy has also had to become global. However, the goal of food policy should not only be food security, which has been defined as a state that “exists when all people at all times have physical, social and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life” (FAO, 2009). The goal of food policy should also be food sovereignty, which could be defined as the local governance of food security (Loos *et al.*, 2014). Although this thesis began in the context of UK food policy, much of the research has focused on, and has taken place in, sub-Saharan Africa, in the context of both food security and food sovereignty, for the following reasons.

Growth in food production has been lower per person in Africa than it has on any other continent, since the FAO records began in 1961 (Pretty *et al.*, 2011). In 2000, sub-Saharan Africans consumed only about 64% of the calories that were consumed per person in industrial countries (FAO, 2006), and in 2005 they consumed only about 17% of the recommended daily amount of animal protein (FAO, 2011). From 2000 to 2050, the population of sub-Saharan Africa is predicted to grow by about 193% to about 1.96 billion people (UN, 2011, medium variant), calorie consumption is predicted to increase by about 29% per person, and meat and dairy consumption are predicted to increase by about 89% and 34% per person (FAO, 2006). These increases are greater than those predicted for the world as whole, any yet a greater percentage of the population in sub-Saharan Africa is predicted to be undernourished in 2050 than in any other developing region (FAO, 2006). For research on food security and food sovereignty, sub-Saharan Africa is the place to be.

Intensification—specifically, “sustainable” intensification—has been suggested as one solution to the problem of food insecurity in sub-Saharan Africa (Sanchez, 2010; Pretty *et al.*, 2011). However, expansion will probably make a greater contribution to the increase in food production in sub-Saharan Africa (about 25% of the increase) than it will worldwide (about 10% of the increase) (Bruinsma, 2009). Therefore, the increase in food production will probably cause a greater loss of natural habitat in sub-Saharan Africa than it will worldwide, and the increase in food production in sub-Saharan Africa will need to be reconciled with biodiversity conservation and other ecosystem services that are provided by natural habitats, such as carbon storage, water catchment, crop pollination, and pest regulation (Daily, 1997; MEA, 2005; Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011). Furthermore, the impacts of climate change on crop productivity could be especially severe in sub-Saharan Africa. For example, a decrease of 19% in maize yield (*Zea mays*) and a decrease of 47% in bean yield (*Phaseolus* spp.) is predicted for East Africa, if there is an increase of 5 degrees Celsius (C) in mean temperature—an increase that could reasonably be expected to take place by 2090 (Thornton *et al.*, 2011). For research on the conflicts between food production, biodiversity conservation, and other ecosystem services (Chapter 3), in the context of changes in climate and changes in land use (Chapters 4 and 5), sub-Saharan Africa is also the place to be.

Kenya and the Taita Hills

In Kenya, 3.2 million tonnes (Mt) of maize were produced in 2010, and maize was the top crop in Kenya that year, in terms of biomass (FAO, 2012). Maize was also the top crop worldwide (840 Mt), whereas rice was second from the top (696 Mt), and wheat was third (654 million Mt) (FAO *et al.*, 2012). In Kenya, from 1961–2010, maize yield increased by 28%, from 1.25 to 1.60 tonnes per hectare (t / ha). In other words, there was an intensification of maize production in Kenya. However, maize yield increased by less in Kenya than it did worldwide, from 1961–2010 (Figure 1.1). Moreover, Kenyan maize yield increased at a slower rate than did the area of land on which maize was grown, whereas worldwide maize yield increased at a faster rate than did the area of land on which maize was grown (Figure 1.2). Furthermore, in most of Kenya, maize yield is not yet biophysically limited in terms of its “agro-climatic potential” (IIASA/FAO, 2012) (Figure 1.3). Maize is a staple crop, but it is not the only crop that is grown in Kenya, and it is used here only to make the point that the trend in Kenyan agriculture has been toward extensification, as opposed to intensification (by comparison to agriculture worldwide), and therefore the *de facto* position of conservation in Kenyan agriculture could be closer to land sharing (wildlife-friendly farming, but also human-wildlife conflict—see below) than it is to land sparing, and there could be substantial potential for agricultural intensification in Kenya. Could it be ecological intensification? Would it do less damage to Kenyan wildlife than would the further expansion of Kenyan agriculture, which is already extensive? Would the loss of biodiversity in Kenyan agroecosystems generate negative feedbacks for food production, or would ecosystem services in Kenyan agroecosystems be resilient to low levels of biodiversity loss? These are some of the questions that framed the research in this thesis.

In this thesis, the research on pollinators and natural enemies in Chapters 4 and 5 took place in the Taita Hills, in Kenya. The Taita Hills are in Southeast Kenya, east of Mount Kilimanjaro, and they are surrounded by Tsavo East and Tsavo West National Parks (see Figure 4.1 in Chapter 4 for maps, and Figures 1.4–1.6 in this chapter for photographs). Smallholder agriculture is widespread throughout the Taita Hills, and the mosaic of agricultural and natural habitats, which extends from the lowlands of the Taita Hills to the coast, was tentatively identified as a global hotspot of conflict between agriculture and nature (Chapter 3). The resolution of such “conservation conflict” (Balmford *et al.*, 2001; Redpath *et al.*, 2013; Baudron & Giller, 2014) will need to be based on an understanding of ecosystem services, ecosystem disservices, and the matrix of crop and non-crop habitats in these agricultural landscapes—landscapes which buffer the National Parks, and which suffer from the raiding of crops by elephants (*Loxodonta africana*) and the killing of livestock by lions (*Panthera leo*) (Patterson *et al.*, 2004), among other ecosystem disservices.

Tsavo has a history of human-wildlife conflict. When the railroad was cut through Tsavo, at the end of the Nineteenth Century, many of the railroad workers were killed and eaten by lions (Kerbis Peterhans & Gnoske, 2001). The “Man-Eaters of Tsavo” are symbols of conservation conflict, which is the focus of Chapter 3, but they are also symbols of another focus of this thesis—the effects of biodiversity loss on ecosystem function, as a result of habitat loss and climate change (Chapters 2, 4, and 5). It was partly as a result of such changes in the Tsavo ecosystem that these lions leaped into history. Kerbis Peterhans & Gnoske (2001) tell the story in compelling detail—so compelling that their publication, in a scientific journal, was on sale to the general public in the gift shop of the Field Museum (Chicago, USA), when I went there to see the skins of the Man-Eaters on display. A brief retelling of the tale will serve as a quick introduction to the greater Tsavo ecosystem, in which the research in Chapters 4 and 5 took place.

Firstly, there had been an outbreak of disease (rinderpest) among the cattle (*Bos taurus*) and buffalo (*Syncerus caffer*), upon which the lions would have depended as their “typical” prey species (a loss of biomass). Secondly, most man-eating incidents in Tsavo take place in the wet seasons, when the typical prey species are dispersed in the dense woody vegetation (not concentrated along rivers or at water holes), and therefore they are difficult to hunt (but season may or may not have affected *the* Man-Eaters of Tsavo). Thirdly, ivory hunters had killed so many elephants in Tsavo that the remaining elephants could not knock over and eat enough of the woody vegetation to maintain a lot of open grassland vegetation, upon which the typical prey species and other herds of grazing animals would have depended. In turn, the Man-Eaters could not have depended upon these herds of grazers as prey, and instead they used the dense woody vegetation as cover for hunting humans. Thus, because of changes in habitat (successional changes in vegetation, from open grassland to closed woodland), changes in climate (seasonal dispersal of typical prey species and seasonal changes in vegetation), and an outbreak of disease (loss of biomass), the predators switched to human prey (change in function).

Human-wildlife conflict continues to be a problem in the Tsavo ecosystem, in the form of crop-raiding elephants and livestock-eating lions (Patterson *et al.*, 2004; Kioko *et al.*, 2006). It is against this backdrop of ecosystem “disservices” that research on ecosystem services in the Tsavo ecosystem has a role to play in the resolution of conservation conflict. In North America and Western Europe, natural habitats in agricultural landscapes are sources of beneficial species, such as pollinators and natural enemies (Chapter 2), and these habitats are sources of net gains in crop yields (Ricketts *et al.*, 2004; Morandin & Winston, 2006; Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011). However, not much research on the relationship between natural habitats and ecosystem services in agricultural landscapes has yet been done in sub-Saharan Africa (but see Gemmill-Herren & Ochieng', 2008; Martins & Johnson, 2009; Hagen & Kraemer, 2010; Otieno *et al.*, 2011; Classen *et al.*, 2014). Therefore, the balance of evidence thus far might be seen as proof that natural habitats in sub-Saharan Africa are sources of net losses in crop yields, by means of ecosystem-disservice providers (such as elephants and lions), instead of being sources of net gains, by means of ecosystem-service providers (such as bees and wasps). Thus, much more research is needed on ecosystem-service providers and the balance between services and disservices in sub-Saharan Africa.

Crop pollination and pest regulation

Honey bees (*Apis mellifera*) are among the most familiar of ecosystem-service providers. For many years, hives of honey bees have been intensively managed to pollinate crops. For example, hives have been moved on the backs of trucks from the South of the United States, where they overwinter, to the West, where they pollinate almonds in early spring, and then to the Northeast, where they pollinate apples, blueberries, and cranberries in late spring and summer (Danka *et al.*, 2012). However, the pollination services of these intensively-managed honey bees may no longer be dependable or sustainable. Catastrophic losses of honey bees ("colony collapse disorder"), as well as losses of wild bees and other wild pollinators, losses of natural habitats, changes in climate, and spatial and temporal mismatches between crops and pollinators have all been seen as signs of an impending "pollination crisis" in crop production (Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998; Potts *et al.*, 2010).

Neonicotinoid pesticides have recently been implicated in colony collapse disorder, and therefore three of these neonicotinoids (clothianidin, imidacloprid, and thiamethoxam) have recently been banned in some parts of the European Union, in order to conserve pollinators (Gross, 2013). Pesticide usage is only one example of the many management actions that have impacts not only on pollinators but also on pests and natural enemies of pests. Therefore, it has been suggested that crop pollination and pest regulation should be jointly managed, as two components of one unified system for the ecological intensification of agriculture (Kremen *et al.*, 2007; Isaacs *et al.*, 2009; Bommarco *et al.*, 2013). The need for joint management could be especially vital to crops that depend on both pollination and pest regulation, because there can be interactions between these ecosystem services (Lundin *et al.*, 2012), and thus a decrease in either pollination or pest regulation could lead to a non-linear decrease in crop yield.

Could pollinators and natural enemies be jointly managed and, if so, how could they be jointly managed? These questions are addressed in Chapters 2, 4, and 5. It is possible that both pollinators and natural enemies would benefit from the conservation of natural habitats in agricultural landscapes (Chapter 2). However, it is not known whether or not this is the case for specific combinations of pollinators and natural enemies, because pollinators and natural enemies have only just begun to be simultaneously studied in the field. Moreover, it is not known whether or not the relationships between pollinators, natural enemies, and natural habitats will change with climate change. Therefore, in Chapter 4, pollinators and natural enemies were simultaneously studied on two environmental gradients in the Taita Hills—a habitat gradient and a climate gradient.

It is also possible that some species of pollinators and natural enemies would benefit from the provision of supplemental nesting sites (*e.g.*, Harris, 1994; Wearing & Harris, 2005). Nesting sites could be indirectly supplied to pollinators and natural enemies, through the conservation of natural habitats in agricultural landscapes (Chapter 2), but they could also be supplied directly, just as nesting boxes are supplied to birds. Some species of bees (crop pollinators) and predatory wasps (natural enemies of crop pests) nest in natural cavities, such as hollow stems, and it is possible to use artificial cavities ("trap nests") to study these bees and wasps (Krombein, 1967). The fact that these bees and wasps will nest in artificial cavities also means that it might be possible to develop them as commercially managed pollinators or natural enemies (*e.g.*, Bosch & Kemp, 2002), and indeed there are already several species of cavity-nesting bees that are commercially managed as pollinators (*e.g.*, Bosch & Kemp, 2001; Bosch *et al.*, 2008; Pitts-Singer, 2008; Pitts-Singer & Cane, 2011). The study of trap-nesting bees and wasps also gives general insight into life history and ecology, because it literally gives insight into the "home life" of these species—a glimpse of what they feed their young and how they decorate the nursery, as it were. Thus, trap nesting is potentially a useful tool for establishing connections between natural enemies and their prey or between pollinators and their plants (if the contents of the nest, with which they feed their young, can be identified). These are some of the reasons that trap nests were used to simultaneously study pollinators and natural enemies in the Taita Hills (Chapters 4–5).

Overview of the research

Set against this background of food insecurity and conflict between agriculture and nature, the research in this thesis is presented as part of a search for compromise between ecosystem services—food production, biodiversity conservation, crop pollination, and pest regulation—and part of a search for a resolution to conservation conflicts. A synopsis of the roles that are played by each of the research chapters (Chapters 2–5), is given in the following sections.

Chapter 2

How could we manage agricultural landscapes to benefit both both pollinators and natural enemies? Would they have similar responses to habitat management on local or landscape scales? Pollinators and natural enemies have only just begun to be simultaneously studied in the field, and therefore this chapter addresses these questions by comparing similar studies from these two separate fields of research. Both a qualitative synthesis (a literature review) and a quantitative synthesis (a meta-analysis) are presented. It is suggested that habitat management might benefit some groups of pollinators and natural enemies, such as bees and spiders, but it might not benefit other groups, such as predatory beetles and parasitic wasps, and it is concluded that specific combinations of pollinators and natural enemies need to be simultaneously studied in the field (addressed in Chapters 4–5).

Chapter 3

Where could agriculture do the greatest damage to nature, and where could it do the least? Where could the conservation of natural habitats in agricultural landscapes have the greatest benefit, and where the least? In this chapter, geospatial data sets and spatial scan statistics are used to address these questions. A global hotspot analysis is presented, as is a conceptual framework for thinking about systematic conservation planning in agricultural landscapes. It is suggested that some of the hottest hotspots of conservation conflict are in East Africa, including the Taita Hills, and it is also suggested that ecological intensification could have a part to play in the resolution of conservation conflict. Together, Chapters 2–3 are a justification for the simultaneous studies of pollinators and natural enemies in the Taita Hills (Chapters 4–5), as part of the ecological intensification of agriculture and the resolution of conservation conflict.

Chapter 4

Could there be specific combinations of bees and wasps that would have similar responses to environmental gradients, and could these species therefore be jointly managed as crop pollinators and natural enemies of crop pests? In this chapter, trap nests are used to compare and contrast the distributions of a pollinator (a leaf-cutting bee) and a natural enemy (a caterpillar-hunting wasp) on gradients of climate (elevation) and habitat (woody vegetation) in the Taita Hills. It is suggested that these species could probably not be jointly managed, if confronted by changes in climate, because they seem to have opposite responses to temperature on the elevation gradient. However, it is also acknowledged that this temperature gradient is confounded by other aspects of elevation. Therefore, Chapter 4 is a justification for the study, in Chapter 5, of the effects of temperature on these two species, in isolation from these other aspects of elevation.

Chapter 5

Could there be a mechanistic connection between temperature and body size, development time, or larval survival in the leaf-cutting bee or the caterpillar-hunting wasp, and would this explain their opposite distributions on the elevation gradient? In this chapter, a temperature gradient is generated in the lab and used to incubate the larvae of the two trap-nesting species, whose nests were collected from the elevation gradient. It is suggested that their opposite distributions on the elevation gradient are supported, but not proved, by their different responses to temperature.

Together, Chapters 2–5 are a search for compromise between food production, biodiversity conservation, crop pollination, and pest regulation, in the context of changes in climate and changes in land use. This research spans many scales of biodiversity, from global communities (the meta-analysis and hotspot analysis of Chapters 2–3), to local communities (Chapter 4), to individuals within species (Chapter 5). There are no simple solutions to the complex conflicts between these ecosystem services, but it is hoped that this research will help to bridge some small gaps in our knowledge of these ecosystem services and the creatures that provide us with these ecosystem services.

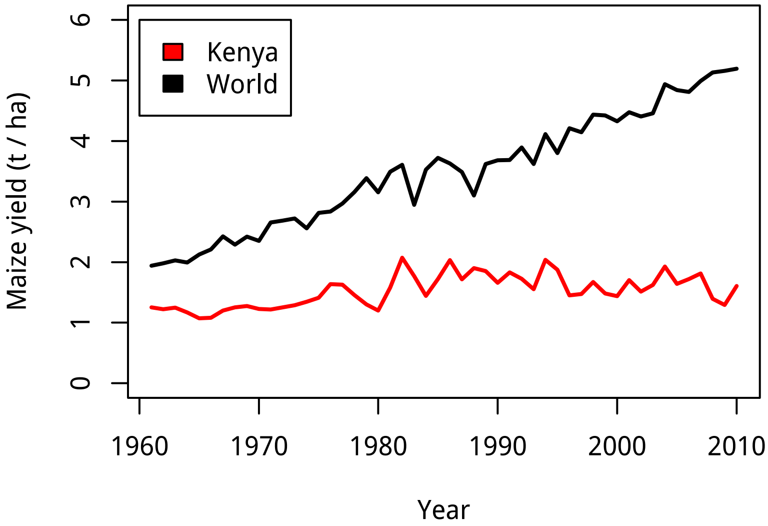


Figure 1.1 Comparison of Kenyan and worldwide maize yields, from 1961–2010 (data from the FAO, 2012).

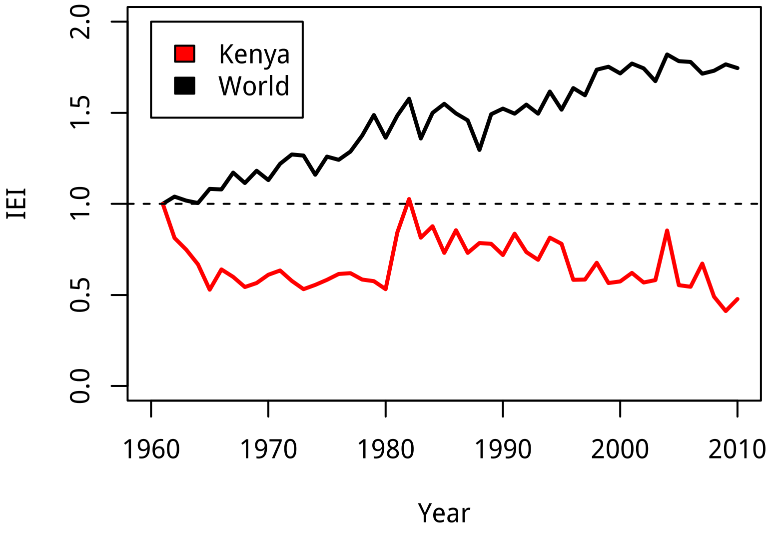


Figure 1.2 Relative changes in the intensification and extensification of maize production in Kenya and worldwide: "extensification" (E) was calculated as the change in the area of land on which maize was grown since 1961, measured in hectares (ha), where $E = \text{ha}_{year} / \text{ha}_{1961}$ from 1961–2010, and "intensification" (I) was calculated as the change in maize yield since 1961, measured in tonnes per hectare (t / ha), where $I = (\text{t} / \text{ha})_{year} / (\text{t} / \text{ha})_{1961}$ for the years from 1961–2010 (data from the FAO, 2012). The index that is suggested here—the "intensification-extensification index" (IEI)—was calculated as I / E. For any given year (1962–2010), an IEI of 1 (indicated by the horizontal line) means that by that year there had been equal changes in intensification and extensification, in comparison with 1961 (*e.g.*, a 10% increase in intensification and a 10% increase in extensification = 10% / 10% = 1). Kenyan maize yield (intensification) increased at a slower rate than did the area of land (extensification) on which maize was grown (IEI < 1), but worldwide maize yield increased at a faster rate than did the area of land on which maize was grown (IEI > 1).

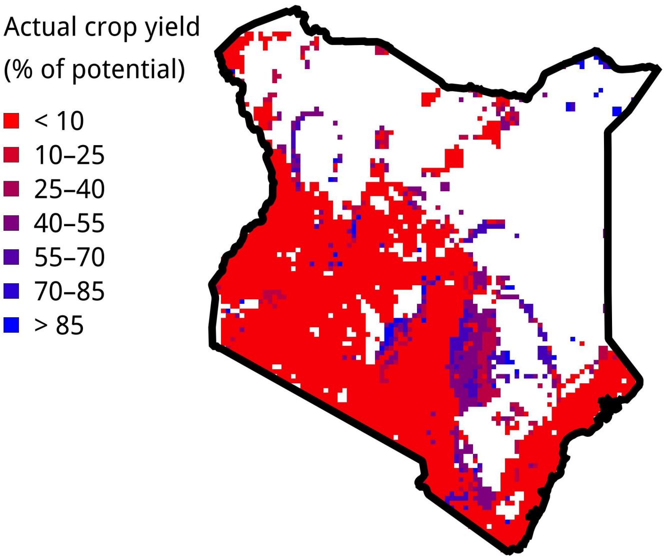


Figure 1.3 Agro-climatic potential of crop production in Kenya, based on data from the Global Agro-Ecological Zones (GAEZ) database (IIASA/FAO, 2012; see Chapter 3). Actual yield is shown as a percentage of potential yield for a combination of “main crops” (including maize, rice, and wheat), provided that “high inputs” of fertilizer and water are used (see GAEZ model documentation in Fischer *et al.*, 2012). High inputs might or might not be available or sustainable, but this high agro-climatic potential could nevertheless be a powerful driver of change in agricultural land use, if demand for food is high, and if there is therefore a large incentive to find sources of fertilizer and water. An abundant source of ground water was recently found in Turkana, in the semi-arid Northwest of Kenya (Marshall, 2013), and this water could be used, sustainably or unsustainably, to intensify crop production.

Figure 1.4 The highlands of the Taita Hills: terraced agricultural land, below the slopes of a hill called Wesu. These trees are mostly non-native plantation species (*e.g.*, *Eucalyptus*), but there are also fragments of native cloud forest on some of the Taita Hills (*e.g.*, Aerts *et al.*, 2011). The highlands of the Taita Hills are relatively cooler and wetter than the lowlands (Chapters 4–5).

Figure 1.5 The lowlands of the Taita Hills: the mist shown here was photographed early in the morning, and it is much hotter and drier in the lowlands than it might appear to be in this photograph (Chapters 4–5).

Figure 1.6 Tsavo West National Park: the greater Tsavo ecosystem surrounds the Taita Hills and is a source of conservation conflict in the area (Chapter 3). The changes in climate on the elevation gradient in the Taita Hills (Chapters 4–5) can be seen by comparing the hot and dry lowlands, shown here, with cool and wet highlands, shown in Figure 1.4.

Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops

Introduction

Agricultural landscapes could and should be managed not only for food production but also for other ecosystem services (MEA, 2005; Foresight, 2011). Both pollination and pest-control services can contribute to crop production, and the economic values of these ecosystem services can be incentives to conserve the habitats and species that provide these services (*e.g.*, Morandin & Winston, 2006). For example, the value of the pollination service that a forest provided to a nearby coffee farm, by supporting populations of wild pollinators, was estimated to be higher than the value of the forested land itself, and this was seen as an incentive to conserve the forest (Ricketts *et al.*, 2004). However, there can also be tradeoffs between ecosystem services (Bennett *et al.*, 2009; Raudsepp-Hearne *et al.*, 2010), such as the tradeoffs between intensive food production and biodiversity conservation (Benton *et al.*, 2003; Green *et al.*, 2005; Gabriel *et al.*, 2010; Kleijn *et al.*, 2011; and see Chapter 3 for hotspots of conflict between food production and biodiversity conservation). To manage agroecosystems for multiple ecosystem services, we need to know whether the management of one service has positive, negative, or no effects on other services.

The biotic pollination of crops (hereafter, “pollination”) and the conservation biological control of crop pests (hereafter, “pest control” or “pest regulation”) are ecosystem services that regulate crop production (MEA, 2005). It has been suggested that the management of pollination and pest-control services might be compatible (*e.g.*, Gurr *et al.*, 2003; Kremen & Chaplin-Kramer, 2007; Fiedler *et al.*, 2008; Stallman, 2011), but this compatibility has not been properly investigated. We suggest that the mechanisms and the interactions of pollination and pest-control services should be quantified, in terms of their effects on crop productivity, and modelled, in response to the management of agroecosystems. We do not yet have quantitative data on the interactions between these ecosystem services. However, we do have quantitative data on the distributions of pollinators and natural enemies, in response to the structure of agroecosystems. These beneficial arthropods may or may not be good predictors of the ecosystem services that they provide, but the data that we have on these arthropods are the best that we have at this point.

We compare the abundance and richness of pollinators and natural enemies, in response to the compositional complexity of agroecosystems, and we present a quantitative meta-analysis of previously published data. We begin with a qualitative synthesis of similarities and differences between pollinators and natural enemies, and we end with the conclusion that both bees (pollinators) and spiders (natural enemies) are positively affected by the complexity of agroecosystems, at both local and landscape scales. We also note that complexity might have stronger effects on the richness than the abundance of beneficial arthropods, and therefore it might have stronger effects on the stability than the magnitude of arthropod-mediated ecosystem services. Only recently have pollinators and natural enemies been studied simultaneously in the field (Otieno *et al.*, 2011; and see Chapter 4), and so we cannot yet conclude that they do not have incompatible responses to the management of agroecosystems or that they do not have negative interactions (see Chapter 4 for incompatible responses). Therefore, we identify the interactions between pollinators and natural enemies and their interacting effects on crop productivity as gaps in our knowledge, and we suggest some future research to plug these gaps. Nevertheless, our present use of meta-analysis enables us to make some tentative, quantitative comparisons between these two groups of beneficial arthropods, which have only begun to be compared in the field.

Qualitative synthesis: literature review

Ecosystem-service providers as indicators of ecosystem-service provision

Both pollination and pest-control services can contribute to the yield and quality of crops. The mechanistic links between pollinators, pollination, and crop productivity have been studied in manipulative experiments, in which the yield or quality of "control" crops are compared to the yield or quality of "treatment" crops (pollinators are supplemented or excluded, or the treatment crops are pollinated by hand) (Greenleaf & Kremen, 2006a; Gemmill-Herren & Ochieng', 2008; Isaacs & Kirk, 2010; Vaissière *et al.*, 2011). Likewise, the mechanistic links between natural enemies, pest control, and crop productivity have also been studied in manipulative experiments (the natural enemies of pests are supplemented or excluded, without excluding the pests) (Menalled *et al.*, 1999; Symondson *et al.*, 2002; Gardiner *et al.*, 2009a). In observational experiments (in contrast to manipulative experiments), pollinators or natural enemies have been sampled in different fields or farms and used as indicators of ecosystem service provision.

In statistical models, the abundance and richness of pollinators can be significant predictors of pollination services (*e.g.*, Greenleaf & Kremen, 2006b; Morandin & Winston, 2006; Hoehn *et al.*, 2008; Carvalheiro *et al.*, 2010; Isaacs & Kirk, 2010; Taki *et al.*, 2010). Likewise, the abundance and richness of natural enemies can be significant predictors of pest-control services (*e.g.*, Symondson *et al.*, 2002; Cardinale *et al.*, 2003; Gardiner *et al.*, 2009a; Letourneau *et al.*, 2009). This is an important link between these services—both pollination and pest control can be provided by beneficial arthropods, and beneficial arthropods can be used as significant predictors of ecosystem-service provision. Isaacs *et al.* (2009) referred to both pollination and pest control as "arthropod-mediated ecosystem services" (AMES), and Kremen *et al.* (2007) suggested that, as "mobile-agent-based ecosystem services" (MABES), both pollination and pest control could be incorporated into the same conceptual framework.

However, the abundance and richness of beneficial arthropods may or may not be good indicators of pollination and pest-control services, because the relationships between biodiversity and ecosystem services are not well understood. For example, a high diversity of natural enemies might be related to a low level of pest control, if some of these natural enemies were to prey on others ["intraguild predation" (Rosenheim *et al.*, 1995)]. We know of no evidence for negative biodiversity-function relationships involving pollinators, but competition between pollinators, because of high diversity, might in theory cause a decrease in the level of service provision. For example, an efficient pollinator might be excluded from a species of flower by an efficient competitor that is an inefficient pollinator. In contrast, a high diversity of pollinators or natural enemies could be related to a high level of pollination or pest control, if some of these pollinators or natural enemies were to cause an increase in the level of service provision by others ["facilitation" (Losey & Denno, 1998; Greenleaf & Kremen, 2006b)]. However, if a high level of service provision is mostly related to a high abundance of one efficient species (*e.g.*, honey bees or classical biological control agents), then diversity *per se* might not be related to service provision (Straub & Snyder, 2006).

Whatever the relationships between biodiversity and ecosystem services turn out to be, the factors that affect the distribution of pollinators and natural enemies in agroecosystems could in turn affect the ecosystem services that they provide to crops. Therefore, we should underpin our management of pollination and pest-control services with an understanding of these factors, if only as a step towards a mechanistic model of service provision (Kremen, 2005; Kremen & Ostfeld, 2005; Letourneau & Bothwell, 2008). However, we should not confuse the service providers with the services themselves. Hereafter, we focus on potential pollinators of crops (hereafter, "pollinators") and potential natural enemies of crop pests (hereafter, "natural enemies"), and we refer to them in general as "beneficial arthropods" or potential "ecosystem-service providers" (ESPs) (Luck *et al.*, 2009).

Management of ecosystem-service providers

In many studies, pollinators are insects, and bees are thought to be the most important pollinators of animal-pollinated crops (Free, 1993; Delaplane & Mayer, 2000; Klein *et al.*, 2007). Birds, bats, butterflies, moths, flies, beetles, ants, and several other taxa have also been identified as pollinators of crops (Westerkamp & Gottsberger, 2000; Blanche & Cunningham, 2005; Martins & Johnson, 2009; Carvalheiro *et al.*, 2010), but herein we focus on bees. Studies of pollination as an ecosystem service have often classified bees into two groups—"managed" or "domesticated" bees (*e.g.*, the honey bee, *Apis mellifera*), and "unmanaged" or "wild" bees (*e.g.*, bumble bees, *Bombus* species) (*e.g.*, Winfree *et al.*, 2009; Isaacs & Kirk, 2010). Parasitic and predatory wasps, beetles, flies, spiders, and several other taxa have been identified as natural enemies of crop pests (Jervis, 2007). Like pollinators, we could classify the laboratory-reared and mass-released populations of natural enemies as "managed" [*cf.* "classical biological control", "inoculation biological control", and "inundation biological control" (Eilenberg *et al.*, 2001)], and we could classify the native or naturalized populations as "unmanaged" (*cf.* "conservation biological control").

However, these distinctions between "managed" and "unmanaged" arthropods will become increasingly unclear as more and more components of agroecosystems become managed (Palmer *et al.*, 2004; Koh *et al.*, 2009; Steingröver *et al.*, 2010). For example, manmade nesting sites and "bee pastures" are forms of management for otherwise unmanaged pollinators (Bohart, 1972; Banaszak, 1992, 1996; Delaplane & Mayer, 2000), and so are "beetle banks" and other forms of habitat management for otherwise unmanaged natural enemies (Barbosa, 1998; Landis *et al.*, 2000). Therefore, we will classify the management of pollinators and natural enemies as either "indirect" ("*in situ*") or "direct" ("*ex situ*").

Direct management could include commercial colonies of bees and classical, inoculative, and inundative releases of natural enemies, maintained *ex situ* and supplied to agroecosystems. Indirect management could include all native or naturalized populations, sustained *in situ*. These terms are readily relatable to the *in situ* and *ex situ* conservation of endangered species, and indeed *in situ* management of ESPs could be considered a form of conservation (conservation biological control and what we could call "conservation pollination"). Hereafter, we focus on the indirect (*in situ*) management of ESPs.

Requirements of ecosystem-service providers

An increase in the intensity of farming on existing farmland, and an increase in the extent of farmland, has caused a decrease in the biodiversity of agroecosystems, by means of a decrease in the compositional complexity of agroecosystems, at local and landscape scales (Benton *et al.*, 2003; Tscharntke *et al.*, 2005; Kleijn *et al.*, 2011). Losses have been reported for pollinators (Ricketts *et al.*, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010) and also for natural enemies (Attwood *et al.*, 2008; Chaplin-Kramer *et al.*, 2011; Letourneau *et al.*, 2011). Compositionally complex agroecosystems are defined as having a high diversity of habitats, not only fields of crops, but also non-crop habitats (*e.g.*, floral margins, fallows, meadows, grassland, and woodland) [*cf.* "compositional heterogeneity" (Fahrig *et al.*, 2011)], and therefore they may offer a high diversity of food and nesting resources to ESPs—resources in both crop and non-crop habitats. Compositional complexity (hereafter, "complexity") is therefore an indirect measure of the diversity of resources that agroecosystems offer to ESPs [*cf.* "indirect resources" (Roulston & Goodell, 2011) and "functional landscape heterogeneity" (Fahrig *et al.*, 2011)]. However, we note that there may be differences between habitat diversity and resource diversity, if non-crop habitats provide many resources, and crop habitats provide few, or *vice versa* [see below ("Effects of compositional complexity on ecosystem-service providers")]. Nevertheless, if complexity has positive effects on both pollinators and natural enemies, a mechanistic explanation could be that they have similar requirements for resources, such as floral resources for food [*cf.* "direct resources" (Roulston & Goodell, 2011)], and that these resources might be better supplied by complex rather than simple agroecosystems.

Bees feed on nectar and pollen (Potts *et al.*, 2003; Michener, 2007), and so do some natural enemies (Wäckers & van Rijn, 2005). Food can be provided by crop or non-crop plants (*e.g.*, when crops are not in flower, or if their nectaries are inaccessible or unattractive) (Landis *et al.*, 2000; Fiedler *et al.*, 2008). Isaacs *et al.* (2009) reported that floral area was the most important predictor of floral attractiveness to both pollinators and natural enemies, and they identified species of flowering plants that were attractive to both. However, Wäckers (2004) reported that, of eleven insect-pollinated plant species, only two species were attractive to natural enemies (*i.e.* as well as insect pollinators) and accessible to natural enemies (*i.e.* accessible nectaries). Moreover, Hogg *et al.* (2011) reported that, of nine plant species, the species that was most attractive to hover flies was least attractive to bees. Therefore, we note that pollinators and natural enemies do not necessarily use the same species of flowering plants, even though they do have similar general requirements for floral resources. Nevertheless, a high diversity of flowering plants could have benefits for both pollinators and natural enemies, because a highly diverse community could include floral resources for both. Moreover, if pollinators and natural enemies do use different species of flowering plants, then they are unlikely to compete with each other for floral resources.

Other similar requirements of pollinators and natural enemies could be their requirements for woody plants or undisturbed soils as nests (Michener, 2007; Holzschuh *et al.*, 2009), and their requirements for non-crop habitats as refuges from disturbance, such as mowing, harvesting, tillage, pesticide usage, or changes in seasonal climate (Landis *et al.*, 2000; Backman & Tiainen, 2002; Pywell *et al.*, 2005; Gemmill-Herren & Ochieng', 2008). It is possible that woody habitats, including orchards and vineyards, could be less disturbed by mowing, harvesting, or tillage than would non-woody habitats, including annual crops, and therefore it is possible that the negative effects of oversimplified agroecosystems could be less extreme in woody (or perennial) crops than they would in non-woody (or annual) crops. For example, management that reduced disturbance (organic rather than conventional farming) did not have positive effects on spiders in woody perennial crops (vineyards), despite the fact that it can have positive effects in annual (non-woody) crops (Bruggisser *et al.*, 2010).

Effects of compositional complexity on ecosystem-service providers

We differentiate between complexity at local and landscape scales. These scales are on the same continuum, and they are relative to one another and the resolution of the study system, and therefore we cannot give them universal definitions. However, for the purposes of this synthesis, we define "local complexity" as a measurement of the diversity of plants, within a field of crops or in its margins (*e.g.,* in polycultures, weedy cultures, or floral margins), or a measurement of the distance from a sample of arthropods (*e.g.,* a pan or pitfall trap, or a transect walk), within a relatively species-poor field of crops, to a relatively species-rich field margin (but see our more restricted definition of "local complexity" for the purposes of our meta-analysis, which did not include the diversity of plants within a field of crops). In contrast, we define "landscape complexity" as a measurement of the diversity of habitats (*e.g.*, the proportion of non-crop habitat) within a wider radius that circumscribes an area beyond the boundaries of a field or a farm, or a measurement of the distance from a sample (*e.g.,* a trap or transect), within a field of crops, to non-crop habitat beyond the margin of a field. Whereas local complexity is a measurement of plant diversity (a finer scale), landscape complexity is a measure of habitat diversity (a coarser scale), and whereas local complexity is measured within a field or in its margins (a finer scale), landscape complexity includes the wider agroecosystem, beyond the margins (a coarser scale).

In the context of local complexity, natural enemies can be more abundant in polycultures than they are in monocultures, more abundant in crops that are surrounded by high-diversity rather than low-diversity field margins (Andow, 1991; Letourneau *et al.*, 2011), and more abundant and diverse when they are sampled close to rather than far from field margins (*e.g.*, Miliczky & Horton, 2005; Clough *et al.*, 2007). Likewise, the diversity of plants (*e.g.*, Banaszak, 1996; Albrecht *et al.*, 2007) and the proximity of margins (*e.g.*, Clough *et al.*, 2007; Tuell *et al.*, 2009) can have positive effects on the abundance and diversity of pollinators. However, the effects of local complexity can depend on the size of fields and/or the size (*i.e.* mobility) of ESPs. For example, only smaller ESPs were significantly affected by the proximity (Albrecht *et al.*, 2007) or the diversity (Thomson & Hoffmann, 2010) of the vegetation that surrounded crops, and predatory arthropods were more abundant in medium (16–256 m^2) than in small (< 16 m^2) plots of diverse vegetation (Bommarco & Banks, 2003). The effects of local complexity can also depend on landscape context (Tscharntke *et al.*, 2005, 2012; Batáry *et al.*, 2011; Kleijn *et al.*, 2011).

At landscape scales, complexity can have overall positive effects on the abundance and richness of natural enemies, and it was most predictive when measured within a radius of *ca.* 1500–2200 m (Chaplin-Kramer *et al.*, 2011). Likewise, landscape complexity had positive effects on the flower-visitation rate and richness of pollinators (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011). The most-predictive scales of landscape complexity have not been summarized for bees, but individual studies have reported similar [*e.g.*, 2400 m (Kremen *et al.*, 2004)] or finer scales [*e.g.*, 750 m (Steffan-Dewenter *et al.*, 2002)] than the most-predictive scales for natural enemies. Like local complexity, the effects of landscape complexity, and the scale at which it is most predictive of ESP abundance and/or richness, may depend on the size (*i.e.* mobility) of ESPs, as well as on their resource requirements. For example, small (*i.e.* less mobile) bees responded to landscapes at finer scales than did large (*i.e.* more mobile) bees (Steffan-Dewenter *et al.*, 2002), and habitat loss had a stronger effect on small polylectic bees than large polylectic bees and small oligolectic bees (Bommarco *et al.*, 2010). Likewise, specialist natural enemies responded to landscape complexity at finer scales than did generalists (Chaplin-Kramer *et al.*, 2011). Large wolf spiders with low dispersal abilities were affected by natural habitat at fine scales, but ballooning spiders with high dispersal abilities were affected at coarse scales (Schmidt *et al.*, 2008), and large carabid beetles with low dispersal abilities were affected negatively by the intensification of agricultural landscapes, but small carabid beetles with high dispersal abilities were affected positively (Burel *et al.*, 2004).

Many studies have measured landscape complexity as the proportion of natural or non-crop habitat surrounding a field of crops, but we need to differentiate between the effects of natural or non-crop habitats *per se* and those of landscape complexity. In landscapes with low proportions of crops, high proportions of natural or non-crop habitats could be measurements of landscape simplicity (*i.e.* a low diversity of habitats, but not necessarily a low diversity of floral or other resources, if natural or non-crop habitats have a higher diversity of plants than crop habitats). Such landscapes are structurally simple (on the coarser scale of habitat diversity), but not necessarily functionally simple (on the finer scale of resource availability) (*cf.* Fahrig *et al.*, 2011). Nevertheless, high proportions of natural or non-crop habitat can have negative effects on ESPs in such structurally simple landscapes (*e.g.*, Winfree *et al.*, 2007; Schmidt *et al.*, 2008). Moreover, there could be a threshold, above which the percentage of natural or non-crop habitat does not have a significant effect on ESPs, and this could be as low as 2–5% (Westphal *et al.*, 2003; Winfree *et al.*, 2009). Higher percentages (*ca.* 20–30%) have been suggested as possible targets for the management of ESPs (Banaszak, 1992, 1996; Tscharntke *et al.*, 2005; Morandin & Winston, 2006), but these targets can depend on the scale of management. For example, watermelons were predicted to be adequately pollinated by wild bees when 30% of the land within 1200 m, or 40% of the land within 2400 m, was natural habitat (Kremen *et al.*, 2004).

We have seen that complexity can have different effects at different scales and on different taxa, but it can also have different effects on two different metrics— abundance and richness. For example, local complexity, including the management of weeds within fields of wheat (organic *versus* conventional), explained the abundance but not the richness of spiders within these fields, and landscape complexity, including the percentage of non-crop habitat surrounding these fields, explained the richness of spiders, but it only explained the abundance of spiders in conventionally managed fields (Schmidt *et al.*, 2005). Similarly, in a meta-analysis of spiders, land management had effects on either the abundance or the richness of spiders, but not both (Prieto-Benítez & Méndez, 2011). At local scales, the richness but not the abundance of bees was explained by the availability of floral (food) and woody (nesting) resources, and the abundance but not the richness of bees was explained by the density of the tree canopy and the frequency of fire (Grundel *et al.*, 2010). Similarly, in a meta-analysis of bees, natural habitats had stronger effects on the richness than the flower-visitation rates of bees in crops (Garibaldi *et al.*, 2011).

Quantitative synthesis: meta-analysis

Hypotheses

As we have seen, the effects of complexity on ESPs in crops can depend on many variables, such as the scale at which complexity is measured (local *versus* landscape), the crop in which in an ESP is sampled (woody/annual *versus* non-woody/perennial), the taxon that is sampled (*e.g.*, species with differences in body size and/or mobility), and the metric that is measured (abundance *versus* richness). Because of this variability in the effects of complexity, and also because of the contradictory effects of complexity from study to study (*e.g.*, negative *versus* positive effects of non-crop habitats), we performed a quantitative synthesis, to complement the narrative synthesis that we presented above. We used meta-analysis to compare the effects of complexity, at local and landscape scales, on pollinators and natural enemies.

Meta-analysis has been used to summarize the effects of landscape complexity on pest control (Chaplin-Kramer *et al.*, 2011) and pollination (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) and to summarize the effects of local complexity on pest control (Letourneau *et al.*, 2011) but not on pollination. However, pollinators and natural enemies have not been simultaneously meta-analyzed or quantitatively compared. We analyzed the effects of local and landscape complexity on the abundance and richness of pollinators of crops and natural enemies of crop pests, sampled in fields, orchards, and vineyards of food crops. We hypothesized that (1) effect sizes would be positive, and significantly different from zero, for both pollinators and natural enemies, and that (2) effect sizes might differ by metric (abundance *versus* richness), (3) by scale (local *versus* landscape complexity), (4) by crop habit (woody *versus* non-woody crops), and (5) by taxon (*e.g.*, beetles *versus* spiders, or pollinators *versus* natural enemies). We tested these hypotheses for bees, as potential pollinators, and predatory beetles, spiders, and parasitic wasps, as potential natural enemies.

Methods

Search strategy and inclusion criteria

We limited our search of the *ISI Web of Knowledge* database to the following terms: Topic=bee OR bees OR pollinator* OR ((beetle* OR "hover fl*" OR hoverfl* OR parasitoid* OR spider* OR wasp*) AND ("biological control" OR "pest control" OR "natural enem*")) AND Topic="ecosystem service*" OR ((crop OR crops OR field*) AND (border OR borders OR boundar* OR edge* OR margin OR margins OR perimeter* OR (landscape* AND scale*) OR ("natural habitat*" AND (area* OR distance* OR isolation OR percent*)))) AND Topic=abundance OR abundant OR rich OR richness OR visits OR visitation AND Year Published=2001-2010. In July of 2011, this search resulted in 350 studies (with "lemmatization" off). We acknowledge that this search was not unbiased, nor is that of any meta-analysis, but it is repeatable, and we suggest that meta-analyses should be repeatable. Access to unpublished data from published studies will not necessarily be granted to future meta-analysts, and therefore we limited our search to published studies, and we did not contact authors for unpublished data on published studies.

Studies were vetted by title and abstract, and relevant studies were read and included if they reported (1) the abundance or richness of *in situ* ESPs (bees, predatory beetles, hover flies, spiders, or parasitic wasps), (2) sampled in fields, orchards, or vineyards of food crops (not in the margins), (3) as an effect of local complexity (proximity to, or diversity of, field margins) or landscape complexity [proximity to, diversity of, or proportion of natural or non-crop habitats, or similar metrics from ordinations of landscape variables (*e.g.*, Gardiner *et al.*, 2009a)]. Studies were not included if their experiments were not replicated (*e.g.,* if they compared only one complex landscape with only one simple landscape). Studies that sampled arthropods in meadows or pastures, rather than in fields of food crops, were not included, because meadows or pastures might provide a greater diversity of floral resources than food crops (especially monocultures), but more importantly because we were interested in the direct contributions of ESPs to food, rather than fodder. Studies of small-scale experimental plots were not included if we considered treatments and controls to have been spatially confounded (*i.e.* if they were separated by < 10 m) and if no spatial statistics were reported. Only measurements of richness that were standardized by sampling effort were included, if both standardized and unstandardized measurements were reported. The percentage of pests that were parasitized by wasps was included as a measurement of parasitoid abundance.

Data from these studies were included if they were reported as exact P-values or other statistics (Z, F, t, r, r^2, or χ^2) with the numbers of replicates or degrees of freedom. Data that were not reported as exact statistics were also included by assuming $P = 1$ for data reported as "non-significant" and $P = 0.05$ for data reported as $P < 0.05$ or "significant" ($P = 0.01$ for data reported as $P < 0.01$, etc.). For data reported as "non-significant" ($P > 0.05$), we assumed that the effect of complexity was negative, in opposition to our first hypothesis. Even though these effects are “non-significant” they nonetheless contribute to the combined effect size by adding to it, or subtracting from it, and we cannot know whether an effect is negative or positive, if we have estimated it from a non-significant difference. This is also why we assumed $P = 1$ for “non-significant” data, because it results in an effect size of zero, and therefore it avoids the need for an additional assumption about the direction of the effect (positive or negative), and therefore it is parsimonious. It is also conservative, because it makes the null hypothesis of no effect more likely. However, we also used sensitivity analyses to evaluate the effects of these assumptions, by assuming $P = 0.5$ for “non-significant” data in one set of sensitivity analyses (SA2 and SA3), and $P = 0.1$ in another set (SA1 and SA4), and also by assuming that “non-significant” effects were negative in one set of sensitivity analyses (SA1 and SA2) and positive in another set (SA3 and SA4).

Data were included from relevant variables in statistical models with multiple variables. This is conservative, because the P-values of these variables are overestimates if they are correlated with other variables in these models (Nakagawa & Cuthill, 2007). If a relevant variable was involved in a significant interaction, then we included the P-value for the interaction, because the P-value of the variable itself is not meaningful if the variable is involved in a significant interaction. Data from omnibus tests (*i.e.* F-tests with more than one degree of freedom in the numerator, factors with multiple levels—*e.g.*, near, middle, and far distances from field margins—or interactions between these factors and other terms) were not included, unless a relevant contrast was reported (*e.g.*, between the near and far distances, rather than between all of these distances), or unless we could code a relevant contrast as “significant” ($P = 0.05$) or “non-significant” (*e.g.*, $P = 1$), based on the data that were presented (*e.g.*, in figures with standard error bars).

If studies classified honey bees as “feral” [*i.e. in situ* ESPs—see above (“Management of ecosystem-service providers”)], because there were no manmade hives or beekeepers in their study areas, then we included their data on these honey bees, but we did not include data on directly managed honey bees. Neither did we include aggregated data on “flower visitors” if they included multiple taxa (*e.g.*, bees and wasps). If a single study reported separate data on multiple taxa, then they were all included as separate data points, but only for predefined groups (bees, predatory beetles, hover flies, spiders, or parasitic wasps), because we had hypothesized that there would be differences between these groups. If a single study reported data on multiple subgroups of these predefined groups (*e.g.*, families of spiders), and if data on the group were also reported (*e.g.*, all spiders), then data on the subgroups were not included. Otherwise, data on multiple subgroups (*e.g.*, Linyphiidae and Lycosidae) were averaged, to generate a single effect size and variance for the group (Borenstein *et al.*, 2009), by assuming a perfect correlation ($r = 1$) between the variances of subgroups in the same study. Assuming some correlation between these variances would probably be more realistic, as a compromise between no correlation ($r = 0$) and perfect correlation ($r = 1$). However this would result in smaller variances, and therefore larger weights [see below ("Statistical analysis")], for studies that reported data on multiple subgroups, and we would argue that these subgroup studies should not be given additional weight (a sort of pseudo-replication), especially because we often had reduced, rather than increased, confidence in effects on subgroups that were not reported as exact statistics (*e.g.,* "non-significant") and that therefore required additional assumptions (*e.g.,* $P = 1$, and a negative effect). Likewise, if data from multiple sampling methods (*e.g.*, pitfall traps and suction samples for spiders), multiple predictor variables at a single scale (*e.g.*, margin diversity and margin proximity), or multiple time-points were reported separately, then these were also averaged, to generate a single effect size and variance. If data from multiple scales or statistical models were reported separately, then data from only the most predictive scale or model were included [*e.g.*, scales with the highest r^2 or models with the lowest Akaike Information Criterion (AIC)] (Chaplin-Kramer *et al.*, 2011). Data were included on the abundance and richness of the same taxon, in the same study, since we had hypothesized that there would be differences between these metrics.

Statistical analysis

We calculated effect sizes (Fisher's Z-transformed r (Z_r)) and their conditional variances, by using published formulae (Cooper & Hedges, 1994; Borenstein *et al.*, 2009). We then combined and modelled these effect sizes, weighted by inverse variance, by using mixed-effects models in R, version 2.12.1 (R Development Core Team, 2010), in the *nlme* package (Pinheiro *et al.*, 2010). To account for the non-independence of data reported in the same study (*e.g.,* abundance and richness), we used study as a random effect in all models (Chaplin-Kramer *et al.*, 2011). For each of our data sets (*e.g.*, pollinators only, natural enemies only, spiders only, or landscape complexity only), we fitted minimum adequate models. We started with maximal mixed-effects models that used effect size as the response variable and metric, scale, crop habit, taxon, and their interactions as predictor variables, and then we used backwards stepwise deletion to select minimum adequate models (Crawley, 2007). We used the *metafor* package (Viechtbauer, 2010) to present these models in graphical form (Figures 2.1–2.3). To test for publication bias, we examined funnel plots and conducted correlation tests for funnel-plot asymmetry. We also used chi-squared tests to compare the number of studies in different categories (*e.g.*, studies on pollinators *versus* studies on natural enemies).

The distributions of residuals were not significantly different from normal for any of the minimum adequate models (Shapiro-Wilk normality tests), except for the model of the parasitoids-only data set. However, this was the smallest of the data sets, with only 13 effect sizes, and a histogram of the residuals looked relatively normal, given the small number of data points. With this caveat, we decided to include this model in our results. Where plots of residuals *versus* fixed effects suggested that variances were unequal, we used "varIdent" to specify the variance structure (Zuur *et al.*, 2009; Pinheiro *et al.*, 2010). Therefore, the assumptions of the statistical models are likely to be valid. Funnel plots were not significantly asymmetrical for any of the data sets, except for the data set on local complexity ($P = 0.0339$, Spearman's $r = 0.3704$). However, for the data set on local complexity, it would take an additional 251 studies, each with an effect size of approximately zero (sampled from a normal distribution with a mean of zero and the same variance as the data set), to make the combined effect size statistically insignificant (at $P < 0.05$). This *Fail Safe N* could be considered robust (for the $N = 20$ studies that we included on local complexity, $5N + 10 = 110$, and $251 > 110$) (Rosenberg, 2005), and our results on local complexity are not likely to be an artifact of publication bias.

Table 2.1 Studies included in the meta-analysis of pollinators (P) and natural enemies (NE): abundance (A), richness (R), animal-pollinated (AP), wind-pollinated (WP), non-woody (NW), and woody (W).

Study	**Continent**	**Taxon**	**Metric**	**Scale**	**Crop**	**Habit**	**Mode**
Ameixa & Kindlmann (2008)	Europe	NE	A	Landscape	Wheat	NW	WP
Anjum-Zubair *et al.* (2010)	Europe	NE	Both	Local	Wheat	NW	WP
Arthur *et al.* (2010)	Australia	P	A	Both	Brassica	NW	AP
Blanche *et al.* (2006)	Australia	P	A	Landscape	Longan	W	AP
Brittain *et al.* (2010)	Europe	P	Both	Landscape	Grape	W	AP
Büchi (2002)	Europe	NE	A	Local	Brassica	NW	AP
Chacoff & Aizen (2006)	S America	P	A	Landscape	Grapefruit	W	AP
Clough *et al.* (2005)	Europe	NE	Both	Both	Wheat	NW	WP
Clough *et al.* (2007)	Europe	Both	R	Local	Wheat	NW	WP
Drapela *et al.* (2008)	Europe	NE	Both	Landscape	Brassica	NW	AP
Eilers & Klein (2009)	N America	NE	A	Both	Almond	W	AP
Forehand *et al.* (2006)	N America	NE	A	Local	Tomato	NW	AP
Gardiner *et al.* (2009a)	N America	NE	A	Landscape	Soybean	NW	AP
Gardiner *et al.* (2009b)	N America	NE	A	Landscape	Soybean	NW	AP
Gardiner *et al.* (2010)	N America	NE	Both	Landscape	Soybean	NW	AP
Gemmill-Herren & Ochieng (2008)	Africa	P	A	Local	Eggplant	NW	AP
Greenleaf & Kremen (2006a)	N America	P	A	Landscape	Tomato	NW	AP
Hajek *et al.* (2007)	N America	NE	A	Local	Soybean	NW	AP
Isaacs & Kirk (2010)	N America	P	A	Local	Blueberry	W	AP
Julier & Roulston (2009)	N America	P	A	Landscape	Pumpkin	NW	AP
Klein *et al.* (2006)	Asia	P	Both	Landscape	Coffee, cacao	W	AP
Klein (2009)	Asia	P	Both	Landscape	Coffee	W	AP
Kremen *et al.* (2002)	N America	P	Both	Landscape	Watermelon	NW	AP
Kremen *et al.* (2004)	N America	P	A	Local	Watermelon	NW	AP
Lee & Heimpel (2005)	N America	NE	A	Local	Brassica	NW	AP
Miliczky & Horton (2005)	N America	NE	A	Local	Orchard crops	W	AP
Morandin & Winston (2006)	N America	P	A	Landscape	Brassica	NW	AP
Morandin *et al.* (2007)	N America	P	Both	Landscape	Brassica	NW	AP
Nash *et al.* (2008)	Australia	NE	A	Local	Cereal crops	NW	WP
Oberg *et al.* (2008)	Europe	NE	Both	Landscape	Barley	NW	WP
Pease & Zalom (2010)	N America	NE	A	Local	Tomato	NW	AP
Pluess *et al.* (2010)	Asia	NE	Both	Landscape	Wheat	NW	WP
Ricketts (2004)	C America	P	Both	Landscape	Coffee	W	AP
Roschewitz *et al.* (2005)	Europe	NE	A	Landscape	Wheat	NW	WP
Rundlof *et al.* (2008)	Europe	P	Both	Landscape	Cereal crops	NW	WP
Saska *et al.* (2007)	Europe	NE	Both	Local	Wheat	NW	WP
Schmidt *et al.* (2005)	Europe	NE	Both	Landscape	Wheat	NW	WP
Schmidt *et al.* (2008)	Europe	NE	Both	Landscape	Wheat	NW	WP
Schmidt-Entling & Dobeli (2009)	Europe	NE	Both	Both	Wheat	NW	WP
Steffan-Dewenter (2003)	Europe	P	Both	Landscape	Orchard crops	W	AP
Thomson & Hoffmann (2010)	Australia	NE	A	Local	Grape	W	AP
Thomson *et al.* (2010)	Australia	NE	A	Landscape	Grape	W	AP
Tuell *et al.* (2009)	N America	P	Both	Local	Blueberry	W	AP
Varchola & Dunn (2001)	N America	NE	Both	Local	Maize	NW	WP
Vollhardt *et al.* (2008)	Europe	NE	Both	Landscape	Wheat	NW	WP
Wyckhuys & O'Neil (2007)	C America	NE	A	Landscape	Maize	NW	WP
Totals	18 N America	28 NE	45 A	30 Landscape	11 Wheat	33 NW	30 AP
	16 Europe	19 P	22 R	20 Local	6 Brassica	13 W	16 WP
	5 Australia				4 Soybean		
	3 C/S America				3 Coffee		
	3 Asia				3 Grape		
	1 Africa				3 Tomato		

Results

Publication bias

We included 88 effect sizes from 46 studies in the meta-analysis. Of these, 29 effect sizes were calculated from 19 studies on pollinators, and 59 effect sizes were calculated from 28 studies on natural enemies (Table 2.1). There was not a significant difference between the number of studies on pollinators and natural enemies (19 *versus* 28 studies, $P = 0.1893$, $\chi^2 = 1.723$, and d.f. = 1 for all χ^2 tests), and so our search strategy and inclusion criteria are not likely to have been significantly biased towards either pollinators or natural enemies. However, there were significantly more studies from Europe and North America combined than all the other continents combined (34 *versus* 12 studies, $P = 0.0012$, $\chi^2 = 10.52$), and there was only one study from Africa that met our inclusion criteria (Gemmill-Herren & Ochieng', 2008). Therefore, our results are likely to be biased towards European and North American agroecosystems.

There were not significant differences between the number of studies of landscape or local complexity (30 *versus* 20 studies, $P = 0.1573$, $\chi^2 = 2$), but there were significantly more studies in non-woody than in woody crops (33 *versus* 13 studies, $P = 0.0032$, $\chi^2 = 8.696$) and significantly more studies of abundance than richness (45 *versus* 22 studies, $P = 0.0050$, $\chi^2 = 7.896$). There was no significant difference between the number of studies of pollinators and natural enemies at landscape scales (14 *versus* 16 studies, $P = 0.7150$, $\chi^2 = 0.1333$), but there were significantly fewer studies of pollinators than natural enemies at local scales (6 *versus* 15 studies, $P = 0.0495$, $\chi^2 = 3.857$). There was no significant difference between the number of studies of natural enemies in wind-pollinated or animal-pollinated crops (15 *versus* 13 studies, $P = 0.7055$, $\chi^2 = 0.1429$), and therefore our results for natural enemies are likely to be relevant to animal-pollinated crops. Of the 350 studies found by our search, 141 studies seemed to be relevant by title or abstract, but we could not access four of these studies, and we could not consider another four that were not written in English. Only three studies reported relevant data on hover flies, and therefore we decided not to include hover flies in the meta-analysis of effect sizes.

Hypothesis tests and summary effects

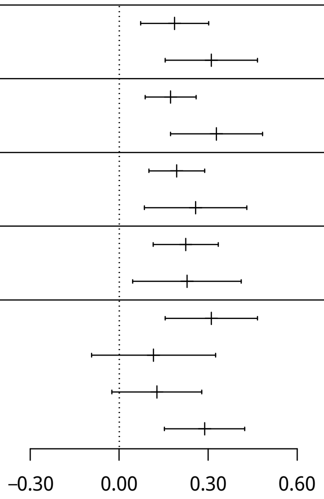
We included 29 effect sizes on bees, 27 on spiders, 19 on predatory beetles, and 13 on parasitoids. The effects of complexity were positive and significantly different from zero for pollinators ($P = 0.0005$, $Z_r = 0.3108$) and also for natural enemies ($P = 0.0024$, $Z_r = 0.1868$). This supports our first hypothesis (positive effects on both pollinators and natural enemies). However, there was no significant difference between the effects of complexity on pollinators and natural enemies ($P = 0.2659$, $t = 1.128$, $Z_r = 0.0974$, SE = 0.0863, when the factor that categorizes ESPs as either pollinators or natural enemies was added to minimum adequate model of the combined data set). This does not support our fifth hypothesis (different effects on pollinators than on natural enemies).

Complexity had positive effects on both abundance and richness, positive effects in both woody and non-woody crops, positive effects at both landscape and local scales, and positive effects on both bees and spiders (Figure 2.1). However, the effects of complexity on beetles and parasitoids were inconclusive, because the results for these subgroups of natural enemies were not robust to sensitivity analysis (Figure 2.2). Results for bees were positive under all sets of assumptions (Figure 2.2: SA1–SA4). Under one set of assumptions (Figure 2.2: SA1) spiders were not significantly affected by complexity, and beetles and parasitoids were only positively affected by complexity under the assumption that effects were positive for data reported as "non-significant" (Figure 2.2: SA3 and SA4).

Complexity had stronger effects on richness than abundance (P = 0.0430, Z_r = 0.1421) in the minimum adequate model of the combined data set (Table 2.2: All ESPs). Crop habit, scale, and taxon were not significant predictors of effect size for this data set (deleted during model selection). These results support our second hypothesis (different effects on abundance and richness), but not our third, fourth, and fifth hypotheses (different effects at different scales, in crops of different habits, or on different taxa). These differences between abundance and richness were larger and more significant in the models of natural enemies only (P = 0.0169, Z_r = 0.2044) and spiders only (P = 0.0112, Z_r = 0.2659), but there was no significant difference between abundance and richness in the models of bees only, beetles only, and parasitoids only (Table 2.2). This suggests that the smaller differences between abundance and richness in the models of all ESPs and all natural enemies (Table 2.2) were driven by the larger difference between the abundance and richness of spiders. In fact, complexity had significantly positive effects only on the richness, but not on the abundance, of spiders (Figure 2.3). Complexity also had significantly stronger effects on the richness than the abundance of ESPs in non-woody crops (P = 0.0412, Z_r = 0.1655), but not in woody crops (deleted during model selection).

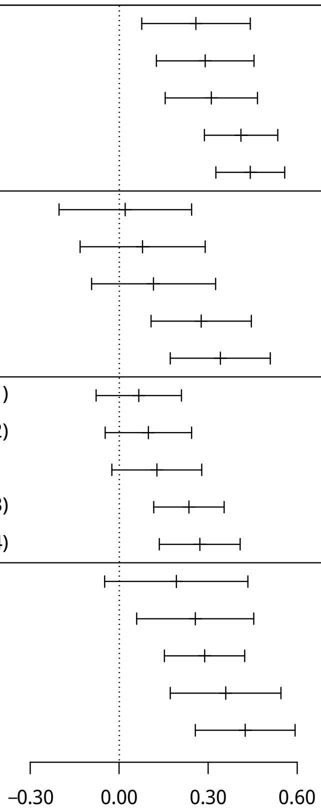
Landscape complexity had significantly stronger effects on ESPs in non-woody crops than it did on ESPs in woody crops (P = 0.0363, Z_r = 0.1975). It also had significantly positive effects on bees and spiders in non-woody crops and on bees but not spiders in woody crops (Figure 2.3). For parasitoids, however, landscape effects were stronger in woody crops than they were in non-woody crops (P = 0.0074, Z_r = 0.3246). This supports our fourth hypothesis (different effects in woody and non-woody crops). Landscape effects on beetles and parasitoids were not significantly positive, but we consider these effects to be inconclusive, because of their sensitivity to our assumptions about "non-significant" results. However, we note that landscape complexity might have significantly stronger effects on bees than beetles (P = 0.0099, Z_r = 0.3738). This supports our fifth hypothesis [different effects on different taxa, and indeed different effects on one taxon of pollinators (bees) than on another taxon of natural enemies (beetles)]. Other than this, we did not detect a significant difference between pollinators and natural enemies (Table 2.2).

We did not detect significant differences between the effects of local and landscape complexity. However, when scale was deleted from the models of the parasitoids-only and spiders-only data sets, there were significant decreases in likelihood. This supports our third hypothesis (different effects of complexity at different scales).



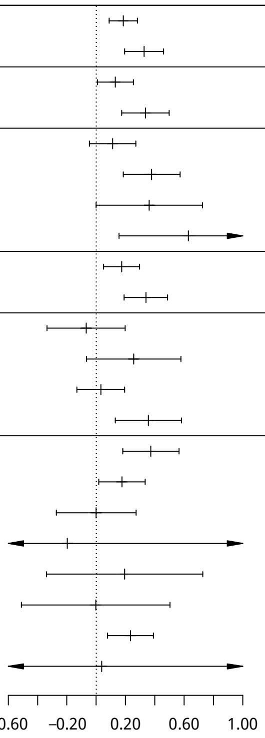
Data set	ES	SE	LL	UL	t	P	N
Enemies	0.1868	0.0560	0.0720	0.3016	3.3338	0.0024	28
Pollinators	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Abundance	0.1735	0.0426	0.0877	0.2593	4.0730	0.0002	45
Richness	0.3280	0.0747	0.1730	0.4830	4.3889	0.0002	22
Landscape	0.1938	0.0460	0.0998	0.2878	4.2100	0.0002	30
Local	0.2576	0.0829	0.0846	0.4306	3.1056	0.0056	20
Non–woody	0.2245	0.0539	0.1148	0.3342	4.1627	0.0002	33
Woody	0.2284	0.0847	0.0455	0.4113	2.6972	0.0183	13
Bees	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Beetles	0.1158	0.0974	–0.0930	0.3247	1.1896	0.2540	14
Parasitoids	0.1269	0.0682	–0.0250	0.2787	1.8611	0.0924	10
Spiders	0.2878	0.0627	0.1524	0.4231	4.5931	0.0005	13

Figure 2.1 The effects of compositional complexity on pollinators and natural enemies, as predicted by random-effects null models (effect sizes ~ 1, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. All effect sizes were significantly positive, except for beetles and parasitoids (but see sensitivity analyses in Figure 2.2).



Data set	ES	SE	LL	UL	t	P	N
Bees (SA1)	0.2588	0.0873	0.0760	0.4417	2.9634	0.0080	19
Bees (SA2)	0.2901	0.0787	0.1254	0.4547	3.6878	0.0016	19
Bees	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Bees (SA3)	0.4108	0.0590	0.2873	0.5344	6.9612	0.0000	19
Bees (SA4)	0.4417	0.0554	0.3257	0.5577	7.9721	0.0000	19
Beetles (SA1)	0.0205	0.1041	−0.2028	0.2438	0.1967	0.8469	14
Beetles (SA2)	0.0791	0.0982	−0.1316	0.2898	0.8051	0.4342	14
Beetles	0.1158	0.0974	−0.0930	0.3247	1.1896	0.2540	14
Beetles (SA3)	0.2763	0.0789	0.1071	0.4455	3.5016	0.0035	14
Beetles (SA4)	0.3408	0.0787	0.1721	0.5095	4.3332	0.0007	14
Parasitoids (SA1)	0.0661	0.0644	−0.0774	0.2097	1.0262	0.3290	10
Parasitoids (SA2)	0.0985	0.0652	−0.0468	0.2439	1.5107	0.1618	10
Parasitoids	0.1269	0.0682	−0.0250	0.2787	1.8611	0.0924	10
Parasitoids (SA3)	0.2351	0.0534	0.1161	0.3541	4.4012	0.0013	10
Parasitoids (SA4)	0.2716	0.0612	0.1353	0.4080	4.4381	0.0013	10
Spiders (SA1)	0.1925	0.1118	−0.0490	0.4340	1.7221	0.1087	13
Spiders (SA2)	0.2563	0.0915	0.0587	0.4539	2.8019	0.0150	13
Spiders	0.2878	0.0627	0.1524	0.4231	4.5931	0.0005	13
Spiders (SA3)	0.3590	0.0863	0.1725	0.5456	4.1586	0.0011	13
Spiders (SA4)	0.4251	0.0778	0.2570	0.5933	5.4623	0.0001	13

Figure 2.2 Sensitivity analyses (SA) of the effects of compositional complexity on pollinators and natural enemies, as predicted by random-effects null models (effect sizes ~ 1, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. Different data sets had different sets of assumptions for data reported as "non-significant" (SA1 and SA2 assumed effects were negative, SA3 and SA4 assumed effects were positive, SA2 and SA3 assumed $P = 0.5$, and SA1 and SA4 assumed $P = 0.1$).



Data set	Factor level	Factor level	ES	SE	LL	UL	t	P	N
All ESPs	Abundance	–	0.1848	0.0481	0.0879	0.2817	3.8413	0.0004	45
	Richness	–	0.3269	0.0641	0.1940	0.4598	5.1034	0.0000	22
Enemies	Abundance	–	0.1312	0.0600	0.0081	0.2543	2.1860	0.0377	27
	Richness	–	0.3356	0.0750	0.1736	0.4976	4.4755	0.0006	13
Spiders	Landscape	Abundance	0.1125	0.0710	−0.0457	0.2707	1.5834	0.1444	10
	Landscape	Richness	0.3784	0.0821	0.1843	0.5725	4.6109	0.0025	7
	Local	Abundance	0.3625	0.1412	−0.0005	0.7255	2.5675	0.0502	5
	Local	Richness	0.6284	0.1486	0.1555	1.1013	4.2282	0.0242	3
Non−woody	Abundance	–	0.1736	0.0605	0.0504	0.2968	2.8716	0.0072	32
	Richness	–	0.3391	0.0698	0.1911	0.4871	4.8607	0.0002	16
Parasitoids	Landscape	Non−woody	−0.0685	0.0620	−0.3353	0.1983	1.1051	0.3843	2
	Landscape	Woody	0.2562	0.0748	−0.0656	0.5780	3.4246	0.0757	2
	Local	Non−woody	0.0315	0.0588	−0.1318	0.1948	0.5353	0.6208	4
	Local	Woody	0.3561	0.0710	0.1301	0.5821	5.0177	0.0152	3
Landscape	Bees	Non−woody	0.3734	0.0813	0.1812	0.5656	4.5938	0.0025	7
	Bees	Woody	0.1759	0.0667	0.0182	0.3336	2.6355	0.0336	7
	Beetles	Non−woody	−0.0004	0.1058	−0.2724	0.2716	0.0035	0.9974	5
	Beetles	Woody	−0.1979	0.1185	−1.7036	1.3078	1.6707	0.3434	1
	Parasitoids	Non−woody	0.1943	0.1240	−0.3392	0.7278	1.5673	0.2576	2
	Parasitoids	Woody	−0.0033	0.1179	−0.5106	0.5040	0.0278	0.9804	2
	Spiders	Non−woody	0.2348	0.0691	0.0785	0.3911	3.3988	0.0079	9
	Spiders	Woody	0.0372	0.1079	−1.3338	1.4082	0.3449	0.7886	1

Figure 2.3 The effects of compositional complexity on pollinators and natural enemies, as predicted by minimum adequate mixed-effects models (effect sizes ~ fixed effects, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. An arrow indicates that the limit of a confidence interval extends beyond the boundaries of the plot.

Table 2.2 Minimum adequate models (effect sizes ~ fixed effects, random effects = ~ 1 | study): the difference [in units of Fisher's *Z*-transformed *r* (Z_r)] and the standard error of the difference (SE) for the contrast between larger (>) and smaller effect sizes. Significant differences are in bold. For some data sets, the minimum adequate model was the null model, and so the only fixed effect was the intercept (1), and there were no significant differences between factor levels.

Data set	**Fixed effects**	**Contrast**	Z_r	**SE**	***t***	***P***
All ESPs	Metric	**Richness > abundance**	0.1421	0.0680	2.0884	**0.0430**
Enemies	Metric	**Richness > abundance**	0.2044	0.0808	2.5291	**0.0169**
Pollinators	1	—	—	—	—	—
Abundance	1	—	—	—	—	—
Richness	1	—	—	—	—	—
Bees	1	—	—	—	—	—
Beetles	1	—	—	—	—	—
Parasitoids	Habit + scale	**Woody > non-woody**	0.3246	0.0912	3.5598	**0.0074**
		Local > landscape	0.0999	0.0331	3.0224	0.0943
Spiders	Metric + scale	**Richness > abundance**	0.2659	0.0889	2.9913	**0.0112**
		Local > landscape	0.2500	0.1438	1.7389	0.1076
Landscape	Habit + taxon	**Non-woody > woody**	0.1975	0.0898	2.1988	**0.0363**
		Bees > beetles	0.3738	0.1204	3.105	**0.0099 ***
		Bees > parasitoids	0.1791	0.1262	1.419	0.4814 *
		Bees > spiders	0.1386	0.1031	1.345	0.5281 *
		Parasitoids > beetles	0.1946	0.1532	1.270	0.5761 *
		Spiders > beetles	0.2351	0.1248	1.884	0.2303 *
		Spiders > parasitoids	0.0405	0.1394	0.291	0.9913 *
Local	1	—	—	—	—	—
Non-woody	Metric	**Richness > abundance**	0.1655	0.077	2.1483	**0.0412**
Woody	1	—	—	—	—	—

* These *P*-values were corrected for multiple comparisons by using the Tukey method in the *multcomp* package (Hothorn *et al.*, 2008).

Discussion

Limitations of this meta-analysis and a framework for future comparisons

We found and included significantly more studies from Europe and North America than from all of the other continents combined. In contrast, we found and included only one study from Africa. This bias needs to be corrected by future research, especially because the “sustainable” intensification of agriculture in sub-Saharan Africa has been presented as a high priority for the future of food security (Sanchez, 2010; Clay, 2011; Pretty *et al.*, 2011), and the “ecological” intensification of agriculture—harnessing ecosystem services, such as pollination and pest control, to increase crop yields—will be a vital part of sustainable intensification (Bommarco *et al.*, 2013). To produce a given amount of food, it is possible that the sustainable intensification of agriculture would do less damage to biodiversity than would the expansion of agriculture (Green *et al.*, 2005; Phalan *et al.*, 2011; and see Chapter 3), but both expansion and intensification could have negative effects on the complexity of agroecosystems, and therefore they could have negative feedback effects on food production, if the crops in these agroecosystems suffer from a decrease in pollination, pest control, or other agroecosystem services.

We should not assume that we can generalize from our results to other continents, especially because there could be differences between temperate agroecosystems, including much of Europe and North America, and tropical agroecosystems. For example, proximity to natural habitat affected the abundance of wild bees more strongly in tropical than temperate studies (Ricketts *et al.*, 2008), and plant diversity had similar latitudinal effects on pest control (Letourneau *et al.*, 2011). Furthermore, Batáry *et al.* (2011) reported that local management affected farmland biodiversity more strongly in simple than in complex landscapes, and therefore—if landscape complexity is correlated with the latitude, intensity, or area of farms—then local management that benefits commercial farmers in Europe and North America might not contribute to crop productivity in the tropics. Indeed, the landscapes of some tropical agroecosystems might not be so simple, or the biodiversity so impoverished, that they have reduced functionality (but see Carvalheiro *et al.*, 2010), and therefore the management of ecosystems services might not have payoffs in these agroecosystems, especially if wildlife-friendly management is not subsidized by agri-environment schemes. Small-scale and/or low-intensity agroecosystems might have well-functioning pollination and pest-control services (Hagen & Kraemer, 2010), and loss of income from these services might be an unintended consequence of rural or agricultural development, if development results in loss of complexity.

We should also not assume that we can generalize from ESPs (pollinators and natural enemies) to the ecosystem services that they provide (pollination and pest control), for the reasons summarized above (“Ecosystem-service providers as indicators of ecosystem-service provision”). However, we propose three criteria for comparing pollinators and natural enemies, in response to the management of agroecosystems, and we think that this framework could be extended to future comparisons of pollination and pest-control services.

We propose that pollinators and natural enemies must both be positively affected (1) by the same driver, (2) at the same scale, and (3) they must not have negative interactions (*cf.* Bennett *et al.*, 2009), if there is to be a synergy (+/+) between their management, for that specific driver, at that specific scale. If one of them is not affected by a positive driver of the other (+/0), then there is not a synergy between their management, for that driver, at that scale, but neither is there a tradeoff. However, if one of them is negatively affected by a positive driver of the other, then there is a tradeoff (+/–) between their management, and they are not compatible, for that driver, at that scale. We discuss the results of this meta-analysis in the context of this framework. The driver is complexity, and the scales are local and landscape. We also discuss the relationship between biodiversity and the stability of ecosystem services in this context, by comparing some taxa that might have different drivers.

Similarities and differences between ecosystem-service providers

Complexity had positive effects on both pollinators and natural enemies (+/+), at both local and landscape scales. This suggests that there could be synergies between pollinators and natural enemies in response to the management of agroecosystems. However, of the natural enemies, complexity had robustly positive effects only on spiders. In two of the four sensitivity analyses (SA3 and SA4), complexity had positive effects on beetles and parasitoids, but not in the other two sensitivity analyses (SA1 and SA2) or in the main meta-analysis, and therefore we consider our results on beetles and parasitoids to be inconclusive. As other meta-analysts have noted (*e.g.*, Gurevitch & Hedges, 2001), it would be useful if exact statistics were published for all results, not only significant results, and not only *P*-values but also sample sizes and standard errors, so that future meta-analysts would not have to discard as much data or deal with sensitive assumptions about the nature of non-significance. Nonetheless, we detected a significant difference between the effects of landscape complexity on bees and beetles, and even if complexity does have positive effects on beetles and parasitoids it seems likely that these effects might differ between taxa.

Other than this difference between bees and beetles, we did not detect a significant difference between the effects of complexity on pollinators and natural enemies *per se* (taxon was not a significant predictor in any of the other models; Table 2.2). However, our results suggest that effects on pollinators (Z_r = 0.3108) might be more strongly positive than effects on natural enemies (Z_r = 0.1868). Moreover, effects on pollinators were less ambiguous than effects on natural enemies—effects on bees were positive in all sensitivity analyses (Figure 2.2). Our results also suggest that some pollinators and natural enemies might have different responses to complexity in woody crops, at landscape scales, or as an effect on abundance rather than richness. For example, in woody crops, landscape complexity had positive effects on bees, but not on natural enemies (+/0). Furthermore, although complexity had significantly stronger effects on the richness than the abundance of natural enemies (spiders), we did not detect a significant difference between its effects on the richness and the abundance of pollinators (bees). Complexity had significantly positive effects on the richness of bees and spiders (+/+), and on the abundance of bees, but not on the abundance of spiders (+/0). All of these differences between pollinators and natural enemies might have important implications for the management of pollination and pest-control services. For example, if it were concluded that the magnitude of pollination and pest-control services depended only on the abundance, but not on the richness, of bees and spiders, then a management strategy that increases the complexity of the agroecosystem might not have positive effects on the magnitude of both pollination and pest control. Furthermore, for woody crops, a management strategy that increases landscape complexity might not have positive effects on spiders, but only on bees.

If there is a difference between landscape effects on bees and beetles, perhaps it could be explained by differences in mobility. Bees and some spiders can move long distances by flying or ballooning through the air (Suter, 1999; Hagen *et al.*, 2011), but predatory ground beetles generally move by walking, not flying (most of the beetles in our meta-analysis were Carabidae and Staphylinidae, not Coccinellidae), and the distances they move (*e.g.*, Firle *et al.*, 1998) might be shorter than the distances moved by bees or spiders. If less-mobile arthropods move through less space, per unit time, than more-mobile arthropods, then it is possible that they are also less able to benefit from resources in both crop and non-crop habitats, per unit time, especially at landscape scales, and it is also possible that they are less able to frequently move back and forth between crop and non-crop habitats than are more-mobile arthropods.

Studies of beneficial arthropods that are seasonal “snapshots” do not give us an overview of annual movements, but annual movements from non-crop to crop and back again might be an important mechanism for the effects of complexity. For example, beetles were more abundant and diverse in corn fields surrounded by simple vegetation (grass) than in corn fields surrounded by complex vegetation (hedges), but only late in the growing season, when the crops were structurally complex (Varchola & Dunn, 2001). Our meta-analysis construes this as a negative effect of local complexity. However, in the same study, early in the growing season, when the crops were structurally simple, beetles were more abundant and diverse in corn fields surrounded by complex vegetation. Our meta-analysis construes this as a positive effect of local complexity. Therefore, the existence of beetles in crop habitats in one season could be dependent upon the existence of non-crop habitats in other seasons (*e.g.*, for overwintering), but not necessarily the season in which they are sampled. Furthermore, subgroups of carabid beetles with different dispersal abilities can have significant but opposite responses to landscape fragmentation, and if the data on these subgroups are analyzed together, it can seem as if fragmentation has a non-significant effect on carabid beetles (Hendrickx *et al.*, 2009). Therefore, we cannot conclude that landscape complexity had no effect on predatory beetles, and we identify the need for research that compares effects on bees and beetles (and other natural enemies), in the context of the distances and frequencies with which they move, on annual and seasonal timescales.

Differences between abundance and richness:
the cultural difference or specialist-generalist mechanism

Complexity had significantly stronger effects on the richness than on the abundance of spiders, and possibly also of some of the other taxa, when sampled in non-woody crops (Table 2.2). A mechanism for these differences between abundance and richness might have two components.

Firstly, an increase in complexity could have a positive effect on the richness of arthropods sampled in crops, because of an increase in the richness of non-crop resources, and a positive effect on the abundance of arthropods sampled in crops, because of an increase in the abundance of non-crop resources, close to the crops. As we defined it in this meta-analysis, complexity was not measured as a property of crops, but as a property of non-crop habitats or proximity to non-crop habitats. The arthropods, however, were sampled in crops, and not in non-crop habitats. Therefore, we might imagine that the only arthropods that could have directly benefitted from the increased resources in non-crop habitats would have been those arthropods that moved between non-crop habitats (where they used these resources) and crop habitats (where they were sampled)—these arthropods are so-called “ecotone species” or “dispersers” (Duelli & Obrist, 2003).

Secondly, in contrast to these ecotone species and dispersers, an increase in complexity could have a neutral or a negative effect on the abundance of arthropods that do not use resources in non-crop habitats, but only in crop habitats, because of a decrease in the abundance of crop habitats—these arthropods are so-called “cultural species” (Duelli & Obrist, 2003). We understand a “cultural species” to be a species that does not depend on non-crop habitats. For example, the abundance of bumble bees was dependent on the area of oilseed rape, a crop, but was not dependent on the area of non-crop habitats, at landscape scales (Westphal *et al.*, 2003), and in this context we could call these bumble bees “cultural species”. It could be that all species depend to some extent on non-crop habitats, and so we will consider a cultural species to be an extreme, along a continuum from no dependency on non-crop habitats (a cultural species) to complete dependency on non-crop habitats [a “stenotopic species” (Duelli & Obrist, 2003)], and we will assume that what seems true for a truly cultural species is somewhat true for a somewhat cultural species.

If complexity has different effects on cultural species, on the one hand, and ecotone species and/or dispersers, on the other, then we think this might be a possible mechanism for the stronger positive effects of complexity on richness. We could imagine that complexity could have a negative effect on the abundance of one or more cultural species (because of a decrease in crop habitats or an increase in competition with ecotone species and/or dispersers), without having a negative effect on the richness of cultural species (*i.e.* without causing the local extinction of one or more cultural species). If, at the same time, we were to imagine that complexity would have positive effects on the abundance and richness of ecotone species and/or dispersers, then this would have a stronger overall effect on richness than it would on abundance (for a hypothetical example, see Figure 2.4). We will call this mechanism the “cultural difference” mechanism, because it is a result of differences between the effects of complexity on cultural species, on the one hand, and ecotone species and/or dispersers, on the other.

The existence of such a mechanism might be supported by the results of another meta-analysis, in which landscape complexity had significantly positive effects on the abundance of generalist natural enemies, but non-significant and possibly negative effects on the abundance of specialist natural enemies (Chaplin-Kramer *et al.*, 2011). In that meta-analysis, specialists were defined as natural enemies of only a single species of pest, and therefore we could probably consider them to be cultural species, at least in terms of their requirements for food or hosts (the pests were defined as pests of crops), if not in terms of their requirements for nesting sites or refuges from disturbance. Therefore, we could also call this mechanism the “specialist-generalist” mechanism. This mechanism might have important implications for the management of agroecosystem services, because it points to the possibility that only some service providers—those that depend on both crop and non-crop habitat—are likely to respond positively to complexity. Therefore, an important question for the managers of agricultural landscapes to answer might be, “Which species in this agroecosystem are effective service providers, and are they cultural species?” If they are cultural species, then managing the agroecosystem for greater complexity might not have positive effects on pollination and/or pest-control services. In contrast, complexity might have negative effects on these services, if the abundance of cultural species decreases when complexity increases [see above (“Ecosystem-service providers as indicators of ecosystem-service provision”)].

We identify the need for research that tests the relative effects of complexity on richness and abundance, and tests this “cultural difference” or “specialist-generalist” mechanism, especially because of its implications for the management of ESPs. If the stability of ecosystem services depends on the richness of ESPs (*e.g.*, Kremen *et al.*, 2002), and if the magnitude, rather than the stability, of ecosystem services depends on the abundance of specific and effective ESPs (*e.g.*, Straub & Snyder, 2006), then the management of agroecosystems for greater complexity could have greater benefits for the stability of ecosystem services than could for the magnitude of ecosystem services, if it proves to be more generally true that complexity does have stronger effects on the richness than it does on the abundance of ESPs [see below ("Diversity and the stability of ecosystem services")].

In their study of the dependency of arthropods on semi-natural habitats, Duelli & Obrist (2003) categorized 56% of the carabid beetles and 35% of the staphylinid beetles as "not depending on semi-natural habitats" ("cultural species" and some "ubiquists"—see their Table 2), compared to only 24% of the spiders and 17% of the aculeate Hymenoptera (bees, ants, and wasps). This supports our results on the significantly different effects of complexity on bees and beetles, because it suggests that these groups might have different dependencies on semi-natural habitats. Likewise, in our meta-analysis, landscape complexity had stronger effects in non-woody than woody crops (Table 2.2), and this might also be explained by differences between cultural species and others. If woody crops are less disturbed than are non-woody crops (*e.g.*, because of harvesting or tillage), then a higher proportion of ESPs in woody crops might be cultural species, or might have viable populations that do not depend on immigration from populations in complex landscapes, but that do depend on local vegetative resources [*e.g.*, if woody crops are "partial habitats" (Westrich, 1996), which offer only some of their resource requirements]. For example, Tscharntke *et al.* (2007) suggested that conservation biological control in perennial crops might be less dependent on the immigration of natural enemies than in annual crops. Our results support this suggestion because local complexity had significant effects on parasitoids in woody crops, but landscape complexity did not (Figure 2.3; Table 2.2). This has implications for the scale of management of ecosystem services in woody crops, and managers should ask themselves whether or not the effective ESPs in these systems are cultural species.

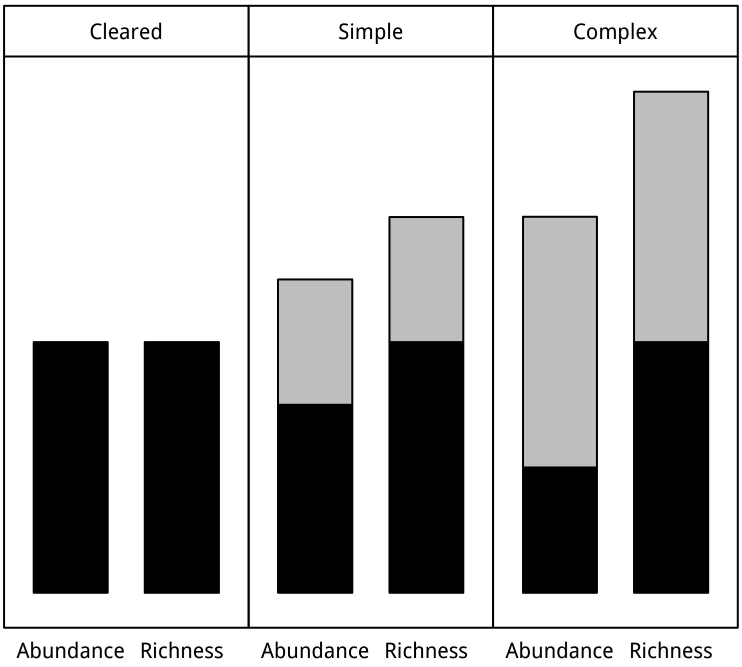


Figure 2.4 The “cultural difference” or “specialist-generalist” mechanism: a possible explanation for the stronger effects of complexity on the richness than on the abundance of arthropods sampled within a crop habitat. In this hypothetical example, complexity has positive effects on abundance, because its positive effects on the abundance of ecotone species and dispersers (gray bars) more than compensate for its negative effects on the abundance of cultural species (black bars). It also has positive effects on the richness of ecotone species and dispersers, but neutral effects on the richness of cultural species (*e.g.*, complexity results in the immigration, into the crop, of ecotone species and dispersers, without causing the local extinction of cultural species). In a so-called “cleared” agroecosystem (Tscharntke *et al.*, 2005), there is little or no non-crop habitat, and therefore we might imagine that there would be few or no ecotone species or dispersers. As complexity increases, from cleared, to simple, to complex agroecosystems, the abundance and richness of ecotone species and dispersers also increase, but the increase in the richness of the arthropod community (relative to the richness of the cleared agroecosystem) is stronger than the increase in the abundance of the arthropod community (relative to the abundance of the cleared agroecosystem).

Diversity and the stability of ecosystem services

Ecosystem functions (including ecosystem services) are thought to be more stable in high-diversity rather than low-diversity communities, because there are more species that have the same functions in high-diversity communities, and this redundancy of species reduces fluctuations in ecosystem functions (the "insurance hypothesis") (McNaughton, 1977; Lawton & Brown, 1993; Yachi & Loreau, 1999; Tscharntke *et al.*, 2005). According to ecological theory, the stability of an ecosystem service could be underpinned by three mechanisms: (1) density compensation, (2) cross-scale resilience, and (3) response diversity (Tilman, 1999; Winfree & Kremen, 2009). In the context of this meta-analysis, density compensation could occur when two species that have the same function (*e.g.,* two species of bees that pollinate the same species of plant, or two species of natural enemies that prey on the same species of pest) also have the same driver (*e.g.,* landscape complexity), but this driver has inverse effects on them (+/–). When the abundance of one species decreases (*e.g.,* an ecotone species, when non-crop habitat is destroyed), the abundance of the other species increases (*e.g.,* a cultural species, when crop habitat is created), and thereby that ecosystem service is stabilized. Cross-scale resilience could occur if two species that have the same function also have the same driver, but are not affected by that driver at the same spatial or temporal scale (*e.g.,* one species is affected by local complexity, and the other is affected by landscape complexity, perhaps because of differences in mobility). Response diversity could occur if two species that have the same function do not have the same driver (*e.g.,* different requirements for floral resources). When the abundance of one species decreases, the abundance of the other species is not affected. For example, as generalist predators, spiders and beetles could be redundant as pest-control agents. If complexity is a strong positive driver of spider diversity but not a strong driver of beetle diversity (+/0), then this could be an example of "response diversity" as a mechanism for stability.

Garibaldi *et al.* (2011) reported that isolation from natural habitats reduced the stability of pollination services by wild bees, and Winfree & Kremen (2009) found evidence for cross-scale resilience and response diversity, but not for density compensation, in the pollination services provided by wild bees. Likewise, we did not find evidence for density compensation (+/–), but our results could be compatible with response diversity (+/0) or cross-scale diversity (+/+ or 0/+ at one scale, and +/0 at another) within the natural enemy community (Figure 2.3; Table 2.2). We note that density compensation shows how ESPs and ecosystem services should not be confused. A tradeoff between two taxa of natural enemies (+/–) could have a positive effect on pest control, by stabilizing the service that either of these taxa could provide, if the system were driven in different directions (+/– or –/+).

Comparisons between this meta-analysis and similar meta-analyses

We believe that this is the first meta-analysis to quantitatively compare pollinators and natural enemies. However, other publications have meta-analyzed either pollinators (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) or natural enemies (Chaplin-Kramer *et al.*, 2011) in response to agricultural complexity, and therefore we will discuss some similarities and differences between our results and theirs.

Our results confirm the conclusions of earlier authors (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) that complex landscapes can have positive effects on bees, but these earlier meta-analyses did not investigate the effects of local complexity. In our meta-analysis, local complexity did not have significantly different effects on bees than did landscape complexity, and the combined effects of local and landscape complexity were significantly positive. We also note that these earlier meta-analyses studied flower visitation by bees rather than bee abundance, and it is good to know that our results agree with theirs despite our somewhat different metrics.

Garibaldi *et al.* (2011) reported that landscape complexity can have stronger effects on the richness than on the flower-visitation rate of bees, and our results seem to confirm this relationship between the richness and the abundance of ESPs in general, but we did not detect a significant difference between the two for bees specifically. However, we report that complexity can have significantly stronger effects on the richness than on the abundance of spiders, and it is good to know that there is evidence of similar effects on bees. Chaplin-Kramer *et al.* (2011) did not detect a significant difference between the richness and the abundance of the natural enemies in their meta-analysis on landscape complexity, but the trend in their data supports our results. Letourneau *et al.* (2011) did not compare the effects of local complexity on abundance and richness, and we note that only landscape complexity, not local complexity, had a significantly stronger effect on the richness than on the abundance of spiders in our meta-analysis (Figure 2.3).

In terms of abundance, Letourneau *et al.* (2011) reported positive effects of local complexity on natural enemies, and Chaplin-Kramer *et al.* (2011) reported positive effects of landscape complexity on natural enemies (generalists, not specialists). The latter study noted no significant differences between subgroups of natural enemies, such as beetles, parasitoids, and spiders, and the former study did not compare subgroups. Our results confirm the conclusions of these authors that complexity can have positive effects on natural enemies, in general, in terms of abundance and richness combined, and at local and landscape scales combined. Our results for spiders show positive but non-significant trends in the effects of both local and landscape complexity on the abundance of spiders, and these trends support the results of the earlier authors. However, our results also show stronger and significantly positive effects on the richness of spiders, and our results on beetles and parasitoids are inconclusive. Therefore, we note that significant trends for ESPs in general might not be significant for subgroups of

ESPs, if one of these subgroups is driving the overall trend (*e.g.*, the abundance-richness difference for spiders), and future meta-analysts should take note of this when drawing conclusions about subgroups from the combined results for the group.

We used the same measure of effect size as Chaplin-Kramer *et al.* (2011), and similar statistical methods, but effects on natural enemies in our meta-analysis [Z_r = 0.1312 (abundance) and Z_r = 0.3356 (richness)] were smaller than theirs [$Z_r \approx 0.3$ (abundance) and $Z_r \approx 0.45$ (richness), estimated from their Figure 1]. Their data set suggested significant publication bias towards large effect sizes, but ours did not, possibly because our assumptions enabled us to include data reported as “non-significant” (their methods and those of these other meta-analyses did not mention their handling of “non-significant” data, and not including this data could bias results). However, the differences between our effect sizes and theirs are probably not statistically significant (looking at the confidence intervals), and we drew the same conclusion that these effects were significantly positive. Nonetheless, these differences in effect sizes might be of interest to future researchers, in parameterizing power analyses, as indeed might all of our reported effect sizes, sample sizes, and standard errors (Figures 2.1–2.3).

Conclusion

We conclude that some pollinators and natural enemies satisfy our first two criteria for synergistic management. Both pollinators and natural enemies can be positively driven by the compositional complexity of agroecosystems, at local and landscape scales. However, we are only confident that this is true of bees (pollinators) and spiders (natural enemies), not beetles or parasitoids (natural enemies), and whereas the abundance and the richness of bees were positively driven by complexity, the abundance of spiders was not (but the trend was positive, and close to significance for local complexity). This suggests that bees and spiders might be managed synergistically, but management might not have positive effects on the abundance of both (+/0). Nevertheless, it might have positive effects on the richness of both (+/+), and this might contribute to the stability of both pest-control and pollination services. Moreover, if the management of agroecosystems for greater complexity does have stronger effects on richness than abundance, as our results suggest, then it could have stronger effects on the stability than the magnitude of ecosystem services.

We cannot yet conclude that pollinators and natural enemies satisfy our third criterion—that they do not have negative interactions—because we do not yet have data on these interactions. For example, we might imagine that some species of natural enemies would prey not only on pests but also on pollinators (a tradeoff between the management of pollinators and the management of natural enemies), or that pollination might have larger effects on the yields of plants that have not been damaged by pests, because these plants have plenty of energy for seed and/or fruit production (a synergy between pollination and pest control). Therefore, we identify the interactions between pollinators and natural enemies, and their interacting effects on the productivity of crops, as gaps in our knowledge. Only one of the studies included in our meta-analysis reported data on both pollinators and natural enemies (Clough *et al.*, 2007), only four reported data on both local and landscape complexity (Clough *et al.*, 2005; Eilers & Klein, 2009; Schmidt-Entling & Dobeli, 2009; Arthur *et al.*, 2010), and the effects of one scale, or one service, might interact with the effects of another. For example, Marshall *et al.* (2006) reported that the effects of local management on spiders depended on the landscape context [*cf.* the "intermediate landscape-complexity" hypothesis (Tscharntke *et al.*, 2005, 2012; Batáry *et al.*, 2011; Kleijn *et al.*, 2011)]. Moreover, we cannot confirm that pollinators and natural enemies are affected by the same components of complexity. For example, managing a floral margin by sowing a mixture of wildflower seeds might produce a complex plant community that has positive effects only on pollinators, because the plant community might be composed of species that are not resources for natural enemies. However, in the one study that reported data on both pollinators and natural enemies (Clough *et al.*, 2007), bees, spiders, and beetles were significantly more diverse at the edges than the centres of wheat fields (*i.e.* there were positive effects of local complexity on both pollinators and natural enemies).

To bridge these gaps in our knowledge, we suggest that the simultaneous effects of land management on pest-control and pollination services should be the subject of future research at several scales, both spatial (local and landscape) and temporal (annual and seasonal), and in several systems (woody and non-woody animal-pollinated crops, with high and low proportions of non-crop habitat). We found significantly fewer studies in woody than non-woody crops, and significantly fewer studies of pollinators than natural enemies in response to local complexity, and future research should correct this bias. Not only natural enemies and pollinators, but also pests, should be researched, because it is possible that pests and pollinators might have similar drivers, and landscape complexity might not be a negative driver of pests, even if it is a positive driver of natural enemies (Chaplin-Kramer *et al.*, 2011), but crop diversification schemes might be positive drivers of natural enemies and negative drivers of pests (Letourneau *et al.*, 2011). This research could look for different effects on functionally redundant species of pollinators and natural enemies, to test the effects of management not only on the magnitude but also on the stability of pollination and pest-control services. This research could also test the specialist-generalist or cultural difference mechanism that we have suggested, and it should take place on both large-scale and/or high-intensity (*e.g.*, commercial) farms and small-scale and/or low-intensity (*e.g.*, subsistence) farms, and in both temperate and tropical agroecosystems.

Finally, future research should not limit itself to the ecology of ecosystem-service providers, but it should model the relationships between ecosystem-service providers and ecosystem services, in terms of the yield and quality of crops. In response to the common criticism that meta-analyses are unfair comparisons of dissimilar organisms—the “apples and oranges” problem (Sharpe, 1997)—some meta-analysts have argued that they were comparing “fruits” in general, and we would argue that we have been comparing beneficial arthropods in general. And yet, if this review has shown that pollinators and natural enemies are more comparable than “apples and oranges” then nonetheless we need to know that pollination and pest-control services are also comparable, and indeed compatible, in terms of crops and yields, not only arthropods. We literally need to compare them in terms of apples, oranges, and other crops, not only bees, beetles, spiders, and parasitoids.

Conservation planning in agricultural landscapes: hotspots of conflict between agriculture and nature

Introduction

From 2005 to 2050, demand for food could as much as double (Tilman *et al.*, 2011). To meet this increase in demand, it has been suggested that there should also be an increase in supply, much of which would need to come from an increase in production (The Royal Society, 2009). However, this suggestion is controversial (Lang & Barling, 2012; Tomlinson, 2013). Such an increase in production, without an increase in distribution, accessibility, and affordability, might meet the demands of the rich, but it would not meet the needs of the poor or the undernourished, and it would have a massive impact on the environment, without insuring food security or food sovereignty (Tilman *et al.*, 2001; Tscharntke *et al.*, 2012; Loos *et al.*, 2014). Moreover, an increase in demand could be met, at least in part, by a decrease in demand for livestock feed and biofuel feedstock, and a decrease in waste, without the need for such a massive increase in production (Foley *et al.*, 2011; Bajzelj *et al.*, 2014).

Agriculture has already done more damage to nature than any other human activity (Balmford *et al.*, 2012), and therefore many conservationists are opposed to an increase in production. However, in view of the "new productivism" in agricultural policy (Horlings & Marsden, 2011; Fish *et al.*, 2013), it looks to us as though an increase is likely to take place—possibly a doubling of agricultural production, and possibly a redoubling of "agribusiness-as-usual"—if the new incentives for overproduction are not replaced with new and renewed incentives for conservation, sustainable production, waste reduction, equitable distribution, accessibility, and affordability (Donald *et al.*, 2002; Schmid *et al.*, 2007; Henle *et al.*, 2008; Fischer *et al.*, 2012b; Loos *et al.*, 2014). Nevertheless, conservationists could reduce the environmental impacts of an increase in food production by answering two questions. Where would an increase in production do the most damage to conservation, and where would it do the least? In other words, where are there "hotspots" of conflict between agriculture and nature, and where are there not? The resolution of these "conservation conflicts" (Balmford *et al.*, 2001; Henle *et al.*, 2008; Dobrovolski *et al.*, 2011; Redpath *et al.*, 2013) could then be prioritized in the "hottest" hotspots.

Fundamentally, these conflicts are driven by the expansion and intensification of agriculture (Lambin & Meyfroidt, 2011; Baudron & Giller, 2014; Laurance *et al.*, 2014). Agricultural expansion takes place at the expense of biodiversity, as natural habitats are cleared to make space for farmland (Gibbs *et al.*, 2010), and habitat loss will probably be the primary driver of biodiversity loss this century (Sala *et al.*, 2000). Clearly, the "agricultural frontiers" of the world are among the hottest hotspots of conflict between agriculture and nature, such as the Amazon and Congo basins, where farmland is being carved out of the wilderness (Phalan *et al.*, 2013). However, agricultural expansion also takes place behind the front lines of these conservation conflicts, where farmland is being carved out of fragments of natural habitat, and small and diversified farms are being enlarged and simplified, often accompanied by the unsustainable use of agrochemical inputs, irrigation water, and soil, under the banner of "conventional" agricultural intensification (Benton *et al.*, 2003; Tscharntke *et al.*, 2012).

Agricultural land has the potential to be wildlife habitat, in and of itself, but it also has the potential to be a vital part of a wildlife-friendly "matrix" of agricultural and natural habitats that buffers protected areas from edge effects and facilitates the movement of wildlife between protected areas (Pimentel *et al.*, 1992; Ricketts, 2001; Hansen & DeFries, 2007; Perfecto & Vandermeer, 2010). In the emerging theory of "countryside biogeography" (Daily, 1997), the habitability and the permeability of the matrix are thought to be the main reasons that small protected areas on land—which were once thought of as "islands" of habitat in an "ocean" of uninhabitable farmland—have lower rates of local extinction, relative to large protected areas, than predicted by the theory of "island biogeography" (Mendenhall *et al.*, 2014). Therefore, the conservation of countryside biodiversity should not only be about restricting agricultural land use in strict protected areas, which has been the focus of "systematic conservation planning" (Margules & Pressey, 2000), but it should also be about buffering and connecting these protected areas with a habitable and permeable matrix (Perfecto & Vandermeer, 2010). We suggest that the matrix should be the target of a new form of systematic conservation planning in agricultural landscapes—a method of identifying agricultural landscapes of especially high quality (not only as wildlife habitats, in and of themselves, but also as buffers and connectors of protected areas), and prioritizing the resolution of conservation conflicts in these landscapes.

Systematic conservation planning is most effective when the costs and benefits of land use are analyzed and optimized (Naidoo *et al.*, 2006). Around the world, a lot of agricultural landscapes have wide "yield gaps" (where actual crop yields are much lower than potential crop yields) (Foley *et al.*, 2011; Mueller *et al.*, 2012), and the closing of the widest yield gaps would confer the greatest benefits on global food production. However, the conservation costs of closing these yield gaps has only just begun to been assessed (Cunningham *et al.*, 2013; Phalan *et al.*, 2014). We suggest that these costs and benefits should be assessed not only in terms of food production, but also in terms of wildlife conservation and the other ecosystem services that these agricultural landscapes could provide as "multiple-use modules" (Noss & Harris, 1986), in which core protected areas could be buffered and connected by a wildlife-friendly matrix.

As a conceptual framework for this cost-benefit analysis, we suggest that the conservation value of a multiple-use module is a function of the quantity and quality of wildlife habitat in the matrix, the number of species that live in or move through the matrix, and the conservation status of these species. We also suggest that the production value of a multiple-use module—and thus the potential for conservation conflict—is a function of the yield gap of the cropland (potential for intensification) and the quantity and quality of non-cropland in the agricultural matrix that could potentially be cleared to make space for new cropland (potential for expansion). As a proof of concept, we used this conceptual framework to search for hotspots of conflict between agriculture and nature, on the global scale. This enabled us to assess priorities for resolving different types of conservation conflict in different places, and it could possibly enable us to steer an increase in food production towards places with low potential for conservation conflict (but only if an increase must take place).

Methods

We used a map of global land cover to randomly sample the agricultural landscapes of the world (see Figure 3.1 for a graphical abstract of these methods). Sampling points were restricted to land that was classified as cropland. For each point, (1) we used the GlobCover 2009 map (raster data with a resolution of about 300 m at the equator) (ESA & UCL, 2010) to calculate the proportion of non-crop habitat within 2 km of that point [see below ("Supporting methods") for the classification of habitat in GlobCover], (2) we used the IUCN Red List of Threatened Species™ maps (vector data) (BirdLife International & NatureServe, 2012; IUCN, 2012) to calculate the number of "threatened" and "Near-Threatened" species of vertebrates (amphibians, birds, mammals, and reptiles) with ranges that included that point (species with potential to live in or move through the matrix), and (3) we used the Global Agro-Ecological Zones (GAEZ) maps (raster data with a resolution of about 10 km at the equator) (IIASA/FAO, 2012) to measure the ratio of actual to potential yield (the yield gap). We deleted points that had no data on yield and points that were within protected areas with restrictions on agriculture, as defined by the GAEZ classification of data from the World Database on Protected Areas.

We then used these data points on non-crop habitat (h), vertebrate species (s), and relative yield (y) to map the potential for conservation conflict (c) on the global scale. We defined c as a function of h, s, and y (Table 3.1), and we assumed that interactions between habitat and yield would result in different types of conflict. For example, we assumed that landscapes with high amounts of habitat and low yields, where an increase in food production could come from both expansion and intensification, would have a different type of conflict (Type III conflict in Table 3.1) than would landscapes with low amounts of habitat and low yields, where an increase could come only from intensification (Type II conflict). We then made heatmaps of the potential for these different types of conflict. Because of the latitudinal gradient in species richness (Whittaker *et al.*, 2001), which is a source of bias towards high c at low latitudes, we also calculated c as a function of habitat and yield only (not species). We made heatmaps by interpolating c onto a 5 arc-minute grid (a resolution of about 10 km at the equator, for comparison with the GAEZ maps) and then deleting pixels that did not have data on relative yields (GAEZ), pixels that were in protected areas with restrictions on agriculture (GAEZ), and pixels that were < 1% cropland (calculated from GlobCover).

We took a closer look at Type III conflict, which we regarded as the highest priority for conflict resolution (both expansion and intensification as a source of conflict). We classified each point as either a “case” or a “control” (Table 3.2), based on its potential for Type III conflict. For example, in analysis H1, points with c-values > 98% of all c-values were defined as cases, and other points were defined as controls. We then used spatial scan statistics to search for “hotspots” of Type III conflict. Spatial scan statistics are usually used to search for significant spatial clusters of disease or crime (hence the terms “case” and “control”), but we used them to search for significant spatial clusters of agricultural land with potential for conservation conflict. We used SaTScan™ (Kulldorff, 2013). For each data point, we searched for nearby data points (the “search area” was a circle with a radius of 100, 200, or 400 km around the data point) and we calculated the proportion of data points that were cases in each search area. We defined “hotspots” as search areas in which the proportion of cases was significantly higher than expected ($P < 0.05$), based on the proportion of cases in all search areas (Bernoulli models in SaTScan™).

We also took a closer look at Type I conflict (expansion, but not intensification, as a source of conflict). We suggest that the potential for Type I conflict is lowest in landscapes with the lowest amounts of habitat (no potential for expansion), the lowest numbers of species, and the lowest yields (potential for intensification). If an increase in food production is inevitable, then “coldspots” of Type I conflict could be the landscapes that are most beneficial for intensification (potential to close the widest yield gaps) and least costly for conservation (potential to threaten the fewest species and the lowest amounts of habitat, if the local intensification of cropland causes the local expansion of cropland into non-crop habitat, by means of the mechanism known as the “rebound effect” or the “Jevons paradox”) (Ewers *et al.*, 2009; Lambin & Meyfroidt, 2011; Phelps *et al.*, 2013). Therefore, without advocating an increase in food production, we used spatial scan statistics to search for coldspots of Type I conflict, as potential hotspots for an increase in food production. Instead of searching for low c-values (Table 3.1), we searched for high i-values (“i” for “intensification”), where $\max(i) \sim \max((1 - h) * (1 - s) * (1 - y))$, because i is maximized only if h, s, and y all have low values, whereas c is minimized if any one of h, s, or y is equal to zero, even if the other two have high values.

To test the sensitivity of these assumptions (H1 and C1 in Table 3.2), we also searched for hotspots and coldspots under other sets of assumptions (H2–H6 and C2–C6 in Table 3.2). For example, in one set of sensitivity analyses (H4 and C4) we used the proportion of grassland within 2 km to calculate h, instead of the proportion of all non-crop habitat (which we defined as grassland + woodland), because fragments of grassland in the agricultural matrix could have different values as buffers and connectors of woodland protected areas than would fragments of woodland, and *vice versa* (Ricketts, 2001). In all sets of analyses, we used search areas of different radii (100, 200, or 400 km), to test the sensitivity of these assumptions to conservation planning on different scales. We then looked for areas where hotspots or coldspots were found in all analyses (the “hottest” hotspots or “coldest” coldspots).

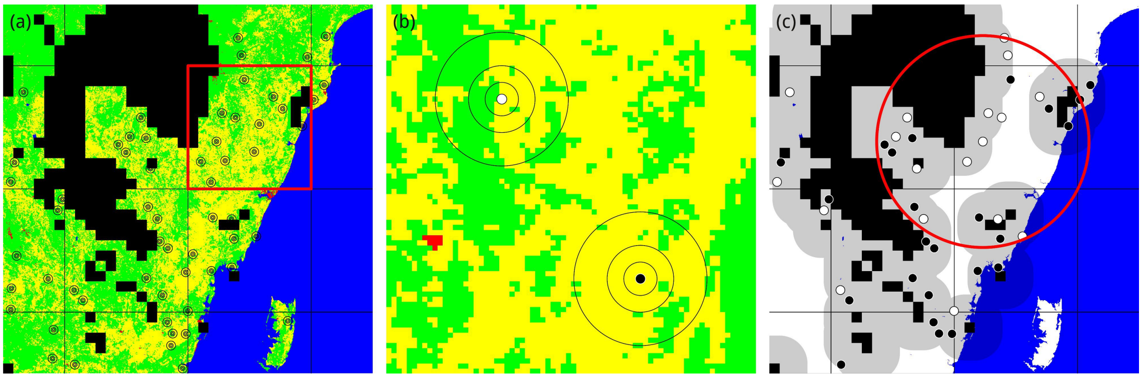


Figure 3.1 Graphical abstract of methods. (a) The globe was split into 1 x 1 degree tiles (*e.g.*, red square). In each tile, crop habitat (yellow area) was sampled with a number of points in proportion to the area of crop habitat in that tile. Points inside protected areas with restrictions on agriculture (black areas) were deleted. (b) The proportion of non-crop habitat (green area) was calculated in buffers around each point (concentric circles). The relative yield of the cropland was calculated at each point, and so was the number of “threatened” and “Near-Threatened” species of amphibians, birds, mammals, and reptiles with ranges that included that point (species with potential to live in or move through the agricultural matrix). Data from all tiles were then combined. (c) Data points were classified as either “cases” (white points) or “controls” (black points), based on the type of conservation conflict (Table 3.1), and spatial scan statistics were used to identify “coldspots” and “hotspots” in the data (areas with significantly high proportions of cases; *e.g.*, red circle). Buffer zones (gray buffers of 25 km) are shown around protected areas with restrictions on agriculture (black areas). Only the subset of data points that were inside these buffers were used in one analysis (H3 hotspots), and only the subset of data points that were outside these buffers were used in another analysis (C3 coldspots; Table 3.2).

Table 3.1 Potential for conservation conflict (c), as a function of habitat (h), species (s), and yield (y). For example, we suggest that the potential for Type III conflict is highest in landscapes with the highest amounts of habitat, highest numbers of species, and lowest yields. Thus, c is maximized as $h * s * (1 - y)$ is maximized. These variables (h, s, and y) could be given equal or unequal weights, based on the circumstances of the conflict, and thus we use the tilde (~) to suggest that these functions are approximations of the potential for conflict, not equations. For each variable (habitat, species, and yield), the measured value at each data point was divided by the maximum value at all data points, and it was thereby transformed into a proportional variable (h, s, and y). Therefore, $1 - h$ and $1 - y$ approach 0 as h and y approach 1.

Type	**Habitat (h)**	**Species (s)**	**Yield (y)**	**Potential for conflict (c)**	**Source of conflict**
I	high	high	high	$\max(c) \sim \max(h * s * y)$	expansion
II	low	high	low	$\max(c) \sim \max((1 - h) * s * (1 - y))$	intensification
III	high	high	low	$\max(c) \sim \max(h * s * (1 - y))$	both expansion and intensification
IV	low	high	high	$\max(c) \sim \max((1 - h) * s * y)$	neither expansion nor intensification

Table 3.2 A data point was defined as either a case or a control, based on its high potential for conservation conflict (*c*) or its low potential for conservation conflict (*i*). For example, for hotspot analysis H3, only data points < 25 km from protected areas were analyzed: a data point was either defined a case if its *c*-value was > 98% of all *c*-values in that analysis, or else it was defined as a control; its *c*-value was calculated from *h*, *s*, and *y* (as opposed to *h* and *y* only), using the formula for Type III hotspots; and its *h*-value was calculated using all non-crop habitat (as opposed to either grassland or woodland). For Type III hotspots, $c = h * s * (1 - y)$, and for Type I coldspots, $i = (1 - h) * (1 - s) * (1 - y)$.

Hotspots	***h***	***c***	**Type**	**Protected areas**
H1	non-crop	> 98%	III (*h*, *s*, *y*)	any distance
H2	non-crop	> 95%	III (*h*, *s*, *y*)	any distance
H3	non-crop	> 98%	III (*h*, *s*, *y*)	points < 25 km
H4	grassland	> 98%	III (*h*, *s*, *y*)	any distance
H5	woodland	> 98%	III (*h*, *s*, *y*)	any distance
H6	non-crop	> 98%	III (*h*, *y*)	any distance

Coldspots	***h***	***i***	**Type**	**Protected areas**
C1	non-crop	> 98%	I (*h*, *s*, *y*)	any distance
C2	non-crop	> 95%	I (*h*, *s*, *y*)	any distance
C3	non-crop	> 98%	I (*h*, *s*, *y*)	points > 25 km
C4	grassland	> 98%	I (*h*, *s*, *y*)	any distance
C5	woodland	> 98%	I (*h*, *s*, *y*)	any distance
C6	non-crop	> 98%	I (*h*, *y*)	any distance

Results

Sampling the cropland of the world resulted in 60,405 data points. Globally, cropland was surrounded by 44 ± 28% non-crop habitat within 2 km [mean ± standard deviation (SD)], it was potentially lived in or moved through by 11 ± 9 “threatened” and “Near-Threatened” vertebrate species (mean ± SD), and its actual yield was about 35% of its potential yield (Table 3.3). On heatmaps of the potential for conservation conflict [Figure 3.2(a–d)], the different types of conflict had distinct global distributions. For example, India was a hotspot of Type II and Type IV conflict, but not Type I or Type III conflict, whereas Indonesia and Malaysia were hotspots of all types of conflict. Therefore, on the global scale, there seemed to be potential to differentiate between regions with different types of conflict. However, the latitudinal gradient in species richness affected the global distribution of hotspots, some of which shifted to higher latitudes when *c* was calculated only from habitat and yield (not species) [Figure 3.2(e–h)]. For example, in Figure 3.2(f–g), Indonesia and Malaysia were not hotspots of Type II or Type III conflict, and large parts of Eurasia and North America, which were coldspots in Figure 3.2(a–d), were hotspots in Figure 3.2(e–h).

These heatmaps offer some insight into the distributions of different types of conservation conflict, but the visual interpretation of these heatmaps is sensitive to the density of cropland, and it is subjective. By comparison, the statistical interpretation of the underlying data points, by means of spatial scan statistics, is not sensitive to the density of cropland, and it is not subjective. In the strict consensus of hotspot analyses H1–H5, the hottest hotspots [Figure 3.3(a)] were all in sub-Saharan Africa, in three sub-regions: (1) West Africa, (2) Eastern and Southern Africa, and (3) Madagascar. In the strict consensus of coldspot analyses C1–C5, the coldest coldspots [Figure 3.3(c)] were widespread, in five regions: (1) the Sahel region of sub-Saharan Africa, (2) North Africa, (3) Eastern Europe, (4) Central Europe, and (5) South Asia. In the strict consensus of analyses H1–H6 or C1–C6, which included the analyses that used only habitat and yield to calculate the potential for conflict (H6 or C6), the results were surprisingly similar to those from the analyses that used habitat, species, and yield (Figure 3.3), but we note that there were no hotspots in Madagascar and fewer hotspots throughout sub-Saharan Africa. Thus, the effects of the latitudinal gradient in species richness were accounted for in the hottest hotspots and coldest coldspots (see Figure 3.4 for hotspots and coldspots from each analysis, H1–H6 and C1–C6).

In the hottest hotspots, cropland was surrounded by 72% ± 10% non-crop habitat within 2 km (mean ± SD), it was potentially lived in or moved through by 26 ± 9 “threatened” and “Near-Threatened” vertebrate species (mean ± SD), and its actual yield was about 15% of its potential yield (100 km search areas; Table 3.3). All of these measurements were significantly different from the global average, and this was also the case for all of the hottest hotspots and coldest coldspots (100–400 km search areas; Table

3.3). In the hottest hotspots, cropland had about 55–58% lower yield, was surrounded by 59–63% more habitat, and it was potentially lived in or moved through by 67–135% more species than the global average. In the coldest coldspots, cropland had about 44–63% lower yield, was surrounded by 24–38% less habitat, and it was potentially lived in or moved through by 5–14% fewer species than the global average.

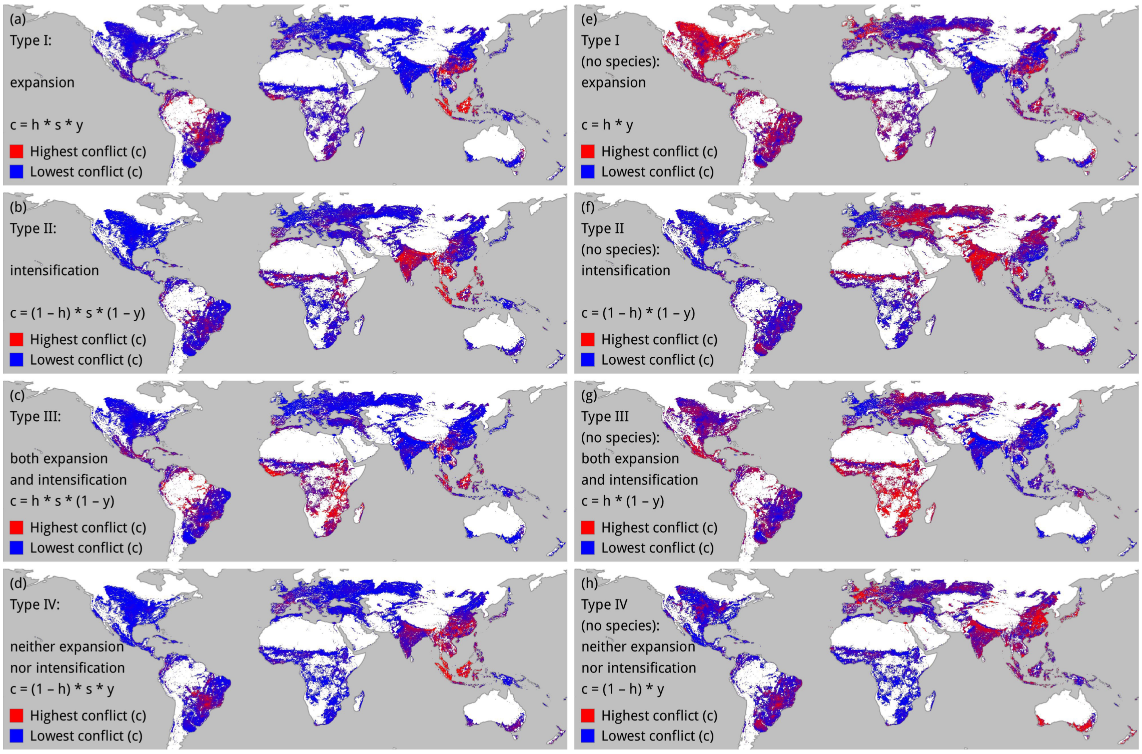


Figure 3.2 Heatmaps of the potential for conservation conflict (*c*), as a function of the proportion of non-crop habitat (*h*) within 2 km of cropland, the number of “threatened” and “Near Threatened” species (*s*) of amphibians, birds, mammals, and reptiles with potential to live in or move through cropland, and the relative yield (*y*) of cropland (panels a–d), or, as above, but as a function of habitat (*h*) and yield (*y*) only, not species (*s*) (panels e–h).

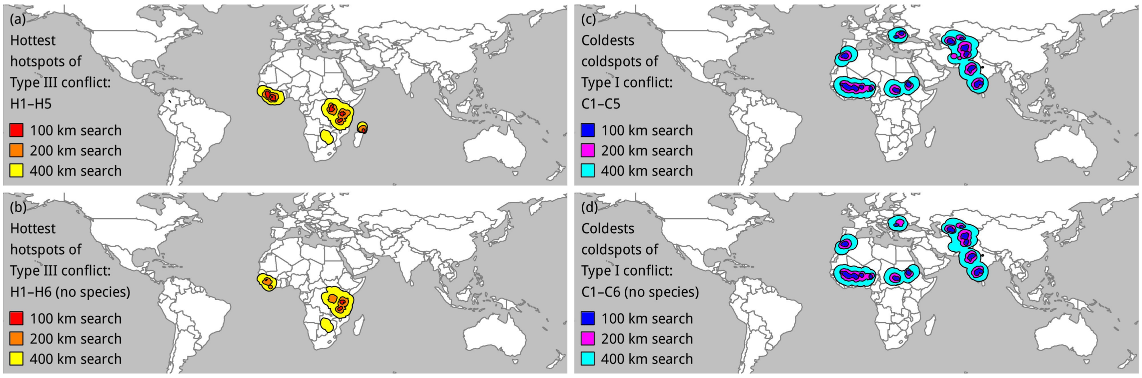


Figure 3.3 The hottest hotspots of Type III conflict and the coldest coldspots of Type I conflict. The hottest hotspots are the intersections between all of the hotspots (Figure 3.4) that resulted from (a) analyses H1–H5, or (b) analyses H1–H6, which included the analysis (H6) that was not based on species. The coldest coldspots are the intersections between all of the coldspots (Figure 3.4) that resulted from (c) analyses C1–C5, or (d) analyses C1–C6, which included the analysis (C6) that was not based on species.

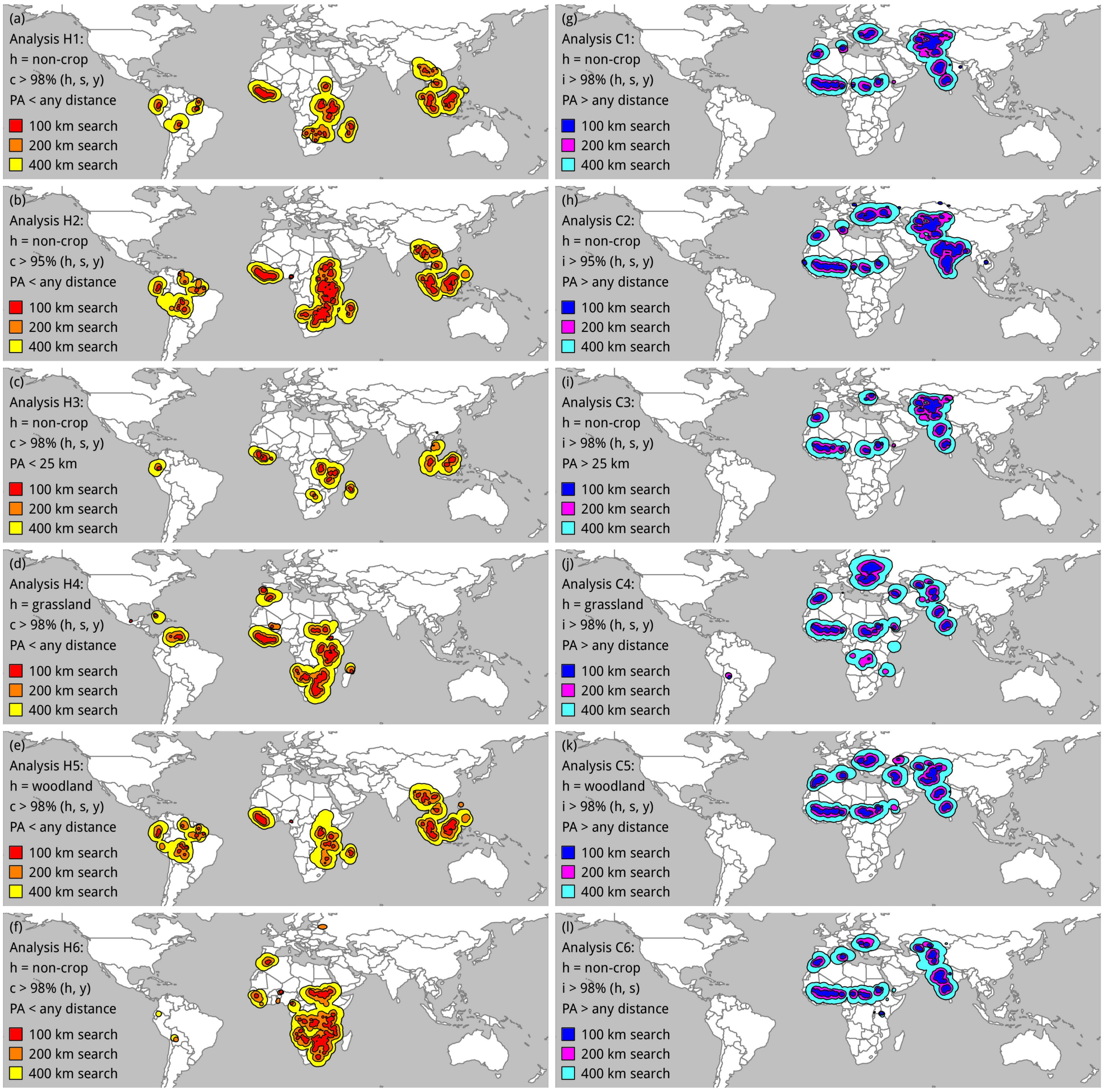


Figure 3.4 Hotspots and coldspots from each analysis (H1–H6 and C1–C6).

Table 3.3 Comparison of data points in the hottest hotspots (H1–H5), the coldest coldspots (H1–H5), and the world: the number of cropland points (*N*), the percentage of non-crop habitat within 2 km of the average point (Habitat), the number of “threatened” and “Near-Threatened” vertebrate species with ranges that included the average point (Species), and the relative yield of the average point, both as a percentage of its potential yield (Yield) and also as its GAEZ yield category (GAEZ), in which 1 is the lowest yield and 7 is the highest yield (average values are shown as mean ± standard deviation (SD)). Comparisons between spot averages and global averages were made using *t*-tests in which t = (spot mean – world mean) / (spot SD / √ spot N), and degrees of freedom = spot N – 1. Because of the high sample sizes (*N*), the *P*-values for all comparisons between spot averages and global averages were significant ($P < 0.0001$), and therefore no *P*-values are shown in the table.

Points	**Search**	***N***	**Habitat**	**Species**	**Yield**	**GAEZ**
H1–H5	100 km	490	72 ± 10%	26 ± 9	15%	2.3 ± 0.5
	200 km	1,101	71 ± 13%	23 ± 8	15%	2.3 ± 0.5
	400 km	2,539	70 ± 15%	19 ± 7	16%	2.4 ± 0.6
C1–C5	100 km	2,495	27 ± 24%	10 ± 3	13%	2.2 ± 0.7
	200 km	5,071	31 ± 25%	10 ± 4	16%	2.4 ± 0.8
	400 km	9,855	34 ± 26%	11 ± 5	20%	2.7 ± 0.8
World	NA	60,405	44 ± 28%	11 ± 9	35%	3.7 ± 1.2

Discussion

Recent debate about the resolution of conservation conflict has been framed in terms of "land sharing" (extensive agriculture that is wildlife-friendly) *versus* "land sparing" (intensive agriculture that is less wildlife-friendly but also less extensive) as methods of growing the most food while doing the least damage to nature (Green *et al.*, 2005; Phalan *et al.*, 2011). It has been concluded that both sharing and sparing could be useful tools for conflict resolution (Hodgson *et al.*, 2010; Tscharntke *et al.*, 2012; Baudron & Giller, 2014; Fischer *et al.*, 2014) However, we suggest that what is needed now is an evidence-based framework for deciding where to implement these tools, with limited amounts of time, money, and land, and how to use these tools to build resilience into the conservation planning system, by buffering and connecting protected areas with habitable and permeable agricultural landscapes.

If the debate between land sharing and land sparing were framed in these terms —that is, in terms of countryside biogeography—then the question would not be *whether* to share land or spare land, but *where* to share and where to spare, in order to maintain the habitability and permeability of the agricultural matrix. The answer to this question would depend upon the type of conservation conflict (expansion, intensification, both, or neither). For example, in hotspots of Type IV conflict (low habitat, high species, high yield), neither would there be a lot of land to spare, nor would there be a lot potential for increased yield to spare land elsewhere, and therefore land sharing could be a higher priority in these hotspots. However, our aim here is not to suggest that sharing should be a higher priority than sparing, or *vice versa*, as a resolution to any particular type of conservation conflict. Instead, our aim is to suggest that both sharing and sparing should be higher priorities in hotspots of conservation conflict than they should be in agricultural landscapes with lower potential for conflict. Therefore, our aim is to suggest that hotspots of conservation conflict could and should be defined and identified.

The present search for hotspots is only a proof of concept, and future research is needed to further develop this concept, and to search for hotspots on scales that are appropriate for conflict resolution. Conservation planning on the global scale has the potential to confer greater benefits and impose lesser costs on nature than conservation planning on finer scales, if the costs and benefits of agriculture are also addressed (Dobrovolski *et al.*, 2014), and therefore the global scale could be an ideal starting point for conservation planning in agricultural landscapes. Conservation and production plans on the national scale have led to the "exportation" of conservation conflicts to developing nations, through the importation of agricultural products by developed nations (Lambin & Meyfroidt, 2011), and thus the plans that are made on the national scale are not independent of trade on the global scale. However, agricultural, ecological, economic, political, and social processes take place on multiple scales and have multiple stakeholders (Sayer *et al.*, 2013), and therefore we suggest that hotspots of conservation conflict should be defined and identified on multiple scales, from local to global (Moilanen & Arponen, 2011; Gonthier *et al.*, 2014), in the context of global trade and the need for local food security and food sovereignty ("distributive" and "procedural" justice) (Loos *et al.*, 2014). In this complex context, our definition of conservation conflict, in terms of habitat, species, and yield only, is obviously an oversimplification. Nevertheless, the limitations of the present search should be seen as possibilities for future research in multiple fields, under multiple sets of assumptions about the value of conservation and production.

For example, we assumed that agricultural landscapes with the most habitat had the highest conservation value (hotspots of Type III conflict). In future research, it could be assumed that landscapes with the least habitat have the highest conservation value, because they could be the last refuges of endemic species, and indeed "biodiversity hotspots" have been identified as landscapes that have lost at least 70% of their natural habitat (Myers *et al.*, 2000). However, we assumed that agricultural landscapes should not be replacements for protected areas, and therefore they should not be evaluated in terms of unprotected species that they could protect on their own, but in terms of species that are nominally protected now (in protected areas) but would not be effectively protected in the future, if these protected areas were to become isolated in an "ocean" of uninhabitable and impermeable agriculture. The effectiveness of protected areas depends on the area of unprotected habitat in the landscapes that surround them (Wiersma *et al.*, 2004), and thus we assumed that agricultural landscapes with the most habitat had the highest conservation value. Therefore, hotspots of Type III conflict are "proactive" as opposed to "reactive" (Dobrovolski *et al.*, 2011; Phalan *et al.*, 2013). However, in future research, it could be assumed that "reactive" conflicts over low levels of habitat (such as Type II and Type IV conflict) should be higher priorities.

We also assumed that agricultural landscapes with the most species had the highest conservation value. This is ethically utilitarian ("the greatest happiness of the greatest number"), and it was based on threat and vulnerability, but other methods of assessment could be used, such as those based on complementarity, representativeness, or any of the core methods of systematic conservation planning (Kukkala & Moilanen, 2013). As opposed to endemism, it could also be assumed that "cosmopolitanism" should be a high priority for conservation planning in agricultural landscapes, because species with wide ranges could have high vulnerability to low matrix quality. However, the extinction of the passenger pigeon, which was widely ranging, but "endemic" to only one type of widely-ranging habitat (Bucher, 1992), exemplifies the limitations of such assumptions.

Considering the costs that some species impose on agriculture (such as elephants that raid crops or lions that kill livestock) and the benefits that some species bestow on agriculture (such as bees that pollinate crops and wasps that kill crop pests), it could be assumed that potential for conservation conflict is highest where the perceived costs outweigh the perceived benefits by the most, and where the species that impose these costs are species of the greatest conservation concern. Research on pollination and pest control has shown that both of these ecosystem services are enhanced by high proportions of non-crop habitat (Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011), and indeed the standard methods in research on pollinators and natural enemies (Shackelford *et al.*, 2013; see Chapter 2) motivated us to sample non-crop habitat as we did, within 2 km of cropland. Therefore, it is possible that "damage costs" from crop raiders and livestock predators and "opportunity costs" from the forgone expansion of cropland (Naidoo *et al.*, 2006) could be offset by benefits from the conservation of natural habitats, such as pollination, pest control, water catchment, and erosion control (Power, 2010). Indeed, the harnessing of ecosystem services for the "ecological" intensification of agriculture (Bommarco *et al.*, 2013) could be vital to conflict resolution, as could payments for ecosystem services, such as carbon storage (Turner *et al.*, 2012; Venter *et al.*, 2013).

In future research, it could also be assumed that agricultural landscapes at different distances from protected areas should have different levels of priority. For example, it was assumed that the intensity of land use in "multiple-use modules" would increase at increasing distances from core protected areas (Noss & Harris, 1986). It is not known whether there is some distance at which unprotected areas would have the strongest effects on conservation in protected areas, but some studies have assumed that areas within 25 km of protected areas would need to be "buffer zones" (Wiersma *et al.*, 2004; DeFries *et al.*, 2005; Beaumont & Duursma, 2012). Therefore, we searched a subset of points that were < 25 km from protected areas (H3), and this caused a lot of hotspots in South America, South East Asia, and sub-Saharan Africa to be subtracted from the strict consensus. Thus, the definition of buffer zones could be vital to the identification of hotspots.

Similarities and differences between protected areas and the habitats that buffer them could also be vital. For example, grassland protected areas might be well buffered by a matrix of grassland habitats, but not by a matrix of woodland habitats, if these habitats differ in their habitability and permeability to grassland species (Ricketts, 2001; Wright *et al.*, 2012; Cunningham *et al.*, 2013) or in their ability to maintain energy flows or disturbance regimes, such as grassland fires that are started by lightning (Hansen & DeFries, 2007). The analysis based on grassland (H4) caused all of the hotspots in South America and South East Asia to be subtracted from the strict consensus, and the analysis based on woodland (H5) caused many of the hotspots in sub-Saharan Africa to be subtracted. Therefore, even though the hottest hotspots were found only in sub-Saharan Africa (where evidently there are significantly high proportions of both grassland and woodland surrounding cropland), parts of both South America and South East Asia would probably be hotspots in future research on woodland protected areas (Figure 3.4).

All of the hottest hotspots, and a lot of the coldest coldspots, were in sub-Saharan Africa. This should be seen as a warning that the "sustainable" intensification of sub-Saharan Africa (Pretty *et al.*, 2011) should proceed only with extreme caution, because sub-Saharan Africa is a huge and heterogeneous region, in which the different sub-regions could have vastly different potentials for conservation conflict. If need be, the coldest coldspots could be considered hotspots for sustainable intensification, but conservation conflict should not be the only consideration here, because the "sustainability" of "sustainable" intensification is controversial (Loos *et al.*, 2014), especially in ecologically fragile sub-regions, such as the Sahel (Tappan & McGahuey, 2007). Central Asia, which also had a lot of the coldest coldspots, also has a history of unsustainable intensification (Cai *et al.*, 2003). We need much more research on soil and water conservation (Foley *et al.*, 2011; Mueller *et al.*, 2012), and the regulation of agrochemicals (Jepson *et al.*, 2014), before we can be confident in the "sustainable" label on agricultural intensification in these regions. We also need much more research on "ecological" intensification in these regions (Steward *et al.*, 2014).

A recent analysis by Phalan *et al.* (2014) considered the conservation consequences of closing (or failing to close) yield gaps. This is the only other analysis (that we know of) that has considered global spatial priorities for nature conservation in agricultural landscapes. Their analysis was framed as a spatial prioritization of either intensification (closing yield gaps and thereby sparing land) or expansion (failing to close yield gaps and thus expanding cropland), whereas our analysis was framed as a spatial prioritization of either production (whether by intensifying or expanding cropland) or conservation (whether by sharing or sparing). They analyzed the interactions between birds and future land use (proportion of cropland), whereas we analyzed the interactions between vertebrates and present land use (proportion of non-cropland that could be cleared or degraded). There was some consensus between our analyses, and this gives us some confidence in our results. For example, in their analysis, Eastern Europe seemed to be among the highest priorities for intensification and the lowest priorities for bird conservation, and in our analysis some of the coldest coldspots of conservation conflict were also in Eastern Europe. In their analysis, parts of the Great Rift Valley, along the African Great Lakes, seemed to be some of the highest priorities for both intensification and bird conservation, and some of the hottest hotspots of conservation conflict were also in these areas in our analysis.

When we searched for hotspots based on the top 95% of points (H2), we found a lot more hotspots than we did based on the top 98% of points (H1), and all of these hotspots could also be prioritized for conflict resolution, if time and money were unlimited. However, the hottest hotspots were all in sub-Saharan Africa, and it could be that our limited time and money should be spent on conflict resolution in sub-Saharan Africa, but this proof of concept should be seen as a call for research, not a call to arms for either conservation or production in either hotspots or coldspots. Moreover, there was high potential for at least one type of conservation conflict in most regions (Type I–IV heatmaps), and the global scale is only one of many scales. Furthermore, the many limitations of the underlying data sets [see below ("Supporting methods")] should be seen as a further call for research and a reason to be circumspect when drawing conclusions from our results.

In conclusion, we suggest that hotspots of conservation conflict could and should be identified, as part of an "assessment phase" in conflict resolution (Henle *et al.*, 2008). But should we fight for nature in these hotspots, or should we cede the field to agriculture, and fight for nature where the costs are lower? To answer these questions scientifically and systematically, we could use cost-benefit analysis to optimize land use. Ethically, however, the answer is not that easy. The value of nature cannot be defined only in terms of the number of species in a landscape, and as we optimize the conservation planning system, we would do well to respect the fact that some things cannot be optimized (Fischer *et al.*, 2014).

Supporting methods

We used R (v3.0.0) (R Core Team, 2013) and QGIS (v2.0) (QGIS Team, 2014) to handle the geospatial data. In particular, we used the R packages *ggplot2*, *gstat*, *raster*, *rgdal*, and *rgeos* (Pebesma, 2004; Wickham, 2009; Bivand & Rundel, 2013; Bivand *et al.*, 2013; Hijmans, 2014) to generate random sampling points in the cropland of the world, to extract data from these sampling points, and to map the results. We used the GlobCover 2009 global land-cover map (ESA & UCL, 2010) to calculate the proportion non-crop habitat surrounding each cropland point. This map was too large to load into R and so we split it into smaller tiles (1° longitude x 1° latitude) for sampling and extracting data (Figure 3.1). Within the cropland of each tile, we generated a number of random points in proportion to the area of cropland (*i.e.* we sampled with equal effort per unit area of cropland), and we then calculated the proportion of non-crop habitat within 1–4 km of each point, based on standard methods in landscape ecology (Shackelford *et al.*, 2013; see Chapter 2). We specified a minimum distance of 8 km between points, so that 4 km radii did not overlap and points were independent samples of land cover from 1–4 km. We did not see clear distinctions between the global distribution of non-crop habitat within 1, 2, and 4 km of cropland, and therefore we used the data on non-crop habitat within 2 km for all analyses.

We defined "cropland" as GlobCover classes 11 and 14 (irrigated and rainfed cropland) and a percentage of classes 20 and 30 (mosaic cropland and mosaic vegetation; see below), we defined "non-crop habitat" as classes 40–180 (grassland, shrubland, forest, etc.) and a proportion of classes 20 and 30 (mosaic cropland and mosaic vegetation; see below), and we did not include classes 190–230 (artificial, bare, permanent snow and ice, water, or no data classes) in calculations of land cover. The proportion of non-crop habitat surrounding a point was calculated by dividing the total area of non-crop habitat by the total area of land, not including classes 190–230 (*e.g.*, not including water), so that the results were not biased against croplands surrounded by these classes (*e.g.*, croplands on the coast). GlobCover classes 20 and 30 have variable percentages of crop and non-crop habitat. Class 20 ("mosaic cropland") is 50–70% cropland and class 30 ("mosaic vegetation") is 20–50% cropland. We defined "mosaic cropland" as 60% cropland (and thus 40% non-crop habitat), and we defined "mosaic vegetation" as 35% cropland (and thus 65% non-crop habitat), for the purposes of calculating the proportion of non-crop habitat surrounding each point. We split all non-crop habitat into either "grassland" or "woodland". We defined "woodland" as 100% of classes described as "forest" or "shrubland" (classes 40–100, 130, 160, and 170), plus 60% of class 110 (a "mosaic" class, which is 50–70% "forest or shrubland"), plus 40% of class 120 (another "mosaic" class, which is 50–70% "grassland"), plus 50% of class 180 ("grassland or woody vegetation on regularly flooded or waterlogged soils"), plus 50% of the non-crop habitat in the aforementioned "mosaic" classes (20% of class 20 and 32.5% of class 30; see above), and we defined "grassland" as 100% of classes described as "grassland or savannah or lichens/mosses" or "sparse vegetation" (100% of classes 140 and 150), plus the remainder of the non-crop habitat in the mosaic classes (classes 20, 30, 110, 120, 150, and 180; see above), such that total "non-crop habitat" = "grassland" + "woodland".

We refer to "protected areas" throughout the text, and we mean "protected areas where restricted agricultural use is permitted" and "strictly protected areas where agricultural use is not permitted" in terms of the GAEZ definitions of these areas. These definitions were based on the World Database of Protected Areas Annual Release 2009 and the NATURA 2000 network—80% of these areas are "strictly protected" areas (*e.g.*, IUCN II National Parks), and 20% are "protected" areas with restrictions on agriculture (*e.g.*, IUCN V Managed Resource). Please see the GAEZ documentation for details (Fischer *et al.*, 2012a). Clearly, there are conservation conflicts on "agricultural frontiers" of the world, at the edge of the wilderness, such as the Amazon and Congo basins, and much of this wilderness is not protected. However, we assumed that conservation planning in agricultural landscapes would not be a replacement for protected areas. We trust that wilderness areas will be designated as protected areas when and where it is possible to do so, and they could then be included in future searches for hotspots of conservation conflict.

We used Bernoulli models in SaTScan™ v9.2 (Kulldorff, 1997, 2013) to search for areas with significantly high proportions of cases ($P < 0.05$). We used SaTScan™ for several reasons. It enabled us to use unprojected coordinates (latitude and longitude), whereas many of the other methods of cluster analysis that we considered did not, and the use of projected coordinates would have resulted in unnecessary distortions to this global analysis. SaTScan™ also accounted for the density of cropland in a search area, by testing for the proportion of cases in each search area, rather than the number of cases, and this resulted in a test statistic for each search area, from which its *P*-value was calculated. We used the default settings in SaTScan™, except that we limited our searches to maximum areas of 100, 200, or 400 km around each point, and we set no restrictions on cluster centers (such that hotspots could overlap, and thus the maximum search areas did not restrict the size of the hotspots, because many small hotspots that overlapped could form hotspots that were larger than the maximum search area). We used the coordinates of the data points as the centers of the search areas (the "coordinates file").

We assumed that points could be prioritized in terms of their relative values (*e.g.*, points with *c*-values that were higher than 98% of other *c*-values were cases). In future research, a balance should be found between points that would seem to be the highest priorities, because they have "superlative" values (*e.g.*, they have the highest proportions of natural habitat), and areas that would not seem to be the highest priorities, but probably should be, because they surpass an agriculturally, biologically, or ecologically meaningful threshold (*e.g.*, they have enough natural habitat to support a minimum viable population of a threatened species), even though they do not have "superlative" values.

In the GlobCover 2009 land-cover map, only about 70% of the land cover was accurately classified (Bontemps *et al.*, 2011). Nonetheless, GlobCover 2009 was the most recent and highest resolution global land-cover map that we knew of (it has a resolution of about 300 m at the equator), and therefore we suggest that it was the most appropriate map for measuring land cover within relatively small distances of cropland points (1–4 km). However, it was not possible to use this map to differentiate between plantation forests and natural forests, for example, or to differentiate between intensive grasslands and extensive grasslands or natural grasslands, and thus it is not possible to argue that the "non-crop habitats" in this analysis are "natural" or "semi-natural" habitats. Nonetheless, "non-crop habitats" are sources of heterogeneity in farming landscapes, and heterogeneity is a driver of biodiversity and ecosystem services (Benton *et al.*, 2003; Shackelford *et al.*, 2013).

The number of threatened species has limitations as a proxy for biodiversity value or vulnerability to agriculture. Only a small proportion of all species are on the IUCN Red List of Threatened Species™, only half of these species have geospatial data, and thus there could have been spatial bias in this search for hotspots, based on spatial bias in the research on threatened species. We had no data on the value of these species in terms of cultural benefits (*e.g.*, as charismatic or endemic species) or in terms of agricultural costs (*e.g.*, as crop raiders or livestock predators), and we had no data on the vulnerability of these species to agricultural intensification (data which does not exist on a global scale, except for extrapolated data on birds) (Phalan *et al.*, 2014).

The data on yield gaps are rough estimates on a coarse scale (Fischer *et al.*, 2012a), and closing these yield gaps might not be possible, if investments in rural infrastructure and agricultural inputs are not forthcoming, in which case the agricultural landscapes with the widest yield gaps might not be at maximum risk of agricultural intensification. However, these landscapes might then be at maximum risk of agricultural expansion, if the local food supply is unable to meet the local food demand. Thus, landscapes with wide yield gaps might nevertheless be hotspots of conflict between agriculture and nature.

Closing yield gaps in areas of food insecurity, or areas with high rural populations and low rural incomes, might be vital for reducing pressures on natural habitats, and data on human populations in the buffer zones of protected areas might be an important predictor of the effectiveness of protected area (Wiersma *et al.*, 2004). We did not use any sociological or economic data sets in searching for hotspots of conservation conflict. However, in Africa, where we found all of the hottest hotspots of conservation conflict, human populations are high where species richness is high (Balmford *et al.*, 2001).

Because of all these limitations, we stress that the present search for hotspots is only a proof of concept, and further research based on this conceptual framework would benefit not only from better biological data but also from economic, political, and sociological data. Furthermore, “monetized data” on biological, sociological, and economic costs and benefits should be used to complement the “non-monetized data” (“threat” and “distance-function” data) that we used in this search for hotspots (Naidoo *et al.*, 2006). Data on the cost of land in different areas would be especially useful, since the expansion of cropland could be a stronger driver of habitat loss in places with lower land costs.

Impediments to the joint management of arthropod-mediated ecosystem services: a case study of trap-nesting pollinators and natural enemies in East Africa

Introduction

The joint management of multiple ecosystem services—balancing costs and benefits, minimizing tradeoffs, and maximizing synergies—has become a motivational goal of multiple fields of research, one of which is landscape ecology (Bennett *et al.*, 2009; Power, 2010; Raudsepp-Hearne *et al.*, 2010). Two ecosystem services that have the potential for joint management in agricultural landscapes are crop pollination and pest regulation (*e.g.*, Kremen *et al.*, 2007; Isaacs *et al.*, 2009; Bommarco *et al.*, 2013; Shackelford *et al.*, 2013). The joint management of these two ecosystem services could be vital to food security, as part of the "ecological" intensification of agriculture (Klein *et al.*, 2007; Bommarco *et al.*, 2013), and it could also be vital to the resolution of conflict between agriculture and nature (Chapter 3). However, there are wide gaps in our knowledge of how to jointly manage pollinators and natural enemies (Chapter 2).

In a meta-analysis of pollinators and natural enemies (Chapter 2; Shackelford *et al.*, 2013), the abundance and species richness of bees (pollinators) and the species richness of spiders (natural enemies) were higher when they were sampled in croplands that were surrounded by high proportions of non-crop habitats, and therefore it might be possible to jointly manage the pollinators and natural enemies that live in and around croplands by conserving the non-crop habitats that surround these croplands. These non-crop habitats, such as hedgerows and woodlots, are thought to be sources of food, shelter, and other resources that are used by both pollinators and natural enemies (Roulston & Goodell, 2011). However, the above meta-analysis was based on pollinators or natural enemies that were studied at different times and different places, using different methods (such as pan traps, pitfall traps, transect walks, or trap nests). Therefore, one gap in our knowledge is that we do not know which species of pollinators and natural enemies will prove to have compatible responses to habitat management, when studied at the same time, in the same place, and using the same methods. Pollinators, pests, and natural enemies of pests have only just begun to be compared in the field, and some of them seem to have incompatible responses to habitat gradients (*e.g.*, Otieno *et al.*, 2011, who found that pollinators and pests had similar responses to land use).

Another gap in our knowledge is that we do not know which species of pollinators and natural enemies will have compatible responses to climate change, or how communities of pollinators and natural enemies will disassemble as different species move to higher latitudes or higher altitudes at different rates. Elevation gradients have been used to study the distributions of pollinators or natural enemies in response to climate change (Hodkinson, 2005; Marini *et al.*, 2012), but not pollinators and natural enemies at the same time, in the same place, or using the same methods. As elevation increases, rainfall increases and temperature decreases. However, these spatial changes in climate are not ideal substitutes for temporal changes in climate, because changes in elevation are correlated with changes in other variables, such as changes in the partial pressures of respiratory gases (oxygen and carbon dioxide), changes in UV radiation, and changes in wind speed (Hodkinson, 2005). Whether or not the distributions of insects on elevation gradients are caused by climate or correlated with some other aspect of elevation, the observation of pollinators and natural enemies on "steep" environmental gradients is nonetheless useful for bridging the gaps in our knowledge of community disassembly in response to environmental changes (Hodkinson, 2005; Grytnes & McCain, 2007; Hoiss *et al.*, 2012). These knowledge gaps need to bridged, and management plans need to be made, if we aim to "harness" the ecosystem services of pollinators and natural enemies, in order to "ecologically" intensify agriculture (Kremen, 2005; Letourneau & Bothwell, 2008; Bommarco *et al.*, 2013).

Much of what we do know about pollinators and natural enemies is based on research that has been biased against smallholder agriculture (Steward *et al.*, 2014), which has been referred to as the "backbone" of food security (Tscharntke *et al.*, 2012a), and biased against agriculture in developing regions, such as sub-Saharan Africa (Steward *et al.*, 2014; and see Chapter 2). These biases need to be corrected. Worldwide, many of the widest gaps between actual crop yields and potential crop yields are in sub-Saharan Africa (Chapter 3), and the conventional intensification of agriculture could have massive impacts on biodiversity and ecosystem services, if croplands are simplified, non-crop habitats are cleared, and agrochemicals are allowed to "spill over" from cropland into non-crop habitats (Benton *et al.*, 2003; Brittain *et al.*, 2010; Baudron & Giller, 2014; and see Chapters 2 and 3). However, the effects of agricultural intensification on pollinators and natural enemies have only just begun to be studied in sub-Saharan Africa, and the negative effects that have been widely found in North America and Western Europe have not yet been widely found in sub-Saharan Africa (but see Gemmill-Herren & Ochieng', 2008), whereas neutral and positive effects of intensification have been found in some African agroecosystems (Hagen & Kraemer, 2010; Otieno *et al.*, 2011; Classen *et al.*, 2014), and "intermediate" amounts of intensification might even be expected to increase the biodiversity of some of these very complex landscapes (Kleijn *et al.*, 2011; Tscharntke *et al.*, 2012b). Climate change could also have especially severe effects on agriculture in sub-Saharan Africa (Thornton *et al.*, 2011), but climate-mediated impacts on pollination, pest regulation, and other "arthropod-mediated ecosystem services" (Isaacs *et al.*, 2009), which in turn will have impacts on agriculture in sub-Saharan Africa, are wide gaps in our knowledge.

Habitat loss, as a result of agricultural expansion and intensification, will probably continue to be the greatest threat to terrestrial biodiversity in this century, but the second greatest threat will probably be climate change (Sala *et al.*, 2000), and the effects of agricultural expansion and intensification could have interactions with the effects of climate change (Stefanescu *et al.*, 2011; Larsen, 2012; Marini *et al.*, 2012). For example, changes in agricultural land use (such as clearing woody vegetation) could cause changes in microclimate (such as lowering humidity and raising temperature), and these changes could interact with the effects of global warming, resulting in climatic conditions that are more extreme in agricultural landscapes with lower proportions of woody vegetation (Larsen, 2012). Therefore, we need to know how pollinators and natural enemies respond to changes in climate at the same time as they respond to changes in land use. Specifically, we need to know whether pollinators and natural enemies—when sampled at the same time, in the same place, and using the same sampling methods—have compatible responses to change in land use and changes in climate, especially in sub-Saharan Africa. We also need to know whether there are specific methods of habitat management, such as the provision of supplemental nesting sites for bees and wasps, which we could use to conserve and eventually to “harness” the services of pollinators and natural enemies. To bridge these gaps in our knowledge, a community of cavity-nesting bees and wasps was observed on a gradient of climate (elevation) and a gradient of habitat (woody vegetation), in the smallholder agricultural landscapes of the Taita Hills, Kenya.

Trap nesting is a method of sampling bees and wasps that nest in natural cavities, such as hollow plant stems, by providing them with artificial nesting sites, such as bundles of paper drinking straws or blocks of wood that have been drilled with holes (*e.g.*, Krombein, 1967; Tscharntke *et al.*, 1998; Steffan-Dewenter, 2002; Hoehn *et al.*, 2009; Schüepp *et al.*, 2011). Trap nesting has three properties that were especially appropriate for this study. Firstly, trap nesting is a method of passive, long-term sampling, and therefore it accounts for the meteorological and seasonal effects of elevation, whereas the short-term, active sampling of bees and wasps is often limited to sunny and windless days, which are less typical of high elevations. Secondly, trap nesting is potentially a method of sampling both pollinators and natural enemies using the same sampling method. Thirdly, trap nesting is potentially a method of sampling pollinators and natural enemies that might be amenable to management, through the provision of supplemental nesting sites (Bosch & Kemp, 2002). Several species of trap-nesting bees, such as the alfalfa leaf-cutting bee (*Megachile rotundata*) and two species of orchard bees (*Osmia* spp.), have been successfully managed as commercial pollinators of crops (Bosch & Kemp, 2002; Pitts-Singer & Cane, 2011). Trap-nesting wasps have not yet been successfully managed as natural enemies of crop pests, but there have been attempts to manage trap-nesting wasps (*Ancistrocerus gazella*) as natural enemies of caterpillars in fruit crops (Harris, 1994; Wearing & Harris, 2005), and supplemental nesting sites have been used to increase populations of paper wasps (*Polistes* spp.) in tobacco crops, as natural enemies of tobacco and tomato hornworms (*Manduca* spp.) (Rabb & Lawson, 1957).

Methods

Selection of sites on climate and habitat gradients

A digital elevation model [the ASTER Global Digital Elevation Model (GDEM) version 2 (METI / NASA, 2011)] was used to divide the agricultural landscapes of the Taita Hills into random sampling strata, such that each sampling stratum represented 50 meters of an elevation gradient, from 600–1700 meters above sea level (masl). Geographical information system (GIS) software [QGIS version 1.7 (QGIS Team, 2012)] was used to delete pixels that had slopes > 6 degrees, and thus to select sampling sites in flat valleys, which were well represented in the Taita Hills by slopes < 6 degrees (personal observation)]. This was done to minimize variation in the data that could have been correlated with variation in slope. In each sampling stratum, twenty random points were generated. A handheld GPS unit [the Garmin eTrex® 20 (Garmin International Inc., Olathe, Kansas, USA)] was then used to find these points in the field.

The aim was to sample pollinators and natural enemies in crop fields, which is where they need to be if they are going to pollinate crops or control crop pests. Therefore, a point was rejected if it was not typical of cropland in the Taita Hills, and typical cropland was defined as a point with maize or maize stubble within 25 meters, because maize is grown on almost all farms in the Taita Hills, and maize plots are small (0.9 ha, or 90 x 100 m) (Soini, 2005). This was done to minimize variation in the data that could have been correlated with variation in land use. A point was also rejected if the owner of the cropland could not be found or would not grant access to his or her land. If a point was rejected, then the next closest point in the sampling stratum was found and assessed, until two points had been found and accepted in each sampling stratum. This resulted in eighteen sampling sites, with elevations from 650–1680 masl, and with two sampling points within each sampling site (Figure 4.1 and Table 4.1). Thus, the sampling points were selected based on elevation (the climate gradient), but not based on woody vegetation (the habitat gradient).

Data loggers [Thermochron® iButtons® (model DS1921G, Maxim Integrated, San Jose, California, USA)] were used to measure the temperature at each sampling site (Figure 4.2), and simple plastic buckets, fitted with funnels (300 mm diameter), were used to measure the rainfall at each sampling site. The temperature was automatically measured every hour, but the rainfall had to be measured manually, and that was only possible every two weeks, when site visits were possible. Evaporation between site visits must have caused a decrease in the accuracy of the rainfall measurements and an increase in the strength of the (negative) correlation between rainfall and temperature, because there must have been higher rates of evaporation where there were higher temperatures, such as the hotter and drier lowlands of the Taita Hills. However, rainfall was less strongly correlated with elevation than was temperature (Figure 4.3). Moreover, the reason that rainfall was measured was to account for differences between sites for which differences in temperature did not account—sites that were relatively drier than would have been predicted from the correlation between temperature and rainfall—and a stronger correlation between the two could have caused a decrease in the significance of both, in statistical models, but it would not have systematically biased the study.

Satellite images (available at earth.google.com and bing.com/maps) were used to calculate the proportion of woody vegetation within 250 m of each sampling point (Table 4.1). A buffer of 250 m (radius) was generated around each sampling point, and the satellite images were used to draw polygons around the woody vegetation within each buffer. The area covered by woody vegetation within each buffer was calculated as a proportion of the total area within each buffer. A buffer of 250 m was used, because land cover within shorter distances (250–750 m) was found to be a better predictor of the species richness of solitary bees and wasps than land cover at longer distances (> 750 m) (Steffan-Dewenter, 2002; Steffan-Dewenter *et al.*, 2002), and also because the buffers of different sampling sites would have overlapped if they had been > 250 m, and therefore they would not have been independent samples of land cover. The proportion of woody vegetation in the landscape has been used as a significant predictor of the nesting success of trap-nesting species in past studies (Schüepp *et al.*, 2011), and therefore it seemed to be a relevant measurement for this study. There are also mechanistic connections between climate and woody vegetation, such as the direct connection between humidity and woody vegetation (Larsen, 2012), and therefore woody vegetation also seemed to be a relevant measurement for a study of the interactions between climate and habitat. For almost all of the sampling sites, it was possible to use the most recent satellite images (2011–2013) to calculate the proportion of woody vegetation, but for one site (1680 masl), a combination of recent (2012–2013) and less recent (2002) images had to be used, because of cloud cover. There was a clear distinction between open, grassy vegetation and closed, woody vegetation in most of the satellite images, and it was even possible to see individual trees in most of these images (Figure 4.4).

Trap nests

Four bundles of trap nests were placed at each sampling point in the Taita Hills, such that one bundle opened in each of the four cardinal directions. Each bundle was placed inside a cylindrical plastic pipe (50 mm x 250 mm), which was horizontally attached to a wooden stake, at a height of about 750 mm from the ground (Figure 4.5). Each bundle was made of 18 paper straws (6 of these straws were 10 x 200 mm, 6 were 8 x 200 mm, and 6 were 6 x 200 mm). Each straw was made of paper (210 mm x 148 mm), which was rolled around a cylinder of 6, 8, or 10 mm in diameter. It was then folded at one end, and that end was closed with tape, such that the tape could be cut, the nest could be unrolled, the inhabitants could be observed, and then the nest could be rerolled and stored while the inhabitants matured. The trap nests were placed at the sampling points in March 2012, and they were collected and replaced every two weeks, during a sampling period of one year, from the beginning of May 2012 to the end of April 2013. Paper drinking straws have been used as trap nests in the past, but this may be the first use of handmade straws as trap nests. Handmade straws are useful inasmuch as straws may be made in sizes which may not otherwise be available from commercial suppliers.

Statistical analysis

R was used to analyze the data with generalized linear models (R Core Team, 2013). For each species of bee or wasp, its “nesting frequency” at each sampling site was calculated as the proportion of site visits on which at least one nest of that species was collected from that sampling site. Nesting frequency was then modelled as a function of mean annual temperature, total annual rainfall, proportion of woody vegetation, and the interactions between these variables. Rainfall and temperature were (negatively) correlated, but both of these variables were used in the statistical models (Freckleton, 2011), to account for differences in rainfall between sites with similar temperatures. The climate gradient was not confounded by the habitat gradient ($P = 0.4592$, $t = –0.758$, d.f. = 16, $r^2 = 0.0256$). The data from the two sampling points within each sampling site were combined, as a method of eliminating pseudo-replication (Crawley, 2007), because the two points within each site were within 250 m of each other and there was only one set of climate data for each site, and therefore the points within each site were not independent samples of climate or habitat. Spatial correlograms were used to test for spatial auto-correlation in the residuals of the models (Zuur *et al.*, 2009), and there was no evidence of significant spatial auto-correlation.

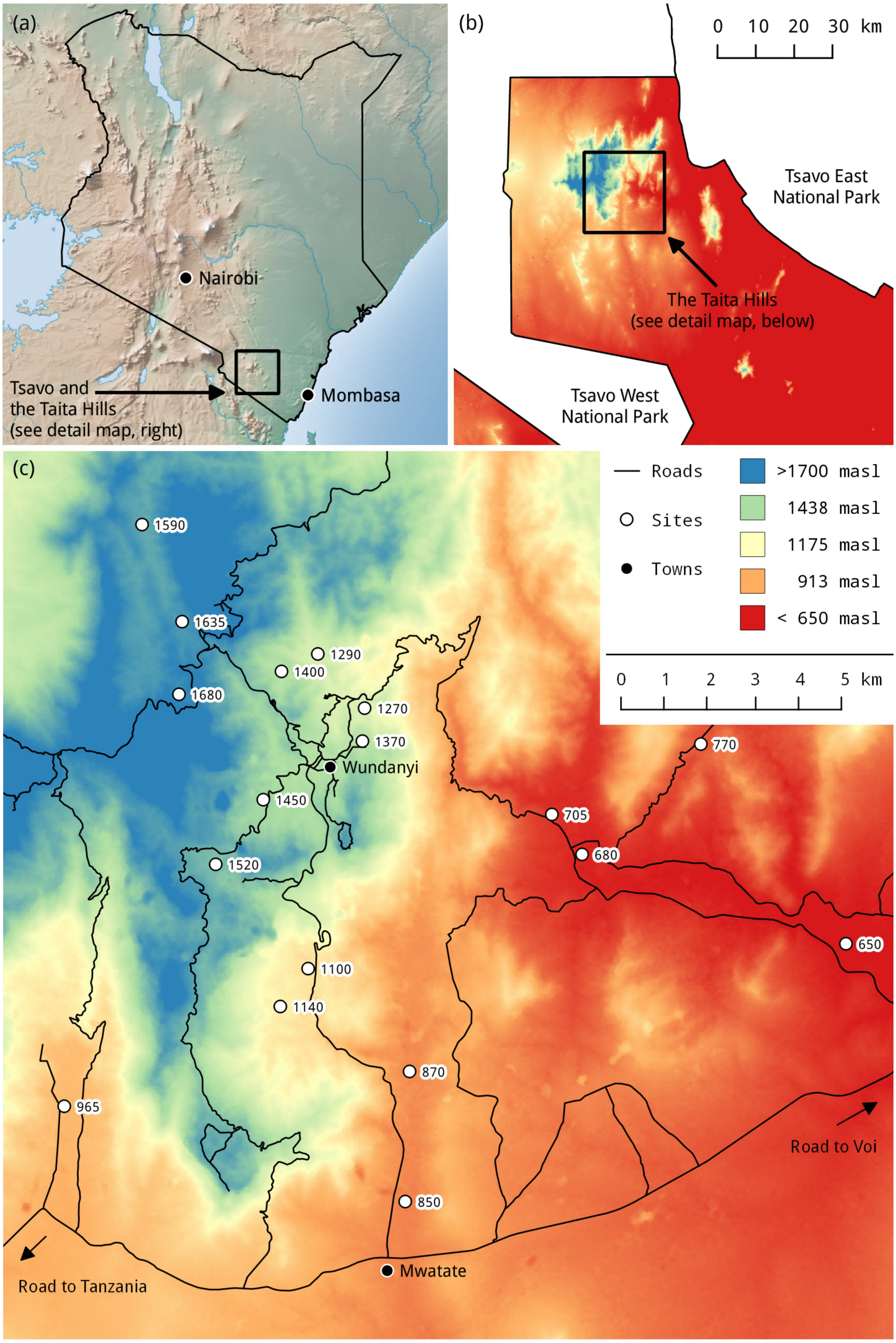


Figure 4.1 Maps of the sampling sites: (a) Kenya (Natural Earth), (b) the Taita Hills and Tsavo (World Database on Protected Areas), and (c) the sampling sites on the elevation gradient in Taita Hills (ASTER GDEM; ASTER GDEM is a product of METI and NASA).

Figure 4.2 A data logger (Thermochron® iButton®) in a homemade stand. Adequate shade and ventilation are needed for making reasonably accurate measurements of air temperature with these data loggers (Hubbart, 2011). The shade was constructed from 1/8 inch plywood (4 x 4 inches), which was glued and nailed onto a wooden stake, which was then hammered into the ground at the field sites (here the shade is pictured in a greenhouse that was not used in this study). The data logger was placed inside a bag that was constructed from mosquito net, which was glued onto the underside of the shade, and which hung at a height of about 4 inches from the ground. The bag was made by folding the mosquito net over a plastic ziplock bag, gluing the edges together, and then cutting away the sides of the plastic bag, such that the ziplock could be used to open and close the net, and the data logger could be removed and replaced in the field. The measurements made with data loggers that were placed in these shaded and ventilated stands were good approximations of the measurements made with handheld thermometers (±1 C), whereas the measurements made with data loggers that were placed in direct sunlight, or that were placed in the plastic cylinders that contained the trap nests, were bad approximations (+20 C in direct sunlight).

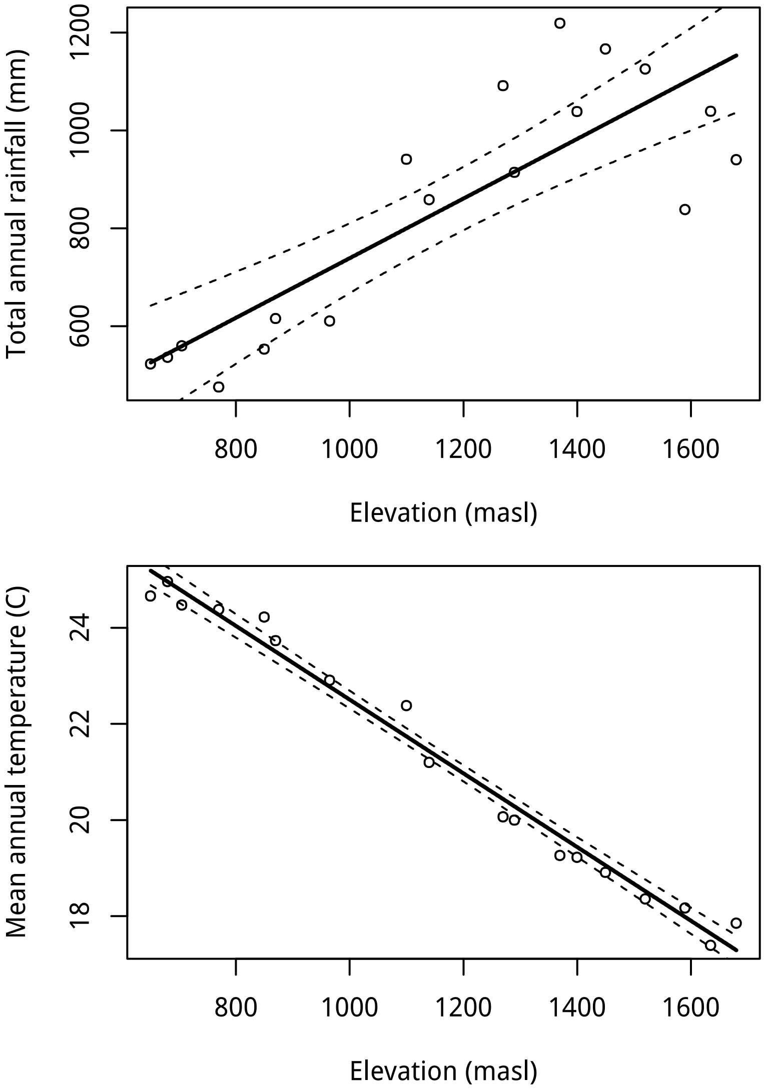


Figure 4.3 The relationships between elevation, rainfall, and temperature on the elevation gradient in the Taita Hills. In linear models, there was higher variation (lower r^2) in rainfall ($r^2 = 0.6968$, $P < 0.0001$, d.f. = 17) than there was in temperature ($r^2 = 0.9821$, $P < 0.0001$, d.f. = 17) on the elevation gradient in the Taita Hills. The solid lines are the predictions of the linear models (rainfall = 0.6095 * elevation + 129.5484; temperature = –0.0077 * elevation + 30.1719), and the dotted lines are the 95% confidence intervals for these predictions. The variation in rainfall clearly increased as the elevation increased, and thus this linear model of rainfall on elevation is not strictly valid (it has “non-constant variance” or “heteroskedasticity”), but this model nonetheless permits a simple comparison between the r^2-value of rainfall-on-elevation and the r^2-value of temperature-on-elevation. The non-constant variance of rainfall-on-elevation could have been caused by topographic effects on climate (“orographic” effects, such as “rain shadows”), which could have been more complex in the highlands than in the lowlands, or it could have been caused by higher rates of evaporation from the rain gauges in the lowlands than in the highlands (see “Methods”).

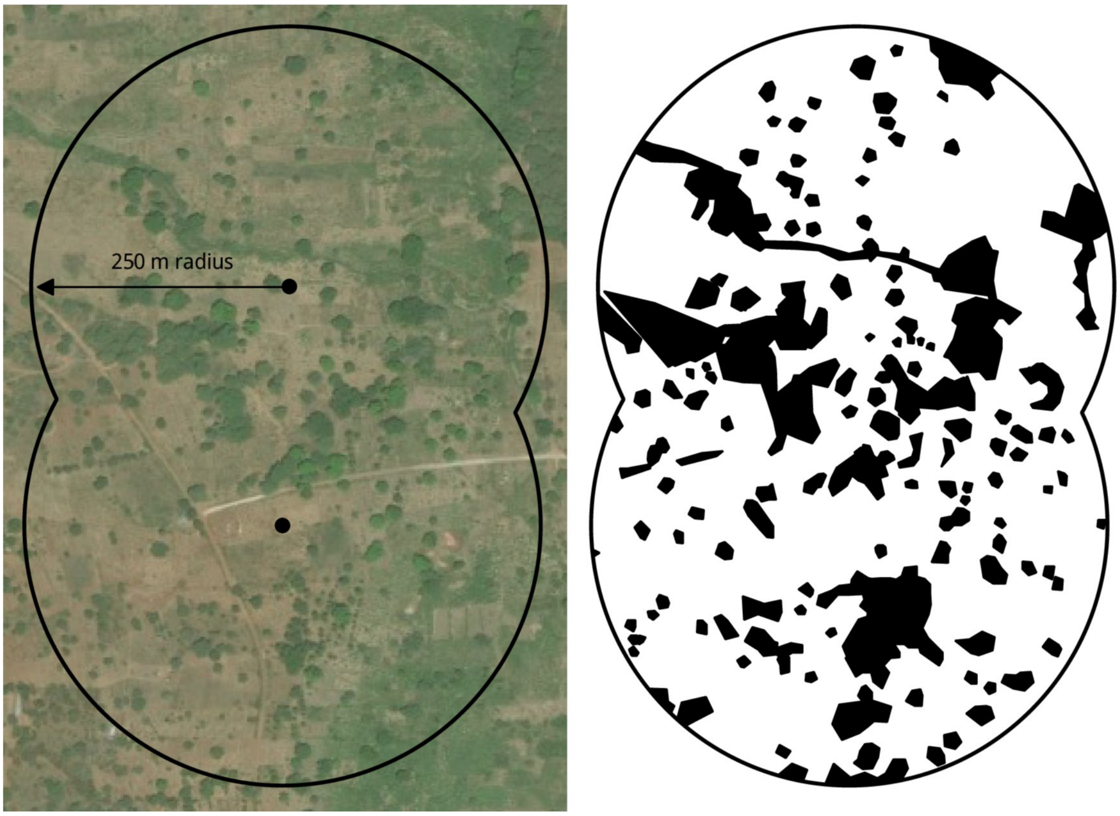


Figure 4.4 An example of mapping the woody vegetation on the elevation gradient in the Taita Hills. A buffer of 250 m radius was generated around the two sampling points at each site, and satellite images were used to draw polygons around the woody vegetation within each buffer. The area covered by woody vegetation within each buffer was then calculated as a proportion of the total area within each buffer. These polygons were rough sketches of the organic shapes that they represented, but they were only used to calculate the relative differences in the proportion of woody vegetation between sites.

Table 4.1 Environmental gradients in the Taita Hills: “latitude” and “longitude” are the coordinates of the sampling points (decimal degrees, WGS84 coordinate reference system), “elevation” is meters above sea level (masl), “rainfall” is total annual rainfall (mm), “temperature” is mean annual temperature in degrees Celsius (C), and “vegetation” is proportion (prop) of woody vegetation within 250 m.

Latitude	**Longitude**	**Elevation (masl)**	**Rainfall (mm)**	**Temperature (C)**	**Vegetation (prop)**
-3.440533	38.469571	650	525	24.68474	0.13
-3.440190	38.470073	“	“	“	“
-3.421845	38.416979	680	539	24.98565	0.32
-3.422859	38.416763	“	“	“	“
-3.414319	38.410455	705	562	24.49886	0.35
-3.414334	38.411083	“	“	“	“
-3.399454	38.440973	770	478	24.40382	0.23
-3.400868	38.440463	“	“	“	“
-3.491792	38.381644	850	556	24.24683	0.28
-3.492465	38.381057	“	“	“	“
-3.467013	38.382159	870	618	23.75722	0.21
-3.464956	38.382219	“	“	“	“
-3.474003	38.312935	965	613	22.93239	0.12
-3.471922	38.312704	“	“	“	“
-3.445153	38.362105	1100	943	22.40454	0.23
-3.445501	38.361546	“	“	“	“
-3.452634	38.356033	1140	861	21.22304	0.22
-3.453271	38.356372	“	“	“	“
-3.392849	38.373361	1270	1094	20.09071	0.31
-3.393096	38.372997	“	“	“	“
-3.382072	38.364057	1290	916	20.02268	0.23
-3.382100	38.363465	“	“	“	“
-3.399236	38.372518	1370	1222	19.28822	0.35
-3.399936	38.372859	“	“	“	“
-3.385701	38.356902	1400	1041	19.24786	0.31
-3.385494	38.356070	“	“	“	“
-3.411241	38.353115	1450	1169	18.93459	0.23
-3.411517	38.352396	“	“	“	“
-3.424591	38.343626	1520	1128	18.38281	0.21
-3.424228	38.342788	“	“	“	“
-3.356727	38.328698	1590	841	18.19481	0.12
-3.355371	38.328182	“	“	“	“
-3.374878	38.336133	1635	1042	17.41698	0.19
-3.376339	38.336846	“	“	“	“
-3.390217	38.336525	1680	943	17.87908	0.18
-3.390229	38.335126	“	“	“	“

Results

The nesting frequency of the most abundant species

From May 2012 to April 2013, 684 trap nests were collected. Most of these nests (about 80% of all nests) were made by only two species: (1) a caterpillar-hunting wasp, and (2) a leaf-cutting bee. The wasp was identified as *Rhynchium marginellum sabulosum* de Saussure 1855 (Hymenoptera: Vespidae: Eumeninae), and it made 285 nests (about 42% of all nests). The leaf-cutting bee was tentatively identified as *Megachile* (*Eutricharaea*) *venusta* Smith 1853 (Hymenoptera: Megachilidae), and it made 257 nests (about 38% of all nests). *Megachile* is a large genus that is difficult to identify to species (Eardley *et al.*, 2010), and although Eardley (2013) has recently revised the genus *Megachile* in Southern Africa, *Megachile* has not been recently revised in Eastern Africa, and therefore this species will hereafter be referred to as an unknown species of *Megachile* (*Megachile* sp. 1, or simply *Megachile*). Voucher specimens were deposited at the National Museums of Kenya (and see Figures 4.6–4.18 for photographs of the bees, the wasps, and the opened trap nests).

This species of *Megachile* may or may not be a pollinator of crops in the Taita Hills, but other species in the genus *Megachile* are important pollinators in other parts of the world. For example, the alfalfa leaf-cutting bee (*Megachile rotundata*) is a pollinator of alfalfa (*Medicago sativa*), canola (*Brassica napus*), and lowbush blueberry (*Vaccinium angustifolium*) in North America (Pitts-Singer & Cane, 2011). As for *Rhynchium*, another species in this genus (*Rhynchium haemorrhoidale*) is known to be a natural enemy of a crop pest (*Agathodes caliginosalis*, a pest of cacao in Indonesia) (Hoehn *et al.*, 2009), and there was some evidence in the Taita Hills (Figure 4.15–4.16) that *Rhynchium marginellum sabulosum* is also a natural enemy of a crop pest (*Crocidolomia pavonana*, the Cabbage Cluster Caterpillar).

Of these two species, which were the most abundant species in the trap nests, one was a potential pollinator (*Megachile*) and one was a potential natural enemy (*Rhynchium*). As a case study in the joint management of pollinators and natural enemies, these two species were compared and contrasted, and there were a number of differences between them. Firstly, *Megachile* was mostly collected from north-facing nests, whereas *Rhynchium* was mostly collected from east-facing nests (Table 4.2). Secondly, *Megachile* was mostly collected from nests of 6 mm in diameter, whereas *Rhynchium* was mostly collected from nests of 10 mm in diameter (Table 4.3).

Thirdly, *Megachile* nests and *Rhynchium* nests were most frequently collected at opposite ends of the elevation gradient. In the statistical models of the distributions of these species on the elevation gradient, temperature was a significant predictor of the nesting frequency of both species (Figure 4.19 and Table 4.4), but *Megachile* nests were more frequently collected where the temperature was lower (*i.e.* in the highlands), and *Rhynchium* nests were more frequently collected where the temperature was higher (*i.e.*

in the lowlands). Fourthly, both rainfall and woody vegetation were statistically significant predictors of the nesting frequency of *Megachile*, but not of *Rhynchium* (Table 4.4). For *Megachile*, there was also a significant interaction between rainfall and woody vegetation (Figure 4.20). Of the sites with low rainfall, *Megachile* nests were more frequently collected from sites with low proportions of woody vegetation. In contrast, of the sites with high rainfall, *Megachile* nests were more frequently collected from sites with high proportions of woody vegetation. In other words, the nesting frequency of *Megachile* was highest at sites in the highlands with low rainfall (relative to other sites in the highlands) and high proportions of woody vegetation, and it was lowest at sites in the lowlands with high rainfall (relative to other sites in the lowlands) and high proportions of woody vegetation.

Whereas it was possible to validate the statistical models of the nesting frequency of *Megachile* and *Rhynchium* (logistic regression models of proportional data), it was not possible to validate statistical models of the number of nests that were collected at each site (Poisson and negative-binomial regression models of count data, with over-dispersion, excess zeros, and patterns in the residuals). However, the sites with high nesting frequencies also had high numbers of nests (Figure 4.21), and therefore the environmental drivers of nesting frequency might also be the drivers of nest abundance.

The species richness of pollinators and natural enemies

Several other species of bees and wasps were also collected from the trap nests, and these other species could also be pollinators of crops or natural enemies of crop pests. However, whereas *Megachile* and *Rhynchium* were continuously distributed along the gradients of climate and habitat (they were each collected from 16 of the 18 sites), these other species were not continuously distributed along these gradients (they were each collected from only 1–4 of the 18 sites), and thus it was not possible to model their nesting frequencies across these gradients. These other species included two species of resin-collecting bees (Hymenoptera: Megachilidae), one of which was collected only from the lowlands, and the other of which was collected only from the highlands; one species of cricket-hunting wasp (Hymenoptera: Sphecidae), which was only collected from the lowlands; another species of leaf-cutting bee (Hymenoptera: Megachilidae), which was collected from one site in the lowlands and three sites in the highlands; and another species of caterpillar-hunting wasp (Hymenoptera: Vespidae: Eumeninae), which was collected only from the lowlands. More species of trap-nesting bees and wasps were collected from the lowlands than the highlands (Figure 4.22), but the effect of elevation on species richness was only marginally significant ($P = 0.0417$, $t = -2.214$, d.f. = 16, $r^2 = 0.1867$).

The effects of temperature and the proportion of woody vegetation were not significant, and these variables were deleted from the minimum adequate model of species richness. When the species richness of bees or wasps were modelled separately, elevation had a significantly negative effect on the species richness of wasps (P = 0.0017, t = –3.761, d.f. = 16, r^2 = 0.4361), but not on the species richness of bees (P = 0.8713, t = 0.165, d.f. = 16, r^2 = 0.0607).

Figure 4.5 Trap nests in the field: wood (left) and paper (right). Only the paper trap nests were used for the research that is reported in this chapter.

Figure 4.6 An unrolled paper trap nest: the cells of a leaf-cutting bee (*Megachile* sp. 1).

Figure 4.7 An unrolled paper trap nest: the larvae of a caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*). In contrast to the larvae observed by Gess & Gess (1991), these larvae did not spin cocoons.

Figure 4.8 An unrolled paper trap nest: the pupae of a caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*).

Figure 4.9 An unrolled paper trap nest: in this case, the leaf-cutting bee (*Megachile* sp. 1) and the caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*) used the same trap nest.

Figure 4.10 Pupae of the leaf-cutting bee (*Megachile* sp. 1; right) and the caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*; left).

Figure 4.11 An adult female of the leaf-cutting bee, *Megachile* sp.1.

Figure 4.12 An adult male of the leaf-cutting bee, *Megachile* sp. 1.

Figure 4.13 An adult female of the caterpillar-hunting wasp, *Rhynchium marginellum sabulosum*.

Figure 4.14 An adult male of the caterpillar-hunting wasp, *Rhynchium marginellum sabulosum*.

Figure 4.15 The Cabbage Cluster Caterpillar, *Crocidolomia pavonana* (Lepidoptera: Crambidae), is a pest of *Brassica oleracea acephala* (“sukuma wiki”).

Figure 4.16 An opened wooden trap-nest, provisioned by *Rhynchium marginellum sabulosum* with *Crocidolomia pavonana*. This trap nest was set among the brassicas that are pictured in Figure 4.15. This is evidence that *Rhynchium marginellum sabulosum* is a natural enemy of a crop pest.

Figure 4.17 Unidentified caterpillars that were preyed upon by *Rhynchium marginellum sabulosum*.

Figure 4.18 Unidentified caterpillars that were preyed upon by *Rhynchium marginellum sabulosum*.

Table 4.2 The number of nests of a pollinator (*Megachile*, a leaf-cutting bee) and a natural enemy (*Rhynchium*, a caterpillar-hunting wasp) that were collected from trap nests that faced in different directions. The results of the chi-squared tests support the conclusion that these species have preferences for nests that face in different directions. *Megachile* was mostly collected from north-facing nests, whereas *Rhynchium* was mostly collected from east-facing nests. These numbers do not include empty nests (nests that were plugged but were not provisioned).

Species	**North**	**East**	**West**	**South**	χ^2	**d.f.**	***P***
Megachile	78	45	44	59	13.40	3	0.0039
Rhynchium	54	113	42	34	63.26	3	< 0.0001

Table 4.3 The number of nests of a pollinator (*Megachile*, a leaf-cutting bee) and a natural enemy (*Rhynchium*, a caterpillar-hunting wasp) that were collected from trap nests of different diameters. The results of the chi-squared tests support the conclusion that these species have preferences for nests of different diameters. *Megachile* was mostly collected from 6 mm nests, whereas *Rhynchium* was mostly collected from 10 mm nests. These numbers do not include empty nests (nests that were plugged but were not provisioned).

Species	**6 mm**	**8 mm**	**10 mm**	χ^2	**d.f.**	***P***
Megachile	161	61	4	167.7	2	< 0.0001
Rhynchium	16	78	149	109.4	2	< 0.0001

Table 4.4 Statistical models of the nesting frequencies of a pollinator (*Megachile*, a leaf-cutting bee) and a natural enemy (*Rhynchium*, a caterpillar-hunting wasp) that were collected from trap nests in the Taita Hills. For *Rhynchium*, the residual deviance of the model (51.319) was much higher than the number of degrees of freedom (16), and therefore it was assumed that the model was over-dispersed, the dispersion parameter was estimated to be 3.047 (51.319 / 16), and the *P*-values were adjusted (using the "quasibinomial" family in R). For *Megachile*, the model had a residual deviance of 22.188 on 16 degrees of freedom. Therefore, it was assumed that the model was not over-dispersed (22.188 / 16 ~ 1), but woody vegetation and the interaction between rainfall and woody vegetation were significant at $P < 0.05$ even when they were adjusted for over-dispersion (the *P*-values shown here for *Megachile* were not adjusted for over-dispersion).

Species	**Variable**	**Estimate**	**SE**	***Z***	***P***
Megachile	Intercept	11.2432	4.4497	2.527	0.0115
	Rainfall	−0.0064	0.0029	−2.221	0.0264
	Temperature	−0.3331	0.1294	−2.575	0.0100
	Vegetation	−23.1158	7.4170	−3.117	0.0018
	Rainfall x vegetation	0.0242	0.0084	2.899	0.0038
Rhynchium	Intercept	−12.0533	2.8304	−4.259	0.0006
	Temperature	0.4615	0.1214	3.801	0.0016

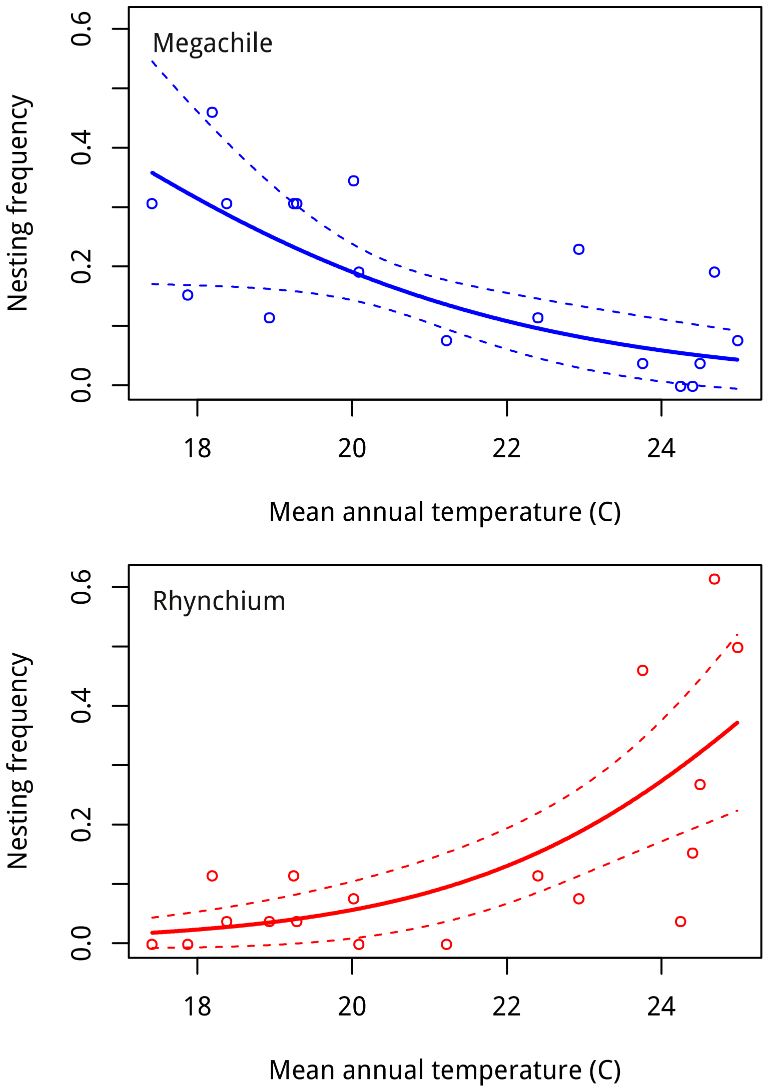


Figure 4.19 Opposite patterns in the nesting frequencies of a pollinator (*Megachile*, a leaf-cutting bee) and a natural enemy (*Rhynchium*, a caterpillar-hunting wasp) that were collected from trap nests on a gradient of temperature (elevation) in the Taita Hills. The solid lines are the predictions of generalized linear models with binomial error distributions, and the dotted lines are 95% confidence intervals for these predictions. *Megachile* nests were more frequently collected where the temperature was lower, and *Rhynchium* nests were more frequently collected where the temperature was higher. In both species, temperature was a significant predictor of nesting frequency ($P < 0.05$).

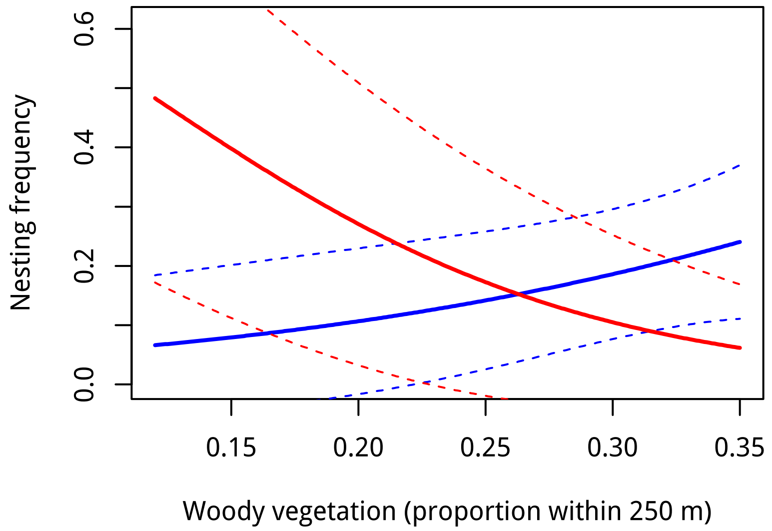


Figure 4.20 Interactions between rainfall and woody vegetation as predictors of the nesting frequency of a cavity-nesting bee (*Megachile*) on an elevation gradient in the Taita Hills. Of the sites with low rainfall (red lines), *Megachile* nests were more frequently collected from sites with low proportions of woody vegetation. In contrast, of the sites with high rainfall (blue lines), *Megachile* nests were more frequently collected from sites with high proportions of woody vegetation. The solid lines are the predictions of a generalized linear model with a binomial error distribution, and the dotted lines are 95% confidence intervals for these predictions.

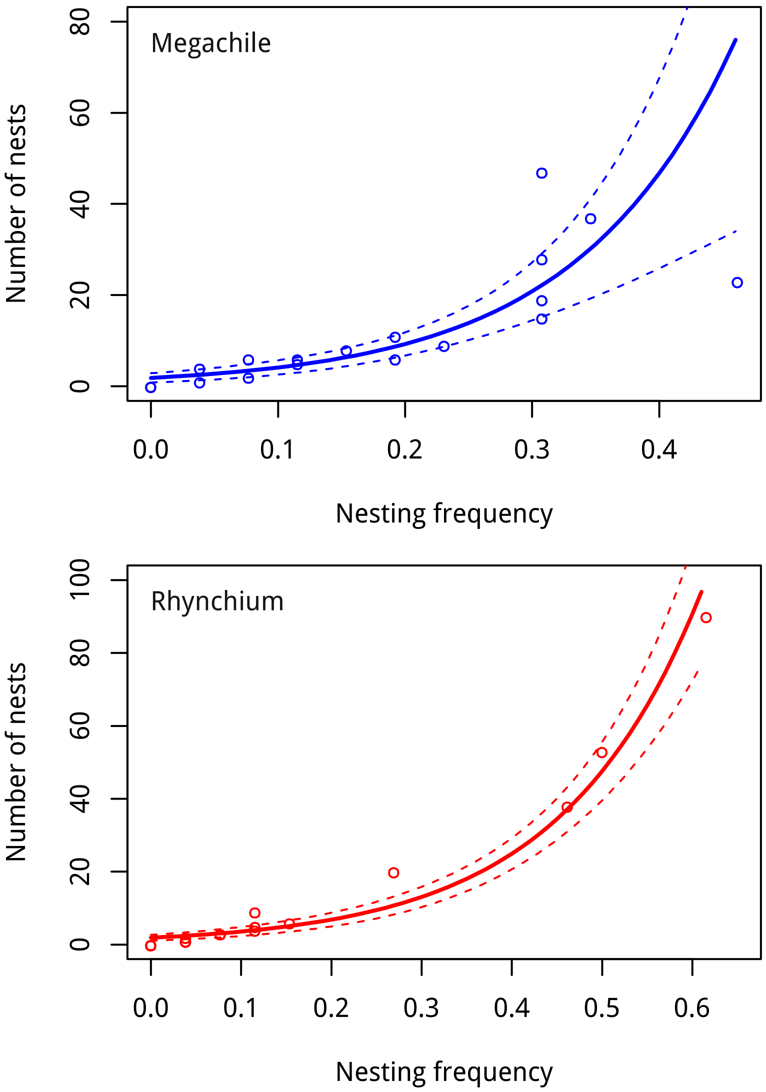


Figure 4.21 The relationships between nesting frequency and the number of *Megachile* or *Rhynchium* nests that were collected on the elevation gradient in the Taita Hills. The solid lines are the predictions of generalized linear models with Poisson (*Rhynchium*) or negative-binomial (*Megachile*) error distributions, and the dotted lines are the 95% confidence intervals for these predictions. In both species, nesting frequency was a significant predictor of the number of nests ($P < 0.05$).

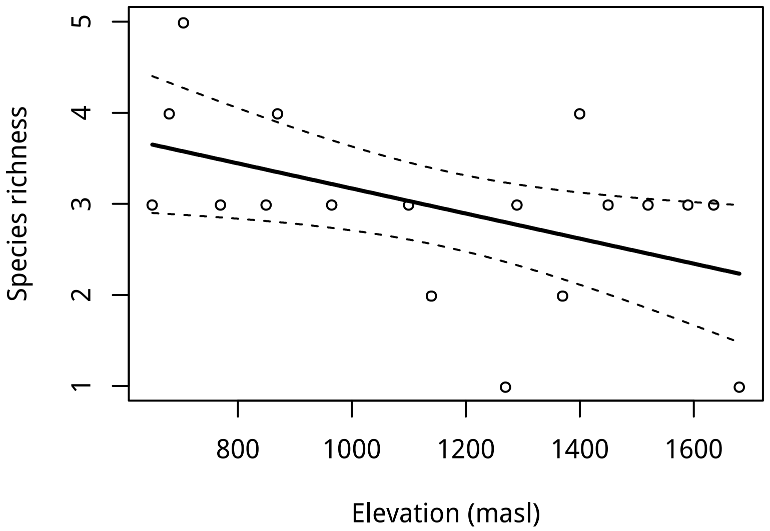


Figure 4.22 Species richness of trap-nesting bees and wasps on an elevation gradient in the Taita Hills. Elevation had a negative effect on species richness, but this effect was only marginally significant ($P = 0.0417$, SE = 0.0006, $t = –2.214$, d.f. = 16) and it explained only about 19% of the variation in species richness ($r^2 = 0.1867$). The solid lines are the predictions of a linear model (species richness = –0.0014 * elevation + 4.546), and the dotted lines are 95% confidence intervals for these predictions.

Discussion

The distributions of pollinators and natural enemies on environmental gradients

On elevation gradients around the world, two general patterns have been found in the distribution of biodiversity: either species richness decreases with elevation, or species richness increases from low to intermediate elevation and then decreases from intermediate to high elevation (Rahbek, 1995; Hodkinson, 2005). In the Taita Hills, the species richness of trap-nesting wasps decreased with elevation (increased with temperature), which agrees with these general patterns, but the species richness of trap-nesting bees did not. It has been suggested that high richness is a function of high abundance—for example, the "more-individuals hypothesis" (Wright, 1983; Srivastava & Lawton, 1998; Clarke & Gaston, 2006)—and thus it is not surprising that the species richness of trap-nesting wasps was highest in the lowlands, where the nesting frequency of *Rhynchium* was also highest. However, it is surprising that the nesting frequency of trap-nesting bees was highest in the highlands, given the general patterns in species richness on elevation gradients, especially for bees (Hodkinson, 2005; Hoiss *et al.*, 2012; Marini *et al.*, 2012).

General patterns in the abundance of insects on elevation gradients have not been widely found, probably because different taxa have different responses to elevation. For example, the abundance of ants, bees, and spiders may decrease with elevation, whereas the abundance of flies and parasitic wasps may increase with elevation (McCoy, 1990; Hodkinson, 2005; Hoiss *et al.*, 2012). For insects that have more than one generation per year, it has been suggested that lower abundances at higher elevations could be a direct result of climate, if the growing seasons at higher elevations are shorter (limited by low temperatures), and if this results in fewer generations per year at higher elevations (Hodkinson, 2005; Hoiss *et al.*, 2012). For *Megachile* and *Rhynchium*, nesting frequency was positively correlated with abundance, but nesting frequency was also an indirect measurement of the number of generations per year, and thus it is especially surprising that the nesting frequency of *Megachile* increased with elevation, which would seem to disagree with the suggestion that there are fewer generations per year at lower elevations.

However, on elevation gradients in seasonal tropical climates, it could be that growing seasons are limited by low rainfall at low elevation and are limited by low temperature only at extremely high elevation. In Indonesia, the abundance of *Rhynchium haemorrhoidale* was correlated with rainfall but not with temperature (Hoehn *et al.*, 2009), and in the highlands of the Taita Hills, crops are grown throughout the year, whereas crops were only grown in the wet seasons in the lowlands (personal observation). However, if a longer growing season could explain the higher nesting frequency of *Megachile* in the highlands, then that would not explain the higher nesting frequency of *Rhynchium* in the lowlands, unless *Rhynchium* has only one generation per year, and thus its nesting frequency is not limited by the length of the growing season. In South Africa, *Rhynchium* had only one or possibly two generations per year (Gess & Gess, 1991), but in the Taita Hills it nested throughout the year. It would be surprising if these opposite patterns in the nesting frequencies of *Megachile* and *Rhynchium* were caused by opposite responses to the length of the growing season or opposite responses to anything abiotic, since these species are similar in so many other ways, both ecologically and evolutionarily, as cavity-nesting and flower-visiting Hymenoptera (but see Chapter 5 for the different responses of these two species to incubation temperature). It would not be surprising if the nesting frequency of either *Megachile* or *Rhynchium* was caused not only by climate but also by something else—something biotic—that was correlated with elevation but was not measured in this study (perhaps the availability of other nesting materials, such as suitable leaves for *Megachile* or suitable soils for *Rhynchium*, which they use to partition their nests into cells).

In the case of *Rhynchium haemorrhoidale* in Indonesia, abundance was negatively correlated with tree cover (Hoehn *et al.*, 2009). Likewise, the proportion of woody vegetation within 250 m had a significantly negative effect on the nesting frequency of *Megachile*, but it did not have a significant effect on the nesting frequency of *Rhynchium*. If woody vegetation was a source of nesting sites for *Megachile*, then it could be that *Megachile* nests were more frequently collected in landscapes with less woody vegetation, because there were fewer natural nesting sites in these landscapes, and therefore a higher proportion of the nesting sites in these landscapes were trap nests. However, it is also possible that woody vegetation provided fewer floral or nesting resources to these bees than did non-woody vegetation, and thus it is possible that landscapes with less woody vegetation did in fact have more of these bees. Elsewhere in Kenya, there were fewer species of bees in woodland than there were in cropland (Hagen & Kraemer, 2010), and there was a lower abundance of bees in cropland surrounded by higher proportions of semi-natural habitat in one study (Otieno *et al.*, 2011), but in another study there was a higher abundance of bees in cropland that was closer to woodland (Gemmill-Herren & Ochieng', 2008). Therefore, there is not yet evidence for a general pattern in the effects of woodland on bees in Kenyan agroecosystems, but this study is further evidence that the conservation of woodland *per se* might not be as important for bees as the conservation of complex agricultural landscapes.

Why was there no effect of woody vegetation on the nesting frequency of *Rhynchium*? In Indonesia, both trap-nesting bees and trap-nesting wasps were more abundant where woodland was less dense (Klein *et al.*, 2002), but *Rhynchium haemorrhoidale* was thought to forage at long distances from its nesting sites (Klein *et al.*, 2004), and if this also the case for *Rhynchium marginellum sabulosum* in the Taita Hills, then it is possible that land use at a larger spatial scales could have had a significant effect on its nesting frequency. It would be surprising if land use had no effect on

Rhynchium in the Taita Hills, but it would not be surprising if land use had different effects on *Megachile* than it did on *Rhynchium*, because land use had different effects on bees and wasps in other cavity-nesting communities (Steffan-Dewenter, 2002; Schüepp *et al.*, 2011).

I am not aware of other studies of bees and wasps that have found significant interactions between climate and habitat, but in Italy the abundance and species richness of wild bees in apple orchards decreased as elevation increased and also decreased as the proportion of apple orchards in the surrounding landscape increased (Marini *et al.*, 2012). In the Taita Hills, the interacting effects of climate and habitat on *Megachile* (Figure 4.20) could be interpreted in terms of changes in the composition of woody vegetation along the elevation gradient. It could be the case that woody species that grow in areas with low rainfall do not provide resources for *Megachile*, whereas woody species that grow in areas with high rainfall do provide resources. This mechanism would need to be understood before we could consider the consequences of these results for the management of woody vegetation under the influence of climate change, because this interaction between climate and habitat could be statistical correlation rather than mechanistic causation.

The management of communities

Much of the research on environmental gradients has focused on patterns in species richness, rather than patterns in abundance (Fischer *et al.*, 2011). However, inasmuch as we are now searching for applied solutions to a “pollination crisis” (Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998)—inasmuch as we are searching for new species of pollinators and natural enemies to develop as ecosystem service providers (Bosch & Kemp, 2002)—we should be searching not only for patterns in species richness, but also for patterns in the abundance of specific pollinators and natural enemies, such as *Megachile* and *Rhynchium*, which we might be able to target for intensive management. Moreover, it might not be practical to target communities, as opposed to species, for intensive management.

Firstly, some natural enemies might compete with or prey upon other natural enemies, some pollinators might rob nectar from flowers or compete with other pollinators, and some natural enemies might prey upon pollinators (Shackelford *et al.*, 2013; Aizen *et al.*, 2014; see Chapter 2). Therefore, a species-rich community of pollinators and natural enemies might or might not be more functional than a species-poor community, in terms of pollination and pest control, and a species-rich community should not necessarily be a target for management (but see Garibaldi *et al.*, 2013).

Secondly, in the Gleasonian “continuity hypothesis” (as opposed to the Clementsian “discontinuity hypothesis”), a community is thought to be a short-term assemblage of species, which will disassemble in response to long-term changes in the environment. The continuity hypothesis has been supported by research on environmental gradients (Grytnes & McCain, 2007)—for example, elevation gradients on which the relationships between plants and pollinators have become uncoupled (Forrest & Thomson, 2011)—and this hypothesis implies that some species of pollinators and natural enemies might not respond to environmental changes in similar ways (*e.g.*, *Megachile* and *Rhynchium* in this study). Therefore, it might not be possible to manage a community of pollinators and natural enemies in the long-term, but only to manage the subset of that community that has compatible responses to environmental changes or to aspects of management that mitigate these environmental changes.

The management of species

In this study, the most abundant species of pollinator and the most abundant species of natural enemy had opposite responses to an environmental gradient. These two species were not the only pollinators and natural enemies in the study system, and if it were concluded that the management requirements of these two species were not compatible, then that would not necessarily be an impediment to the joint management of pollinators and natural enemies in the Taita Hills. However, the fact that two such ecologically and evolutionarily similar species could have such different responses suggests that we should be cautious when we make assumptions about the conditions under which joint management might be possible.

To take an optimistic viewpoint, diverse responses to environmental gradients (but not opposite responses) could be seen as opportunities for joint management. For example, if *Rhynchium* has no response to woody vegetation at small scales, then it might be possible to manage woody vegetation at small scales for the benefit of *Megachile,* at no cost to *Rhynchium*. Thus, it might be possible to make separate management plans for each species of ecosystem-service provider, such that the management of one species would not have negative effects on other species. For example, in providing supplemental nesting sites for *Megachile* and *Rhynchium*, it might possible to reduce competition for nesting sites by providing 10 mm nests that face east for *Rhynchium* and 6 mm nests that face north for *Megachile*, considering their different preferences for nests of these different diameters and orientations (Tables 4.2–4.3).

This case study is a step towards the joint management of beneficial arthropods in an African agroecosystem. Further steps might be to test the effectiveness of these species as pollinators and natural enemies, and then to establish protocols for rearing these species in the lab or increasing their abundance in the field. For example, in the Taita Hills, *Brassica* crops are mostly grown in the highlands, and it is possible that *Rhynchium* could be managed as a natural enemy of a *Brassica* pest (*Crocidolomia pavonana*), but the abundance of *Rhynchium* in the highlands is lower than it is in the lowlands. If something other than climate is limiting the abundance of *Rhynchium* in the highlands, then perhaps its abundance could be increased through management. In field trials, it was concluded that *Ancistrocerus gazella* is not an effective natural enemy of orchard pests, because it is polyphagous (Wearing & Harris, 2005), and this could also be the case for *Rhynchium marginellum sabulosum*, which is also polyphagous (Figures 4.17–4.18). In contrast to *Ancistrocerus gazella*, it was concluded that there was good potential for the management of *Rhynchium haemorrhoidale* (through the management of nesting sites) as a natural enemy of coffee pests (Hoehn *et al.*, 2009), and it is possible that *Rhynchium marginellum sabulosum* also has good potential for management as a generalist natural enemy of crop pests. However, we will need to study the basic biology and ecology of species such as *Rhynchium marginellum sabulosum*, before we have a mechanistic understanding of their applied potential as ecosystem-service providers. Studies of communities should not be used as substitutes for studies of species, because the responses of important species of ecosystem-service providers within these communities might not be compatible (as suggested by the results of this study), and I would recommend a renewed focus on the species as a unit of study, and also as a unit of management within the community.

Mismatches between pollinators and natural enemies in a changing climate: temperature, development time, and body size in trap-nesting bees and wasps

Introduction

The global food system will have to confront a “perfect storm” before the end of the century, and it will be a storm on many fronts—economic, ecological, and climatic (Beddington, 2009). There will be an increase of about 50–100% in demand for food from 2005 to 2050 (The Royal Society, 2009; Foley *et al.*, 2011; Tilman *et al.*, 2011; Bajzelj *et al.*, 2014), but there will also be an unsustainable decrease in soil and water conservation, crop pollination, pest regulation, and other ecosystem services, unless we are able to stop the expansion and unsustainable intensification of agriculture (Chapters 1–3). From 2000 to 2100, there will also be an increase of about 1–5 degrees Celsius (C) in global mean surface temperatures (IPCC, 2013), an increase in heat waves and other extreme climatic events (Diffenbaugh & Field, 2013), and a decrease in the fitness of crop varieties, livestock breeds, and other forms of “planned” and “associated” biodiversity (Vandermeer *et al.*, 1998), such as crop pollinators and natural enemies of crop pests, unless they are able to adapt to life in a warmer world (Hegland *et al.*, 2009; Thomson *et al.*, 2010; Thornton *et al.*, 2011). If the impact of these global changes cannot be predicted and mitigated—both changes in climate and changes in land use—then there will be a decrease in the sustainable supply of food, and we will not be able to meet the increase in demand.

In sub-Saharan Africa, an increase of 5 C could cause a massive decrease in crop yields, such as a 19% decrease in maize yield and a 47% decrease in dry bean yield in East Africa, from 2000 to 2090 (Thornton *et al.*, 2011). These decreases in yields were predicted from the agro-climatic potentials of these crops, but not from the agro-climatic potentials of the ecosystem services that support and regulate the yields of these crops, and therefore they should be seen as the minimum decreases in the sustainable yields of these crops, in case the species that provide these ecosystem services at present (such as pollinators and natural enemies) are unable to adapt to climate change and thus are unable to provide these ecosystem services in the future. This is especially worrying in sub-Saharan Africa, in which the “sustainable” or “ecological” intensification of agriculture—the “harnessing” of ecosystem services, such as crop pollination and pest regulation, to increase the food supply (Bommarco *et al.*, 2013)—has been presented as a high priority for food security (Pretty *et al.*, 2011; The Montpellier Panel, 2013). Much of the future increase in demand for food will come from sub-Saharan Africa (Foresight, 2011), but much of the research on ecological intensification, by means of crop pollination and pest regulation, has been done in North America and Western Europe (Chapter 2; Steward *et al.*, 2014). Worldwide, the impact that climate change could have on crop pollinators and natural enemies needs to be predicted and mitigated (Hegland *et al.*, 2009; Thomson *et al.*, 2010), and such research could be especially important in sub-Saharan Africa, where the “perfect storm” could be “even more perfect” than it could in other regions. Therefore, the research in this chapter is a case study of the effects of temperature on pollinators and natural enemies in East Africa.

Most species of pollinators and natural enemies are insects (Chapter 2), and insects are ectotherms, which are particularly sensitive to temperature (Deutsch *et al.*, 2008). Most of sub-Saharan Africa is tropical, and adapting to climate change will be especially challenging for tropical ectotherms, which will have lower rates of survival and reproduction in a warmer world—especially in comparison to temperate ectotherms—because tropical temperatures are closer to critical maximum temperatures (Deutsch *et al.*, 2008). Moreover, the adaptations of pollinators and natural enemies might not “match” the adaptations of the crops that they pollinate or the pests that they regulate, and a “mismatch” might be spatial (for example, a pest might have, or might evolve, the ability to disperse to a higher elevation, in response to global warming, but its natural enemy might not), or it might be temporal (for example, at a higher temperature, a crop might mature a little earlier in the year, but its pollinator might mature a lot earlier) (Hegland *et al.*, 2009; Thomson *et al.*, 2010). Therefore, the impact of global warming on crops, pollinators, pests, and natural enemies should be predicted in terms of traits that are related to spatial mismatch, such as dispersal ability, and temporal mismatch, such as development time (Berg *et al.*, 2010). The impact of global warming can be predicted by experimentally manipulating temperature and statistically modelling the responses of different individuals to different temperatures. The shapes and slopes of these statistical models—which are known as “generalized thermal reaction norms”—can then be compared between species (Sarkar & Fuller, 2003; Martin *et al.*, 2011; Rocha & Klaczko, 2012). If the shapes and slopes of the reaction norms of different species are similar, then there is a smaller chance of a mismatch between these species than there is if the reaction norms are dissimilar, or non-linear (Hegland *et al.*, 2009).

Many immature insects that develop at higher temperatures mature earlier in the year than they do at lower temperatures (Nylin & Gotthard, 1998), which is a direct effect of temperature on a trait that is related to temporal mismatch (development time). Many immature insects that develop at higher temperatures also mature at smaller body sizes—“Bergmann's rule” (Shelomi, 2012)—which is a direct effect of temperature on a trait that is related to dispersal ability (body size), if larger individuals are better dispersers (Greenleaf *et al.*, 2007; Jenkins *et al.*, 2007). Both of these developmental changes are forms of “phenotypic plasticity” in response to temperature—variation in the expression of phenotypic traits, such as body size and development time, which are a product of the interaction between the genotype and the environment (Nylin & Gotthard, 1998).

Phenotypic plasticity could be a mechanism by which insects could adapt to a warmer world, either directly (plasticity as adaptation), indirectly (plasticity as heritable variation upon which evolution could act by natural selection), or both. Phenotypic plasticity could also be a mechanism by which a mismatch between pollinators and crops, or natural enemies and crop pests, could be prevented.

If climate change does cause a decrease in either crop pollination or pest regulation, it could cause a decrease in crop yields that would not be proportional to the decrease in either of these ecosystem services on their own, because there could be interactions between them (Chapter 2; Lundin *et al.*, 2012). Thus, climate change could have an impact on agriculture not only by causing a mismatch between crops and pollinators, or crop pests and natural enemies, but also by causing a mismatch between crop pollination and pest regulation. Therefore, these ecosystem services should be studied simultaneously (Chapters 2 and 4), and the impacts of climate change on multiple species should be compared (Berg *et al.*, 2010), especially because crops (primary producers), pollinators (primary consumers), pests (primary consumers), and natural enemies (secondary consumers) are on different trophic levels, and species on higher trophic levels are expected to have stronger responses to climate change (Voigt *et al.*, 2003; Berg *et al.*, 2010).

When trap-nesting pollinators and natural enemies were simultaneously studied on an elevation gradient in the Taita Hills, in Kenya (Chapter 4), the nests of the most abundant species of pollinator were more frequently collected from the highlands, where the temperatures were low, whereas the nests of the most abundant species of natural enemy were more frequently collected from the lowlands, where the temperatures were high. However, elevation gradients are gradients not only in temperature but also in humidity, rainfall, vegetation, and other climatic and biotic variables (Hodkinson, 2005), and thus these species could have been responding not to temperature *per se* but to some other aspect of elevation, or more than one aspect of elevation, or an interaction between these aspects. Therefore, to test the direct effects of temperature on these species, in isolation from the effects of these other aspects of elevation, their nests were collected from the field and brought back to the lab, where the immature bees and wasps were incubated at different temperatures. The results of these tests are presented in this chapter.

Some of the bees and wasps were incubated at temperatures that were similar to the temperatures on the elevation gradient, and others were incubated at higher temperatures, to test for limitations in their thermal responses that could be caused by climate change. Six hypotheses were tested: (1) body size decreases as mean temperature increases, in both species (Bergmann's rule); (2) development time decreases as mean temperature increases, in both species, (3) the survival of the pollinator decreases as mean temperature increases above the mean in the highlands, whereas the survival of the natural enemy decreases as mean temperature decreases below the mean in the lowlands, which could explain their distributions on the elevation gradient; and (4–6) these species have different responses to temperature, in terms of (4) body size, (5) development time, and (6) survival, measured in terms of the shapes or slopes of their generalized thermal reaction norms for these variables. Hypotheses 3–6 were tested as possible explanations for the apparently opposite responses of these species to temperature on the elevation gradient. Thus, the present research, which was based on experimental manipulations of temperature in the lab, was designed to complement past research, which was based on observations of climate in field (Chapter 4), and also to provide some mechanistic evidence of the direct effects that temperature could have on these species, for use in future models of climate change and species distribution.

Methods

Immature bees and wasps were collected from trap nests, which were placed on an elevation gradient (650–1680 meters above sea level), in the Taita Hills, Kenya (Chapter 4). The wasp was identified as *Rhynchium marginellum sabulosum* de Saussure 1855 (Hymenoptera: Vespidae: Eumeninae). The bee was identified as a species of *Megachile* (Hymenoptera: Megachilidae; possibly *Megachile venusta* Smith 1853) and it will be referred to hereafter simply as *Megachile*. Voucher specimens were deposited at the National Museums of Kenya (and see the photographs in Chapter 4).

The nests were collected from the field every two weeks from 19 July–28 September 2012 (the cold dry season). Thus, the nests could have been as much as two weeks old when they were collected and opened. Each cell was separated from the others, placed into a plastic specimen jar (125 ml), and sealed with an airtight lid, but only if it contained a living larva. Cavity-nesting bees and wasps develop in a naturally low-oxygen environment (Abdelrahman *et al.*, 2014), and the airtight lid did not prevent them from completing their development inside the incubator. *Megachile* used leaves to partition its nests into cells, and each cell was placed into a specimen jar, but because each cell had been completely covered with leaves by the mother bee, it was impossible to tell whether or not each cell contained a larva or a pupa and whether or not it was alive or dead. Each jar was labeled with its nest number and cell number, and it was incubated from the morning after it was collected until something emerged or the experiment ended (30 December 2012). *Rhynchium* used mud to partition its nests into cells, but the cells were open along the sides of the cavity. Therefore, it was possible to see inside the cells, and only living larvae were incubated.

This study took place in rural Kenya, and the incubator (Figures 5.1–5.2) was constructed with hand tools, from materials that were available in the local hardware stores, with the exception of the plug timers, which were available in Nairobi. Therefore, this incubator could serve as a model for studies of thermal reaction norms in places with poor access to materials. The incubator was a wooden cabinet (72 inches tall x 24 inches wide x 24 inches deep on the inside), which had a cover of 1/8 inch thick plywood, over a framework of 1 x 1 inch lengths of wood. Imperial measurements were used, because plywood is usually available in 48 x 96 inch (4 x 8 foot) sheets. Wood glue and 1/2 inch nails were used for construction. The inside of the incubator had wooden shelves (22 x 2 x 1/8 inches) on three sides, at intervals of 6 inches above the floor (12 heights from 0–66 inches above the floor). The fourth side had two doors (36 x 24 x 1/8 inches) and no shelves. There was one upper door (for access to the shelves from 66–36 inches above the floor) and one lower door (for access to the shelves from 30–0 inches above the floor). The doors were attached to the framework with hinges (cloth tape) on their upper edges and were latched on their bottom edges with nails that could be pivoted into position to lock the doors. The outside of the incubator was insulated on all sides with low-density foam (1 inch thick).

The inside of the incubator was heated by five 25 W tungsten light bulbs. The bulbs were at the center of the incubator, and the bottoms of the bulbs were about 6 inches below the tops of the beams from which they were hung (the tops of the beams were at 24, 36, 48, 60, and 72 inches above the floor). The bulbs at 24, 48, and 72 inches were plugged into one timer, which switched on at 6:00 and switched off at 18:00 each day (a 12:12 light:dark cycle), and the bulbs at 36 and 60 inches were plugged into another timer, which switched on at 9:00 and switched off at 15:00 each day. On each shelf, the temperature was measured every hour, on the hour, by a Thermochron® iButton® (model DS1921G, Maxim Integrated, San Jose, California, USA), which was placed inside a plastic specimen jar, just like the bee and wasp cells.

The temperature gradient inside the incubator was based on the fact that heat rises, and thus the top shelf (Shelf 1) was the hottest, and the bottom shelf (Shelf 12) was coldest. Fluctuating temperatures have different effects on the development of bees and wasps than do constant temperatures (Radmacher & Strohm, 2011; Foray *et al.*, 2014), and therefore the daily fluctuations inside the incubator (controlled by the plug timers) were based on the daily fluctuations on the elevation gradient, to create a temperature gradient that was as realistic as possible (Figure 5.3), within the limitations of these simple materials (*i.e.* rising temperatures in the morning, maximum temperatures in the afternoon, and falling temperatures in the evening). The maximum temperature inside the incubator increased as height increased, as did the mean temperature and the standard deviation of the mean (SD), but the minimum temperature did not (when the light bulbs were off and it was night) (Figure 5.4 and Table 5.1). In contrast, on the elevation gradient, the maximum, minimum, mean, and SD all increased as elevation decreased (Figure 5.4). Thus, it must be stressed that the incubator did not simulate the temperature gradient on elevation gradient in all aspects (especially minimum temperature), but it did enable temperature to be studied in isolation from rainfall, humidity, atmospheric pressure, and the other environmental variables that confounded the elevation gradient (Hodkinson, 2005). Although the temperature gradient inside the incubator resulted from the heat of light bulbs, it was not confounded by a light gradient, either when three bulbs were on (P = 0.6143, r^2 = 0.0710), or when five bulbs were on (P = 0.3080, r^2 = 0.0138).

Each cell was randomly assigned to one shelf in the incubator, such that no two cells from one nest were assigned to the same shelf. Each cell was placed on its assigned shelf, inside its specimen jar, on the morning after it was collected from the field. The incubator was inspected every morning, and for every bee or wasp that had emerged as an adult, the number of days that it had been inside the incubator was calculated ("development time" = date of emergence – date of incubation), and its "intertegular span" or "intertegular distance" (ITD) was measured, using vernier calipers (with a precision of 0.02 mm). ITD is the distance between the bases of its wings, which is a standard measurement of body size in bees (Cane, 1987; Greenleaf *et al.*, 2007).

Body size, development time, and larval survival ("survival" = number of adults / number of larvae) were statistically modelled as functions of temperature inside the incubator ("generalized thermal reaction norms"). R was used for all statistical analysis (R Core Team, 2013). Both linear and non-linear models were fit to the data, using the forward stepwise methods of model selection described by Rocha & Klaczko, because reaction norms are frequently non-linear (Rocha & Klaczko, 2012). To compare the generalized thermal reaction norms of *Megachile* and *Rhynchium*, the slopes of the linear models for these species were compared, using *t*-tests for unequal sample sizes and unequal variances, and using the Welch-Satterthwaite equation to estimate the degrees of freedom (Welch's *t*-test). To test for differences between nests, which could be attributed to differences in genotype (different parents) or differences in age at incubation (nests were only collected from the field every two weeks), both linear and non-linear mixed-effects models were also fit to the data, using the R package *nlme* (Pinheiro *et al.*, 2010), and either the intercept (reaction norm ~ temperature, random = ~ 1 | nest) or both the slope and the intercept (reaction norm ~ temperature, random = ~ temperature | nest) were allowed to vary randomly by nest. The Akaike Information Criterion (AIC) and ANOVA tests were used to select the best models (Crawley, 2007; Zuur *et al.*, 2009; Rocha & Klaczko, 2012), and the best models were used to make predictions about the impacts of climate change.

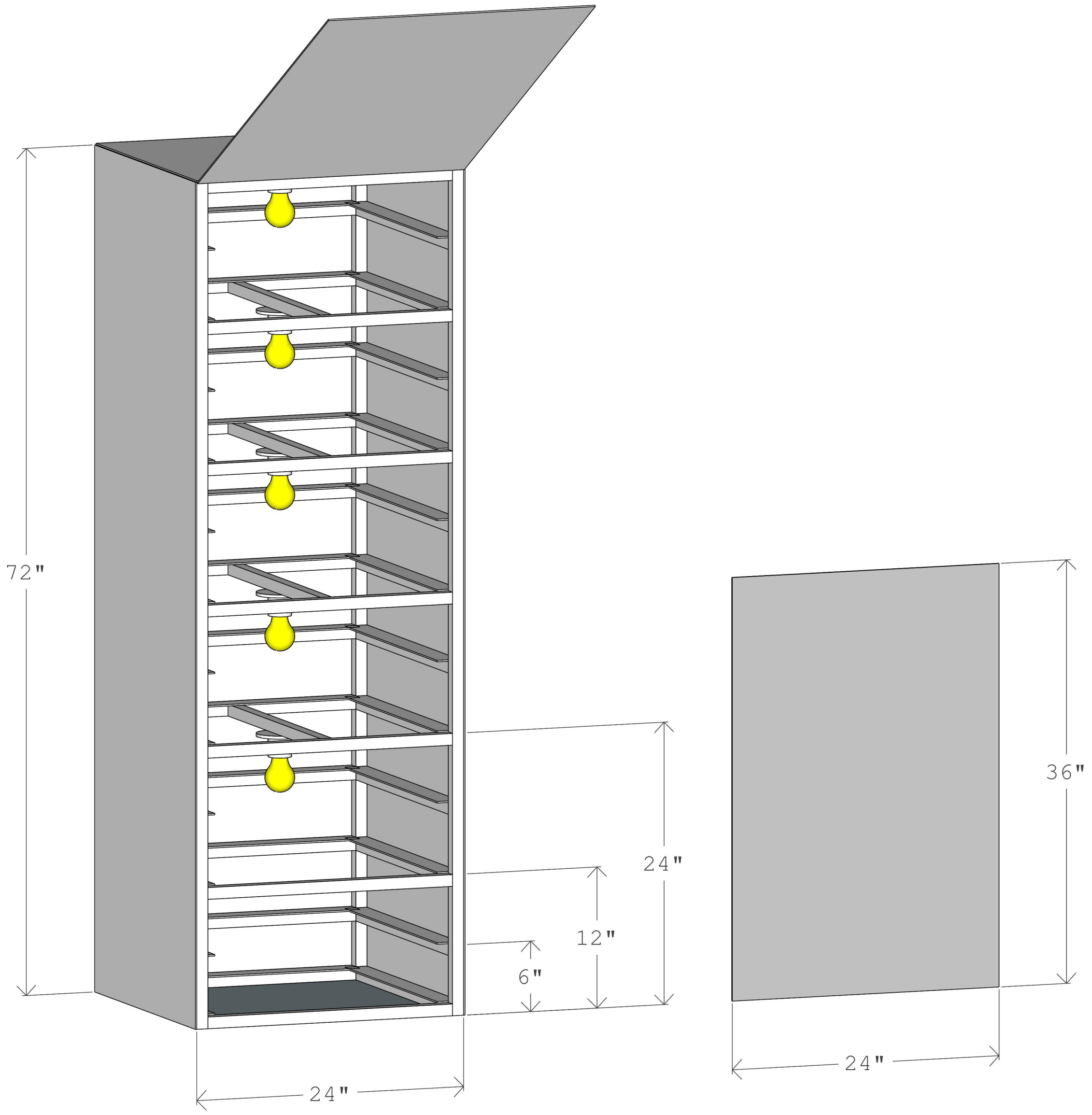


Figure 5.1 The incubator. The upper door is shown in an open position, and the lower door has been removed, to reveal the inside of the incubator. The insulation on the outside of the incubator is not shown, and neither are the wires or timers. The light bulbs are shown in yellow.

Figure 5.2 The immature bees and wasps, inside their specimen jars, inside the incubator.

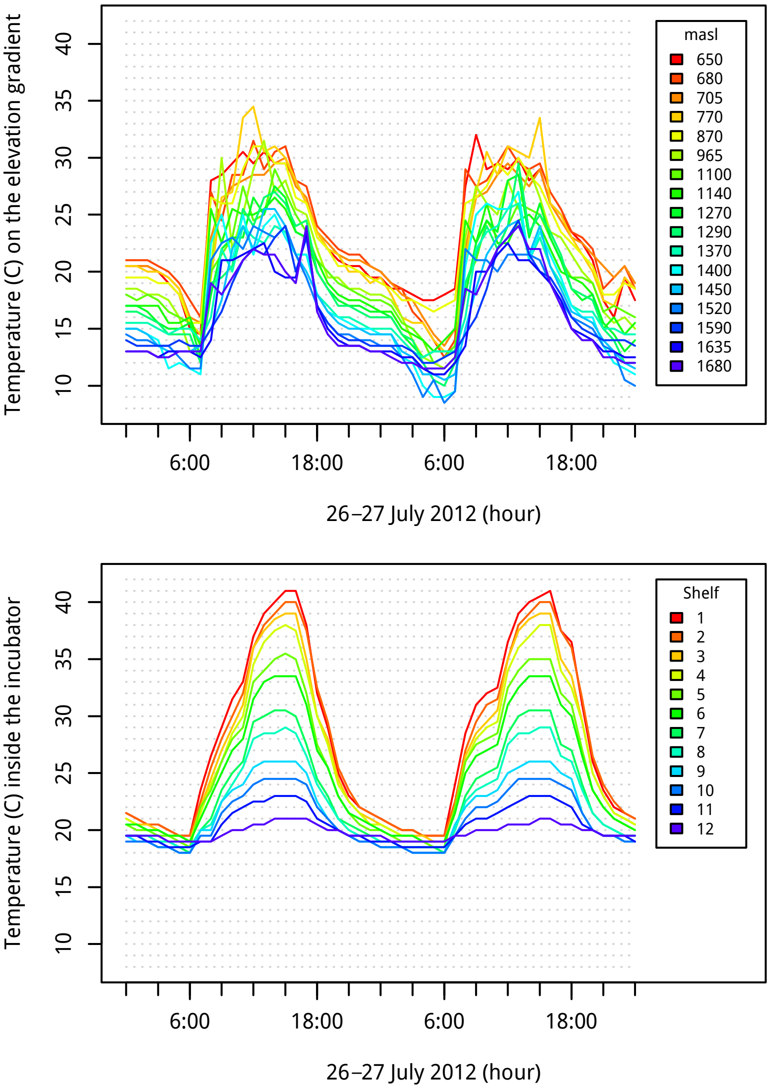


Figure 5.3 Comparison of the daily fluctuations in temperature on the elevation gradient and inside the incubator. The colors represent the temperatures at different elevations in the Taita Hills, in meters above sea level (masl), or the temperatures on different shelves inside the incubator (Shelf 1 was at the top of the incubator and Shelf 12 was at the bottom).

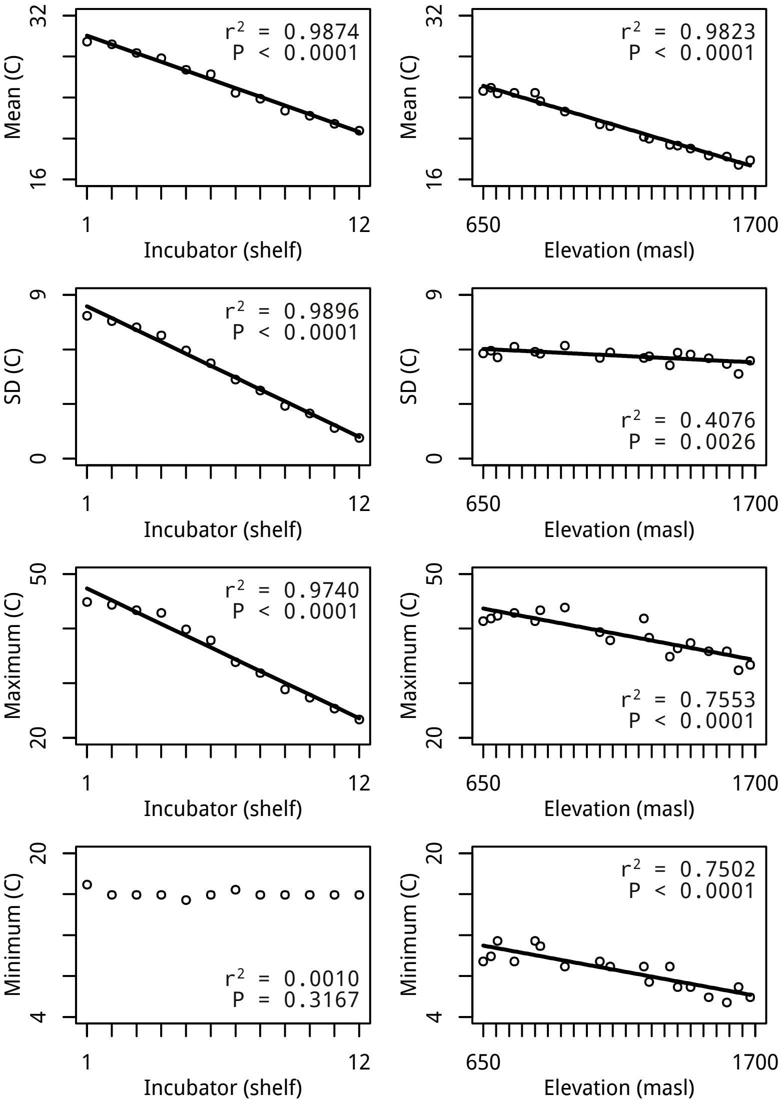


Figure 5.4 Comparison of the temperature gradient inside the incubator (data in Table 5.1) and the temperature gradient on the elevation gradient (data in Table 5.2). Shelf 1 was at the top of the incubator and Shelf 12 was at the bottom.

Table 5.1 The temperature gradient inside the incubator (20 July–30 December 2012). Maximum and mean temperatures decreased as height decreased, and so did the standard deviations of the mean temperatures (SD), but the minimum temperatures did not (Figure 5.4). Therefore, the temperature gradient inside the incubator was a gradient in maximum and mean temperatures, but not in minimum temperatures, and it was also a gradient in the variability of temperatures (SD). Because of the seasonal increase in temperature from 20 July, when the experiment began, to 30 December, when the experiment ended, there was also a seasonal increase in temperature inside the incubator, and therefore the lowest mean temperature (20.8449 C on Shelf 12) was higher than planned, based on the lowest mean temperature when the experiment began (19.5497 C on Shelf 12, in the first week, and 21.7161 C, in the last week). However, the unique temperature to which each bee or wasp was subjected, during its unique development time in the incubator, was used in the statistical models, and thus the seasonal increase in temperature is only a problem inasmuch as there is no data on the effects of the lowest mean temperatures on the elevation gradient (17.5029 C at 1635 masl; Table 5.2). Several other combinations of light bulbs and timers were tested, but it was not possible to generate mean temperatures as high as 29.5 C at the top of the incubator and simultaneously to generate mean temperatures as low as 17.5 C at the bottom of the incubator, while maintaining clear distinctions between the temperatures on different shelves (Figure 5.3). “Extreme” temperatures were defined statistically (based on the distribution of temperatures on each shelf) as temperatures with $P < 0.025$ (the upper tail of the distribution, or temperatures > Mean + 1.96 * SD) (Jentsch *et al.*, 2007; Smith, 2011). Even the highest extreme temperature on the elevation gradient (36.7381 C; Table 5.2) was not statistically extreme on the top five shelves of the incubator, and thus the incubator simulated an increase in the frequency of statistically extreme temperatures (Diffenbaugh & Field, 2013).

Shelf	Height (in)	Mean (C)	SD (C)	Max (C)	Min (C)	Extreme (C)
1	66	29.5292	7.8923	45.0	17.0	44.9981
2	60	29.2764	7.5982	44.5	16.0	44.1689
3	54	28.4254	7.2546	43.5	16.0	42.6444
4	48	27.9103	6.8121	43.0	16.0	41.2620
5	42	26.7858	5.9837	40.0	15.5	38.5139
6	36	26.3448	5.2804	38.0	16.0	36.6944
7	30	24.5188	4.3832	34.0	16.5	33.1099
8	24	23.9539	3.7828	32.0	16.0	31.3682
9	18	22.7908	2.9431	29.0	16.0	28.5593
10	12	22.3030	2.5242	27.5	16.0	27.2504
11	6	21.5048	1.7252	25.5	16.0	24.8862
12	0	20.8449	1.1817	23.5	16.0	23.1610

Table 5.2 The temperature gradient on the elevation gradient (20 July–30 December 2012). Maximum, mean, and minimum temperatures all decreased as elevation increased, and so did the standard deviations of the mean temperatures (SD) (Figure 5.4). Extreme temperature events ("Extreme") were defined statistically (based on the distribution of temperatures at each elevation) as temperatures with $P < 0.025$ (the upper tail of the distribution, or temperatures > Mean + 1.96 * SD) (Jentsch *et al.*, 2007; Smith, 2011).

Elevation (masl)	**Mean (C)**	**SD (C)**	**Max (C)**	**Min (C)**	**Extreme (C)**
650	24.7081	5.8209	41.5	9.5	36.1171
680	25.0343	5.9713	42.0	10.0	36.7381
705	24.4796	5.6022	42.5	11.5	35.4598
770	24.5342	6.1963	43.0	9.5	36.6789
850	24.5419	5.9165	41.5	11.5	36.1381
870	23.7134	5.8066	43.5	11.0	35.0943
965	22.7007	6.2451	44.0	9.0	34.9412
1100	21.4503	5.5723	39.5	9.5	32.3721
1140	21.2638	5.8765	38.0	9.0	32.7817
1270	20.2225	5.5686	42.0	9.0	31.1369
1290	20.0586	5.6668	38.5	7.5	31.1655
1370	19.4545	5.1672	35.0	9.0	29.5823
1400	19.3818	5.8614	36.5	7.0	30.8703
1450	19.0941	5.7634	37.5	7.0	30.3904
1520	18.4095	5.5566	36.0	6.0	29.3003
1590	18.3168	5.2428	36.0	5.5	28.5927
1635	17.5029	4.6968	32.5	7.0	26.7086
1680	17.9461	5.4201	33.5	6.0	28.5695

Results

In both *Megachile* and *Rhynchium*, development time decreased significantly as mean incubation temperature increased, in the linear models (Figure 5.5). There was a significant difference between the slopes of the model of *Megachile* and the model of *Rhynchium* ($P < 0.0001$, $t = –10.22$, d.f. = 83.55, $\text{mean}_1 = –5.5429$, $\text{mean}_2 = –1.1970$, $N_1 = 94$, $N_2 = 20$, $\text{SD}_1 = 3.224$, $\text{SD}_2 = 1.185$). In other words, *Megachile* had significantly greater phenotypic plasticity in development time, as an effect of temperature, than did *Rhynchium*. In the model of *Megachile*, the rate of change in development time (a slope of –5.5429) was about 4.6 times higher than it was in the model of *Rhynchium* (a slope of – 1.1970). Mean incubation temperature explained about 75% of the variation in the development time of *Megachile*, but only about 50% of the variation in the development time of *Rhynchium*, in these linear models.

In terms of development time, the linear mixed-effects model with different intercepts for different nests was the best model for *Rhynchium* (Table 5.3; the model with the lowest AIC in its class of models), but the cubic mixed-effects model with different intercepts and different slopes for different nests was the best model for *Megachile* (Table 5.4). Therefore, in terms of development time, the generalized thermal reaction norm was best described by a linear model for *Rhynchium* (Figure 5.5), but it was best described by a non-linear model for *Megachile* (Figures 5.6–5.7). The linear mixed-effects model for *Megachile* is also shown in Figure 5.7, because it illustrates an interesting pattern more clearly than does the non-linear model—specifically, there was more variation between nests at low mean temperatures than there was at high mean temperatures. This pattern is discussed, below, in terms of constraints on phenotypic plasticity at high temperatures.

Mean incubation temperature did not have significant effects on the larval survival of either species, or on the body size of *Megachile*, but it did have a marginally significant effect on the body size of *Rhynchium* males (Figure 5.8), which decreased in size as temperature increased ($y = –0.0471x + 4.4087$, $r^2 = 0.2812$, SE = 0.0197, $t = – 2.386$, $P = 0.0361$). In terms of body size, the generalized thermal reaction norm for *Rhynchium* males was best described by a linear model (Table 5.3). In both species, males were significantly smaller than females (Table 5.5), but the development times of females were not significantly longer than they were for males (Table 5.6).

Predicted effects of temperature

At the mean temperature on the elevation gradient (21.27 C), the linear fixed-effects models predicted a development time of about 64 days for *Megachile* and about 29 days for *Rhynchium*. The minimum mean temperature in the incubator was 20.84 C (Table 5.1), whereas the minimum mean temperature on the elevation gradient was 17.50 C (Table 5.2), and therefore predictions for the full range of temperatures on the elevation gradient could not be made based on the statistical models that were made from the incubator data. However, an increase in mean temperature of 7.53 C (the change in mean temperature on the elevation gradient) was predicted to cause a decrease in the development time of *Megachile* by about 42 days (67.11%). By comparison, an increase in mean temperature of 7.53 C was predicted to cause a decrease in the development time of *Rhynchium* by only about 9 days (26.89%). Therefore, the changes in temperature on the elevation gradient could have had an effect on the development time of both species, but a stronger effect on *Megachile* than on *Rhynchium*. However, it is not clear that this would necessarily have caused their distinct distributions on the elevation gradient.

The change in mean temperature on the elevation gradient (7.53 C) was larger than the change that is expected from global warming (about 1–5 C), and therefore predictions were also made for an increase of 2 C or 4 C (Table 5.7). For an increase in mean temperature of 2–4 C, the linear fixed-effect models predicted an 18.25–36.51% decrease in the development time of *Megachile* and an 8.25–16.50% decrease in the development time of *Rhynchium*. Because these models were linear, they made the same predictions for an increase of 2–4 C from different baseline temperatures. By comparison, for an increase in mean temperature of 2–4 C, the cubic fixed-effect model predicted a 34.07–45.79% decrease in the development time of *Megachile* from a baseline of 21.27 C, but it predicted a 40.01–56.59% decrease from a baseline of 20.11 C (the lowest mean temperature that was recorded for any bee in the incubator), because of the steep slope of the cubic model at low mean temperatures (Figure 5.6).

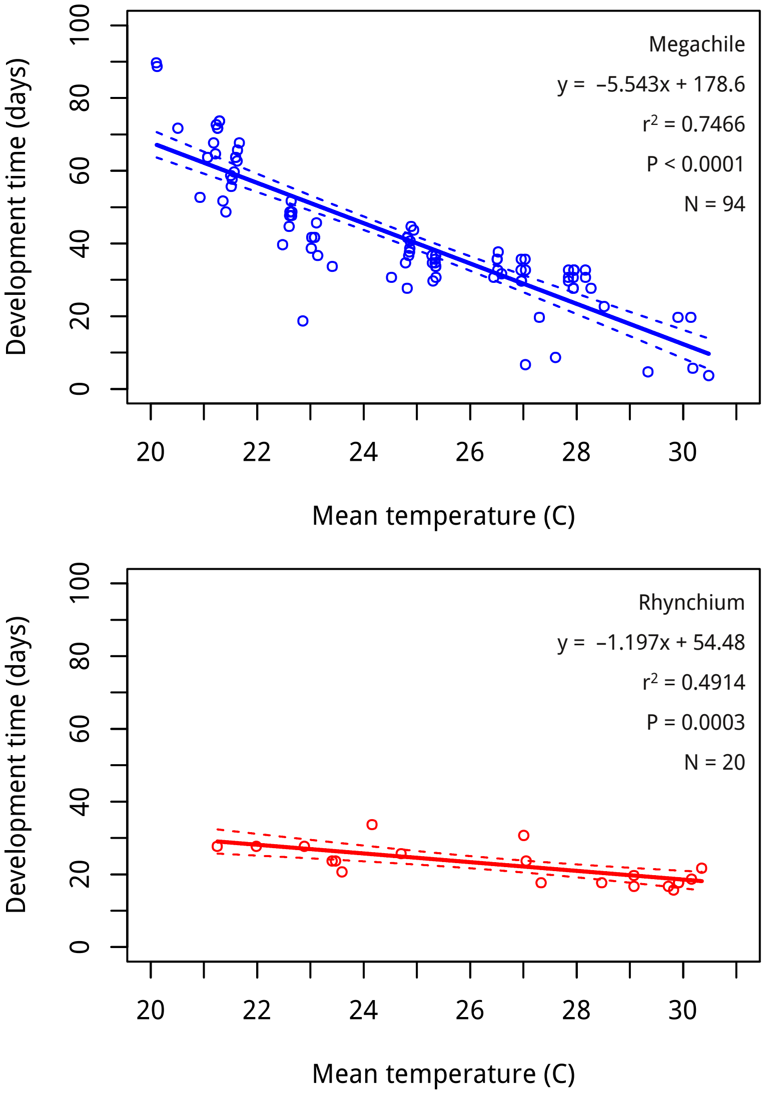


Figure 5.5 Generalized thermal reaction norms (fixed-effect models): linear responses of development time to mean incubation temperature in *Megachile* (a leaf-cutting bee) and *Rhynchium* (a caterpillar-hunting wasp).

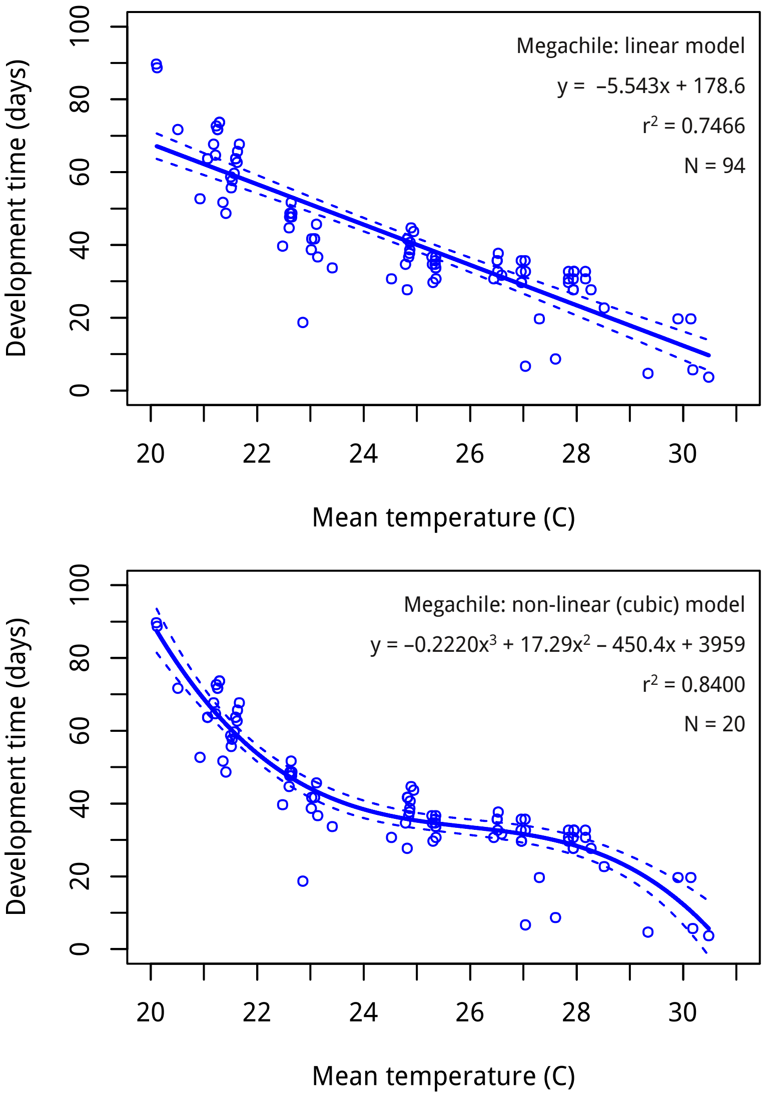


Figure 5.6 Generalized thermal reaction norms (fixed-effect models): linear and non-linear (cubic) responses of development time to mean incubation temperature in *Megachile* (a leaf-cutting bee).

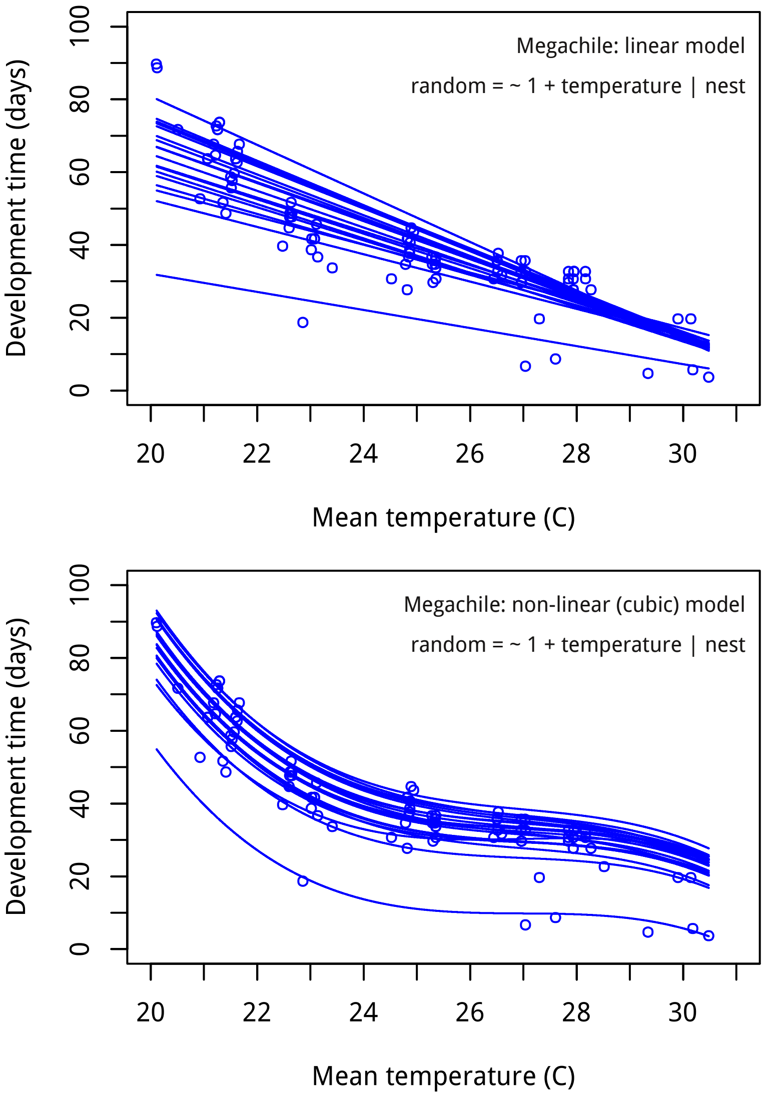


Figure 5.7 Generalized thermal reaction norms (mixed-effects models): linear and non-linear (cubic) responses of development time to mean incubation temperature in *Megachile* (a leaf-cutting bee). Each line represents a different nest.

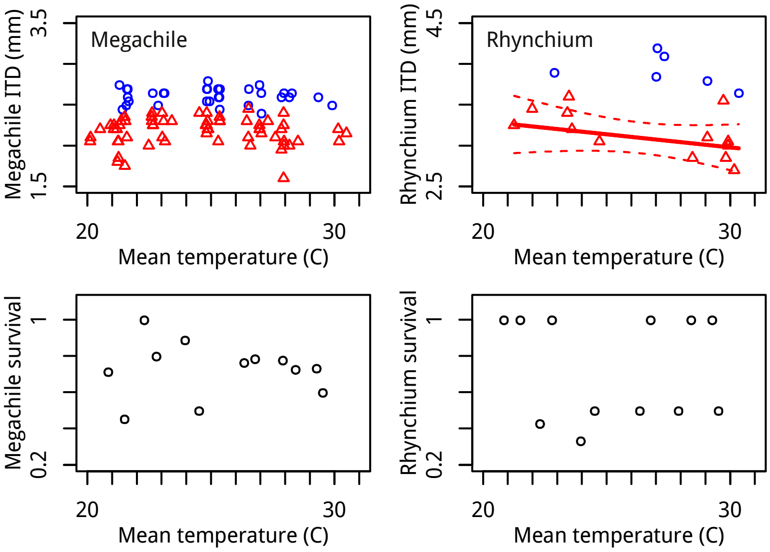


Figure 5.8 Generalized thermal reaction norms (fixed-effect models): body size (ITD) and larval survival (proportion of cells that produced adults) in *Megachile* (a leaf-cutting bee) and *Rhynchium* (a caterpillar-hunting wasp), in response to mean incubation temperature. In the plot of body size on mean temperature, males are shown as red triangles and females are shown as blue circles. Because of sexual dimorphism in body size (see Table 5.5), males and females were modelled separately. Temperature did not have significant effects on the body size of *Megachile* male or females, or *Rhynchium* females, but it did have significant effects on the body size of *Rhynchium* males, which decreased in body size as temperature increased ($y = -0.04707x + 4.4087$, $r^2 = 0.2812$, SE = 0.01972, $t = -2.386$, $P = 0.0361$).

Table 5.3 Models of generalized thermal reaction norms for *Rhynchium*. In the syntax of the R package *nlme* (Pinheiro *et al.*, 2010), the mixed-effects models had either a random intercept (random = ~ 1 | nest) or a random slope and a random intercept (random = ~ 1 + temp | nest). Within a group of models, the "best" model is the model with the lowest AIC. For example, within the group of models of development time, the best model is the mixed-effects model with different intercepts for different nests (AIC = 105.5).

Reaction norm	**Fixed**	**Random**	**AIC**
Body size (female)	~ 1	—	—
Body size (male)	~ temp	—	33.92
	~ $temp^2$ + temp	—	34.87
	~ temp	~ 1 | nest	42.67
	~ temp	~ 1 + temp | nest	46.67
Development time	~ temp	—	113.3
	~ $temp^2$ + temp	—	114.5
	~ temp	~ 1 | nest	105.5
	~ temp	~ 1 + temp | nest	109.5
Survival	~ 1	—	—

Table 5.4 Models of generalized thermal reaction norms for *Megachile*. In the syntax of the R package *nlme* (Pinheiro *et al.*, 2010), the mixed-effects models had either a random intercept (random = ~ 1 | nest) or a random slope and a random intercept (random = ~ 1 + temp | nest). Within a group of models, the "best" model is the model with the lowest AIC. For example, within the group of models of development time, the best model is the cubic mixed-effects model with different intercepts and different slopes for different nests (AIC = 570.8).

Reaction norm	**Fixed**	**Random**	**AIC**
Body size	~ 1	—	—
Development time	~ temp	—	681.4
	~ $temp^2$ + temp	—	669.8
	~ $temp^3$ + $temp^2$ + temp	—	640.1
	~ $temp^4$ + $temp^3$ + $temp^2$ + temp	—	641.6
	~ temp	~ 1 | nest	672.7
	~ temp	~ 1 + temp | nest	663.8
	~ $temp^3$ + $temp^2$ + temp	~ 1 | nest	576.2
	~ $temp^3$ + $temp^2$ + temp	~ 1 + temp | nest	570.8
Survival	~ 1	—	—

Table 5.5 Mean body sizes (intertegular distances) of *Megachile* and *Rhynchium*, at the temperatures that were tested inside the incubator. The “tegulae” are morphological characters at the bases of the wings, and the “intertegular” distance is the distance between the tegulae (the distance between the shoulder blades, in anthropomorphic terms). Comparisons between males (M) and females (F) were made using linear models (SE, *t*, and *P*), and there were statistically significant differences between males and females, in both species (males were smaller than females).

Taxon	**mm (F)**	**SE**	**mm (M)**	**SE**	***t***	***P***
Megachile	2.614	0.0262	2.175	0.0322	–13.63	< 0.0001
Rhynchium	3.917	0.1065	3.158	0.1288	–5.893	< 0.0001

Table 5.6 Mean development times of *Megachile* and *Rhynchium* (number of days in the incubator), at the temperatures that were tested inside the incubator. Comparisons between males (M) and females (F) were made using linear models (SE, *t*, and *P*), and there were not statistically significant differences between males and females, in either species.

Taxon	**Days (F)**	**SE**	**Days (M)**	**SE**	***t***	***P***
Megachile	40.03	3.129	42.66	3.853	0.683	0.497
Rhynchium	23.83	1.852	21.08	2.239	–1.231	0.235

Table 5.7 Predicted effects of an increase in mean temperature on development time in *Megachile* and *Rhynchium*, based on the linear and cubic (fixed-effect) models. The mean temperature on the elevation gradient was 21.27 C, and predictions were made for increases of 2 C and 4 C, from a baseline mean temperature of 21.27 C, to warmer mean temperatures of 23.27 C and 25.27 C. For example, for an increase of 2 C (from 21.27 C to 23.27 C), the linear model predicted a change of –11.09 days (Δ Days), from 60.73 days to 49.64 days (60.73 days – 11.09 days), which is a change of –18.25% [Δ Days (%)]. For the cubic model, predictions were also made for increases from a baseline mean of 20.11 C (the lowest mean temperature that was recorded for an individual in the incubator), to show that the cubic model predicted greater changes in development time for increases from a lower baseline than it did from a higher baseline (because of its greater slope at lower mean temperatures). The linear models, because they were linear, made the same predictions from different baselines.

Species	**Model**	**C**	**Days**	**Δ C**	**Δ Days**	**Δ Days (%)**
Megachile	linear	21.27	60.73	+ 2	-11.09	-18.25
“	“	“	“	+ 4	-22.17	-36.51
“	cubic	21.27	64.14	+ 2	-21.85	-34.07
“	“	“	“	+ 4	-29.36	-45.79
“	cubic	20.11	87.51	+ 2	-35.02	-40.01
“	“	“	“	+ 4	-49.53	-56.59
Rhynchium	linear	21.27	29.02	+ 2	- 2.39	- 8.25
“	“	“	“	+ 4	- 4.79	-16.50

Discussion

Hypothesis tests

In both species, development time decreased as temperature increased, but temperature had significantly stronger effects on the development time of *Megachile* than it did on the development time of *Rhynchium*. Temperature also had significant effects on the body size of *Rhynchium* males, but it did not have significant effects on the body size of *Megachile*, and it did not have significant effects on the survival of either species. Thus, there was support for hypothesis 1 (Bergmann's rule) in *Rhynchium*, but not in *Megachile*, and there was support for hypothesis 2 in both species (development time decreases as temperature increases), but there was no support for hypothesis 3 (different levels of survival at different temperatures). There was strong support for hypotheses 4 and 5 (different thermal reaction norms in different species). Firstly, for body size, the slope of the reaction norm was significantly different than zero for *Rhynchium* but not for *Megachile*. Secondly, for development time, the slope of the reaction norm was significantly steeper for *Megachile* than it was for *Rhynchium*. Thirdly, for development time, the shape of the reaction norm was best described by a linear model for *Rhynchium* and a non-linear model for *Megachile*. However, for survival, the slope of the reaction norm was not significantly different than zero for either species, and so there was no support for hypothesis 6.

Mechanistic effects of temperature: hypothesis tests and the elevation gradient

Between hypotheses 4 and 5, there was only weak support for the conclusion that the different distributions of these species on the elevation gradient could have been driven by different responses to temperature. There would have been stronger support for this conclusion, if there were a mechanistic connection between development time and nesting frequency that could explain these different distributions. A decrease in development time could cause a decrease in generation time, and thus an increase in the number of generations per year (an increase in “voltinism”) (Bale *et al.*, 2002; Tobin *et al.*, 2008), which could be a mechanistic connection between development time and nesting frequency. However, such a mechanism would suggest that the nesting frequencies of both *Megachile* and *Rhynchium* should be higher in the lowlands, where the temperatures are higher and the development times of both species should be shorter, which is not what was observed on the elevation gradient.

If a decrease below, or an increase above, some optimum development time could be shown to cause a decrease in survival or reproduction, and if survival or reproduction could then be shown to cause a decrease in nesting frequency, then that would be a better mechanism for explaining these different distributions on the elevation gradient, because different species could have different optimum development times. Temperature did not have significant effects on larval survival in *Megachile* or

Rhynchium, over the range of temperatures that were tested, and the effects of development time on adult survival and reproduction were not tested. However, temperature does have significant effects on adult survival and reproduction in other species of Hymenoptera (Foray *et al.*, 2014), and therefore this mechanism is not an impossible explanation for these different distributions.

If temperature were to have no effects on the survival or reproduction of *Megachile* or *Rhynchium*, in terms of development time, it could still have effects on other species, and thus the distributions of *Megachile* and *Rhynchium* could still be explained by temperature, in terms of interactions with other species (such as competition, predation, and mutualism). Indeed, it could be hypothesized that *Megachile* and *Rhynchium* would interact with one another, and that the outcomes of these interactions would depend on temperature. *Megachile* and *Rhynchium* have preferences for nests of different sizes and different orientations (Chapter 4), and therefore they would probably not compete for nests. However, they could have other antagonistic interactions. For example, the nests of one species might attract generalist natural enemies to a shared nesting site, which might attack the other species (MacIvor & Salehi, 2014), and this might result in “apparent competition” (Holt, 1977) between these species, the outcome of which might depend on temperature. However, a mechanistic connection between different temperatures and the different distributions of these two species has not been proved (or disproved) by the results of this experiment.

Predicted effects of temperature: body size and development time

The predicted effects of temperature on development time and body size might be qualitatively accurate as predictions of the effects of global warming—development time will probably decrease, in both species—but they might not be quantitatively accurate, for two reasons. Firstly, global warming will be accompanied by many other changes in climate. East Africa will probably get hotter and wetter, not hotter and drier (Washington & Pearce, 2012). Therefore, on the elevation gradient in the Taita Hills—on which rainfall and temperature are negatively correlated at present (Chapter 4)—the relationship between rainfall and temperature will probably become uncoupled in the future. Secondly, the simulation of global warming in the incubator was not perfectly realistic. As well as extremely high temperatures, extremely low temperatures are known to limit the distribution of some species, such as trees (Jentsch *et al.*, 2007), and differences in minimum temperatures were not simulated in the incubator, which could have had an effect on the development of *Megachile* and *Rhynchium*.

Nevertheless, it might be meaningful to consider the consequences of the predicted effects of global warming on development time and body size in the Taita Hills. The bees and wasps that were incubated in this experiment were collected from nests that were constructed in the cold dry season (roughly July–September). If the mean development time in *Megachile* is about 64 days at 21.27 C, as predicted by the cubic model, then an egg that is laid in the middle of the cold dry season will probably emerge as an adult in the short wet season (roughly October–December), and if the development time is about 88 days at 20.11 C (in the highlands of the Taita Hills, where *Megachile* nests more frequently), then an egg that is laid at any time from the middle of July to the middle of September will probably emerge in the short wet season. However, if the Taita Hills warms up by 2–4 C, and mean development time decreases by about 22–29 days (from a baseline of 64 days) or 35–50 days (from a baseline of 88 days), as predicted by the cubic model (Table 5.7), then an egg that is laid in the beginning or middle of the cold dry season will probably emerge in the cold dry season. This might be lethal, if there are fewer floral resources in the cold dry season than there are in the short wet season.

By comparison, the mean development time of *Rhynchium* (about 29 days) is much shorter than the length of the cold dry season (about 90 days), and therefore an egg that is laid in the middle of the cold dry season will probably emerge in the cold dry season, whether or not there is global warming. Thus, the consequence of a change in development time (as a consequence of global warming) could be much more biologically meaningful for *Megachile* than it would for *Rhynchium*, if it would mean a change in the season of emergence for *Megachile* but not for *Rhynchium*. Such a change in season could mean a mismatch between *Megachile* and the crops that it pollinates. However, many crops are grown year-round in the highlands of the Taita Hills, and therefore a change in phenology might not cause a mismatch between *Megachile* and the crops that it pollinates—if indeed it pollinates crops, which remains to be determined, but other species of *Megachile* are crop pollinators, such as *Megachile rotundata*, the alfalfa leaf-cutting bee, which is commercially managed as a pollinator of alfalfa (*Medicago sativa*) and other crops (Pitts-Singer & Cane, 2011). In general, a mismatch between mutualists might be less likely in environments with low variation between seasons (Rafferty *et al.*, 2014).

It is strange that temperature had statistically significant effects on *Rhynchium* males but not on *Rhynchium* females, and this was probably caused by differences in statistical power (only 6 *Rhynchium* females were incubated, compared to 14 males, and the effect on males was only marginally significant), rather than being caused by differences in the biological effect of temperature on the body sizes of males and females. However, it should be noted that Hymenoptera are “haplodiploid” (males are produced from unfertilized eggs and have a haploid number of chromosomes, but females are produced from fertilized eggs, and have a diploid number of chromosomes), and therefore there is less genetic variation between males from one nest than there is between females. This could mean that it is easier to detect statistical patterns in the reaction norms of male Hymenoptera than female Hymenoptera (such as body size in this experiment). This difference between male and female Hymenoptera could be exploited in future research on genotypic *versus* phenotypic adaptation.

Bergmann's rule is not as strict a rule in ectotherms as it is in endotherms, and an “inverse Bergmann cline” (an increase in body size with an increase in temperature) has been observed in some ectotherms (Shelomi, 2012). However, for species that are described by Bergmann's rule, an increase in development time could cause a decrease in dispersal ability, if individuals with smaller bodies are worse dispersers (Jenkins *et al.*, 2007). It has been suggested that species have two choices when faced with climate change: “adapt or disperse” (Berg *et al.*, 2010). The converse could also be true for species that have a phenotypic decrease in body size when faced with climate change (“fail to adapt and fail to disperse”), because a phenotypic decrease in body size (a maladaptive response, in terms of dispersal ability), if not counteracted by a genotypic increase in body size (an adaptive response, in terms of dispersal ability), could cause a decrease in dispersal ability and an increase in dispersal failure. Thus, there could be situations in which plasticity could be maladaptive.

Megachile is a smaller species than *Rhynchium* (Table 5.5), and thus its dispersal ability could be more limited than the dispersal ability of *Rhynchium*. *Megachile* is also a species of higher elevations than is *Rhynchium* (Chapter 4). Therefore, if both *Megachile* and *Rhynchium* are faced with the same two choices (“adapt or disperse”), then “disperse” could be a worse choice for *Megachile* that it could for *Rhynchium*, because the availability of higher elevations (to which *Megachile* would need to disperse, in order to reach a relatively cooler climate) is more limited than the availability of lower elevations (to which *Rhynchium* would need to disperse, in order to reach a relatively cooler climate), and also because the dispersal ability of *Megachile* could be more limited than the dispersal ability of *Rhynchium*. As a smaller species, with a larger ratio of surface area to volume, *Megachile* could also have a lower ability to resist convective heat exchange with the environment (Stevenson, 1985), and this could be a reason that *Megachile* nested more frequently at higher elevations, or a reason that temperature had a stronger effect on *Megachile* than it did on *Rhynchium*.

It is surprising that temperature did not have a significant effect on the larval survival of either species, but it would seem that the temperatures that were tested inside the incubator were still within the “thermal buffers” of these species (Deutsch *et al.*, 2008), at least in terms of larval survival. High temperatures have been shown to have negative effects on larval survival in other species of trap-nesting bees (Pitts-Singer & James, 2008; Hranitz *et al.*, 2009), and thus it is possible that the temperatures that were tested in this experiment were not high enough. However, the temperatures that were statistically “extreme” (Jentsch *et al.*, 2007) on the elevation gradient, even at the hottest elevations (Table 5.2), were not statistically extreme on the top five shelves of the incubator (Table 5.1), and thus it would seem that neither an increase in mean temperatures nor an increase in the frequency of statistically extreme temperatures had a significant effect on larval survival. This supports the suggestion that “extremes” should be defined not only statistically, but also ecologically (Jentsch *et al.*, 2007; Smith, 2011). However, it is possible that larval survival in the incubator was artificially high, because leaf-cutting bees can have higher levels of larval survival in environments with lower levels of oxygen (Abdelrahman *et al.*, 2014), and thus the airtight jars in which the larval bees and wasps were incubated could have had an effect on larval survival.

Phenotypic plasticity: variation in reaction norms and adaptation to climate change

Reaction norms were originally used to study phenotypic plasticity within a genotype, but here they were used to study phenotypic plasticity at a higher level of biodiversity—between genotypes (one nest *versus* another) and between species (*Megachile versus Rhynchium*)—and therefore, they are “generalized” reaction norms (Sarkar & Fuller, 2003). They are also “realized” reaction norms (as opposed to “fundamental” reaction norms), inasmuch as they are based on fluctuating temperatures as opposed to constant temperatures (Paaijmans *et al.*, 2013). However, the fluctuating temperatures in this experiment were not completely realistic (they were not fluctuations in minimum temperatures), and therefore these reaction norms were only incompletely “realized” in this experiment.

This experiment was much better replicated than a standard experiment on reaction norms, which might use only two or three experimental treatments—such as the three treatments of the “three-point-curve” experimental design (Rocha & Klaczko, 2012)—to model the shape of the reaction norm. In this experiment, there were effectively 94 replicates of *Megachile* and 20 replicates of *Rhynchium* (in terms of development time), because the variation in the temperature inside the incubator, from day to day, and the variation in the development time, from individual to individual, meant that each individual was an independent data point in terms of temperature, averaged over the course of its individual development period, and therefore individuals were treated as replicates in the statistical models.

Because this experiment was better replicated than a “three-point curve” experiment, the shapes of the reaction norms could also be better modelled. Whether or not a linear model should be used to describe a reaction norm, based on only two or three experimental treatments, has been debated (Rocha & Klaczko, 2012), and the results of the present experiment support both the “optimistic view” that a linear model could be used (*Rhynchium*), and also the “pessimistic view” that a linear model should not be used (*Megachile*), to describe a reaction norm. This experiment also shows that development time can be better described by non-linear models than by linear models (*Megachile*), which is good to know, because development time was the only trait that was not better described by non-linear models in the study by Rocha & Klaczko (2012). Reaction norms of different shapes (linear *versus* non-linear) resulted in very different predictions about the effects of temperature on development time in *Megachile* (Table 5.7). Therefore, the debate about the shape of the reaction norm is not only of theoretical significance. It is also of applied significance, if reaction norms are used to predict and mitigate the impacts of climate change.

In the linear mixed-effects model of development time (Figure 5.7), there was less variation between nests at high temperatures than there was at low temperatures. This supports the suggestion that there is less phenotypic plasticity in upper thermal limits (such as the critical thermal maximum) than there is in lower thermal limits, in insects (Hoffmann *et al.*, 2013). If there is a lack of phenotypic variation at high temperatures (variation upon which evolution could act by natural selection), then this could be a negative feedback mechanism—in other words, an increase in temperature could cause a decrease in phenotypic variation (the raw material of natural selection), and thus a decrease in the potential for genotypic adaptation.

Adaptation** versus **mitigation

Could there be methods of habitat management in agricultural landscapes that would mitigate the impact of global warming on trap-nesting pollinators and natural enemies? Agroforestry is common in the highlands of the Taita Hills, and it is possible that supplemental nesting sites could be placed under shade trees, in order to mitigate an increase in temperature. In the grasslands of the Central Valley of California (Hranitz *et al.*, 2009), leaf-cutting bees that developed in shaded traps nests had lower levels of heat stress than did leaf-cutting bees that developed in unshaded trap nests. However, they also had higher levels of parasitism, and thus there was no overall improvement in survival in the shaded trap nests. Therefore, there might be tradeoffs between abiotic conditions and biotic interactions, in terms of efforts to mitigate the effects of global warming. There might also be tradeoffs between mitigation (by means of habitat management) and adaptation (by means of genotypic and phenotypic change). For example, by placing supplemental nests in colder habitats, mitigation might disrupt the process of adaptation, such as the process of "heat hardening" (upregulating the production of heat shock proteins in larvae that develop in warmer habitats) (Hoffmann *et al.*, 2013). Alternatively, there might be synergies between mitigation and adaptation, if adaptation is genotypically or phenotypically constrained at high temperatures (see Figure 5.7) (Hoffmann *et al.*, 2013), or if adaptation does not happen faster than the "velocity of climate change" (Diffenbaugh & Field, 2013), and if mitigation provides more time for adaptation at lower temperatures, at which there could be higher levels of phenotypic plasticity (upon which evolution could act by natural selection).

Conclusion

Temperature has different effects on different traits and different species. This could cause a mismatch between crops and their pollinators, or pests and their natural enemies, but it could also cause a mismatch between crop pollination and pest regulation. The prediction and mitigation of such mismatches should be based on models of the mechanistic connections between changes in temperatures and changes in traits, in multiple species, and on multiple trophic levels. This implies a high level of experimental complexity, which may be impractical for a preliminary study, such as this (which is possibly the first study to compare the thermal reaction norms of pollinators and natural enemies, and is probably the first study to do so in sub-Saharan Africa). However, even at this low level of experimental complexity, there was a clear distinction between the thermal reaction norms of these two trophic levels. Therefore, there seems to be a distinct possibility that this small community of trap-nesting pollinators and natural enemies in the Taita Hills will disassemble in response to global warming. This might or might not be a problem for crop pollination, pest regulation, and crop production in the Taita Hills. The most that can be said at this point is that biodiversity seems to stabilize ecosystem function (McNaughton, 1977; and see "Diversity and the stability of ecosystem services" in Chapter 2), and this seems to be the case for crop pollination and pest regulation, in response to global changes (Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011, 2013; Rader *et al.*, 2013). Therefore, it would seem to be vital for us to conserve biodiversity in agricultural landscapes.

In opposition to the observation that climate has stronger effects on higher trophic levels (Voigt *et al.*, 2003), temperature had stronger effects on a primary consumer (the pollinator) than it did on a secondary consumer (the natural enemy), in this experiment. This suggests that climate and trophic level could have a complicated or idiosyncratic relationship, and therefore it will be reiterated that we need models of the mechanistic connections between changes in climate and changes in traits, in multiple species, and on multiple trophic levels. Such research on climate change has so far been biased against sub-Saharan Africa (Parmesan, 2006), and so has research on pollination and pest regulation (Chapter 2; Steward *et al.*, 2014). The present research is a step towards correcting this bias, but much more research is needed—and soon, before the "perfect storm" hits land.

Biodiversity and ecosystem services: prospects for future research on pollinators, natural enemies, and conservation conflicts in sub-Saharan Africa

Conclusion to the thesis

Throughout this thesis, the proportion of “habitat” in an agricultural landscape is presented as a driver of biodiversity. “Non-crop” habitat is presented as a driver of the abundance and richness of pollinators and natural enemies (Chapter 2) and of the richness of threatened species (Chapter 3). “Woody” habitat is presented as a driver of the abundance of leaf-cutting bees in trap nests (Chapter 4). However, “habitat” is a generic term for an environment that is lived in by a given species, and “habitat” could be a protected area, a fragment of natural grassland or woodland in an unprotected agricultural landscape, or it could be an agricultural monoculture, from the viewpoint “cultural species” (see Chapter 2), such as some bees, some natural enemies, and many species of crop pests (which may be why these species are pests). The mechanistic connection between species and habitats has been demonstrated for species throughout the world, by modelling the “species-area relationship” (*e.g.*, Rosenzweig, 2003a), which basically states that there are more species where there is more area (in part, because there is more habitat). The species-area relationship is fundamental to biogeography, conservation biology, and ecology, but as a theory of island biogeography, it is not well supported by the distribution patterns of mainland biodiversity in “islands” of protected habitat, surrounded by “oceans” of unprotected agricultural land (Mendenhall *et al.*, 2014). However, in the emerging theory of countryside biogeography (Daily, 1997), it has been shown that, from the viewpoint of species in a terrestrial protected area, the “area” in the species-area relationship can also mean the agricultural “matrix” of crop and non-crop habitat (Ricketts, 2001; Perfecto & Vandermeer, 2010; Mendenhall *et al.*, 2014). It is in this context—the context of countryside biogeography—that this thesis has focused on the synthesis of two divergent perspectives on the species-area relationship.

The first perspective is that of productionists (including the proponents of “sustainable” or “ecological” intensification), whose vantage point is in the farmland, and who therefore see the species-area relationship from the perspective of agriculture, by looking out at the wilderness that surrounds them, and thinking of the benefits that biodiversity could provide to agriculture, through pollination, pest regulation, and other ecosystem services, and the costs that biodiversity could impose on agriculture, through ecosystem disservices, such as crop raiding. The second perspective is that of conservationists, whose vantage point is in the wilderness, and who therefore see the species-area relationship from the perspective of nature, looking out across the farmlands that surround them, and thinking of the benefits that agriculture could provide to nature, and the costs that agriculture could impose.

There could be a third perspective, which could be a synthesis of the first and second. There are some of us whose vantage point is the ivory tower, looking down at both the farmland and the wilderness from high above, and thinking of the benefits that could be heaped upon benefits, if only we could optimize the costs. However, if I were a poor farmer at the edge of Tsavo, whose crops had been raided, or a child whose teacher had been killed by an elephant (which happened in the time that I was living in the Taita Hills), then I would struggle not to hate wildlife, and I would struggle not to clear away the thickets of dense woodland, which were once the hunting grounds of the Man-Eaters of Tsavo, if that would mean more charcoal, more farmland, and fewer lions and elephants. It must be remembered that the ivory tower is made of ivory, and those of us whose prosperity rests upon the poaching of the past are not above reproach.

Nevertheless, there could be a third perspective. There could be potential for "win-win ecology" or "reconciliation ecology" (Rosenzweig, 2003a, 2003b). Some compelling research has been done in Kenya on the use of bee hives, hung on fences, both to prevent elephants from raiding crops (elephants are afraid of bees, and the bees defend their hives when the elephants run into the fences and disturb the hives) and also to provide sustainable livelihoods by means of honey production (King *et al.*, 2011). Of course, this is not a "win" for the elephants, whose goal is to raid the crops—it is not a resolution of the conservation conflict, but it is at least a mitigation. It seems to me that a resolution will be found in the thoughtful use of the species-area relationship to mend the relationship between agriculture and nature—a relationship that has been referred to as a marriage of "trouble and strife" (Baudron & Giller, 2014). A resolution will be found by finding compromises between agriculture and nature, such as land sharing and land sparing, and coupling these compromises with quantitative evaluations of ecosystem services and disservices (Chapter 3). It has been suggested in this thesis, as it has been suggested elsewhere, that the exchange of species between agricultural and natural habitats could be of benefit to both agriculture and nature, but there are also costs and risks associated with such an exchange of benefits, and these will need to be predicted and mitigated. However, the lesson that we seem to be learning from the valuation of ecosystem services is that they are highly valuable—not to mention priceless—and therefore there would seem to be potential for the valuation of, and payment for, ecosystem services to allow the people of the greater Tsavo ecosystem not to hate wildlife, and possibly even to value it.

Vital to such valuations will be a mechanistic understanding of the relationships between natural habitats and ecosystem-service providers (species-area relationships), such as the relationships between crop pollinators, pests, natural enemies of crop pests, and non-crop habitats. This is the context in which the community of cavity-nesting pollinators and natural enemies was studied in the Taita Hills. However, much more research is needed. First and foremost, we need to bridge the gaps in our knowledge between ecosystem-service providers, on the one hand, and ecosystem services, on the other. Secondly, we need to bridge the gap between natural habitats and ecosystem-service providers, and thereby to make a mechanistic connection between natural habitats and ecosystem services. Thirdly, we need to take the first and second steps while keeping an eye on climate change, which is likely to change the relationships between natural habitats, ecosystem-service providers, and ecosystem services (Chapters 4–5). The research in this thesis has taken steps toward bridging the second and third gaps, but the first gap continues to be wide and deep, especially in terms of the interactions between crop pollination and pest regulation.

Future research on crop pollination, pest regulation, conflict resolution, and food security in the Taita Hills

To bridge this first gap in our knowledge—the connection between ecosystem-service providers and ecosystem services—we need simultaneous experimental manipulations of pollinators, pests, and natural enemies, coupled with measurements of crop yield, such as the groundbreaking work by Lundin *et al.* (2012), who manipulated bumble bees as pollinators (*Bombus terrestris*) and weevils as pests (*Apion* spp.), and studied their interacting effects on the yield of red clover (*Trifolium pratense*) in field cages.

In the Taita Hills, my field assistant and I designed and constructed a series of field cages for such experimental manipulations (Figures 6.1–6.2), and I attempted to rear experimental colonies of leaf-cutting bees (*Megachile* sp. 1) and caterpillar-hunting wasps (*Rhynchium marginellum sabulosum*) for use in such manipulations (Figures 6.3–6.4), but I was unsuccessful in the time I had available to me. I also designed and constructed a series of smaller field cages, and I attempted to study the interacting effects of pollination and pest-control deficits on the yield of courgettes (*Cucurbita pepo*), which could have been experimentally manipulated by hand pollination, and which are obligately dependent upon cross-pollination (Klein *et al.*, 2007). Some farmers in the Taita Hills told me that courgettes invariably suffered from powdery mildew (a pest species, which could have been experimentally manipulated by fungicide), but the courgettes that were planted in my field cages were never infected by powdery mildew, and many of the field cages were soon destroyed by wild puppies (Figures 6.5–6.6), and there the experiment ended. Nonetheless, experiments such as these could be a good way forward, for studying the interactions between crop pollination and pest regulation, and I would recommend them to future researchers in the Taita Hills.

However, in designing these experiments—in identifying crops that are grown in the Taita Hills that might suffer from pollination and pest control deficits—I began to question the role of pollination in the food security of the Taita Hills. Two thirds of crop species are dependent, to a greater or lesser degree, upon pollination by animals (Klein *et al.*, 2007), but of the “main crops” that are grown in the Taita Hills (Soini, 2005), only one—mango (*Mangifera indica*)—is more than a little dependent on animal pollination (Table 6.1). The pollination and yield of mango decreased with increasing distance from natural habitat in South Africa (Carvalheiro *et al.*, 2010), and so did the pollination and yield of papaya in Kenya (*Carica papaya*), which is also grown in the Taita Hills (Martins & Johnson, 2009). Therefore, it is possible that the pollination of fruit trees in the greater Tsavo ecosystem could offer some compensation for the ecosystem disservices that stem from natural habitats, such as crop raiding by elephants. However, the assessment of pollination deficits in perennial crops, such as fruit trees, is complicated by differential resource allocation from season to season (Vaissière *et al.*, 2011), and it remains to be seen whether or not the pollination deficits that have been reported for perennial crops are repeatable from season to season.

Moreover, the two top crops in the Taita Hills are maize and beans (which are both annual crops, and thus the assessment of their pollination deficits is less complicated than it is for perennial crops), but maize yield is not at all dependent upon animal pollination (maize is wind pollinated), and bean yield is only reduced by 0–10%, in the absence of animal pollinators. Of the other crops that are grown in the Taita Hills (Soini, 2005), avocado, coffee, guava, loquat, macadamia nut, passion fruit, paw paw (papaya), pepper (hot and sweet), pumpkin, and sunflower are at least a little dependent upon animal pollination (Klein *et al.*, 2007). In the interviews that were reported by Soini (2005), farmers in the Taita Hills did not say that they grew courgette or watermelon (*Citrullus lanatus*), but both of these crops were grown in the Taita Hills when I was there, and together with the other species of crops in the Cucurbitaceae family (such as pumpkin, which was reported by Soini), as well as papaya and passion fruit, these are among the most pollinator-dependent crops in the Taita Hills (Klein *et al.*, 2007). If demand for these animal-pollinated crops increases in the future, which seems to be the trend worldwide (Aizen *et al.*, 2008), then the value of animal pollination to food security in the Taita Hills could also increase. However, animal-pollinated crops are also valuable sources of nutrients (Eilers *et al.*, 2011) and income (Soini, 2005), and therefore animal pollination would seem to have a role to play in the food security of the Taita Hills. Nevertheless, it seems to me that pest regulation could have a larger and more widespread role to play in food security that could pollination, because all crops—not only animal-pollinated crops, but also wind-pollinated crops, and especially cereal crops, which are the top crops worldwide (FAO, 2012)—are potentially in need of pest control.

As a source of food security in the Taita Hills, I would also add that although dairy and meat production is an inefficient use of prime agricultural land, it could be an efficient use of sub-prime agricultural land, especially in semi-arid areas or other agricultural landscapes in which food production is constrained by climate change (Jones & Thornton, 2009). In the semi-arid areas of the Taita Hills, I often saw goats browsing and grazing amid the woody vegetation and in the fields of failed crops in the lowlands. As we seem to be learning, biodiversity is a source of stability in ecosystem function (*e.g.*, McNaughton, 1977; Chaplin-Kramer *et al.*, 2011; Garibaldi *et al.*, 2011, 2013; Letourneau *et al.*, 2011; Rader *et al.*, 2013; and see Chapter 2). Specifically, agricultural biodiversity is a source of a stability in food production, and therefore food production should include both wind-pollinated crops and animal-pollinated crops and both vegetable foods and animal foods (in moderation). However, much more research is needed on the optimal use of agricultural landscapes, in order to find a balance between food production, biodiversity conservation, and other ecosystem services.

A personal view of the way forward

Intensive farming in agricultural landscapes that are ecologically dead is not a sustainable method of food production. Agricultural landscapes need to be managed not as ecological graveyards but as living landscapes that integrate non-crop habitats with crop habitats. Both land sharing and land sparing will have roles to play in solving the problems of food insecurity and biodiversity loss, but their roles will be different in different geographical regions, and much more research will be needed before we will know how and where a balance between food production and biodiversity conservation is to be found.

However, instead of concluding this thesis with a pessimistic view of how much more research is needed, before the coming of the “perfect storm” in the global food system, I would prefer to conclude with an optimistic view of the bridges that have been crossed by this thesis. I would also like to conclude with an optimistic view of the skills that I have learned and demonstrated in the process of doing this research and writing this thesis (because it was, of course, an exercise in education). In this thesis, I learned and demonstrated skills in systematic literature review and meta-analysis (Chapter 2), geographic information systems and hotspot analysis (Chapter 3), the design of observational experiments on environmental gradients (Chapter 4), the design of manipulative experiments in the lab (Chapter 5), the collection, identification, and curation of insect samples (Chapters 4 and 5), statistical data analysis (all chapters), the writing and revising of scientific manuscripts (all chapters), and the negotiation of the peer-review process (Chapters 2 and 3). All of these chapters required sampling strategies to be designed, whether the croplands of the world (hotspot analysis), the croplands of the Taita Hills (gradient analysis), or studies in the literature (meta-analysis) were being sampled, and all of these chapters also required the results to be statistically analyzed (whether in hotspot maps, forest plots, or scatter plots and tables).

Some small gaps in our knowledge of ecosystem services and service providers have also been bridged by this research. These bridges were built from biological and ecological theory, by testing hypotheses on species-area relationships (Chapters 2 and 4), species-climate relationships (Chapter 4), and the effects of temperature on development and phenotypic plasticity (Chapter 5). A conceptual framework for nature conservation in agricultural landscapes was built from the theories of island biogeography and countryside biogeography, with support from the concepts of buffer zones and multiple-use modules, in the context of the debate between land sharing and land sparing, and in the context of the latitudinal gradient in species richness (Chapter 3). Thus, the process of doing this research and writing this thesis has also been a process of education in some aspects of ecological theory, and in the process I was also able to suggest some ecological theory of my own, in the form of the “cultural difference mechanism” (Chapter 2).

This thesis has gone from the very big picture (worldwide hotspot analysis and meta-analysis) to the very small picture (physiological responses of single species), and from the community (big picture) to the species (small picture). In the process, it has become clear to me that we need to focus on biodiversity at all of these scales. By the time the “perfect storm” hits land, it seems impossible to me that we will have had the time to do all of the research that is clearly needed. However, if this thesis has given me any hope that we might be able weather the storm, it is this—biodiversity enhances and stabilizes ecosystem services, and therefore we would do well to conserve as much biodiversity in agricultural landscapes as is humanly possible.

Figure 6.1 An experimental field cage in the Taita Hills.

Figure 6.2 Francis Namisiko, my field assistant, constructing an experimental field cage.

Figure 6.3 A caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*), feeding from the flowers of *Tagetes minuta*, which is a non-native plant in the Taita Hills.

Figure 6.4 A caterpillar-hunting wasp (*Rhynchium marginellum sabulosum*), feeding from a bowl of honey and water in an experimental field cage in the Taita Hills.

Figure 6.5 Courgettes (*Cucurbita pepo*) in experimental field cages.

Figure 6.6 The trials and tribulations of field research: courgettes (*Cucurbita pepo*) in an experimental field cage that is being invaded and destroyed by puppies (*Canis familiaris*).

Table 6.1 The dependence of the main crops in the Taita Hills on animal pollination, based on the review by Klein *et al.* (2007). The crops are listed in order of decreasing popularity in the Taita Hills, in terms of the number of farmers that grow them, based on the survey of farmers in the Taita Hills by Soini (2005). The dependence of a crop on animal pollination is assessed in terms of a decrease in its yield (“direct decrease”) and a decrease in its seed production (“indirect decrease”), in the absence of animal pollinators. Green gram was not assessed by Klein *et al.* (2007).

Common name	**Scientific name**	**Direct decrease**	**Indirect decrease**
Maize	*Zea mays*	No	No
Bean	*Phaseolus* spp.	Yes (0–10%)	Yes
Cassava	*Manihot esculenta*	No	Yes *
Cowpea	*Vigna unguiculata*	Yes (0–10%)	Yes
Mango	*Mangifera indica*	Yes (40–90%)	Yes
Pigeon pea	*Cajanus cajan*	Yes (0–10%)	Yes
Banana	*Musa* spp.	No	Yes *
Millet	Various genera	No	No
Green gram	*Vigna radiata*	NA	NA
Cabbage	*Brassica* spp.	No	Yes
Irish potato	*Solanum tuberosum*	No	Yes *
Sweet potato	*Ipomoea batatas*	No	Yes *
Tomato	*Lycopersicon esculentum*	Yes (0–10%)	Yes

* Animal pollination causes an increase in seed production in these crops, but they are typically propagated vegetatively, not by seed, and the seeds are not eaten by humans. Therefore, animal pollination does not cause an increase in the supply of food from these crops (but it could be vital to traditional crop breeding and the maintenance of genetic diversity in these crops).

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