Effects of Hedgerow Rejuvenation Management on Invertebrates with Particular Reference to Habitat Structure

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Abstract

Hedgerows are an important semi-natural habitat for invertebrates and other wildlife within agricultural landscapes. Hedgerow quality can be greatly affected either by over- or under-management. Neglect of hedgerows is an increasingly important issue as traditional management techniques such as hedgelaying become economically unviable. In the UK, funding for hedge management is available under agri-environment schemes but relatively little is known about how this impacts on wider biodiversity. This thesis describes a randomised block experiment used to investigate how habitat structural change, arising from a range of techniques to rejuvenate hedgerows (including more economic/mechanised alternatives to traditional hedgelaying) affected invertebrate abundance and diversity throughout the year. A novel technique of digital image analysis was combined with estimates of foliage biomass and quality, hedge dimensions and microclimate at the base of the hedge to show which aspects of hedge structure were affected by the rejuvenation treatments. All investigated aspects of habitat structure varied considerably with management type. For example, treatments where the hedge was laid all increased foliage biomass but resulted in differing widths of hedge, and those subjected to more intensive cutting resulted in a lower foliage C:N ratio. For invertebrates utilising the canopy from spring-autumn, the abundance of herbivores and predators was affected primarily by foliage density, with which there was a positive correlation, whilst detritivore abundance was most strongly correlated (negatively) with variation in hedge gap size. For invertebrates overwintering in the soil beneath the hedge, herbivore abundance was positively correlated the maximum temperature at ground level which itself was affected by hedge density, though structural measures did not directly relate to invertebrate parameters.

The results suggest that habitat structure is an important organising force in invertebrate community interactions and that management technique may affect trophic groups differently. Specifically, this thesis shows that alternative methods of hedgerow rejuvenation could support abundances of invertebrates comparable or even higher than traditional hedgelaying, with positive implications for the restoration of a larger area of hedgerow habitat on a limited budget.

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Author’s declaration

I hereby declare that this thesis has been composed by myself and has not been accepted in any previous application for a degree. Some early data from this thesis were published in the following conference proceedings paper:

Staley, J.T., Amy, S., Facey, S.L. and Pywell, R.F. (2012) Hedgerow Conservation and Management: A review of 50 years of applied research in the UK. In: *Hedgerow Futures* (ed. Dover JW). Published by the Tree Council for Hedgelink. Staffordshire University, Stoke-on-Trent, UK, pp. 111-133

A significant portion of the work within this thesis, forming the entirety of chapter 2, has been published in a peer-reviewed journal. As first author I collected the majority of the data, completed all statistical analyses, and wrote the work up as a complete manuscript, with supporting input from my co-authors. The reference is as follows:

Amy, S.R., Heard, M.S., Hartley, S.E., George, C.T., Pywell, R.F. & Staley, J.T. (2015) Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure. *Basic and Applied Ecology*, **16**, 443–451.

I also extended parts of the digital image analysis I formulated and carried out as part of this theses further, incorporating additional data collected at a later date by myself and colleagues, to contribute to the following peer-reviewed paper:

Staley, J.T., Amy, S.R., Adams, N.P., Chapman, R.E., Peyton, J.M. & Pywell, R.F. (2015) Re-structuring hedges: Rejuvenation management can improve the long term quality of hedgerow habitats for wildlife in the UK. *Biological Conservation*, **186**, 187–196.

Information drawn from other sources and assistance received are duly acknowledged below. The initial experimental setup was designed and implemented by Dr Jo Staley as part of Defra grant BD2114, with practical input regarding hedge management techniques from Nigel Adams. Image analysis work was made possible by input from Charles George, who wrote script in ENVI (Elexis Visual information Systems) to enable automated extraction of the data from multiple files output from the ERDAS IMAGINE analysis I performed.

1. Introduction

1.1. The hedgerow habitat

Hedgerows are a linear habitat comprising a number of woody, climbing and herbaceous plant species (Critchley *et al.* 2013). One of the UKs most extensive semi-natural habitats, there is over 450,000km present just within England (Norton *et al.* 2012). This habitat been defined by the Department for Environment Food and Rural Affairs (Defra) as ‘any boundary line of trees or shrubs over 20m long and less than 5m wide between major woody stems at the base, provided that at one time the trees or shrubs were more or less continuous’ (Defra 2007). Many other authors stress the anthropogenic nature of hedgerows, with their origins in historic boundary marking, stock-proofing and as a source of products such as wood and berries, and with some form of management inherent to their definition (e.g. Baudry, Bunce & Burel 2000). One of few semi-natural habitats within intensively farmed agricultural landscapes, hedgerows support over 1500 species of invertebrate (UK Steering Group 1995) as well as many birds (Hinsley & Bellamy 2000) and mammals (Macdonald, Tew & Todd 2004; Barr *et al.* 2005).

Whilst Hawthorn *Crataegus monogyna* followed by Blackthorn *Prunus spinosa* are the most common shrubs forming the hedgerow canopy in the UK (French & Cummins 2001; see Table 2), species-rich hedgerows dominated by Hazel *Corylus avellana* are particularly prominent in the South West. Although over 500 native plant species may be found in UK hedgerows (of which approximately half can be thought of as ‘hedgerow species’; Barr *et al.* 2005), Plymouth Pear *Pyrus cordata* (Red Data Book, Schedule 8) may be the only plant occurring almost exclusively within this habitat (Hooper 1987; Stace 2010). As well as the woody species forming the hedgerow canopy, a wide range of herbaceous plant species found also in woodland, arable, wetland and pasture habitats, comprise the basal flora (French & Cummins 2001; Deckers *et al.* 2004; Critchley *et al.* 2013). Where hedgerows have more ancient origins, for example those assarted (cut out) from ancient woodland as it was cleared, they can be considerably more species-rich botanically (Rackham 2003; Barr *et al.* 2005). There are seven Biodiversity Action Plan (BAP) species described as having ‘significant associations’ with hedgerows (Wolton 2009), including the nationally scarce Purple Ramping Fumitory *Fumaria purpurea*, which is endemic to Great Britain, Ireland and the Channel Islands. Hedgerow plant species diversity has declined and homogenised over the last few decades, with more competitive species and those tolerant of high soil fertility becoming more dominant (Barr *et al.* 2005; Critchley *et al.* 2013; Staley *et al.* 2013). This is probably due to a combination of adjacent land use (i.e. negative impacts of fertiliser and pesticide use; French & Cummins 2001; Critchley *et al.* 2013), and the decline of traditional hedgerow management (Staley *et al.* 2013).

Hedgerow flowers and foliage provide food and shelter for invertebrates (Maudsley 2000a; Merckx & Berwaerts 2010), whilst berries provide food for small mammals such as the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolu*; Pollard & Relton 1970) and a range of farmland birds (Hinsley & Bellamy 2000). For birds, hedgerows also provide nesting, roosting and foraging sites which, with a paucity of other suitable habitat in many agricultural landscapes, can be very important (Hinsley & Bellamy 2000). For some mammals hedgerows provide a habitat comparable to that of woodland (i.e. the common dormouse *Muscardinus avellanarius*; Bright & MacPherson 2002), whilst others are more selective; yellow-necked mice (*Apodemus flavicollis*), for example, require a particularly well-established hedge and may prefer the presence of a ditch (Kotzageorgis & Mason 1997). Hedgerows were found to be the preffered habitat for European hedgehogs (*Erinaceus europaeus*) within the agricultural environment (Hof & Bright 2010), providing nesting and hibernation sites (Barr *et al.* 2005) with protection from predators, a macro-invertebrate food source, and are also used for dispersal through arable habitat (Doncaster, Rondinini & Johnson 2001). Hedgerows can also provide connectivity in the landscape for other taxa, facilitating the movement of birds (Hinsley & Bellamy 2000) and certain insects (Dover & Sparks 2000; Cranmer, McCollin & Ollerton 2012). Some bat species such as *Plecotus auritus* (Entwistle, Racey & Speakman 1996) and *Pipistrellus* species (Boughey *et al.* 2011) are known to use linear features such as hedgerows as commuting routes between roosting and foraging habitats, in preference to more direct open routes. This may be due to the provision of cover from predators, as well as potentially aiding orientation and providing additional foraging opportunities (Entwistle, Racey & Speakman 1996), and the presence of hedgerow trees may be particularly important (Boughey *et al.* 2011).

As well as providing hibernation sites for small mammals during winter when cover is often scarce in the surrounding agricultural habitat, hedgerows also provide shelter for many invertebrates with a dormant phase during this time (Maudsley *et al.* 2002b; Pywell *et al.* 2005). This may then provide a souce of natural enemies to aid in crop pest control (Varchola & Dunn 2001; Senoussi, Dutoit & Debras 2011; Morandin, Long & Kremen 2014) although it has also been suggested that invertebrate pest species may themselves find refuge in the hedgerow habitat only to return to crops in the spring (Way & Cammell 1982). Support by hedgerows also extends to other ecosystem services such as pollination (Jacobs *et al.* 2009b), as well as a wider range of regulatory services such as air quality, climate change mitigation, and those related to water quality and flow (Wolton *et al.* 2014).

1.2. The history of hedgerows and their management and conservation

Hedgerows occur in many countries worldwide, but have been most extensively studied and documented in Europe (Baudry, Bunce & Burel 2000). In the UK the most common woody species found in hedgerows is Hawthorn *Crataegus monogyna*, which has been planted since Roman times and was particularly used during enforcement of the eighteenth and nineteenth century Parliamentary Enclosure Acts which resulted in the planting of a large proportion of hedgerows in the UK, particularly in the period from 1750 – 1850 and in the Midlands and the South of England (Rackham 2003).

There was a sharp decline of hedgerow habitat in the UK (loss of ~50%) in the 20th century post-WWII (Barr & Parr 1994), due to intensification of agriculture which meant that the use of larger machinery and conversion of pasture to arable land rendered many hedges redundant and they were therefore removed (Petit *et al.* 2003). Losses of about 23% of hedgerow length in Great Britain between 1984 and 1990 were followed by a period of stability between 1990 and 1998, due primarily to a reduction in their removal rather than an increase in the rate of planting (Petit *et al.* 2003). However, under-management is also of considerable concern, thought to be responsible for a 6% decrease in the length of hedgerow between 1998 and 2007. Data gathered as part of the 2007 Countryside Survey of Great Britain showed that only 48% of hedgerows were in 'good' structural condition (Norton *et al.* 2012). The criteria for 'good' condition were drawn from the BAP favourable condition targets (Defra 2007), and were that hedgerows must be at least 1m high, 1.5m wide, have a cross-section >3m, a canopy base <0.5m high, and a maximum of 10% gaps of which any one should be <5m in length (Norton *et al.* 2012).

Traditionally in much of the UK and other parts of Europe, hedgerows were periodically managed by hedgelaying, whereby some stems and branches are removed and remaining stems are partially cut near the base and laid along the line of the hedge, with specific methods and style differing according to region. This practice removes large gaps and encourages new vertical growth, resulting in a thicker, more stock proof hedge (Brooks & Agate 1998). Coppicing hedges for firewood, where stems are removed to the base from which they then re-grow, has also historically been widely practiced in some areas (Rackham 2003). Another such traditional management is pollarding, which is essentially coppicing but at a height on the main stem above which animals can graze new growth, though this was more typical of wood pasture (Rackham 2003). Modern machinery, increased labour costs, and resulting changes in agricultural practice (i.e. a move towards widespread arable farming) has meant that annual post-harvest flailing is now preferentially practiced, whilst in some cases management has ceased entirely, leading to widespread changes in the structural quality of hedges (Croxton *et al.* 2004). Intensive cutting can lead to shorter hedges and reduce berry food resources (Staley *et al.* 2012), while cessation or relaxation of cutting leads to 'gappy' hedges (Croxton 2002) which eventually grow into lines of trees (Croxton *et al.* 2004).

Since hedgerows are of ecological and cultural value, reductions in their quantity and quality have attracted intensive conservation efforts. Ancient and/or species-rich hedgerows were recognised as a BAP habitat in 1994. This definition was later expanded to include all hedgerows consisting predominantly (at least 80%) of one or more native woody species, and the habitat remains a priority in the UK Post-2010

Biodiversity Framework and European Union (EU) Biodiversity Strategy (JNCC & Defra, 2012). The removal of hedgerows in the British countryside is prohibited in most cases by the Hedgerow Regulations 1997.

The EU's agricultural subsidy scheme requires farmers to comply with a set of statutory management requirements (Cross Compliance), in order to receive payments. Cross compliance places restrictions on dates for hedgerow cutting/trimming to protect birds during the breeding and rearing season (1st March and 31st August inclusive), and the application of fertilisers or pesticides within 2m of the centre of a hedgerow (Defra 2015). Voluntary agri-environment schemes (AES), implemented in many EU Member States including the UK, enable land managers to receive additional payments to compensate for altering certain management practices to benefit the farm landscape and biodiversity. AES play a key role in the promotion of sensitive hedgerow management in the UK; approximately £50 million annually has in recent years been available for management aiming to improving hedge structure and resource provision to wildlife (Hedgelink 2011).

The main focus for hedgerows of AES in the UK is on relaxed cutting regimes; either biennially or triennially, and in winter rather than autumn (Staley *et al.* 2010), and the restrictions on dates for hedgerow cutting/trimming may be extended further. The ecological benefits of recent advice to incrementally cut hedgerows, whereby some newer growth (c.a. 10cm) is left on the hedge when it is cut (Hedgelink 2014) are currently the subject of scientific investigation (Defra-funded project BD2114). This practice, if widely implemented in the future, could increase the use of intermittant rejuvenation management such as that practiced historically; over time incrementally cut hedges will increase in height and width such that they eventually require rejuvenating.

The potential benefits of hedgerow rejuvenation are also recognised within these schemes. Provision for such management was extended from the targeted Higher Level Scheme to the more broad and shallow Entry Level Environmental Stewardship Scheme in 2013 (Natural England 2013), and also features in the new Countryside Stewardship Scheme (Natural England 2015), though cost does remain a limiting factor. To try and encourage a return to rejuvenation management for hedgerows, there is an obvious benefit to be found in identifying techniques more economical than traditional hedgelaying or coppicing, and of comparable ecological value. One example that has been introduced in Buckinghamshire, is a novel method called ‘wildlife hedging’ using a chainsaw and digger to mimic manual hedgelaying at speed. This technique has been advocated for its benefit to wildlife (Dodds 2005) though as yet there is no scientific evidence to support this claim.

1.3. Invertebrates and the hedgerow habitat

Invertebrates comprise a large portion of the biodiversity found in hedgerows, with the number of species depending on the botanical composition of the hedgerow, its structural diversity and the shelter it provides (Maudsley 2000). The UK Biodiversity Action Plan (UK Steering Group 1995) reports that over 1500 invertebrate species are associated with hedgerows, though this figure may be considerably higher. Looking at botanical composition of hedgerows can inform on their potential as habitat for invertebrates. French & Cummins (2001) classified British Hedges into 11 classes using multivariate analysis, based on the woody species composition of a total of 1213 10x1 m plots sampled in 1978 and 1979 across Britain and stratified by land class (Bunce *et al.* 1996).

The Biological Record Centre’s Database of Insects and their Food Plants (DBIF; (Smith & Roy 2008) contains records of 1800 species of insects and mites having an association with one of the woody hedgerow taxa listed by French & Cummins (2001; excluding planted exotics). As these records are almost exclusively herbivores, the consideration of higher trophic levels indirectly reliant on these species would probably increase this figure somewhat. Though not exhaustive, and with caveats such as variable time lapses since certain families have been updated and bias towards more heavily studied taxa, DBIF probably constitutes the most comprehensive database available for the herbivorous invertebrate fauna of Great Britain (Smith & Roy 2008).

Table 1: Species present in > 20% of plots and mean cover > 5% for each hedge class (French & Cummins, 2001).

Hedge class	Main species included in DBIF output
Hawthorn-dominant	*Crataegus monogyna*
Blackthorn	*Acer campestre, C. monogyna, Prunus spinosa*
Mixed-hazel	*Corylus avellana, C.monogyna, Ilex aquifolium, P.spinosa*
Rich-hawthorn	*A.campestre, C.monogyna, Fraxinus excelsiour, Sambucus nigra*
Elm	*C.monogyna, Ulmus spp.*
Elder-hawthorn	*C.monogyna, Sambucus nigra*
Beech	*Buxus sempervirens, C.monogyna, Fagus sylvatica*
Gorse	*Ulex spp.*
Willow	*Salix spp.*
Wild Privet	*Ligustrum vulgare*

Table 2: Estimated potential maximum number of herbivorous invertebrate species supported by each hedge class (after French & Cummins, 2001), based on data extracted from DBIF.

Hedge class	No. plots[1]	Acari	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera (butterflies)	Lepidoptera (macro-moths)	Lepidoptera (micro-moths)	Thysanoptera	Total invertebrate species
Hawthorn-dominant	552	5	27	4	33	3	4	111	17	1	205
Blackthorn	270	27	46	15	64	16	7	175	87	1	438
Mixed-hazel	157	23	84	15	91	23	10	198	104	1	549
Rich-hawthorn	61	25	55	21	77	11	6	149	49	4	397
Elm	49	15	92	17	83	12	8	149	51	5	432
Elder-hawthorn	40	6	28	9	34	5	4	115	19	3	223
Beech	19	15	92	17	83	12	8	149	51	5	432
Gorse	8	3	29	4	13	0	9	19	14	5	77
Willow	6	13	180	40	100	73	7	247	74	4	418
Wild Privet	5	3	3	0	4	1	2	32	7	0	19

[1] No. Plots refers to the number of 10x1m Countryside Survey plots within which each hedge class was recorded in the dataset used by French and Cummins (2001).

For the ‘main’ hedgerow species listed by French & Cummins (2001; Table 1), the number of insect (and mite) species by order recorded for each, was extracted from DBIF to compile maximum counts for each hedge class (Table 2). Although the hawthorn-dominant class is by far the most common, representing 47% of the total sample (French & Cummins 2001), its largely single-species status means it is likely to harbour considerably fewer invertebrate species than many of the other more varied types (Table 2). The blackthorn, mixed-hazel, rich-hawthorn and beech hedges unsurprisingly support relatively high numbers of invertebrates due to their multi-species status.

Flowering hedgerow plants provide an important pollen and nectar source for invertebrates, particularly Diptera and Hymenopera, as well as other pollinating insects; this can extend over a long period where a mixture of species found in hedgerows, either woody or herbaceous, flower successionally (Maudsley 2000) . Fruit set in hedgerow plants is significantly reduced when insects are excluded from flowers (Jacobs *et al.* 2009a) indicating the importance of pollinating insects for the provision of berries for other wildlife. Invertebrates are likely to have an uneven and clumped distribution within hedgerows (Joyce 1998; Maudsley *et al.* 2002b; Pollard & Holland 2006), as indeed is often the case in other habitats (Pearce & Zalucki 2006). This may be related to factors such as variability in soil moisture, monocotyledon biomass (i.e. overwintering Carabidae; Maudsley *et al.* 2002b), litter biomass (i.e. for Araneae; Rypstra *et al.* 1999), or plant species distribution (i.e. for phytophagous insects).

Predators can form a large contingent of the hedgerow invertebrate fauna (Pollard & Holland 2006) with potential value for integrated pest management, though the possibility that some hedgerows may harbour pests has also been considered (Way & Cammell 1982). Hedgerows can provide alternate hosts for certain parasitoids in spring, when populations of phytophages on crops are low. For example, the larval parasitoid *Diadegma fenestralis* (Hymenoptera), which preys on the diamondback moth (*Plutella xylostella*), a pest on oilseed rape, has an overwintering generation that uses *Swammerdamia lutarea*, an yponomeutid caterpillar on hawthorn as a host (van Emden 2003). Invertebrates overwintering in hedgerows are also thought to disperse into surrounding fields (Alvarez, Frampton & Goulson 2000; Geiger, Wäckers & Bianchi 2009) including natural enemies of pest species (Landis, Wratten & Gurr 2000).

Much research into invertebrates in hedgerows has focussed on either pest or beneficial predator species, and it was highlighted in an extensive review of hedge management by Barr *et al.* (2005) that other taxa such as Psocoptera, dependent entirely on the woody hedge vegetation, warrant closer consideration. One exception to this rule is the relatively well-studied Lepidoptera (Dover, Sparks & Greatorex-Davies 1997; Dover & Sparks 2000; Merckx *et al.* 2009; Merckx & Berwaerts 2010). Though hedgerows may not support any species of butterfly uniquely, they provide an important resource within the agricultural landscape (Dover & Sparks 2000). Dover *et al.* (1997) investigated the sheltering effect of hedgerows for butterflies, highlighting the importance of the density of hedges, as well as their height, in this respect.

1.3.1. Hedgerow impact on invertebrates in the wider agricultural landscape

Hedgerows can act as a windbreak for crops and livestock, potentially ‘catching’ species not specifically utilising the habitat (a consideration to bear in mind when sampling from hedgerows; Bowden & Dean 1977). This effect may also concentrate immigrating pest species in adjacent fields (Lewis 1969), although within orchards Debras *et al.* (2008) found pest populations of Psyllidae to be negatively affected by the wind-protection conferred by a hedge. Whilst hedgerows may have a positive effect as corridors for certain invertebrates such as butterflies (Dover & Sparks 2000) and bumblebees (*Bombus* spp.; Cranmer, McCollin & Ollerton 2012), they are known to function as a barrier to others, such as Carabidae (Mauremooto *et al.* 1995). For butterflies the effect of hedgerows as either a corridor or barrier to dispersal appears to be very much species specific (Dover & Sparks 2000). There is a consensus that hedgerows are an important semi-natural refuge habitat for invertebrates within intensively managed agricultural landscapes (Maudsley 2000; Pollard & Holland 2006), though it is clear that the diversity of invertebrates in hedgerows is also affected by the surrounding vegetation (Dover & Sparks 2000; Maudsley 2000; Barr *et al.* 2005). For example, the presence of trees within the hedgerow can increase the diversity of moths (Merckx *et al.* 2009), and probably other invertebrate species (Lawton 1983).

Invertebrates in temperate climates are described as having an ‘overwintering’ stage to their lifecycle, during which they exist in an altered physiological state for the purposes of survival in the adverse conditions of winter; this may be intermittent in response to sudden changes in abiotic conditions, or a more long-term state of dormancy (Leather, Walters & Bale 1993). In order to avoid predation or extremes of climatic conditions, for example, the choice of site for overwintering can be critical (Leather, Walters & Bale 1993). Within the agricultural environment, hedgerows provide a suitable overwintering habitat for many predatory invertebrates including Staphylinidae, Carabidae (Coleoptera; Sotherton 1984; Griffiths *et al.* 2007), and Araneae (Pywell *et al.* 2005). Overwintering habitat provided by hedgerow cover may also have a positive impact on the biological control of crop pests by increasing natural enemy abundance, with potential knock-on effects on crop-pest predation, though research in this area is limited (Griffiths *et al.* 2008; Morandin, Long & Kremen 2014). Predatory Coccinellidae, for example, have been shown to be more abundant up to 200m into fields adjacent to hedgerows, with a concurrent reduction in the aphid population (Morandin, Long & Kremen 2014). In contrast to classical biological control where the abundance of a key predator is supported (often through managed introductions), such support of the overall natural predator diversity and abundance is known as conservation biological control (Eilenberg, Hajek & Lomer 2001).

Pywell *et al*. (2005) found higher abundance and species richness of Coleoptera and Araneae overwintering in hedgerow habitat compared to field margins. This was attributed to a sheltering effect of the woody hedge vegetation, although other semi-natural habitats such as beetle banks can support comparable or even higher densities of polyphagous predators than hedgerows (Collins *et al.* 2003). Shelter provided by shrub cover is likely to have a moderating effect on microclimate (Noemí Mazía, Chaneton & Kitzberger 2006). This can be beneficial to overwintering invertebrates, being unable to regulate their own temperature, and vegetation cover may also provide access to prey or other food sources (Thomas, Mitchell & Wratten 1992). Whilst some invertebrate taxa such as spiders are likely to favour the hedgerow canopy as a site for overwintering (Pekár 1999), the soil is often utilised by insects overwintering due to its temperature being relatively warm and stable in comparison to the air (Leather, Walters & Bale 1993). Although the focus of past research has been largely on predatory arthropods due to their relevance for crop protection, herbivorous and detritivorous beetles are also known to overwinter in hedgerows (Pywell *et al.* 2005), and it is likely this extends to other taxa also.

1.4. Hedgerow rejuvenation management impacts on invertebrates

The majority of research into effects of hedge management on invertebrates relates to the frequency and timing of regular trimming (Maudsley, Marshall & West 2002; Facey *et al.* 2014). ‘Rejuvenation’ is a term that can be applied to the more periodic but substantial management such as the hedgelaying, coppicing or pollarding used traditionally (see section 1.2. above; Hedgelink 2014; Staley *et al.* 2015).

There has been relatively little research published looking directly at the effect of hedgerow rejuvenation management on invertebrate wildlife, but those studies that do exist suggest hedgelaying may be beneficial to invertebrate biodiversity. A study in Ireland (McAdam, Bell & Henry 1994; McAdam, Bell & Gilmore 1996) compared layed, coppiced and low-pollarded plots with an uncut control at 10 sites. Invertebrates were monitored during May in two years with shelter traps, the data presented as mean number of orders per treatment, with significantly more orders recorded in the laid plots than the control in 1992, and the pollard in 1993 (Henry *et al.* 1994; McAdam, Bell & Gilmore 1996). Dover *et al*. (1997) found more than double the total number of butterflies adjacent to 5-6 year old laid and coppiced sections of hedge compared with unmanaged sections.

Coppicing has obvious negative impacts for any wildlife reliant on the physical structure or specific woody species within the hedge in the early years after implementation (Maudsley, Marshall & West 2002), as well as loss of purpose in terms of stock-proofing/shelter. However, coppicing can actually increase plant species diversity immediately after management (McAdam, Bell & Gilmore 1996), as light reaches the ground flora. This may be viewed as essentially a change of habitat type to field margin grassland however, and the loss of hedgerow species is likely to impact the overall diversity of the boundary vegetation. A woody hedge once coppiced will generally grow to form a recognisable hedge in a few years (subject to grazing pressure), though woody species differ in their response to restoration management (Croxton *et al.* 2004), with likely impacts on the invertebrate community. Although the novel technique of 'wildlife hedging', whereby a chainsaw and digger are employed to push over and 'lay' a hedge with considerably more speed than traditional hedgelaying, has been posited as producing considerable benefits for wildlife (Dodds, 2005), it has also been met with concern from the hedgelaying community (Portas, 2009). The quality of overwintering habitat afforded by different rejuvenation treatments may change with microclimate and quantity of leaf litter (Maudsley *et al.* 2002), both being likely to differ with the amount of brash removed from the hedge and the density of vegetation remaining. Wildlife hedging may prove favourable in this sense as the hedge volume remains considerably larger than with other management techniques, and denser than uncut hedges (Amy *et al.* 2015). It has also been suggested that this technique may provide deadwood habitat for saproxylic invertebrates (Dodds, 2005). When considering strategies for the restoration of hedgerows the value of habitat heterogeneity should not be neglected (Maudsley *et al.* 2002). This may include sections of seemingly poor habitat; Griffiths *et al.* (2007) showed the overall diversity of Carabid and Staphylinid beetles may be highest when hedgerow, degraded hedgerow and fence boundary types are present, highlighting the fallibility of a purely hierarchical view of habitat value. In terms of effects of restoration techniques on invertebrates, it may be beneficial to consider implementing a variety of methods within the farm or even field-scale.

1.5. Invertebrates and habitat structure

Habitat structure can be defined as the composition and arrangement of objects in space (McCoy & Bell 1991), is a term applied to a range of concepts at many different scales, and has often been shown to affect invertebrate communities

(Langellotto & Denno 2004; Janssen *et al.* 2007; Woodcock & Pywell 2009), as well as other taxa such as birds (MacArthur & MacArthur 1961), small mammals (Kotzageorgis & Mason 1997), intertidal gastropods (Beck 2000), coral reef fish (Rogers, Blanchard & Mumby 2014) and even micro-organisms (Altermatt & Holyoak 2012). A meta-analysis of studies where habitat structure was manipulated suggested that enhancement of habitat complexity (i.e. increased detritus, plant species diversity, leaf and branch density or structure of domatia) resulted in a significant increase in predator and parasitoid abundance (Langellotto & Denno 2004). Whilst this was generally not the case for herbivores, it is not clear whether this is due to increased predation. The study found that effects of structural changes on the abundance of natural enemies were greatest at the habitat scale in the detritus layer, and were also found at the habitat scale where vegetation was enhanced (i.e. intercropping, polyculture, no-till/mowing) and at the within-plant scale (i.e. leaf and branch density, structure of domatia; Langellotto & Denno 2004).

Although fewer studies demonstrate a link between structure and predator diversity compared to structure and predator abundance, Woodcock *et al.* (2007) found that enhanced structural complexity, defined as a diversity measure derived from drop-pin contacts with vegetation, increased the diversity of predatory invertebrate communities. In the literature the term ‘complexity’ is frequently used in relation to habitats, plants or plant architecture, though it can be equated to widely varying factors as evidenced in Table 3, where a wide range of vegetation measures are used to relate habitat structure to invertebrate communities.

Table 3: Examples of the range of factors to which the terms habitat, plant, architectural or structural 'complexity' is applied in studies looking at effects of habitat structure on invertebrate communities. Scale refers to detritus (D), within-plant (P) or within-habitat (H), after Langellotto & Denno (2004).

Measure of complexity	*Scale*	*Reference*
Presence/absence of thatch substrate (real)	D	(Riechert & Bishop 1990)* (Finke & Denno 2006) (Langellotto & Denno 2006)
Presence/absence of thatch substrate (real/artificial)	D	(Schmidt & Rypstra 2010)
Proportion of flat/bent leaves in litter (real/artificial)	D	(Bultman & Uetz 1984)
Amount of vegetation (LAI as proxy)	P	(Schmidt & Rypstra 2010)
No. junctions on a stem and number of plants	P	(Gagnon & Brodeur 2014)
No. modules of primary/secondary ramifications of plants	P	(Araujo *et al.* 2006)
Number of second-order branches, shoots and leaves (NB. Plant height and biomass referred to separately)	P	(Lara *et al.* 2008)
Connections and surface area of artificial plants	P	(Gingras & Boivin 2002)
Amount of vegetation and branching (real/artificial)	P	(Mcnett & Rypstra 2000)
No. ramifications, vegetation cover and stalk number	P	(Obermaier *et al.* 2008)
Natural/reduced foliage (needle) density	P	(Gunnarsson 1990)*
Leaf domatia added/removed	P	(Agrawal 1997)*
Leaf area, edge and junctions	P	(Legrand & Barbosa 2003)
Height/width of plants (real and artificial)	P	(Schmidt & Rypstra 2010)
'Branchiness' and amount of vegetation	P	(Riihimaki *et al.* 2006)
Number of branching angles, total biomass (as a proxy for surface area) and diameter at breast height	P	(Halaj, Ross & Moldenke 1998)
Vertical drop-pin data condensed into a modified Shannon-Weiner diversity index	H	(Woodcock *et al.* 2007)
Tree/shrub canopy cover; ground herb cover; soil moisture; amount of leaf litter/ logs/ rocks/ debris	H	(Lassau *et al.* 2005)
Bare earth versus grassy tussocks	H	(Dennis, Thomas & Sotherton 1994)
Cut (10cm)/uncut (20cm) grass	H	(Sanders *et al.* 2008)
Mono- and biculture	H	(Coll & Bottrell 1995)*
Mono- and polyculture	H	(Andow & Risch 1985)* (Wetzler & Risch 1984)

* denotes those studies that do not themselves refer to 'complexity' but to which Langellotto & Denno (2004) attribute this concept.

The more ‘complex’ structures described by studies such as those listed in Table 3, may allow more effective prey capture (Denno *et al.* 2002), provide refuge from intraguild predation (Finke & Denno 2002; Janssen *et al.* 2007) or cannibalism (Langellotto & Denno 2006; Schmidt & Rypstra 2010), or provide access to alternative resources when prey is scarce (Langellotto & Denno 2004). More effective prey capture has been suggested as a possible mechanism for increased predator abundance with a perceived enhancement of structural complexity (Langellotto & Denno 2004). The spider *Pardosa milvina*, for example, was better able to capture planthopper (*Prokelesia*) prey where habitat structure was enhanced through the addition of thatch, possibly allowing it better access to prey located on the leaves above (Denno *et al.* 2002). However, in contrast, Mcnett & Rypstra (2000) found that although the abundance of the orb-weaving spider *Argiope trifasciata* was positively correlated with an increase in web attachment sites within the vegetation (provided by thistles and introduced artificial structures with varying levels of branching), this did not translate to increased prey capture. The identity of the prey in this study was not given, but in another study where Auchenorrhyncha was preyed upon by the closely related spider *Argiope bruennichi*, a positive effect on predation was found with the removal of thatch and reduction in grass height (termed ‘low-structured’ vegetation; Sanders *et al.* 2008). Whilst this might be expected to reduce the number of web attachment sites and have the opposite effect, the suggested explanation given was a higher number of available refuges for prey when thatch was present (Sanders *et al.* 2008).

In an example using *Coccinella septempunctata* (Coccinellidae), partitioning of leaf surface area in the form of a higher number of smaller leaves led to a reduced new search area/foraging efficiency (Legrand & Barbosa 2003). In another study, the same species (and other Coccinelidae) was impaired by a seemingly opposing aspect of habitat structure in a different plant species; the flat, smooth surface of larger leaves with fewer edges resulted in more frequent falling from the plant (Grevstad and Klepetka 1992). However, habitat structure may also affect intraguild predation of Coccinelidae, as has been found with many other taxa (Janssen *et al.* 2007). For example, *Coleomegilla maculata* were better able to avoid intraguild predation in mesocosms with more complex substrate than in petri-dishes (Noppe, Michaud & De Clercq 2012), with a potential cascading effect on the shared aphid prey.

In fact the potential role that refuge from intraguild predation or cannibalism plays in the increased abundances of many predatory invertebrate taxa with changes to habitat structure, is widely documented (Janssen *et al.* 2007), and can lead to increased suppression of shared prey (Finke & Denno 2002). For example, increased thatch reduced the occurrence of cannibalism in the wolf spiders *Pardosa milvina* (Schmidt & Rypstra 2010) and *P.littoralis* (Langellotto & Denno 2006), and intraguild predation of mirid bugs (*Tytthus vagus*) by *P.littoralis,* leading to an increase in the combined effectiveness of their suppression of planthopper prey (*Proklesioa* spp.; Finke & Denno 2002). Other examples include those of predatory mites finding refuge from intraguild predation in leaf domatia (Agrawal 1997), and decreased intraguild predation of the parasitoid wasp (*Aphidius ervi*) by carabid beetles (primarily *Pterostichus melanarius*) with taller plants (Snyder & Ives 2001).

It is often difficult to separate structural components from other factors. For example, structural change may be correlated with increases in alternative resources for non-obligate predators, such as pollen and nectar (Langellotto & Denno 2004). This may be the case where structure has been altered by increased plant species diversity (Landis *et al.* 2005), or management (Pywell *et al.* 2011). As for predators, structure may also alter the availability of resources for herbivores (i.e. plant biomass and, less so, species diversity; Lawton, 1983; Denno *et al.* 2002; Sanders *et al.* 2008). Changes in the physical attributes of habitat structure can also impact on the quality of resources for herbivores. For example, where the mechanical disturbance or cutting of a plant leads to the production of young leaves, this may decrease the ratio of total carbon (C) to nitrogen (N) in foliage as well as altering the physical structure of the plant (Havill and Raffa 2000; Mediene *et al.* 2002). A review by Chen, Olson, & Ruberson (2010) showed that changes in N fertilization of plants can alter their suitability for herbivores, affect the nutritional quality of herbivores for natural enemies, as well as the foraging efficiency of the latter though herbivore-induced volatile organic compounds (VOCs) and provision of alternative food sources (i.e. pollen and nectar) and shelter (i.e. leaf domatia and biomass). This illustrates how the potential effects of such changes to resource quality on herbivores can also cascade to other trophic levels. A recent review by Moreira *et al.* (2016) looking at effects of plant diversity on higher trophic levels, highlights the fact that whilst intraspecific variation has been shown to affect ecosystem functioning, mediating interactions among and between herbivores and their natural enemies, our mechanistic understanding of such processes is lacking (Moreira *et al.* 2016).

Whilst a general pattern of increased natural enemy abundance with increased habitat structural complexity has been described (Langellotto & Denno 2004), the examples given above illustrate that effects of habitat structure on invertebrate interactions are not clear cut. Their direction and magnitude are dependent on the habitat and species' in question (Klecka & Boukal 2014) and the nature of multi-trophic interactions occurring, as well as the way in which structure is quantified and the scale at which it is observed.

1.5.1. How changes in hedgerow habitat structure may affect invertebrates

In the context of hedgerows, Maudsley (2000) highlights the relationship between invertebrate diversity and hedge architecture in terms of botanical composition and the presence of hedgerow trees, as well as the spatial distribution of plant material. Hedgelaying appears to have a positive effect on invertebrate diversity and abundance (Henry, Bell & McAdam 1994; McAdam, Bell & Gilmore 1996), and this may be due to the compact structure and vigorous new growth (Maudsley 2000). The increased butterfly abundance found by Dover *et al.* (1997) next to areas of laid hedge was also attributed to higher foliage density, in this case due to the shelter it provided to adjacent habitat, though of course this represents a more transient use of the hedgerow habitat.

In contrast, an experiment where architectural changes from hedgerow cutting management were measured (hedge height and width, number and biomass of leaves, branching density and length), found no effect of these changes on moth abundance or parasitism (Facey *et al.* 2014). However, as the management here was trimming (i.e. maintenance), it is likely the structural changes were not as drastic as would be expected following rejuvenation management.

1.6. Scope and aims of this thesis

This thesis describes the impacts of habitat structure on invertebrate communities using hedgerows as a model system. It also assesses the practical effects of different hedgerow rejuvenation management techniques on invertebrate abundance and diversity. A multi-site replicated experiment (Appendix 1) designed to compare a range of different hedge rejuvenation management treatments (and a control that was not rejuvenated), was used to test the hypothesis that more economical methods, used in place of traditional hedgelaying, can support a similar abundance and trophic diversity of invertebrates. The methods assessed ranged from 50% of the cost of a traditional hedgerow rejuvenation technique, to just 15% of this cost for a perhaps less analogous but still potentially valuable technique (Staley *et al.* 2015), and thus could hold real potential for increasing the length of hedgerow rejuvenated in the UK. The hedges used in this experiment fall within the most common category identified in Britain by French & Cummins (2001), 'Hawthorn-dominated', as well as the relatively frequent 'Rich-Hawthorn' category.

Invertebrates using the canopy of the hedge throughout the growing season, as well as those utilising the soil and litter beneath the hedge to overwinter, were surveyed. In addition to comparing effects of different management treatments, this thesis investigates how invertebrate abundance and diversity in hedgerows is affected by the differences arising in localised habitat structure (i.e. woody biomass distribution), microclimate, and habitat quality (nutritional value of foliage for herbivores). Looking at how differences in structure arising from management of hedges of the same age and woody species composition affect invertebrate interactions, the focus is primarily on habitat structure at the within-plant scale. As well as plant architecture, foliage biomass is considered, recognising that this represents both a structural and resource component of the system. Comparing differences between trophic groups, the hypothesis is tested that increasing the spatial variation in hedgerow structure will increase predator abundance but that herbivores will be more affected by changes in the nutritional quality of food resources.

In order to start to investigate potential mechanisms by which habitat structure might affect differences in ratios of predator:prey invertebrates, a bioassay with herbivore bait was trailed within the hedge rejuvenation experimental setup (Appendix 5). This aimed to test the hypothesis that where changes in habitat structure show an increase in predator abundance, there will be a related increase in rates of predation on bait prey species.

The specific hypotheses addressed in this thesis are as follows:

(i) Increasing the spatial variation of within-habitat hedgerow structure will increase predator abundance (Chapter 2).

(ii) The nutritional quality of food resources will have a greater effect than within-habitat hedgerow structure on herbivores abundance (Chapter 2).

(iii) Aspects of hedge structure related to increased shelter and protection (hedge height and width, hedge:gap ratio) and associated changes to microclimate (temperature at ground level) will affect the abundance of overwintering invertebrates (Chapter 3).

(iv) Hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, will support a similar abundance and trophic diversity of invertebrates in the canopy during spring, summer and autumn, as those rejuvenated with traditional hedgelaying, (Chapter 2).

(v) Hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, will support a similar abundance and trophic diversity of invertebrates in the soil beneath the hedge during winter as those rejuvenated with traditional hedgelaying (Chapter 3).

2. Hedgerow rejuvenation management affects canopy invertebrate communities through changes to habitat structure

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Additional related information and data are included in appendices 1-3, referenced at relevant points in the text.

2.1. Introduction

Habitat structure, defined as the composition and arrangement of objects in space within a habitat (McCoy & Bell 1991), is widely known to affect interactions within invertebrate communities (Langellotto & Denno 2004). A meta-analysis of 67 manipulative studies found that enhancement of habitat structure resulted in a significant increase in predator and parasitoid abundance (Langellotto & Denno 2004), concluding that increases in predators did not follow prey abundance but rather occurred through increased efficiency of prey capture. However, despite the finding of this study that there is a general trend towards accumulation of invertebrate predators in ‘complex-structured’ habitats (Langellotto & Denno 2004) the direction and magnitude of these effects are likely to be dependent on the system in question, and the way in which structure is quantified. For example, predators may also be impaired by increased complexity of habitat structure, for example through reduced foraging efficiency (Legrand & Barbosa 2003), or a higher number of refuges for prey (Sanders *et al.* 2008).

At the within-habitat scale, structure may affect invertebrate interactions by altering the availability of resources for herbivores (Denno *et al.* 2002; Sanders *et al.* 2008), the ease with which predators are able to capture their prey (Schmidt & Rypstra

2010), or the degree of interference among predators (Janssen *et al.* 2007). Alterations to habitat structure may concurrently alter resource quality. For example, the proliferation of young leaves resulting from mechanical disturbance results in a decreased ratio of total carbon (C) to nitrogen (N; Havill & Raffa 2000; Mediene *et al.* 2002), which can have effects on herbivores that cascade to other trophic levels (Chen, Olson & Ruberson 2010).

Hedgerows are a man-made linear habitat covering over 450,000 km in England alone (Norton *et al.* 2012), supporting a wide range of plants (Critchley *et al.* 2013), birds, mammals (Barr *et al.* 2005), and over 1500 species of invertebrate (UK Steering Group 1995). Traditional management by hedgelaying, whereby some stems are removed and those remaining are partially cut near the base and laid along the line of the hedge, has given way to intensive cutting by modern tractor and flail machinery or in some cases neglect. Resulting widespread changes in the structural quality of hedges (Croxton *et al.* 2004) include reductions in berry resources for wildlife (Staley *et al.* 2012) and 'gappy' hedges (Croxton 2002) or lines of trees (Croxton *et al.* 2004). A 6% decrease in the length of hedgerow between 1998 and 2007 was attributed largely to under-management, and in 2007 it was also estimated that only 48% of hedges were in 'good' structural condition (Norton *et al.* 2012). Valued as a priority habitat for conservation (JNCC & Defra 2012), sensitive management of hedgerows, including rejuvenation, is promoted in the UK through agri-environment scheme funding (Natural England 2013), making investigation into the potential of more economical methods pertinent.

Few formal comparisons have been made between the impacts of hedge rejuvenation management on invertebrates (Henry, Bell & McAdam 1994) though different methods lead to widely divergent habitat structures which are likely to impact differently on invertebrate community composition. In this study, we tested how invertebrate abundance and diversity in hedgerows was affected by changes in localised habitat structure (i.e. woody biomass distribution) and habitat quality (nutritional value of foliage for herbivores) using a multi-site manipulative field experiment at which hedgerow rejuvenation treatments were applied. We also measured foliage biomass, recognising that this represents both a structural and resource component of the system. We focussed on differences between trophic groups, testing the following hypotheses:

- Increasing the spatial variation of (within-habitat) hedgerow structure will increase predator abundance, but herbivores will be more affected by the nutritional quality of food resources.
- Hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, will support a similar abundance and trophic diversity of invertebrates as those rejuvenated with traditional hedgelaying.

2.2. Materials and methods

2.2.1. Experimental design

A randomised block experiment was established at four lowland arable sites in East and Southeast England; Newbottle Estate (NE; Buckinghamshire), Utcoate Grange (UG; Bedfordshire), Monks Wood (MW; Cambridgeshire) and Wimpole Hall (WH; Cambridgeshire; Appendix 1). At each site, four rejuvenation techniques and an unmanaged control (Table 4) were randomly allocated and applied in October 2010 to 15 m contiguous sections (plots) of uniform hedgerows (see Appendix 2) that had received little management for some years. Treatments were replicated two or three times at each site, depending on the length of hedgerow available, giving 10 experimental blocks in total (each treatment replicated once per block). All experimental plots within one block were on the same hedge, and orientation varied between the hedges in the experiment. Hedges were typical for lowland England being largely dominated by hawthorn (*Crataegus monogyna*), with some blackthorn (*Prunus spinosa*) and field maple (*Acer campestre*; French & Cummins 2001).

Table 4: Description of experimental hedge management treatments.

Management	Description
Midland-style hedgelaying	Traditional style designed for heavy stock-proofing; some branches are removed, the rest laid to one side of the hedge with frequent stakes and top binders to secure. Results in all foliage being pushed to one side of the hedge, with the other side remaining relatively devoid of foliage during the following year
Conservation hedgelaying	Reduced labour method of hedgelaying; similar to the Midland-style but with stems along the line of the hedge rather than to one side, stakes used extremely sparingly, and binders omitted
Wildlife hedging (mechanical laying)	Novel method where the hedge is laid using heavy machinery; a chainsaw is used to make basal cuts, and a tractor with telescopic handler pushes the hedge over along its length. No brash is removed, and some stems may be severed
Circular saw re-shaping	A tractor with circular saw attachment is used to re-shape the hedge. This gives a much cleaner cut than the flail attachment used for regular management, and enables larger volumes of brash to be cut and easily removed from the hedge
Control	The hedge remains unmanaged

2.2.2. Invertebrate sampling

Invertebrates were sampled from each plot on three occasions during 2011 (May, July & September). At 3 m, 6 m & 9 m along the plot a 2 m length of guttering was inserted through the hedge (approximately 50 cm above ground level). The canopy was beaten five times with a stick 1 m above each guttering length. Falling invertebrates were swept from the guttering into a labelled plastic bag with a soft paintbrush and refrigerated (Maudsley *et al.* 2002). Transferred to 70% Industrial Methylated Spirits, samples were later sorted to order or in some cases family (i.e. Coleoptera) and assigned to a trophic group where possible (predators, herbivores and detritivores; Appendix 3). Taxa for which it was not possible to differentiate between feeding preferences at this taxonomic resolution (including Acari, Diptera and Heteroptera; Appendix 3) were excluded. For each group, the Shannon diversity index (*H'*) of taxa was calculated as $H' = -\sum p_i \ln(p_i)$, where i = order and p =

proportion of invertebrates in that order. The Shannon index, based on information theory, gives a measure of the amount of order within a community (Krebs 1999). This index was used as it incorporates both the richness and evenness of the community, providing the same answer regardless of sample size, as long as the number of species (or taxa) and their proportions are held constant (Magurran 2004).

2.2.3. Habitat structure and foliage quality: destructive sampling

Destructive leaf samples were collected in July 2011 from four three-dimensional (8000 cm^3) quadrats per plot, at 70 cm height; two positioned at the outer edge of the hedge and two half way into the centre, to encompass variation in foliage density. Leaves were dried at 80 °C for 48 hours and biomass determined. Within these quadrats the length (cm) and width (<0.5 cm, 0.5-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm) of each twig was measured, from which woody volume (v) was estimated using the equation $v = \sum_{i=1}^{6} (\pi {a_i}^2) b_i$, where a is the median width and b is the total length of the twig recorded for each class i.

In spring 2011, hedge height and width (at 1 m height) was measured with a pole to the nearest 10 cm at five positions for each plot, and mean height and width calculated per plot. Leaves from six *C. monogyna* branch tips collected at random alongside each invertebrate sample were freeze-dried (Heto PowerDry PL3000) and finely ground. Total carbon (C) and nitrogen (N) content was determined by gas chromatography (Matejovic 1995) in a Costech Elemental Combustion System CHNS-O (MI, Italy).

2.2.4. Habitat structure: Digital image analyses

Digital photographs were taken of plots in January 2011, with leaves absent, holding a white sheet behind the hedge to illuminate gaps. Images were converted to a standard resolution (0.25 cm/pixel) and a standardised area of interest was used for analysis (30-90 cm above hedge base; compatible with invertebrate sampling region). Pixels were assigned to binary values denoting either hedge or gap, using a signature file created iteratively from the image(s) in a batch supervised classification with ERDAS IMAGINE 9.3 software (Figure 1; Intergraph, 2013). For each gap the coordinates of the centre point and area (cm^2) were extracted using ENVI 5.1 software, from which the number of gaps and coefficient of variation (CV) of gap area was then calculated. The ratio of woody hedge:gap was also calculated as the proportion of total pixels of each value.

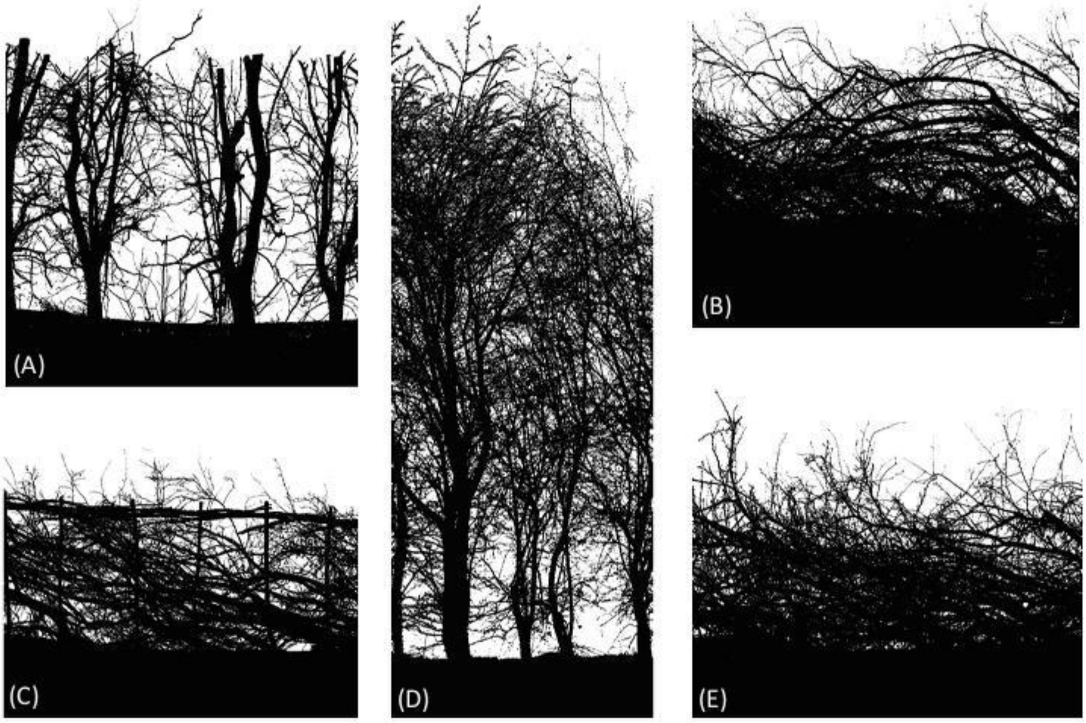

Figure 1. Classified images. Example binary images of treatments (average height m ± SE) (A) circular saw (1.85 m ± 0.11), (B) wildlife hedging (2.00 m ± 0.12), (C) Midland-style hedgelaying (1.45 m ± 0.03), (D) control (4.17 m ± 0.10) and (E) conservation hedgelaying (1.40 m ± 0.04) treatments.

2.2.5. Data analyses

The invertebrate abundance data were analysed initially as absolute values which, as the beating method used sampled a constant height of the hedge above the guttering collection tray (1 m), represent an abundance per unit height of hedge. These data were also scaled (multiplied) by hedge height, to give a closer approximation of the relative abundances of invertebrates supported by the actual volume of habitat resulting from different treatments. The latter were used to look at the effects of rejuvenation treatment only, and results compared with the non-scaled data (see Figure 2 below). Linear models were used to test relationships between rejuvenation treatment and habitat structure (coefficient of variation in gap area, number of gaps /m^2, lateral branch volume, hedge:gap ratio, foliage biomass) and the quality of herbivore resources (C:N ratio of foliage). Site and block were initially included as factors in linear models. Block did not contribute to the explanatory power of the models, and so was removed from final analyses.

The effects of rejuvenation treatment and habitat variables on abundance and diversity of invertebrates in different trophic levels were tested. Spearman's rank correlation was calculated and a cut-off coefficient value of 0.5 used to identify excessively collinear explanatory variables (Zuur *et al.* 2009), resulting in hedge:gap ratio being excluded from the analysis. Linear models containing these variables, and site, were constructed for each of nine responses relating to invertebrate community composition (abundance and diversity, and ratios between each trophic group), and simplified using backwards selection. Where a significant effect of rejuvenation treatment was shown *post hoc* Tukey tests were used to determine which treatment levels differed. As habitat variables were collinear with treatment, separate models containing only treatment and site were used to assess management effect. The fits of the two models were compared using Corrected Akaike's Information Criteria for small sample sizes (AICc) to assess the relative importance of treatment versus the continuous measures of hedge structure that may represent mechanistic drivers behind the impacts of management on invertebrate responses.

Data were transformed (natural log, square root, arcsin or squared) to meet assumptions of normality where necessary and untransformed means (± standard error) reported in results. All analyses were carried out in R version 3.0.1 (R Core Team 2013), with packages glmulti (Calcagno & Mazancourt 2010) and multcomp (Hothorn, Bretz & Westfall 2008).

2.3. Results

In total 10,769 invertebrates were collected from beating the hedge canopy in 2011; no interactions were found between treatment and month (see Appendix 4) so data were summed across months for further analysis. The most abundant taxa in decreasing order were Collembola (n = 4554), Acari (n = 1322), Coleoptera (n = 1197), Araneae (n = 811), Psocoptera (n = 597), Heteroptera (n = 570), Diptera (n = 447) and Psylloidea (n = 400). For all other taxa <250 individuals were sampled. Of the predators the most abundant taxa were Araneae (60%), parasitic Hymenoptera (17%) and Dermaptera (11%). Herbivores were more diverse, but dominated by Psyllidae (31%), Curculionidae (17%) and Aphididae (11%), and the most abundant detritivore taxa were Collembola (79%), Psocoptera (10%) and Lathridiidae (10%).

2.3.1. Relationships between rejuvenation treatment and invertebrate community composition

Rejuvenation method affected the number of invertebrates in each trophic group (Figure 2 and Table 5). In the three laid treatments detritivores were on average 2.1 and 1.5 times more abundant than the control or circular saw treatments respectively (Tukey's HSD $P<0.01$), and herbivores were on average 1.4 times more abundant than in the latter (Tukey's HSD $P< 0.05$). The abundance of predators was 1.9 times greater in the Midland-style hedgelaying and wildlife hedging than either the control or the circular saw treatments (Tukey's HSD $P< 0.01$) . When data were scaled to account for hedge height, the effect of rejuvenation treatment remained significant for predators ($F_{(4,42)} = 8.21$, $P = <0.001$) and herbivores ($F_{(4,42)} = 9.23$, $P <0.001$) similarly. The control treatment supported 2.2 times more herbivores and 1.9 times more predators than the average of all other treatments except the wildlife hedging. The Midland and wildlife hedging treatments also had 1.6 times more herbivores (Figure 2A) and 1.7 times more predators (Figure 2B) than the circular saw treatment (Tukey's HSD $P < 0.05$). Detritivore abundance scaled by hedge height was 1.3 times greater in the Midland and wildlife hedging than the circular saw treatment (all Tukey's HSD $P < 0.05$; overall treatment effect $F_{(4,42)} = 3.91$, $P <0.001$; Figure 2C).

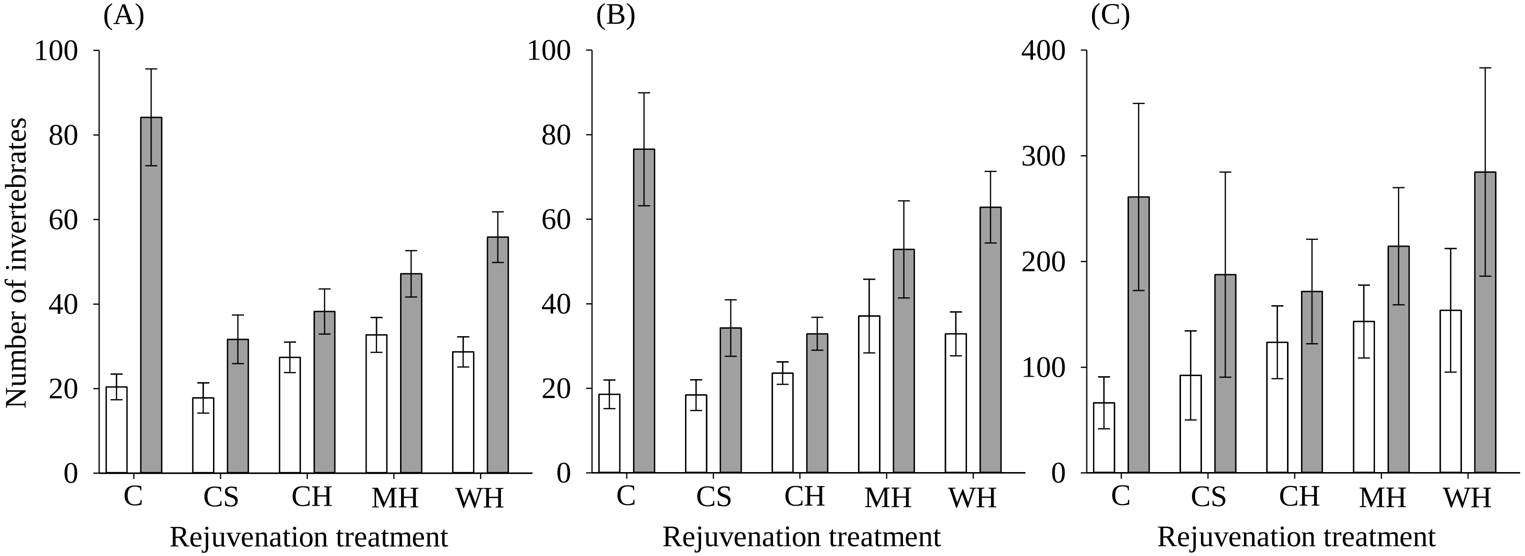

Figure 2. Mean abundance (±SE) of (A) herbivores, (B) predators and (C) detritivores, against rejuvenation treatment. Bars are white for sample abundances, and grey for abundances scaled by the mean hedge height (m). Treatments are control (C), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

2.3.2. Relationships between rejuvenation treatment and habitat factors

Treatment affected all habitat variables tested (Table 4). The C:N ratio of foliage was lowest in the circular saw and highest in the control. The midland-style and conservation hedgelaying, and the wildlife hedging were intermediate. All three laying techniques increased foliage biomass (g/m^3), particularly the Midland-style, which was was over 2.5 times that of the control and 1.5 times that of the wildlife hedging (Table 6).

The control had a smaller volume of lateral branches per unit area than the conservation hedgelaying and wildlife hedging (Table 6). The coefficient of variation of gap area (CV), which indicates a more variable structure containing open areas (see Figure 1), was largest in the control and circular saw treatments, and smallest in the wildlife hedging. The total proportion of hedge:gap was collinear with lateral branch volume and CV (Spearman rank correlation: $r_s = 0.56$ and $r_s = 0.67$ respectively, $P < 0.001$), but in contrast differed between wildife hedging and other laid treatments. The lowest proportion of hedge:gap was found in the circular saw treatment and the highest in the wildlife hedging.

Although some treatments showed concomitant increases in foliage biomass and decreases in CV, the Midland-style hedgelaying treatment had a significantly higher foliage biomass than the wildlife hedging, but no difference in CV. A very weak correlation (Spearman rank correlation: $r_s = -0.24$, $P = 0.09$) between width and foliage biomass x CV, suggests there were no confounding effects of increased width (i.e. of wildlife hedging).

Table 5: Relative effects of treatment and habitat variables on invertebrate community composition. Results of separate models containing explanatory variables of treatment (M1) or habitat variables (M2) on those measures of invertebrate community composition for which significant effects were found. Model in bold minimises AICc.

Response[a]	Model	Parameter	Estimate (±SE)	$F_{(d.f)}$	*P*	Adj. R^2	AICc
P abundance	M1	Foliage biomass[b]	0.03 (0.009)	$11.14_{(1,45)}$	<0.01	0.43	408.27
	M2	Treatment		$6.29_{(4,42)}$	<0.001	0.58	65.47
H abundance	M1	Foliage biomass	0.001 (0.038)	$7.50_{(1,45)}$	<0.05	0.37	69.42
	M2	Treatment		$5.20_{(4,42)}$	<0.001	0.47	65.56
D abundance	M1	CV for gap area	-0.33 (0.06)	$26.13_{(1,45)}$	<0.001		
	M1	Number of gaps	0.001 (0.0004)	$5.54_{(1,45)}$	<0.05	0.71	119.62
	M2	Treatment		$7.71_{(4,42)}$	<0.001	0.72	122.44
H:D ratio	M1	CV for gap area	0.028 (0.01)	$12.10_{(1,45)}$	<0.001	0.61	-71.49
	M2	Treatment		$2.87_{(4,42)}$	<0.05	0.59	-63.13
D:P ratio	M1	CV for gap area	-0.037 (0.012)	$7.38_{(1,45)}$	<0.01	0.62	n/a
H diversity	M1	CV for gap area	-0.057 (0.02)	$7.90_{(1,42)}$	<0.01		
	M1	Number of gaps	0.00037 (0.00013)	$7.90_{(1,42)}$	<0.01	0.47	n/a

[a] Trophic groups are summarised as P (predators), H (herbivores) and D (detritivores). Response data were transformed prior to analysis to meet assumptions of normality with log (all abundance variables) square root (H:D ratio) or squared (D:P ratio) transformations. Only significant results are reported. [b] Foliage biomass is measured in g/m3.

Table 6: Relative effects of treatment on habitat variables and mean (±SE) per treatment. Treatments are control (C), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH), and different letters denote treatments are significantly different at $P < 0.05$ according to post hoc Tukey's HSD test.

Response	C	CS	CH	MH	WH	$F_{4,42}$	*P*
Mean C:N ratio of foliage	0.36 (0.02)a	0.27 (0.01)c	0.32 (0.01)ab	0.31 (0.02)bc	0.33 (0.01)ab	8.91	<0.001
Foliage biomass (g/m^3)	247 (39)b	225 (26)b	581 (53)a	637 (72)a	432 (72)a	20.11	<0.001
CV for gap area (cm^2)	4.90 (0.62)a	4.25 (0.35)a	2.62 (0.33)b	2.31 (0.29)b	1.68 (0.33)c	13.45	<0.001
Lateral branches (% volume)	0.32 (0.11)b	0.30 (0.11)b	0.88 (0.28)a	0.77 (0.18)a	0.55 (0.11)a	4.4	<0.01
Ratio of hedge:gap	0.66 (0.06)c	0.63 (0.05)c	0.80 (0.03)b	0.88 (0.02)b	0.95 (0.02)a	21.62	<0.001

2.3.3. Habitat factors affecting invertebrate community composition

Foliage biomass had a positive effect on herbivore and predator abundance, with a 500 g/m^2 increase equating to an average increase of five and 15 individuals respectively (Table 5; Figure 3A and 3B), although there was no effect on the ratio of predators to herbivores. Detritivore abundance was related most strongly (negatively) to CV (Figure 3C), decreasing from approximately 200 to just a few individuals over the measured range. The ratio of detritivores to predators was also negatively correlated with CV (Table 5; Figure 3D), and to herbivores slightly less so (Table 5). The quality of resources for herbivores (C:N ratio of foliage), was not a significant factor for any invertebrate community response variable tested, despite differing between treatments. Treatment did not affect the Shannon diversity index for any trophic group. The diversity of herbivores was negatively correlated with CV, with a slightly positive relationship to number of gaps /m^2 (Table 5); across the range of CV there was an average loss of three herbivore taxa ($F_{(1,45)} = -2.52$, $P < 0.05$).

Variation in most invertebrate community response variables was better explained by treatment than by the structural variables (Table 5). As the management treatments are the cause of structural changes, this is to be expected, but one exception was the detritivore to predator ratio, for which the variation in gap size had an effect independent of treatment.

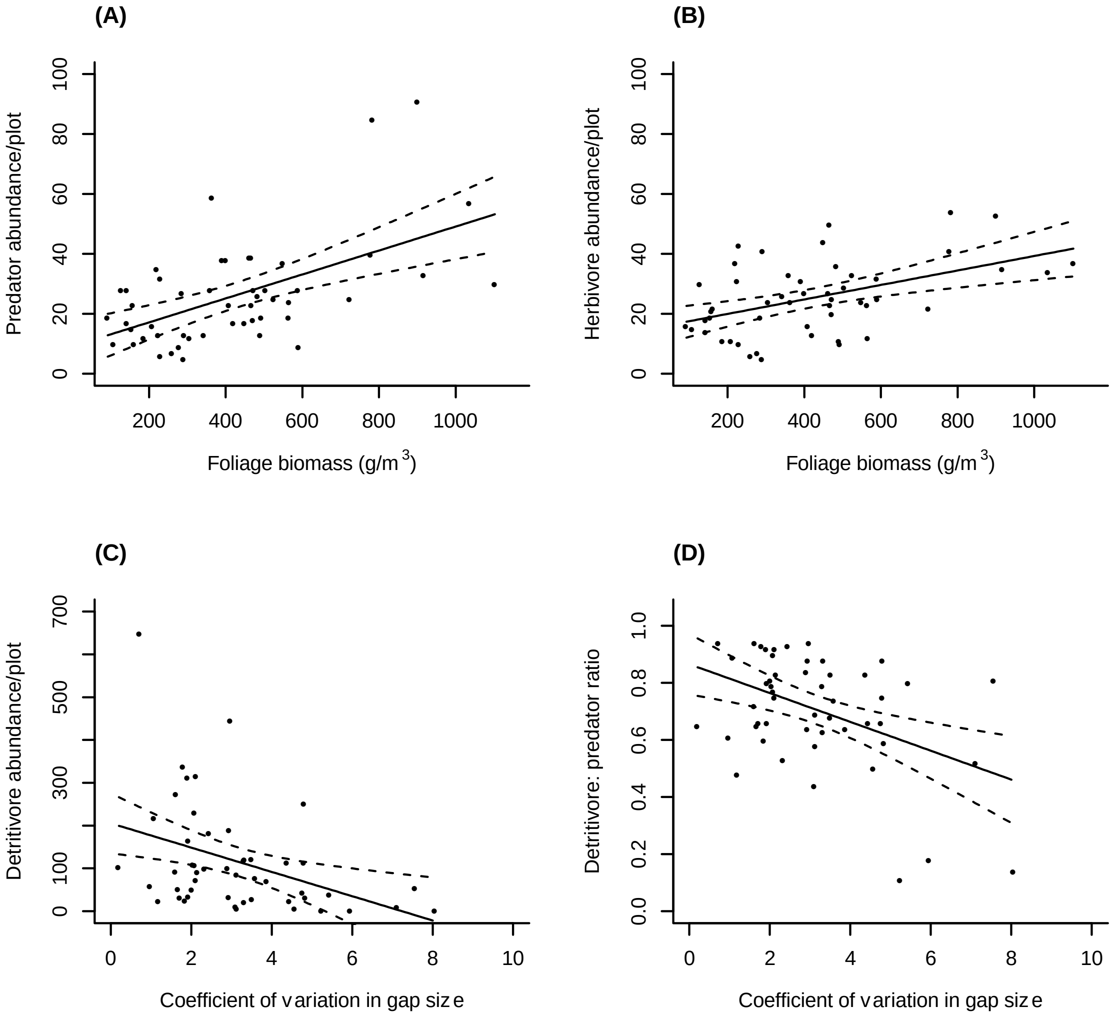

Figure. 3. Relationships between (A) foliage biomass and predator abundance, (B) CV gap area and herbivore abundance, (C) CV gap area and detritivore abundance, and (D) CV gap area and detritivore:predator ratio. Regression lines (solid) and 95% confidence intervals (dashed) are univariate relationships only, included to provide a visual reference.

2.4. Discussion

2.4.1. Hedgerow management affecting invertebrates

Hedge rejuvenation method resulted in considerable immediate differences in the structure and quality of hedgerow habitat which had knock-on effects on invertebrate communities. Techniques where the hedge was laid increased foliage biomass, though less so in the mechanical wildlife hedging. A positive relationship between foliage biomass and invertebrate abundance corroborates previous findings, particularly for spiders (Gunnarsson 1990), and herbivores (Whitfeld *et al.* 2012). Greater net positive effects of foliage biomass on predator abundance compared to herbivores were found, which could potentially reflect increased availability of refugia from intra-guild predation for predators (Gunnarsson 1990), or increased prey availability enhancing population growth (Denno *et al.* 2002). However, the ratio of these two trophic groups did not relate significantly to either treatment or habitat structure parameters, so the data does not strongly support the hypothesis that within-habitat spatial variation in structure differentially affects herbivores and predators. An increase in the foliage quality for herbivores (C:N ratio; Mattson, 1980), was found in treatments where considerable cutting had occurred (circular saw, Midland-style and conservation hedgelaying; Mediene *et al.* 2002), but the hypothesis that herbivore abundance would be more affected by the nutritional quality of foliage than by habitat structure, was not supported. It is possible that fecundity increased (Awmack & Leather 2002) whilst other factors such as interactions with predators and parasitoids reduced abundance (Havill & Raffa 2000). Further research employing smaller-scale mesocosm experiments (e.g. Langellotto & Denno 2004; Woodcock & Heard, 2011) could be used to elucidate these mechanisms.

Detritivore abundance has previously been shown to correlate with branch biomass (Halaj, Ross & Moldenke 2000). However, we found heterogeneity (CV) of gaps to be more relevant with lower CVs (less variation) related to higher abundances. Psocoptera and Lathridiidae are specifically associated with bark (New, 1970; Lawrence & Newton, 1980), while Collembola benefit from the retention of dead foliage within the canopy habitat, both of which a more closed and clumped distribution of branches (lower gap area CV) is likely to provide. Why less variation in gap size related to increased diversity of herbivorous taxa is less clear. One line of enquiry that could be explored in future studies is whether there is any relationship to the provision of nectar and pollen resources important to herbivores (Wäckers, Romeis & van Rijn 2007).

2.4.2. Implications for rejuvenation management practice

Our study is unique in its use of a multi-site, replicated manipulative field experiment to compare the relative effects of different hedgerow rejuvenation techniques. Few previous studies addressing habitat structural effects on invertebrate abundance have also quantified resource quality for primary consumers within an arboreal context (but see Facey *et al.* 2014). We found that when the overall size of hedge was taken into consideration, the unmanaged hedge supported the highest abundances of predatory and herbivorous invertebrates. However, rejuvenation treatments are designed to prevent hedgerows from developing into a line of trees and in this context management impacts are important to consider if farmer goals (e.g. management efficiency and effectiveness) are to be better aligned with optimising the value of hedge habitats for wildlife. Farmer goals are rarely about optimising invertebrate abundance, but rather the maintenance of a reasonably compact hedge habitat. Moreover, we assessed the response of invertebrate community over the spring – autumn following winter hedgerow rejuvenation. Over the longer term the effects of rejuvenation may reduce as the hedgerow plants grow and structural differences diminish, especially between the three laid rejuvenation methods.

In contrast to Henry, Bell & McAdam (1994), where number of insect orders increased with hedgelaying (though their comparison was only against pollarding), treatments had no effect on invertebrate diversity at the level of order/family. While reshaping a hedgerow with a circular saw reduced the abundance of invertebrates in the first year after management, other techniques performed similarly to the traditional Midland-style laying. This supports our hypothesis that the wider use of these more economical methods is unlikely to have detrimental effect on the abundance of invertebrates. Consideration of ease of future management is required for some techniques e.g.wildlife hedging, but this should be offset with their potential benefits e.g. supporting more invertebrates than other techniques. Overall the techniques we tested reduced the cost of traditional hedgelaying from half to less than a quarter. As such they represent a more efficient and cost effective way of rejuvenating a greater number of hedgerows (e.g. under AES) without compromising a key element of the biodiversity they foster.

3. Hedgerow rejuvenation management affects invertebrates overwintering in the soil

3.1. Introduction

Interest in the management of semi-natural non-crop habitats such as hedgerows to support natural enemies of crop pests (‘conservation biological control’; Tscharntke *et al.* 2007; Griffiths *et al.* 2008), has increased in recent years (Perdikis, Fantinou & Lykouressis 2011; Morandin, Long & Kremen 2014). Hedgerows, amongst other non-crop habitats within the agricultural landscape, could play such a role by providing permanent vegetation cover for overwintering predatory invertebrates (Tscharntke *et al.* 2007). However, Griffiths *et al.* (2008) have warned that in fact woody non-crop habitats such as hedgerows, whilst they support higher abundance and diversity of predatory invertebrates, may actually inhibit their movement. They also suggest there is little evidence for actual impact on pest-suppression from conservation biological control, with only the potential for benefits explicitly demonstrated (Griffiths *et al.* 2008). However, there is now at least some compelling evidence; a study by Morandin, Long & Kremen (2014) found that pest populations were significantly lower, and the abundance of predatory invertebrates higher, in crops ajacent to hedgerows. The negative effect on aphid populations (predated largely by Coleoptera) extended to 200m from the hedgerows, and that on on stink bugs (with parasitoid natural enemies) to 100m from hedgerows (Morandin, Long & Kremen 2014). Studies such as these support the theory that the relative abundance of predatory invertebrates present in different hedgerow habitats could potentially impact on the degree of biological pest-control occuring within adjacent crops.

Although above-ground habitat such as the hedgerow canopy is utilised by some overwintering invertebrates (Pekár 1999), many insects favour the soil environment due to the relatively warm and stable temperature it provides (Leather, Walters & Bale 1993). Woody habitats such as hedgerows clearly can provide valuable protection for overwintering invertebrates; higher abundances and species richness of Coleoptera and Araneae in hedgerows compared to field margins were attributed to shelter provided by woody vegetation (Pywell *et al*. 2005), and greater beetle activity, biomass and diversity recorded in shrub microsites relative to a surrounding bare-soil matrix was attributed to the moderating effect on climate provided by the woody shrubs (Noemí Mazía, Chaneton & Kitzberger 2006).

Just as grass species with a tussock-forming habit can provide a more stable temperature than those with a mat-forming habit (Thomas, Mitchell & Wratten 1992), it might be expected that in the larger scale of woody species in hedgerows, the density of the vegetation will also affect temperature variability or range. Perhaps surprisingly, Griffiths *et al.* (2007), using emergence traps to assess Carabidae and Staphylinidae (Coleoptera) using the soil to overwinter, found that fence habitat had a considerably higher density (160.40 m^{-2}) than either the hedgerow (31.29 m^{-2}) or degraded hedgerow (53.69 m^{-2}) habitats. They also found that in terms of the species diversity of these taxa, the more open fence habitats were as valuable as hedgerows and degraded hedgerows, all of which supported unique species with a similar species richness. Within the hedgerow habitats, however, Carabid and Staphylinid species richness was greatest where the canopy was tall, wide and continuous (Griffiths *et al*. 2007).

Chapters 1 and 2 have discussed the ecological importance of the hedgerows in general and in particular for invertebrates, as well as the need for rejuvenation management and the relative paucity of studies assessing its impact on these taxa. This chapter investigates the effect of hedgerow rejuvenation management on invertebrates overwintering in the soil beneath the hedge, and incorporates the four rejuvenation management treatments and an uncut control described in Chapter 2 (Table 4), as well as an additional coppicing treatment. Coppicing, where the main stems of the hedge are cut to just above ground level, is another method of long-term management that has historically been utilised instead of hedge laying in places (Rackham 2003), providing a source of firewood. This management technique leaves no vegetation cover initially. Shoots soon re-grow from the coppiced basal stool and, although browsing by deer can be a problem (Staley *et al.* 2015), over time can form a thick hedge once again. Whilst this treatment was omitted from canopy sampling described in Chapter 2 due to the lack of any woody material remaining in the year following management when data was collected, this was not an issue for sampling of overwintering invertebrates inhabiting the soil, and provided a potentially interesting contrast to assess the effect of a complete lack of woody vegetation cover.

Although hedgerows provide overwintering habitat for a wide range of functional groups of invertebrates (Pywell *et al.* 2005), the majority of discussion and investigation on this topic has focussed on those predatory taxa that may play a role in the biological control of crop pests (Griffiths *et al.* 2008; Morandin, Long & Kremen 2014), and their use of hedgerows as an alternative habitat when arable fields are fallow. This experiment tests the hypotheses that:

- Aspects of hedge structure related to increased shelter and protection (hedge height and width, hedge:gap ratio) and related changes to microclimate (temperature at ground level) will affect the abundance of overwintering invertebrates.
- Hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, will support a similar abundance and trophic diversity of overwintering invertebrates as those rejuvenated with traditional hedgelaying.

3.2. Materials and methods

3.2.1. Experimental design

The data presented in this chapter was collected from the same randomised block field experiment as described in Chapter two, with the inclusion also of an additional treatment where the hedge was coppiced to approximately 5 cm above ground using a hand-held chainsaw (at the same time other management treatments were implemented in October 2010). Similarly to all other treatments, this was replicated amongst and within sites.

3.2.2. Invertebrate sampling

Sampling of overwintering invertebrates across the four experimental sites took place between 8th February and 14th March 2011. Four soil samples, including the leaf litter directly above, were taken from each plot (depth: 10cm, diameter: 11cm; two per side, randomly positioned and at 60cm from the hedge centre). Ideally all samples would have been taken from the centre of each plot, but the considerable width of the wildlife hedging meant this was not possible in this case; 60cm from the centre of the hedge was as far into the plot as was accessible. With the intention of standardising the methodology across treatments, this was therefore taken as a set distance from the centre of the hedge from which to sample. Soil samples were refrigerated at 4.5°C for up to two weeks before being sorted by hand for three minutes to remove the largest invertebrates, and then placed in Tullgren funnels (Burkard Scientific funnels; 40W bulb) for 24 hours to remove smaller species e.g. mites. Emerging invertebrates were collected and then stored in 70% Industrial Methylated Spirits (IMS).

All invertebrates were later sorted to order and in some cases family (i.e. Coleoptera) and assigned to one of three trophic groups where possible (predators, herbivores and detritivores; Appendix 3). Taxa for which it was not possible to differentiate between feeding preferences at this taxonomic resolution (including Acari, Diptera and Heteroptera; Appendix 3) were excluded. For each trophic group, Shannon-Weaver diversity (H') was calculated based on the taxonomic resolution to which different groups were identified as $H' = -\sum p_i \ln(p_i)$.

3.2.3. Hedge dimensions

In late spring, hedgerow height was measured using a range pole placed against the face of the hedge at five locations. At the same positions width was measured by inserting the range pole through the hedgerow at a height of 1m, with one person either side of the hedge recording the position of the widest points. Height and width were recorded to the nearest 10cm, and measurements were averaged for each plot.

3.2.4. Microclimate

Data loggers (Gemini, Tinytag Plus 2) were put out at four of the five sites for seven days concurrent with the invertebrate sampling at each site (between 8th February and 14th March 2011), with readings taken every minute; one site (NE) was considered not secure enough to leave equipment out in the field as it was adjacent to a busy footpath. Loggers were placed at the ground surface level in the centre of each plot, and at the mid-point of the hedge.

3.2.5. Data analyses

Abundances of invertebrates in each trophic group found overwintering in the soil/leaf litter were over-dispersed count data, so quasipoisson generalised linear models (GLMs) were used to model the effect of treatment, with site as a factor. The use of quasipoisson GLMs precluded the use of Akaike’s Information Criterion to assess whether effects of habitat structure (or microclimate) were independent of treatment as was done in Chapter 2. GLMs were also used to test treatment effects on ratios of trophic groups and microclimate, with site as a factor, and data were transformed to approximate a normal distribution where necessary. Where negative values were present within temperature data, a constant value of 5 was added to all values prior to log transforming. Where a significant effect of rejuvenation treatment (or interaction of treatment and site) was found, *post hoc* Tukey tests were used to determine which treatment levels differed, using the multcomp package (Hothorn, Bretz & Westfall 2008).

3.3. Results

A total of 11,869 invertebrates were collected from soil samples beneath the hedge canopy in late winter (Feb - March) 2011. The most abundant taxa in decreasing order were Acari (n = 5692), Coleoptera (n = 2898, of which 252 larvae), Collembola (n = 1808), Oligochaeta (n = 480), Isopoda (n = 301), Araneae (n = 219). For all other taxa < 200 individuals were sampled. Staphylinidae were by far the most abundant Coleoptera (n = 1588), representing 76% of the predatory trophic group. Areneae (10%), parasitic Hymenoptera (9%) and Carabidae (4%) accounted for much of the remainder of predators. Of the herbivores, the most abundant taxa were the Curculionidae (21%), Nitidulidae (20%), Apionidae (15%) and Chrysomelidae (14%) families of the Coleoptera. Collembola were the most abundant detritivores (52%), followed by Oligochaeta (14%), Lathridiidae (Coleoptera; 9%), Cryptophagidae (Coleoptera; 9%), and Isopoda (8%).

3.3.1. Relationships between rejuvenation treatment and invertebrate community composition

Rejuvenation method affected the number of invertebrates in some trophic groups (Table 7). There was a significant effect of treatment on herbivore abundance (χ^2_5 = 37.32, $P < 0.05$); Figure 4A), although an interaction between treatment and site (χ^2_{15} = 64.27, $P < 0.01$) makes the results complex to interpret. *Post hoc* Tukey tests show the overall treatment effect was due to the circular saw resulting in over twice as many herbivores as the conservation hedgelaying ($P < 0.05$), but that this was driven by differences between a single site (WH; primarily the circular saw treatment) and all others ($P < 0.05$). There was also a significant effect of treatment (χ^2_5 = 82.10, $P < 0.05$; Figure 4B) and site (χ^2_3 = 1294, $P < 0.01$) on the abundance of predators overwintering in the soil and leaf litter beneath hedgerow plots, although not interaction between the two. *Posthoc* Tukey tests reveal that the only significant treatment difference was between the wildlife and conservation hedging ($P < 0.05$), with a marginally non-significant trend between the conservation and control treatments ($P = 0.063$), but that there were significant differences between all sites ($P < 0.05$). The conservation hedging had the lowest number of predatory invertebrates; the wildlife hedging had approximately 1.6 times as many individuals. There was no relationship between rejuvenation treatment and the abundance of detritivores extracted from soil samples, or on the total abundance of invertebrates.

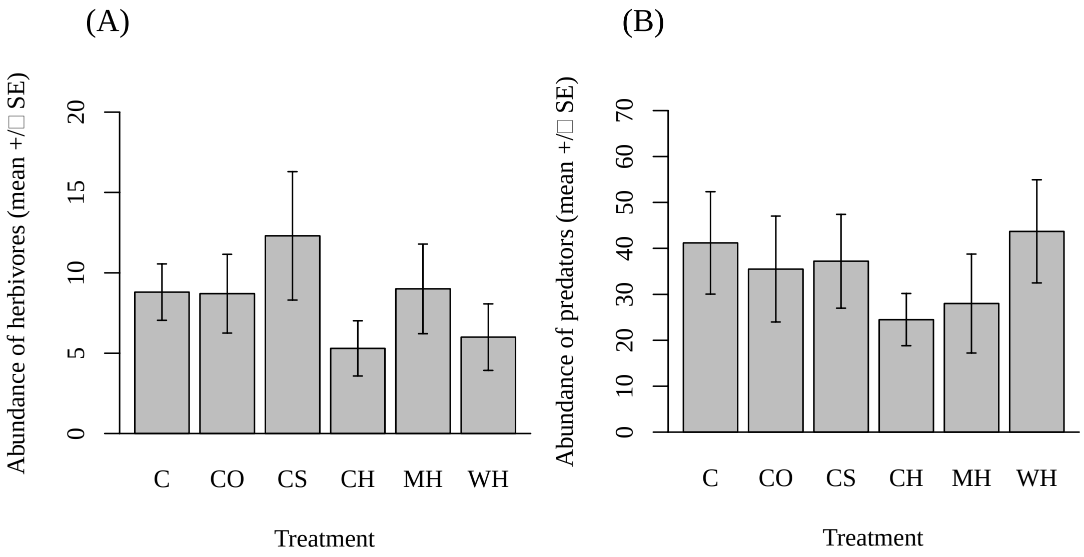

Figure 4: Abundance of A) herbivores and B) predators (± standard error) extracted from soil samples, by rejuvenation management treatment. Treatments are control (C), coppice (CO), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

Rejuvenation method affected the ratio of predators to herbivores ($F = 3.21_{(5,51)}$, $P < 0.05$; Figure 5); wildlife hedging had a significantly higher ratio of predators to herbivores than the control, coppice and midland hedgelaying treatments (*post hoc* Tukey test $P < 0.05$). There was no relationship between rejuvenation treatment and the diversity of taxa in soil samples either within or across trophic groups.

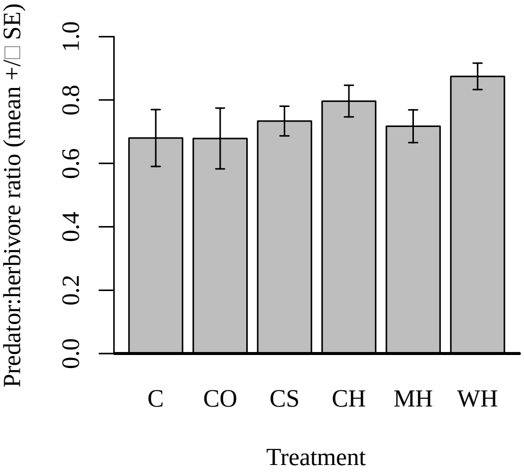

Figure 5: Ratio of predators:herbivores (± standard error) extracted from soil samples, by rejuvenation management treatment. Treatments are control (C), coppice (CO), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

Table 7: Effects of rejuvenation treatment on invertebrate community composition.

Response	Test statistic	P	Adj. R^2
P abundance	$\chi^2_5 = 82.10$	<0.05	
H abundance	$\chi^2_5 = 37.32$	<0.05	
P:H ratio	$F = 3.21_{(5,51)}$	<0.05	0.50
H:D ratio	$F = 2.96_{(5,51)}$	<0.05	0.39

[a]Trophic groups are summarised as P (predators), H (herbivores) and D (detritivores). Response data subjected to general linear models were transformed prior to analysis to meet assumptions of normality with squared (P:H ratio) or square root (H:D ratio) transformations. Only significant results (P = <0.05) are reported.

3.3.2. Relationships between rejuvenation treatment, vegetation cover and temperature

Excluding the coppice plots, which had no woody vegetation cover at the time of survey, rejuvenation management treatment had a significant effect both on the width ($F_{(42,4)} = 57.01$, $P < 0.001$, $R^2 = 0.83$) and height ($F_{(42,4)} = 143.58$, $P < 0.001$, $R^2 = 0.92$) of hedge plots (Figure 6). The only treatments that did not differ significantly in width were the control and wildlife hedging, and the circular saw and conservation hedging respectively (Figure 6A; *post hoc* Tukey test $P < 0.01$). For height, the wildlife and circular saw treatments, and the conservation and midland hedgelaying respectively, were not significantly different from one another (Figure 6B; *post hoc* Tukey test $P < 0.001$).

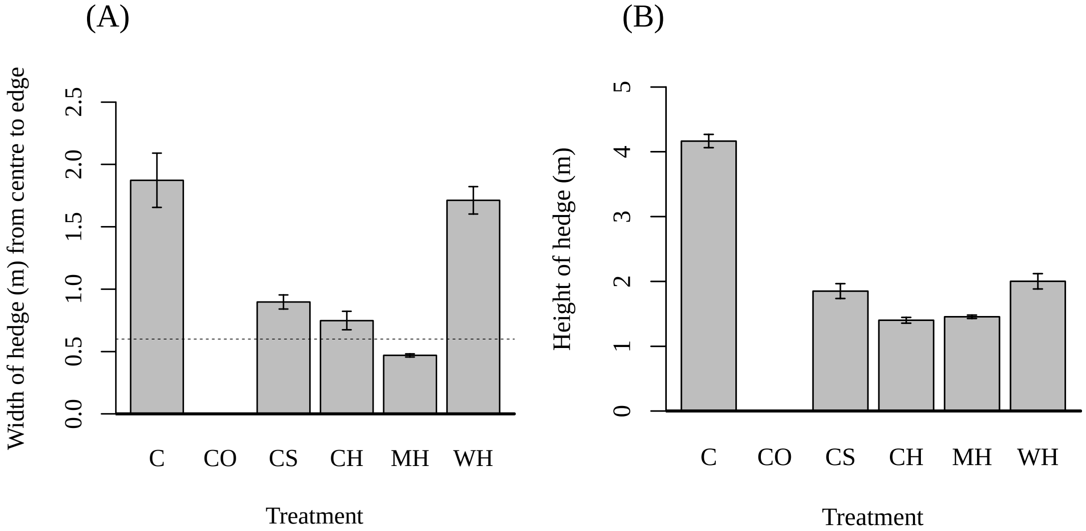

Figure 6: Effect of rejuvenation management treatment on A) width and B) height of hedge. The dashed line in plot a represents the point (60cm from the centre of hedge) at which soil samples for invertebrate samples were taken; hedge widths below this therefore denote a lack of woody vegetation cover directly above the point of sampling. Treatments are control (C), coppice (CO), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

The total proportion of woody material calculated from digital images gives an indication of the density of cover provided by the hedge for overwintering invertebrates. In the basal portion of the hedge (0-90cm height) there was a significant effect of treatment on the overall amount of woody material in the hedge (hedge:gap ratio; $F_{(4,22)} = 21.62$, $P < 0.001$, $R^2 = 0.68$; Figure 7).

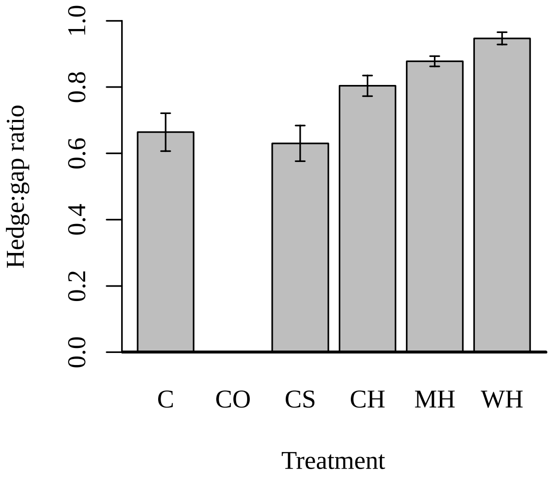

Figure 7: Effect of rejuvenation management treatment on the hedge:gap ratio calculated from digital images taken in January 2011 (i.e. the proportion of woody material). Treatments are control (C), coppice (CO), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

There was a significantly lower proportion of woody material in the control and circular saw treatments than all three laid treatments, and the wildlife hedging had a significantly higher proportion of woody material than the conservation and Midland-style hedging (*post hoc* Tukey tests $P < 0.05$). Images of the control treatment show an open structure despite its relatively large width, whilst the dense structure depicted in images of the wildlife hedging on the other hand may be influenced by its relatively large width (Figure 1).

Temperature range was strongly negatively correlated with the minimum temperature (Spearman rank correlation = $r_s = -0.72$, $P < 0.001$), and positively correlated with the maximum temperature (Spearman rank correlation = $r_s = 0.97$, $P < 0.001$). Minimum and maximum temperature were also correlated (Spearman rank correlation = $r_s = -0.56$, $P < 0.001$). This was related to the cover provided by the hedge; increased hedge:gap ratio had a small but significant positive effect on the maximum temperature at ground level ($F_{(38,1)} = 6.68$, $P < 0.05$, $R^2 = 0.12$). Across all treatments including coppice, there was a significant treatment effect on the minimum (but not maximum) temperature ($F_{(34,5)} = 7.96$, $P < 0.001$, $R^2 = 0.57$; Figure 8A) and the temperature range ($F_{(34,5)} = 4.02$, $P < 0.01$, $R^2 = 0.31$; Figure 8B) at ground level in late winter. This was due to the coppice plots having a significantly lower minimum temperature than all other treatments (*post hoc* Tukey test, $P <$

0.01), and a significantly narrower temperature range (by approximately 10˚C) than the Midland-style and conservation hedgelaying (*post hoc* Tukey test, $P > 0.001$).

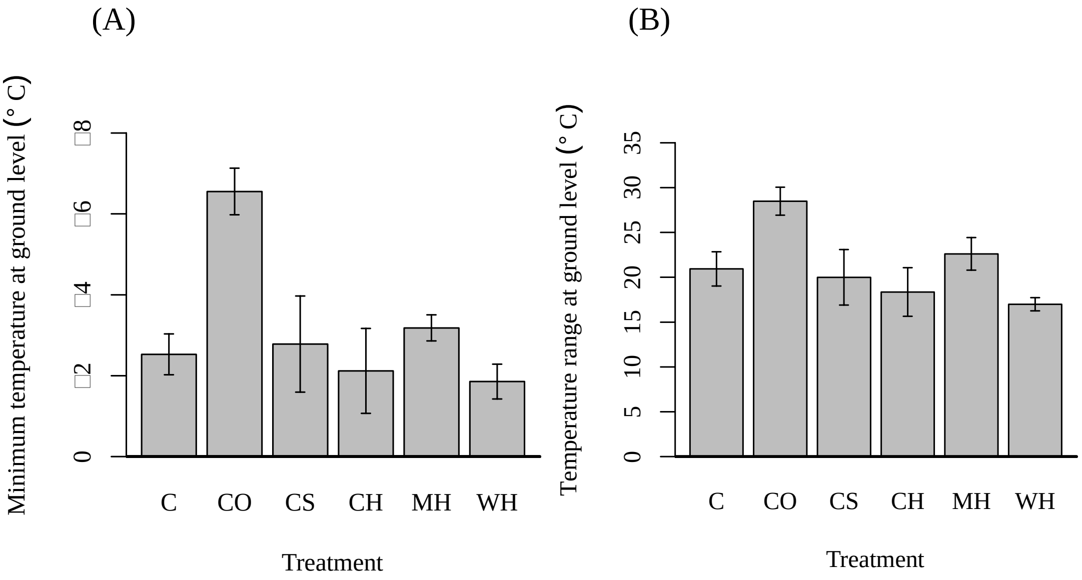

Figure 8: Effect of rejuvenation management treatment on A) minimum temperature at ground level (˚C) and B) temperature range at ground level. Treatments are control (C), coppice (CO), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

3.3.3. Relationships between vegetation cover, temperature and invertebrate community

The mean width of most treatments was above 1.2m (Figure 6A), which is the point at which we would expect the invertebrate samples (taken 60cm from the hedge centre) to have no vegetation cover immediately above them. However, soil samples with overwintering invertebrates from the midland hedgelaying were taken just outside of the mean width of the hedge (0.94m ± 0.02m in total or 0.47m ± 0.01m from the hedge centre), meaning they would have no woody vegetation cover directly above (Figure 6A). However, as this relates to a maximum sampling distance <15cm from the edge of the hedge, there is likely to still be a considerable degree of shelter from the vegetation. For the conservation hedgelaying treatment mean hedge width was not much above 1.2m and the soil sample for at least one plot was taken outside of the width of the hedge (1.5m ± 0.15m; Figure 6A). However, neither the width nor height of the hedge, or the proportion of woody material as calculated from digital images, was found to significantly affect the abundance of invertebrates in any of the three trophic groups collected from soil samples. Temperature had a small but significant effect on the abundance of herbivores; their abundance was positively correlated with the maximum temperature ($\chi^2_1 = 20.44$, $P < 0.05$) and the range in temperature ($\chi^2_1 = 19.38$, $P < 0.05$; Figure 9).

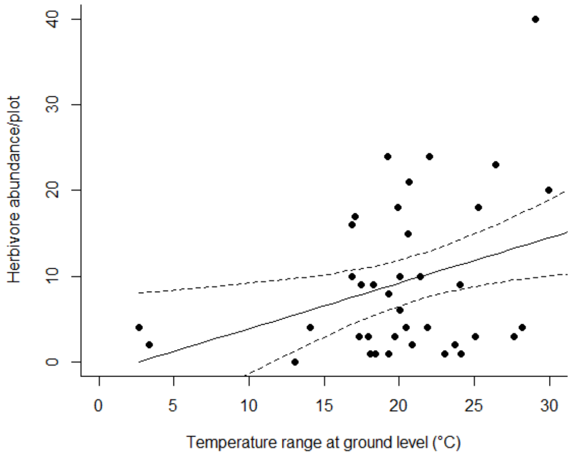

Figure 9: The relationship between herbivore abundance and the temperature range (˚C) at ground level in the centre of the hedge.

Three outliers were identified using the boxplot function in R (those >1.5 times outside the interquartile range for each variable); the two data points with the lowest temperature range, and the data point with the highest herbivore abundance. The analysis repeated without these outliers found a similar pattern for the range in temperature, though the effect was marginally non-significant ($\chi^2_1 = 12.33$, $P = 0.05486$), but the effect of maximum temperature was no longer apparent. However, caution is advised with regards to the removal of such outliers, particularly without good reason to suspect error in the data as is the case here (Zuur, Ieno & Elphick 2010), and so the following discussion considers the results of the full dataset. There was no relationship between the abundance of either detritivores or predators and the temperature at ground level.

3.4. Discussion

3.4.1. Hedgerow management affecting overwintering invertebrates

Different management treatments resulted in varying degrees of shelter above the soil from which overwintering invertebrtes were sampled, in terms of the height and width of the hedge, and the resulting microclimate. The hypothesis that hedge structure and microclimate would affect the abundance of overwintering invertebrates was not strongly supported, as no effects of hedgerow dimensions or density of woody material were found. However, although the hedge dimensions alone did not affect invertebrate abundance directly, the temperature range at ground level did have some effect on herbivore abundance. Whilst it might be expected that in general a more limited range of temperatures might be more favourable to overwintering invertebrates (Leather, Walters & Bale 1993), the results here do not support this; abundances of herbivores were in fact slightly greater with a larger range in temperature. More intuitively, there was a positive relationship between herbivore abundance and maximum temperature at ground level. Overall, temperature explained relatively little variation in the invertebrate communities, suggesting that other factors may play an important role. Overwintering in insects is most commonly cued by photoperiod and temperature, often in combination (Leather, Walters & Bale 1993), which may be affected by basal vegetation beneath or adjacent to hedges (Pywell *et al.* 2005; Thomas, Mitchell & Wratten 1992), as well as the woody canopy. Although the present study didn’t record basal vegetation, there appeared to be very little vegetation growing where samples were taken from (personal observation). In any case, the reason usually cited for the relevance of herbaceous vegetation in providing a suitable habitat for overwintering invertebrates is the moderating effect on microclimate, which has been considered. The provision of enhanced cover from predators by any basal flora present (Collins *et al.* 2003) as well as the woody vegetation could theoretically be a driver of herbivore abundance, rather than temperature change *per se*. However, this is perhaps less likely as invertebrates overwintering in the soil are relatively protected from predation by winter-active animals such as birds (Leather, Walters & Bale 1993).

The present study measured temperature for a period of 7 days concurrent with the invertebrate sampling. Although the presence of invertebrates overwintering in the soil could potentially be affected by temperature differences throughout the autumn and winter, the timing of sampling (between 8th February and 14th March 2011) was relatively soon after the coldest time of year in the UK (Parker, Legg & Folland 1992) and hence representative of the extremity of conditions invertebrates overwintering in the soil are likely to endure, particularly as changes in soil temperatures lag behind that of the air (Zheng, Hunt & Running 1993). It is possible that the methodology of sampling invertebrates at a standard distance from the hedge (60cm), rather than at the centre of the hedge where temperature was recorded, has introduced some degree of disparity between the latter and the true microclimate of the invertebrate sampling point. In future such studies it would be prudent to take both samples (invertebrates and temperature) from exactly the same place and, as the centre point of the hedge was not possible in this case, perhaps the mid-point between the edge and the centre of the hedge would be more appropriate as a method of standardising between treatments.

The hypothesis that alternative, more economical, rejuvenation methods could support a similar abundance of invertebrates to traditional Midland-style hedgelaying is supported by the data. Slightly higher abundances of herbivores were supported by the circular saw treatment, although this was dominated by the effect at a single site (WH). The wildlife hedging treatment supported the highest abundance of predators and ratio of predators to herbivores. Although not significantly different to the Midland-style hedgelaying, the conservation hedging appeared to provide, by a small margin, the poorest conditions for invertebrates overwintering in the soil beneath the hedge. Results showed that this treatment supported fewer overwintering predators than the wildlife hedging, and fewer overwintering herbivores than hedges managed by circular saw. This was unexpected as, based on the variables measured, the conservation hedging appeared to provide similar conditions to the Midland-style hedgelaying; neither the density of the hedge (illustrated by the hedge:gap ratio calculated from digital images) nor the temperature at ground level differed. Although the circular saw treatment resulted in a wider hedge than the conservation hedging, thus providing more direct cover over the region from which samples were taken, the latter was wider than the Midland-style hedgelaying, and the higher density of woody material might also be expected to provide more cover for invertebrates.

Results showed that temperature, hedge dimensions and hedge density differed between rejuvenation treatments, though there are other factors that could have affected the presence of overwintering invertebrates. Increased detritus at either the habitat or within-plant scale can have a positive effect on the abundance of natural enemies (Langellotto & Denno 2004). Leaf litter was not sampled in this study, but as the wildlife hedging management involved leaving all branches within the hedge (i.e. no brash was removed), and these hedges were significantly higher than the other laid treatments, it is probable that there was more leaf litter on the ground in this treatment. The ratio of predators to herbivores was higher in the wildlife hedging than the control, coppice or midland treatments, suggesting that from a conservation biological control perspective, this treatment may be worthy of further study.

Although the soil/leaf litter is a favoured location for many overwintering species (Sotherton 1984; Pfiffner & Luka 2000), other species are known to overwinter in the canopy (Pollard, Hooper & Moore 1974; Pekár 1999), and so soil sampling alone may be limited in terms of getting a complete overview of the suitability of different hedgerow habitats for overwintering invertebrates. The extraction method used could be biased toward those soil fauna taxa that are most able to move away from the dry/warm conditions caused by the Tullgren lamps; invertebrates that either over-winter as immobile larvae or are particularly moisture dependent such that they desiccate before escaping may have been under sampled, though the employment of pre-hand sorting will have located many of the larger pupae. Although heat extraction can over-represent those species present as larvae that hatch due to accelerated incubation, this is unlikely to be a problem given the relatively short timescale of 24 hours used. Another consideration is that management was implemented in the October (2010) prior to sampling in March 2011, so some invertebrates may have already located overwintering sites prior to this point.

Regardless of the above caveats, this study represents a novel insight into the effects of hedge rejuvenation management treatments on the abundance and trophic diversity of invertebrates overwintering in the soil beneath the hedge. Pollard &

Holland (2006) found that soil-dwelling arthropods beneath a hedgerow had a clumped distribution above that explained by measured habitat variables, and cautioned that a high level of replication is required in studies, which is indeed provided by the present experiment.

3.4.2. Implications for rejuvenation management practice

Whilst the present study found relatively subtle effects of rejuvenation treatment at the level of abundance within trophic groups, results did confirm that more economic methods of hedgerow rejuvenation were comparable in their ability to support invertebrates to traditional Midland-style hedgelaying. In fact, the wildlife hedging and circular saw treatment resulted in the highest abundances of herbivores and predators respectively, though significantly higher than only the conservation hedging. The latter in particular is surprising, as reshaping with a circular saw results in such a sparsely vegetated hedge which appears to provide the least amount of shelter beneath (Figure 1A). The findings of Griffiths *et al.* (2007) highlight the possibility that there may be considerable differences in the species composition of different field boundary habitats, which could also be the case with different rejuvenation treatments. For example, Griffiths *et al.* (2007) found large differences in species composition of Carabidae and Staphylnidae between managed hedges with a closed canopy, and unmanaged gappy hedges/lines of trees (relict hedges), the latter of which may be analagous to the uncut control treatment in this study. However, given that the primary concern here is to compare between traditional Midland-style hedgelaying and alternative, more economical methods, it is more difficult to surmise whether differences in species composition of specific invertebrate groups such as these might be likely.

Hedgerows have been suggested as potentially valuable habitats for conservation biological control, whereby they may act as a natural source for predatory invertebrates (Tscharntke *et al.* 2007; Morandin, Long & Kremen 2014). In this context the finding that wildlife hedging, a particularly novel method of rejuvenation with machinery employed to push over the hedge at particularly fast rate, may support a higher ratio of predators to herbivores, could be worthy of further study.

4. General discussion and conclusions

This thesis has assessed the abundance and trophic diversity of invertebrates at several time points through the year, utilising hedgerow habitats typical of those across much of the UK, which had been subjected to different hedgerow rejuvenation management techniques within a multi-site replicated experiment. As well as considering practical implications in terms of the application of specific techniques, the scale of resulting differences in habitat structure allowed for an investigation of how different structural factors might affect suitability of the habitat for invertebrates.

Table 8: Summary of the main findings regarding effects of hedgerow rejuvenation on habitat structure and invertebrate community composition.

Main findings	Related hypotheses
Invertebrates utilising the canopy during spring-autumn	
- More economic rejuvenation methods were comparable to traditional hedgelaying in terms of invertebrate abundance	(iv)
- Abundance in all 3 trophic groups was generally higher in treatments	(iv)
- Circular saw reshaping = fewer invertebrates/unit area than laid treatments	(iv)
- Scaled by hedge height, the uncut control and wildlife hedging supported most invertebrates	(iv)
- Diversity at the level of order/family did not differ with treatment	(iv)
- Foliage biomass positively correlated with herbivore & predator abundance	(i) & (ii)
- Variation in gap size negatively correlated with abundance of detritivores	(i) & (ii)
- Variation in gap size negatively correlated with diversity of herbivores	(i) & (ii)
Invertebrates overwintering in the soil	
- More economic rejuvenation methods were comparable to traditional hedgelaying in terms of invertebrate abundance	(v)
- Overwintering predators more abundant in wildlife hedging than conservation hedgelaying	(v)
- Wildlife hedging had the highest ratio of predators to herbivores	(v)
- Circular sawing supported more herbivores than conservation hedging	(v)
- Diversity at the level of order/family did not differ with treatment	(v)
- Hedge dimensions were not correlated with invertebrate abundance	(iii)
- Herbivore abundance was positively correlated with the range in, and maximum, temperature	(iii)

Summarised in Table 8, the main findings of this thesis include evidence to support the wider application of alternative rejuvenation techniques, some of which could be relevant in terms of conservation biological control, as well as insight into differential effects of habitat structure across trophic groups.

The overwintering habitat provided by hedgerows for many predatory invertebrate species (Varchola & Dunn 2001; Pywell *et al.* 2005), may provide a conservation biological control function to neighbouring crops. A recent study by Morandin *et al.* (2014) found that the ratio of predators:herbivores was greater in crops with adjacent hedgerows, suggesting that beneficial spillover effects in terms of pest control were occurring. Whilst the present study certainly found that predatory invertebrates were overwintering in the soil beneath hedges, it is not possible to quantify the likelihood of these predators moving into crops in the spring. However, it is interesting to note that the ratio of predators:herbivores was higher in the wildlife hedging than the uncut control, coppice and midland hedgelaying treatments, and so in relative terms this management could have increased potential as a source of natural enemies for crop pests.

Trophic groups are often affected differently by aspects of habitat structure; the findings of a meta-analysis by Langellotto & Denno (2004) suggested that increased complexity of hedgerow habitat structure might preferentially benefit predators over herbivores. In this study, the hypotheses that increasing the spatial variation of within-habitat hedgerow structure would increase predator abundance (i) whilst herbivores would be more affected by foliage quality (ii), were rejected. In terms of invertebrates utilising the hedge canopy during the growing season (spring, summer and autumn), predators and herbivores were similarly affected by foliage biomass; there was a positive correlation between foliage biomass and the abundance of these groups. Variation in hedge gap size was also found to be a relevant structural measure, primarily to the abundance of detritivores with which it was negatively correlated, but it was aso negatively correlated with herbivore diversity at the level of order/family discerned.

In both these cases, however, there is the potential for resource provision to be a factor, and so one cannot be certain that the effects are based on purely physical structural differences. Variation in gap size could be related to the provision of resources for detritivores such as decaying bark, for example, and foliage biomass has an obvious effect on the abundance of resources for herbivores, although results suggested not on the quality. This demonstrates that resource availability and habitat or host plant structure cannot be simply seperated as implied in some previous studies (Langellotto & Denno 2004). A review of the literature regarding effects of habitat structure on invertebrate community composition and interactions also revealed confusion caused by the term ‘complexity’ in relation to habitat structure, due to a plethora of different and often conflicting interpretations of its meaning, highlighting the mportannce of discussing and quantifying the specific alterations to habitat structure under investigation, particularly as individual genera or i may be differentially affected (Klecka & Boukal 2014).

The hypothesis (iii) that aspects of hedge structure related to increased shelter and protection (i.e. hedge height and width, hedge:gap ratio) and associated changes to microclimate (temperature at ground level) would affect the abundance of overwintering invertebrates, was only partly supported. For invertebrates overwintering in the soil, the stuctural measures assessed (hedge height and width, and density as reflected by hedge:gap ratio) were not directly correlated with abundance or diversity of any trophic groups. However, temperature at ground level was influenced by the cover provided by the hedge, and this in turn influenced herbivore abundance (but not that of predators or detritivores); there was a positive relationship with maximum temperature or temperature range.

A replicated, large-scale field experiment such as that described in this thesis has obvious benefits in terms of realism and relevance to the habitat in question. However, in order to investigate some of the theories surrounding mechanisms by which habitat structure affects predator-prey interactions discussed in chapter 1 (i.e. Agrawal 1997; Denno *et al.* 2002; Legrand & Barbosa 2003; Janssen *et al.* 2007; Schmidt & Rypstra 2010; Snyder & Ives 2010) more closely controlled experiments are necessary. Future work could focus on some of the key taxa found here, and use field or laboratory mesocosm experiments mimicing the differences in habitat structure measured in this study with a limited number and quantity of selected species introduced. For example, small hawthorn plants within enclosures could be manipulated in different ways by cutting some to encourage increased foliage density and lower variation in gap size, and differential effects on the prey-capture rate of species of Araneae with differing hunting strategies, could be observed.

The management techniques used were chosen because they represented more economic alternatives to traditional Midland-style hedgelaying (Staley *et al.* 2015), as cost and related changes in farming practices are a key factor in the decline of this practice and resulting increase in neglect of hedgerows (Croxton *et al.* 2004). The hypotheses that hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, would support a similar abundance and trophic diversity of invertebrates as those rejuvenated with traditional hedgelaying, both in the canopy during spring, summer and autumn (iv), and overwintering in the soil (v), was supported. Methods where the hedge is laid over and hence rejuvenated at the base as well as higher up, such as conservation hedgelaying and wildlife hedging, supported comparable abundances of invertebrates across trophic groups to the traditional technique tested, both for insects utilising the hedge during spring-autumn, and those overwintering in the soil beneath the hedge.

When canopy invertebrate data were scaled by hedge height, the wildlife hedging outperformed other laid treatments in terms of invertebrate abundance. This was similar to the uncut control, but unfortunately the technique may also share some of the practical constraints of leaving a hedge unmanaged; management is necessary to retain the hedgerow habitat which supports species across a range of taxa that a line of trees may not (i.e. Hinsley & Bellamy 2000; Deckers *et al.* 2004; Griffiths *et al.* 2007; Kotzageorgis & Mason 1997) and the large volume of hedge left by wildlife hedging may be impractical for farmers or contractors (Portas, 2009).

Reshaping the hedge by circular saw represented a somewhat different approach, with cutting (and hence any resulting vigorous growth) occurring only at the top and sides of the canopy, but was also by far the cheapest (approximately 15% of the cost of Midland-style hedgelaying; Staley *et al.* 2015). Measured per unit area, hedges managed by circular saw supported significantly fewer invertebrates in the leafy canopy than the laid treatments, although when scaled by hedge height, this effect was negated. Surprisingly, for overwintering invertebrates this treatment was found to support over twice the abundance of herbivores than the conservation hedglaying, and the reason for this is unclear. It is important to note that this data was collected in the year following management, and that structural differences between management treatments may actually decrease over time (Staley *et al.* 2015).

Whilst diversity at the relatively coarse scale of order/family did not differ between different management types, species level differences may well be present and future work assessing at the level of species for certain groups would be very interesting (Griffiths *et al.* 2007), particulary as some taxanomic groups were necessarily excluded from the taxonomic grouping due to the range of feeding behaviours they display. For example, the Acari were among the most abundant taxa and whilst many species (i.e. the within the order Orabatida) are detritivores, other species (i.e. Phytoseiidae spp.) are known to be effective biological control agents against other pest Acari species (i.e. spider mites; Tetrenychidae; (Barber *et al.* 2003; Fitzgerald, Pepper & Solomon 2007).

In conclusion, this study provides evidence that more economic rejuvenation techniques can support a comparable or even higher abundance of invertebrates throughout the year to traditional Midland-style hedgelaying, treatments have a range of specific benefits and caveats for each treatment (Table 9). The conservation and habitat value for invertebrates provided by different management treatments are highly relevant to the rejuvenation of under-managed hedgerows under AES, for which there are limited funds. This study is one of few to specifically address effects of hedgerow rejuvenation on invertebrates (Henry, Bell & McAdam 1994; McAdam, Bell & Gilmore 1996; Dover *et al.*1997), and several of the novel techniques addressed here, as far as I am aware, have not been formally studied (i.e. wildlife hedging, conservation hedging and reshaping by circular saw).

Differences in habitat structure accounted for some of the variation recorded in invertebrate community structure across treatments, and specifically foliage biomass (for predators and herbivores) and variation in gap area (for detritivores) were important. Given the differences in structural features identified between certain management techniques (i.e. laid treatments and reshaping with a circular saw), one option for land managers wishing to lessen the impact of hedgerow management on wildlife is to maintain hedgerows on a rotational basis, perhaps even employing more than one rejuvenation method across the farm, ensuring a range of hedgerow structures are present at any time. Heterogeneity in habitat is likely to increase plant species diversity (Deckers *et al.* 2004), and benefit a range of animal taxa such as small mammals (Kotzageorgis & Mason 1997) and birds (MacArthur & MacArthur 1961; Hinsley & Bellamy 2000) as well as invertebrates (Griffiths *et al.* 2007), some of which may play a role in biological control of crop pests (Tscharntke *et al.* 2007).

Table 9: Summary of benefits and caveats of hedgerow rejuvenation techniques.

Rejuvenation management	Benefits	Caveats
Uncut control	Larger volume = higher overall invertebrate abundance in canopy.	Will revert to line of trees; not stock-proof. Lower canopy invertebrate abundance per unit/area than laid treatments.
Coppice	Method can be used for very neglected hedges with stems too thick to be layed; should eventually result in thicker hedge.	Initially results in no woody habitat or shelter; not stock-proof.
Circular saw	Fewer invertebrates/unit area in canopy than laid treatments, but highest abundances overwintering in the soil.	The internal hedge structure is not altered; large gaps remain so not stock-proof. Lower canopy invertebrate abundance per unit/area than laid treatments.
Conservation hedgelaying	Results in neat, compact, stock-proof hedge.	Supported lower overwintering herbivore abundance in the soil than circular saw reshaping.
Midland-style hedgelaying	Traditional management, resulting in neat, compact, stock-proof hedge.	Expensive to implement
Wildlife hedging	Results in stock-proof hedge. Larger volume = higher overall invertebrate abundance in canopy. Highest ratio of predators:herbivores overwintering in the soil.	Hedge remains very wide, untidy, and future management likely to be difficult.

Appendices

Appendix1: Location of experimental sites

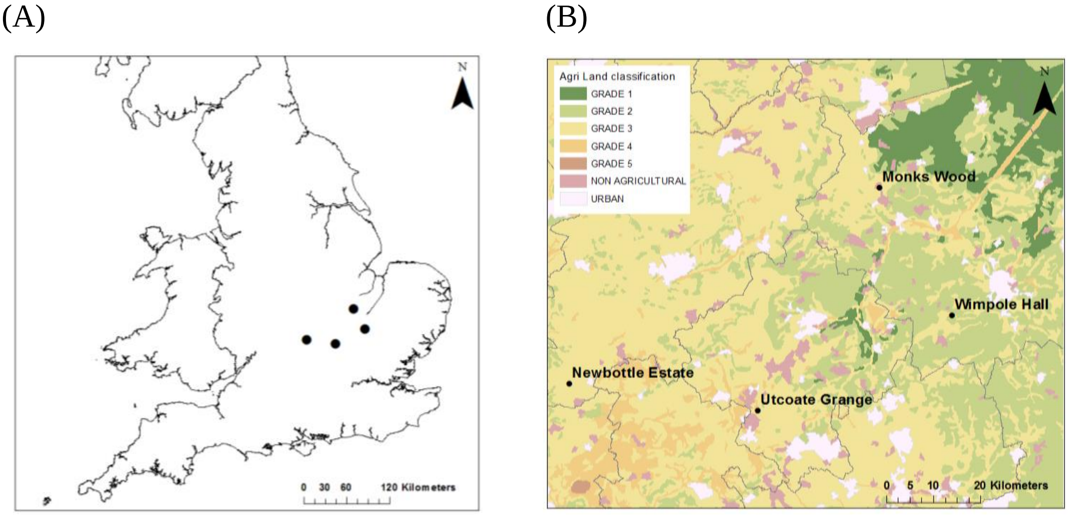

Figure A1: Location of experimental sites a) within the UK and b) in terms of the underlying agricultural land classification, which refers to the quality of the land for agriculture, based on a range of attributes such as climate, soil properties, topography and flood risk. Grade 1 = excellent quality; Grade 2 = very good; Grade 3 = good to moderate; Grade 4 = poor; Grade 5 = very poor (MAFF 1988).
© Natural England copyright. Contains Ordnance Survey data © Crown copyright and database right [2014].

Appendix 2: Woody vegetation composition prior to management

The height and width of hedges, as well as the presence and surface percentage cover of woody plant species (including climbers such as *Rosa canina* and *Rubus fruticosus*) for one standardised aspect of each plot, was recorded prior to management. Although experimental hedgerows differed significantly in height between sites prior to management ($F_{3,46} = 8.38$, $P<0.01$), with the mean height of MW approximately 20% higher than NE and UG (TukeyHSD tests, $P = <0.01$), there was no significant difference between the height of plots randomly selected for different treatments. Similarly, there was no significant difference in species-richness of woody plants in the hedgerow between treatments prior to implementation of management. There were inter-site differences ($F_{3,34} = 24.39$, $P<0.001$) in woody species-richness, with NE and MW significantly less species-rich than UG and WH (TukeyHSD tests, all $P < 0.05$) .

Appendix 3: Allocation of invertebrate taxa sampled to trophic levels

Table A3: Allocation of invertebrate taxa sampled to trophic levels.

Trophic level	Definition	Invertebrate taxa
Detritivore	Feeds on decaying plant material, or associated fungal material/lichens	Coleoptera (Cryptophagidae, Endomychidae, Lathridiidae, Leiodidae, Ptiliidae, Scirtidae, Silphidae), Collembola, Diplopoda, Isopoda, Polyxenida, Psocoptera
Herbivore	Feeds on living plant material	Coleoptera (Bruchidae, Cerambycidae, Chrysomelidae, Coccinellidae[1], Curculionoidea, Elateridae, Lagridiidae, Malachiidae, Mordellidae, Nitidulidae, Oedemeridae, Phalacridae, Salpingidae, Scraptiidae), Aphididae, Auchennorrhyncha, Lepidoptera, Orthoptera, Psylloidea, Symphyta, Thysanoptera
Predator	Feeds on other invertebrates for at least part of the life cycle (includes parasitoids)	Araneae, Coleoptera (Cantharidae, Carabidae, Coccinellidae[1], Pselaphidae, Staphylinidae), Dermaptera, Mecoptera, Neuroptera, Hymenoptera (Formicidae, Parasitica), Diptera (Syrphidae)
Mixed	Feeding preferences variable within taxa and hence excluded from analyses based on trophic group	Acari, Anthicidae, Diptera, Heteroptera, Hydrophilidae, Tenebrionidae, Trichoptera

[1] Coccinellidae were identified to species and then assigned to ‘trophic level’ according to their feeding preference.

Appendix 4: Seasonal changes in canopy invertebrate community composition

Seasonal differences found in the abundance of trophic groups were in line with existing knowledge of invertebrate phenology. Herbivores were most abundant in the spring (largely due to the Psilloidea), coinciding with a significantly lower carbon:nitrogen ratio than either summer or autumn ($F_{(138)} = 31.99$; post hoc Tukey’s HSD $P<0.001$). Whilst in spring the number of herbivores was generally higher than predators, the reverse was true in autumn. Psylloidea are known to peak in fecundity when leaves are more tender and nutrient-rich (Southwood *et al.* 2004), and spring foliage is generally more palatable to herbivores (Awmack & Leather 2002). The overall detritivore abundance peaked in the summer, though this was disproportionately due to the Collembola population at one site (Utcoate Grange), with higher abundances seen more widely in autumn (Figure A4).

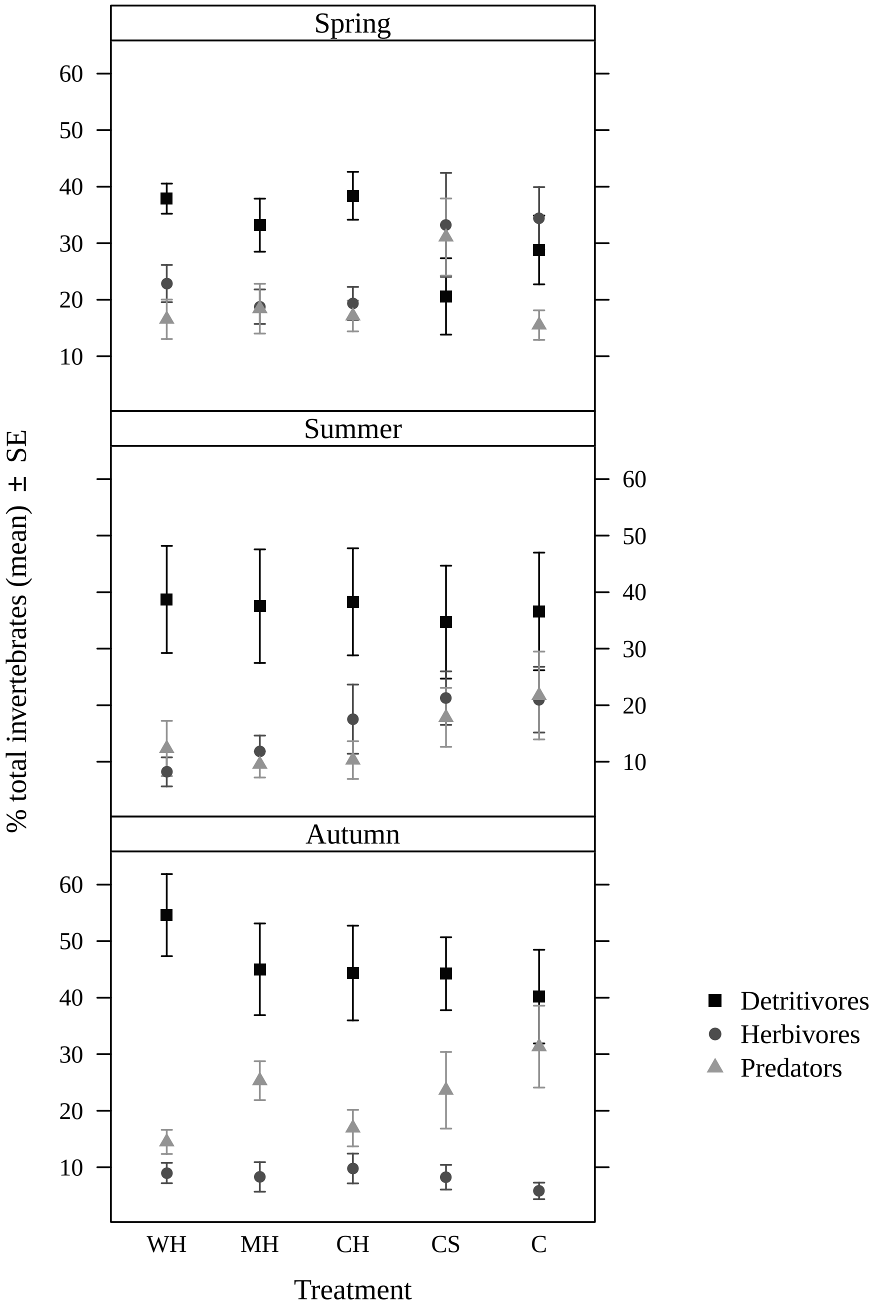

Figure A4: Means ± standard errors for relative abundance of invertebrates in each of three trophic groups (% of total) sampled by beating the hedge canopy, by treatment and season. Spring = May, Summer = July, Autumn = September.

]

However, there were no significant interactions between treatment and season on the abundance or diversity of any of the three trophic groups, so these response variables were summed across the three seasons for further analysis.

Appendix 5: Predation bait bioassay using live Lepidoptera larvae in semi-enclosed cages

Introduction and Methods

A bait bioassay trial was carried out in May 2013, using free-roaming *Opisthograptis luteolata* (Brimstone moth; Lepidoptera) larvae. This is a common and widespread herbivore species in the UK, flying from April to October in the South of the UK, the larvae of which feed on a range of trees including *Crataegus monogyna*. Semi-enclosed cages (40cm long x 30cm diameter) were constructed from a metal frame with organza material, designed to keep live larvae bait in (i.e. not to fall on the ground), and to deter predation by birds but to let arthropod predators in. A 10cm hole was present at either end of the cage, which was positioned around a branch, so that predators could enter by flying or by walking along the branch (Figure A5.1). In order to avoid escape by the bait species, *Opisthograptis luteolata* (Brimstone moth; Lepidoptera) was chosen as it is thought to be relatively sedentary (M. Botham, personal communication), using a masquerade strategy whereby they resemble a twig in order to avoid predation (Skelhorn *et al.* 2010).

Figure A5.1. Semi-enclosed bait bioassay cages.

This bioassay was carried out on spatially separated (>10m) sections of wildlife hedging and Control (i.e. uncut) hedge (n = 5) of a single site (NE). For each treatment, 5 cages were each be placed around a branch of *C.monogyna* from which existing invertebrates were removed, and twenty larvae of *O. luteolata* were placed out within each cage. Replicates were at least 10m apart. The number of larvae placed in each cage reflected the fact that although *O. luteolata* are not particularly gregarious they are unlikely to travel too far once hatched provided food is present. It also reflects the need to ensure that food was not a limiting factor within the enclosure for the duration of the experiment, whilst also ensuring that a good estimate of mortality can be achieved. A control cage completely enclosed to exclude all predators was also placed out to enable assesment of the potential for cannibalism within the prey species. After 24 hours, cages were checked for remaining larvae. As many larvae were easily visible, it appeared unlikely that significant losses to predation had occured, and the experiment was run for a further 24 hours. After a total of 48 hours, each caged branch was removed from the hedge. The branch was searched thoroughly for remaining larvae, which were counted. The biomass of foliage and branches was measured in each case, and any predators found within the cage collected and preserved in alcohol.

Predation rates were expected to reflect different levels of predators present in the vicinity and/or scarcity of alternative prey. To test this, the hedges were sampled for invertebrates by beating, once the cages were collected in. In the vicinity of each cage, the hedge was beaten at 3 positions, and invertebrates collected in a section of guttering inserted into the hedge were swept into a plastic bag. Samples were pooted and stored in 70% IMS prior to identifying to order/family, and assigned to a trophic group as above. To test whether the density of foliage differed between the two treatments, destructive foliage samples were taken concurrent with the bioassay experiment, from which biomass was measured as described previously in Chapter 2 (2.2.2; p.22).

For results from the field experiment bioassay to measure rates of predation, the relationship between management treatment and number of larvae remaining, as well as abundance and diversity of predators sampled from beating were tested using ANOVA. All analyses were carried out in R version 3.0.1 (R Core Team, 2013).

Results

As found previously, foliage samples collected from a standardised area within plots concurrent with the bait bioassay experiment showed significantly higher biomass in the wildlife hedging than the control ($F_{(1,8)} = 31.68$, $P < 0.001$), with means and standard errors of 391.7 (±37.5) and 129.3 (±25) respectively. When the biomass of leaves contained within the actual cage was measured, no significant differences were found between the two treatments, reflecting the fact that cages were placed on a single branch, and that it may be the density of branches, rather than the density of leaves on each branch, which casues the wildlife hedging to have a higher biomass.

No significant difference was found in the number of prey remaining (mean ± SE; i.e. rate of predation) of *O. luteolata* larvae between the wildlife hedging and control after 48 hours. Invertebrate samples collected by beating the hedge canopy at the time the bioassay experiment ended showed a significantly higher abundance of detritivores in the wildlife hedging ($X^2_1 = 31.69$, $P < 0.001$), but not so with herbivores or predators (Figure A2). There was also no significant difference in the overal ratio of predators:non-predators between the two treatments. Additional invertebrates captured within the cage at the end of the experiment also showed this trend with detritivores ($X^2_1 = 8.56$, $P < 0.01$) and predators, though in this case there were also significantly more herbivores found in the wildlife hedging than the control ($X^2_1 = 8.99$, $P = 0.01$). Again, there was also no significant difference in the overal ratio of predators:non-predators between the two treatments. No significant difference was found between the control and wildlife hedging in the number of larvae remaining within the cages after 48 hours (Figure A5.2).

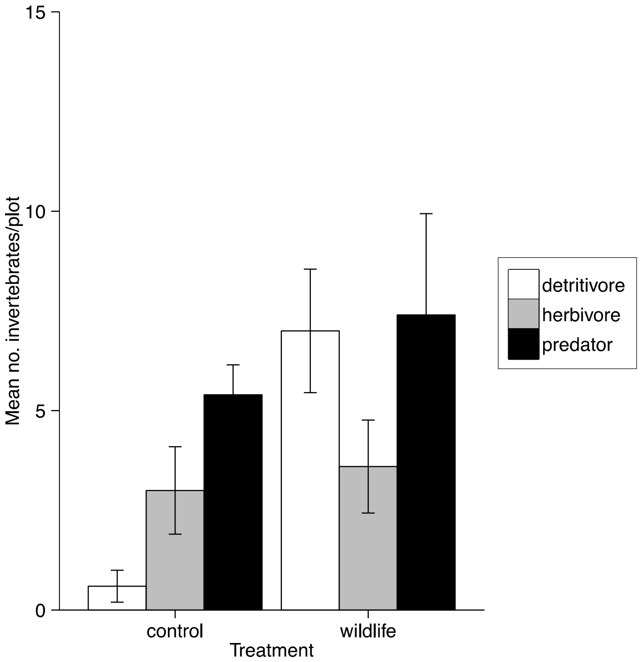

Figure A5.2: Mean (± SE) number of invertebrates in each of three trophic levels (detritivore, herbivore, and predator), for each of the control and wildlife hedging treatments.

Discussion

Anecdotally, a large proportion of the larvae collected after 48 hours were found towards the centre of the cage near the leaf on which they were imported, in line with the understanding of their masquerading strategy, and suggesting they weren't travelling far and hence loss is likely due to predation. However, results showed no significant differences between treatments in the number of prey remaining (i.e. losses to predation).

Despite seeing the expected differences in habitat structure (significantly higher biomass in the wildlife hedging), the results do not support the hypothesis that there would be a higher abundance of predators relative to non-predators in hedgerows managed by wildlife hedging compared with an uncut control. However, as the number of individuals collected in the beating samples was generally quite low, it is possible that subtle differences in the abundance of predators between treatments were not picked up. In line with previous results, the wildlife hedging was found to have a significantly higher abundance of detritivores, probably due to the increased density of woody material and possibly an increased amount of dead wood remaining in the hedge following management (Dodds 2005). Invertebrates collected within the cages at the end of the experiment also had a higher abundance of herbivores within the wildlife hedging which, along with the increased detritivore abundance, may constitute an increase in prey choice and/or abundance for predators thus reducing pressure on the bait prey. However, the fact that the ratio of predators:non-predators was not significantly different between the two treatments lessens the strength of this argument.

List of references

Agrawal, A. (1997) Do leaf domatia mediate a plant-mite mutualism? An experimental test of the effects on predators and herbivores. *Ecological Entomology*, **22**, 371–376.

Altermatt, F. & Holyoak, M. (2012) Spatial clustering of habitat structure effects patterns of community composition and diversity. *Ecology*, **93**, 1125–33.

Alvarez, T., Frampton, G.K. & Goulson, D. (2000) The role of hedgerows in the recolonisation of arable fields by epigeal Collembola. *Pedobiologia*, **44**, 516–526.

Amy, S.R., Heard, M.S., Hartley, S.E., George, C.T., Pywell, R.F. & Staley, J.T. (2015) Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure. *Basic and Applied Ecology*, **16**, 443–451.

Andow, D.A. & Risch, S.J. (1985) Predation in diversified agroecosystems : relations between a Coccinellid predator Coleomegilla maculata and Its food. *The Journal of Applied Ecology*, **22**, 357.

Araujo, A.P.A., De Paula, J.D., Carneiro, M.A.A. & Schoereder, J.H. (2006) Effects of host plant architecture on colonization by galling insects. *Austral Ecology*, **31**, 343–348.

Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, **47**, 817–44.

Barber, a., Campbell, C. a. M., Crane, H., Lilley, R. & Tregidga, E. (2003) Biocontrol of Two-spotted Spider Mite Tetranychus urticae on Dwarf Hops by the Phytoseiid Mites Phytoseiulus persimilis and Neoseiulus californicus. *Biocontrol Science and Technology*, **13**, 275–284.

Barr, C.J., Britt, C.P., Sparks, T.H. & Churchward, J.M. (2005) *Hedgerow Management and Wildlife: A Review of Research on the Effects of Hedgerow Managament and Adjacent Land on Biodiversity*. Defra publications, London.

Barr, C.J. & Parr, T.W. (1994) Hedgerows: linking ecological research and countryside policy. *Hedgerow Management and Nature Conservation. University of London.* (eds T.A. Watt), & G.P. Buckley), pp. 119– 136. Wye College Press, Wye College.

Baudry, J., Bunce, R.G.H. & Burel, F. (2000) Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management*, **60**, 7–22.

Beck, M. (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods.

Journal of experimental marine biology and ecology, **249**, 29–49.

Boughey, K.L., Lake, I.R., Haysom, K.A. & Dolman, P.M. (2011) Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation*, **144**, 1790–1798.

Bowden, J. & Dean, G.T.W. (1977) The distribution of flying insects in and near a tall hedgerow. *Journal of Applied Ecology*, **14**, 343–354.

Bright, P. & MacPherson, D. (2002) *Hedgerow Management , Dormice and Biodiversity for Nature Tomorrow*. English Nature, Peterborough.

Brooks, A. & Agate, E. (1998) *Hedgeing: A Practical Handbook, 2nd Edition*. BTCV.

Bultman, T.L. & Uetz, G.W. (1984) Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. *American Midland Naturalist*, **111**, 165–172.

Bunce, R.G.H., Barr, C.J., Gillespie, M.K. & Howard, D.C. (1996) The ITA Land Classification: providing an environmental stratification of Great Britain. *Environmental Monitoring and Assesment*, **39**, 39–46.

Calcagno, V. & de Mazancourt, C. (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1–29.

Chen, Y., Olson, D.M. & Ruberson, J.R. (2010) Effects of nitrogen fertilization on tritrophic interactions. *Arthropod-Plant Interactions*, **4**, 81–94.

Coll, M. & Bottrell, D.G. (1995) Predator-prey association in mono- and dicultures: Efect of maize and bean vegetation. *Agriculture Ecosystems and Environment*, **54**, 115–125.

Collins, K.L., Boatman, N.D., Wilcox, A. & Holland, J.M. (2003) A 5-year comparison of overwintering polyphagous predator densities within a beetle bank and two conventional hedgebanks. *Annals of Applied Biology*, **143**, 63–71.

Cranmer, L., McCollin, D. & Ollerton, J. (2012) Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos*, **121**, 562–568.

Critchley, C.N.R., Wilson, L.A., Mole, A.C., Norton, L.R. & Smart, S.M. (2013) A functional classification of herbaceous hedgerow vegetation for setting restoration objectives. *Biodiversity and Conservation*, **22**, 701–717.

Croxton, P.J. (2002) A farm-scale evaluation of the influence of hedgerow cutting frequency on hawthorn (Crataegus monogyna) berry yields. *Agriculture*, *Ecosystems & Environment*, **93**, 437–439.

Croxton, P.J., Franssen, W., Myhill, D.G. & Sparks, T.H. (2004) The restoration of neglected hedges: a comparison of management treatments. *Biological Conservation*, **117**, 19–23.

Debras, J., Senoussi, R., Rieux, R., Buisson, E. & Dutoit, T. (2008) Spatial distribution of an arthropod community in a pear orchard (southern France). Identification of a hedge effect. *Agriculture, Ecosystems & Environment*, **127**, 166–176.

Deckers, B., Hermy, M. & Muys, B. (2004) Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica*, **26**, 23–37.

Deckers, B., Verheyen, K., Hermy, M. & Muys, B. (2004) Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology*, **5**, 551–566.

Defra. (2007) *Hedgerow Survey Handbook: A Standard Procedure for Local Surveys in the UK*. Defra, London.

Defra. (2015) *The Guide to Cross Compliance in England*. Defra, London.

Dennis, P., Thomas, M.B. & Sotherton, N.W. (1994) Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *Journal of Applied Ecology*, **31**, 361–370.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, **83**, 1443–1458.

Dodds, M.J.W. (2005) Mechanical hedge-laying for wildlife. *Conservation Evidence*, **2**, 55–56.

Doncaster, C.P., Rondinini, C. & Johnson, P.C.D. (2001) Field test for environmental correlates of dispersal in hedgehogs Erinaceus europaeus. *Journal of Animal Ecology*, **70**, 33–46.

Dover, J. & Sparks, T. (2000) A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, **60**, 51–63.

Dover, J.W., Sparks, T.H. & Greatorex-Davies, J. (1997) The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation*, **1**, 89–97.

Eilenberg, J., Hajek, A. & Lomer, C. (2001) Suggestions for unifying the terminology in biological control. *BioControl*, **46**, 387–400.

van Emden, H. (2003) Conservation biological control: From theory to practice. *Proceedings of the International Symposium Biological Control of Arthropods,* *Honolulu, Hawaii, 14-18 January 2002* (ed R. VanDriesche), pp. 199–208. USDA Forest Service, Morgantown, WV.

Entwistle, A.C., Racey, P.A. & Speakman, J.R. (1996) Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philosophical Trasactions of the Royal Society of London B*, **351**, 921–931.

Facey, S.L., Botham, M.S., Heard, M.S., Pywell, R.F. & Staley, J.T. (2014) Moth communities and agri-environment schemes: Examining the effects of hedgerow cutting regime on diversity, abundance, and parasitism. *Insect Conservation and Diversity*, **7**, 543–552.

Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: Implications for prey supression. *Ecology*, **83**, 643–652.

Finke, D.L. & Denno, R. (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia*, **149**, 265–75.

Fitzgerald, J.D., Pepper, N. & Solomon, M.G. (2007) Interactions among predators and phytophagous mites on apple; possible impact on biocontrol of Panonychus ulmi by Typhlodromus pyri in orchards. *Biocontrol Science and Technology*, **17**, 1009–1019.

French, D.D. & Cummins, R.P. (2001) Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science*, **4**, 213–228.

Gagnon, A.-È. & Brodeur, J. (2014) Impact of plant architecture and extraguild prey density on intraguild predation in an agroecosystem. *Entomologia Experimentalis et Applicata*, **152**, 165–173.

Geiger, F., Wäckers, F.L. & Bianchi, F.J.J.A. (2009) Hibernation of predatory arthropods in semi-natural habitats. *BioControl*, **54**, 529–535.

Gingras, D. & Boivin, G. (2002) Effect of plant structure, host density and foraging duration on host finding by Trichogramma evanescens (Hymenoptera:Trichogrammatidae). *Environmental Entomology*, **31**, 1153–1157.

Griffiths, G.J.K., Holland, J.M., Bailey, A. & Thomas, M.B. (2008) Efficacy and economics of shelter habitats for conservation biological control. *Biological Control*, **45**, 200–209.

Griffiths, G.J.K., Winder, L., Holland, J.M., Thomas, C.F.G. & Williams, E. (2007) The representation and functional composition of carabid and staphylinid beetles in different field boundary types at a farm-scale. *Biological Conservation*, **135**, 145–152.

Gunnarsson, B. (1990) Vegetation structure and the abundance and size distribution of spruce-living spiders. *The Journal of Animal Ecology*, **59**, 743–752.

Halaj, J., Ross, D.W. & Moldenke, A.R. (1998) Habitat structure and prey availability as predictors of the abundance and community organization of spiders in Western Oregon forest canopies. *Journal of Arachnology*, **26**, 203–220.

Halaj, J., Ross, D.W. & Moldenke, A.R. (2000) Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, **90**, 139–152.

Havill, N.P. & Raffa, K.F. (2000) Compound effects of induced plant responses on insect herbivores and parasitoids: implications for tritrophic interactions. *Ecological Entomology*, **25**, 171–179.

Hedgelink. (2011) Environmental Stewardship and hedgerows Briefing for Change – Key facts, figures and pointers, http://www.hedgelink.org.uk/cms/cms_content/files/97_hedgelink_-_environmental_stewardship_and_hedgerows,_briefing,_final,_27_jan_2011,_rob_wolton.doc.

Hedgelink. (2014) Hedgerow Management, http://www.hedgelink.org.uk/hedgerow-management.htm

Henry, T., Bell, A.C. & McAdam, J.H. (1994) The effect of restoration strategies on the flora and fauna of overgrown hedges and methods of repairing gaps in over-managed hawthorn hedges. *Field Margins: Integrating Agriculture and Conservation. BCPC Monograph No. 58.* (ed N. Boatman), British Crop Protection Council, Farnham.

Hinsley, S.A. & Bellamy, P.E. (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *Journal of Environmental Management*, **60**, 33–49.

Hof, A.R. & Bright, P.W. (2010) The value of agri-environment schemes for macro-invertebrate feeders: Hedgehogs on arable farms in Britain. *Animal Conservation*, **13**, 467–473.

Hooper, M.D. (1987) Conservation interest in plants of field margins. *Field Margins. BCPC Monograph No. 35* (eds J.M. Way), & P.W. Greig-Smith), pp. 49–52. British Crop Protection Council, Thornton Heath.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Jacobs, J.H., Clark, S.J., Denholm, I., Goulson, D., Stoate, C. & Osborne, J.L. (2009a) Pollinator effectiveness and fruit set in common ivy, Hedera helix (Araliaceae). *Arthropod-Plant Interactions*, **4**, 19–28.

Jacobs, J.H., Clark, S.J., Denholm, I., Goulson, D., Stoate, C. & Osborne, J.L.

(2009b) Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set. *Annals of botany*, **104**, 1397–404.

Janssen, A., Sabelis, M.W., Magalhães, S., Montserrat, M. & van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology*, **88**, 2713–2719.

JNCC & Defra (on behalf of the Four Countries' Biodiversity Group). (2012) *UK Post-2010 Biodiversity Framework*. JNCC, Peterborough.

Joyce, K. (1998) *The Role of Hedgerows in the Ecology of Invertebrates in Arable Landscapes*. University of Southampton.

Klecka, J. & Boukal, D.S. (2014) The effect of habitat structure on prey mortality depends on predator and prey microhabitat use. *Oecologia*, **176**, 183–191.

Kotzageorgis, G.C. & Mason, C.F. (1997) Small mammal populations in relation to hedgerow structure in an arable landscape. *Journal of Zoology*, **242**, 425–434.

Krebs, C. (1999) Ecological Methodology.

Landis, D.A., Menalled, F.D., Costamagna, A.C. & Wilkinson, T.K. (2005) Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, **53**, 902–908.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests. *Annual Review of Entomology*, **45**, 175–201.

Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

Langellotto, G.A. & Denno, R.F. (2006) Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecological Entomology*, **31**, 575–581.

Lara, D.P., Oliveira, L.A., Azevedo, I.F.P., Xavier, M.F., Silveira, F.A.O., Carneiro, M.A.A. & Fernandes, G.W. (2008) Relationships between host plant architecture and gall abundance and survival. *Revista Brasileira de Entomologia*, **52**, 78–81.

Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions Distributions*, **11**, 73–82.

Lawrence, J.F. & Newton, A.F. (1980) Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). *The Coleopterists Bulletin*, **34**, 129–143.

Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.

Leather, S.R., Walters, K.F.A. & Bale, J.S. (1993) *The Ecology of Insect Overwintering*. Cambridge University Press.

Legrand, A. & Barbosa, P. (2003) Plant morphological complexity impacts foraging efficiency of adult Coccinella septempunctata L . (Coleoptera : Coccinellidae). *Environmental Entomology*, **32**, 1219–1226.

Lewis, T. (1969) The distribution of flying insects near a low hedgerow. *Journal of Applied Ecology*, **6**, 443–452.

MacArthur, R.H. & MacArthur, J.W. (1961) On Bird Species Diversity. *Ecology*, **42**, 594–598.

Macdonald, D.W., Tew, T.E. & Todd, I.A. (2004) The ecology of weasels (Mustela nivalis) on mixed farmland in southern England. *Biologia*, **59**, 235–241.

MAFF. (1988) *Agricultural Land Classification of England and Wales: Revised Guidelines and Criteria for Grading the Quality of Agricultural Land*.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing Ltd.

Mattson, W.J. (1980) Herbivory in relation to plant Nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.

Maudsley, M.J. (2000) A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management*, **60**, 65–76.

Maudsley, M.J., Marshall, E.J.P. & West, T.M. (2002) *Guidelines for Hedge Management to Improve the Conservation Value of Different Types of Hedge. Based on Results of DEFRA Project BD2102*. IACR - Long Ashton Research Station.

Maudsley, M., Seeley, B., Lewis, O. & Seely, B. (2002) Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables. *Agriculture, Ecosystems & Environment*, **89**, 77–89.

Mauremooto, J.R., Wratten, S.D., Worner, S.P. & Fry, G.L.A. (1995) Permeability of hedgerows to predatory carabid beetles. *Agriculture, Ecosystems and Environment*, **52**, 141–148.

McAdam, J.H., Bell, A.C. & Gilmore, C. (1996) The effects of different hedge restoration strategies on biodiversity. *Aspects of Applied Biology*, **44**, 363–367.

McAdam, A., Bell, J. & Henry, T. (1994) The effect of restoration techniques on flora and microfauna of hawthorn-dominated hedges. *Hedgerow Management and Nature Conservation* (eds T. Watt), & G. Buckley), pp. 25–32. Wye College Press, Ashford, Kent.

McCoy, E. & Bell, S. (1991) Habitat structure: The evolution and classification of a complex topic. *Habitat structure: the physical arrangement of objects in space* (eds S. Bell),, E. McCoy), & H. Mushinsky), pp. 3–27. Chapman and Hall.

Mcnett, B.J. & Rypstra, A.L. (2000) Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecological Entomology*, **25**, 423–432.

Mediene, S., Jordan, M.O., Pagès, L., Lebot, J. & Adamowicz, S. (2002) The influence of severe shoot pruning on growth, carbon and nitrogen status in young peach trees (Prunus persica). *Tree physiology*, **22**, 1289–96.

Merckx, T. & Berwaerts, K. (2010) What type of hedgerows do Brown hairstreak (Thecla betulae L.) butterflies prefer? Implications for European agricultural landscape conservation. *Insect Conservation and Diversity*, **3**, 194–204.

Merckx, T., Feber, R.E., Riordan, P., Townsend, M.C., Bourn, N.A.D., Parsons, M.S. & Macdonald, D.W. (2009) Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems & Environment*, **130**, 177–182.

Morandin, L. a., Long, R.F. & Kremen, C. (2014) Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, **189**, 164–170.

Moreira, X., Abdala-roberts, L., Rasmann, S., Castagneyrol, B. & Mooney, K.A. (2016) Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. *Current Opinion in Insect Science*, **14**, 1–7.

Natural England. (2013) *Entry Level Stewardship Environmental Stewardship Handbook, Fourth Edition - January 2013*. Natural England.

Natural England. (2015) *Countryside Stewardship Manual. Applies to All 1st January 2016 Multi-Year Agreements*. Natural England.

New, T. (1970) The relative abundance of some British Psocoptera on different species of trees. *The Journal of Animal Ecology*, **39**, 521–540.

Noemí Mazía, C., Chaneton, E.J. & Kitzberger, T. (2006) Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. *Journal of Arid Environments*, **67**, 177–194.

Noppe, C., Michaud, J.P. & De Clercq, P. (2012) Intraguild predation between lady beetles and lacewings: Outcomes and consequences vary with focal prey and arena of interaction. *Annals of the Entomological Society of America*, **105**, 562–571.

Norton, L.R., Maskell, L.C., Smart, S.S., Dunbar, M.J., Emmett, B. a, Carey, P.D., Williams, P., Crowe, A., Chandler, K., Scott, W. a & Wood, C.M. (2012) Measuring stock and change in the GB countryside for policy-key findings and developments from the Countryside Survey 2007 field survey. *Journal of* *environmental management*, **113**, 117–27.

Obermaier, E., Heisswolf, A., Poethke, H.J., Randlkofer, B. & Meiners, T. (2008) Plant architecture and vegetation structure : Two ways for insect herbivores to escape parasitism. *European Journal of Entomology*, **105**, 233–240.

Parker, D.., Legg, T.. & Folland, C.. (1992) A new daily central England temperature series 1772-1991. *International Journal of Climatology*, **12**, 317–342.

Pearce, S. & Zalucki, M.P. (2006) Do predators aggregate in response to pest density in agroecosystems? Assessing within-field spatial patterns. *Journal of Applied Ecology*, **43**, 128–140.

Pekár, S. (1999) Some observations on overwintering of spiders (Araneae) in two contrasting orchards in the Czech Republic. *Agriculture, Ecosystems & Environment*, **73**, 205–210.

Perdikis, D., Fantinou, A. & Lykouressis, D. (2011) Enhancing pest control in annual crops by conservation of predatory Heteroptera. *Biological Control*, **59**, 13–21.

Petit, S., Stuart, R.C., Gillespie, M.K. & Barr, C.J. (2003) Field boundaries in Great Britain: stock and change between 1984, 1990 and 1998. *Journal of Environmental Management*, **67**, 229–238.

Pfiffner, L. & Luka, H. (2000) Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment*, **78**, 215–222.

Pollard, K.A. & Holland, J.M. (2006) Arthropods within the woody element of hedgerows and their distribution pattern. *Agricultural and Forest Entomology*, **8**, 203–211.

Pollard, E., Hooper, M.D. & Moore, N.W. (1974) *Hedges*. Collins, London.

Pollard, E. & Relton, J. (1970) Hedges. V. A study of small mammals in hedges and cultivated fields. *Journal of Applied Ecology*, **7**, 549–557.

Pywell, R.F., James, K.L., Herbert, I., Meek, W.R., Carvell, C., Bell, D. & Sparks, T.H. (2005) Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biological Conservation*, **123**, 79–90.

Pywell, R.F., Meek, W.R., Hulmes, L., Hulmes, S., James, K.L., Nowakowski, M. & Carvell, C. (2011) Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. *Journal of Insect Conservation*, **15**, 853–864.

R Core Team. (2013) R: A language and environment for statistical computing.

Rackham, O. (2003) *An Illustrated History of the Countryside*. Weidenfeld &

Nicholson Ltd.

Riechert, S.E. & Bishop, L. (1990) Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology*, **71**, 1441–1450.

Riihimaki, J., Vehvilainen, H., Kaitaniemi, P., Koricheva, J., Riihimäki, J. & Vehviläinen, H. (2006) Host tree architecture mediates the effect of predators on herbivore survival. *Ecological Entomology*, **31**, 227–235.

Rogers, A., Blanchard, J.L. & Mumby, P.J. (2014) Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity. *Current biology : CB*.

Rypstra, A.L., Carter, P.E., Balfour, R.A. & Marshall, S.D. (1999) Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology*, **27**, 371–377.

Sanders, D., Nickel, H., Grützner, T. & Platner, C. (2008) Habitat structure mediates top–down effects of spiders and ants on herbivores. *Basic and Applied Ecology*, **9**, 152–160.

Schmidt, J.M. & Rypstra, A.L. (2010) Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia*, **164**, 899–910.

Senoussi, R., Dutoit, T. & Debras, J.F. (2011) Hedgerow effects on the distribution of beneficial arthropods in a pear orchard in Southern France. *Ecologia mediterranea*, **37**, 75–83.

Skelhorn, J., Rowland, H.M., Speed, M.P. & Ruxton, G.D. (2010) Masquerade: camouflage without crypsis. *Science*, **327**, 51.

Smith, M. & Roy, D.B. (2008) Revealing the foundations of biodiversity: The Database of Insects and their Foodplants. *British Wildlife*, **20**, 17–25.

Snyder, W.E. & Ives, A.R. (2001) Generalist predators disrupt biological control by a specialist parasitoid. *Ecological Society of America*, **82**, 705–716.

Sotherton, N.W. (1984) The distribution and abundance of predatory arthropods overwintering on farmland. *Annals of Applied Biology*, **105**, 423–429.

Southwood, T.R.E., Wint, G.R.W., Kennedy, C.E.J. & Greenwood, S.R. (2004) Seasonality , abundance , species richness and specificity of the phytophagous guild of insects on oak (Quercus) canopies. *European Journal of Entomology*, **101**, 43–50.

Stace, C. (2010) *New Flora of the British Isles*, Third. Cambridge University Press.

Staley, J.T., Amy, S.R., Adams, N.P., Chapman, R.E., Peyton, J.M. & Pywell, R.F. (2015) Re-structuring hedges: Rejuvenation management can improve the long term quality of hedgerow habitats for wildlife in the UK. *Biological*

Conservation, **186**, 187–196.

Staley, J.T., Amy, S., Facey, S.L. & Pywell, R.F. (2010) Hedgerow Conservation and Management : A review of 50 years of applied research in the UK. *Hedgerow Futures* (ed J.W. Dover), pp. 111–134.

Staley, J.T., Bullock, J.M., Baldock, K.C.R., Redhead, J.W., Hooftman, D. a. P., Button, N. & Pywell, R.F. (2013) Changes in hedgerow floral diversity over 70years in an English rural landscape, and the impacts of management. *Biological Conservation*, **167**, 97–105.

Staley, J.T., Sparks, T.H., Croxton, P.J., Baldock, K.C.R.R., Heard, M.S., Hulmes, S., Hulmes, L., Peyton, J., Amy, S.R. & Pywell, R.F. (2012) Long-term effects of hedgerow management policies on resource provision for wildlife. *Biological Conservation*, **145**, 24–29.

Thomas, M., Mitchell, H. & Wratten, S. (1992) Abiotic and biotic factors influencing the winter distribution of predatory insects. *Oecologia*, **89**, 78–84.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T. a., Tylianakis, J.M., Nouhuys, S. Van, Vidal, S., Bonmarco, R. & Tylaianakis, J. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.

UK Steering Group. (1995) *Biodiversity: The UK Steering Group Report, Volume 2: Action Plans. (Annex F, Annex G).* HMSO, London.

Varchola, J.M. & Dunn, J.P. (2001) Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. *Agriculture, Ecosystems & Environment*, **83**, 153–163.

Wäckers, F.L., Romeis, J. & van Rijn, P. (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annual review of entomology*, **52**, 301–23.

Way, M.J. & Cammell, M.E. (1982) The distribution and abndance of the spindle tree, Euonymus europaeus, in Southern England with particular reference to forecasting infestations of the black bean aphid, Aphis fabae. *Journal of Applied Ecology*, **19**, 929–940.

Wetzler, R.E. & Risch, S.J. (1984) Experimental studies of beetle diffusion in simple and complex crop habitats. *Journal of Animal Ecology*, **53**, 1–19.

Whitfeld, T., Novotny, V., Miller, S. & Hrcek, J. (2012) Predicting tropical insect herbivore abundance from host plant traits and phylogeny. *Ecology*, **93**, S211–S222.

Wolton, R. (2009) *UK Biodiversity Action Plan: Priority Species Linked to Hedgerows. A Report to Hedgelink.*

Wolton, R., Pollard, K., Goodwin, A. & Norton, L. (2014) *Regulatory Services Delivered by Hedges: The Evidence Base*. LM0106 Report for Defra and Natural England.

Woodcock, B.A. & Heard, M.S. (2011) Disentangling the effects of predator hunting mode and habitat domain on the top-down control of insect herbivores. *The Journal of animal ecology*, **80**, 495–503.

Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, a. J., Lambert, M., Harris, S.J. & Brown, V.K. (2007) The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecological Entomology*, **32**, 302–311.

Woodcock, B.A. & Pywell, R.F. (2009) Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity and Conservation*, **19**, 81–95.

Zheng, D., Hunt, E.R. & Running, S.W. (1993) A daily soil temperature model based on air temperature and precipitation for continental applications. *Climate Research*, **2**, 183–191.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.