The value of agri-environment schemes and farm woodland for bats and nocturnal insects

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Declaration

I hereby declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

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Summary

Many bat species in Europe have undergone severe population declines during the last century and one of the driving causes is believed to be the loss of roosting and foraging habitat through agricultural expansion and intensification. Modern agricultural practices have also had strong negative effects on many insect groups, such as moths, which are important components of the diets of many bat species. Agri-environment schemes (AES) have been introduced in many countries as an attempt to counteract the negative effects of intensive agriculture on biodiversity by providing financial incentives for farmers to adopt environmentally-sensitive agricultural practices. AES are potentially beneficial to bats and nocturnal insects, but the response of these taxa to their implementation had not been assessed prior to this study. Here, the potential benefits (or otherwise) that bats and their insect prey species gain from the implementation of certain AES management prescriptions was assessed using ultrasonic detectors (to assess bat activity levels) and heath light traps (to quantify nocturnal insect abundance) at 18 pairs of AES and conventionally-managed farms. In addition, the influence of the surrounding landscape on bats and insects was quantified to evaluate the relevance of a landscape-scale management approach for the conservation of these taxa. Some of the AES prescriptions assessed in this study benefited moths (and are potentially beneficial for moth-eating bats), but not Pipistrelle bats nor their insect prey. The most important factors associated with bat activity on farmland were metrics related to woodland configuration in the surrounding landscape, which suggests that conservation efforts for bats should focus on the creation and management of this habitat. Currently, some AES prescriptions aim to increase the amount and quality of woodland on agricultural land, but little is known about how woodland character relates to bat abundance and insect prey availability; therefore, recommendations for woodland creation and management rarely consider the requirements of foraging bats. Here, the influence of woodland character (e.g. vegetation structure and patch configuration) on bats and nocturnal insects was assessed. Vegetation surveys were conducted and Geographic Information Systems (GIS) were used to quantify the vegetation character and spatial configuration of 34 woodland patches within farmland. Two complementary methods (acoustic monitoring and bat trapping assisted by an acoustic lure) were used to assess the influence of woodland vegetation character, patch configuration and the surrounding landscape on bat populations. Nocturnal insect abundance at each site was assessed using heath light traps. Data presented here demonstrate that bats show species-specific associations with woodland vegetation structure and patch configuration; patterns of higher bat abundance and activity at small and isolated woodland patches suggest that bats utilize this habitat more intensively in landscapes where woodland is scarce. This thesis also shows that moths are strongly influenced by woodland character; in general, large woodland patches of compact shapes, composed of a large number of native tree species and a dense understory cover, and located close to other woodlands were associated with high moth abundance and species richness (and are potentially valuable for moth-eating bats). Other nocturnal insects (mainly Diptera) were not influenced by woodland character. This study also shows that bats and nocturnal insects are influenced by the landscape context; moths are mainly influenced by the extent of semi-natural environment (such as rough grassland and scrub) within small spatial scales (within 250 m; although effects of woodland extent were detected at larger spatial scales for woodland specialists moths). Bats are mainly influenced by woodland-related landscape metrics. Some bat species are influenced by the surrounding landscape at large spatial scales (within 3 km) and would benefit from woodland creation and management at a wide-landscape-scale. The findings presented in this thesis have important management implications for the design of agri-environment schemes. A list of management recommendations to optimize the benefits that bats and nocturnal insects gain from these schemes is presented in the final section.

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"Twinkle, twinkle little bat!
How I wonder what you're at!
Up above the world you fly,
like a tea tray in the sky.
Twinkle, twinkle little bat!
How I wonder what you're at…"

The Mad Hatter
(in "Alice in Wonderland" by Lewis Carroll)

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Chapter 1

General introduction

1.1. Biodiversity crisis: the role of agricultural intensification

Biodiversity is defined as any form of variation within living systems, at all levels of organization – from genes within a single local population or species, to the species composing a local community, and to the communities which form the living parts of the ecosystems of the world (Wilson 1997). The term 'biodiversity' is most commonly used to refer to the number of species present in an area. The number of species described to date approximates 1.5 million, but the total number is certainly much higher (estimates range from 10 – 100 million species; Lovejoy 1997). Maintaining biological diversity is essential given that it provides vital resources (e.g. food and timber) and ecosystem services (e.g. pollination and nutrient cycling) on which we are entirely dependent (Lovejoy 1997). However, populations of many species are declining and species extinctions are occurring at an alarming rate (Ehrlich 1988; Brook, Sodhi & Ng 2003). The number of species being lost is hard to estimate and different calculations lead to different results. Still, there is no doubt that extinction rates are much higher now than prior to the 1800s and that, if current trends continue, they may lead to the most extreme biodiversity loss seen in millions of years (Wilson 1988). In order to conserve biological diversity, it is necessary to understand the life history and ecology of species; only then, can the causes of population declines be identified and actions be taken to halt or reverse the negative trends.

The increasing demands of an ever-growing human population have led to the widespread destruction of habitats. Habitat loss and fragmentation are regarded by many as the greatest current threats to biological diversity (Wilcox & Murphy 1985; Ehrlich 1988; Sisk *et al.* 1994; Tilman *et al.* 1994; Laurance *et al.* 2002; Fahrig 2003) and agricultural expansion has played a major role in this process. Many species which have very specific habitat requirements do not occur at all in agricultural environments and have undergone particularly marked population declines. Many other species, however, have become adapted to living in low intensity arable systems. Farmland represents the major land use in many parts of the world and, as a consequence, a substantial proportion of the world's biodiversity now exists within this habitat. Nonetheless, since the second half of the twentieth century there have been major changes in farming practices related to more intensive methods that seek to maximise the production of food per unit area. These include (modified from Boatman 2006):

- Increased mechanisation and use of agrochemicals (fertilisers and pesticides, directly affecting some species and indirectly affecting many others by reducing invertebrate prey availability).
- Creation of larger fields with the consequent loss of non-crop features (e.g. hedgerows).
- Simplification of crop rotations and specialisation of farms (resulting in less diverse landscapes).
- Changes in crop sowing time (from spring to autumn, which affects the abundance of spring-germinating weeds and the availability of suitable nesting habitat for birds, many of which prefer shorter crops).
- Increased land drainage and reseeding of grasslands (usually replacing previously diverse swards with monocultures).
- Increased stocking densities (high grazing pressure generally reduces botanical diversity and structural complexity of the sward).

These intensive farming practices are part of a complex array of factors which are associated with a general decline in farmland biodiversity (Fig. 1.1), and there is overwhelming evidence demonstrating that many taxa (e.g. plants, insects, amphibians, reptiles, birds and mammals) have suffered population declines in response to agricultural intensification (e.g. Krebs *et al.* 1999; Stoate *et al.* 2001; Robinson & Sutherland 2002; Kleijn *et al.* 2009).

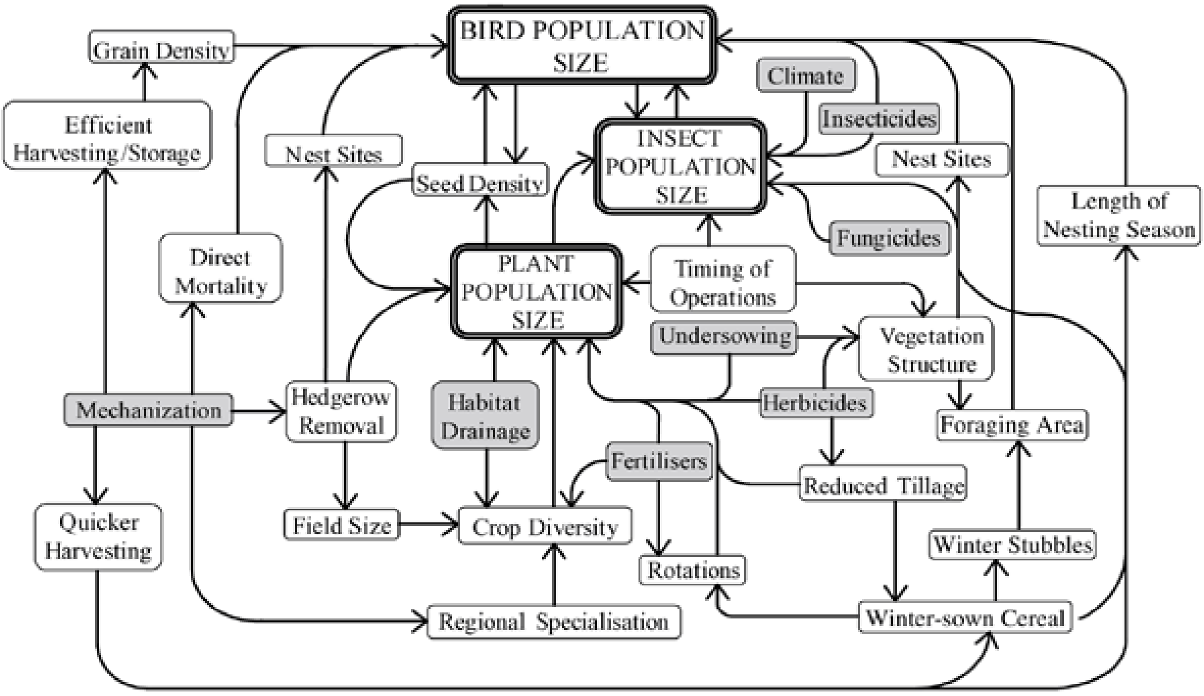

Figure 1.1. Factors related to agricultural intensification which affect farmland biodiversity (plant, insect and bird populations in this case). The major drivers are highlighted in grey. From Robinson & Sutherland (2002).

1.2. Agri-environment schemes: an attempt to improve farmland biodiversity

In the past, efforts to conserve biodiversity focused almost exclusively on the protection of particular species with localised distributions or of important semi-natural habitat sites (e.g. through the creation of nature reserves). However, it is now recognised that for many species inhabiting agricultural landscapes this strategy is not good enough. Furthermore, many modern farming systems are neither economically (e.g. farming has been underpinned by subsidies for so long that some business are now untenable without them) nor environmentally sustainable (Hunt 2006). Therefore, the need to conserve biodiversity (and the associated ecosystem services that it provides) in harmony with agriculture is beginning to be acknowledged and actions which meet both business and environmental goals are being sought (Krebs *et al.* 1999; Feber, Asteraki & Firbank 2007).

Agri-environment schemes (AES) have been introduced in Europe and North America as an attempt to reverse declines in farmland biodiversity by providing financial incentives for farmers to adopt less intensive, environmentally-sensitive agricultural practices. In Europe, AES are co-funded by the European Union (EU) – providing between 50 and 75 % of the costs – and its Member States, and large sums of money are spent on these schemes (e.g. nearly €9 billion were granted by the EU for the UK Rural Development Programme 2007–2013 to support sustainable agriculture throughout the countryside; DEFRA 2008). All EU Member States are currently required to implement AES as part of their Rural Development Programmes, but participation by land owners is not compulsory (e.g. operates on a voluntary basis; Kleijn *et al.* 2006). The aims and specifics of these programmes depend on the environmental and ecological issues related to agriculture in each country (although political situation and socio-economic problems are reflected as well). As a consequence, AES vary markedly between countries (Kleijn & Sutherland 2003), but most of them consist of a set of environmentally-sensitive management prescriptions – such as the maintenance of landscape features (e.g. hedgerows) and reductions in stocking densities or chemical inputs (EEA 2005) – to be implemented by farmers on their land. AES are considered by many as the most important policy instruments to protect biodiversity in agricultural landscapes (EEA 2005; Boatman 2006; Feber, Asteraki & Firbank 2007). Although organic farming (a production system in which the use of chemical inputs, such as synthetic fertilizers and pesticides, is largely restricted) is an agri-environment scheme (e.g. is co-funded by the EU under the same regulation), its main objectives are not necessarily biodiversity conservation and do not require the creation of new habitats or landscape features. Even though the practices adopted on organic farms are beneficial to many farmland species (Hole *et al.* 2005), the mechanisms by which they benefit biodiversity might be quite different from those of other AES; therefore, a distinction will be made between the two in this thesis.

Even though AES have been in place in Europe for nearly 20 years, very little information on their effects on biodiversity was available until quite recently (Kleijn & Sutherland 2003). The last decade, however, witnessed a boost in the number of studies conducted to assess the effects of AES on biodiversity (Whittingham 2006, 2011). Still, consistent patterns are hard to find. Research has shown that AES have had mixed effects on different taxa; some groups show positive responses, many show no response at all, and others even show negative responses to the implementation of AES (Kleijn & Sutherland 2003; Kleijn *et al.* 2006; Whittingham 2007, 2011). For instance, AES are often (but not always) successful at enhancing the abundance and diversity of plants and invertebrates – the former as a result of reduced fertilizer and herbicide applications, and the latter as a result of reduced pesticide applications and the positive impact of AES on plant communities (Kleijn *et al.* 2006). The effects of AES on farmland birds are less consistent; in many cases, it has proved difficult to enhance their populations and the general trend has been a persistent decline (although at a slower rate during the last decade; Whittingham 2011). Still, AES have been very successful at increasing the populations of certain bird species (e.g. corn bunting, black grouse, stone curlew and corncrake in the UK); these cases usually derive from intensive research of target species and management programmes which are closely supervised by conservation organisations (e.g. Vickery *et al.* 2004; Perkins *et al.* 2011). Only a few studies have assessed the effects on AES on mammals and, again, the results are contrasting and the benefits rather limited. For instance, Hof & Bright (2010) found that AES field margins were selected by hedgehogs when compared to other habitats such as arable land, pasture, woodland and amenity grassland (however, AES field margins were not compared to non-AES field margins, and so the value of AES management remains questionable). Bates & Harris (2009) found no benefits of hedgerow management regimes for small mammals, whereas Fischer, Thies & Tscharntke (2011) found that AES measures only enhance small mammal populations in simple (but not in complex) landscapes. Research has also shown that whereas common and widespread species can be enhanced with relatively simple modifications in farming practices and usually respond to positively to the implementation of AES, uncommon species (e.g. species included in the IUCN Red List) rarely benefit from AES and may require more elaborate conservation measures (Vickery *et al.* 2004; Kleijn *et al.* 2006). In summary, the general outcome seems to be that AES have had 'marginal to moderately positive effects on biodiversity' (Kleijn *et al.* 2006), but that much still needs to be done to maximize their effectiveness.

As a consequence of the varied success of AES in conserving biodiversity, the cost-effectiveness of the schemes has been questioned (e.g. Kleijn *et al.* 2001). Indeed, there are studies which suggest that there is no relationship between biological diversity and the amount of AES subsidies invested in an area (Zechmeister *et al.* 2003). Adequate design and implementation of AES are of utmost importance in determining the efficiency of the schemes, but regular monitoring to evaluate biodiversity gains is also essential (Kleijn & Sutherland 2003; Kleijn *et al.* 2006). Adaptive management (an iterative process of decision-making that combines research with management, enabling practitioners to learn and actively adapt actions), which integrates design, management and monitoring is crucial to maximize the success of AES (Salafski *et al.* 2002; Perkins *et al.* 2011; Whittingham 2011). However, monitoring programmes are not a compulsory element of AES and the conservation outcomes delivered by the schemes are hardly ever assessed. Nonetheless, it is still widely accepted that AES offer the greatest potential to reverse population declines and enhance biodiversity in agricultural areas (Vickery *et al.* 2004; Whittingham 2011).

1.2.1. The importance of a landscape-scale management approach

Insights derived from island biogeography theory (IBT; MacArthur & Wilson 1967) could be incorporated into the design of AES to increase their efficiency. IBT maintains that the number of species inhabiting an island depends on the island's size and isolation. Larger islands can support larger populations (which are in turn less prone to local extinction) than small islands, while less isolated islands have higher immigration rates and are more likely to be colonized by new species. The conceptual framework of IBT has been extended from real islands to terrestrial ecosystems of habitat patches in order to understand the effects of habitat loss and fragmentation on biodiversity. IBT has also been applied in conservation science to nature reserve design, sparking considerable debate about the importance of reserve size (e.g. whether a single large reserve will be more efficient protecting biodiversity than several small reserves of equivalent size) and of the presence of corridors linking patches of suitable habitat (Diamond 1975; Simberloff & Abele 1982; Wilcox & Murphy 1985; Patterson & Atmar 1986; Shafer 1995). Taking IBT knowledge into consideration for the spatial design of AES could be greatly beneficial.

Agri-environmental prescriptions are often applied to very small areas of land (e.g. field margins or individual fields) and create a mosaic of habitats of different quality with an erratic spatial distribution (Kleijn *et al.* 2006). This may offer insufficient resources to counteract the negative effects of an intensively managed surrounding landscape (Whittingham 2007). Therefore, it has been suggested that a landscape-scale management approach may be more beneficial than small-scale targeted AES prescriptions (Hole *et al.* 2005; Donald & Evans 2006). Whittingham (2007) suggests that adopting a 'protected area' approach (e.g. whole farms or groups of adjacent farms incorporating AES) may yield greater biodiversity gains from AES. Spatial targeting – use of Geographic Information Systems (GIS) as a spatial analysis tool to identify the most relevant areas for policy intervention – is recognised as a potentially useful means to increase the efficiency of AES (van der Horst 2007). Given that a species' mobility may influence its response to the implementation of AES, this approach may benefit some species more than others. In particular, taxa with poor dispersal abilities require a well connected network of habitats and even relatively small distances between suitable habitat patches may reduce the likelihood of a patch being colonized (Geertsema 2005). Species with high dispersal abilities, on the other hand, may be enhanced by structurally complex landscapes which compensate for local high-intensity management (Tscharntke *et al.* 2005).

However, the contribution of IBT to understanding some of the most important phenomena affecting fragmented landscapes (e.g. edge effects, permeability of surrounding matrix, importance of spatial heterogeneity), is limited (Laurance 2008). With regards to this, Donald & Evans (2006) suggest that AES could increase the permeability of the agricultural matrix surrounding patches of semi-natural habitat (e.g. by making it a less hostile environment), therefore compensating some of the negative impacts of habitat fragmentation on biodiversity. As a consequence, AES may have wider benefits than previously thought, and they could benefit not only characteristic farmland species, but also species which do not typically occur on agricultural land. Benefits may, therefore, go undetected if monitoring focuses purely on agricultural land / AES features.

A number of studies have highlighted the importance of the surrounding landscape on farmland biodiversity and on the effectiveness of AES (e.g. Tscharntke *et al.* 2005). It is often assumed that a particular AES will have similar efficacy on a target species across the whole range at which the scheme operates (Whittingham 2007, 2011). However, it has been shown that landscape character (e.g. heterogeneity, proportion of non-cropped areas and surrounding woodland) plays an important role and that AES yield greater benefits if implemented in areas that still support high levels of biodiversity (e.g. extensively farmed areas vs. intensively managed areas; Hendrickx *et al.* 2007; Kleijn *et al.* 2009). Nonetheless, other evidence suggests that AES are actually more effective (e.g. the difference between conventional and AES management is bigger) in simple than in complex landscapes and that the farming regime in an area also affects the efficiency of AES (Batáry *et al.* 2011). For instance, within arable land species richness is enhanced by AES in simple but not in complex landscapes (presumably because complex landscapes already support high species richness), whereas within grassland AES increase species richness regardless of the landscape context (presumably because it is usually less intensively managed than arable land) (Fig. 1.2; Batáry *et al.* 2011). Gabriel *et al.* (2009) suggest that AES (organic farming in their study) would be more cost-efficient in agriculturally less-favoured areas where the loss of production due to conversion to organic farming will be relatively small and thus economic incentives do not need to be high. In addition, the outcomes of AES also depend on the nature of the taxa under study (Gabriel *et al.* 2010; Batáry *et al.* 2011). For these reasons, AES would be more efficient if they were targeted to species groups and took into account the farming regimes and the landscape character of the regions in which they are to be implemented (Batáry *et al.* 2011). In general, AES prescriptions aimed at enhancing or maintaining landscape complexity would be highly effective in conserving biodiversity in agricultural landscapes (Concepción, Díaz & Baquero 2008).

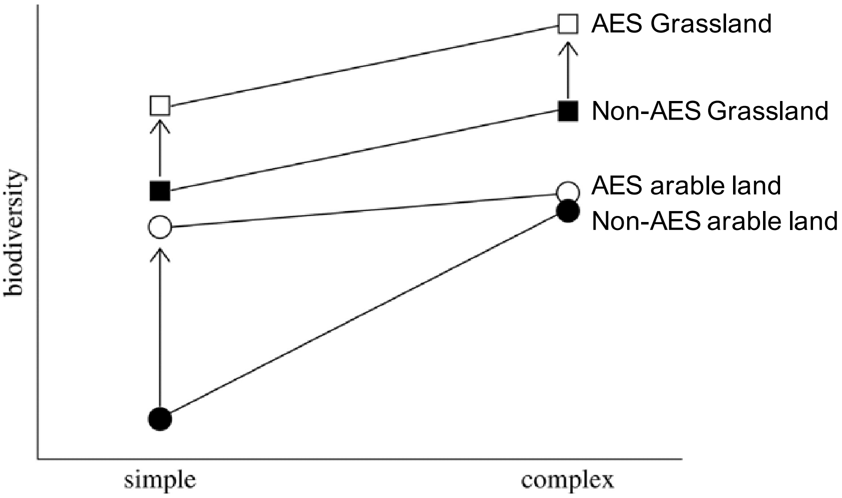

Figure 1.2. Hypothesized relationship between biodiversity gains (species richness) in response to AES in dependence of the complexity of the landscape (simple ≤ 20% cover of semi-natural habitat; complex > 20% semi-natural habitat). Black arrows indicate benefits to biodiversity when implementing AES. Modified from Batáry *et al.* (2011).

1.2.2. How agri-environment schemes operate in the United Kingdom

Approximately 45% of agricultural land in the UK is under AES management (DEFRA 2008). Agri-environment schemes in the UK are part of the Rural Development Programmes and operate independently within each country. In Scotland, AES are co-funded by the Scottish Government and the EU; their main purpose is to encourage farmers to manage their land while providing benefits for Scotland's wildlife and habitats. AES have operated in Scotland since 1987. They are reviewed frequently and, as a consequence, their names, specifics and the scale at which they operate have changed over time (Fig. 1.3). The first Scottish AES – Environmentally Sensitive Areas (ESA) – were designed to protect large areas of land important for biodiversity which were at risk of being affected by farming practices. Similarly, the Habitat Scheme operated at relatively large scales and included the set-aside or limited grazing of whole fields. These schemes were primarily about maintaining large areas relatively undisturbed from agricultural activities. Forestry Schemes involved the creation of new woodlands, as well as woodland management over time. From the Countryside Premium Scheme (CPS) onwards, AES have incorporated specific prescriptions targeted at the creation and/or management of landscape features on relatively small areas of land (e.g. hedgerows and field margins), although prescriptions at larger (e.g. field size) scales also exist (e.g. creation of species-rich grasslands). The duration of the schemes (e.g. minimum period of time during which a farmer agrees to stick to AES management) is also variable, and whereas some agreements will be running for up to 40 years (e.g. ESA), others – like the Rural Stewardship Scheme (RSS) – last a maximum of 5 years (but with a chance to renew). Although applications for most of these schemes are now closed, payments are scheduled to continue until the date stated in the original agreements (http://www.scotland.gov.uk/Topics/farmingrural/Agriculture/Environment/Agrienvironment).

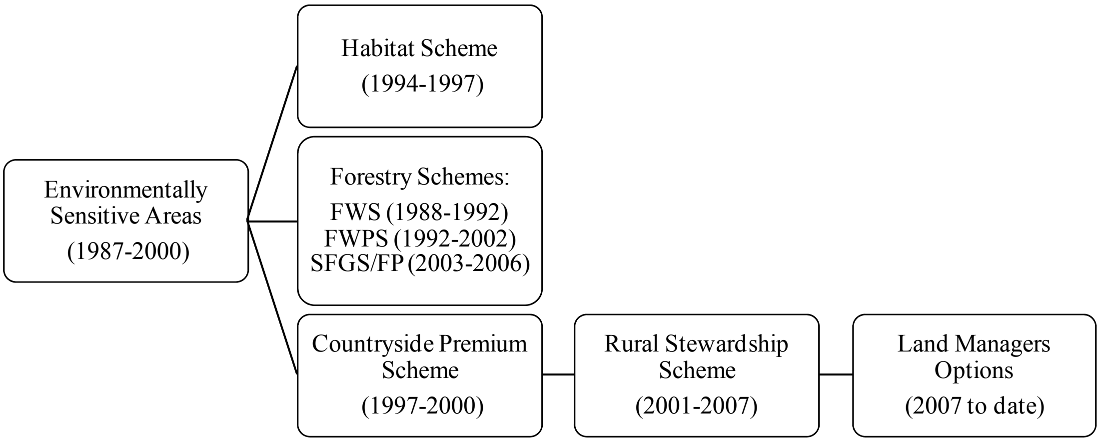

Figure 1.3. Agri-environment schemes which have operated in Scotland since 1987. Dates refer to when applications were received, but payments are scheduled to continue until the date stated in the original agreements (even if schemes have now closed to new applications). FWS: Farm Woodland Schemes; FWPS: Farm Woodland Premium Schemes; SFGS/FP: Scottish Forestry Grant Scheme / Farmland Premium.

The RSS was the Scottish AES in place when this research project started in 2007. It formed part of the Scottish Rural Development Programme and was a competitive scheme (i.e. used a ranking system to select successful applications) that required participants to comply with general environmental conditions (the Standard of Good Farming Practice, which applies over the whole farm) and manage specified areas of land in accordance with the requirements of the particular management prescriptions chosen (Table 1.1). Each management option available to farmers had an associated fixed payment rate (per area/length unit), designed to cover the cost of operations, including profits foregone and capital costs, and to provide a degree of financial incentive (Anonymous 2006). The RSS was superseded by the Rural Development Contracts - Land Managers Options (LMO) in 2007. Unlike RSS, LMO is a non competitive scheme. Some options require a five year commitment while others are for one year only. Compliance with Good Agricultural and Environmental Conditions and Statutory Management Requirements over the whole farm is mandatory. The management options available for farmers to choose from are very similar to those included in the RSS. All these schemes are non-spatially targeted.

AES in the rest of the UK resemble Scottish AES in some aspects, but in some cases they operate in a somewhat different way. In England, the Environmental Stewardship Scheme is the main AES providing funding to farmers to deliver effective environmental management. The main difference with Scottish AES is that English AES are divided into Entry Level Stewardship (ELS) – non-competitive scheme incorporating simple, non spatially-targeted land management prescriptions – and Higher Level Stewardship (HLS) – competitive scheme incorporating more complex management prescriptions tailored to specific local targets (http://www.naturalengland.org.uk/ourwork/farming/funding/es/default.aspx). Northern Ireland (NI) runs the Countryside Management Scheme (CMS), which is a competitive scheme (http://www.dardni.gov.uk/ruralni/index/environment/countrysidemanagement/schemes.htm). Wales is currently in the process of restructuring their AES; from 2012 onwards, the five existing agri-environment schemes will be replaced by one scheme, Glastir (http://wales.gov.uk/topics/environmentcountryside/farmingandcountryside/farming/agrienvironmentschemes/?lang=en). Despite their operational differences, most of these schemes incorporate similar management prescriptions.

Table 1.1. RSS management options available for farmers to choose from (Anonymous 2006).

Prescriptions predominantly for bird life
Extensive Management of Mown Grassland for Birds
Management of Open Grazed Grassland for Birds
Extensive Management of Mown Grassland for Corncrakes
Management of Early and Late Cover for Corncrakes
Management of Wet Grassland for Waders
Creation and Management of Early and Late Cover for Corncrakes
Prescriptions for species-rich areas
Management of Species-Rich Grassland (SRG)
Bracken Eradication Programme for SRG, Coastal or Lowland Heath
Creation and Management of SRG
Management of Coastal Heath
Management of Lowland Heath
Prescriptions for moorland
Moorland - Moorland Management
Stock Disposal
Muirburn and Heather Swiping
Bracken Eradication Programme for Moorland
Prescriptions for wetland features
Management of Wetland
Management of Lowland Raised Bogs
Creation and Management of Wetland
Management of Water Margin
Management of Flood Plain
Management of Basin and Valley Mire Buffer Areas
Prescriptions for field margins and boundaries
The Management of Grass Margin or Beetlebank in Arable Fields
Management of Conservation Headlands
Management of Extended Hedges
Management of Hedgerows
Prescriptions for arable areas
Introduction or Retention of Extensive Cropping
Spring Cropping
Management of Cropped Machair
Unharvested Crops
Prescriptions for woodland and scrub
Management of Scrub (including Tall Herb Communities)
Management of Native or Semi Natural Woodland
Management of Ancient Wood Pasture

There have been very few evaluations of any Scottish AES. Only a few published studies have compared biodiversity metrics of AES, as operated within Scotland, to conventional farming. Lye *et al.* (2009) studied the availability of foraging and nesting habitat resources for bumblebee queens; they concluded that some AES management prescriptions (e.g. field margins) were beneficial, but others (e.g. hedgerows) were not. Perkins *et al.* (2011) measured changes in breeding abundance of a severely declining bird species (corn bunting) in response to AES in Scotland; bird populations declined in conventionally-managed farms, but remained stable in AES farms. Recently, the Scottish Government commissioned an evaluation of Scottish AES (CPS and RSS, plus the Organic Aid Scheme) and the results revealed that these schemes generated little benefits to biodiversity; birds showed relatively strong responses to the implementation of the schemes, but the vegetation and invertebrate communities showed little changes (Scott Wilson Scotland Ltd. 2009). However, this study presents some limitations – e.g. it did not evaluate specific AES prescriptions and monitoring effort per farm was rather limited for some taxa – and its findings should be considered with caution. A previous report on Forestry Schemes (the Farm Woodland Premium Scheme; FWPS) concluded that the woodlands created within the scheme had considerable benefits for biodiversity (mainly plants, invertebrates and birds; Crabtree 1996). None of these studies have assessed the potential benefits of AES on bats or their insect prey.

1.3. Bats

Amongst mammals, bats (order Chiroptera) are one of the most numerous and diverse taxa. There are 18 families and over a thousand species of bat (representing about a quarter of all mammalian species) distributed all around the world, except for the most extreme polar regions. Bats have very diverse diets and ecological roles (Altringham 1996, 2003; Dietz, von Helversen & Nill 2009). Some species are carnivorous (e.g. feeding on fish, amphibians, reptiles, birds or mammals) and a few others (only three species) feed on blood. Many species are nectarivorous or frugivorous (about 25% of all species) and have crucial ecological roles as pollinators and seed dispersers (Altringham 1996, 2003; Dietz, von Helversen & Nill 2009). However, the vast majority of bats (about 70% of all species) are insectivorous and have important ecological and economic roles (e.g. they control damaging agricultural pests; Boyles *et al.* 2011; Kalka, Smith & Kalko 2008; Williams-Guillén, Perfecto & Vandermeer 2008).

1.3.1. Threats and conservation actions for bats

Nearly 15% of all bat species are listed as threatened (e.g. Critically Endangered, Endangered or Vulnerable and therefore facing a high risk of extinction; IUCN 2001) by the IUCN Red List, while a further 7% are classed as nearly threatened (IUCN 2011). Even species which are not included in the IUCN Red List have seen their local populations drastically reduced in many places, whereas for numerous other species population estimates are absent or unreliable (e.g. over 200 bat species are classed as Data Deficient by the IUCN Red List). The threats affecting bat populations are many and include: Destruction and disturbance of roost sites (e.g. caves and mines), disease (e.g. the rapidly expanding white-nose syndrome affecting North American bats), over exploitation for food (e.g. of flying foxes in the Pacific Ocean islands) and persecution by humans caused by fear (e.g. of rabies transmission) and misinformation. Habitat loss or modification, however, stands out as the worldwide major threat to bats (Altringham 1996; Mickleburgh, Hutson & Racey 2002; see also Cosson, Pons & Mason 1999 and Meyer & Kalko 2008), with increasing demands for land, food and other resources from an ever-growing human population resulting in the loss and degradation of many habitats.

Woodland is one of the most important habitats for bats, as it offers roosting and feeding opportunities for many species (Dietz, von Helversen & Nill 2009). It has been, however, badly affected by habitat fragmentation, loss and degradation. For instance, forestry practices can have strong effects on forest structure which can negatively affect bat populations (e.g. by reducing roosting and feeding opportunities; Erickson & West 2003; Yates & Muzika 2006; Lacki, Amelon & Baker 2007). Moreover, woodland habitat is often highly fragmented; small and isolated woodland patches within a hostile matrix are usually characterized by having an altered vegetation structure and spatial configuration, which can also impact bat populations (Yates & Muzica 2006). The intensification and expansion of agriculture have played a major role in the destruction and fragmentation of woodland by converting this and many other habitats into arable/pastoral lands. Inland water bodies (e.g. lakes, reservoirs, rivers and canals), which are used by many bat species as feeding sites (Walsh & Harris 1996; Vaughan, Jones & Harris 1997; Russ & Montgomery 2002; Downs & Racey 2006), have also been affected by agricultural intensification (e.g. reduction in water quality and removal of riparian vegetation). Furthermore, linear landscape features (e.g. hedgerows and tree lines), which are used by bats for commuting and feeding (Verboom & Huitema 1997; Downs & Racey 2006) which were once common in agricultural areas, have too been lost due to agricultural intensification (e.g. creation of larger fields).

Most British bat species are adapted for living and foraging in a heterogeneous landscape (a mixture of native woodland, water and open areas of heath and unimproved grassland; Altringham 2003); therefore, landscape simplification, along with the extensive use of pesticides in modern agriculture, have reduced food availability (Benton *et al.* 2002) and made intensively managed farmland (e.g. arable land and improved grassland) a hostile environment for many bat species (Walsh & Harris 1996; Wickramasinghe *et al.* 2003). The loss of roosting and foraging habitat through agricultural intensification is thought to be one of the main drivers behind the drastic population declines of many bat species in the UK during the 20th century (Harris *et al.* 1995; Walsh & Harris 1996). As a result, all species of bats and their roosts are protected under national (Wildlife and Countryside Act 1981 (as amended)) and international (Directive on the Conservation of Natural Habitats and of Wild Flora and Fauna 1992 (Annex IV)) legislation. In addition, in response to the1992 Convention on Biological Diversity (CBD) the UK Government launched the UK Biodiversity Action Plan (BAP), which identifies species and habitats of special conservation concern; seven bat species are currently considered ‘priority’ species under the UK BAP (JNCC 2011). In addition to legally protecting bats and their roosts in the UK, conservation actions for bats have resulted in the establishment of legally protected areas. SSSIs (Sites of Special Scientific Interest) have been designated all over the UK, some of them specifically to protect key bat sites (primarily roost sites) where relatively rare species (e.g. horseshoe and Bechstein’s bats) occur (Altringham 2003). However, these protected sites cover a very small proportion of the UK’s land (e.g. < 8 % in England, and only a few sites being relevant to bats). At a wider scale, conservation actions have focused on creating artificial roosts for bats, e.g. by setting up “bat boxes” for replacing natural roosts lost to forestry operations. These artificial roosts have had varying degrees of success depending on their location and the species of bat that use them (Altringham 2003).

Whilst bats, their roosts and some specific areas important for bats are now legally protected in the UK and artificial roosting opportunities are provided within many areas (e.g. within forestry plantations), foraging sites remain vulnerable to development and changes in land use. Conservation actions to create/manage foraging habitat for bats are rare (but see Hutson 1993). In addition, although agricultural intensification has been recognized as one of the main threats affecting bat populations, few specific actions have been taken to enhance bat populations in agricultural areas. As a consequence, there are very few examples of conservation actions for bats which incorporate habitat management guidelines to improve feeding areas in the countryside (e.g. for *Rhinolophus ferrumequinum*; English Nature 2003).

1.3.2. The ecology of British bats

The greatest diversity of bat species is concentrated in the tropics, while the number of species in higher latitudes is relatively low. In Europe, there are 35 bat species (Mickleburgh, Hutson & Racey 2002). Of those, seventeen species are considered as resident in the United Kingdom (UK), but only nine occur in Scotland (Richardson 2000; Altringham 2003; Jan *et al.* 2010). They all belong to the Vespertilionidae family, a very diverse and widespread family with nearly 350 species, and feed mainly on insects. All British bats hibernate during the winter. In the spring they abandon their hibernation sites and move into summer roosts; females roost communally and form nursery colonies, while males roost alone or in small groups with other males (although they may be present in significant numbers in nursery colonies of some species). Pups are born in late June – early July and weaning occurs from late July through August. Nursery colonies break up at the end of the summer and mating takes place during the autumn, sometimes extending to the early stages of hibernation (Altringham 2003). Relevant ecological information for each of the nine species resident in Scotland is presented next (modified from Altringham 2003 and Dietz, von Helversen & Nill 2009 unless otherwise stated; distribution data within Britain obtained from Richardson 2000).

Common Pipistrelle bat (*Pipistrellus pipistrellus*)

This species is widely distributed across Europe and it is the most common bat species in Britain (estimated population 2,430,000 individuals; JNCC 2007), although they are relatively less common in the north. They occur in a broad variety of habitats (e.g. woodland, water, hedgerows, grassland, farmland, suburban and urban areas). They hibernate in crevices in old buildings. Summer nursery roosts (usually 50 – 100 individuals) are almost always found in buildings. They commute on average 1.5 km from their roosts to their foraging sites (which are approximately 1500 ha in size; Nicholls & Racey 2006a). They catch their prey by aerial hawking, and their diet consists mainly of Diptera (suborder Nematocera), although other Diptera, Trichoptera, Neuroptera, Coleoptera, Lepidoptera and Hymenoptera are consumed in small proportions (Barlow 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK since 1999: increasing according to the National Bat Monitoring Programme (NBMP 2010).

Soprano Pipistrelle bat (*Pipistrellus pygmaeus*)

This species occurs throughout south and central Europe. It is the second most common bat species in Britain (estimated population 720,000 individuals; JNCC 2007), although it may be more common than *P. pipistrellus* in the north. They are more strongly associated with riparian woodland and water than Common Pipistrelles, although woodland edge, tree lines, hedges, suburban gardens and parks are also used. They avoid agricultural areas and grassland. Little is known about their hibernation sites, but they have been reported in buildings, trees, bat boxes and only rarely in underground sites. Nursery roosts (usually 500 – 700 individuals) are usually found in buildings, but tree holes and bat boxes are also used. Even though individuals from this species commute relatively large distances (an average of 1.7 km) from their roost to their foraging sites, they have smaller foraging areas (approximately 500 ha; Nicholls & Racey 2006a) than the Common Pipistrelle (Davidson-Watts & Jones 2006). Their diet is also very similar to that of the Common Pipistrelle (mainly insects from the dipteran suborder Nematocera), but Soprano Pipistrelles consume a greater proportion of aquatic flies (e.g. Chironomidae and Ceratopogonidae; Barlow 1997), which they catch by aerial hawking. Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species; classed as a Priority Species under the UK Biodiversity Action Plan (BAP) because of a long term population decline in the UK. Current population trend in the UK: increasing (NBMP 2010).

Nathusius' Pipistrelle bat (*Pipistrellus nathusii*)

They are widely distributed in Europe. They are a migratory species which was only recently recognised as a resident in Britain, where it is only rarely recorded. Nathusius'

Pipistrelles are strongly associated with woodland, preferring damp lowland woods, riparian forests and parkland. Winter roosts are usually found in tree holes, but crevices in buildings, caves and cliffs are also used. Nursery colonies (20 – 200 individuals) in Europe usually found in trees; bat boxes and wooden structures (e.g. shooting towers) are sometimes used. In Britain, nursery roosts have been found in buildings. They commute up to 6.5 km from their roosts to their hunting sites, which can be as large as 2000 ha. They feed mainly on Diptera; however, Trichoptera, Hemiptera, Neuroptera and Lepidoptera are occasionally consumed (Vaughan 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK: insufficient data (NBMP 2010).

Brown long-eared bat (*Plecotus auritus*)

Their distribution covers all of Europe and it is widely distributed across Britain, where they're probably the next most common species after the Common and Soprano Pipistrelles (estimated population in Britain 200,000 individuals; 30,000 in Scotland). They are a woodland specialist species (although they occur also in parkland and gardens in towns), and they have short and broad wings which allow slow and highly manoeuvrable flight amongst vegetation. They hibernate in underground sites, usually near the entrances of mines and caves, and tree holes. Their nursery roosts (10 – 50 individuals, a large proportion of males often present) are located in trees and old buildings close to wooded areas. They usually commute only short distances (e.g. 500 m) to their foraging grounds. They locate their prey by listening to their rustling sounds, and catch them by gleaning them off the vegetation or by aerial hawking. They feed mainly on moths (Lepidoptera), but Coleoptera, Trichoptera, Diptera and non-flying invertebrates (e.g. Dermaptera and Arachnida) are also consumed (Vaughan 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species and as a Priority Species under the UK BAP because of a long term population decline in the UK. Current population trend in the UK: stable (NBMP 2010).

Natterer’s bat (*Myotis nattereri*)

They are widely distributed across most of Europe and Britain (estimated population in Britain 100,000 individuals; 17,500 in Scotland). They are found in woodland (including dense coniferous plantations), parkland and gardens; open areas are rarely used. They hibernate almost exclusively in mines and caves, often into crevices but sometimes also hanging in the open. Their nursery roosts (up to 200 individuals but usually 20 – 50, males making up approximately 25%) are usually found in buildings (e.g. old castles, stone walls and bridges), tree holes and bat boxes. They can commute up to 4 km from their roosts to their foraging sites, which are on average 215 ha. Their broad wings allow great manoeuvrability and a very versatile hunting style; they can hawk flying insects, glean them off the vegetation and even catch spiders from their webs. This is reflected in their varied diet, which includes mainly Diptera, Coleoptera, Lepidoptera, Arachnida, Neuroptera, Hymenoptera and Trichoptera. Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK: increasing (NBMP 2010).

Daubenton’s bat (*Myotis daubentonii*)

This species is distributed across most of Europe and parts of Asia. It is also widely distributed in Britain (estimated population size 150,000 individuals; 40,000 in Scotland). They are strongly associated with water and feed over lakes and rivers; woodland and parkland are also used, especially if water bodies are located nearby. They usually hibernate in crevices in underground sites (e.g. caves, mines and tunnels), but tree holes and rock crevices are also used. In the summer, their roosts are found in tree holes, underground sites (e.g. bridges over canals) and occasionally in old buildings, but always close to water. Nursery colonies usually include 20 – 50 individuals (but can exceptionally hold up to 600 bats). Males form their own colonies, but they are also present in nursery colonies. Daubenton’s bats frequently switch roosting sites during the summer. They typically forage within 2 – 3 km of the roost, but can occasionally commute considerably longer distances (up to 15 km). They have a distinctive fast and agile flying style, foraging very close (<1 m) to water surfaces; they take insects from the air, but also the water surface. They feed mainly on aquatic Diptera (especially Chironomidae midges), but Trichoptera can make up an important part of their diet; Lepidoptera, Ephemeroptera, Coleoptera, Neuroptera are also consumed (Vaughan 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK: stable (NBMP 2010).

Whiskered bat (*Myotis mystacinus*)

They are widely distributed across Europe and the south of Britain (England and Wales) and their distribution reaches the south of Scotland, where they are less common (estimated population in Britain 40,000 individuals; 1,500 in Scotland). They are mainly a woodland species, associated with trees and riparian habitats; they also use open landscapes with isolated woodland patches and hedges, and gardens in suburban areas. They hibernate in caves and mines, in crevices or in the open. Summer nursery roosts (usually 20 – 60 bats) are almost exclusively comprised of females and found in trees and buildings; males roost individually. Roosting sites are changed frequently. They travel up to 2.8 km from their roosts to their foraging sites. They hunt mainly by aerial hawking, but they can also catch their prey close to – or glean off – the vegetation surface. Their diet is quite varied, including mainly Diptera and Lepidoptera, but also a considerable proportion of Arachnida, Coleoptera, Neuroptera, Trichoptera and Hymenoptera (Vaughan 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK: stable (data incorporates *M. mystacinus* and *M. brandtii*; NBMP 2010).

Noctule bat (*Nyctalus noctula*)

Their distribution covers most of Europe and parts of Asia. In Britain, they are found as far north as south-west Scotland (estimated population in Britain 50,000 bats; only a few hundred in Scotland). Woodland and water are their preferred habitats, but given that they are fast fliers capable of commuting long distances between roosts and foraging sites, they can use a variety of other environments. They hibernate mainly in tree holes, where they gather in small groups; buildings are sometimes also used. During the summer they form small nursery colonies (< 20 bats in Britain, larger in continental Europe), while males roost singly or in small groups. These colonies are located almost exclusively in tree holes (woodpecker holes are heavily favoured, as are beech trees; coniferous trees are rarely used), although bat boxes and man-made structures are occasionally used. Roosts are frequently changed. They usually forage within 2.5 km of their roosts, although much longer flights (e.g. 26 km) have been reported. They feed in the open, often over trees and water, eating predominantly large insects within the orders Diptera, Lepidoptera and Coleoptera (Vaughan 1997). Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species and as a Priority Species under the UK BAP because of a long term population decline in the UK. Current population trend in the UK: stable (NBMP 2010).

Leisler's bat (*Nyctalus leisleri*)

They are distributed across southern and central Europe. They are relatively rare in Britain (estimated population size 10,000 bats), where their distribution extends as far north as south-west Scotland. They prefer woodland (and woodland edge), parkland, pasture and riparian habitats. Nursery colonies (usually 20 – 50 bats, in Ireland over 500 females) are typically found in naturally developed holes in trees (beeches and oaks are favoured), although bat boxes and man-made structures are used too. They change their roost locations frequently. Their long and narrow wings allow fast flight and they can commute long distances (up to 5.7 km) from their roosts to their foraging sites (Waters, Jones & Furlong 1999), although occasional flights of up to 17 km have been reported. Leisler's bats feed mainly on Diptera (suborder Nematocera), although Coleoptera, Lepidoptera and Trichoptera are also an important part of their diet (Vaughan 1997; Waters, Jones & Furlong 1999). They hibernate in tree holes and less commonly in buildings. Conservation status: classed as a species of Least Concern by the IUCN Red List of Threatened Species. Population trend in the UK: insufficient data (NBMP 2010).

1.4. Nocturnal insects

Insects (class Insecta) are the most diverse animal taxa on Earth, with more than a million species described (about 100,000 in Europe and 20,000 in Britain) and estimates of total diversity reaching up to 30 million species (Chinery 1993). Insects play many important ecological roles; the vast diversity of forms and life-styles includes nutrient recyclers, predators, pollinators, parasites and scavengers. They are also a key part of the food chain and an important component of the diet of many animal groups, such as birds and mammals (including bats). Despite being such an abundant and diverse group, the ecology and conservation status of many insect species are still unknown (e.g. only 0.3% of species described have been evaluated by the IUCN; www.iucnredlist.org/ documents/summarystatistics/ 2011_1_RL_Stats_Table_1.pdf).

Many insect groups have been badly affected by habitat loss and degradation caused by agricultural intensification (Feber *et al.* 1997; Benton *et al.* 2002). Relatively little is known about the nocturnal insects on which bats feed, but there is evidence which suggests that the intensification of agriculture has had strong negative effects on the abundance and diversity of insects which are important components of the diets of many bat species (Wickramasinghe *et al.* 2004). Declines in insect prey abundance associated with agricultural intensification may be linked to bat populations declines (Stebbings 1988), in the same way that they have been linked to population declines of farmland birds (Vickery *et al.* 2001; Benton *et al.* 2002). Low insect abundance has also been linked to low bat activity in forestry plantations (Tibbels & Kurta 2003). Therefore, maintaining large insect populations should be taken into consideration in bat conservation actions. Because food resources are limited on intensively managed agricultural land, even small insect-rich areas (e.g. water bodies and woodland patches) could represent important local foraging patches for bats (Park & Cristinacce 2006) and should, therefore, be maintained or created.

Coleoptera, Diptera, Lepidoptera and Hymenoptera are the most diverse insect orders; the first three (and the fourth to a lesser extent) are also some of the most important components in the diets of British bats. Amongst them, Lepidoptera stand out because, despite being so abundant and diverse, they are relatively easy to sample and identify. In addition, Lepidoptera are considered a sensitive indicator group for biodiversity because they show strong responses to agricultural intensification and forest quality (Kitching *et al.* 2000; Summerville, Ritter & Crist 2004; Jennings & Pocock 2009). For these reasons, they are given special attention in this thesis.

1.4.1. Moths

Lepidoptera are one of the most abundant and diverse insect orders, with more than 150,000 named species (about 5,000 in Europe; Chinery 1993). They are commonly divided into macrolepidoptera (a group of moth families containing mostly large species or "macromoths", plus all butterfly families) and microlepidoptera (a group of moth families comprising mostly smaller species or "micromoths"), of which *ca.* 900 and 1700 species occur in the UK, respectively (Chinery 1993; Waring & Townsend 2003). The majority of Lepidoptera are moths, with butterflies representing less than 10 % of the order. Moths are mostly nocturnal (although there are crepuscular and diurnal species) and they occupy a wide variety of habitats, including grassland, heathland, scrub, wetland, woodland, farmland and urban areas (Waring & Townsend 2003). Moths have important roles as pollinators (Proctor, Yeo & Lack 1996) and are essential food resources for many species of birds, bats and small mammals (Vaughan 1997; Wilson *et al.* 1999).

1.4.1.1. The ecology of British moths

All Lepidoptera pass through the four stages of metamorphosis (egg, larva, pupa and imago). The eggs are laid singly or in groups (from just a few up to several hundreds), usually on (or near) the plant on which the larva will feed when it emerges. The egg state usually lasts two to three weeks (except in species that lay eggs in late summer and overwinter as eggs). When the larvae (or caterpillars) hatch, they feed on mainly on plant leaves, but flowers, fruits, stems and roots are also consumed by some species. The caterpillars of many moths specialise on a particular food-plant, whereas others feed on a much broader range. The larval stage may be short (e.g. three weeks), or last for months in species which hibernate as larvae. Caterpillars moult (typically four to five times) as they grow; once they are fully grown the larvae use their silk glands to build a cocoon (although some species build chambers in the soil and others may not be covered at all) and pupate on their food-plant, in the leaf litter, soil or moss. The time spent in the pupal stage also varies greatly and could last just a couple of weeks in the spring or early summer; however, most British moths overwinter as pupae, and therefore spend up to 10 months in this stage. After the adult moths emerge, they feed mainly on nectar, although sap leaking from tree trunks and honeydew excreted by aphids and accumulated on leaves are also consumed; adults of some species do not feed at all. Adult moths then find a mate and lay their eggs; many species have more than one brood per year (usually two, rarely three or four; Chinery 1993). This stage is usually short and lasts only a few days or weeks (usually two to three weeks, although some species overwinter as adults and live for months), but it is the best opportunity for moths to disperse (Chinery 1993; Waring & Townsend 2003). Some species (such as many micromoths and geometrids) move just a few hundred meters during their adult lifespan, but others (such as most noctuids) are much more mobile and can fly very long distances (up to 3 km). Some are even migratory and reach Britain as immigrants from Europe and north Africa (Nieminen, Rita & Uuvana 1999; Doak 2000; Merckx *et al.* 2009a, 2010a,b).

1.4.1.2. Threats and conservation actions for moths

Ecological research and conservation efforts for Lepidoptera have been largely focused on butterflies. Relatively little attention has been given to macromoths and even less to the conservation status and habitat requirements of micromoths, even though they comprise a large proportion of most local lepidopteran assemblages (Bland & Young 1996; New 2004). Many moth species have undergone severe population declines. One of the most important threats to moth populations is habitat loss and fragmentation caused mainly by the expansion of modern agricultural practices (Conrad *et al.* 2004; New 2004); changes in the structure, management and spatial configuration of habitats (e.g. woodlands) have also been linked to declines of certain species (Fox *et al.* 2006). In the UK, more than 60 species became extinct during the twentieth century (Fox *et al.* 2006) and many common and widespread macromoth species have showed significant population declines over the last few decades (Conrad *et al.* 2006). To date, only a handful of moth species are protected by law under the UK's Wildlife and Countryside Act 1981 (as amended); 81 species have been identified as national priorities for conservation by the UK BAP, whereas a further 71 species are included in the UK BAP priority species list labelled as ‘widespread and common, but rapidly declining’ (e.g. their population declines have been so severe that if IUCN criteria were to be applied at a national scale they would be regarded as threatened; Conrad *et al.* 2006). Conservation actions for moths sometimes focus on setting aside small areas to protect populations of a particular species (e.g. the burnet moth *Zygaena viciae*; Young & Barbour 2004). However, on top of preserving isolated areas in the form of reserves, conservation actions (lead by Butterfly Conservation in the UK) now aim to restore and manage larger areas of the countryside working in conjunction with landowners and Government organisations (e.g. Scottish Natural Heritage and Forestry Commission).

1.5. Study aims and thesis outline

Although agricultural expansion and intensification have been recognized as major threats affecting bat populations, no specific actions have been taken to enhance bat populations in agricultural areas. Agri-environment schemes have been introduced in the UK as an attempt to counteract the negative effects of intensive agriculture on biodiversity. However, current AES prescriptions have been specifically designed to benefit taxa such as birds and pollinators, and do not take the needs of bats and many of their insect prey into consideration. Whilst some AES prescriptions are potentially beneficial to bats, to date no study has quantified the response of either bats, or their prey species, to the implementation of AES. While most AES prescriptions are designed to be implemented on arable/pastoral land (e.g. creation of wide grassy field margins and species-rich grasslands), some others aim to increase the amount and quality of woodland on agricultural land. Surprisingly, despite woodland being one of the most important habitats for bats, little is known about how its character relates to prey availability and bat abundance and diversity; as a result, woodland management guidelines for bats are scarce, and the ones that exist focus on creating/maintaining roosting opportunities rather than enhancing good foraging habitat (Anonymous 2005; but see Entwistle *et al.* 2001). In addition, different bat species may have different habitat requirements, so scientific research to produce practical management recommendations is essential.

The purpose of this thesis is to assess the effectiveness of commonly employed agri-environmental management prescriptions for bats and nocturnal insects and to produce management recommendations which improve the benefits that these taxa gain from AES. In particular, the aims of this study are:

1. To assess the benefits (or otherwise) of four commonly employed AES management prescriptions and the importance of a landscape-scale management approach for bats and nocturnal insects (Chapters 2 and 3).
2. To assess the relative importance of woodland vegetation character (e.g. tree species richness), patch configuration (e.g. size and shape) and surrounding landscape (e.g. proportion of woodland cover) on bats and nocturnal insects in order to increase the knowledge required to adequately design AES prescriptions for woodland creation and management (Chapters 4 and 5).

Chapter 2

Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions

An adapted version of this chapter has been published as:

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2.1. Summary

Agricultural intensification is a major cause of biodiversity declines. Agri-environment schemes (AES) have been introduced in many countries as an attempt to counteract the negative effects of intensive agriculture by providing financial incentives for farmers to adopt environmentally-sensitive agricultural practices. We surveyed 18 pairs of AES and conventionally-managed farms in central Scotland (United Kingdom) to evaluate the effects of specific AES management prescriptions (field margins, hedgerows, species-rich grasslands and water margins) on foraging bats and nocturnal insects. In addition, we assessed the importance of habitat in the wider landscape at several spatial scales on foraging bats and their insect prey. *Pipistrellus pygmaeus* and *Pipistrellus pipistrellus* were the most commonly recorded species, accounting for 98% of total bat activity levels. Overall levels of bat activity and the abundance of their insect prey (mainly Diptera and Trichoptera) were lower (by 40–50%) on farms participating in AES than on non-participating farms. Differences in insect abundance were also significant when we compared specific AES management prescriptions with equivalent conventionally-managed features. The surrounding landscape influenced bat activity; fragmentation metrics related to woodland configuration were the most important landscape characteristics influencing bat activity levels. However, the two Pipistrelle species responded differently to the surrounding landscape, *P. pipistrellus* being strongly influenced by the landscape at large scales (e.g. within 2 km of the monitoring site) and *P. pygmaeus* being most influenced by the landscape at smaller scales (within 500 m of the monitoring site). Insect abundance was positively affected by the percentage cover of semi-natural environment within 500 m of trapping sites. We suggest that the implementation of the four common AES management prescriptions assessed in this study does not benefit Pipistrelle bats nor other bat species foraging on

similar prey. Such species may respond more positively to a landscape-scale management approach focused mainly on the creation and management of woodland.

2.2. Introduction

Farmland represents the major land use throughout Europe. In the United Kingdom (UK) agricultural land occupies approximately 75% of the land area (DEFRA 2008) and most of this is under intensive agricultural practices aimed at maximising the production of food (Stoate *et al.* 2001). The intensification and expansion of modern agricultural practices have led to the biological simplification of the farmed environment, which has resulted in declines in farmland biodiversity during the last century (Krebs *et al.* 1999; Robinson & Sutherland 2002). Agri-environment schemes (AES) have been introduced in Europe and North America as an attempt to reverse these declines by providing financial incentives for farmers to adopt less intensive, environmentally-sensitive agricultural practices (e.g. extensive grazing, reductions in chemical inputs and maintenance of landscape features; EEA 2005). Approximately 45% of agricultural land in the UK is under AES management (DEFRA 2008) and large amounts of money are spent by the Government on these schemes. For instance, the European Union (EU) funded the UK Rural Development Programme 2007 - 2013 with nearly €9 billion to support sustainable agriculture throughout the countryside (DEFRA 2008). Despite these high financial inputs, the implementation of AES has had mixed results for different taxa (Kleijn *et al.* 2006), and monitoring and evaluation of these schemes is imperative to improve their efficiency and maximize the conservation outcomes.

Many bat species in Europe have suffered severe population declines during the 20th century (Harris *et al.* 1995), with one of the main drivers believed to be the loss of roosting and foraging habitat through agricultural intensification (Walsh & Harris 1996). Avoidance by foraging bats of intensively managed agricultural land has been noted in previous studies (e.g. Wickramasinghe *et al.* 2003); it has been suggested that declines in insect prey abundance (associated with the intensification of agriculture) may have contributed to declines in bat populations (Stebbings 1988), in the same way that they have been linked to declines in farmland bird populations (Vickery *et al.* 2001; Benton *et al.* 2002). In the UK, all species of bats and their roosts are protected under national (Wildlife and Countryside Act 1981 (as amended)) and international legislation, but foraging sites remain vulnerable to development and changes in land use (Hutson 1993). Even small insect-rich areas in agricultural landscapes may be used by bats and could represent important local foraging patches (Park & Cristinacce 2006). Previous studies have shown positive effects of organic farming (a production system in which the use of chemical inputs, such as synthetic fertilizers and pesticides, is largely restricted) on bat populations and the nocturnal insects on which they feed (Wickramasinghe *et al.* 2003, 2004); however, organic farming currently represents a very small proportion of the farmed areas in the UK (~ 2%; DEFRA 2008), so it may offer limited benefits to these groups on a large scale. In contrast, AES – other than organic farming – operate on a much larger scale, and even though they are largely designed for birds and invertebrates, AES may potentially benefit other taxa. To date, the potential benefits they may offer to bat populations have not been assessed.

It has been suggested that the effectiveness of AES depends on species' mobility, and that a landscape-scale management approach may be more beneficial than small-scale targeted AES prescriptions (Hole *et al.* 2005; Donald & Evans 2006;

Gabriel *et al.* 2009, 2010). Structurally complex landscapes enhance local diversity in agro-ecosystems, which may compensate for local high-intensity management. This is particularly true for species with high dispersal abilities (Tscharntke *et al.* 2005). The direct impact of habitat composition and configuration of the surrounding landscape on bat communities has been measured in previous studies (e.g. Perry, Thill & Leslie 2008; Klingbeil & Willig 2009), but these studies have usually been conducted in predominantly forested areas (e.g. Amazonian forest) and only rarely in farmland-dominated landscapes (e.g. Duchamp & Swihart 2008).

We assessed the benefits (or otherwise) of four commonly employed AES management prescriptions and the influence of the surrounding landscape to foraging bats and nocturnal insects in Scotland, UK. We addressed two particular questions:

1. Are farms involved in AES associated with higher levels of bat activity and greater insect abundance than conventionally-managed farms and, if so, which specific AES management options have the greatest effect on bat activity and nocturnal insects?
2. Is a landscape-scale management approach important for the conservation of bats and, if so, which is the most appropriate scale?

2.3. Materials and methods

2.3.1. Study sites

We used a paired survey design to quantify bat activity levels and nocturnal insect abundance on 18 pairs of AES and conventional farms in central Scotland (Fig. 2.1) between June and September 2008. We selected 18 farms which had been participating in the Scottish Rural Stewardship Scheme (RSS) since 2004. The RSS forms part of the

Scottish Rural Development Programme, although it was superseded by the Rural Development Contracts - Land Managers Options (LMO) in 2007. It is a competitive scheme (i.e. uses a ranking system to select successful applications) that requires participants to comply with general environmental conditions (the Standard of Good Farming Practice, which applies over the whole farm) and manage specified areas of land in accordance with the requirements of the particular management prescriptions chosen (Anonymous 2006). Each selected AES farm incorporated at least three of the following AES management prescriptions which we felt would be most likely to benefit foraging bats: a) field margins or beetlebanks (present in 15 farms); b) hedgerows (13 farms); c) water margins (17 farms); and d) species-rich grasslands (16 farms). The following descriptions have been modified from Anonymous (2006).

a) *Management of field margins or beetlebanks in arable fields.* This prescription aims to provide habitat for beneficial insects and cover and food for birds. It involves the creation and management of strips of between 1.5 m and 6 m in width sowed with a suitable mix of grass seed, which may be located around or across an arable field. Fertiliser, pesticide and grazing restrictions apply.
b) *Management of hedgerows.* This prescription is meant to provide improved habitat for invertebrates, birds and small mammals. It targets existing hedgerows and involves restrictions on pesticide input. Gaps in the hedge must be filled in, the hedge bottom must not be mown, cutting is restricted to once every three years and timing restrictions apply.
c) *Management of water margins.* This prescription aims to protect water margins from erosion and permit development of tall waterside vegetation for the benefit of freshwater life, invertebrates, water voles, otters and bats. It targets land

bordering still water or watercourses. The water margin must be at least 3 m wide. Fertiliser, pesticide, mowing and grazing restrictions apply.

d) *Creation and management of species-rich grassland.* This prescription aims to convert arable or improved grassland to species-rich grassland for the benefit of pollinator species such as butterflies and bumblebees. Its creation involves the destruction of any previously existing grassland cover and the establishment of a new sward by sowing the land with a low productivity grass and herb mix. Fertiliser and pesticides input restrictions apply; mowing and grazing are not allowed during the summer.

We paired each AES farm with nearby conventionally-managed farms to act as counterparts (see Table 2A-1. in Appendix 2A for details on the pairing design). These were not involved in any AES and are referred to as conventional farms hereafter. Each of these conventional farms was within 8 km of its corresponding AES farm, conducted similar farming activities (arable, pastoral or mixed; 7, 2, and 9 pairs of farms respectively) and was of similar size (farm area range: 51 – 607 ha; mean difference within paired sites ± standard error (SE): 63 ± 36 ha). In each conventional farm we selected conventionally-managed field margins, hedgerows and water margins to compare with the equivalent habitat features under AES management. The selection of conventionally-managed features was performed carefully to control for as many variables as possible other than AES management. Activities conducted in adjacent fields (pastoral or arable) and proximity to non-targeted features such as woodland and roads were considered in the pairing design. AES species-rich grasslands were compared to either improved pasture or crop fields in the conventional farms; the

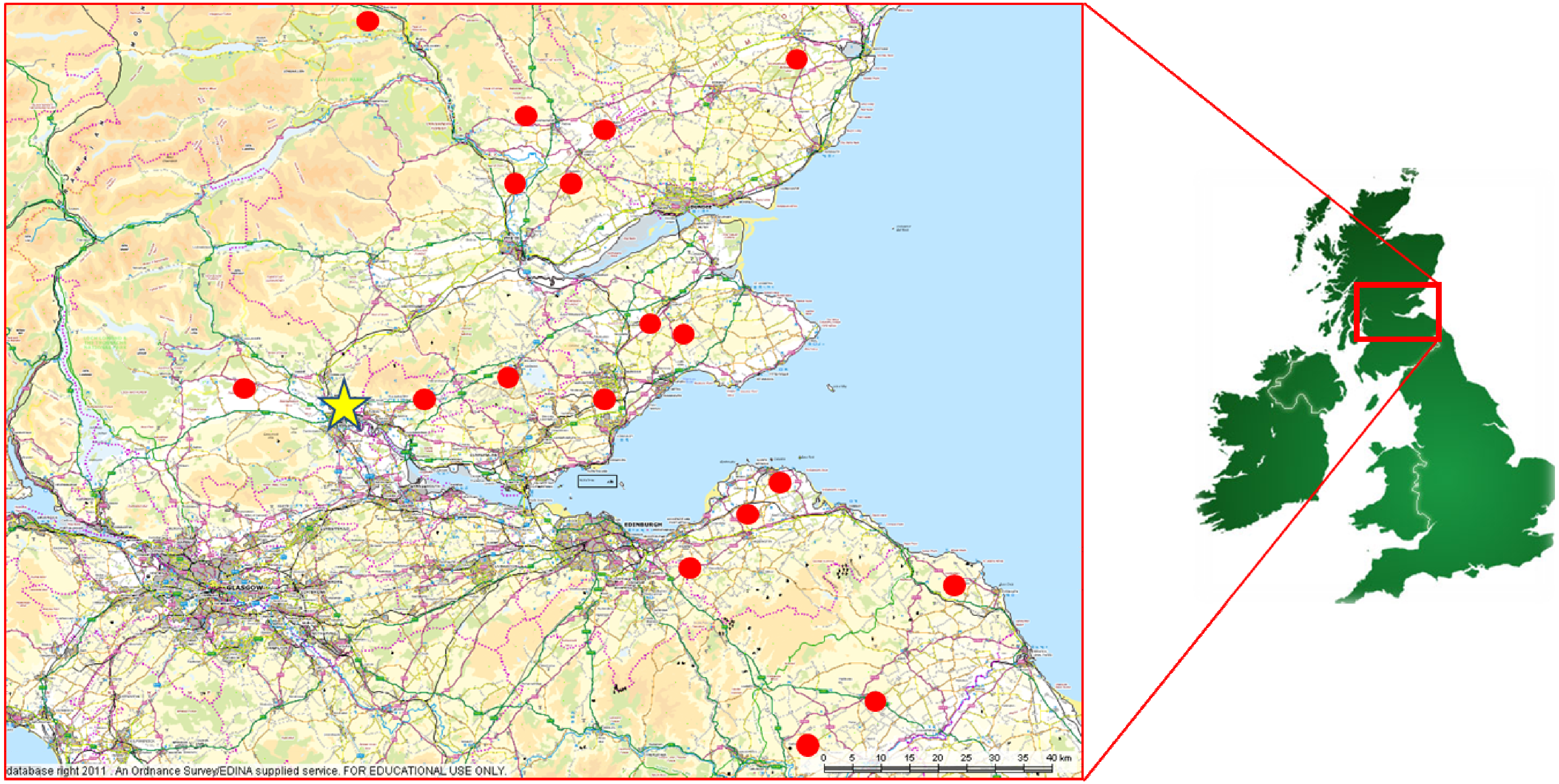


Figure 2.1. Map of central Scotland showing approximate locations of AES-conventional farm pairs (red dots) surveyed during 2008. Yellow star represents the University of Stirling.

selection of either of these two habitats was based upon land use of the species-rich grassland prior to AES conversion.

2.3.2. *Sampling methods*

We sampled each farm once during the summer (mid June to early September) of 2008. Although variations in bat activity and insect abundance occur between nights, our paired design allowed us to make a robust comparison between AES and conventionally-managed farms. Farms within a pair (AES farm and its conventional counterpart) were surveyed during the same night to minimize weather variation. Temperature and wind speed were recorded on each farm immediately before and after sampling. If temperature fell below 8˚C, wind force exceeded Beaufort scale 4, or heavy rain fell, sampling was abandoned.

2.3.2.1. *Insect sampling*

We collected nocturnal insects using portable 6 W heath light traps (3 – 4 traps per farm, depending on the number of AES prescriptions within the site) powered with 12 V batteries. The traps were ≥ 100 m apart from each other to prevent the lights from interfering with each other (Merckx *et al.* 2009a). The traps were activated 15 minutes after dusk adjacent to each AES management prescription or equivalent conventional feature (either centred or ≥ 100 m from the edge of each feature) and switched off after 4 hours using automatic timers. The light traps were then sealed and transported to the laboratory. The collected insects were euthanized by dropping a cotton pad soaked with ethyl acetate into each trap, left overnight, placed in sample bottles and refrigerated for later identification to order level (suborder for Diptera). Lepidoptera were excluded from the analyses presented here given that they represent a very small proportion (< 2 % in terms of number of individuals per faecal pellet) in the diet of Pipistrelle bats (the most common species in the area) in the UK (Swift, Racey & Avery 1985; Hoare 1991). Data on the abundance and diversity of Lepidoptera in relation to AES are presented elsewhere (Chapter 3).

2.3.2.2. Bat monitoring and sound analysis

Acoustic surveys were performed to assess bat activity using a frequency division bat detector (Anabat SD1, Titley Electronics) attached to a PDA device (HP iPAQ) and a GPS unit (Compact Flash, GlobalSat). When echolocation calls were detected they were automatically stored into a file including the time and exact location of the recording. Monitoring was continuous along transects which incorporated the AES prescriptions (or equivalent features on conventionally-managed farms) within the farms. Transects were walked at a constant pace (approx. 3.5 km/hr), and the bat detector was held at waist height with the microphone angled up at 45°. The length of transects varied between pairs (2.5 − 3.7 km) depending on the number of features surveyed. Transects within paired farms were of similar length and included similar proportions of habitat features (e.g. hedgerows; see Table 2A-2 in Appendix 2A for details on the proportions covered by each habitat). Sampling began 45 minutes after sunset to avoid peak emergence times for different bat species (and therefore avoided recording bats commuting to feeding sites). The two farms within a pair were surveyed during the same night one immediately after the other; the order of sampling (AES *vs.* conventional farm) was alternated to avoid temporal effects on bat activity.

We analysed all bat recordings using AnalookW (Corben 2006). We identified bat species and counted total numbers of bat passes (defined as at least two echolocation calls within one second of each other; Fenton 1970; Walsh & Harris 1996), social calls and feeding buzzes emitted when attempting prey capture (Griffin, Webster & Michael 1960). There are four bat genera present in the study area (*Pipistrellus, Myotis, Nyctalus* and *Plecotus*; Richardson 2000), and all can be identified based on characteristics of their search-phase echolocation calls. However, in some cases it is difficult to distinguish between species within a genus due to similarities in call structure. Such is the case of the *Myotis* (*M. daubentonii*, *M. nattereri* and *M. mystacinus*) and *Nyctalus* species (*N. noctula* and *N. leisleri*) found in the area, which were therefore grouped as *Myotis* sp. and *Nyctalus* sp., respectively. *Plecotus* is represented by only one species in the area (*P. auritus*), but it is rarely recorded because of its quiet echolocation calls. The *Pipistrellus* species present in the UK can be distinguished on the basis of the characteristic frequency of their search-phase echolocation calls. Bat passes with a Fc between 49 and 51 kHz were classed as unknown *Pipistrellus* sp.. Calls unsuitable for identification were classed as unknown.

2.3.3. Landscape analysis

We used ArcGIS 9.2 (ESRI Inc. 2006) to create buffers of 250, 500, 1000, 1500, 2000, 2500 and 3000 m around each farm transect. We selected these different scales because the smallest represents site-specific characteristics, whereas the others cover the home ranges of low (e.g. *P. auritus*) and intermediate (e.g. *P. pygmaeus*) mobility species; the largest scale approximates an upper limit to home range sizes of more mobile bat species (e.g. *P. pipistrellus*; Entwistle, Racey & Speakman 1996; Nicholls & Racey

2006a). Within each buffer, we reclassified feature classes obtained from OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service) into five categories (hereafter referred to as biotopes). These were: 1) urban areas (buildings, structures and roads); 2) farmland; 3) water (inland and tidal water); 4) semi-natural environment (rough grassland and scrub); and 5) woodland (coniferous, deciduous and mixed trees and areas covered by scattered trees). We then used Fragstats 3.3 (McGarigal *et al.* 2002) to calculate a selection of landscape metrics for each biotope and a landscape heterogeneity index (Shannon diversity) taking into account the number of different biotopes and their proportional abundance within the buffers (Table 2.1). A correlation matrix of the landscape parameters for each of the buffer sizes is presented in Appendix 2B.

2.3.4. Data analysis

Statistical analyses were conducted using the statistical software R version 2.11.1 (R Development Core Team 2010) and the packages lme4 (Bates & Maechler 2010) and MASS (Venables & Ripley 2002). Linear regression analyses (Generalised Linear Models) were used to evaluate the effect of each landscape parameter at each different spatial scale on insect biomass, insect abundance and the number of bat passes. Individual models (one for each landscape parameter at each spatial scale) were performed using Gaussian errors when the response variable was continuous (insect biomass, log transformed) and quasi-Poisson errors for count data (Crawley 2007). R^2 values were calculated to select the landscape parameter that explained the highest variation in the data; for models using quasi-Poisson errors, pseudo R^2 values (hereafter referred to as R^2 values) were calculated by correlating the values predicted by each

Table 2.1. Description of landscape metrics used for landscape analysis and significance values [a] from regression analyses between landscape metrics at each spatial scale and the number of bat passes of *P. pipistrellus*. R^2 values from regression analyses are shown in Figure 2.4.

Landscape metric	Description [b]	Scale						
		250 m	500 m	1 km	1.5 km	2 km	2.5 km	3 km
Shannon diversity	Minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion.	ns	ns	*	*	**	*	*
% Urban	Percentage of the landscape comprised of buildings, structures and roads.	ns	ns	ns	ns	ns	ns	ns
% Farmland	Percentage of the landscape comprising agricultural land.	ns	*	ns	**	**	*	*
% Water	Percentage of the landscape comprising inland and coastal water (includes waterways and standing water).	ns	ns	ns	ns	ns	ns	ns
% Semi-natural	Percentage of the landscape comprising rough grassland and scrub.	ns	ns	ns	ns	ns	ns	ns
% Woodland	Percentage of the landscape comprising coniferous, deciduous and mixed woodland and scattered trees areas.	*	**	**	**	**	**	*
Water-LPI	Percentage of the landscape comprising the largest water patch.	ns	ns	ns	ns	ns	ns	ns
Water-ENN	Mean value of Euclidean nearest neighbour distances between all water patches within the landscape.	ns	ns	ns	ns	ns	ns	ns
Wood-LPI	Percentage of the landscape comprising the largest woodland patch.	*	*	*	*	*	◌̇	◌̇
Wood-ENN	Mean value of Euclidean nearest neighbour distances between all woodland patches within the landscape.	ns	ns	ns	ns	ns	ns	ns
Wood-ED	The sum of the lengths of all woodland edge segments divided by the total landscape area.	*	*	*	**	**	**	*

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, ' ◌̇ ' $p \leq 0.1$, "ns" $p \geq 0.1$.
[b] Modified from (McGarigal *et al.*, 2002).

model with the observed data (Zuur *et al.* 2009). The most important landscape parameter at the most relevant scale (highest R^2 value) for each response variable was later included as one of the potential explanatory variables in subsequent models.

We then performed Generalised Linear Mixed-Effects Models (GLMMs; Zuur *et al.* 2009) to determine which of the variables evaluated had significant effects on bat activity and insects. We conducted two sets of analyses, one to assess the effect of AES at the farm level ("farm level" analysis) and another one to assess the effect of specific AES management prescriptions ("feature level" analysis, performing pair-wise comparisons between AES prescriptions versus their equivalent conventionally-managed features).

When assessing bat activity levels at the farm level, we used the total number of bat passes (of each bat species) per farm as the response variable. The following were included in the models as potential explanatory variables: land management type (AES or conventional) and farming activity (arable or mixed; pastoral farms were excluded from this analysis as our sample size was too small, n = 4 farms) were included as fixed effects; "pair" was included in all models as a random effect (grouping variable) to account for the paired-site sampling design; the landscape parameter with the highest R^2 value for each bat species (see section 2.3.4, first paragraph), site altitude, date and ambient temperature were covariates. The length of the transect surveyed at each farm was included in the model as an offset. Insect abundance and biomass were assessed at the farm level in the same way (except the number of traps within a farm was used as the offset), using the sum of the values of all traps within a farm as the response variable. A correlation matrix of all potential explanatory variables (excluding landscape metrics) was created to check for possible collinearity between predictors.

None of them were significantly intercorrelated ($p \geq 0.05$, Pearson correlation coefficient ≤ 0.3).

When assessing bat activity levels at the feature level, we used the number of bat passes per AES prescription (or equivalent conventionally-managed feature) as the response variable. We used ArcGIS 9.2 (ESRI Inc. 2006) to plot bat passes on OS digital map layers (EDINA Digimap Ordnance Survey Service). Each bat pass was then assigned to the AES prescription (or conventional equivalent feature) immediately adjacent (≤ 20 m) to the location of the recording. When there were several habitat features within 20 m of the recording location, a proportion of each pass was assigned to each habitat (e.g. 1 bat pass adjacent to both hedgerow and water margin: 0.5 pass was assigned to each habitat). Management type (AES or conventional) and habitat feature (field margin, hedgerow, water margin, species-rich grassland, or their equivalent conventional features) were included in these models as fixed factors; "pair" was included as a random effect (grouping variable) to account for the paired-site sampling design; the length of the transect covered by each habitat feature at each farm was included as an offset. Insect abundance and biomass were also assessed at the feature scale, using the total values per trap as the response variable, management type and habitat feature as fixed factors, and "pair" as a random effect.

Models were fitted using Poisson errors (or quasi-Poisson whenever the data were overdispersed) when the response variables were counts (e.g. number of bat passes) and Gaussian errors on transformed data when the response variables were continuous (e.g. insect biomass; Crawley 2007). For the "farm level" analysis, an information-theoretic approach to model selection based on AIC_C – a corrected method of Akaike's information criterion (AIC) particularly suited for small sample sizes (Akaike 1974; Hurvich & Tsai 1989) – was adopted. For each response variable, we compared models with every possible combination of explanatory variables. For simplicity, here we present the results of the most parsimonious models (lowest AIC_C). Possible alternative models within a 95% confidence interval – based on AIC_C weights (relative probabilities of each model being the best model) – are shown in Appendix 2C. Because the "feature level" analysis consisted only of pair-wise comparisons between AES prescriptions and their equivalent conventionally-managed features, no model selection was performed.

2.4. Results

2.4.1. Nocturnal insect abundance

We collected a total of 15,232 insects from 122 trap samples in 488 hours of sampling. The most abundant insect orders were Diptera, Lepidoptera and Trichoptera, which comprised 97% of the total catch (Table 2.2).

2.4.1.1. Effects of the surrounding landscape on nocturnal insects

The percentage cover of semi-natural environment within 500 m of the trapping sites was the only landscape metric showing a significant correlation (+) with insect abundance (p = 0.025, R^2 = 9.39%). Insect biomass was not significantly correlated with any of the landscape parameters at any scale; it showed the strongest non-significant correlation (+) with the percentage cover of semi-natural environment within 500 m of the trapping sites (p = 0.182, R^2 = 13.82%). Therefore, this landscape parameter was included as a potential explanatory variable in subsequent models for insect abundance and biomass.

Table 2.2. Summary table showing abundance of nocturnal insects collected at agri-environmental and conventional farms.

	AES farms		Conventional farms		Total	
Insect order	Abundance	% of total catch	Abundance	% of total catch	Abundance	% of total catch
Diptera (Nematocera)	1540	10.11	6166	40.48	7706	50.59
Diptera (Brachycera)	1072	7.04	1528	10.03	2600	17.07
Lepidoptera (micro) [a,b]	390	2.56	199	1.31	589	3.87
Lepidoptera (macro) [a,b]	1377	9.04	917	6.02	2294	15.06
Trichoptera	434	2.85	1168	7.67	1602	10.52
Coleoptera	57	0.37	97	0.64	154	1.01
Hymenoptera	40	0.26	45	0.30	85	0.56
Hemiptera	59	0.39	23	0.15	82	0.54
Other [c]	70	0.46	50	0.33	120	0.79
Total	5039	33.08	10193	66.92	15232	100

[a] Excluded from food availability analyses. See methods for further details.
[b] Data presented elsewhere (Chapter 3).
[c] Includes orders representing < 0.5% of the total catch.

2.4.1.2. Effects of agri-environment schemes on nocturnal insects

At the farm level, insect abundance was lower at farms participating in AES than at non participating farms, representing only 57% of the abundance observed at conventional farms (based on differences in fitted median values; Table 2.3 & Fig. 2.2a). Insect biomass was also lower at AES farms, although this difference was not significant (Table 2.3 & Fig. 2.2b). The landscape parameter included in the farm level analysis (percentage cover of semi-natural environment within 500 m of trapping site) remained a significant predictor for insect abundance (but not biomass; Table 2.3).

At the feature level, significantly fewer insects were captured at each of the AES prescriptions than at their equivalent conventional features, but for field margins this difference was not significant (Table 2.4 & Fig. 2.3a). Insect abundance at AES field margins, hedgerows, species-rich grasslands and water margins represented only 47.8, 50.0, 88.3 and 75.4% respectively (based on differences in observed median values) of the abundance observed at their conventional counterparts (Table 2.4 & Fig. 2.3a). There were no significant differences in biomass between AES and conventionally-managed features (Table 2.4 & Fig. 2.3b).

2.4.2. Bat activity

We surveyed a total of 106.6 km of transects and recorded a total of 1965 bat passes. Bat activity was recorded on 34 of 36 farms. We identified five bat species / genera. The most commonly recorded species was *P. pygmaeus*, followed by *P. pipistrellus*, *Myotis* sp., *P. auritus* and *Nyctalus* sp. (Table 2.5). The two Pipistrelle species alone comprised nearly 98% of all bat passes; there were insufficient data to perform

Table 2.3. Summary table of the farm level analysis showing significance values, parameter estimates (±SE) and the goodness of fit of the most parsimonious GLMMs (lowest AIC_C). Possible alternative models (95% confidence set based on model $wAIC_C$) are shown in Appendix 2C. Management = farms involved in agri-environment schemes *vs.* conventionally-managed farms. Activity = arable *vs.* mixed (arable and pastoral activities within a farm). Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$ and 'ns' $p \geq 0.1$.

	Management [a]	Activity	Landscape parameter [b]	Altitude	Temperature	Date	Model $wAIC_C$ [c]	Model R^2 [d]	Model distribution
Insect abundance	-0.68 ± 0.02 ***	ns	0.18 ± 0.01 ***	-0.02 ± 0.00 ***	ns	ns	0.423	91.20%	Poisson
Insect biomass	ns	ns	ns	ns	ns	ns	0.583	NA	Gaussian
P. pygmaeus	-0.21 ± 0.06 **	ns	-0.02 ± 0.00 ***	ns	ns	ns	0.461	63.51%	Poisson
P. pipistrellus	-0.44 ± 0.13 ***	ns	0.02 ± 0.00 ***	0.01 ± 0.00 **	ns	ns	0.495	63.35%	Poisson
Feeding buzzes	-0.87 ± 0.20 ***	ns	-	ns	ns	ns	0.150	57.86%	Poisson
Feeding buzz ratio	ns	ns	-	ns	ns	ns	0.925	NA	Gaussian

[a] Negative values indicate a negative effect of the implementation of AES.

[b] Landscape parameters included in the models varied depending on the response variable being assessed. Percentage cover of semi-natural environment at the 500 m scale was used for insect abundance and biomass, woodland ENN at the 500 m scale was used for *P. pygmaeus* and woodland ED at the 2 km scale was used for *P. pipistrellus*. For a description of landscape metrics see Table 2.1.

[c] AIC_C weights: Relative probability of each model being the best model (based on AIC_C). $wAIC_C = \exp(-\Delta AICc_i / 2) / \sum(\exp(-\Delta AICc_j / 2)$.

[d] R^2 values for models with a Gaussian error distribution were calculated with the formula: 1 − (Residual Sum of Squares / Total Sum of Squares). Pseudo-R^2 values for models with a Poisson error distribution were calculated with the formula: (Deviance explained by model / Null deviance) * 100 (Zuur *et al.*, 2009). This value was not available (NA) when none of the potential explanatory variables remained in a model and is not adjusted for the number of explanatory variables included in a model.

Table 2.4. Summary table showing post hoc analyses comparing AES prescriptions versus conventionally-managed features.

	Field margins		Hedgerows		Species-rich grasslands		Water margins		Model $R^{2\,c}$	Model distribution
	Estimate [ab]	*SE*	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*		
Insect abundance	-0.89 ◌̇	0.46	-1.06 *	0.54	-1.09 ***	0.31	-1.00 ***	0.30	30.72%	Quasi-Poisson
Insect biomass	-0.78 ◌̇	0.46	-0.09	0.49	-0.02	0.44	-0.83 ◌̇	0.43	53.32%	Gaussian
P. pygmaeus	0.77	0.49	-0.84	0.84	-0.61	0.75	-0.56	0.44	16.76%	Quasi-Poisson
P. pipistrellus	1.48 ◌̇	0.81	-1.02	0.73	-0.95	0.89	-0.81	0.51	17.36%	Quasi-Poisson

[a] Significance codes: $p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’.

[b] Negative values indicate that insect abundance/biomass and/or bat activity levels were lower at AES prescriptions than at conventionally-managed features.

[c] R^2 values for models with a Gaussian error distribution were calculated with the formula: 1 − (Residual Sum of Squares / Total Sum of Squares). Pseudo-R^2 values for models using quasi-Poisson errors were calculated by correlating the values predicted by the final GLMMs (fitted values) with the observed data. This value is not adjusted for the number of explanatory variables included in a model.

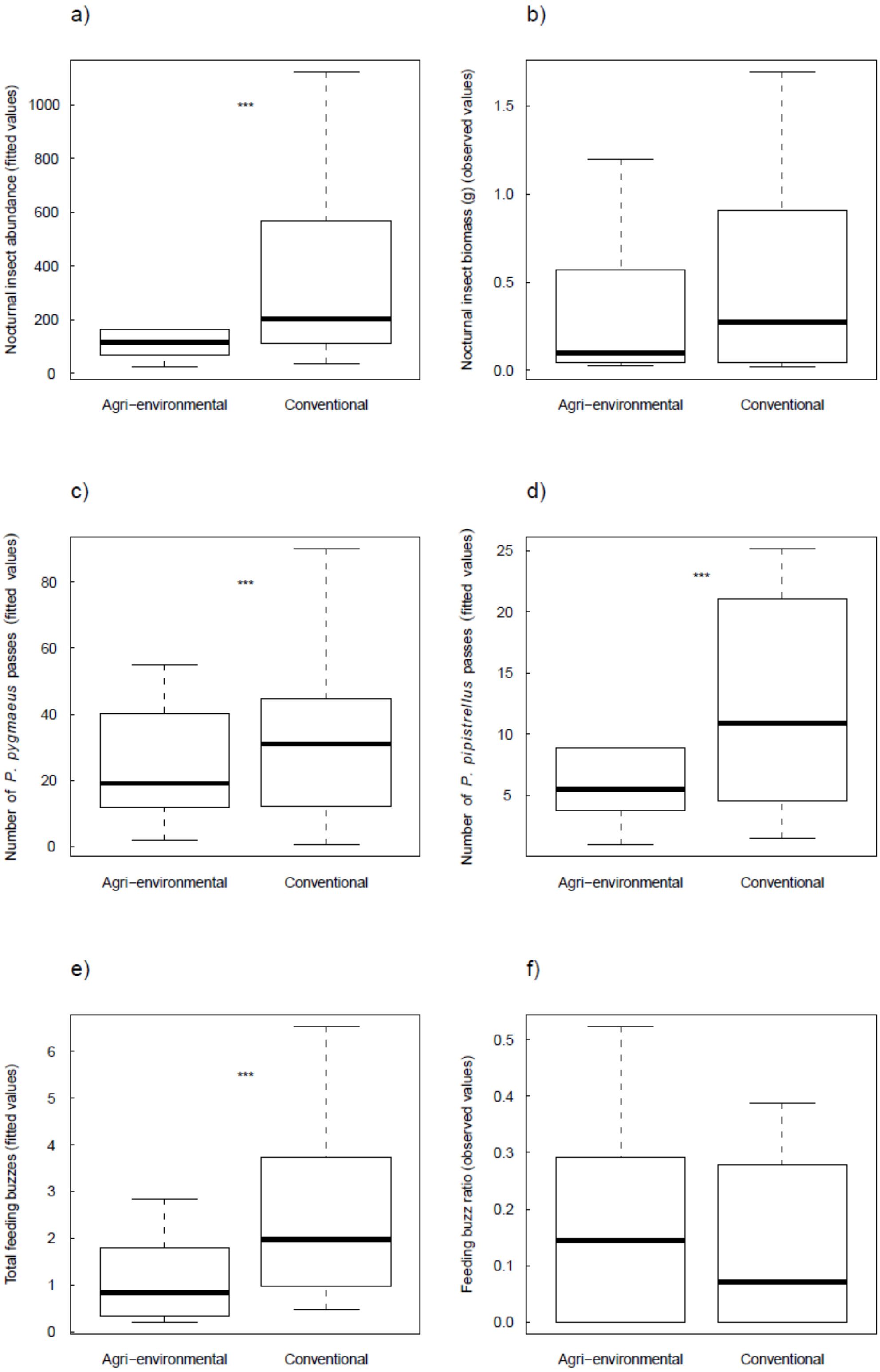


Figure 2.2. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the fitted values predicted by the most parsimonious GLMMs at the farm level for a) nocturnal insect abundance, b) nocturnal insect biomass, c) *P. pygmaeus* activity, d) *P. pipistrellus* activity, e) total number of feeding buzzes and f) feeding buzz ratio (number of feeding buzzes per bat pass). Variables included in each final model are summarized in Table 2.3. Original values are shown instead of fitted values for b) and f) because there were no significant predictors in the selected models. Stars indicate significant differences due to management type. Significance codes: $p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’.

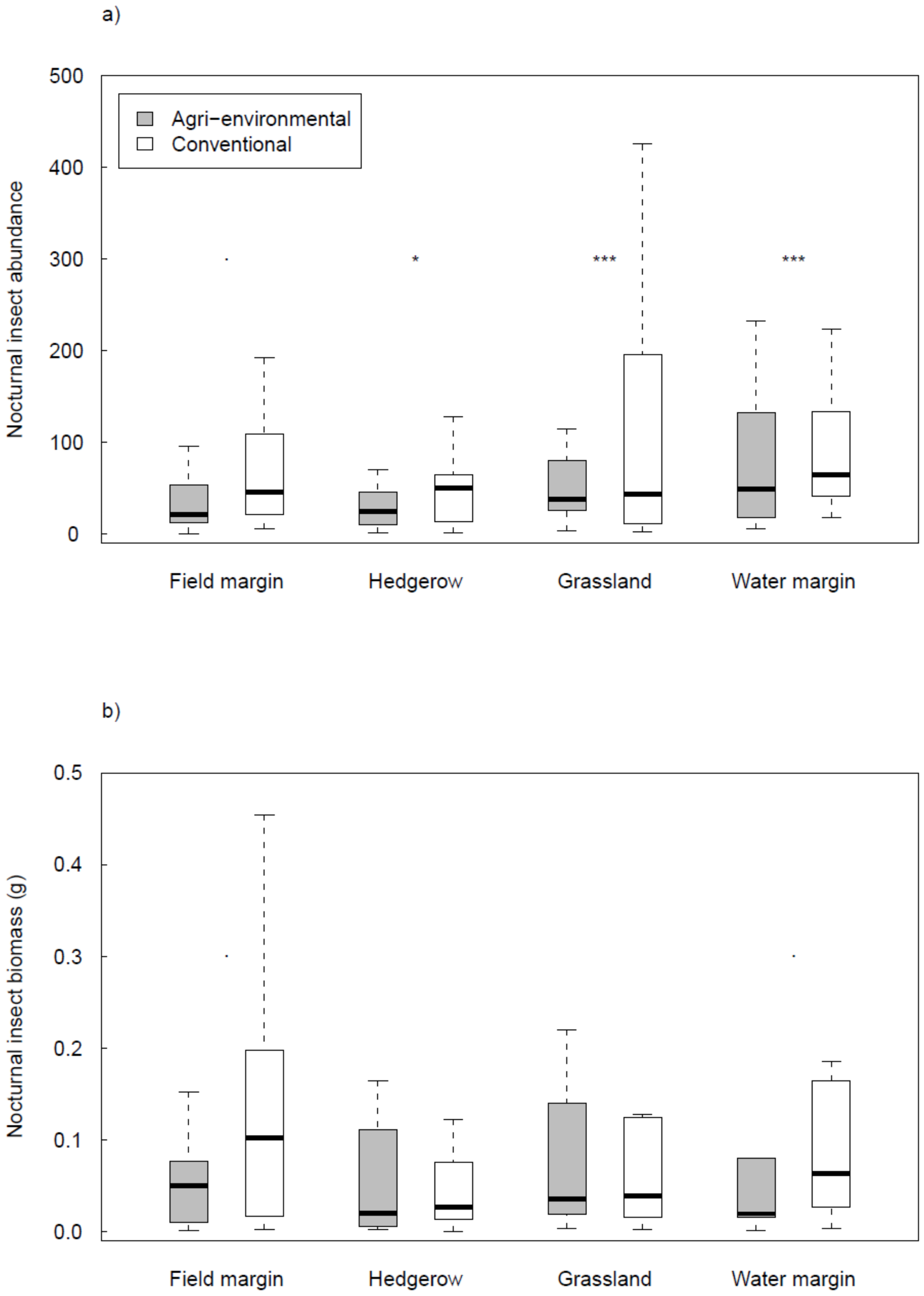


Figure 2.3. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the pair-wise comparisons between AES and conventionally-managed features for: a) nocturnal insect abundance and b) nocturnal insect biomass. Stars indicate significant differences within a habitat feature due to management type. Significance codes: $p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’.

statistical analyses on any other bat species.

2.4.2.1. Effects of the surrounding landscape on bat activity

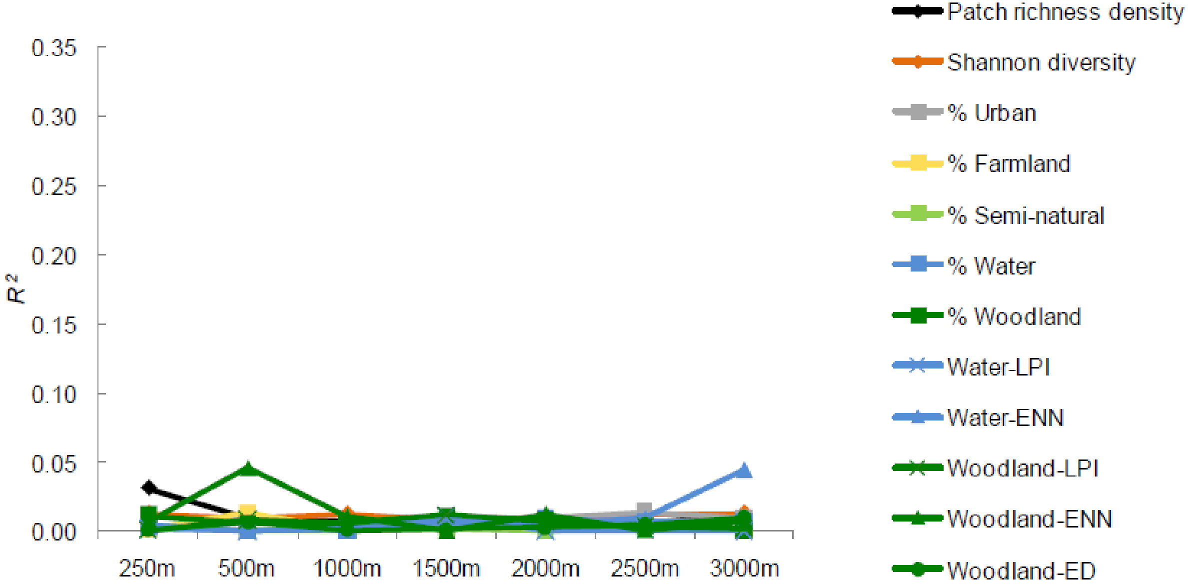
Metrics relating to woodland were the most important predictors for both *P. pygmaeus* and *P. pipistrellus* but the scale and magnitude of their effect on activity levels differed substantially between the two species. The surrounding landscape explained a low variation in activity levels of *P. pygmaeus.* Woodland Euclidean nearest neighbour (ENN) distance between patches (Table 2.1), a measure of woodland isolation, within 500 m of the transects was the landscape metric that showed the strongest relationship (-) to the number of bat passes of this species ($p = 0.094$, $R^2 = 4.55\%$; Fig. 2.4a). Water ENN within 3 km of the transects showed a similar non-significant relation (-) to the number of *P. pygmaeus* passes ($p = 0.247$, $R^2 = 4.44\%$; Fig. 2.4a). However, given that woodland ENN explained a slightly higher variation than water ENN in the data (in terms of both higher model R^2 and higher statistical significance), the former was selected over the latter to be included as a potential explanatory variable in subsequent models for this species. In contrast, a high proportion of the variation in *P. pipistrellus* activity levels was explained by the surrounding landscape (Table 2.1 & Fig. 2.4b). Woodland edge density within 2 km from transects showed the strongest relationship (+) to the number of *P. pipistrellus* bat passes ($p = 0.009$, $R^2 = 31.24\%$) and was therefore included as a potential explanatory variable in subsequent models concerning this species. The percentage of woodland cover, woodland largest patch index and the index of landscape heterogeneity (Shannon diversity index) also showed strong significant positive relationships to this species’ activity levels, but these landscape parameters were strongly positively correlated with woodland edge density (Appendix 2B) and not included in the subsequent models. The percentage cover of farmland was negatively related to the number of *P. pipistrellus* bat passes. These metrics showed the strongest relationship to *P. pipistrellus* activity levels when assessed within 1 – 2 km of the transects, although the relationships remained significant at the largest scale (3 km) assessed (Table 2.1 & Fig. 2.4b).

2.4.2.2. Effects of agri-environment schemes on bat activity

At the farm level, bat activity was significantly lower on AES farms than on conventionally managed farms (Table 2.3), with the number of *P. pygmaeus* and *P. pipistrellus* passes at AES farms representing only 62 and 50%, respectively, that of their conventional pair (Figs. 2.1c & 2.1d). Foraging activity was also significantly lower on AES farms than on conventional farms, with the total number of feeding buzzes on AES farms representing just 43% that of conventionally managed farms (Table 2.3 & Fig. 2.2e). Foraging effort, indicated by the number of feeding buzzes per bat pass (feeding buzz ratio), did not differ significantly between the two types of farms (Table 2.3 & Fig. 2.2f). The landscape parameters included in the farm level models remained as significant predictors of bat activity levels for the two species (Table 2.3).

At the feature level, no significant differences were observed between AES prescriptions and conventionally-managed features for either of the two Pipistrelle species, although the differences for three of the four prescriptions were in the same direction as the farm level analysis (e.g. lower activity at AES compared with conventional). Only AES field margins had a positive effect on *P. pipistrellus* activity, but this was not statistically significant (Table 2.4 & Fig. 2.5).

a) *P. pygmaeus*



b) *P. pipistrellus*

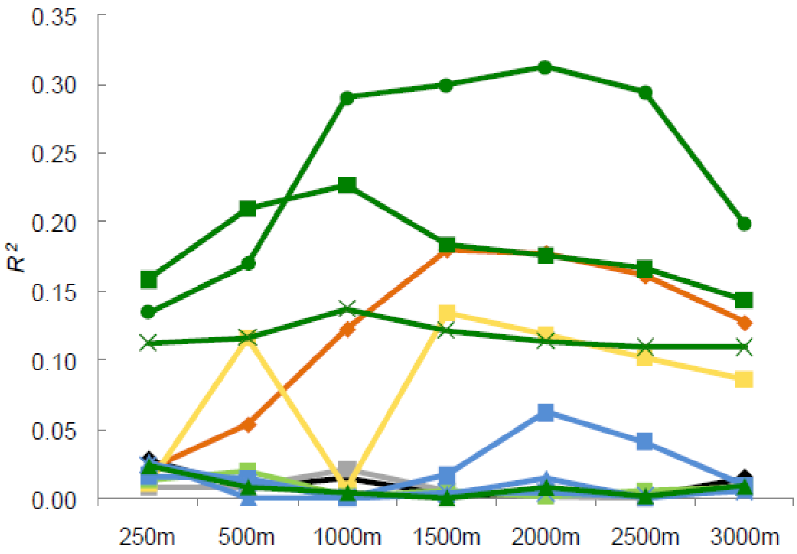
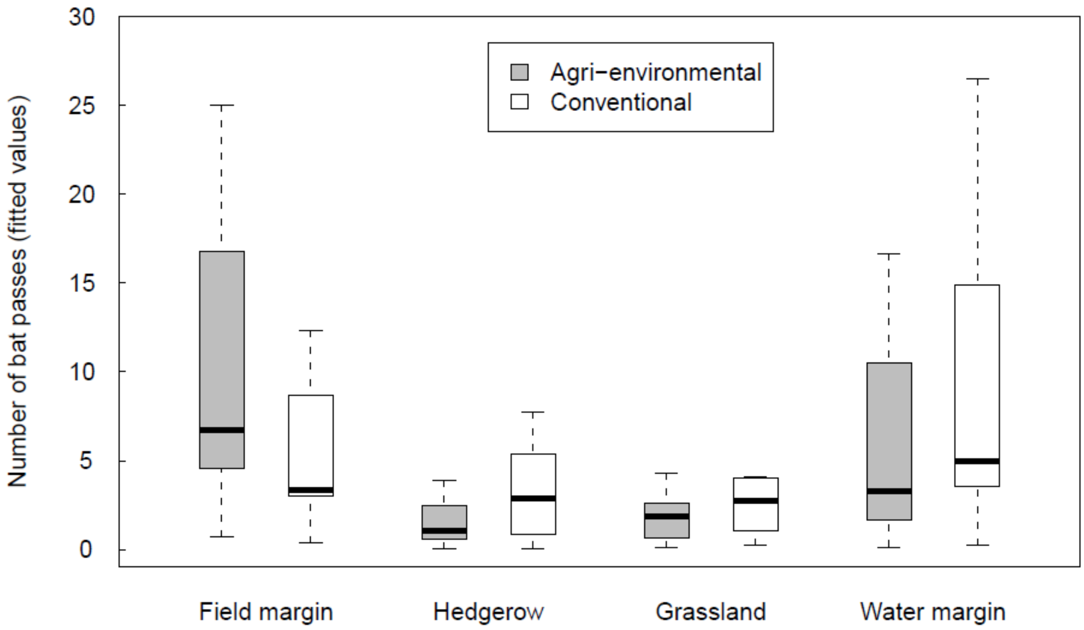


Figure 2.4. R^2 values obtained from regression analyses between landscape metrics at seven spatial scales and the number of bat passes of: a) *P. pygmaeus* and b) *P. pipistrellus*. Woodland-ENN at the 500 m scale was the only marginally significant ($p = 0.094$) R^2 value for *P. pygmaeus.* Significance values for *P. pipistrellus* and a description of the landscape metrics are shown in Table 2.1. LPI = largest patch index; ENN = Euclidean nearest neighbour distance; ED = edge density.

Table 2.5. Summary table showing bat passes recorded at agri-environmental and conventional farms.

	AES farms		Conventional farms		Total	
Bat pass classification	Number	% of all bat passes	Number	% of all bat passes	Number	% of all bat passes
Pipistrellus sp.	765	38.9	1156	58.8	1921	97.8
Myotis sp.	10	0.5	7	0.4	17	0.9
Plecotus auritus	4	0.2	1	0.1	5	0.3
Nyctalus sp.	3	0.2	0	0.0	3	0.2
Unknown bat	8	0.4	11	0.6	19	1.0
Pipistrellus pygmaeus	537	27.3	794	40.4	1331	67.7
Pipistrellus pipistrellus	159	8.1	312	15.9	471	24.0
Unknown *Pipistrellus* sp.	69	3.5	50	2.5	119	6.1
Social call	73		120		193	
Feeding buzz	37		85		122	
All bat passes	790	40.2	1175	59.8	1965	100.0

a) *P. pygmaeus*



b) *P. pipistrellus*

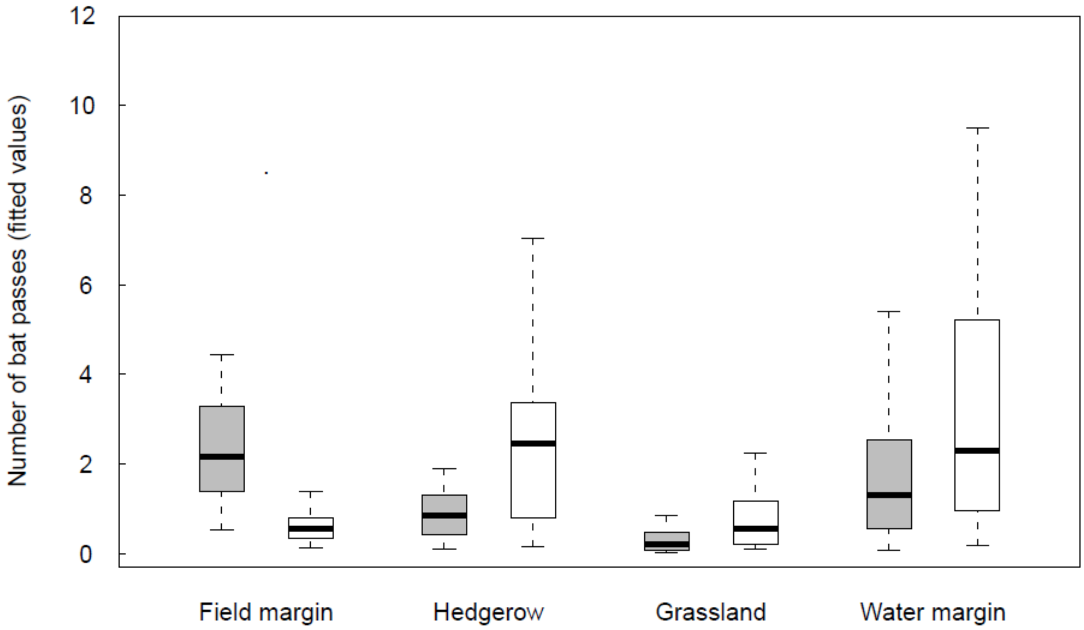


Figure 2.5. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the pair-wise comparisons between AES and conventionally-managed features for: a) *P. pygmaeus* and b) *P. pipistrellus*. Fitted values predicted by the GLMM at the feature level were used. Stars indicate significant differences within a habitat feature due to management type. Significance codes: $p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’.

2.5. Discussion

In this study we assessed the effectiveness of AES as they currently operate in Scotland on Pipistrelle bats and their insect prey. We also considered the influence of the surrounding landscape to assess the importance of a landscape-scale management approach for their conservation. We believe our results provide relevant information to be applied by land managers and policy makers involved in bat conservation.

2.5.1. Nocturnal insect abundance

Nearly 70% of the insects sampled were Diptera, which form the main diet of many European bats (including Pipistrelles), and over 10% were Trichoptera, which also form an important part of their diet (Vaughan 1997). Our results indicate that overall insect abundance (not including Lepidoptera) was almost twice as high on conventional farms compared to AES farms; insect abundance was significantly lower at three of the four AES prescriptions assessed in this study than at their equivalent conventionally-managed features, whilst biomass showed similar non-significant trends at both farm and feature levels. This indicates that food availability for Pipistrelle bats is actually lower in farms participating in AES than in non-participating farms. Whilst the mechanism for this reduced insect availability is currently unclear, one possible explanation for this outcome is that many AES prescriptions (e.g. field margins/beetlebanks) have been designed to enhance populations of predatory insects, while others are known to benefit some bird species (Newton 2004). Insectivorous birds and predatory insects are likely to prey on both the immature and adult stages of Diptera. Given that some AES prescriptions (e.g. management of species-rich grasslands) involve grazing restrictions, it is also possible that farms not involved in

AES have higher densities of grazing stock and, therefore, larger amounts of organic matter (dung) which are associated with high numbers of dung-dwelling insects, such as many Diptera (D'Arcy-Burt & Blackshaw 1991; McCracken, Foster & Kelly 1995).

Our results appear in contrast with other studies (e.g. Benton *et al.* 2002; Wickramasinghe *et al.* 2004), which have found that the abundance, biomass and diversity of aerial insects are negatively associated with agricultural intensification. However, conventional farms are not necessarily more intensively-managed than AES farms. In fact, our pairing design showed that attributes such as field size and density of linear features (which have been used as indices of agricultural intensification by other authors; e.g. Pocock & Jennings, 2008) were similar between AES and conventional farms (Appendix 2A in the supplementary material). It is also important to note that many insect groups (e.g. bumblebees, hoverflies and butterflies) show positive responses to the implementation of some AES (Albrecht *et al.* 2007; Lye *et al.* 2009). In particular, a parallel study conducted at the same sites as the bat surveys indicated that these same AES do benefit moth populations in agricultural environments (Chapter 3), which form the main diet of *P. auritus* in Scotland and other bat species (e.g. *Barbastella barbastellus*) in southern parts of the UK (Vaughan 1997). Therefore, AES could potentially benefit some bat species (e.g. moth-eating bats) by increasing foraging resources for them.

2.5.2. Bat activity

2.5.2.1. Effects of the surrounding landscape on bat activity

Several studies have highlighted differences in the diet, habitat selection and foraging range of the cryptic species *P. pygmaeus* and *P. pipistrellus* (e.g. Barlow 1997;

Vaughan, Jones & Harris 1997; Nicholls & Racey 2006a,b). In this study the two species responded differently to the composition and configuration of the surrounding landscape. Whilst activity of both species showed the strongest correlations with the configuration of woodland patches, the specific parameters (e.g. proximity between patches *vs.* edge density), the scale (distance from monitoring site) and the magnitude of the responses (R^2 values from regression analyses) were substantially different.

In general, individual landscape metrics explained a low proportion of variation (< 5%) in activity levels of *P. pygmaeus.* The proximity between woodland patches (ENN distance) within 500 m of the transects showed a negative non-significant correlation ($p = 0.094$) with this species' activity levels, meaning that as the distance between woodland patches increases, bat activity decreases. However, when woodland ENN was included along with other explanatory variables in subsequent models of *P. pygmaeus* activity, it became strongly significant, highlighting the importance of this landscape metric on this species when taking into account other environmental variables (e.g. temperature) and explanatory variables (e.g. land management type), and suggesting that this species requires a well-connected network of suitable habitat to capitalize on available resources. The fact that *P. pygmaeus'* strongest response to the landscape was shown at the 500 m scale concurs with previous information on its home range size (~ 500 ha; Nicholls & Racey 2006a). Given that *P. pygmaeus* has been reported to preferentially forage over riparian habitats (Nicholls & Racey 2006b), it was surprising that it did not respond to any of the landscape metrics involving water (although water ENN within 3 km of the transects showed a non-significant negative relationship with this species activity, only slightly weaker than that of woodland ENN within 500 m). It should be noted, however, that the amount of water (and variation between sites) was low in this study (1.26 ± 0.24% at the 3 km scale).

Pipistrellus pipistrellus responded strongly to the surrounding landscape (~ 30% of the variation in the data explained by a single landscape parameter). In particular, the percentage of woodland cover in the landscape and the spatial configuration of this habitat (e.g. edge density and largest patch index) were strongly positively correlated with the number of *P. pipistrellus* bat passes. These findings are in accordance with studies reporting this bat species preferentially forages around woodland edges (Walsh & Harris 1996). It has been well documented that woodland is an important habitat for many bat species because of both foraging and roosting opportunities (Vaughan, Jones & Harris 1997; Russ & Montgomery 2002; Smith & Racey 2008); a conservation management strategy involving the creation and management of woodland is therefore likely to benefit bat populations. Landscape heterogeneity (Shannon diversity index) was also strongly related to *P. pipistrellus* activity levels, suggesting that a highly diverse landscape enhances this species' foraging activity. The responses of this species to the landscape were strongest at the 1 – 2.5 km scale, which coincides with *P. pipistrellus* home range size (~ 1500 ha; Nicholls & Racey 2006a) being larger than that of *P. pygmaeus.* Although the magnitude of the responses of *P. pipistrellus* to the landscape declined at the largest scale evaluated (3 km), most were still statistically significant; this fact emphasizes the necessity of a wide-landscape-scale management approach to be incorporated in conservation efforts targeted to enhance populations of *P. pipistrellus*.

2.5.2.2. Effects of agri-environment schemes on bat activity

Unexpectedly, bat activity levels were generally lower on farms involved in AES than on conventionally-managed farms, in accordance with patterns of prey abundance. At the feature level, hedgerows, species-rich grasslands and water margins all showed no effect of participation within AES, although non-significant trends were towards higher levels of bat activity at conventionally-managed features than at AES prescriptions (note that models for the 'feature level' analysis were fitted using quasi-Poisson errors, which are less powerful than the Poisson errors used to fit the models for the 'farm level' analysis). This may be a result of the lower numbers of nocturnal insects on AES prescriptions than on their conventional counterparts, providing reduced food resources for foraging bats. Agri-environmentally-managed field margins were associated with marginally higher levels of bat activity (for *P. pipistrellus*) than conventionally-managed field margins. The selection by bats of linear features has been well documented (e.g. Verboom & Huitema 1997; Russ & Montgomery 2002; Downs & Racey 2006). AES field margins are wider and the vegetation is higher than in conventional ones (Lye *et al.* 2009), which might provide bats with better navigation landmarks than narrower linear features. Although we did not assess the correct implementation of AES prescriptions (e.g. differences in vegetation height and width when compared to conventionally-managed features), poor implementation could potentially explain the lack of benefits of AES for *P. pipistrellus* and *P. pygmaeus*. For instance, a parallel study conducted during the same year in a random subset (n = 5 farm pairs) of our field sites (Lye *et al.* 2009) found that although AES species-rich grasslands had slightly taller vegetation (1.30 *vs.* 1.00 m) than that of their conventional counterparts, they had fewer broad-leaved plant species and lower spring flower abundance. However, AES field margins and hedgerow margins were, on average, wider (6.20 *vs.* 1.81 m and 2.40 *vs.* 1.78 m, respectively) and the vegetation was taller (1.39 *vs.* 0.64 and 0.96 *vs.* 0.53 m, respectively) than that of their conventional counterparts; no information is available for water margins. These differences in the vegetation character of the habitat features suggest that these AES prescriptions have been implemented reasonably well in the field. However, our results raise questions on the value of these AES prescriptions as they currently operate and suggest the lack of benefits for bats and their prey derives from an inappropriate design. It is important to acknowledge that the AES management prescriptions assessed in this study were not specifically designed for bats. Nonetheless, our findings highlight the necessity of incorporating features selected by bats (e.g. tree lines; Walsh & Harris 1996) into AES management recommendations if Pipistrelle bats (and other bat species foraging on similar prey) are to benefit. Given the strong relations to woodland-related metrics shown by the two Pipistrelle species (*P. pipistrellus* in particular), AES prescriptions involving the creation and management of this habitat seem of great importance; more research is required to ensure they fulfil the requirements of bats.

It has been suggested that the effectiveness of AES is influenced by the landscape context and that AES are more effective in simple than in complex landscapes because structurally complex landscapes may compensate for local high-intensity management and enhance local diversity in agroecosystems (Tscharntke *et al.* 2005; Batáry *et al.* 2011). However, the landscape surrounding our study area was relatively simple (Batáry *et al.* 2011 consider landscapes with < 20 % of semi-natural environment as 'simple'), with farmland and urban areas comprising *ca.* 80% of the landscape within 1.5 km of the transects in both AES and conventional farms (Table 2A-1 in Appendix 2A). Hence, this possible interaction between AES management and the landscape context is unlikely to be the cause of the lack of benefits of AES for bats and nocturnal insects in our study. Given that the proportion of non-AES farmers who refused to participate in our study when first approached was relatively high (although quantitative data is not available), it is also possible that the lack of benefits of AES we observed was due to a non-representative sample of non-AES farmers. Conventional farmers who agreed to participate may potentially be more inclined towards environmental issues than farmers who chose not to take part in the study. If this was the case, differences between AES and conventional farms may have been minimised. However, a parallel study focussing on the effectiveness of AES on moths (Chapter 3), conducted in the same sites and during the same year, found positive effects of the implementation of AES; therefore, the possibility of an unrepresentative subset of non-AES farms having obscured the effects of AES is unlikely.

2.5.3. Limitations

i) Temporal variations: Our study was conducted during one year only and we performed a single survey per farm. We recognise that bat activity and insect populations may show large variations between and within years. In addition, previous research has found that the value of AES may vary seasonally (e.g. Carvell *et al.* 2007). We believe that our pairing design improves the robustness of our results despite the mentioned constraints. Nonetheless, future work should consider the potential importance of seasonal interactions. ii) Sample size: Our sample size compares reasonably well with similar studies using paired designs (e.g. Wickramasinghe *et al.* 2003; Gibson *et al.* 2007; Bates & Harris 2009) and it allowed us to find significant differences due to management type for insect abundance and bat activity at the farm level. When data were analysed at the feature level the direction of the differences between AES and conventional remained the same (with the exception of field margins) but these were no longer statistically significant. Therefore, it is unlikely that lack of statistical power at the feature level resulted in our not detecting a positive effect of

AES prescriptions on bat activity. iii) Geographic area: Lastly, our results reflect the effectiveness of the Scottish RSS (although the specific management prescriptions evaluated in our study are widely used in other AES in the UK and Europe), and they may have geographic limitations.

2.6. Conclusions

In summary, our findings demonstrate that the implementation of most AES management prescriptions assessed does not benefit foraging Pipistrelle bats; overall, there was significantly lower activity of both *P. pipistrellus* and *P. pygmaeus,* and fewer prey insects on farms with AES prescriptions compared to conventional farms. Only AES field margins had non-significant trends towards higher levels of bat activity than their conventionally-managed counterparts; AES field margins may benefit bats by providing them with better navigation landmarks than narrower linear features. The surrounding landscape significantly affected bat activity. Fragmentation metrics related to woodland configuration were the most important landscape characteristics influencing bat activity levels. Furthermore, the effects of the surrounding landscape on Pipistrelle bats (particularly on *P. pipistrellus*) were significant even at large spatial scales (e.g. 3 km). These findings have important conservation management implications. We suggest that the AES management prescriptions assessed here have had no positive effect on Pipistrelle bats or their insect prey and that the implementation of AES prescriptions applied to relatively small areas is not enhancing their populations in agricultural environments. A landscape-scale management approach – with a focus on the creation and management of woodland and woodland edge habitat – seems essential to effectively contribute to the conservation of bats.

2.7. Acknowledgements

We would like to thank the Scottish Government for providing information on farms participating in the RSS, the landowners and Estate managers who granted us access to their land, R. Trodden, L. Dockray and G. Lye for their logistic assistance and help with fieldwork, J. Smith for her help with insect identification, M. Vallejo-Marín and J. Minderman for their advice on statistical analyses, M. O'Brien for initial advice on agri-environment scheme data, D. Chamberlain and two anonymous reviewers for their valuable comments on this manuscript. We would also like to thank CONACyT for providing a graduate scholarship (189261) to E.F.M., and the People's Trust for Endangered Species for their financial support.

Appendix 2A. Details of pairing design.

Table 2A-1. Summary table showing statistical analyses to check that pairing between AES and conventional farms was adequate. No significant differences were found for any of the attributes.

Attribute	AES farms (mean ± SE)	Conventional farms (mean ± SE)	*t* [a]	*p*	Statistical analysis
Farm altitude (m)	110.44 ± 17.86	92.50 ± 13.16	1.28	0.217	Paired t-test
Farm mean field area (ha)	7.87 ± 0.86	7.56 ± 0.99	0.25	0.805	Paired t-test
Farm field perimeter : field area (m/ha)	161.36 ± 8.10	171.42 ± 11.08	-0.77	0.450	Paired t-test
Farm green linear features : field area (m/ha) [b]	29.42 ± 3.54	34.82 ± 5.08	-1.03	0.318	Paired t-test
Farmland within 250 m of transect (%)	83.54 ± 2.30	85.74 ± 2.40	53.00	0.163	Wilcoxon
Woodland within 250 m of transect (%)	9.61 ± 1.47	9.02 ± 2.06	95.00	0.695	Wilcoxon
Urban areas within 250 m of transect (%)	1.36 ± 0.17	1.74 ± 0.34	311.00	0.954	Wilcoxon
Farmland within 1.5 km of transect (%)	78.50 ± 3.76	77.27 ± 3.21	104.00	0.433	Wilcoxon
Woodland within 1.5 km of transect (%)	12.88 ± 1.91	14.56 ± 2.60	67.00	0.433	Wilcoxon
Urban areas within 1.5 km of transect (%)	1.76 ± 0.22	2.47 ± 0.49	228.00	0.157	Wilcoxon

[a] *t* values are shown when the data were normally distributed and paired *t*-tests could be performed. Wilcoxon statistics are shown when normality could not be achieved and Wilcoxon signed-rank tests were used.

[b] Green linear features included hedgerows and tree lines.

Table 2A-2. Percentage of bat monitoring transect covered by each AES prescription or equivalent conventionally-managed feature.

Habitat feature	AES farms [a] (mean ± SE)	Conventional farms (mean ± SE)
Field margin	33.34 ± 2.49 %	35.17 ± 2.90 %
Hedgerow	16.67 ± 1.41 %	18.83 ± 2.02 %
Water margin	21.03 ± 2.55 %	19.88 ± 2.06 %
Species-rich grassland	13.79 ± 2.22 %	10.90 ± 1.76 %
Woodland [b]	13.37 ± 2.42 %	11.15 ± 2.45 %
Urban [c]	1.80 ± 0.91 %	4.07 ± 1.56 %
Combined [d]	17.49 ± 4.11 %	8.35 ± 3.22 %

[a] Includes conventionally-managed features within AES farms (70.71 ± 2.39 %of the transects within AES farms was managed under AES prescriptions).

[b] Woodland was not an AES prescription.

[c] Includes buildings and tracks.

[d] Percentage of transect in which there were several habitat features within 20 m of the recording location (e.g. hedgerow adjacent to water margin).

Appendix 2B. Correlation matrices of landscape parameters.

Table 2B-1. Correlation matrix of landscape parameters within 250 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI
URBAN%	0.086						
FARMLAND%	**-0.969 *** **	-0.054					
WATER%	0.322 ◌̇	-0.089	-0.268				
NATURAL%	**0.645 *** **	-0.192	**-0.615 *** **	0.047			
WOODLAND%	**0.805 *** **	-0.021	**-0.880 *** **	0.190	0.220		
WOOD.LPI	**0.519 *** **	0.129	**-0.650 *** **	-0.015	0.041	**0.806 *** **	
WOOD.ED	**0.613 *** **	0.297 ◌̇	**-0.613 *** **	0.179	-0.050	**0.745 *** **	**0.524 *** **

Table 2B-2. Correlation matrix of landscape parameters within 500 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED
URBAN%	0.147							
FARMLAND%	**-0.954 *** **	-0.105						
WATER%	**0.434 ** **	-0.084	**-0.392 ** **					
NATURAL%	**0.597 *** **	-0.179	**-0.601 *** **	0.029				
WOODLAND%	**0.843 *** **	0.021	**-0.918 *** **	**0.382 * **	0.288 ◌̇			
WOOD.LPI	**0.620 *** **	0.171	**-0.752 *** **	0.175	0.261	**0.791 *** **		
WOOD.ED	**0.630 *** **	0.325 ◌̇	**-0.595 *** **	0.240	-0.005	**0.683 *** **	0.308 ◌̇	
WOOD.ENN	**-0.400 * **	-0.142	**0.351 * **	-0.257	0.054	**-0.426 ** **	-0.206	**-0.699 *** **

Table 2B-3. Correlation matrix of landscape parameters within 1000 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED	WOOD. ENN	WATER. ENN
URBAN%	0.306 ◌̇									
FARMLAND%	**-0.668** ***	**-0.442** ***								
WATER%	0.049	**0.472** **	**-0.714** ***							
NATURAL%	**0.500** **	-0.185	**-0.443** **	-0.047						
WOODLAND%	**0.816** ***	0.013	**-0.493** **	-0.169	0.319 ◌̇					
WOOD.LPI	**0.591** ***	0.192	**-0.447** **	-0.060	0.150	**0.812** ***				
WOOD.ED	**0.679** ***	0.207	-0.253	-0.209	0.046	**0.714** ***	**0.406** *			
WOOD.ENN	**-0.519** ***	**-0.364** *	**0.399** *	-0.174	-0.018	**-0.414** *	-0.258	**-0.629** ***		
WATER.ENN	-0.209	-0.275	0.232	-0.169	-0.046	-0.097	-0.064	-0.260	**0.439** **	
WATER.LPI	0.067	**0.483** **	**-0.714** ***	**0.997** ***	-0.050	-0.164	-0.058	-0.202	-0.177	-0.171

Table 2B-4. Correlation matrix of landscape parameters within 1500 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED	WOOD. ENN	WATER. ENN
URBAN%	**0.413** *									
FARMLAND%	**-0.892** ***	-0.251								
WATER%	**0.721** ***	**0.423** **	**-0.603** ***							
NATURAL%	**0.485** **	-0.194	**-0.664** ***	0.090						
WOODLAND%	**0.810** ***	0.206	**-0.908** ***	**0.603** ***	**0.348** *					
WOOD.LPI	**0.481** **	0.304 ◌̇	**-0.639** ***	**0.463** **	0.065	**0.785** ***				
WOOD.ED	**0.741** ***	**0.420** *	**-0.652** ***	**0.612** ***	0.084	**0.740** ***	**0.460** **			
WOOD.ENN	**-0.622** ***	**-0.337** *	**0.473** **	**-0.489** **	-0.032	**-0.543** ***	-0.245	**-0.763** ***		
WATER.ENN	-0.252	-0.273	0.158	-0.268	-0.050	-0.098	-0.081	**-0.370** *	**0.458** **	
WATER.LPI	**0.585** ***	**0.360** *	**-0.452** **	**0.913** ***	0.113	**0.385** *	0.243	**0.378** *	**-0.398** *	-0.223

Table 2B-5. Correlation matrix of landscape parameters within 2000 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED	WOOD. ENN	WATER. ENN
URBAN%	**0.400 ***									
FARMLAND%	**-0.890 *****	-0.219								
WATER%	**0.702 *****	**0.395 ***	**-0.614 *****							
NATURAL%	**0.474 ****	-0.220	**-0.645 *****	0.060						
WOODLAND%	**0.804 *****	0.173	**-0.907 *****	**0.643 *****	0.318 ◌̇					
WOOD.LPI	**0.460 ****	0.236	**-0.605 *****	**0.462 ****	0.001	**0.776 *****				
WOOD.ED	**0.789 *****	**0.402 ***	**-0.704 *****	**0.679 *****	0.091	**0.793 *****	**0.503 ****			
WOOD.ENN	**-0.630 *****	**-0.396 ***	**0.463 ****	**-0.495 ****	0.048	**-0.557 *****	-0.256	**-0.800 *****		
WATER.ENN	-0.226	-0.260	0.105	**-0.346 ***	0.044	-0.078	-0.037	**-0.353 ***	**0.413 ***	
WATER.LPI	**0.611 *****	**0.403 ***	**-0.527 *****	**0.929 *****	0.090	**0.500 ****	0.320 ◌̇	**0.505 ****	**-0.427 ****	-0.290 ◌̇

Table 2B-6. Correlation matrix of landscape parameters within 2500 m of transects. Pearson correlation values and significance codes are given ($p \leq 0.001$ ‘ *** ‘, $p \leq 0.01$ ‘ ** ‘, $p \leq 0.05$ ‘ * ’, $p \leq 0.1$ ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED	WOOD. ENN	WATER. ENN
URBAN%	**0.397 ***									
FARMLAND%	**-0.896 *****	-0.203								
WATER%	**0.639 *****	0.310 ◌̇	**-0.560 *****							
NATURAL%	**0.566 *****	-0.142	**-0.719 *****	0.141						
WOODLAND%	**0.789 *****	0.135	**-0.895 *****	**0.553 *****	**0.388 ***					
WOOD.LPI	**0.472 ****	0.180	**-0.576 *****	**0.361***	0.055	**0.767 *****				
WOOD.ED	**0.765 *****	**0.366 ***	**-0.697 *****	**0.591 *****	0.166	**0.794 *****	**0.504 ****			
WOOD.ENN	**-0.562 *****	**-0.369 ***	**0.436 ****	**-0.439 ****	0.028	**-0.552 *****	-0.266	**-0.775 *****		
WATER.ENN	-0.105	-0.261	0.071	-0.277	0.080	-0.067	-0.013	**-0.344 ***	**0.355 ***	
WATER.LPI	**0.507 ****	0.301 ◌̇	**-0.449 ****	**0.934 *****	0.148	**0.385 ***	0.205	**0.371 ***	-0.324 ◌̇	-0.267

Table 2B-7. Correlation matrix of landscape parameters within 3000 m of transects. Pearson correlation values and significance codes are given (*p* ≤ 0.001 ‘ *** ‘, *p* ≤ 0.01 ‘ ** ‘, *p* ≤ 0.05 ‘ * ’, *p* ≤ 0.1 ’ ◌̇ ’). A description of each landscape metric is available from Table 2.1 on the main manuscript. LPI = Largest Patch Index; ED = Edge Density; ENN = Euclidean Nearest Neighbour Distance.

	Shannon	URBAN%	FARMLAND%	WATER%	NATURAL%	WOODLAND%	WOOD. LPI	WOOD. ED	WOOD. ENN	WATER. ENN
URBAN%	0.314 ◌̇									
FARMLAND%	**-0.901 *** **	-0.142								
WATER%	**0.529 *** **	0.089	**-0.442 ** **							
NATURAL%	**0.637 *** **	-0.121	**-0.775 *** **	0.131						
WOODLAND%	**0.781 *** **	0.067	**-0.890 *** **	**0.411 * **	**0.453 ** **					
WOOD.LPI	**0.497 ** **	0.132	**-0.573 *** **	0.212	0.142	**0.756 *** **				
WOOD.ED	**0.743 *** **	**0.342 * **	**-0.705 *** **	**0.460 ** **	0.238	**0.795 *** **	**0.536 *** **			
WOOD.ENN	**-0.563 *** **	**-0.372 * **	**0.479 ** **	**-0.404 * **	-0.073	**-0.562 *** **	-0.286 ◌̇	**-0.771 *** **		
WATER.ENN	-0.083	-0.312 ◌̇	0.059	-0.220	0.130	-0.086	-0.001	**-0.390 * **	**0.384 * **	
WATER.LPI	**0.448 ** **	0.152	**-0.393 * **	**0.877 *** **	0.195	0.283 ◌̇	0.095	0.227	-0.244	-0.187

Appendix 2C. Details on model selection (information-theoretic approach based on $\mathrm{AIC_C}$).

For the “farm level” analysis, an information-theoretic approach to model selection based on $\mathrm{AIC_C}$ was adopted. For each response variable, we compared models with every possible combination of explanatory variables – management, activity, altitude, temperature, date and a landscape parameter (except for ‘feeding buzzes’ and ‘feeding buzz ratio’ models). Table 2C-1 summarizes the most parsimonious models within a 95% confidence interval – based on relative probabilities of each model being the best model ($\mathrm{AIC_C}$ weights) – but it is not a comprehensive list of all the models compared. For each response variable, different numbers of models appear in Table 2C-1 because this depended on the particular set of models compared (95% confidence intervals are constructed by starting with the model with the highest $\mathrm{AIC_C}$ weight and repeatedly adding the model with the next highest weight until the cumulative $\mathrm{AIC_C}$ weight exceeds 0.95). For most response variables, there was little model uncertainty ($\mathrm{AIC_C}$ weight of the most parsimonious model much higher than those of other models; Table 2C-1). In cases where there was considerable model uncertainty, the relative importance (sum of $\mathrm{AIC_C}$ weight of all models within the 95% confidence set which include a specific predictor) of significant predictors from the most parsimonious model was high (Table 2C-1), indicating that a predictor was highly likely to be included in possible alternative models within the 95% confidence interval.

Table 2C-1. The 95% confidence (based on AIC$_C$ weights) set of models for each response variable. Each first model corresponds to the most parsimonious model (lowest AIC$_C$). The relative importance of each explanatory variable (sum of wAIC$_C$ of all models within the 95% confidence set which include that variable) is shown. Landscape parameters included in the models varied depending on the response variable being assessed. Percentage cover of semi-natural environment at the 500 m scale was used for insect abundance and biomass, woodland ENN at the 500 m scale was used for *P. pygmaeus* and woodland ED at the 2 km scale was used for *P. pipistrellus*. No landscape parameters were included in the models for 'feeding buzzes' and 'feeding buzz ratio'.

Insect abundance	Rank	ΔAIC$_C$	wAIC$_C$	ModLikAIC$_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.423	1.000	X		X	X		
	2	0.201	0.383	0.904	X		X	X	X	
	3	2.748	0.107	0.253	X	X	X	X	X	
	4	3.181	0.086	0.204	X	X	X	X		
Relative importance					1.000	0.194	1.000	1.000	0.490	0.000
Insect biomass	Rank	ΔAIC$_C$	wAIC$_C$	ModLikAIC$_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.583	1.000						
	2	3.393	0.107	0.183					X	
	3	3.738	0.090	0.154		X				
	4	3.829	0.086	0.147	X					
	5	5.162	0.044	0.076		X			X	
	6	5.842	0.031	0.054			X			
	7	7.391	0.014	0.025	X				X	
Relative importance					0.100	0.134	0.031	0.000	0.165	0.000
P. pygmaeus	Rank	ΔAIC$_C$	wAIC$_C$	ModLikAIC$_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.461	1.000	X		X			
	2	1.662	0.201	0.436	X		X		X	
	3	2.601	0.126	0.272	X		X	X		
	4	3.499	0.080	0.174	X	X	X			
	5	4.406	0.051	0.111	X		X	X	X	
	6	5.597	0.028	0.061	X	X	X		X	
	7	6.442	0.018	0.040	X	X	X	X		
Relative importance					0.965	0.127	0.965	0.195	0.280	0.000

Table 2C-1 (cont.)

P. pipistrellus	Rank	ΔAIC_C	$wAIC_C$	$ModLikAIC_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.495	1.000	X		X	X		
	2	0.882	0.318	0.644	X		X	X	X	
	3	4.580	0.050	0.101	X		X			
	4	5.461	0.032	0.065	X		X		X	
	5	5.668	0.029	0.059	X	X	X	X		
	6	6.321	0.021	0.042	X	X	X	X	X	
	7	7.697	0.011	0.021	X	X	X		X	
Relative importance					0.956	0.061	0.956	0.863	0.382	0.000
Feeding buzzes	Rank	ΔAIC_C	$wAIC_C$	$ModLikAIC_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.150	1.000	X		-			
	2	0.067	0.145	0.967	X		-		X	X
	3	0.401	0.123	0.818	X		-	X		
	4	0.881	0.096	0.644	X		-			X
	5	1.109	0.086	0.574	X	X	-	X		
	6	1.300	0.078	0.522	X		-		X	
	7	1.444	0.073	0.486	X	X	-			
	8	1.449	0.073	0.485	X		-	X	X	
	9	2.072	0.053	0.355	X		-	X	X	X
	10	2.219	0.049	0.330	X	X	-	X	X	
	11	3.125	0.031	0.210	X		-	X		X
Relative importance					0.957	0.208	-	0.415	0.398	0.326
Feeding buzz ratio	Rank	ΔAIC_C	$wAIC_C$	$ModLikAIC_C$	Management	Activity	Landscape	Altitude	Temperature	Date
	1	0.000	0.925	1.000			-			
	2	6.479	0.036	0.039	X		-			
Relative importance					0.036	0.000	-	0.000	0.000	0.000

Chapter 3

The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach

An adapted version of this chapter has been published as:

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3.1. Summary

Agricultural intensification and expansion are regarded as major causes of worldwide declines in biodiversity during the last century. Agri-environment schemes (AES) have been introduced in many countries as an attempt to counteract the negative effects of intensive agriculture by providing financial incentives for farmers to adopt environmentally-sensitive agricultural practices. We surveyed 18 pairs of AES and conventionally-managed farms in central Scotland (UK) to evaluate the effects of specific AES management prescriptions (field margins, hedgerows, species-rich grasslands and water margins) on farmland moths. We also measured the influence of the surrounding landscape on moth populations at three spatial scales (250 m, 500 m and 1 km radii from each trapping site) to assess at which scale management was most important for the conservation of farmland moths. In general, percentage cover of rough grassland and scrub within 250 m of the trapping site was the most important landscape predictor for both micro- and macromoth abundance and macromoth species richness, although negative effects of urbanisation were found at wider scales (within 1 km), particularly for macromoth species richness. The abundance and species richness of micromoths was significantly higher within field margins and species-rich grasslands under AES management in comparison to their conventional counterparts, whereas AES water margins increased micromoth abundance, but not species richness. AES species-rich grasslands and water margins were associated with an increased macromoth abundance and species richness, and macromoths considered "widespread but rapidly declining" also gained some benefits from these two AES prescriptions. In contrast, hedgerows under AES management enhanced neither micromoth nor macromoth populations. *Synthesis and applications:* Our findings indicate that increasing the percentage cover of semi-natural environment at a local scale (e.g. within

250 m) benefits both micro- and macromoth populations, and that the implementation of simple AES management prescriptions applied to relatively small areas can increase the species richness and abundance of moth populations in agricultural environments.

3.2. Introduction

Declines in farmland biodiversity during the last century have been widely attributed to the intensification and expansion of modern agricultural practices (Krebs *et al.* 1999; Robinson & Sutherland 2002). This is of particular concern in the United Kingdom (UK) where approximately 75% of land is classed as agricultural (DEFRA 2008). Agri-environment schemes (AES) have been introduced in Europe and North America as an attempt to reverse declines in farmland biodiversity by providing financial incentives for farmers to adopt less intensive, environmentally-sensitive agricultural practices. Approximately 45% of agricultural land in the UK is under AES management (DEFRA 2008) and large amounts of money are spent by the government on these schemes. For instance, the EU funded the UK Rural Development Programme 2007 - 2013 with nearly €9 billion to support sustainable agriculture throughout the countryside (DEFRA 2008). Despite these high financial inputs, the implementation of AES has had mixed results for different taxa (Kleijn *et al.* 2006). Monitoring and evaluation of these schemes is imperative in order to improve their efficiency and maximize the conservation outcomes. It has been argued that uncommon species rarely benefit from these schemes (Hole *et al.* 2005; Kleijn *et al.* 2006; but see Merckx *et al.* 2010a). It has also been suggested that the effectiveness of AES depends on species' mobility (Merckx *et al.* 2009a), and that a landscape-scale management approach may be more beneficial than small-scale AES prescriptions (Donald & Evans 2006; Merckx *et al.* 2009b).

Lepidoptera are one of the most abundant and diverse insect orders, including more than 150,000 named species (Chinery 1993). They are commonly, but arbitrarily, divided into macrolepidoptera (a group of moth families containing mostly large species, “macromoths”, plus all butterfly families) and microlepidoptera or “micromoths” (a group of moth families comprising mostly smaller species), of which *ca.* 900 and 1700 species occur in the UK, respectively (Chinery 1993; Townsend & Waring 2007). Moths are an important food resource for many species of birds, bats and small mammals (Vaughan 1997; Wilson *et al.* 1999). They are also considered a sensitive indicator group for biodiversity (Jennings & Pocock 2009). To date, ecological research and conservation efforts for Lepidoptera have been largely focused on butterflies, with relatively little attention given to macromoths and even less to the conservation status and habitat requirements of micromoths, which comprise a large proportion of most local lepidopteran assemblages (Bland & Young 1996; New 2004). Some authors consider that the most important threat to moths is habitat change, involving fragmentation and loss of prime natural and semi-natural vegetation biotopes through the expansion of modern agricultural practices (Conrad *et al.* 2004; New 2004). Over a period of 35 years, over two-thirds of 337 common and widespread macromoth species studied by Conrad *et al.* (2006) showed significant population declines in Britain. Furthermore, for some of these species the declines have been so severe that if IUCN criteria were to be applied at a national scale, 71 species would be regarded as threatened (Conrad *et al.* 2006). These species have now been added to the UK Biodiversity Action Plan (BAP) priority species list, labelled as ‘widespread and common, but rapidly declining – research only’. The BAP working group mentions the need for research to look at wide changes in the countryside that may be affecting their populations (Fox *et al.* 2006).

Previous studies have shown positive effects of organic farming on moth populations (Wickramasinghe *et al.* 2004; Taylor & Morecroft 2009). Organic farming currently represents a very small proportion of the land area in the UK (*ca.* 2%; DEFRA 2008), so it may offer limited benefits to these groups on a large scale. In contrast, land under agri-environment schemes (other than organic farming) covers a much larger proportion (45%) of the UK's agricultural areas and there is evidence that some of these schemes may also benefit moth populations (Merckx *et al.* 2009a,b; Taylor & Morecroft 2009). However, to the best of our knowledge, at a local scale, only AES field margins and hedgerow trees as management options have been assessed and these studies deal exclusively with macromoths (Merckx *et al.* 2009a,b). Furthermore, although Merckx *et al.* (2009b) show that the degree of landscape-scale AES uptake matters, the direct impact of land-use composition of the surrounding landscape on moth communities has rarely been assessed (but see Ricketts *et al.* 2001; Summerville & Crist 2004; Kivinen *et al.* 2006; Ekroos, Heliölä & Kuussaari 2010). Hence, Merckx *et al.* (2009a,b)'s recommendation for moving from a field/farm-scale to a landscape-scale approach for farmland moth conservation requires further testing. Given that micromoths are usually low mobility species (Nieminen, Rita & Uuvana 1999), it is likely that they might be most influenced by their immediate surroundings and hence show stronger responses to AES applied at local scales than high mobility species (e.g. certain macromoths such as Noctuids). As a result, the latter might be more affected by the surrounding landscape at relatively larger scales (Ricketts *et al.* 2001) and may require a wider-scale conservation strategy (Merckx *et al.* 2009a).

To the best of our knowledge only one published study has compared biodiversity metrics of AES, as operated within Scotland, to conventional farming, and this study focused on the availability of foraging and nesting habitat resources for bumblebee queens (Lye *et al.* 2009). Here, we assess the benefits (or otherwise) of four different AES management prescriptions and the influence of the surrounding landscape at three spatial scales on farmland moth communities in Scotland. We addressed three questions in particular:

1. Do farmland moths benefit from common AES and, if so, which specific AES management options have the greatest effect on farmland moth abundance and diversity?
2. Is a landscape-scale management approach important for the conservation of farmland moths and, if so, which is the more appropriate scale?
3. Does the effectiveness of AES differ between micro- (low mobility) versus macro- (high mobility) moth species and, if so, are different conservation strategies required to enhance micro- and macromoth populations?

3.3. Materials and methods

3.3.1. Study sites

We used a paired survey design to quantify moth abundance and species richness on 18 pairs of AES and conventional farms in central Scotland (Fig.2.1 in Chapter 2) between June and September 2008. We selected 18 farms participating in the Scottish Rural Stewardship Scheme (RSS) since 2004. Each farm incorporated at least three of the following AES management prescriptions: a) field margins or beetlebanks; b) hedgerows; c) water margins; and d) species-rich grasslands. The following descriptions have been modified from Anonymous (2006).

a) *Management of field margins or beetlebanks in arable fields.* This prescription aims to provide habitat for beneficial insects, and cover and food for birds. It involves the creation and management of strips between 1.5 m and 6 m in width sowed with a suitable mix of grass seed, which may be located around or across an arable field. Fertiliser, pesticide and grazing restrictions apply.

b) *Management of hedgerows.* This prescription is aimed at providing improved habitat for invertebrates, birds and small mammals. It targets existing hedgerows and involves restrictions on pesticide input. Gaps in the hedge must be filled in, the hedge bottom must not be mown, cutting is restricted to once every three years and timing restrictions apply.

c) *Management of water margins.* This prescription aims to protect water margins from erosion and permit development of tall waterside vegetation for the benefit of freshwater life, invertebrates, water voles, otters and bats. It targets land bordering still water or watercourses. The water margin must be at least 3 m wide and fertiliser, pesticide, mowing and grazing restrictions apply.

d) *Creation and management of species-rich grassland.* This prescription aims to convert arable or improved grassland to species-rich grassland for the benefit of pollinator species such as butterflies and bumblebees. Its creation involves the destruction of any previously existing grassland cover and the establishment of a new sward by sowing the land with a low productivity grass and herb mix. Fertiliser and pesticides input restrictions apply, and mowing and grazing are not allowed during the summer.

We paired each AES farm with nearby conventionally-managed farms to act as counterparts. These were not involved in any AES and are referred to as conventional farms hereafter. Each of these conventional farms was within 8 km of its corresponding AES farm, conducted similar farming activities (arable, pastoral or mixed; 7, 2, and 9 pairs of farms respectively) and was of similar size (difference within paired sites 63 ± 36 ha; mean ± SE). In each conventional farm we selected conventionally-managed field margins, hedgerows and water margins to compare with the equivalent habitat features under AES management. The selection of conventionally-managed features was performed carefully to control for as many variables as possible other than AES management. Activities conducted in adjacent fields (pastoral or arable) and proximity to non-targeted features such as woodland and roads were considered in the pairing design. AES species-rich grasslands were compared to either improved pasture or crop fields in the conventional farms; the selection of either of these two habitats was based upon land use of the species-rich grassland prior to AES conversion.

3.3.2. Sampling methods

We sampled each farm once during the summer of 2008. Farms within a pair (one AES farm and its conventional counterpart) were surveyed simultaneously in order to minimize the effects of weather variation on insect abundance. Temperature and wind speed were recorded on each farm immediately before and after sampling. If temperature fell below 8˚C, wind force exceeded Beaufort scale 4, or heavy rain occurred, sampling was abandoned. Moths were caught using portable 6 W heath light traps (3 – 4 traps per farm, depending on the number of AES prescriptions present at each site) powered with 12 V batteries. The traps were ≥ 100 m apart from each other to prevent the light traps from interfering with each other (Dodd, Lacki & Rieske 2008; Merckx *et al.* 2009b). The traps were activated 15 minutes after sunset adjacent to each AES management prescription (or equivalent conventional feature) and switched off after 4 hours using automatic timers. The light traps were then sealed and transported to the laboratory. The collected insects were euthanized by dropping a cotton pad soaked with ethyl acetate into each trap and left overnight. Micromoths were wrapped in tissue paper and placed in sample bottles for later identification; individuals were dissected to examine genitalia whenever species identification required it. Macromoths were pinned for later identification following Townsend & Waring (2007). Rarer moths were unavoidably killed along with other insects after collection. However, trapping took place during one night only at each site, which is unlikely to adversely affect populations. No species protected under the UK's Wildlife and Countryside Act 1981 (as amended) were collected.

3.3.3. Landscape analysis

Using data from OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service), we used ArcGIS 9.2 (ESRI Inc. 2006) to create circles of 250 m, 500 m and 1 km radius around the location of each trap. We selected these three different scales because the smallest (250 m) covers the dispersal distances of low mobility moth species, whereas the largest (1 km) approximates an upper limit to dispersal distances of many moth species (Nieminen, Rita & Uuvana 1999; Doak 2000; Ricketts *et al.* 2001; Summerville & Crist 2004; Merckx *et al.* 2009a). We reclassified the feature classes from the topography layers into five categories (hereafter referred to as biotope types). These were: 1) urban areas (buildings, structures and roads); 2) farmland (both AES and conventionally-managed); 3) water (inland and tidal water); 4) semi-natural environment (rough grassland and scrub); and 5) woodland (coniferous, deciduous and mixed trees and areas covered by scattered trees). We then used Fragstats 3.3 (McGarigal *et al.* 2002) to calculate a selection of landscape metrics for each biotope type within the circles, including the proportion of land covered, the number of patches, mean patch area, total edge density, area-perimeter ratio and Euclidean nearest neighbour distance. A Shannon diversity index taking into account the number of different biotopes and their proportional abundance was also computed as a measure of landscape heterogeneity.

3.3.4. Data analysis

We calculated diversity indices for micro- and macromoths using PAST (Hammer, Harper & Ryan 2001). We selected the α log series diversity index because of its good discriminant ability, its low sensitivity to sample size and the fact that a number of previous studies have shown the index to be particularly suited to the description of moth populations (Taylor, Kempton & Woiwod 1976; Magurran 1988).

All statistical analyses were conducted using R version 2.11 (R Development Core Team 2010). Linear regression analyses were used to evaluate the effect of a selection of landscape parameters at different spatial scales (Table 3.1) on moth abundance, richness and diversity in order to select the parameter that explained the highest variation in moth communities (highest R^2 value); this was later included as one of the potential explanatory variables in subsequent models. To avoid pseudo-replication caused by overlapping buffers within sites, one trap per farm was randomly selected to be included in this analysis. We then performed Generalised Linear Mixed-Effects Models (GLMMs; Bates & Maechler 2009; Zuur *et al.* 2009) to determine which of the variables evaluated had the greatest effect on farmland moths (the response variables are listed in Table 3.2). The following factors were included in the

Table 3.1. Description and summary statistics (mean ± SE) of landscape metrics used for landscape analysis and GLMMs.

Landscape metric	Description	Scale		
		250 m	500 m	1 km
Shannon diversity [a]	Index of landscape heterogeneity. Equals minus the sum, across all biotope types, of the proportional abundance of each biotope type multiplied by that proportion.	0.32 ± 0.02	0.45 ± 0.02	0.57 ± 0.02
% Urban	Percentage of the landscape comprised of buildings, structures and roads.	2.16 ± 0.22	2.41 ± 0.18	3.06 ± 0.21
% Farmland	Percentage of the landscape comprised of agricultural land.	89.34 ± 1.09	86.02 ± 1.02	82.19 ± 1.03
% Water	Percentage of the landscape comprised of inland and coastal water.	0.42 ± 0.15	0.51 ± 0.18	0.72 ± 0.14
% Semi-natural	Percentage of the landscape comprised of rough grassland and scrub.	2.75 ± 0.67	2.59 ± 0.44	2.65 ± 0.42
% Woodland	Percentage of the landscape comprised of coniferous, deciduous, mixed woodland and scattered trees areas.	5.33 ± 0.75	8.47 ± 0.80	11.38 ± 0.81

[a] Modified from McGarigal *et al.* (2002).

Table 3.2. Summary table showing significance values of the explanatory variables and the goodness of fit of the final GLMMs. Management = farms involved in agri-environment schemes *vs.* conventionally-managed farms. Habitat = field margins, hedgerows, species-rich grasslands (improved grassland/arable fields in conventional farms) and water margins. Farming activity = arable and mixed.

	Management	Habitat	Farming activity	Management*Habitat	Management*Activity	Surrounding landscape [c]	Final model R^2 [d]
Micromoth abundance [a,b]	-	-	**<0.001**	**<0.001**	0.550	0.699	72.25 %
Micromoth richness	-	-	0.136	**0.073**	0.253	**0.007**	71.95 %
Micromoth diversity	0.855	0.713	0.102	0.937	0.499	0.106	NA
Macromoth abundance	-	-	-	**0.001**	**0.015**	**<0.001**	82.94 %
Macromoth richness	-	-	0.156	**0.071**	0.102	0.312	67.62 %
Macromoth diversity	0.775	0.135	0.566	0.201	0.809	0.630	NA
Declining species abundance	-	-	-	**0.011**	**<0.001**	**<0.001**	72.20 %
Declining species richness	0.635	0.696	0.255	0.237	0.111	0.306	NA

[a] A dash indicates that the significance of a factor was not assessed in the model given that it was involved in a significant interaction.

[b] Significance values in bold indicate that a factor has been included in the final GLMM.

[c] Percentage cover of semi-natural environment at the 250 m scale was included in all models except for: a) micromoth richness, percentage cover of farmland at the 1 km scale was used; b) micromoth diversity, percentage cover of urban areas at the 1 km scale was used; and c) macromoth diversity, percentage cover of water at the 250 m scale was used.

[d] Pseudo R^2 values for each model were calculated by correlating the values predicted by the final GLMMs (fitted values) with the observed data. This value was not available (NA) when none of the evaluated factors remained significant in the final model.

starting models as potential explanatory variables (fixed effects): land management type (AES or conventional), habitat feature (field margin, hedgerow, water margin, species-rich grassland or their equivalent conventional features), farming activity (arable or mixed; pastoral farms were excluded from this analysis as our sample size was too small, n = 8 trap samples) and the landscape parameter with the highest R^2 value for each response variable (see above). Two-way interactions between land management type and habitat feature and between land management type and farming activity were also included in the model. “Pair” was included in the models as a random effect (grouping variable) to account for the paired-site sampling design. A backwards step-wise approach to model simplification was adopted. All models were also assessed using Akaike’s information criterion (AIC). For all response variables the model selected by the stepwise approach matched the model with the lowest AIC value. Where the response variables were counts (e.g. moth abundance and species richness) models were fitted using Poisson errors (or quasi-Poisson whenever the data were overdispersed); for continuous variables (e.g. macromoth diversity) we used a Gaussian error on log transformed data (Crawley 2007). Whenever a significant effect was found, pair-wise post hoc comparisons were conducted to assess differences between groups; significance values were assessed using the Bonferroni method for multiple comparisons (Sokal & Rohlf 1995).

3.4. Results

We collected a total of 589 micromoths and 2294 macromoths from 122 trap samples (Table 3.3). A total of 61 micromoth species belonging to the families Blastobasidae, Coleophoridae, Crambidae, Elachistidae, Gelechiidae, Oecophoridae, Pterophoridae, Pyralidae, Tortricidae and Yponomeutidae, and 81 macromoth species from the families Noctuidae, Geometridae, Arctiidae and Hepialidae were identified (Appendix 3A). Seventeen macromoth species sampled are classed as "widespread but rapidly declining species" (hereafter referred to as "declining macromoth species") and are of special conservation concern within Britain (Conrad *et al.* 2006; Fox *et al.* 2006).

3.4.1. *Effects of the surrounding landscape*

A correlation matrix of all landscape metrics obtained from the landscape analysis showed that, for each biotope type, most are significantly correlated with each other ($p < 0.05$ in 87% of cases). For instance, at the 250 m scale the percentage of land covered by semi-natural environment was significantly correlated with number of patches, mean patch area, total edge density and Euclidean nearest neighbour distance (all $p < 0.05$) but not with area-perimeter ratio. As a result, we selected the proportion of each of five biotope types and a landscape heterogeneity index (Shannon diversity) at the three spatial scales as representative variables to be used in subsequent analyses. The following results are based on 36 traps (one trap per farm, randomly selected). However, results were largely unchanged when all traps (n = 122) were included in the landscape analysis.

Micromoth abundance was positively related to the percentage cover of semi-natural environment ($t = 3.1$, df = 35, $p = 0.004$, $R^2 = 38.49\%$; Fig. 3.1a) at the 250 m scale. None of the landscape metrics at either 500 or 1000 m scale were significantly related to micromoth abundance. Micromoth species richness was positively related to landscape heterogeneity ($t = 2.1$, df = 35, $p = 0.048$, $R^2 = 7.55\%$) whilst negatively related to the percentage cover of farmland ($t = 2.0$, df = 35, $p = 0.049$, $R^2 = 8.20\%$; Fig. 3.1b) at the 1 km scale, although the amount of variation in species richness

Table 3.3. Summary table showing moth abundance, species richness and diversity indices at agri-environmental (AES) and conventionally-managed habitat features.

Habitat feature	n traps	Micromoth abundance	Micromoth richness	Micromoth diversity	Macromoth abundance	Macromoth richness	Macromoth diversity	Declining spp. abundance	Declining spp. richness
Field margins	30	74	25	15.32	501	47	12.8	56	11
AES field margins	15	57	24	19.1	294	34	10.02	24	6
Conventional field margins	15	17	8	6.97	207	38	13.79	32	10
Hedgerows	26	145	36	16.22	422	40	10.95	57	9
AES hedgerows	13	64	25	16.99	219	33	10.93	26	6
Conventional hedgerows	13	81	25	12.99	203	32	10.78	31	7
Water margins	34	171	34	14.76	734	57	14.75	92	13
AES water margins	17	113	25	11.38	498	48	13.41	65	7
Conventional water margins	17	58	24	23.27	236	44	16.46	27	12
Species-rich grasslands	32	199	34	12.62	637	52	13.7	65	11
AES species-rich grasslands	16	156	24	8.40	366	46	14.38	44	10
Conventional species-rich grasslands	16	43	19	16.29	271	33	10.05	21	9
AES farms	61	390	51	16.77	1377	71	16.11	159	13
Conventional farms	61	199	43	18.61	917	61	14.88	111	17
All farms	122	589	61	18.18	2294	81	16.56	270	17

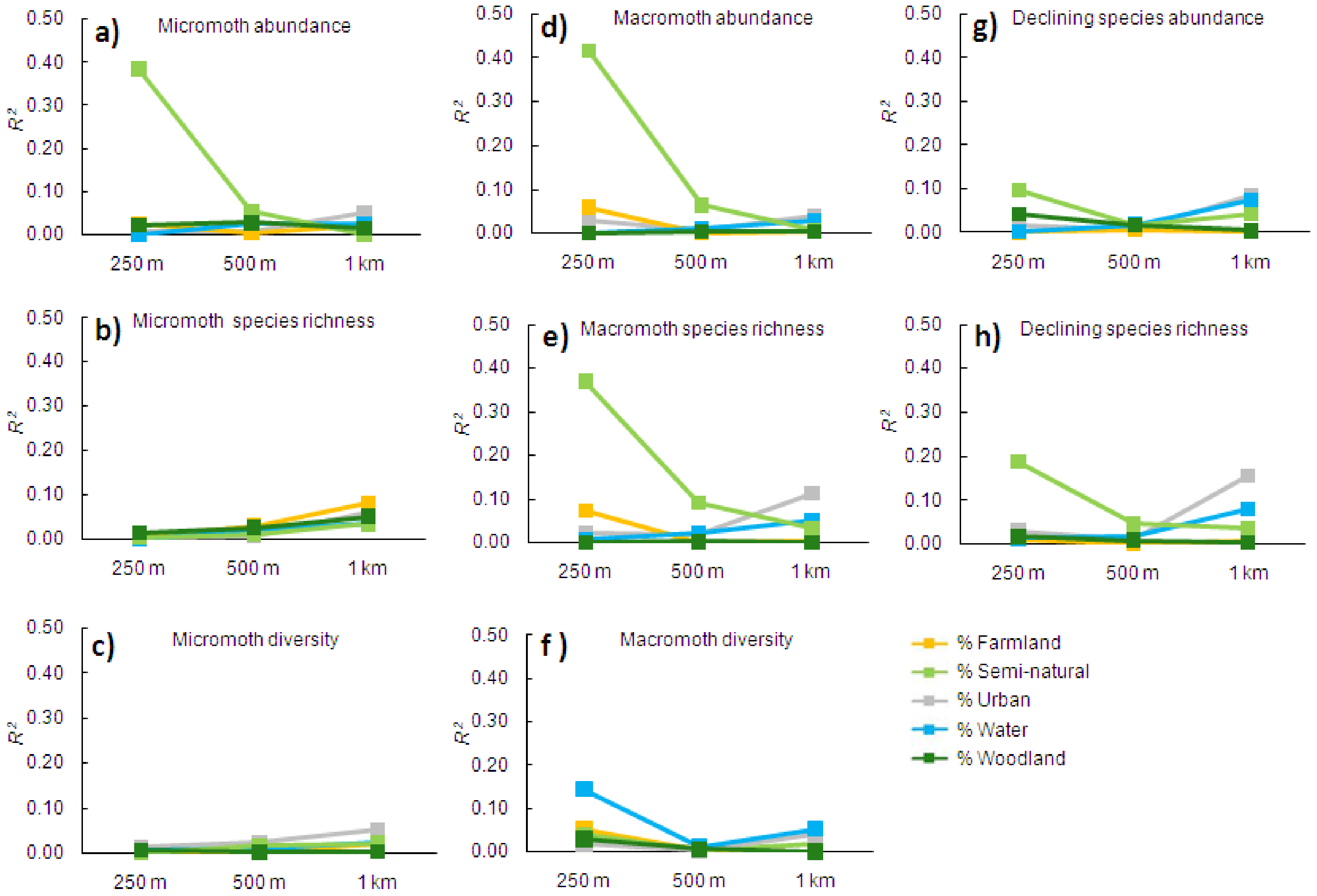

Figure 3.1. R^2 values obtained from regression analyses between the percentage of land covered by each biotope type at three spatial scales and: a) micromoth abundance, b) micromoth species richness, c) micromoth diversity, d) macromoth abundance, e) macromoth species richness, f) macromoth diversity, g) declining macromoth species abundance and h) declining macromoth species richness. To avoid pseudo-replication caused by overlapping buffers within sites, one trap per farm was randomly selected to be included in this analysis, therefore n = 36. Significance values are discussed in the text.

explained by these landscape parameters was relatively low. Micromoth diversity was not significantly related to any of the landscape parameters (Fig. 3.1c).

A very high proportion of the variation in macromoth abundance was positively explained by the percentage of semi-natural environment at the 250 m scale (t = 3.4, df = 35, p = 0.002, R^2 = 41.73%; Fig. 3.1d). Macromoth species richness was also positively related to the percentage cover of semi-natural environment at the 250 m scale (t = 3.5, df = 35, p = 0.001, R^2 = 36.91%; Fig. 3.1e), whilst negatively (but not significantly) related to the percentage cover of urban areas at the 1 km scale (t = 1.8, df = 35, p = 0.088, R^2 = 11.38%). Macromoth diversity was positively related to the percentage of water at the 250 m scale (t = 2.4, df = 35, p = 0.022, R^2 = 14.41%; Fig. 3.1f).

Declining macromoth species showed a similar response to the surrounding landscape as all macromoth species combined. Their abundance showed the strongest response to the percentage cover of semi-natural environment at the 250 m scale, although this was not statistically significant (t = 1.4, df = 35, p = 0.165, R^2 = 9.63%; Fig. 3.1g). Declining macromoth species richness was positively related to the percentage cover of semi-natural environment at the 250 m scale (t = 2.2, df = 35, p = 0.034, R^2 = 18.77%; Fig. 3.1h); and negatively (but non-significantly) to the percentage cover of urban areas at the 1 km scale (t = 1.8, df = 35, p = 0.078, R^2 = 15.61%).

The landscape analysis consistently indicated that the percentage cover of semi-natural environment within 250 m of the sampling site was the most important predictor for both micro- and macromoth abundance and macromoth species richness. This parameter was included as a potential explanatory variable in the subsequent models, except for: a) micromoth species richness, b) micromoth diversity, and c) macromoth diversity, where the percentage cover of farmland within 1 km, urban areas within 1 km, and water within 250 m, were respectively selected as the best potential landscape predictors to include in the models.

3.4.2. Effects of agri-environment schemes

All final models explained a large proportion of the variation observed within the datasets, except for macromoth diversity and declining macromoth species richness models, where none of the variables included were significant (Table 3.2). Post hoc analyses for significant factors are summarized in Table 3.4. Significance values given in the text are not corrected for multiple comparisons, but they remained significant in all cases after using the Bonferroni correction method. The magnitude of the differences (based on median values) between AES prescriptions and conventionally-managed features is also shown.

In general, moth abundance and species richness were higher in farms participating in AES than in non-participating farms (Table 3.3). For micromoth abundance, there was a significant interaction between land management type (AES *vs*. conventional) and habitat feature (Table 3.2). More micromoths were found adjacent to AES field margins ($z = 4.782$, $p < 0.001$, 3.7 x more), water margins ($z = 4.789$, $p < 0.001$, 2.2 x more) and species-rich grasslands ($z = 7.940$, $p < 0.001$, 4.0 x more) than on their conventional counterparts, but no difference was observed between AES and conventionally-managed hedgerows (Table 3.4a & Fig. 3.2a). The same interaction was also significant for micromoth species richness, with more species present at AES field margins ($z = 3.463$, $p < 0.001$, 3.8 x more) and species-rich grasslands ($z = 2.565$, $p = 0.010$, 2.3 x more) than at their conventional counterparts (Fig. 3.3a).

Table 3.4. Summary table showing post hoc analyses for: a) pair-wise comparisons between agri-environmental prescriptions and conventionally-managed features (interaction between management and habitat type), and b) pair-wise comparisons for the interaction between management type (agri-environmental *vs.* conventional) and farming activity (arable and mixed). Only the models with significant interactions are shown. Negative values indicate that moth abundance/richness was lower in conventionally-managed features/farms (with bold font indicating where this is significant at α 0.05). Significance values shown are not corrected for multiple comparisons, but they remained significant in all cases after using the Bonferroni correction method.

a)	Field margins		Hedgerows		Species-rich grasslands		Water margins	
	Estimate [a]	*SE*	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
Micromoth abundance	**-1.330 *****	0.278	0.039	0.174	**-1.381 *****	0.174	**-0.788 *****	0.164
Micromoth richness	**-1.249 *****	0.378	-0.170	0.248	**-0.706 ***	0.286	-0.413	0.244
Macromoth abundance	-0.174	0.120	0.099	0.127	0.098	0.114	**-0.347 ****	0.112
Macromoth richness	-0.027	0.166	-0.014	0.167	**-0.565 *****	0.171	-0.206	0.141
Declining species abundance	-0.220	0.303	-0.490	0.317	**-1.009 ****	0.325	**-1.340 *****	0.312

b)	Arable		Mixed	
	Estimate [a]	*SE*	*Estimate*	*SE*
Macromoth abundance	**-0.439 *****	0.098	-0.174	0.120
Declining species abundance	**-1.079 ****	0.330	-0.022	0.467

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$ and '*' $p \leq 0.05$.

There was also a significant interaction between land management type (AES *vs.* conventional) and habitat feature for macromoth abundance (and marginally significant for macromoth species richness), with higher abundances recorded at AES water margins ($z = 3.110$, $p = 0.002$, 1.6 x more) and more species collected at AES species-rich grasslands ($z = 3.313$, $p = 0.001$, 1.8 x more) than at their conventionally-managed counterparts (Figs. 3.2b & 3.3b). No differences were observed between AES and conventionally-managed hedgerows or field margins. The abundance of declining macromoth species showed the same significant interaction between land management type and habitat, again with AES water margins ($z = 4.298$, $p < 0.001$, 1.5 x more) and species-rich grasslands ($z = 3.111$, $p = 0.002$, 1.1 x more) having higher abundance than their conventional counterparts (Fig. 3.2c). The number of declining macromoth species collected at each farm (on any habitat) was not affected by participation within AES.

Farming activity had a significant effect on micromoth abundance, with more micromoths being collected at arable farms than at mixed ones (Table 3.2). For macromoth abundance, there was a significant interaction between land management type and farming activity, with the effect of adopting agri-environment schemes being noticeable on arable farms but not in mixed farms (Table 3.4b & Fig. 3.4b). This was also true for the abundance of declining macromoth species (Fig. 4c).

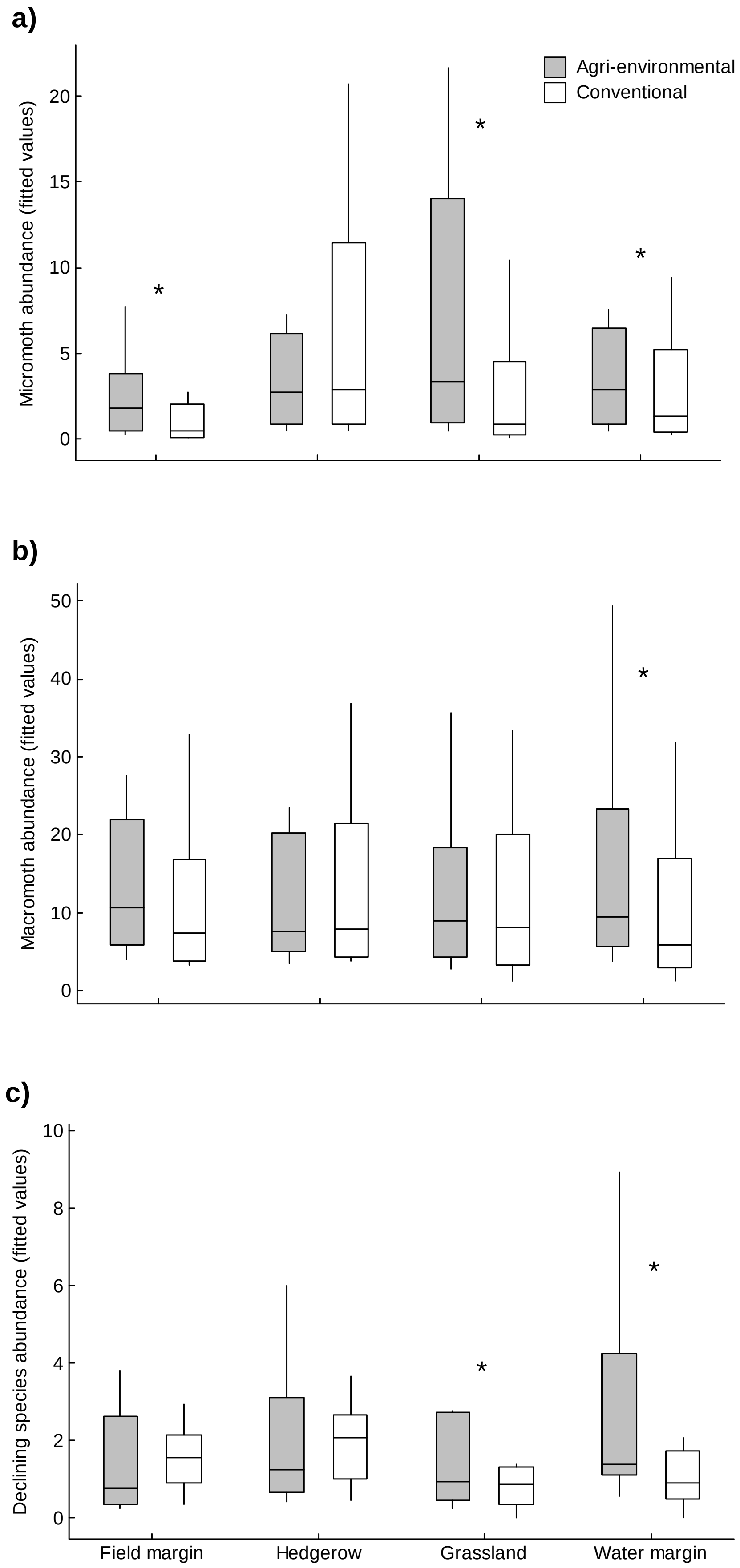

Figure 3.2. Boxplots of fitted values predicted by the final GLMMs showing the effect of the interaction between management type and habitat feature on the abundance of: a) micromoths, b) macromoths and c) declining macromoth species. Stars indicate significant differences within a habitat feature due to management type.

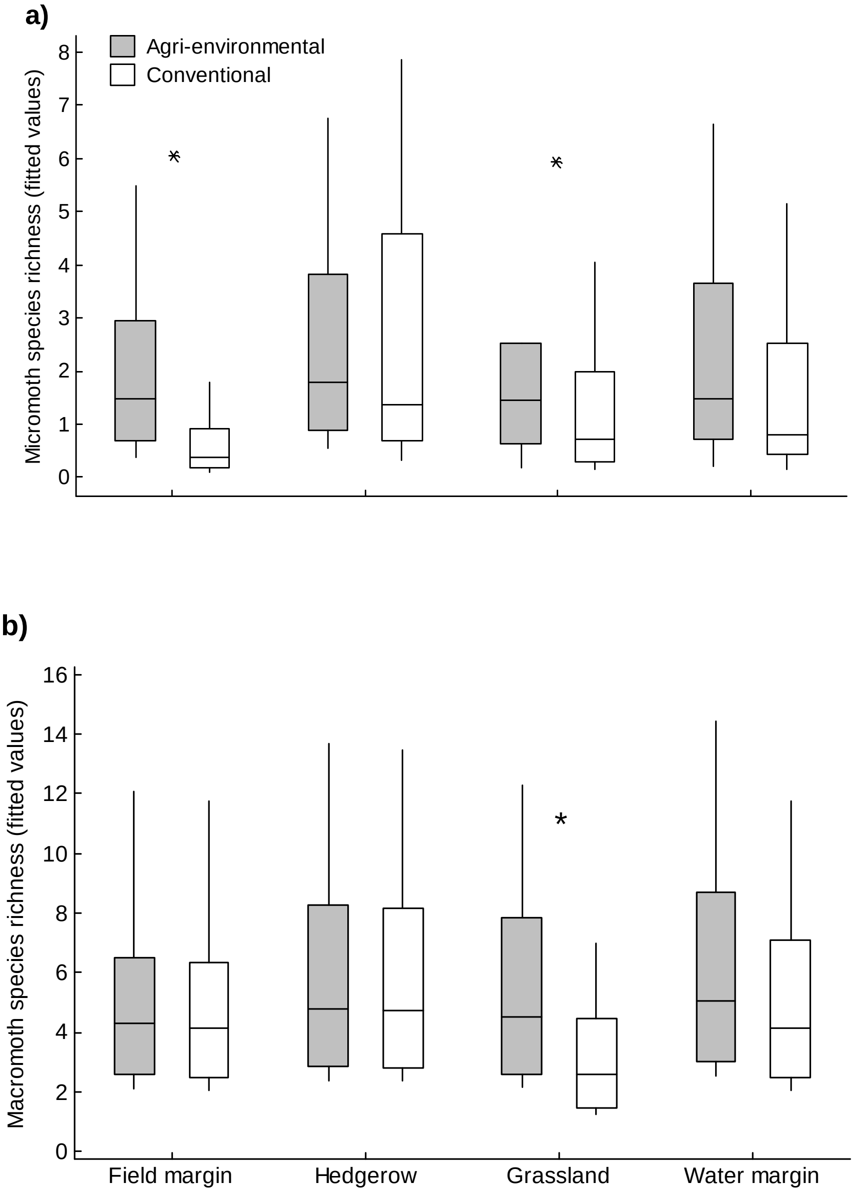

Figure 3.3. Boxplots of fitted values predicted by the final GLMMs showing the effect of the interaction between management type and habitat feature on species richness of: a) micromoths and b) macromoths. Stars indicate significant differences within a habitat feature due to management type.

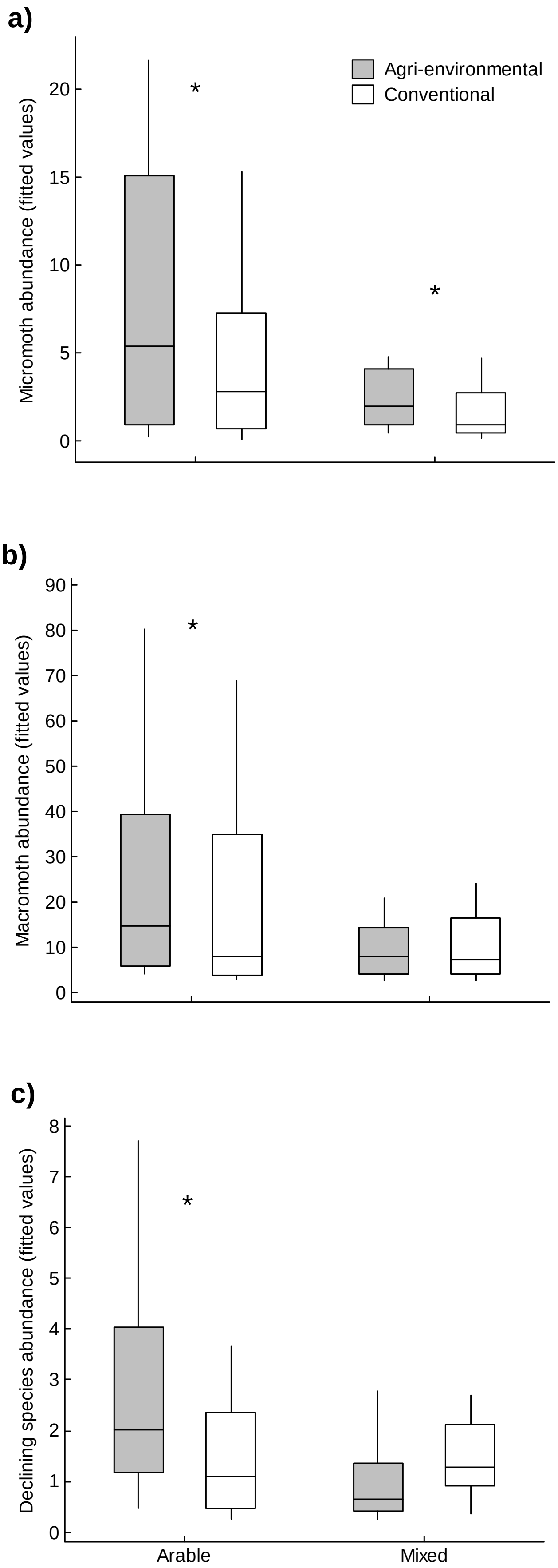

Figure 3.4. Boxplots of fitted values predicted by the final GLMMs showing the effect of the interaction between management type and farming activity on the abundance of: a) micromoths, b) macromoths and c) declining macromoth species. Stars indicate significant differences within arable or mixed farms due to management type. Pastoral farms were excluded from this analysis due to small sample size.

3.5. Discussion

In this study we assessed the value of AES as they currently operate in Scotland and the influence of the surrounding landscape (up to 1 km from trapping site) on assemblages of both macromoths and the relatively poorly studied micromoths. The diversity of the latter group and the fact that it comprises a substantial proportion of lepidopteran assemblages highlights its potential to yield relevant information to land managers (New 2004).

The results derived from the landscape analysis revealed that moth populations are enhanced by a high proportion of nearby semi-natural environment (rough grassland or scrub). Kuussaari *et al.* (2007) also found that semi-natural grasslands benefit lepidopteran communities. Micromoth abundance was significantly related to the percentage cover of semi-natural environment within 250 m of the collection site, but this parameter was not a significant predictor when included in the final explanatory model. Although the percentage of farmland cover within 1 km significantly related to micromoth species richness, this variable only explained a very small amount (< 10 %) of the variation in the data. This indicates that micromoths are influenced mainly by nearby habitat features and suggests that some of the currently operating AES prescriptions applied to relatively small areas are enhancing micromoth populations. Macromoth abundance and species richness were both also most strongly influenced by the percentage cover of semi-natural environment within 250 m of the trap. Given that most micromoths usually have lower dispersal abilities than macromoths (Nieminen, Rita & Uuvana 1999), it is somewhat surprising that the response of the two groups to the surrounding landscape was similar, although the negative effects of urbanisation for macromoth (and declining macromoth) species richness at a wider scale of 1 km was higher, in general, than for micromoths.

Our assessment of Scottish AES revealed that, in general, the abundances and species richness of both micro- and macromoths were higher on farms involved in agri-environment schemes than on conventionally-managed farms. Most of the specific AES prescriptions assessed (except hedgerows) had at least some positive effects on moth populations. Our results concur with those of Taylor & Morecroft (2009) who investigated the impact of the implementation of AES on an English farm and found that moth abundance and species richness significantly increased over a 12-year monitoring period which started prior to the implementation of the schemes. However, since this study focuses at the farm level (e.g. assessing overall abundance at the farm) we cannot use it to evaluate specific prescriptions. Furthermore, their results cannot clearly be attributed to the implementation of AES given that these were implemented at their study site at the same time that conversion to organic farming took place (Taylor & Morecroft 2009).

We evaluated the effects of the implementation of specific AES management prescriptions and found that water margins and species-rich grasslands showed the most general benefits for all groups. The presence of agri-environmentally managed field margins promoted only micromoth (but not macromoth) populations, whereas hedgerows under AES management did not offer any benefit over conventionally-managed hedges for micromoths or macromoths.

AES management of water margins consistently increased the abundance of micro- and macromoths (including rapidly declining species). These wide grassy strips (≥ 3 m) look fairly similar to AES field margins, but often show higher structural complexity (e.g. taller non-woody vegetation, presence of shrubs and young trees; EFM pers. obs.) which might be beneficial for insect communities (Dennis, Young & Gordon 1998; Kuussaari *et al.* 2007). They also differ from AES field margins in that AES water margins management prescriptions do not involve the sowing of a seed mix and so the vegetation associated with them results from natural regeneration. This suggests that simple and inexpensive AES management options may fulfil the habitat requirements of some farmland moths.

Agri-environmentally managed species-rich grasslands also resulted in higher moth abundance and species richness than their conventional counterparts. The vegetation of this habitat is taller than that of its conventional equivalent (Lye *et al.* 2009) and this increased structural diversity could be providing moths with shelter and protection from predators in addition to providing more feeding niches. This is supported by Kuussaari *et al.* (2007), who found a positive effect of increased vegetation height of semi-natural grasslands on moth species richness.

Field margins managed under AES agreements increased the abundance and species richness of micromoths; this prescription increases plant species richness and vegetation height which may provide higher larval food plant availability and shelter from potential predators (Marshall, West & Kleijn 2006; Lye *et al.* 2009). In contrast, abundance, species richness and diversity of macromoths were similar to conventional field margins. This relates to the findings of Merckx *et al.* (2009a), who show that low mobility species (such as micromoths) exhibit stronger responses to the presence of this prescription than more mobile species.

Hedgerows under AES management did not offer any benefit over conventionally-managed hedges for micromoths or macromoths. Similarly, Lye *et al.*

(2009) found that hedgerows under AES management were no more attractive to queen bumblebees (*Bombus* sp.) than conventional hedges, raising questions as to the value of this scheme option as it currently operates. Merckx *et al.* (2009b, 2010b) recommend the establishment and retention of hedgerow trees to be incorporated into AES hedgerow prescriptions, as it has the potential to increase macromoth abundance and diversity.

The effects of implementing AES management for both macromoths (all species) and declining macromoth species abundance was only significant on arable farms. Micromoth abundance and richness were higher at both AES arable and AES mixed farms than at their conventional counterparts, although more micromoths were collected at arable farms than at mixed ones. These effects could be due to the detrimental effects of grazing, which have been noted for moths and other insects in previous studies (Young & Barbour 2004; Pöyry *et al.* 2005; Littlewood 2008; Redpath *et al.* 2010). Grazing over the summer months does not allow for plants to flower and seed, and may therefore result in changes to vegetation composition and structure (Stewart & Pullin 2008). Even though most of the current AES prescriptions do incorporate restrictions regarding grazing regimes over the summer months, a farm-scale effect due to the presence of grazing stock in neighbouring fields may be limiting moth populations regardless of the operation of AES applied at a field scale. Therefore, the implementation of AES at larger scales, increasing not only the area but also the connectivity between patches of suitable habitat (e.g. species-rich grasslands), may be required as part of a more effective conservation strategy, and this might be particularly important in farms involving pastoral activities.

It has often been argued that differences observed between conventional and agri-environmental farms are not necessarily derived directly from the implementation of AES. Farms involved in these schemes might intrinsically be of higher environmental quality than conventionally-managed farms (Hole *et al.* 2005); also, farmers involved in AES may be more inclined to manage their land in an environmentally-friendly way than farmers who choose not to take part in such schemes (Kleijn & Sutherland 2003). These effects are difficult to disentangle, but the approach of Taylor & Morecroft (2009) in using a long-term study to follow the conversion of a conventional farm to an organic farm involved in AES suggests that some differences at least are due to the implementation of less intensive agricultural practices.

Some authors (e.g. Conrad *et al.* 2006) have highlighted the importance of monitoring population changes, not only of common species, but also of rare ones. In this study we show that declining macromoth species seem to respond to AES management prescriptions and to the surrounding landscape as do the rest of the macromoth species. Therefore, a conservation strategy beneficial to macromoth communities in general, would also benefit some species of special conservation concern. Conservation of natural habitats without specific focus on individual species has been regarded as an effective strategy because greater inclusive benefits may occur when focusing at the community level (New 2004).

In summary, our findings demonstrate that the implementation of current AES management prescriptions, targeted to relatively small areas, is an effective method to enhance both micro- and macromoth populations in agricultural environments. However, amendments are required to improve the performance of AES hedgerow management prescriptions and to minimise the detrimental effects of pastoral activities on farmland moths, where actions such as increasing the percentage cover of semi-natural environment in adjacent fields (within 250 m) may be required to maximize the benefits that moth populations gain from existing agri-environment schemes.

3.6. Acknowledgements

We would like to thank the Scottish Government for providing information on farms participating in the RSS, the landowners and Estate managers who granted us access to their land, R. Trodden, L. Dockray and G. Lye for their logistic assistance and help with fieldwork, R. Dawson and E. Heskey for their help with macromoth identification, M. Vallejo-Marín for his advice on statistical analyses, M. O'Brien for initial advice on agri-environment scheme data and T. Merckx, M. Pocock and an anonymous reviewer for their valuable comments on this manuscript. Special thanks to K. Bland (National Museums of Scotland) for identifying micromoth specimens. We would also like to thank CONACYT for providing a graduate scholarship (189261) to E.F.M., and the People's Trust for Endangered Species for their financial support.

Appendix 3A. List of moth species collected at agri-environmental farms and conventionally managed features during study. Mean numbers ± SE of moths captured per trap are shown.

Species[a]	Common name[b, c]	n	AES (mean ± SE)	Conventional (mean ± SE)
Agapeta hamana	Hook-marked Straw Moth (T)	13	0.11 ± 0.07	0.10 ± 0.04
Agriphila straminella	Pearl Veneer (P)	29	0.30 ± 0.15	0.18 ± 0.10
Agriphila tristella	(P)	115	1.74 ± 1.26	0.15 ± 0.08
Agrochola litura	Brown-spot Pinion (N) *	9	0.07 ± 0.05	0.08 ± 0.04
Amphipyra tragopoginis	Mouse Moth (N)*	38	0.25 ± 0.09	0.38 ± 0.18
Apamea lithoxylaea	Light Arches (N)	19	0.18 ± 0.09	0.13 ± 0.07
Apamea monoglypha	Dark arches (N)	144	1.11 ± 0.43	1.25 ± 0.65
Arctia caja	Garden Tiger (A) *	8	0.10 ± 0.06	0.03 ± 0.02
Autographa gamma	Silver Y (N)	8	0.03 ±0.02	0.10 ± 0.05
Blastobasis adustella	(B)	19	0.18 ± 0.07	0.13 ± 0.10
Blastobasis lacticolella	(B)	7	0.10 ± 0.06	0.02 ± 0.02
Campaea margaritata	Light Emerald (G)	10	0.02 ± 0.02	0.15 ± 0.13
Camptogramma bilineata	Yellow Shell (G)	8	0.07 ± 0.04	0.07 ± 0.03
Caradrina morpheus	Mottled Rustic (N) *	5	0.02 ± 0.02	0.07 ± 0.04
Catoptria falsella	(P)	11	0.10 ± 0.07	0.08 ± 0.07
Celypha lacunana	(T)	10	0.10 ± 0.06	0.07 ± 0.04
Cerapteryx graminis	Antler Moth (N)	57	0.64 ± 0.34	0.30 ± 0.13
Chloroclysta truncata	Common Marbled Carpet (G)	5	0.02 ± 0.02	0.07 ± 0.04
Chrysoteuchia culmella	Garden Grass-veneer (P)	11	0.13 ± 0.08	0.05 ± 0.04
Cnephasia asseclana	Flax Tortrix (T)	66	0.41 ± 0.18	0.67 ± 0.34
Cnephasia incertana	Light Grey Tortrix (T)	10	0.11 ± 0.06	0.05 ± 0.04
Cnephasia stephensiana	Grey Tortrix (T)	6	0.00 ± 0.00	0.10 ± 0.07
Colostygia pectinataria	Green Carpet (G)	16	0.08 ± 0.04	0.18 ± 0.06
Diachrysia chrysitis	Burnished Brass (N)	44	0.46 ± 0.21	0.26 ± 0.12
Diarsia mendica mendica	Ingrailed Clay (N)	8	0.11 ± 0.06	0.02 ± 0.02
Diarsia rubi	Small Square-spot (N) *	22	0.25 ± 0.08	0.11 ± 0.07
Dipleurina lacustrata	(P)	9	0.10 ± 0.08	0.05 ± 0.03
Eana osseana	(T)	6	0.03 ± 0.03	0.07 ± 0.07
Epiblema roborana	(T)	5	0.03 ± 0.02	0.05 ± 0.04
Epirrhoe alternata	Common Carpet (G)	16	0.13 ± 0.04	0.13 ± 0.05
Eucosma cana	(T)	13	0.20 ± 0.09	0.02 ± 0.02
Eucosma hohenwartiana	(T)	21	0.20 ± 0.08	0.15 ± 0.10
Eulithis pyraliata	Barred Straw (G)	29	0.33 ± 0.15	0.15 ± 0.06
Hepialus fusconebulosa	Map-winged Swift (H)	9	0.08 ± 0.04	0.07 ± 0.04
Hofmannophila pseudospretella	Brown House Moth (O)	5	0.03 ± 0.02	0.05 ± 0.03

Species[a]	Common name[b, c]	n	AES (mean ± SE)	Conventional (mean ± SE)
Hoplodrina alsines/blanda	The Uncertain/The Rustic (N) *	17	0.25 ± 0.10	0.03 ± 0.02
Hydraecia micacea	Rosy Rustic (N) *	54	0.33 ± 0.16	0.56 ± 0.27
Hydriomena furcata	July Highflyer (G)	5	0.05 ± 0.03	0.03 ± 0.02
Hypena proboscidalis	The Snout (N)	35	0.30 ± 0.17	0.28 ± 0.10
Luperina testacea	Flounced Rustic (N)	11	0.10 ± 0.04	0.08 ± 0.04
Mesapamea secalis/didyma	Common Rustic/Lesser Common Rustic (N)	357	3.26 ± 0.93	2.59 ± 0.88
Mythimna conigera	Brown-line Bright-eye (N)	6	0.07 ± 0.03	0.03 ± 0.02
Mythimna ferrago	The Clay (N)	9	0.08 ± 0.04	0.07 ± 0.04
Mythimna impura	Smoky Wainscot (N)	415	4.97 ± 1.77	1.84 ± 0.66
Mythimna pallens	Common Wainscot (N)	151	1.07 ± 0.31	1.41 ± 0.45
Naenia typica	The Gothic (N)	5	0.07 ± 0.05	0.02 ± 0.02
Noctua comes	Lesser Yellow Underwing (N)	58	0.44 ± 0.19	0.51 ± 0.28
Noctua janthe	Lesser Broad-bordered Yellow Underwing (N)	39	0.48 ± 0.18	0.16 ± 0.05
Noctua pronuba	Large Yellow Underwing (N)	189	1.80 ± 0.46	1.30 ± 0.49
Oligia fasciuncula	Middle-barred Minor (N)	5	0.05 ± 0.04	0.03 ± 0.02
Pandemis heparana	Dark Fruit-tree Tortrix (T)	11	0.10 ± 0.04	0.08 ± 0.04
Photedes captiuncula expolita	Least Minor (N)	8	0.10 ± 0.07	0.03 ± 0.02
Photedes minima	Small Dotted Buff (N)	16	0.08 ± 0.04	0.18 ± 0.09
Pleuroptya ruralis	Mother of pearl (P)	12	0.13 ± 0.06	0.07 ± 0.05
Scoparia ambigualis	(P)	21	0.28 ± 0.11	0.07 ± 0.04
Scoparia pyralella	(P)	9	0.10 ± 0.07	0.05 ± 0.03
Scotopteryx chenopodiata	Shaded Broad-bar (G) *	94	1.26 ± 0.53	0.28 ± 0.10
Spilosoma lubricipeda	White Ermine (A) *	5	0.02 ± 0.02	0.07 ± 0.04
Trachycera advenella	(P)	7	0.08 ± 0.05	0.03 ± 0.03
Udea lutealis	(P)	7	0.08 ± 0.05	0.03 ± 0.02
Udea prunalis	(P)	12	0.16 ± 0.10	0.03 ± 0.02
Xanthorhoe montanata	Silver-ground Carpet (G)	49	0.36 ± 0.19	0.44 ± 0.19
Xestia baja	Dotted Clay (N)	64	0.89 ± 0.38	0.16 ± 0.08
Xestia sexstrigata	Six-striped Rustic (N)	26	0.31 ± 0.15	0.11 ± 0.07
Xestia triangulum	Double Square-spot (N)	27	0.25 ± 0.12	0.20 ± 0.10
Xestia xanthographa	Square-spot Rustic (N)	16	0.16 ± 0.10	0.10 ± 0.06

[a] Only species with total abundance higher than five are shown.

[b] Letters account for Families: A = Arctiidae, B = Blastobasidae, G = Geometridae, H = Hepialidae, N = Noctuidae, O = Oecophoridae, P = Pyralidae, and T = Tortricidae.

[c] Species classed as “rapidly declining species” according to (Conrad *et al.* 2006) are indicated by a star.

Chapter 4

Effects of woodland character and configuration on bats and nocturnal insects within farmland: implications for woodland management and creation schemes

4.1. Summary

Woodland is one of the most important habitats for bats because it offers roosting and feeding opportunities for many species. As a consequence of long-term deforestation, woodland cover in the United Kingdom has been drastically reduced and remaining woodland is highly fragmented. Agri-environment schemes aim to increase the amount and quality of woodland on agricultural land; however, little is known about how woodland character relates to bat abundance and diversity (and to prey availability) and recommendations for woodland creation and management for foraging bats are scarce. We conducted vegetation surveys and used Geographic Information Systems (GIS) software to quantify vegetation character and spatial configuration of 34 woodland patches within farmland. We used two complementary methods (acoustic monitoring and bat trapping assisted by an acoustic lure) to assess the influence of woodland vegetation character, patch configuration and surrounding landscape on bat populations in farm woodlands. Insect prey availability at each site was assessed using heath light traps. At the local scale, woodland vegetation character appeared more important than patch configuration. In general, high activity levels of both *Pipistrellus* species were related to relatively low tree densities, an open understorey cover and a closed canopy cover, while *Myotis* bats showed the opposite trend (i.e. high tree densities and a relatively open canopy cover). The presence of grazing stock was associated with high activity of *P. pipistrellus* and *Myotis* bats. Higher bat abundance and activity levels were detected for some species (e.g. *P. pygmaeus*) in small and isolated woodland fragments, which suggested a more intensive use of woodland in landscapes where this habitat is scarce. The surrounding landscape influenced bat abundance and activity. Woodland fragmentation metrics were the most important landscape parameters influencing all bat species. Water metrics were related to the abundance and activity of

P. pygmaeus. This species was influenced by the surrounding landscape at small spatial scales (<1 km), but others (e.g. *P. pipistrellus* and *Myotis* sp.) were influenced at larger spatial scales (e.g. within 3 km). Insect prey availability (mainly Diptera) was not affected by woodland vegetation or patch configuration; but it was higher in woodland edges that in woodland interior. This pattern was not reflected in bat activity, which was similar (for *P. pipistrellus*) or higher in interior compared to edge (for *P. pygmaeus* and *Myotis* sp.). *Synthesis and applications*: Our results provide relevant information for the design of farm woodland management and creation schemes. Woodland planting should be prioritised in areas where this habitat is scarce. A landscape-scale approach would benefit more mobile bat species. Habitat heterogeneity should be maintained in order to meet the requirements of different bat species.

4.2. Introduction

Woodland is one of the most important habitats for bats because it offers roosting and feeding opportunities for many species (Dietz, von Helversen & Nill 2009). Worldwide longstanding deforestation has resulted in many bat species suffering severe population declines (Harris *et al.* 1995; Mickleburgh, Hutson & Racey 2002). Remaining woodland is often highly fragmented and degraded, consisting of a large number of relatively small and isolated patches immersed in an agricultural matrix. Vegetation structure and spatial configuration are often highly altered in fragmented woodlands. For instance, small fragments with complex shapes have a higher proportion of edge exposed to the surrounding matrix, which can in turn modify the vegetation structure and composition (Laurance 2008).

Woodland vegetation structure is of great importance in determining habitat quality and availability for bats. Although the concept of 'quality' depends on the specific requirements of a particular species, in general, mature hardwood forest stands with high availability of large diameter snags, dense canopy cover and reduced clutter (e.g. low tree density and understorey cover) are often associated with high bat activity levels because they provide roosting and foraging opportunities for bats (Erickson & West 2003; Yates & Muzika 2006; Lacki, Amelon & Baker 2007).

The configuration and extent of a woodland patch can also have a strong influence on bat communities. Island biogeography theory (IBT; MacArthur & Wilson 1967) suggests that the number of species inhabiting an island depends on its size and isolation. Its conceptual framework has been extended from real islands to terrestrial ecosystems of habitat patches in order to understand the effects of habitat loss and fragmentation on biodiversity. Patterns of bat species richness and occurrence on real islands (e.g. archipelagos) are consistent with those predicted by IBT (e.g. positively related to area and negatively related to isolation; Frick, Hayes & Heady 2008a,b). Despite expectations derived from IBT, however, large woodland patches do not necessarily support more species or larger populations of bats than small patches (Law, Anderson & Chidel 1999; Estrada & Coates-Estrada 2002; Lesinski *et al.* 2007). Relatively small woodland fragments may provide roosting opportunities and support populations of many bat species, especially if they are located relatively close to other fragments and have a high structural diversity (Estrada & Coates-Estrada 2002; Meyer & Kalko 2008; Boughey *et al.* 2011a;). However, different bat species respond to woodland fragmentation in different ways. Fast-flying species adapted to forage in uncluttered environments are relatively tolerant to habitat fragmentation; some species even show higher abundance and activity levels in small and isolated fragments

(Estrada-Villegas, Meyer & Kalko 2010) or in sparsely wooded landscapes (Klingbeil & Willig 2009). Slow-flying and highly manoeuvrable species, on the other hand, are usually more reluctant to make use of open areas; therefore, these species are more sensitive to habitat isolation and show positive associations with woodland availability (e.g. patch size; Law, Anderson & Chidel 1999; Duchamp & Swihart 2008; Meyer & Kalko 2008). Roosting ecology and edge-affinity have also been identified as good predictors of bat species' sensitivity to habitat fragmentation; 'woodland interior' species (often tree-roosting bats) are negatively affected by fragmentation, as opposed to species which show affinity for woodland edges (often roosting in human-made structures; Meyer *et al.* 2008; Struebig *et al.* 2008).

Many bat species are highly mobile; therefore, it is likely that they will be influenced not just by the local character of a woodland patch, but also by the surrounding landscape (Thornton, Branch & Sunquist 2011). Bats are strongly influenced by the landscape context at relatively large spatial scales (e.g. within 5 km; Gorresen, Willig & Strauss 2005; Boughey *et al.* 2011a; Klingbeil & Willig 2009; Chapter 2 of this thesis). In fact, the total amount of woodland in the landscape (rather than the size of a particular patch) has been identified as a good predictor for bat species abundance, richness and distribution. Furthermore, woodland availability in the landscape appears more important than its spatial configuration (Jaberg & Guisan 2001; Meyer & Kalko 2008; Perry, Thill & Leslie 2008).

As a consequence of long-term deforestation, woodland cover in the United Kingdom (UK) has been drastically reduced. At the beginning of the 20th century woodland comprised a mere *ca.* 5% of the UK's land area, but programmes of afforestation over the last 50 years have increased this figure to approximately 12%

(Mason 2007). Much of this consists of forestry plantations, which in many cases have low species richness (exotic fast growing conifers) and structural diversity, and which provide fewer roosting and feeding opportunities (e.g. they support less diverse insect communities) for bats than ancient semi-natural woodland (Altringham 2003; but see Mortimer 2006, who shows that commercial coniferous plantations adequately managed for wildlife can be valuable for Natterer's bats). The remaining woodland is highly fragmented and consists of a large number of relatively small patches (< 100 ha) within agricultural landscapes (Watts 2006). Currently in the UK, a number of agri-environment schemes (AES; financial incentives used in Europe and North America for farmers to adopt less intensive, environmentally-sensitive agricultural practices) aim to increase the amount and quality of woodland on agricultural land. Despite the importance of woodland habitat for all UK bat species (Walsh & Harris 1996; Vaughan, Jones & Harris 1997; Russ & Montgomery 2002; Altringham 2003), little is known about how woodland character relates to prey availability and bat abundance and diversity (but see Hill & Greenaway 2008). To date, most studies assessing the effects of woodland character and fragmentation on bats have been conducted in tropical ecosystems and/or predominantly forested areas, and only rarely in farmland-dominated landscapes where the effects of woodland fragmentation are likely to be stronger (Andrén 1994). As a result, recommendations for the creation and management of farm woodland to improve habitat for wildlife in the UK (and many other countries) seldom take the needs of bats and many of their insect prey into consideration; therefore, management guidelines for bats are scarce, and the ones that exist focus on creating/maintaining roosting opportunities rather than enhancing good foraging habitat (Anonymous 2005; but see Entwistle *et al.* 2001). Furthermore, studies that investigate the effect of woodland character at several spatial scales (e.g. incorporating local character and surrounding landscape effects) on bat populations are few.

Here, we examine bat populations (and insect prey availability) in woodland patches within agricultural landscapes to assess the effects of woodland vegetation character (e.g. tree species richness), patch configuration (e.g. size and shape) and surrounding landscape (e.g. proportion of woodland cover) on foraging bats in central Scotland. In particular, we addressed three specific questions:

1. Do bat abundance and activity levels relate to woodland vegetation character and patch configuration and, if so, to which specific attributes?
2. Does the surrounding landscape influence bat abundance and activity levels in woodland patches and, if so, to what spatial extent?
3. What is the relative importance of woodland vegetation character, patch configuration and surrounding landscape for enhancing bat populations (e.g. is local management of woodlands sufficient or is a landscape-scale management approach important)?

4.3. Materials and methods

4.3.1. Site selection and study design

Ordinance Survey digital maps (EDINA Digimap Ordnance Survey Service) were used to select 34 woodland patches within agricultural land in central Scotland (Fig. 4.1). All woodland patches were at least 60 years old (EDINA Historic Digimap Service); they were selected based upon their size (0.1 – 30 ha) and shape (ranging from compact to

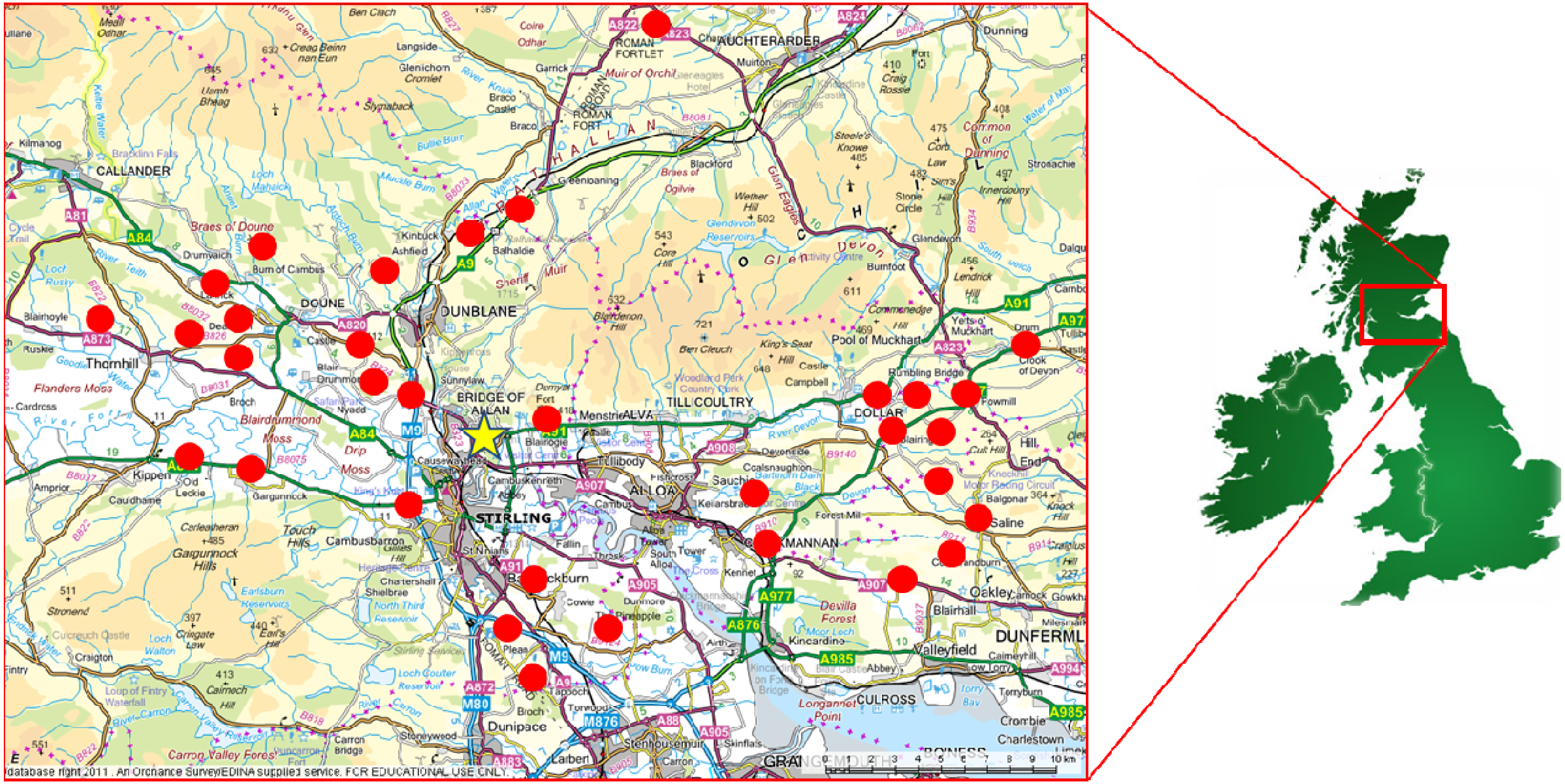

Figure 4.1. Map of central Scotland showing approximate locations of woodland patches (red dots) surveyed during 2009/2010. Yellow star represents the University of Stirling.

complex). All sites were surveyed for vegetation, nocturnal insects and bats once during the summers of 2009 (June to August, 20 sites) and 2010 (May to July, 14 sites). Vegetation surveys were conducted no more than two weeks before the nocturnal surveys. Bat surveys and insect sampling occurred simultaneously and were only conducted in dry weather, when temperature was ≥ 8 °C and wind force ≤ Beaufort scale 4 (temperature and wind speed were recorded on each site immediately before and after sampling).

4.3.2. Vegetation surveys

Vegetation surveys were conducted along transects 100 m in length. Transects within a woodland patch were located in an area considered to be representative of the whole site (after exploration and visual assessment of the woodland). The number of transects per site depended on the size of the woodland; one transect was used for patches of 0.1 – 3 ha, two transects for patches of 3 – 10 ha, and three transects for patches of 10 – 30 ha. Points were established every 15 m along each transect and tree species richness, tree density and tree basal area (only trees and saplings ≥ 7 cm in diameter at breast height were measured) were determined using the point-centred quarter method (Southwood & Henderson 2000). Canopy cover (%) was assessed using a sighting tube with an internal crosshair; presence of canopy was recorded if the crosshair intersected canopy vegetation; this was repeated 10 times at 1 m intervals perpendicular to the transect at each point. Each point also served as the corner of a 10 x 10 m quadrat (used to visually assess understorey percentage cover using the Domin scale; Kent & Coker 1992) and a 2 x 2 m quadrat (used to visually determine the dominant ground cover type).

4.3.3. Invertebrate sampling

Nocturnal invertebrates were collected using portable 6W heath light traps powered with 12 V batteries, which were activated 15 min after sunset and switched off after 4 h using automatic timers. The number of heath traps per site depended on the size of the woodland; two traps were used in patches of 0.1 – 3 ha, four traps in patches of 3 – 10 ha, and six traps in patches of 10 – 30 ha). The traps were ≥ 100 m apart to prevent the lights from interfering with each other (Dodd, Lacki & Rieske 2008; Merckx *et al.* 2009a). If the woodland patch was too small to allow for this distance between traps, we ensured trees or shrubs interrupted visibility between the lights. At each patch, an equal number of heath traps were located at the edge (‘edge’ traps) and the interior (‘interior’ traps, as far away from the edges as possible). After the surveys, the heath traps were sealed and transported to the laboratory. The collected insects were euthanized by dropping a cotton pad soaked with ethyl acetate into each trap/bag and left overnight. They were placed in sample bottles and stored in 70% ethanol for later identification to order level (suborder for Diptera) following Chinery (1993). Lepidoptera were either pinned (macromoths) or wrapped in tissue paper (micromoths) and subsequently identified to species level.

4.3.4. Bat surveys

Bat surveys started 45 minutes after sunset to avoid peak emergence times for different bat species (and therefore avoid recording bats commuting to feeding sites) and finished 4 hours later. Two complementary methods (sound recording and trapping) were used to assess species presence, bat abundance and bat activity at each woodland patch.

4.3.4.1. Sound recording and analysis

Bat activity was assessed using a frequency division bat detector (Anabat SD1, Titley Electronics) mounted on a 1 m high pole with the microphone pointing upwards. The detector was positioned in the interior of each woodland patch (as far away from the edges as possible) and moved between four different points (≥ 20 m from each other; located adjacent to the trapping points described in section 4.3.4.2) every 30 minutes to maximise the surveyed area. We analysed all bat recordings using AnalookW (Corben 2006). We identified bat species and counted total numbers of bat passes (defined as at least two echolocation calls within one second of each other; Fenton 1970; Walsh & Harris 1996), social calls and feeding buzzes emitted when attempting prey capture (Griffin, Webster & Michael 1960). There are four bat genera present in the study area (*Pipistrellus, Myotis, Nyctalus* and *Plecotus*; Richardson 2000), and all can be identified based on characteristics of their search-phase echolocation calls. The *Pipistrellus* species present in the UK can be distinguished on the basis of the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls. However, in some cases it is difficult to distinguish between species within a genus due to similarities in call structure (especially in cluttered environments; Schnitzler & Kalko 2001). Such is the case of the *Myotis* (*M. daubentonii, M. nattereri* and *M. mystacinus*) and *Nyctalus* species (*N. noctula* and *N. leisleri*) found in the area. *Plecotus* is represented by only one species in the area (*P. auritus*), but it is rarely recorded because of its quiet echolocation calls. Therefore, for *Myotis, Nyctalus* and *Plecotus* species the best way to confirm their presence within a site is by capturing and examining individuals in the hand.

4.3.4.2. Bat trapping

Bat abundance was quantified using an Austbat harp trap (2.4 x 1.8 m) and three mist nets (2.4 x 6 m each), which were located in the interior (as far away from the edges as possible and avoiding paths where these were present) of the woodland patch ≥ 20 m from each other. Bats can be extremely difficult to capture in woodlands. Therefore, an acoustic lure for bats – a bat call synthesizer (the Sussex AutoBat; Hill & Greenaway 2005) – was used. This lure offers huge potential for surveying bats in conditions under which ultrasonic detectors perform poorly (e.g. cluttered woodland) and species with quiet echolocation calls, such as *P. auritus* (Hill & Greenaway 2005). The AutoBat was positioned next to one of the nets/trap and moved along to the next one every 30 minutes. Four different synthesized bat call types (which were switched every 15 minutes and played in the same order every night) were used to attract a wide variety of bat species (F. Greenaway personal communication). All nets were checked every 15 minutes to extract any captured bats, which were then identified to species, sexed, aged, weighed and temporarily marked by fur clipping; morphometric measures, pictures and ultrasonic recordings were taken before releasing each bat to aid with species identification. Data from bat activity and bat captures were combined to obtain records of species presence for each woodland patch.

In addition, point counts (10 minutes duration) were conducted at different locations within and around each woodland patch using a frequency division bat detector (Anabat SD1, Titley Electronics) to compare bat activity in the woodland interior, edge and surrounding matrix. At each patch, an equal number of point counts were conducted at the interior (as far away from the edges as possible) and the edge of the woodland; the total number of points per site depended on the size of the woodland; 2 interior, 2 edge and 2 matrix points were used for patches of 0.1 – 3 ha, 3 interior, 3 edge and 2 matrix points for patches of 3 – 10 ha, and 4 interior, 4 edge and 2 matrix points for patches of 10 – 30 ha. Bat recordings were analysed as described in section 4.3.4.1.

4.3.5. Landscape analysis

We used ArcGIS 9.2 (ESRI Inc. 2006) to create circles of 250, 500, 1000, 1500, 2000, 2500 and 3000 m radius around the centre of each woodland patch. We selected these different scales because the smallest represents site-specific characteristics, whereas the others cover the home ranges of low (e.g. *P. auritus*) and intermediate (e.g. *P. pygmaeus*) mobility species; the largest scale approximates an upper limit to home range sizes of more mobile bat species (e.g. *P. pipistrellus*; Entwistle, Racey & Speakman, 1996; Nicholls & Racey 2006a). We used data from OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service) to reclassify the landscape within each circle into five biotope types. These were: (i) urban areas (buildings, structures and roads); (ii) farmland; (iii) water (inland and tidal water); (iv) semi-natural environment (rough grassland, scrub and scattered trees); and (v) woodland (coniferous, deciduous and mixed trees). We then used Fragstats 3.3 (McGarigal *et al.* 2002) to calculate the proportion of land covered by each biotope type and a landscape heterogeneity index (Shannon diversity) within each circle. Based on published literature on bat ecology, we considered ‘woodland’ and ‘water’ as the most important biotope types for bats; we therefore calculated an additional selection of landscape metrics for these two biotopes, including largest patch index (LPI, percentage of the landscape comprising the largest patch of a type), Euclidean nearest neighbour distance (ENN, mean value of ENN distances between all patches of a type within the landscape) and total edge density (ED, the sum of the lengths of all woodland edge segments divided by the total landscape area; calculated for woodland only).

4.3.6. Data analysis

All statistical analyses were conducted using R version 2.11 (R Development Core Team 2010). We performed Generalised Linear Models (GLMs) to determine the influence of woodland character on bats and nocturnal insects. Based on previous knowledge on the ecology of woodland bats, we selected the following potential explanatory variables to be included in the starting models: (i) vegetation character variables: woodland type (broadleaved or broadleaved-conifer mix), tree species richness, tree density, understorey cover (%), canopy cover (%), surrounding matrix type (arable, pastoral or mixed) and presence/absence of in-site grazing, and (ii) patch configuration variables: woodland patch size, shape (patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area; equals 1 when the patch is maximally compact and increases as shape becomes more irregular; McGarigal *et al.* 2002) and isolation (proximity to nearest woodland site ≥ 0.19 ha, which equals the size of smallest woodland patch included in surveys). ‘Year’ was included as a factor to account for potential variation between the two sampling periods. Date and temperature at sunset were included as covariates. Occasionally (seven times), bat surveys lasted < 4 h (due to heavy rain or malfunction of the AutoBat’s internal battery); therefore, survey duration was included in the ‘bat abundance’ models as an offset. A correlation matrix of all potential explanatory variables (excluding landscape metrics) was created to check for possible collinearity between predictors (Pearson correlation coefficient ≤ 0.6 in all cases). A backwards step-wise approach to model simplification was adopted, using $p \leq 0.1$ as a criteria for factor retention or removal. All models were validated by visual examination of residuals (e.g. plotting residuals *vs*. fitted values to check for constant variance, and plotting histograms of residuals to check for normality of errors; Crawley 2007). These models are referred to as 'woodland character' models hereafter.

Linear regression analyses were used to evaluate the effect of the surrounding landscape on bats and nocturnal insects. Individual models (one for each landscape parameter at each spatial scale) were performed and R^2 values calculated to assess the relative importance of each landscape parameter (e.g. identify those which explained the highest variation in the data). These models are referred to as 'landscape' models hereafter. For the 'woodland character' and 'landscape' models, we used total values per site for bat abundance and activity, and mean values per trap for invertebrate abundance as response variables (n = 34 in all cases).

In addition, Generalised Linear Mixed-effects Models (GLMMs; Zuur *et al.* 2009) were conducted to assess differences in invertebrate abundance and bat activity between woodland interior, woodland edge and surrounding matrix (for bat activity only). Invertebrate abundance per trap (n = 126) and total number of bat passes (per species) per point count type (data pooled together to reduce the number of zeroes; n = 105) were used as response variables. 'Location' – interior, edge or surrounding matrix (for bat activity only) – and 'Year' were included in the models as fixed factors, whereas 'site' was used as a random factor (to account for variation between sites). Date and temperature were included as covariates. Because the number of point counts per site depended on the size of the woodland, this value was included in the models for bat activity as an offset.

All continuous variables were standardized (by subtracting the sample mean from all input variable values, and subsequently dividing these values by the sample standard deviation) following Schielzeth (2010) in order to allow meaningful comparisons of the relative importance of predictors within a model. Models were fitted using Gaussian errors (on log transformed data) for continuous variables (e.g. mean invertebrate abundance), Poisson errors (or quasi-Poisson whenever the data were overdispersed) when the response variables were counts (e.g. bat abundance/activity) and binomial errors for species presence-absence data (Crawley, 2007). Models' R^2 values were calculated as follows: for models with a Gaussian error distribution $R^2 = 1 - $ (Residual Sum of Squares/Total Sum of Squares); for models with a Poisson error distribution $R^2 =$ (Deviance explained by model/Null deviance) × 100; for models using quasi-Poisson errors, R^2 values were calculated by correlating the values predicted by each model with the observed data; for models using binomial errors, R^2 values were calculated as the proportion of correct predictions of presence/absence derived from the model (a probability of 0.5 was used as a cut-point threshold; >0.5 = presence; <0.5 = absence; Fielding & Bell 1997; Crawley 2007; Zuur *et al.* 2009). These values are not adjusted for the number of explanatory variables included in a model (except for models with a Gaussian error).

4.4. Results

We identified a total of 34 tree species (listed in Appendix 4A). Vegetation character varied widely between sites, with tree species richness ranging from 2 to 15 species per site and tree density from 181 to 2512 trees per ha. The characteristics of each site are summarized in Appendix 4B.

4.4.1. Nocturnal invertebrates

We collected a total of 14,739 invertebrates from 126 trap samples. The most abundant insect orders were Diptera and Lepidoptera, which comprised nearly 90% of the total catch (Table 4.1). Given that Lepidoptera represent a very small proportion (<2% in terms of number of individuals per faecal pellet) in the diet of *Pipistrellus* sp. (Swift, Racey & Avery 1985; Hoare 1991), but are an important component in the diet of *Myotis* sp. and (particularly) *P. auritus* (Vaughan 1997), data relating to this group is presented separately from the ‘non-Lepidoptera’ group (which consists mainly of Diptera). Woodland vegetation character had a weak influence on non-Lepidoptera insects, with tree density having a marginally significant negative effect on their abundance (Table 4.2). No other vegetation character or patch configuration variables influenced non-Lepidopterans. More non-Lepidopterans were collected in woodland edge than in woodland interior ($p<0.001$, model $R^2 = 67.6\%$; Fig. 4.2a), and the same trend was observed for macro-Lepidoptera ($p<0.001$, model $R^2 = 57.3\%$; Fig. 4.2c); micro-Lepidoptera showed a contrasting response and were more abundant in woodland interior than in woodland edge $p<0.001$, model $R^2 = 73.6\%$; Fig. 4.2b). The surrounding landscape had no significant influence on non-Lepidopterans’ abundance. The effects of woodland vegetation character, patch configuration and surrounding landscape on Lepidoptera are presented in Chapter 5.

Table 4.1. Summary table of invertebrates collected with heath traps.

Order	Mean per trap (±SE)	Abundance	% of total catch
Diptera (Nematocera)	51.0 ± 4.8	6432	43.6
Diptera (Brachycera)	10.0 ± 1.3	1258	8.5
Lepidoptera (macro)	27.9 ± 1.9	3518	23.9
Lepidoptera (micro)	13.4 ± 1.5	1674	11.4
Trichoptera	3.8 ± 0.6	479	3.2
Coleoptera	2.9 ± 0.5	363	2.5
Hymenoptera	2.8 ± 0.3	353	2.4
Hemiptera	2.3 ± 0.5	286	1.9
Araneae	1.5 ± 0.4	194	1.3
Ixodida	0.7 ± 0.2	87	0.6
Others *	0.1 ± 0.0	95	0.6
Total	117.0 ± 7.4	14739	100.0

* Includes orders representing <0.5% of the total catch and unidentified insects.

4.4.2. Bats

We recorded a total of 13,723 bat passes and captured a total of 184 bats during 133.5 hours of monitoring. Six bat species were identified; these were *P. pygmaeus, P. pipistrellus, Plecotus auritus, M. nattereri, M. daubentonii* and *M. mystacinus* (Table 4.3). Bat abundance and activity were significantly correlated for *P. pygmaeus* (Pearson coefficient = 0.42, p=0.012) and *Myotis* sp. (Pearson coefficient = 0.48, p=0.004). However, because analyses using abundance and activity yielded somewhat different results, here we present both. For *P. pipistrellus* only five individuals were caught in the nets/traps and for this reason only activity was used as a response variable in subsequent analyses. For *P. auritus*, few individuals were caught (12 bats) and few were recorded (11 passes; Table 4.3); therefore, we combined both detection methods and used bat presence/absence as a response variable.

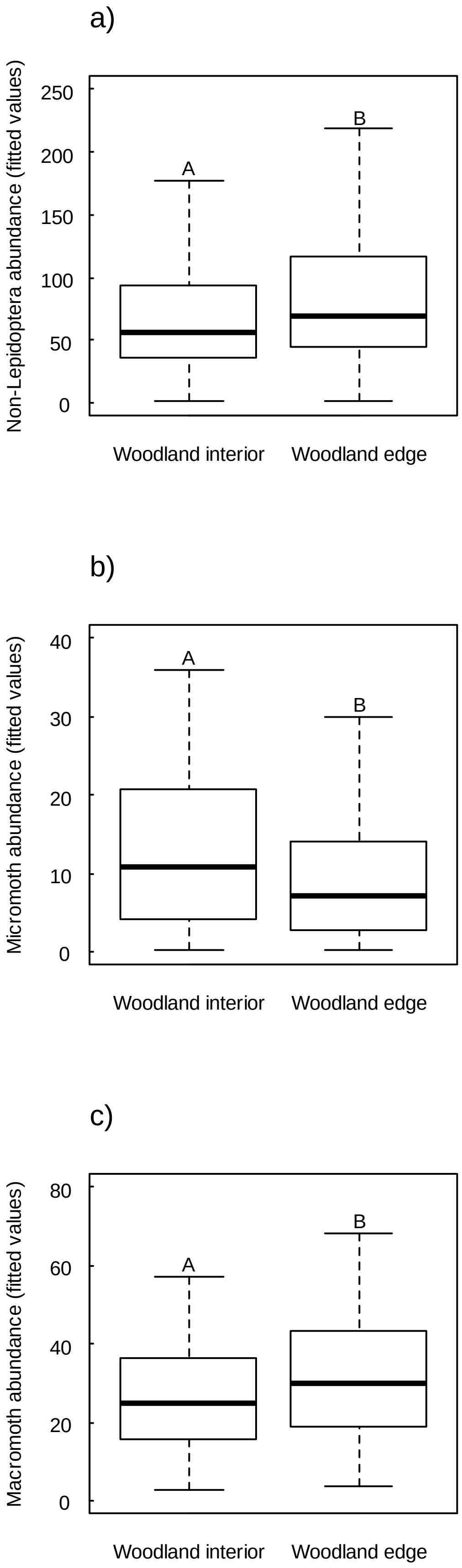

Figure 4.2. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the abundance of different invertebrate groups (a) Non-Lepidoptera, b) Micro-Lepidoptera, and c) Macro-Lepidoptera) at woodland interior and edge. Fitted values predicted by GLMMs are used. Capital letters indicate significant differences between groups at $p \leq 0.05$.

Table 4.2. Summary table showing the influence of woodland character on bats and nocturnal invertebrates. Parameter estimates (±SE; standardized for continuous variables), significance values, and goodness of fit (model R^2) of the models are shown. Significance codes: ‘***’ $p \leq 0.001$, ‘**’ $p \leq 0.01$, ‘*’ $p \leq 0.05$, ‘ ◌̇ ’ $p \leq 0.1$, “-” $p \geq 0.1$.

						Vegetation character					Patch configuration				
Response variable	Year	Date	Temp	Matrix type	Grazing	Wood type	Tree species richness	Tree density	Canopy cover	Understorey cover	Wood size	Wood shape	Wood isolation	Model error	Model R^2
Invertebrates (abundance) *	-	-	0.53 (0.15) ***	-	-	-	-	-0.27 (0.14) .	-	-	-	-	-	Gaussian	35.7 %
P. pipistrellus (activity)	3.62 (0.72) ***	-	-	-	3.52 (0.62) ***	-	-	-0.73 (0.26) *	1.14 (0.45) *	-0.75 (0.22) **	-	-0.41 (0.23) .	-	Quasi-Poisson	96.8 %
P. pygmaeus (abundance)	-	0.33 (0.15) *	0.51 (0.13) ***	-	-	-	0.35 (0.14) *	-	-	-	-0.33 (0.17) .	-	-	Quasi-Poisson	69.0 %
P. pygmaeus (activity)	1.23 (0.43) **	0.66 (0.20) **	0.43 (0.18) *	-	-	0.80 (0.31) *	-	-1.60 (0.44) **	-	-	-	-	0.45 (0.07) ***	Quasi-Poisson	97.2 %
Myotis sp. (abundance)	-	-	-	-	-	-	-	0.44 (0.17) *	-	-	-	-	-	Quasi-Poisson	12.3 %
Myotis sp. (activity)	-	0.64 (0.20) **	0.44 (0.20) *	-	1.80 (0.46) ***	-	-	0.70 (0.17) ***	-0.45 (0.20) *	-	-0.45 (0.26) .	-	-	Quasi-Poisson	92.0 %
P. auritus (presence)	-	-	-	-	-	1.23 (0.73) .	-	-	-	-	-	-	-	Binomial	64.7 %

* Excludes Lepidoptera. The effects of woodland vegetation character, patch configuration and surrounding landscape on Lepidoptera are presented elsewhere (Chapter 5).

Table 4.3. Summary table for bats/bat passes per species and detection method.

Bat species	Detection method	Mean per site (±SE)	Total	% of total	Sites detected	
P. pygmaeus	Trapping	3.6 ± 0.6	126	68.5	27	34
	Acoustic	252.2 ± 93.0	8575	62.5	34	
P. pipistrellus	Trapping	0.2 ± 0.1	5	2.7	3	28
	Acoustic	131.3 ± 47.7	4464	32.5	28	
Myotis sp.	Trapping	1.2 ± 0.3	41 [a]	22.3	19	26
	Acoustic	3.9 ± 1.2	133	1.0	21	
P. auritus	Trapping	0.4 ± 0.1	12	6.5	8	15
	Acoustic	0.3 ± 0.1	11	0.1	8	
All species	Trapping	5.4 ± 0.7	184 [b]	100.0	33	34
	Acoustic	389.8 ± 105.9 [c]	13723 [c]	100.0	34	

[a] 38 *M. nattereri*, 2 *M. daubentonii* and 1 *M. mystacinus*.

[b] Over 70 % of bats were captured using the acoustic lure (Fuentes-Montemayor *et al.* unpublished data).

[c] Includes unidentified bat calls (mostly *Pipistrellus* sp.).

4.4.2.1. Effects of woodland vegetation character and woodland patch configuration on bats

After accounting for the effects of year, date and temperature, bats were significantly influenced by variables related to both woodland vegetation character and woodland patch configuration (Table 4.2). *Pipistrellus pipistrellus* activity was higher in sites with dense canopy cover and low tree density and understorey cover; woodland patches with in-site grazing and with compact shapes were also related to high *P. pipistrellus* activity. *Pipistrellus pygmaeus* abundance was positively related to tree species richness and negatively (but only marginally) to patch size. *Pipistrellus pygmaeus* activity was influenced by woodland type (higher in broadleaved-conifer mix than in broadleaved only), tree density (negatively) and woodland isolation (positively). The abundance and activity levels of *Myotis* sp. were positively related to tree density; these species' activity was also negatively influenced by canopy cover and (marginally) by woodland patch size and positively affected by in-site grazing. The presence of *P. auritus* in a site was only related to woodland type (marginally higher probability of presence in broadleaved-conifer mix than in broadleaved only woodlands).

4.4.2.2. Effects of the surrounding landscape on bats

In general, metrics relating to woodland and water were amongst the most important landscape parameters influencing bat abundance and activity. However, the scale and magnitude of the effects of specific metrics varied between species (Fig. 4.3 & Appendix 4C). *Pipistrellus pipistrellus* activity was influenced by the surrounding landscape mostly at large spatial scales (≥ 1500 m; Fig. 4.3a). Percentage cover of semi-natural environment and woodland were positively and negatively related, respectively, to this species' activity, which was also positively related to woodland isolation (ENN). *Pipistrellus pygmaeus* was most strongly influenced by the landscape at relatively small spatial scales (≤ 1000 m), although weaker landscape effects were still significant at larger scales (Figs. 4.3b & 4.3c). Water metrics (% cover, LPI and ENN) were positively related to *P. pygmaeus* abundance and activity. Woodland isolation and edge density had positive and negative effects, respectively, on this species' activity, which was also related to the percentage cover of farmland and urban areas (positively) and to landscape heterogeneity (negatively). *Myotis* species were affected by woodland metrics at both small (≤ 250 m) and large (≥ 2500 m) spatial scales (Figs. 4.3d & 4.3e); woodland % cover, LPI and edge density were negatively related to *Myotis* sp. activity, whereas woodland and water isolation were positively related to this group's abundance and activity. None of the landscape parameters significantly influenced *P. auritus*; semi-natural environment % cover had the strongest (marginally significant) influence on this species presence (p=0.085; R^2=12.59%).

4.4.2.3. Use of woodland interior, woodland edge and surrounding matrix by bats

In total, 260 point counts (10 minutes each) were conducted at different locations within and around each woodland patch and 2657 bat passes – 1810 *P. pygmaeus*, 719 *P. pipistrellus*, 33 *Myotis* sp., 6 *P. auritus* and 89 unidentified (mostly *Pipistrellus* sp.) – were recorded. Bat activity in woodland was higher than in the surrounding matrix for all species, but preference for woodland interior or edge was species-specific (Fig. 4.4). *Pipistrellus pipistrellus* activity was similar in woodland interior and edge (p = 0.706) and lower in the surrounding matrix $p \leq 0.001$; model R^2 = 79.0 %). *Pipistrellus pygmaeus* activity was higher in woodland interior than in woodland edge ($p \leq 0.001$, but difference between median fitted values was very small; Fig. 4.4b) and lower in the surrounding matrix ($p \leq 0.001$; model R^2 = 63.7 %). The activity of *Myotis* species was higher in woodland interior than either woodland edge (p = 0.045) or surrounding matrix (p = 0.013); the activity of this group did not differ between woodland edge and surrounding matrix (p = 0.269; model R^2 = 33.3 %). *Plecotus auritus* data was insufficient to assess use of woodland interior, edge and surrounding matrix.

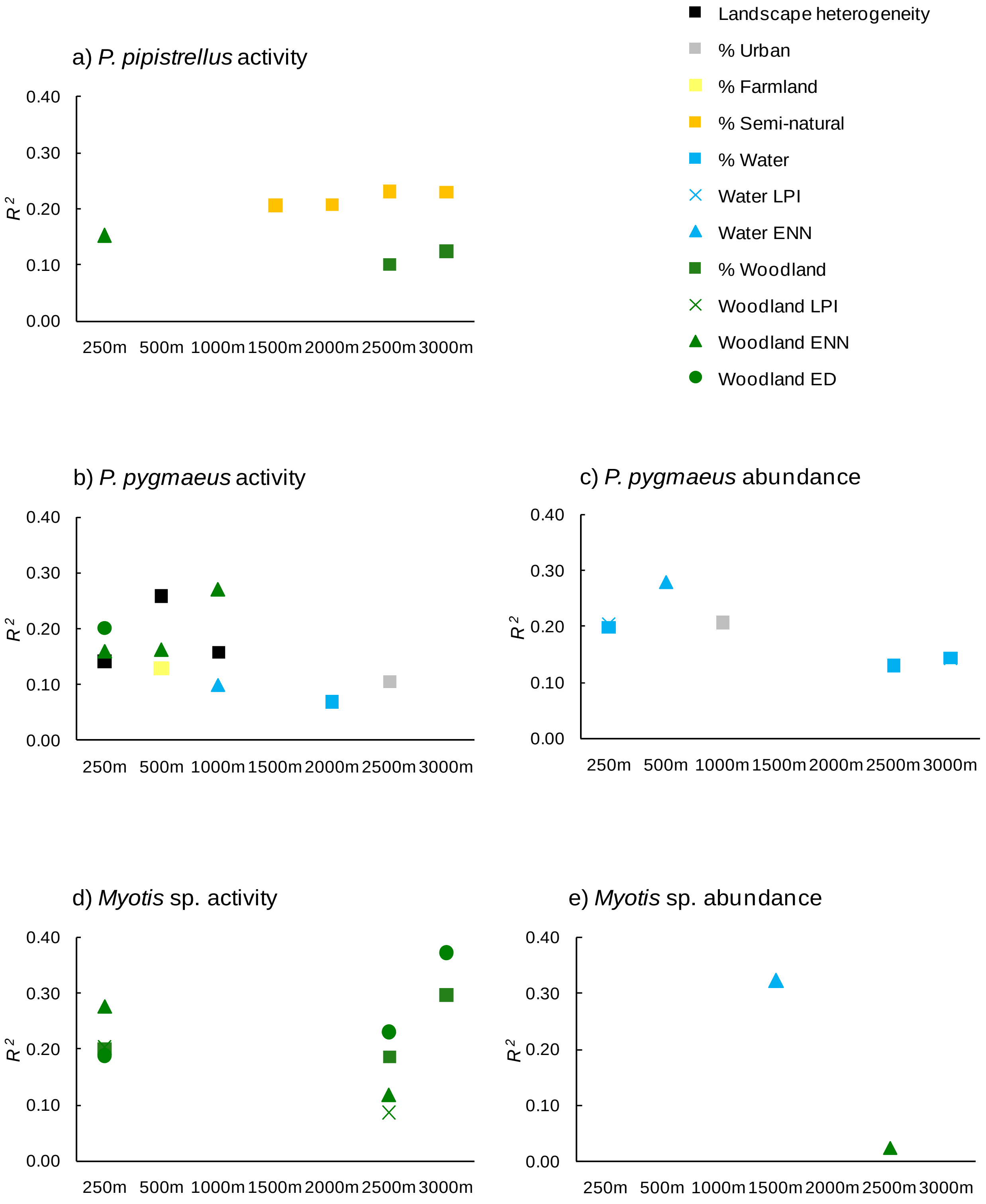

Figure 4.3. R^2 values obtained from regression analyses between landscape metrics and bat abundance and activity for *P. pipistrellus* (a), *P. pygmaeus* (b & c), and *Myotis* species (d & e). Only significant effects ($p \leq 0.05$) are shown. The directions of the effects are discussed in the text and the magnitudes (e.g. parameter estimates) are presented in Appendix 4C.

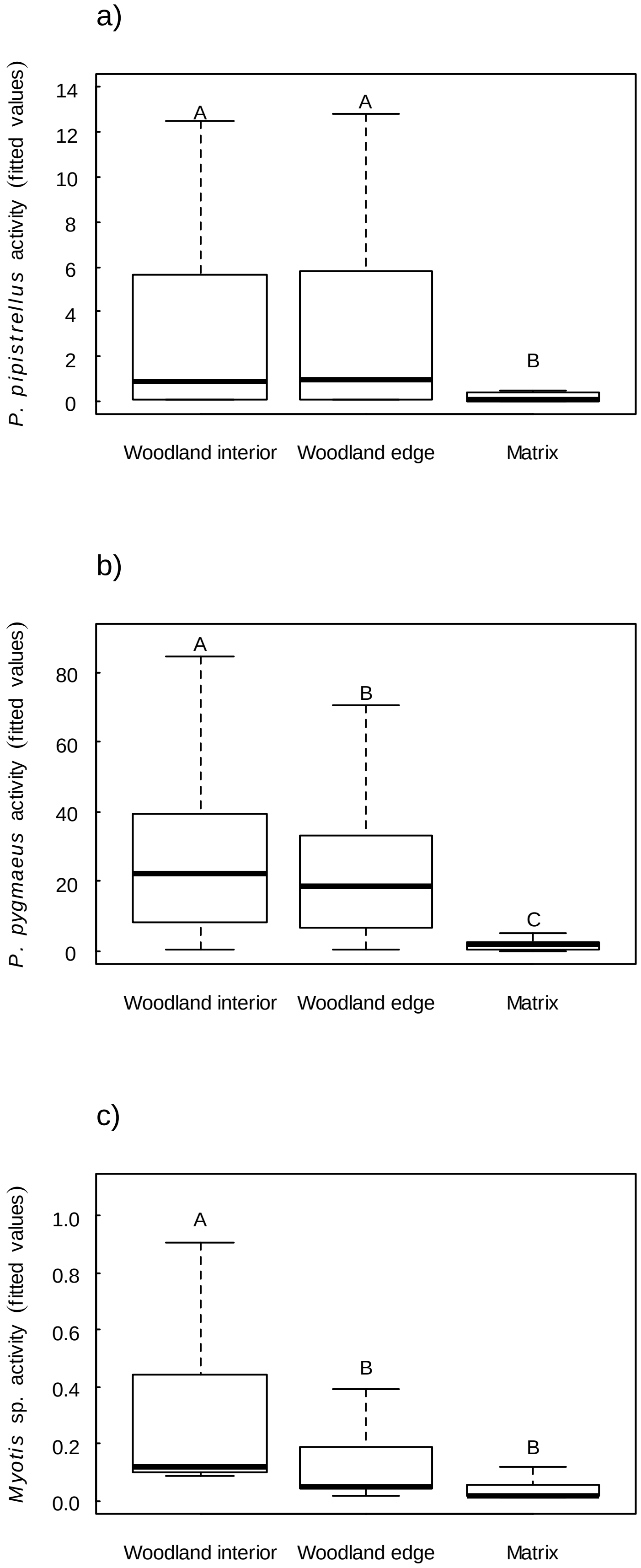

Figure 4.4. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the activity (number of bat passes per point count type) of a) *P. pipistrellus*, b) *P. pygmaeus*, and c) *Myotis* sp. at woodland interior, woodland edge and surrounding matrix. Fitted values predicted by GLMMs are used. Capital letters indicate significant differences between groups at $p \leq 0.05$.

4.5. Discussion

We assessed the effects of woodland vegetation character and patch configuration (local-scale characteristics) and of the surrounding landscape on bats and their insect prey within a farmland-dominated landscape. Our results provide relevant information to be applied by land managers and policy makers involved in woodland management and creation schemes.

Neither woodland vegetation nor patch configuration influenced the availability of non-Lepidoptera (mainly Diptera) insects, which are the main component in the diet of *Pipistrellus* bats (Swift, Racey & Avery 1985; Hoare 1991) and an important component in the diet of *Myotis* bats (Vaughan 1997). In contrast, Lepidoptera – the main component in the diet of *P. auritus* and another important constituent in the diet of *Myotis* species (Vaughan 1997) – show strong associations with woodland vegetation character and patch configuration (Chapter 5). This suggests that food availability for moth-eating bats is higher in large and well connected woodland patches, with a species-rich vegetation and a dense understorey cover (Chapter 5). However, the associations of *Myotis* species with woodland vegetation character did not reflect those of Lepidoptera (see relevant discussion in following paragraph). Within a woodland patch, woodland edge had a higher abundance of non-Lepidopterans compared to woodland interior. This agrees with previous findings (e.g. Morris, Miller & Kalcounis-Rueppell 2010) and suggests that foraging opportunities for bats feeding on this kind of prey are higher in woodland edges, probably because these have a higher structural complexity than woodland interior (Murcia 1995). Macro-Lepidoptera were also more abundant in woodland edges, suggesting that food availability for moth-eating bats is also higher here than in woodland interior; although the pattern shown by micro-Lepidoptera shows the opposite trend, the abundance of this group was much lower than that of macro-Lepidoptera; hence, overall moth availability remains higher in woodland edges.

Bats showed species-specific associations with woodland vegetation character. Woodlands with high tree species richness were associated with higher *P. pygmaeus* abundance. High activity levels of both Pipistrelle species were related to relatively low tree densities (<1000 trees per hectare), an open understorey cover and a relatively closed canopy cover (> 60% canopy cover; the latter two affecting only *P. pipistrellus*), which is consistent with findings for other Pipistrelle species (e.g. *P. subflavus*; Yates & Muzica 2006). In contrast, *Myotis* species' abundance and activity were higher in dense woodlands with a relatively open canopy (50 – 75% cover), contradicting previous findings of negative associations between tree density/clutter and *Myotis* sp. activity (Brigham *et al.* 1997; Erickson & West 2003). These species-specific and conflicting responses to vegetation structure suggest that habitat heterogeneity should be maintained in order to meet the requirements of different bat species. Woodlands with conifer and broadleaved trees had higher *P. pygmaeus* activity and higher probability of *P. auritus* occurrence than woods with broadleaved trees only. Broadleaved woodland is usually regarded as a higher quality habitat for bats than coniferous or mixed woodland (Walsh & Harris 1996). However, conifer (e.g. Scots and Corsican pines) plantations have been found to be valuable for some bat species (e.g. *M. nattereri*; Mortimer 2006). Mixed woodlands might be related to a higher structural complexity and, therefore, to higher roosting and foraging resources for bats. The presence of grazing stock in a woodland was associated with higher activity levels of *P. pipistrellus* and *Myotis* sp. Grazing has been linked to changes in woodland vegetation structure and composition, such as reduced sapling recruitment, shrub and herb cover (Pettit, Froend

& Ladd 1995; Hester, Mitchell & Kirby 1996); reduced clutter caused by grazing might potentially facilitate hunting for aerial hawkers (such as *P. pipistrellus*; Schnitzler & Kalko 2001). Large amounts of organic matter (dung) are associated with high numbers of dung-dwelling insects, such as many Diptera (D'Arcy-Burt & Blackshaw 1991; McCracken, Foster & Kelly 1995); hence, the presence of grazing stock might result in higher food availability for some bat species (although we did not detect such effect on invertebrate abundance). Nonetheless, in-site grazing has strong negative effects on moth abundance (Chapter 5), which might reduce foraging resources for moth-eating bats.

In general, the influence of woodland patch configuration on bat abundance and activity was weaker than that of woodland vegetation character (e.g. less significant associations and lower standardised parameter estimates). Unexpectedly, we found positive effects of woodland patch isolation (for *P. pygmaeus* activity, although the standardized parameter estimate for this variable was relatively low when compared to other predictors within the model) and marginally significant negative associations with woodland patch size (for *P. pygmaeus* abundance and *Myotis* sp. activity). In addition, woodland extent and isolation at the landscape scale had the same effects on bats (negative and positive, respectively). Positive effects of woodland fragmentation have been reported for some bat species (e.g. those adapted for hunting in open areas; Klingbeil & Willig 2009; Estrada-Villegas, Meyer & Kalko 2010). However, given the strong evidence supporting the importance of woodland habitat for British bats (e.g. Walsh & Harris 1996; Vaughan, Jones & Harris 1997; Russ & Montgomery 2002; Altringham 2003), our results were rather surprising. Positive effects of woodland fragmentation in other studies have been linked to increases in woodland edge density (Grindal & Brigham 1999); this and other linear landscape features (e.g. hedgerows) are intensively used by many bat species as navigational references, sources of insect prey, shelter from wind, and protection from predators (Hein, Castleberry & Miller 2009; Morris, Miller & Kalcounis-Rueppell 2010). However, our results showed that woodland edge density was negatively related to the activity of *P. pipistrellus* and *Myotis* species. In addition, we found no evidence of higher bat activity at woodland edges compared to woodland interior (in fact, *Myotis* sp. and *P. pygmaeus* activity was higher in woodland interior than in woodland edge). One potential explanation is that the higher bat abundance and activity levels detected for some species in small and isolated woodland fragments are a consequence of a more intensive use of woodland by bats in landscapes where this habitat is scarce. Flight is energetically expensive (Thomas & Suthers 1972) and intensively-managed agricultural land is a hostile (low permeability) matrix which is avoided by bats (Walsh & Harris 1996; Wickramasinghe *et al.* 2003). Therefore, bats might 'choose' to use nearby resources more intensively rather than commute long distances to remote foraging areas. Tree lines, hedgerows and riparian corridors linking otherwise isolated woodland patches might act as commuting routes for bats (Verboom & Huitema, 1997; Downs & Racey 2006; Boughey *et al.* 2011b) and allow access to feeding sites over a wider area.

The surrounding landscape had a relatively strong influence on bat abundance and activity (e.g. individual landscape parameters explaining *ca.* 10 – 30 % of data variation for most species). Woodland was the most important habitat for bats, being related to the abundance/activity of all bat species (except *P. auritus*; but note that limited data only allowed us to assess presence/absence of this species, which is a coarser variable than abundance/activity). Woodland cover and edge density were negatively related to bat abundance and activity, whereas woodland isolation at the landscape scale (mean value of ENN distances between all woodland patches within the landscape) was positively associated with these parameters (see pertinent discussion in previous paragraph). Water metrics were mainly positively related to the abundance and activity of *P. pygmaeus*, which is consistent with this species' preference to forage over riparian habitats (Davidson-Watts, Walls & Jones 2006; Nicholls & Racey 2006b). The amount of urban areas was also positively related to *P. pygmaeus'* activity, probably because it is associated with availability roosting sites (Walsh & Harris 1996). The extent of semi-natural environment (e.g. rough grassland) was positively related to *P. pipistrellus* activity. Grassland and scrub are regarded as poor quality habitats for British bats (Walsh & Harris 1996); however, a high proportion of this habitat has been linked to high abundances of insects included in the diet of *P. pipistrellus* (Chapter 2), which might explain the positive relation. At the landscape level, *Myotis* species were almost exclusively influenced by woodland metrics, which is consistent with the strong association with woodland shown by many *Myotis* sp. (e.g. *M. nattereri*, which comprised nearly 90 % of *Myotis* species abundance in our study; Smith & Racey 2008). The scale at which bats were most strongly influenced by the surrounding landscape varied between species. *Plecotus auritus* was not significantly influenced by the surrounding landscape at any spatial scale; furthermore, the strongest (marginally significant) landscape effect was observed within 250 m, which is consistent with observations of this species foraging mostly within 0.5 km of the roost (Entwistle, Racey & Speakman 1996). *Pipistrellus pipistrellus* responded to landscape metrics mostly at large spatial scales (≥ 1500 m), whereas *P. pygmaeus* responded more strongly to the landscape at relatively small spatial scales (≤ 1000 m). These findings agree with studies showing that *P. pipistrellus* has larger home ranges (~1500 ha) and is influenced by the surrounding landscape at larger spatial scales (e.g. within 3 km) than *P. pygmaeus* (~500 ha and within 500 m, respectively; Nicholls & Racey 2006a;

Chapter 2 in this thesis). *Myotis* species were influenced by the landscape at both small (≤ 250 m) and large (≥ 2500 m) spatial scales. This double peak might reflect the use of foraging areas close to roosting sites (as observed for other bat species; Entwistle, Racey & Speakman 1996) and within the wider landscape. *Myotis* species can travel relatively long distances (e.g. up to 4 km in the case of *M. nattereri*; Dietz, von Helversen & Nill 2009) to their foraging sites and have been shown to be more strongly associated with the landscape at large than at small spatial scales (Boughey *et al.* 2011a). Given that the response of bats (particularly *Myotis* sp. and *P. pipistrellus*) to the surrounding landscape was strong even at large spatial scales (up to 3 km as assessed in our study, although it probably extends even further), a wide-landscape-scale management approach is required for highly mobile bat species.

In summary, bat populations in woodland patches within a farmland-dominated landscape were influenced by both local and landscape-level attributes. At the local scale, woodland vegetation character appears more important than patch configuration; however, given that habitat associations are species-specific – e.g. Pipistrelle species were positively associated with open understorey and closed canopy cover, whilst *Myotis* species showed the opposite trend – habitat heterogeneity (within or between woodland patches) seems essential to fulfil the requirements of different bat species. Patterns of higher bat abundance and activity at small and isolated woodland patches might be a consequence of a more intensive use of this habitat in landscapes where woodland and other good quality foraging areas are limited. At the landscape scale, woodland extent and configuration were the most important metrics explaining bat abundance and activity. Some species were influenced by the surrounding landscape at large spatial scales (e.g. within 3 km) and would benefit from woodland creation and management at a landscape-scale.

4.6. Acknowledgements

We wish to thank the landowners and Estate managers who granted us permission to conduct this study on their land, and L. Cavin, J. Wallace and K. Wolf for their help conducting field work and analysing ultrasonic recordings. Thanks to CONACyT for providing a graduate scholarship (189261) to E.F.M., and to Bat Conservation International, the British Ecological Society and the People’s Trust for Endangered Species for their financial support.

Appendix 4A. List of tree species recorded during surveys.

Latin name	Common name	Native to Britain	Relative abundance (%)
Betula pubescens	Downy birch	Yes	21.97
Betula pendula	Siver birch	Yes	15.83
Acer pseudoplatanus	Sycamore	No *	9.91
Quercus petraea	Sessile oak	Yes	6.78
Picea abies	Norway spruce	No	5.68
Fraxinus excelsior	Common ash	Yes	5.39
Fagus sylvatica	Common beech	Yes	5.22
Pinus sylvestris	Scots pine	Yes	5.10
Sorbus aucuparia	Common rowan	Yes	3.65
Quercus robur	English oak	Yes	3.30
Picea sitchensis	Sitka spruce	No	2.90
Salix caprea	Goat willow	Yes	2.20
Larix decidua	European larch	No	1.68
Sambucus nigra	Elder	Yes	1.45
Crataegus monogyna	Common hawthorn	Yes	1.33
Ulmus glabra	Wych elm	Yes	1.16
Salix cinerea	Grey sallow	Yes	0.99
Tsuga heterophylla	Western hemlock	No	0.87
Pseudotsuga menziesii	Douglas fir	No	0.75
Abies grandis	Grand fir	No	0.70
Alnus glutinosa	Common alder	Yes	0.64
Prunus avium	Wild cherry	Yes	0.58
Corylus avellana	Common hazel	Yes	0.46
Tilia platyphyllos	Broadleaved lime	Yes	0.41
Populus alba	White poplar	Yes	0.17
Populus nigra ssp. *betulifolia*	Wild black poplar	Yes	0.17
Rhododendron ponticum	Common rhododendron	No	0.17
Aesculus hippocastanum	Horse chestnut	No *	0.12
Chamaecyparis lawsoniana	Lawson cypress	No	0.12
Ilex aquifolium	Common holly	Yes	0.06
Quercus rubra	Red oak	No	0.06
Tilia x *europaea*	Common lime	Yes	0.06
Ulmus procera	English elm	Yes	0.06
x *Cupressocyparis leylandii*	Leyland cypress	No	0.06

* Naturalised

Appendix 4B. Descriptive table showing in-site characteristics of the 34 woodland patches surveyed during 2009/2010.

Site	Woodland size (ha)	Woodland shape [a]	Woodland isolation (m) [b]	Surrounding matrix	In-site grazing	Woodland type [c]	Tree species richness	Dominant tree species [d, e]	Tree density (per ha)	Understorey cover [f]	Canopy cover (%)
1	0.19	2.52	165.10	Pastoral	No	Mixed	4	*P. sitchensis* (64%)	1236.72	3	94.29
2	0.24	1.36	149.93	Pastoral	Yes	Broad	2	*Q. petraea* (92%)	237.14	0	71.43
3	0.37	2.75	109.66	Pastoral	Yes	Broad	7	*T. platyphyllos* (25%)	259.22	7	65.71
4	0.40	1.13	117.18	Arable	No	Mixed	3	*Q. robur* (71%)	209.40	2	75.00
5	0.88	1.29	277.89	Mixed	Yes	Broad	2	*B. pubescens* (93%)	602.10	0	54.29
6	1.01	1.16	74.85	Pastoral	No	Mixed	7	*A. pseudoplatanus* (57%)	399.54	4	80.00
7	1.20	1.75	245.93	Mixed	No	Broad	12	*B. pendula* (21%)	477.99	8	64.29
8	1.32	1.17	674.50	Arable	No	Mixed	5	*P.abies+B.pubescens+B.pendula* (25% each)	549.65	0	75.71
9	1.34	3.08	133.12	Mixed	No	Mixed	8	*B. pubescens* (32%)	2381.20	2	71.43
10	1.59	1.55	32.98	Pastoral	Yes	Broad	3	*B. pendula* (61%)	822.86	8	65.71
11	1.66	1.96	117.61	Mixed	No	Broad	6	*B.pubescens+S.aucuparia* (39% each)	534.69	6	74.29
12	2.21	4.09	159.10	Pastoral	No	Broad	6	*B.pubescens+S.aucuparia* (36% each)	366.89	3	52.86
13	2.82	2.27	103.90	Arable	No	Mixed	9	*B. pubescens* (36%)	1395.64	2	81.43
14	3.14	1.56	223.09	Mixed	No	Broad	8	*B. pubescens* (46%)	413.41	3	81.43
15	3.95	4.18	218.52	Mixed	No	Broad	11	*F. excelsior* (27%)	503.13	3	75.71
16	4.08	1.87	127.02	Pastoral	Yes	Broad	9	*F. excelsior* (27%)	180.59	1	62.14
17	4.29	1.33	75.74	Pastoral	No	Broad	7	*B. pendula (52%)*	389.31	7	59.29
18	4.45	1.69	58.67	Pastoral	No	Broad	3	*B. pendula (54%)*	304.40	4	32.86
19	5.17	2.73	97.10	Mixed	No	Mixed	5	*F. excelsior (41%)*	1663.55	2	90.71
20	5.64	1.47	200.60	Pastoral	No	Broad	7	*B. pubescens (30%)*	358.28	2	59.23
21	5.89	1.20	65.12	Mixed	No	Mixed	7	*B. pubescens (52%)*	747.50	0	85.00
22	6.52	4.50	138.29	Pastoral	No	Mixed	11	*Q. robur (29%)*	730.74	1	68.57
23	7.15	1.39	51.48	Pastoral	No	Broad	5	*B. pubescens (66%)*	852.29	2	79.29
24	7.86	2.59	30.08	Arable	No	Mixed	12	*F. sylvatica (39%)*	680.83	3	93.50

Appendix 4B (cont.)

Site	Woodland size (ha)	Woodland shape [a]	Woodland isolation (m) [b]	Surrounding matrix	In-site grazing	Woodland type [c]	Tree species richness	Dominant tree species [d, e]	Tree density (per ha)	Understorey cover [f]	Canopy cover (%)
25	9.04	1.48	5.10	Mixed	No	Mixed	6	*B. pubescens* (54%)	2512.55	1	78.57
26	9.19	2.35	5.70	Pastoral	No	Mixed	9	*B. pubescens* (30%)	604.75	5	62.14
27	10.83	2.35	6.32	Mixed	No	Broad	5	*B. pubescens* (39%)	670.17	4	74.29
28	16.36	2.22	7.60	Mixed	No	Mixed	5	*Q. petraea* (75%)	483.65	2	75.00
29	17.55	5.43	7.80	Mixed	No	Mixed	10	*A. pseudoplatanus* (31%)	514.86	1	82.00
30	18.35	1.83	16.74	Pastoral	No	Mixed	4	*P. sylvestris* (39%)	1237.03	0	70.95
31	18.79	1.25	7.28	Mixed	No	Broad	7	*B. pubescens* (35%)	578.47	1	63.50
32	18.81	3.68	7.00	Mixed	No	Mixed	15	*A. pseudoplatanus* (38%)	691.00	5	74.50
33	21.16	3.46	17.05	Pastoral	No	Mixed	10	*P. abies* (30%)	611.10	4	73.50
34	29.60	2.88	8.60	Pastoral	Yes	Mixed	8	*B. pendula* (64%)	448.68	4	60.00

[a] Equals the patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the corresponding patch area. When the patch is maximally compact ‘woodland shape’ = 1, and increases without limit as the patch shape becomes more irregular. Modified from McGarigal et al (2002).

[b] Proximity (edge-to-edge distance) to closest woodland patch ≥ 0.19 ha (size of smallest woodland patch included in surveys).

[c] ‘Broad’ refers to sites where only broadleaved trees were present; ‘Mixed’ refers to sites with both broadleaved and conifer trees present.

[d] See Appendix 4A for a full list of tree species.

[e] Dominant tree species relative abundance.

[f] Domin scale (Kent & Coker 1992) was used: 0= no understorey; 1 = cover of ≤ 4 % with few individuals; 2 = cover of ≤ 4 % with several individuals; 3 = cover of ≤ 4 % with many individuals; 4 = cover of 4 – 10 %; 5 = cover of 11 – 25 %; 6 = cover of 26 – 33 %; 7 = cover of 34 – 50 %; 8 = 51 – 75 %; 9 = 76 – 90%; 10 = 91 – 100 %.

Appendix 4C. Standardized parameter estimates (±SE) and significance values obtained from linear regression analyses between landscape metrics and bat abundance/activity. Only significant effects (p<0.05) are shown.

	250m	500m	1000m	1500m	2000m	2500m	3000m
P. pipistrellus activity							
% Natural	-	-	-	0.50 * (0.22)	0.55 * (0.22)	0.58 * (0.23)	0.58 * (0.26)
% Woodland	-	-	-	-	-	-1.29 * (0.53)	-1.35 * (0.55)
Woodland ENN	0.70 * (0.34)	-	-	-	-	-	-
P. pygmaeus abundance							
% Urban	-	-	0.39 ** (0.14)	-	-	-	-
% Water	0.22 * (0.10)	-	-	-	-	-	0.23 * (0.10)
Water LPI	0.23 * (0.10)	-	-	-	-	-	0.23 * (0.10)
Water ENN	-	0.40 * (0.17)	-	-	-	-	-
P. pygmaeus activity							
Landscape heterogeneity	-0.74 * (0.28)	-0.78 ** (0.27)	-0.63 * (0.29)	-	-	-	-
% Urban	-	-	-	-	-	0.51 * (0.22)	-
% Farmland	-	0.62 * (0.31)	-	-	-	-	-
% Water	-	-	-	-	0.45 ** (0.15)	-	-
Water ENN	-	-	0.48 * (0.21)	-	-	-	-
Woodland ENN	0.56 * (0.27)	0.40 * (0.18)	0.56 ** (0.18)	-	-	-	-
Woodland ED	-0.83 * (0.35)	-	-	-	-	-	-
Myotis sp. abundance							
Water ENN	-	-	-	0.74 *** (0.16)	-	-	-
Woodland ENN	-	-	-	-	-	0.55 ** (0.20)	-
Myotis sp. activity							
% Woodland	-0.85 * (0.39)	-	-	-	-	-1.10 * (0.42)	-1.29 ** (0.45)
Woodland LPI	-0.86 * (0.39)	-	-	-	-	-0.85 * (0.42)	-
Woodland ENN	0.88 ** (0.31)	-	-	-	-	0.54 ** (0.19)	-
Woodland ED	-0.85 * (0.34)	-	-	-	-	-0.92 ** (0.32)	-1.08 ** (0.33)

Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, "-" $p \geq 0.05$.

Chapter 5

Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes

5.1. Summary

As a consequence of long-term deforestation, woodland cover has been drastically reduced in the United Kingdom (UK). A large proportion of the remaining woodland consists of small and highly fragmented patches within farmland. A number of agri-environment schemes (AES) aim to increase the amount and quality of woodland on agricultural land, but there is limited information on moths' associations with woodland characteristics which can be used to produce practical recommendations for woodland creation and management. We conducted vegetation surveys and used Geographic Information Systems (GIS) software to quantify vegetation character and spatial configuration of 34 woodland patches within farmland. We assessed the influence of these parameters on micro- and macromoth communities, which were collected using heath light traps. In addition, we measured the influence of the surrounding landscape at several spatial scales to assess the potential importance of a landscape-scale management approach for moth conservation. Variables related to woodland vegetation character influenced moth abundance, richness and diversity. In general, high tree species diversity and a high proportion of native tree species were related to higher moth abundance and species richness. The presence of grazing stock in woodlands had negative effects on moths. The spatial configuration of woodland patches strongly influenced moth assemblages. Moth abundance and richness were higher in large woodland patches located close to other woodlands. Moth assemblages differed between woodland interior and edge, indicating that some moth species are associated with woodland core habitat. Woodlands with compact shapes (with proportionally less edge exposed to the surrounding matrix) had higher numbers of 'woodland species'. Small woodland patches can potentially maintain relatively high moth abundance and richness, but shape and proximity to other woodlands are of particular importance in these cases. Woodland cover was the most important landscape parameter affecting moths, mostly at relatively small spatial scales (within 500 m); macromoth 'woodland species' were influenced by the surrounding woodland at larger spatial scales (within 1500 m) and are more likely to benefit from a wider landscape-scale management approach. *Synthesis and applications*: Our results contribute to a better understanding of the effects of habitat fragmentation on biodiversity and have important implications for the design and management of woodland patches of high conservation value within agricultural land.

5.2. Introduction

As a consequence of long-term deforestation, woodland cover in Europe has been drastically reduced. In the United Kingdom (UK), the decrease has been so severe that at the beginning of the 20th century woodland was estimated to comprise *ca.* 5% of the land area (Mason 2007). Programmes of afforestation over the last 50 years have increased this figure to approximately 12% cover (Mason 2007). Much of this consists of forestry plantations, which in many cases have low species richness (exotic fast growing conifers) and low structural diversity (Mason 2007). The remainder is highly fragmented and consists of a large number of relatively small woodland patches (< 100 ha) within agricultural landscapes (Watts 2006).

Moths occupy a variety of habitats, but many species (e.g. about two-thirds of British macromoths) occur regularly in woodlands and are associated with native tree species (Waring 1989; Young 1997). Ecological research and conservation efforts for Lepidoptera have been largely focused on butterflies. Relatively little attention has been given to macromoths and even less to the conservation status and habitat requirements of smaller micromoths, even though they comprise a large proportion of most local lepidopteran assemblages (Bland & Young 1996). Many moth species have undergone severe population declines. In the UK, 62 species became extinct during the twentieth century (Fox *et al.* 2006) and many common and widespread macromoth species have showed significant population declines over the last few decades (Conrad *et al.* 2006). Moths are a sensitive indicator group for agricultural intensification and forest quality (Kitching *et al.* 2000; Jennings & Pocock 2009) and an important food resource for many species of birds, bats and small mammals (Vaughan 1997; Wilson *et al.* 1999).

One of the most important threats to moths is habitat loss and fragmentation (Conrad *et al.* 2004), although changes in the structure, management and spatial configuration of woodlands have also been linked to declines of certain species (Fox *et al.* 2006). Moth abundance and species richness tend to increase with woodland patch size; woodland quality also influences moth populations, with herbaceous plant species richness, tree species diversity and tree basal area positively affecting moth abundance and species richness (Usher & Keiller 1998; Summerville & Crist 2002, 2003, 2004). Whilst the effects of patch configuration (e.g. shape and isolation) have rarely been assessed in these studies, Usher & Keiller (1998) found that compact patches had higher richness of woodland specialist species than elongated patches, while increased patch isolation reduced species richness of woodland macromoths. In addition, although it has been shown that the surrounding landscape influences lepidopteran communities – e.g. positive effects of landscape heterogeneity, proportion of open semi-natural environment and woodland within up to 2 km from a locality (e.g. Ricketts *et al.* 2001; Ekroos, Heliölä & Kuussaari 2010; Chapter 3 in this thesis) – it has seldom been evaluated when studying moths in woodland fragments (but see Summerville & Crist

(2004) who showed that the percentage cover of woodland within 1 km positively affects the abundance and species richness of woodland specialists).

In the UK, a number of agri-environment schemes (AES) which aim to increase the amount and quality of woodland on agricultural land have been in place for the past 20 years (Crabtree 1996). However, recommendations for the creation and management of woodland to improve habitat for wildlife are strongly biased towards birds and mammals (e.g. Blakesley & Buckley 2010), often disregarding smaller taxa (e.g. arthropods; but see Anonymous 2007). In addition, the value of these woodland patches, in terms of biodiversity gains, is rarely assessed (but see Crabtree 1996). Here, we examine both micro- and macromoth communities in woodland patches within agricultural landscapes to assess the effects of woodland vegetation character (e.g. tree species richness), patch configuration (e.g. size and shape) and surrounding landscape (e.g. proportion of woodland cover) on moth assemblages. In particular, we addressed three specific questions:

1. Do moth abundance and species richness relate to woodland vegetation character and patch configuration and, if so, to which specific attributes?
2. Does the surrounding landscape influence moth populations in woodland patches and, if so, to what spatial extent?
3. What is the relative importance of woodland vegetation character, patch configuration and surrounding landscape for enhancing moth populations (e.g. is local management of woodlands sufficient or is a landscape-scale management approach important for moth conservation)?

Given that micromoths are usually low mobility species (Nieminen, Rita & Uuvana 1999), they might be more influenced by the local habitat, and by patch isolation, compared to high mobility species (e.g. certain macromoths such as Noctuids), which might be more affected by the habitat at relatively larger scales (Tscharntke *et al.* 2002). Therefore, we expect the relative importance of vegetation character, patch configuration and surrounding landscape to differ between micro- and macromoths. Furthermore, given that woodland specialists are more affected by woodland habitat quality and quantity than generalist species (Summerville & Crist 2008), we expect this group to show stronger associations with the woodland character than other species.

5.3. Materials and methods

5.3.1. Site selection and sampling design

Ordinance Survey digital maps (EDINA Digimap Ordnance Survey Service) were used to select 34 woodland patches within agricultural land in central Scotland (Fig. 4.1 in Chapter 4). All woodland patches were at least 60 years old (EDINA Historic Digimap Service); they were selected based upon their size (from 0.1 up to 30 ha) and shape (ranging from compact to complex). All sites were surveyed for vegetation and nocturnal moths once during the summers of 2009 (June to August, 20 sites) and 2010 (May to July, 14 sites).

Vegetation surveys were conducted along transects 100 m in length. Transects within a woodland patch were located in an area considered to be representative of the whole site (after exploration and visual assessment of the woodland); one transect was used for patches of 0.1 – 3 ha, two transects for patches of 3 – 10 ha, and three transects for patches of 10 – 30 ha. Points were established every 15 m along each transect and the following data were collected using the point-centred quarter method (Southwood &

Henderson 2000): tree species richness, tree density and tree basal area (only trees ≥ 7 cm in diameter at breast height were measured). Each point also served as the corner of a 10 x 10 m quadrat – which was used to visually assess understory cover (%) using the Domin scale (Kent & Coker 1992) – and a 2 x 2 m quadrat – used to visually determine the dominant ground cover type. Vegetation surveys were conducted no more than two weeks before the nocturnal moth surveys.

Moths were collected using portable 6 W heath light traps powered with 12 V batteries, which were activated 15 min after sunset and switched off after 4 h using automatic timers. Surveys were only conducted in dry weather, when temperature was ≥ 8 °C and wind force ≤ Beaufort scale 4. Two traps were used in woodland patches of 0.1 – 3 ha, four traps in patches of 3 – 10 ha, and six traps in patches of 10 – 30 ha. The traps were ≥ 100 m apart from each other to prevent the lights from interfering with each other (Merckx *et al.* 2009a). If the woodland patch was too small to allow for this distance between traps, we ensured trees or shrubs interrupted visibility between the lights. At each patch, an equal number of traps were located at the edge and the interior (as far away from the edges as possible) of the woodland. The collected insects were euthanized and stored for later identification; individuals were dissected to examine genitalia whenever species identification required it. Macromoth species for which woodland is listed as the main habitat where species occurs (according to Waring & Townsend 2003) and/or for which the larval food is strongly associated with woodland (e.g. woody plants) were assigned to the 'woodland species' guild. Micromoths were not included in this classification because information regarding this group is more limited.

5.3.2. Landscape analysis

We used ArcGIS 9.2 (ESRI Inc. 2006) to create circles of 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m radius around the centre of each woodland patch. The smallest radius (250 m) covers the dispersal distances of low mobility moth species, the intermediate ones (e.g. 1.5 km), the dispersal distances of many common moth species, and the largest (3 km) approximates an upper limit to dispersal distances of more mobile non-migratory moth species (Nieminen, Rita & Uuvana 1999; Merckx *et al.* 2009a, 2010b). Using data from OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service) we reclassified the landscape within each circle into six biotope types: (i) urban areas (buildings, structures and roads); (ii) farmland; (iii) water (inland and tidal water); (iv) semi-natural environment (rough grassland and scrub); (v) scattered trees; and (vi) woodland (coniferous, deciduous and mixed trees). We then used Fragstats 3.3 (McGarigal *et al.* 2002) to calculate the proportion of land covered by each biotope type and a landscape heterogeneity index (Shannon diversity) within each circle.

5.3.3. Data analysis

We calculated diversity indices for micro- and macromoths using PAST (Hammer, Harper & Ryan 2001). We selected the α log series diversity index (defined by $S=a*\ln(1+n/a)$ where S is number of taxa, n is number of individuals and a is the alpha index) because of its good discriminant ability, its low sensitivity to sample size and the fact that a number of previous studies have shown the index to be particularly suited to the description of moth populations (Magurran 1988).

All statistical analyses were conducted using R version 2.11 (R Development Core Team 2010). We performed Generalised Linear Mixed-Effects Models (GLMMs; Zuur *et al.* 2009) to determine which of the woodland character variables evaluated had an influence on moths. We used total values per trap (e.g. moth abundance, richness or diversity) as response variables (n = 126). Based on published literature on the ecology of woodland moths, we selected the following potential explanatory variables to be included in the starting models: (i) vegetation character variables: woodland type, tree species richness, relative abundance of native tree species, tree density, average tree basal area, understory percentage cover, dominant ground cover type, surrounding matrix type and presence or absence of in-site grazing; and (ii) patch configuration variables: woodland patch size (and its quadratic term to consider a potential non-linear effect), woodland patch shape, woodland patch isolation, trap location (woodland interior *vs.* woodland edge) and their respective two-way interactions. See notes in Table 5.1 for a full description of each variable. Date and temperature at sunset were included as covariates. A correlation matrix of all potential explanatory variables was created to check for possible collinearity between predictors. ‘Site’ and ‘year’ (‘site’ nested within ‘year’) were originally included in the models as random (grouping) factors, but because variation between years was negligible (variance close to zero) this factor was excluded and only ‘site’ was used. All continuous variables were standardized (by subtracting the sample mean from all input variable values, and subsequently dividing these values by the sample standard deviation) following Schielzeth (2010) in order to allow meaningful comparisons of the relative importance of predictors within a model, and interpretation of main effects where these are involved in interactions. Models were fitted using Poisson errors where the response variables were counts (e.g. moth abundance and species richness) and Gaussian errors (on log transformed data to achieve normality where necessary) for continuous variables (e.g. moth diversity). A backwards step-wise approach to model simplification was adopted, removing the least significant predictor from a model and using Akaike's information criterion (AIC; Akaike 1974) to reassess the model at each simplification step. Here we present the results of the simplified models. All models were validated by visual examination of residuals (e.g. plotting residuals *vs*. fitted values to check for constant variance, and plotting histograms of residuals to check for normality of errors; Crawley 2007). These models are referred to as 'woodland character' models hereafter.

The effect of the surrounding landscape on moths was assessed in two steps: Firstly, we used linear regression analyses to evaluate the effect of each landscape parameter at different spatial scales on moth abundance, richness and diversity. We used mean values per trap as response variables (log transformed to achieve normality where necessary; n = 34) and Gaussian error types. Secondly, we selected the landscape parameter that explained the highest overall variation in moth communities (highest R^2 value from linear regressions averaged across spatial scales) and added it, at each landscape scale, to the final 'woodland character' models (see above). We compared the models without any landscape metrics against the new models incorporating landscape metrics to assess whether they provided a better fit to the data, based on AIC values. Significance tests based on differences in deviance values between models (χ^2 test; Zuur *et al.* 2009) are also presented.

We calculated an index of dissimilarity using PAST (Hammer, Harper & Ryan 2001) to assess whether micro- and macromoth species composition differed between woodland interior and woodland edge and whether these differences were influenced by patch configuration metrics – patch size (and its quadratic term), patch shape, patch isolation, and their respective two-way interactions. We selected the Bray-Curtis dissimilarity index because it has been extensively used in ecological studies and can be easily interpreted (Waite 2000). We used the total abundance of each species collected at each site (all ‘interior’ traps pooled together *vs*. all ‘edge’ traps) to obtain a dissimilarity value for each woodland site (n = 34). Linear models were fitted using Gaussian error types on log transformed data.

5.4. Results

We identified a total of 34 tree species (Appendix 4A in Chapter 4). Tree species richness ranged from 2 to 15 per site; tree density ranged from 181 to 2512 trees per ha and average tree basal area from 0.03 to 0.43 m^2. Table 5.1 summarizes the characteristics of each site.

We collected a total of 1674 micromoths, belonging to 66 species (Table 5A-1 in Appendix 5A) and 14 families, and 3518 macromoths, belonging to 146 species (Table 5A-2 in Appendix 5A) and 8 families. Of these, 62 macromoth species are strongly associated with woodland habitat (Waring & Townsend 2003) and were analysed as a separate group because they are likely to show stronger responses to woodland character. Eighteen moth species (all macromoths) are classed as common but rapidly declining and are of special conservation concern (Fox *et al.* 2006).

5.4.1. Effects of woodland vegetation character and woodland patch configuration

After accounting for the effects of date and temperature, moth abundance, richness and diversity were significantly influenced by variables related to both woodland vegetation character and woodland patch configuration (Table 5.2).

Micromoth abundance was positively related to the relative abundance of native trees and the percentage cover of understory in a woodland patch. In-site grazing had negative effects on micromoth abundance and species richness (fewer individuals and fewer species in sites where grazing stock was present). Woodland patch size had positive effects on micromoth abundance and species richness (Figs. 5.1a & 5.1b), whereas patch isolation had negative effects on both (Figs. 5.2a & 5.2b), with more moths and more species being collected in large patches and in patches located close to other woodlands. Micromoth abundance was higher in woodland interior than in woodland edge. ‘Trap location’ was involved in an interaction with ‘woodland isolation’, indicating that the negative effect of woodland isolation on micromoth abundance and species richness was stronger in woodland edge than in woodland interior. Micromoth species richness was higher in broadleaved than in mixed (broadleaved and conifer mix) woodland patches. Micromoth diversity was only influenced by the dominant ground cover type – ‘grass’ and ‘litter’ had lower diversity than ‘other’ (based on visual examination within this group, ‘moss’ < ‘herbs’ < ‘ferns’ < ‘bare ground’).

Macromoth abundance and species richness were positively affected by tree species richness and by the relative abundance of native trees in a woodland patch. Of dominant ground types, ‘grass’ and ‘litter’ had higher abundances and species richness than ‘other’ (within this group, ‘bare ground’ < ‘herbs’ < ‘moss’ < ‘ferns’). In-site grazing had negative effects on macromoth abundance, richness and diversity (fewer

Table 5.1. Descriptive table showing in-site characteristics of the 34 woodland patches surveyed during 2009/2010.

Site	Woodland size (ha)	Woodland shape [a]	Woodland isolation (m) [b]	Woodland in landscape (%) [c]	Surrounding matrix	Woodland type [d]	Tree species richness	Native trees (%) [e]
1	0.19	2.52	165.10	4.22	Pastoral	Mixed	4	25.00
2	0.24	1.36	149.93	12.33	Pastoral	Broad	2	92.31
3	0.37	2.75	109.66	6.42	Pastoral	Broad	7	57.14
4	0.40	1.13	117.18	7.31	Arable	Mixed	3	80.95
5	0.88	1.29	277.89	6.62	Mixed	Broad	2	100.00
6	1.01	1.16	74.85	27.24	Pastoral	Mixed	7	32.14
7	1.20	1.75	245.93	2.70	Mixed	Broad	12	82.14
8	1.32	1.17	674.50	1.68	Arable	Mixed	5	75.00
9	1.34	3.08	133.12	6.99	Mixed	Mixed	8	64.29
10	1.59	1.55	32.98	3.04	Pastoral	Broad	3	100.00
11	1.66	1.96	117.61	12.01	Mixed	Broad	6	100.00
12	2.21	4.09	159.10	0.85	Pastoral	Broad	6	100.00
13	2.82	2.27	103.90	13.57	Arable	Mixed	9	96.43
14	3.14	1.56	223.09	4.56	Mixed	Broad	8	100.00
15	3.95	4.18	218.52	4.89	Mixed	Broad	11	92.86
16	4.08	1.87	127.02	6.63	Pastoral	Broad	9	85.71
17	4.29	1.33	75.74	22.75	Pastoral	Broad	7	96.43
18	4.45	1.69	58.67	19.69	Pastoral	Broad	3	100.00
19	5.17	2.73	97.10	6.16	Mixed	Mixed	5	73.21
20	5.64	1.47	200.60	7.02	Pastoral	Broad	7	100.00
21	5.89	1.20	65.12	23.58	Mixed	Mixed	7	94.64
22	6.52	4.50	138.29	5.91	Pastoral	Mixed	11	67.86
23	7.15	1.39	51.48	17.97	Pastoral	Broad	5	98.21
24	7.86	2.59	30.08	8.11	Arable	Mixed	12	78.57
25	9.04	1.48	5.10	18.95	Mixed	Mixed	6	57.89
26	9.19	2.35	5.70	31.23	Pastoral	Mixed	9	64.29
27	10.83	2.35	6.32	18.78	Mixed	Broad	5	91.07
28	16.36	2.22	7.60	26.66	Mixed	Mixed	5	67.86
29	17.55	5.43	7.80	14.53	Mixed	Mixed	10	39.29
30	18.35	1.83	16.74	29.64	Pastoral	Mixed	4	71.43
31	18.79	1.25	7.28	32.23	Mixed	Broad	7	86.90
32	18.81	3.68	7.00	22.15	Mixed	Mixed	15	54.76
33	21.16	3.46	17.05	30.06	Pastoral	Mixed	10	50.00
34	29.60	2.88	8.60	31.27	Pastoral	Mixed	8	97.62

Table 5.1 (cont.).

Site	Dominant tree species [f, g]	Tree density (per ha)	Tree basal area (m^2)	Understory cover [h]	Dominant ground [i]	In-site grazing
1	*P. sitchensis* (64%)	1236.72	0.12	3	Grass	No
2	*Q. petraea* (92%)	237.14	0.26	0	Grass	Yes
3	*T. platyphyllos* (25%)	259.22	0.43	7	Bare	Yes
4	*Q. robur* (71%)	209.40	0.27	2	Litter	No
5	*B. pubescens* (93%)	602.10	0.06	0	Grass	Yes
6	*A. pseudoplatanus* (57%)	399.54	0.31	4	Litter	No
7	*B. pendula* (21%)	477.99	0.08	8	Herb	No
8	*P.abies+B.pubescens+B.pendula* (25% each)	549.65	0.11	0	Ferns	No
9	*B. pubescens* (32%)	2381.20	0.07	2	Litter	No
10	*B. pendula* (61%)	822.86	0.03	8	Grass	Yes
11	*B.pubescens+S.aucuparia* (39% each)	534.69	0.34	6	Grass	No
12	*B.pubescens+S.aucuparia* (36% each)	366.89	0.27	3	Grass	No
13	*B. pubescens* (36%)	1395.64	0.12	2	Grass	No
14	*B. pubescens* (46%)	413.41	0.22	3	Litter	No
15	*F. excelsior* (27%)	503.13	0.09	3	Litter	No
16	*F. excelsior* (27%)	180.59	0.33	1	Grass	Yes
17	*B. pendula* (52%)	389.31	0.15	7	Grass	No
18	*B. pendula* (54%)	304.40	0.05	4	Moss	No
19	*F. excelsior* (41%)	1663.55	0.05	2	Litter	No
20	*B. pubescens* (30%)	358.28	0.14	2	Grass	No
21	*B. pubescens* (52%)	747.50	0.09	0	Litter	No
22	*Q. robur* (29%)	730.74	0.13	1	Litter	No
23	*B. pubescens* (66%)	852.29	0.05	2	Grass	No
24	*F. sylvatica* (39%)	680.83	0.08	3	Litter	No
25	*B. pubescens* (54%)	2512.55	0.03	1	Litter	No
26	*B. pubescens* (30%)	604.75	0.08	5	Litter	No
27	*B. pubescens* (39%)	670.17	0.10	4	Litter	No
28	*Q. petraea* (75%)	483.65	0.06	2	Herb	No
29	*A. pseudoplatanus* (31%)	514.86	0.14	1	Litter	No
30	*P. sylvestris* (39%)	1237.03	0.05	0	Litter	No
31	*B. pubescens* (35%)	578.47	0.12	1	Ferns	No
32	*A. pseudoplatanus* (38%)	691.00	0.10	5	Litter	No
33	*P. abies* (30%)	611.10	0.10	4	Litter	No
34	*B. pendula* (64%)	448.68	0.06	4	Grass	Yes

[a] Equals the patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the corresponding patch area. When the patch is maximally compact 'woodland shape' = 1, and increases without limit as the patch shape becomes more irregular. Modified from McGarigal *et al.* (2002).

Table 5.1 (cont.).

[b] Proximity (edge-to-edge distance) to closest woodland patch ≥ 0.19 ha (size of smallest woodland patch included in surveys).

[c] Woodland cover (%) within a 500 m radius around the centre of each woodland patch.

[d] ‘Broad’ refers to sites where only broadleaved trees were present; ‘Mixed’ refers to sites with both broadleaved and conifer trees present.

[e] Relative abundance of native tree species.

[f] See Appendix 4A in Chapter 4 for a full list of tree species.

[g] Dominant tree species relative abundance.

[h] Domin scale (Kent & Coker 1992) was used: 0= no understory; 1 = cover of ≤ 4 % with few individuals; 2 = cover of ≤ 4 % with several individuals; 3 = cover of ≤ 4 % with many individuals; 4 = cover of 4 – 10 %; 5 = cover of 11 – 25 %; 6 = cover of 26 – 33 %; 7 = cover of 34 – 50 %; 8 = 51 – 75 %; 9 = 76 – 90%; 10 = 91 – 100 %.

[i] For analysis purposes ‘bare ground’, ‘ferns’, ‘herb’ and ‘moss’ were grouped in the ‘other’ category, because they were the dominant ground cover type in ≤ 2 sites.

Table 5.2. Summary table showing parameter estimates ± SE (for main effects only, no interactions), significance values, and goodness of fit (model R^2) of the 'woodland character' models. Non-significant predictors are not shown. The effects of categorical variables with more than one level ('matrix type' and 'dominant ground') are discussed in the text. Surrounding woodland cover was incorporated to the 'woodland character' models at a later stage to assess the importance of a landscape-scale management approach; the most relevant spatial scale (the one that produced the model with the lowest AIC value) and its correspondent parameter estimates (±SE) and model R^2 values are indicated (see Table 5B-1 in Appendix 5B for further details).

	Woodland vegetation character										Woodland patch configuration								Landscape		
	Date$^{a, b}$	Temperature^{b}	Woodland type$^{c, d}$	Matrix type^{c}	In-site grazing^{c}	Tree species richness^{b}	Native trees^{b}	Tree basal area^{b}	Understory cover^{b}	Dominant ground^{c}	Woodland size^{b}	Woodland shape^{b}	Woodland isolation^{b}	Trap location$^{c, e}$	Trap location * Wood isolation	Woodland size * Woodland shape	Woodland size * Woodland isolation	Model R^2 (%)^{d}	Surrounding woodland cover^{b}	Most relevant spatial scale (m)	Model R^2 (%)$^{f, g}$
Micromoth abundance	1.27 ±0.25 ***	ns	ns	ns	-1.10 ±0.55 *	ns	0.42 ±0.21 *	ns	0.56 ±0.22 *	ns	0.57 ±0.26 *	ns	-0.41 ±0.23 ◌̇	0.53 ±0.06 ***	**	ns	ns	74.97	0.67 ±0.31 *	500	75.17
Micromoth richness	0.70 ±0.14 ***	ns	-0.67 ±0.27 *	ns	-0.74 ±0.33 *	ns	ns	ns	ns	ns	0.36 ±0.15 *	ns	-0.26 ±0.15 ◌̇	ns	*	ns	ns	52.09	ns	-	-
Micromoth diversity	0.26 ±0.07 ***	0.14 ±0.07 *	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	32.03	0.15 ±0.07 *	250	34.65
Macromoth abundance (all species)	0.45 ±0.08 ***	ns	ns	*	-0.91 ±0.27 ***	0.26 ±0.11 *	0.49 ±0.12 ***	ns	ns	***	0.87 ±0.34 *	ns	-1.60 ±0.46 ***	-0.13 ±0.04 ***	***	ns	**	59.85	ns	-	-
Macromoth richness (all species)	0.39 ±0.06 ***	ns	ns	**	-0.89 ±0.19 ***	0.23 ±0.07 ***	0.35 ±0.08 ***	ns	ns	**	0.39 ±0.22 ◌̇	ns	-0.71 ±0.30 *	ns	ns	ns	*	55.66	0.28 ±0.10 **	500	57.11
Macromoth diversity (all species)	1.90 ±0.70 ***	ns	-3.89 ±1.66 *	ns	-4.42 ±2.04 *	ns	ns	ns	ns	ns	1.38 ±0.81 ◌̇	ns	ns	ns	ns	ns	ns	42.27	ns	-	-
Macromoth abundance (woodland species)	ns	ns	ns	*	-1.13 ±0.51 *	0.54 ±0.21 *	0.54 ±0.19 **	-0.33 ±0.17 *	ns	ns	ns	ns	-0.93 ±0.30 **	0.31 ±0.06 ***	*	*	ns	64.81	1.17 ±0.45 *	250	65.28
Macromoth richness (woodland species)	0.22 ±0.09 *	ns	ns	**	-1.33 ±0.30 ***	0.45 ±0.11 ***	0.36 ±0.11 ***	ns	ns	*	ns	-0.28 ±0.11 **	-0.58 ±0.15 ***	0.28 ±0.09 **	*	ns	ns	57.29	0.26 ±0.10 *	1500	58.97

Table 5.2 (cont.).

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '.' $p \leq 0.1$ and 'ns' $p \geq 0.1$.

[b] Standardized parameter estimates are shown for continuous variables.

[c] Non-standardized parameter estimates are shown for categorical variables.

[d] Negative values indicate a negative effect of 'mixed' woodlands (with respect to 'broadleaved').

[e] Negative values indicate lower moth abundance/richness in woodland interior than in woodland edge.

[f] R^2 values for models with a Gaussian error distribution were calculated with the formula: 1 − (Residual Sum of Squares / Total Sum of Squares). Pseudo-R^2 values for models with a Poisson error distribution were calculated with the formula: (Deviance explained by model / Null deviance) * 100 (Zuur *et al.* 2009). This value is not adjusted for the number of explanatory variables included in a model.

[g] R^2 value after incorporating surrounding woodland cover at the most relevant spatial scale to the 'woodland character' models.

moths, fewer species and less diverse communities in sites where grazing stock was present). There were fewer species and a lower abundance of moths in sites surrounded by arable land than in sites surrounded by pastoral or mixed (pastoral and arable mix) land. Woodland size was positively related to macromoth abundance (Fig. 5.1d) – the same (marginally-significant) trend was observed for species richness and diversity (Figs. 5.1e & 5.1f) – whereas woodland isolation was negatively related to macromoth abundance and richness (Figs. 5.2d & 5.2e). Significant interactions between ‘woodland size’ and ’woodland isolation’ indicated that whereas small woodlands generally have lower macromoth abundance and richness, these increase if the patch is located close to other woodlands. Macromoth abundance was higher in woodland edge than in woodland interior. A significant interaction between ‘trap location’ and ‘woodland isolation’ indicated that the negative effect of woodland isolation on macromoth abundance was stronger in the woodland edge than in the interior. Macromoth diversity was affected by woodland type (higher in broadleaved than in mixed woodland patches).

Macromoth ‘woodland species’ (those strongly associated with woodland) responded to vegetation character variables in a similar way to all macromoth species (Table 5.2). Tree species richness and relative abundance of native trees had positive effects on macromoth ‘woodland species’ abundance and richness. Tree basal area was negatively related to the number (but not abundance) of macromoth ‘woodland species’. The dominant ground type affected the richness of ‘woodland species’ – ‘grass’ and ‘litter’ had more species than ‘other’ (within this group, ‘bare ground’ < ‘herb’ < ‘moss’ < ‘ferns’). In-site grazing had negative effects on the abundance and richness of ‘woodland species’, and there were fewer species and a lower abundance of moths in sites surrounded by arable land than in sites surrounded by pastoral or mixed land.

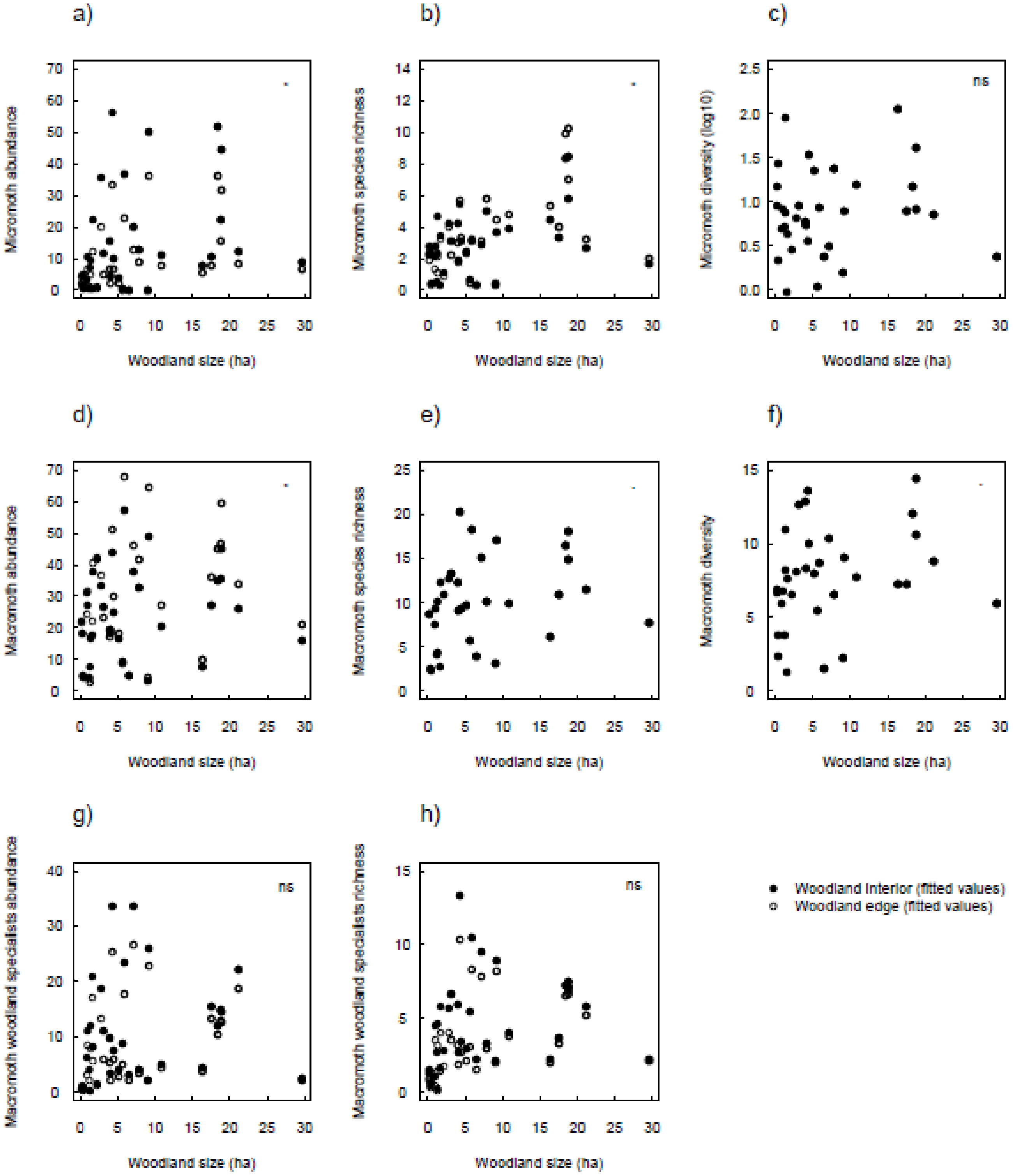

Figure 5.1. Effect of woodland patch size and trap location (woodland interior *vs.* woodland edge) on moth abundance, species richness and diversity for: micromoths (a, b & c), macromoths (d, e & f) and macromoth woodland species (g & h). Fitted values produced by the final GLMMs for each response variable are shown. Only one type of dot is shown for models where trap location and its interaction with woodland patch size were not significant. Significance codes for woodland patch size are shown at the top right corner of each plot: ‘***’ $p \leq 0.001$, ‘**’ $p \leq 0.01$, ‘*’ $p \leq 0.05$, ‘.’ $p \leq 0.1$ and ‘ns’ $p \geq 0.1$.

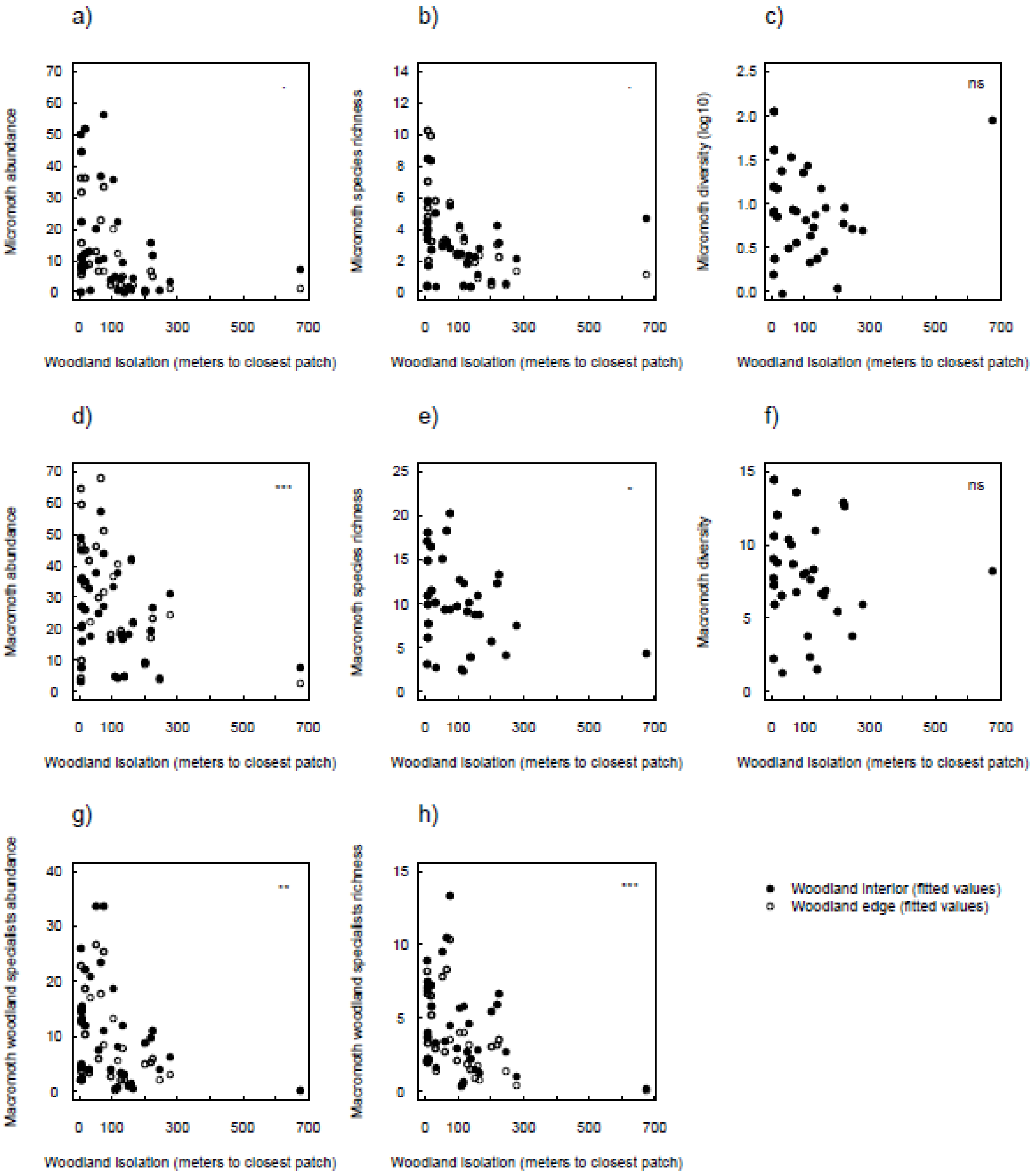

Figure 5.2. Effect of woodland isolation and trap location (woodland interior *vs.* woodland edge) on moth abundance, species richness and diversity for: micromoths (a, b & c), macromoths (d, e & f) and macromoth woodland species (g & h). Fitted values produced by the final GLMMs for each response variable are shown. Only one type of dot is shown for models where trap location and its interaction with woodland isolation were not significant. Significance codes for woodland isolation are shown at the top right corner of each plot: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '.' $p \leq 0.1$ and 'ns' $p \geq 0.1$.

The response of ‘woodland species’ to woodland configuration variables was somewhat different to that of all macromoths (Table 5.2). A significant interaction between woodland size and shape indicated that small woodland patches with complex shapes have the lowest abundance of ‘woodland species’; however, abundance is relatively high in small woodlands with compact shapes and in large woodlands with complex shapes. Woodlands with complex shapes also had reduced ‘woodland species’ richness. Woodland isolation had negative effects on both abundance and richness of macromoth ‘woodland species’ (Figs. 5.2g & 5.2h). However, significant interactions between ‘woodland isolation’ and ‘trap location’ indicated that the negative effects of isolation were stronger in woodland edge than in interior. The overall abundance and richness of ‘woodland species’ were higher in woodland interior than in woodland edge.

The species composition of both micro- and macromoths differed between woodland interior and woodland edge (Bray-Curtis dissimilarity index $\neq 0$; t=10.06, p<0.001 for micromoths; t=12.29, p<0.001 for macromoths). In the case of macromoths, these differences were caused by changes in the abundance and richness of ‘woodland species’ collected in interior *vs.* edge; in total 693 individuals belonging to 55 species strongly associated with woodland were collected in woodland interior (representing 43.2% in abundance and 45.5% in species richness of the total macromoth catch in interior traps), as opposed to 543 individuals from 46 species collected in woodland edge (representing 28.4% in abundance and 38.0% in species richness). Macromoth ‘woodland species’ which were collected in both interior and edge had an average ‘interior/edge ratio’ (mean abundance per ‘interior’ trap / mean abundance per ‘edge’ trap) of 1.57 ± 0.23; for macromoth species not strongly associated with woodland this ratio was 1.03 ± 0.19. We used this 1.57 ‘interior/edge ratio’ value as a threshold to identify putative micromoth ‘woodland species’ (since specific habitat information is lacking for most species); based on this criterion, thirteen micromoth species were recognized as ‘woodland species’ (Appendix 5A). Woodland patch configuration – woodland size (*p*=0.015), its quadratic term (*p*=0.029) and a marginally significant interaction between patch size and shape (*p*=0.052) – affected the similarity of micromoth (but not macromoth) species collected in woodland interior *vs.* edge. Woodland interior and woodland edge were more dissimilar (in terms of micromoth species composition) in larger woodland patches, although the interaction between woodland size and shape indicated that edge and interior are more similar in small woodlands with complex shapes and less similar in small patches with compact shapes.

5.4.2. Effects of the surrounding landscape

In general, linear regression analyses indicated that the percentage cover of woodland and semi-natural environment showed the strongest (positive) relations with moth abundance and species richness (Fig. 5.3). The percentage cover of farmland and the landscape heterogeneity index were also significantly related (negatively and positively, respectively) to moth abundance and richness, but only at relatively small scales (e.g. 250 and 500 m). The percentage cover of urban areas related only to micromoth diversity (positively) at large scales (e.g. 2500 and 3000 m). Given that the percentage cover of woodland was the landscape parameter that significantly related to more response variables (five out of eight) and at more spatial scales (e.g. significantly related to ‘woodland species’ abundance at all spatial scales), we selected this as the landscape parameter to include in the ‘woodland character’ models. After incorporating this landscape metric to the ‘woodland character‘ GLMMs, the percentage cover of woodland in the surrounding landscape significantly improved the models for most response variables at least at one spatial scale (Table 5.2 & Table 5B-1 in Appendix 5B). The models with the lowest AIC values were usually those which incorporated woodland cover at the 250 and 500 m scales. However, for ‘woodland species’ richness the model with the lowest AIC was the one which incorporated the proportion of woodland cover at a larger spatial scale (1500 m; Table 5.2 & Table 5B-1 in Appendix 5B). The results of similar analyses incorporating landscape metrics into the ‘woodland character‘ GLMMs, but using other parameters (percentage cover of ‘semi-natural environment’ and ‘urban areas’) instead of ‘woodland’ are presented in Tables 5B-2 & 5B-3 in Appendix 5B.

5.5. Discussion

In this study we assessed the effects of woodland vegetation character, patch configuration and surrounding landscape on assemblages of both macromoths and the relatively poorly studied micromoths. Moths were significantly influenced by variables related to woodland vegetation character, woodland patch configuration and the surrounding landscape. Our results contribute to a better understanding of the effects of habitat fragmentation on biodiversity and have important implications for the design and management of woodland patches of high conservation value within agricultural landscapes.

Variables related to the woodland vegetation character had an influence on both micro- and macromoth abundance and richness. In general, woodlands composed of broadleaved trees only and a large number of tree species supported high moth abundance and species richness. Tree species richness/diversity has been recognised in

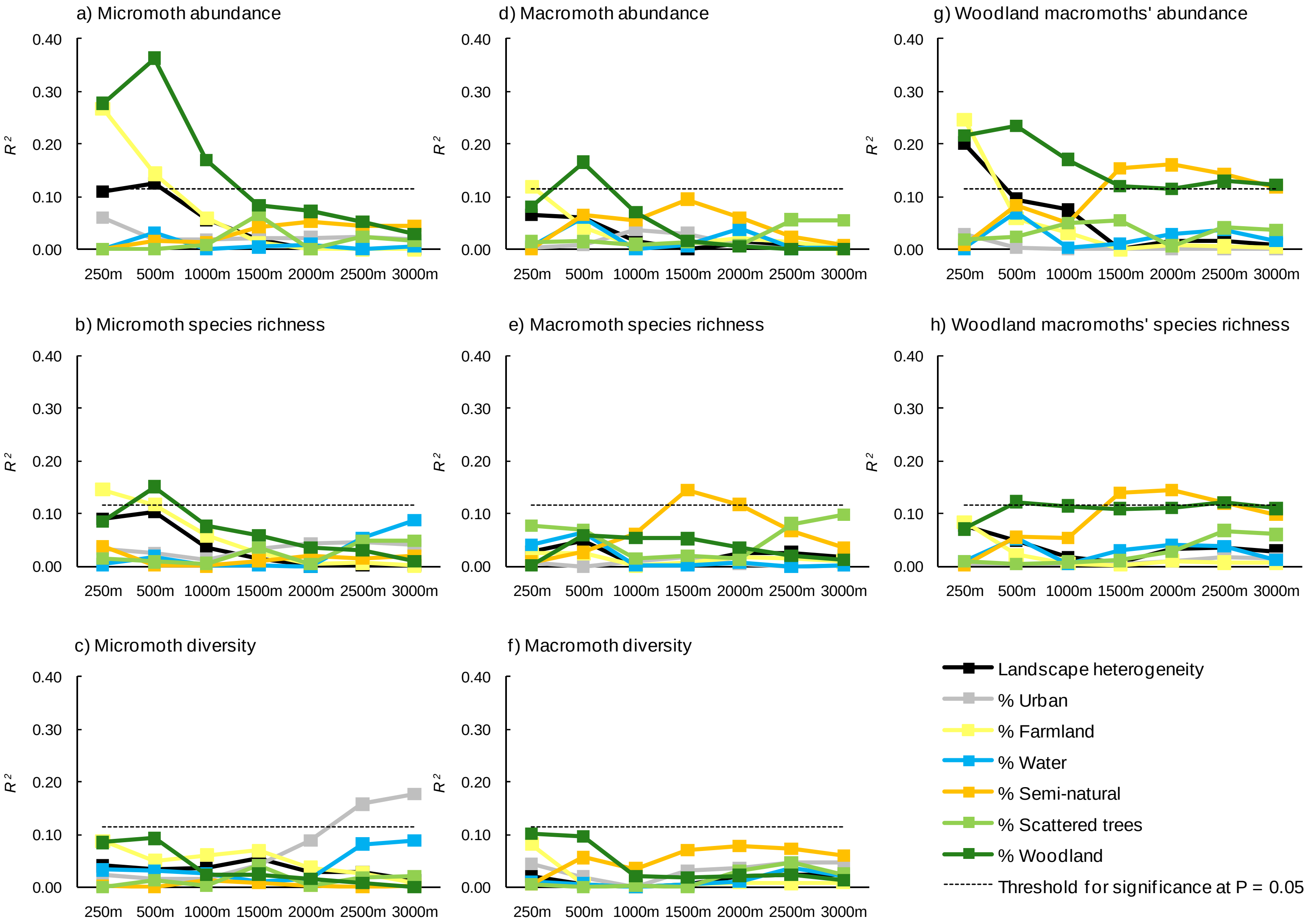

Figure 5.3. R^2 values obtained from linear regression analyses between the percentage of land covered by each biotope type at several spatial scales and: a) micromoth abundance, b) micromoth species richness, c) micromoth diversity, d) macromoth abundance, e) macromoth species richness, f) macromoth diversity, g) ‘woodland species’ abundance and h) ‘woodland species’ richness. We used mean values per trap as response variables (n = 34).

previous studies as one of the most important predictors for moth abundance and species richness (Usher & Keiller 1998; Summerville & Crist 2004). We also found the relative abundance of native tree species in a woodland patch to be of higher importance in most cases, presumably because non-native trees are unlikely to serve as food-plants for native moth species. The dominant ground cover type was also an important predictor for some response variables; sites where grass or litter was the dominant ground cover type had higher moth abundance and species richness than sites dominated by 'other' ground cover. A high percentage of understory cover was beneficial (for micromoth abundance only), probably because it increases structural complexity and provides shelter.

Characteristics related to woodland management also had an influence on moths; for instance, the presence of grazing stock in a site consistently had strong negative effects on moth communities. Grazing has been linked to changes in vegetation structure and composition (Stewart & Pullin 2008) and its detrimental effects on moths have been noted in previous studies (e.g. Young & Barbour 2004). However, the negative effects of grazing are not necessarily even across all moth species (Littlewood 2008). In this study we found that sites surrounded only by arable land had lower macromoth abundance and fewer species than sites adjacent to pastoral or mixed fields, probably because an arable matrix is more homogeneous than a mixed or pastoral matrix.

Variables related to the spatial configuration of woodland patches had a profound impact on moth assemblages. Their relative importance was usually higher than that of vegetation character variables, particularly for macromoths. In general, both micro- and macromoth abundance and species richness were higher in large woodland patches located close to other woodlands. Arthropods are one of the taxa that best fulfil the theoretical expectations of greater species richness within larger fragments (Debinski & Holt 2000). Previous studies show that the size of a woodland patch appears to be one of the most important factors influencing species abundance and richness of different taxa, including moths (Usher & Keiller 1998; Summerville & Crist 2003, 2004), whereas the spatial configuration of the fragmented woodland seems to be less crucial (McGarigal & McComb 1995; Lee *et al.* 2002; Dolman *et al.* 2007). However our results show that woodland isolation in particular has strong negative effects on moths (see also Usher & Keiller 1998).

The responses of micro- and macromoths to the configuration of a woodland patch were somewhat different; although the two groups were affected by woodland size and isolation, for micromoths the former was more important than the latter, whereas for macromoths the opposite was observed. The negative effects of isolation were noticeable at smaller distances on micro- than on macromoths (e.g. micromoth abundance and richness decreased drastically above 100 m, whereas for macromoths the decrease was more gradual). For low mobility species (such as most micromoths) even short distances between woodland patches might act as dispersal barriers, increasing the relative importance of the size of their existing patch. Significant interactions between ‘woodland isolation’ and ‘trap location’ indicated that the negative effects of isolation are stronger in woodland edge than in interior. The interactions between woodland patch size and isolation (significant only for macromoths) suggest that even small woodland patches can be beneficial for moths if they are located in proximity to other woodlands, which may act as sources of individuals/species to colonize nearby woodland patches. This observation – along with the overall importance of woodland isolation on moth communities – highlights the importance of incorporating aspects of spatial configuration in the creation of new woodlands during afforestation programmes.

The shape of the woodland patch was important only for macromoth woodland species, suggesting that patches of compact shapes (with proportionally less edge exposed to the surrounding matrix) sustain a larger number of woodland species. Even though woodland shape *per se* did not affect the abundance of woodland species, it was involved in an interaction with woodland size; this highlights the importance of designing patches of compact shapes, especially when the patch to be created is small. Usher & Keiller (1998) also found that only moth species dependent upon woodland habitat show a relationship to shape, and suggested that this group of moths benefits from large woodland core habitat in woods of compact shapes. This is supported by our observations of higher richness and abundance of woodland species in woodland interior than in woodland edge – and by the higher ‘interior/edge ratio’ showed by woodland species when compared to non-woodland species – and suggests the existence of edge effects experienced by this group of moths. Edge effects have been identified as one of the main driving forces behind changes in insect populations in forest fragments (Didham *et al.* 1996). Conversely, the abundance (but not richness) of all macromoth species was higher in woodland edge than in interior; this observation is most likely driven by a few abundant species, well adapted to agricultural environments (cf. species replacement hypothesis in Summerville & Crist 2003, 2004).

Micromoth assemblages also differed between woodland interior and edge. These differences were accentuated by woodland size and shape. Micromoth species composition was more dissimilar between interior and edge in large woodland patches; the interaction between size and shape indicated that edge and interior moth communities are more similar in small woodlands with complex shapes than in small patches with compact shapes, but the effect of shape was not noticeable in large woodlands. This shows that there are micromoth species associated with woodland core habitat which would benefit from large woodlands, and even from small woodlands of compact shapes. Summerville & Crist (2001, 2004) maintain that small (2 – 25 ha) woodland fragments can support many moth species if the habitat within them is good, whereas Usher & Keiller (1998) identify woodlands under 1 ha as not able to support characteristic communities of woodland moths, and woodlands of more than 5 ha as generally able to support more stable moth communities. Our results showed that woodlands < 1 ha were indeed poor in species richness and abundance, while woodlands > 5 ha had the highest values; however, relatively small patches (e.g. woodlands between 1 – 5 ha) seem to sustain relatively large moth populations. This study and work by others (e.g. Ekroos, Heliölä & Kuussaari 2010) highlight the importance of increasing habitat availability and connectivity for habitat specialists (such as macromoth 'woodland species') and poor dispersers (such as many micromoths) to avoid biotic homogenization in intensively cultivated landscapes with simplified landscape structure.

Both micro- and macromoth communities were influenced to some extent by the surrounding landscape. They were influenced by the percentage cover of woodland in the surrounding landscape at relatively small spatial scales (≤ 500 m), suggesting that local habitat management (or a landscape management at this spatial scale) would be suitable for moth conservation. Macromoth 'woodland species' richness, however, was influenced by woodland cover at larger spatial scales, the most relevant being 1500 m. These findings are in accordance with those of Ricketts *et al.* (2001) and Summerville & Crist (2004), who found that the amount of nearby woodland cover (within 1 – 1.4

km) positively affects moth abundance and richness. The total amount of woodland in the landscape has been recognized as being more important than woodland patch size or spatial pattern in other animal groups (i.e. birds; McGarigal & McComb 1995; Lee *et al.* 2002; Dolman et al 2007). Our observations suggest that macromoth 'woodland species' in particular would benefit from a wider landscape-scale management of woodland habitat. Conservation strategies are increasingly incorporating the concept of habitat networks in an attempt to minimise the effects of habitat fragmentation and conserve woodland biodiversity (Watts 2006; Quine & Watts 2009). Our results highlight the importance of designing action plans which perceive the landscape as a whole, and emphasize the need to take into account the surrounding landscape and the location of a woodland patch within it.

In summary, woodland vegetation character, woodland patch configuration and the surrounding landscape all influenced moth populations in farmland woodlands. The design and management of woodland patches within agricultural landscapes should take into consideration the following points to ensure the creation/protection of habitat of high conservation value for moths:

1. Woodlands composed of a large number of tree species (and a high proportion of native species) support high moth abundance and species richness.
2. The presence of grazing stock in a woodland patch has strong negative effects on moth abundance and diversity.
3. Large woodland patches of compact shapes (with a large proportion of woodland core habitat), located close to other woodlands are associated with high moth abundance and species richness. Small woodland patches can potentially maintain a relatively high abundance and species richness of moths,

but shape and proximity to other woodlands are of particular importance in these cases.

4. Moths are influenced by the surrounding woodland mostly at small spatial scales (within 500 m); however, macromoth ‘woodland species’ are influenced at larger (≤ 1500 m) spatial scales and are, therefore, likely to benefit from a wider landscape-scale management approach taking into consideration woodland cover within the landscape, habitat connectivity and the location of woodland patches with respect to other woodlands.

5.6. Acknowledgements

We wish to thank the landowners and Estate managers who granted us permission to conduct this study on their land, L. Cavin and J. Wallace for their help with field work, and R. Dawson and R. Griffiths for their help with macromoth identification. Special thanks to K. Bland (National Museums of Scotland) for identifying micromoth specimens, to J. Minderman for his advice on statistical analyses and to M. Usher for his valuable comments on this manuscript. Thanks also to CONACYT for providing a graduate scholarship (189261) to E.F.M., and to Bat Conservation International, the British Ecological Society and the People’s Trust for Endangered Species for their financial support.

Appendix 5A. List of moth species collected during surveys.

Table 5A-1. List of micromoth species.

Latin name [a]	Common name (Family) [b]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE) [c]	Abundance per trap – edge (mean ± SE)
Scoparia ambigualis	(Crambidae)	7.10 ± 1.07	9.52 ± 1.92 [c]	4.73 ± 0.86
Apotomis betuletana	(Tortricidae)	1.04 ± 0.30	1.48 ± 0.56 [c]	0.60 ± 0.22
Eudonia truncicolella	(Crambidae)	0.88 ± 0.34	1.31 ± 0.66 [c]	0.46 ± 0.16
Agriphila straminella	Pearl Veneer (Crambidae)	0.82 ± 0.19	0.68 ± 0.27	0.97 ± 0.26
Cnephasia asseclana	Flax Tortrix (Tortricidae)	0.38 ± 0.09	0.45 ± 0.13	0.32 ± 0.12
Yponomeuta evonymella	Bird-cherry Ermine (Yponomeutidae)	0.30 ± 0.10	0.21 ± 0.07	0.38 ± 0.19
Pleuroptya ruralis	Mother of pearl (Crambidae)	0.26 ± 0.10	0.18 ± 0.08	0.35 ± 0.18
Udea lutealis	(Crambidae)	0.20 ± 0.05	0.11 ± 0.05	0.29 ± 0.09
Pandemis heparana	Dark Fruit-tree Tortrix (Tortricidae)	0.19 ± 0.04	0.21 ± 0.07	0.17 ± 0.05
Eudonia mercurella	(Crambidae)	0.14 ± 0.04	0.16 ± 0.06	0.13 ± 0.06
Agriphila tristella	(Crambidae)	0.14 ± 0.04	0.03 ± 0.02	0.24 ± 0.08
Argyresthia goedartella	(Yponomeutidae)	0.14 ± 0.10	0.03 ± 0.02	0.24 ± 0.19
Blastobasis lacticolella	(Blastobasidae)	0.14 ± 0.03	0.13 ± 0.05	0.14 ± 0.05
Tinea semifulvella	(Tineidae)	0.13 ± 0.05	0.21 ± 0.09 [c]	0.05 ± 0.04
Dipleurina lacustrata	(Crambidae)	0.11 ± 0.04	0.11 ± 0.06	0.11 ± 0.05
Elophila nymphaeata	Brown China-mark (Crambidae)	0.10 ± 0.04	0.05 ± 0.03	0.14 ± 0.07
Eucosma hohenwartiana	(Tortricidae)	0.10 ± 0.03	0.10 ± 0.04	0.10 ± 0.05
Eucosma cana	(Tortricidae)	0.09 ± 0.03	0.03 ± 0.02	0.14 ± 0.06
Celypha lacunana	(Tortricidae)	0.09 ± 0.03	0.10 ± 0.04	0.08 ± 0.03
Blastobasis adustella	(Blastobasidae)	0.05 ± 0.02	0.06 ± 0.04 [c]	0.03 ± 0.02
Chrysoteuchia culmella	Garden Grass-veneer (Crambidae)	0.05 ± 0.02	0.02 ± 0.02	0.08 ± 0.03
Cnephasia incertana	Light Grey Tortrix (Tortricidae)	0.05 ± 0.02	0.02 ± 0.02	0.08 ± 0.03
Endothenia quadrimaculana	(Tortricidae)	0.05 ± 0.03	0.03 ± 0.02	0.06 ± 0.05
Epinotia abbreviana	(Tortricidae)	0.05 ± 0.04	0.02 ± 0.02	0.08 ± 0.08
Nymphula stagnata	Beautiful China-mark (Crambidae)	0.05 ± 0.03	0.02 ± 0.02	0.08 ± 0.07

Table 5A-1 (cont.)

Latin name [a]	Common name (Family) [b]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE) [c]	Abundance per trap – edge (mean ± SE)
Ypsolopha parenthesella	(Yponomeutidae)	0.05 ± 0.03	0.02 ± 0.02	0.08 ± 0.05
Bryotropha similis	(Gelechiidae)	0.04 ± 0.02	0.05 ± 0.04	0.03 ± 0.02
Catoptria margaritella	(Crambidae)	0.04 ± 0.03	0.06 ± 0.06 [c]	0.02 ± 0.02
Epinotia brunnichana	(Tortricidae)	0.03 ± 0.02	0.02 ± 0.02	0.05 ± 0.03
Tortrix viridana	Green oak trotrix (Tortricidae)	0.03 ± 0.02	0.03 ± 0.03	0.03 ± 0.02
Aphomia sociella	Bee moth (Pyralidae)	0.02 ± 0.01	0.03 ± 0.02 [c]	0.02 ± 0.02
Catoptria falsella	(Crambidae)	0.02 ± 0.02	0.02 ± 0.02	0.03 ± 0.03
Crambus lathoniellus	(Crambidae)	0.02 ± 0.02	0.05 ± 0.05 [c]	-
Epiblema uddmanniana	Bramble Shoot Moth (Tortricidae)	0.02 ± 0.01	0.03 ± 0.02 [c]	0.02 ± 0.02
Eurrhypara hortulata	Small magpie (Crambidae)	0.02 ± 0.02	0.05 ± 0.04 [c]	-
Plutella xylostella	Diamond-back Moth (Yponomeutidae)	0.02 ± 0.02	-	0.05 ± 0.04
Agonopterix heracliana	(Oecophoridae)	0.02 ± 0.01	-	0.03 ± 0.02
Depressaria pulcherrimella	(Oecophoridae)	0.02 ± 0.01	-	0.03 ± 0.02
Aphelia paleana	Timothy Tortrix (Tortricidae)	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Batrachedra praeangusta	(Batrachedridae)	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Caloptilia alchimiella	(Gracillariidae)	0.02 ± 0.01	-	0.03 ± 0.02
Caloptilia syringella	(Gracillariidae)	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Coleophora flavipennella	(Coleophoridae)	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Epinotia tedella	(Tortricidae)	0.02 ± 0.01	0.03 ± 0.02 [c]	-
Hedya nubiferana	Marbled Orchard Tortrix (Tortricidae)	0.02 ± 0.01	0.03 ± 0.02 [c]	-
Yponomeuta padella	Orchard Ermine (Yponomeutidae)	0.02 ± 0.01	-	0.03 ± 0.02
Acompsia cinerella	(Gelechiidae)	0.01 ± 0.01	0.02 ± 0.02 [c]	-
Aethes cnicana	(Tortricidae)	0.01 ± 0.01	0.02 ± 0.02	-
Agonopterix arenella	(Oecophoridae)	0.01 ± 0.01	0.02 ± 0.02	-
Aleimma loeflingiana	(Tortricidae)	0.01 ± 0.01	-	0.02 ± 0.02
Platyptilia pallidactyla	(Pterophoridae)	0.01 ± 0.01	0.02 ± 0.02	-
Anthophila fabriciana	Nettle-tap (Choreutidae)	0.01 ± 0.01	-	0.02 ± 0.02
Argyresthia brockeella	(Yponomeutidae)	0.01 ± 0.01	0.02 ± 0.02	-

Table 5A-1 (cont.)

Latin name [a]	Common name (Family) [b]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE) [c]	Abundance per trap – edge (mean ± SE)
Bactra lancealana	(Tortricidae)	0.01 ± 0.01	0.02 ± 0.02	-
Clepsis spectrana	Cyclamen Tortrix (Tortricidae)	0.01 ± 0.01	-	0.02 ± 0.02
Cnephasia stephensiana	Grey Tortrix (Tortricidae)	0.01 ± 0.01	0.02 ± 0.02	-
Coleophora mayrella	(Coleophoridae)	0.01 ± 0.01	-	0.02 ± 0.02
Coleophora striatipennella	(Coleophoridae)	0.01 ± 0.01	0.02 ± 0.02	-
Elachista canapennella	(Elachistidae)	0.01 ± 0.01	-	0.02 ± 0.02
Epinotia ramella	(Tortricidae)	0.01 ± 0.01	-	0.02 ± 0.02
Evergestis forficalis	Garden pebble (Crambidae)	0.01 ± 0.01	0.02 ± 0.02	-
Nemapogon cloacella	Cork Moth (Tineidae)	0.01 ± 0.01	0.02 ± 0.02	-
Pandemis cerasana	Barred Fruit-tree Tortrix (Tortricidae)	0.01 ± 0.01	-	0.02 ± 0.02
Scoparia subfusca	(Crambidae)	0.01 ± 0.01	-	0.02 ± 0.02
Carpatolechia proximella	(Gelechiidae)	0.01 ± 0.01	0.02 ± 0.02	-
Ypsolopha sequella	(Yponomeutidae)	0.01 ± 0.01	0.02 ± 0.02	-

[a] Genitalia were examined whenever necessary to confirm species identification.

[b] In some classifications the Crambidae family is only recognised as a subfamily within the Pyralidae.

[c] Identified as woodland species because ‘interior/edge ratio’ ≥ 1.57 or because it was only collected in woodland interior (≥ 2 individuals).

Table 5A-2. List of macromoth species.

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Noctua pronuba	Large yellow underwing (N)	4.06 ± 0.76	2.52 ± 0.65	5.60 ± 1.35
Alcis repandata	Mottled beauty (G) [b]	1.89 ± 0.29	2.19 ± 0.47	1.59 ± 0.35
Campaea margaritata	Light emerald (G) [b]	1.59 ± 0.26	1.70 ± 0.38	1.48 ± 0.36
Mythimna impura	Smoky wainscot (N)	1.44 ± 0.35	0.54 ± 0.17	2.35 ± 0.66
Cerapteryx graminis	Antler moth (N)	1.37 ± 0.30	0.63 ± 0.24	2.11 ± 0.54
Hepialus fusconebulosa	Map-winged swift (H)	1.27 ± 0.37	1.60 ± 0.64	0.94 ± 0.37
Hydriomena furcata	July highflyer (G) [b]	1.00 ± 0.19	1.16 ± 0.30	0.84 ± 0.24
Mesapamea secalis / M. didyma	Common rustic / Lesser common rustic (N)	0.81 ± 0.21	0.27 ± 0.10	1.35 ± 0.40
Colostygia pectinataria	Green carpet (G)	0.67 ± 0.15	0.79 ± 0.21	0.56 ± 0.20
Xestia baja	Dotted clay (N) [b]	0.62 ± 0.14	0.48 ± 0.15	0.76 ± 0.24
Oligia fasciuncula	Middle-barred minor (N)	0.62 ± 0.17	0.79 ± 0.30	0.44 ± 0.18
Diarsia rubi	Small square-spot (N) [c]	0.62 ± 0.14	0.56 ± 0.21	0.68 ± 0.18
Perizoma didymata	Twin-spot carpet (G)	0.62 ± 0.21	0.84 ± 0.37	0.40 ± 0.18
Ochropacha duplaris	Common Lutestring (T) [b]	0.59 ± 0.14	0.89 ± 0.26	0.29 ± 0.09
Perizoma alchemillata	Small rivulet (G)	0.35 ± 0.07	0.22 ± 0.08	0.48 ± 0.12
Xanthorhoe montanata	Silver-ground carpet (G)	0.33 ± 0.07	0.37 ± 0.12	0.30 ± 0.08
Cabera pusaria	Common white wave (G) [b]	0.30 ± 0.07	0.37 ± 0.10	0.24 ± 0.09
Pertophora Chlorosata	Brown silver-line (G) [b]	0.29 ± 0.20	0.38 ± 0.35	0.21 ± 0.21
Venusia cambrica	Welsh wave (G) [b]	0.29 ± 0.08	0.32 ± 0.11	0.27 ± 0.12
Diarsia mendica	Ingrailed clay (N)	0.29 ± 0.08	0.27 ± 0.11	0.30 ± 0.10
Rivula sericealis	Straw dot (N)	0.29 ± 0.06	0.17 ± 0.08	0.40 ± 0.09
Photedes minima	Small dotted buff (N)	0.28 ± 0.09	0.30 ± 0.14	0.25 ± 0.10
Eulithis populata	Northern spinach (G)	0.26 ± 0.13	0.35 ± 0.24	0.17 ± 0.09
Ptilodon capucina	Coxcomb prominent (No) [b]	0.25 ± 0.05	0.32 ± 0.08	0.19 ± 0.07
Apamea monoglypha	Dark arches (N)	0.25 ± 0.06	0.24 ± 0.08	0.27 ± 0.08
Ecliptopera silaceata	Small phoenix (G) [c]	0.25 ± 0.09	0.24 ± 0.09	0.27 ± 0.15

Table 5A-2 (cont.)

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Geometra papilionaria	Large emerald (G) [b]	0.25 ± 0.06	0.37 ± 0.12	0.13 ± 0.04
Xestia triangulum	Double square-spot (N) [b]	0.24 ± 0.06	0.14 ± 0.05	0.33 ± 0.10
Idaea aversata	Riband wave (G)	0.24 ± 0.05	0.25 ± 0.08	0.22 ± 0.07
Lomaspilis marginata	Clouded border (G) [b]	0.20 ± 0.05	0.19 ± 0.06	0.21 ± 0.09
Hypena proboscidalis	Snout (N)	0.20 ± 0.07	0.24 ± 0.11	0.16 ± 0.06
Diachrysia chrysitis	Burnished brass (N)	0.19 ± 0.05	0.22 ± 0.08	0.16 ± 0.06
Diarsia brunnea	Purple clay (N) [b]	0.19 ± 0.07	0.17 ± 0.08	0.21 ± 0.10
Scotopteryx chenopodiata	Shaded broad-bar (G) [c]	0.19 ± 0.06	0.06 ± 0.03	0.32 ± 0.11
Xestia sexstrigata	Six-striped rustic (N)	0.18 ± 0.05	0.11 ± 0.05	0.25 ± 0.09
Lycophotia porphyrea	True lover's knot (N)	0.18 ± 0.14	0.33 ± 0.28	0.03 ± 0.02
Spilosoma lubricipeda	White ermine (A) [c]	0.18 ± 0.06	0.17 ± 0.08	0.19 ± 0.10
Cabera exanthemata	Common wave (G) [b]	0.17 ± 0.05	0.17 ± 0.05	0.17 ± 0.09
Laothoe populi	Poplar hawk-moth (S) [b]	0.17 ± 0.05	0.19 ± 0.08	0.16 ± 0.06
Xanthorhoe designata	Flame carpet (G)	0.17 ± 0.04	0.14 ± 0.04	0.19 ± 0.07
Eulithis pyraliata	Barred straw (G)	0.15 ± 0.04	0.14 ± 0.05	0.16 ± 0.06
Noctua janthe	Lesser broad-bordered yellow underwing (N)	0.14 ± 0.05	0.14 ± 0.08	0.14 ± 0.07
Pheosia gnoma	Lesser swallow prominent (No) [b]	0.14 ± 0.04	0.10 ± 0.04	0.19 ± 0.06
Deileptenia ribeata	Satin beauty (G) [b]	0.14 ± 0.04	0.16 ± 0.06	0.13 ± 0.06
Epirrhoe alternata	Common carpet (G)	0.13 ± 0.05	0.13 ± 0.08	0.13 ± 0.05
Autographa pulchrina	Beautiful golden Y (N)	0.12 ± 0.04	0.06 ± 0.04	0.17 ± 0.07
Axylia putris	Flame (N)	0.12 ± 0.05	0.06 ± 0.03	0.17 ± 0.10
Colocasia coryli	Nut-tree tussock (N) [b]	0.12 ± 0.05	0.11 ± 0.08	0.13 ± 0.07
Herminia grisealis	Small fan-foot (N) [b]	0.12 ± 0.04	0.13 ± 0.05	0.11 ± 0.05
Chortodes pygmina	Small wainscot (N)	0.11 ± 0.07	0.05 ± 0.03	0.17 ± 0.14
Cosmia trapezina	Dun-bar (N) [b]	0.10 ± 0.04	0.14 ± 0.07	0.06 ± 0.05
Idaea biselata	Small fan-footed wave (G) [b]	0.10 ± 0.04	0.08 ± 0.03	0.13 ± 0.06
Xestia xanthographa	Square-spot rustic (N)	0.10 ± 0.05	0.10 ± 0.08	0.10 ± 0.05

Table 5A-2 (cont.)

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Plusia festucae / P. putnami	Gold spot / Lempke's gold spot (N)	0.09 ± 0.04	0.02 ± 0.02	0.16 ± 0.08
Noctua comes	Lesser yellow underwing (N)	0.09 ± 0.04	0.03 ± 0.02	0.14 ± 0.07
Oligia strigilis / O. latruncula / O. versicolor	Marbled minor / Tawny marbled minor / Rufous minor (N)	0.09 ± 0.03	0.10 ± 0.04	0.08 ± 0.04
Hylaea fasciaria	Barred red (G) [b]	0.08 ± 0.03	0.08 ± 0.05	0.08 ± 0.04
Gymnoscelis rufifasciata	Double-striped pug (G)	0.08 ± 0.03	0.05 ± 0.04	0.11 ± 0.05
Nudaria mundana	Muslin footman (A)	0.08 ± 0.04	0.10 ± 0.06	0.06 ± 0.04
Crocallis elinguaria	Scalloped oak (G) [b]	0.08 ± 0.04	0.11 ± 0.07	0.05 ± 0.03
Thera britannica	Spruce carpet (G) [b]	0.08 ± 0.05	0.14 ± 0.10	0.02 ± 0.02
Euthrix potatoria	Drinker (L) [b]	0.07 ± 0.03	0.08 ± 0.04	0.06 ± 0.04
Ochropleura plecta	Flame shoulder (N)	0.07 ± 0.02	0.05 ± 0.03	0.10 ± 0.04
Anaplectoides prasina	Green arches (N) [b]	0.06 ± 0.02	0.05 ± 0.03	0.08 ± 0.04
Eupithecia absinthiata	Wormwood pug (G)	0.06 ± 0.02	0.08 ± 0.03	0.05 ± 0.03
Eupithecia subfuscata [d]	Grey pug (G)	0.06 ± 0.03	0.05 ± 0.04	0.08 ± 0.05
Chloroclystis v-ata	V-pug (G)	0.06 ± 0.03	0.05 ± 0.04	0.06 ± 0.04
Eupithecia vulgata [d]	Common pug (G)	0.06 ± 0.03	0.08 ± 0.06	0.03 ± 0.02
Lacanobia thalassina	Pale-shouldered brocade (N) [b]	0.05 ± 0.03	0.06 ± 0.05	0.03 ± 0.02
Hoplodrina blanda / H. alsines	Rustic / Uncertain (N) [c, e]	0.05 ± 0.02	0.02 ± 0.02	0.08 ± 0.03
Autographa gamma	Silver Y (N)	0.05 ± 0.02	0.05 ± 0.04	0.05 ± 0.03
Opisthograptis luteolata	Brimstone moth (G) [b]	0.04 ± 0.02	0.03 ± 0.02	0.05 ± 0.04
Chlorochlista truncata	Common marbled carpet (G)	0.04 ± 0.02	0.02 ± 0.02	0.06 ± 0.04
Hepialus hecta	Gold swift (H) [b]	0.04 ± 0.02	0.06 ± 0.03	0.02 ± 0.02
Acronicta rumicis	Knot grass (N)	0.04 ± 0.03	0.02 ± 0.02	0.06 ± 0.06
Brachylomia viminalis	Minor shoulder-knot (N) [b, c]	0.04 ± 0.03	0.05 ± 0.05	0.03 ± 0.02
Cosmorhoe ocellata	Purple bar (G)	0.04 ± 0.02	0.03 ± 0.02	0.05 ± 0.03
Autographa jota	Plain golden Y (N)	0.04 ± 0.02	0.02 ± 0.02	0.06 ± 0.03
Apamea scolopacina	Slender brindle (N) [b]	0.04 ± 0.02	0.05 ± 0.03	0.03 ± 0.02
Lacanobia oleracea	Bright-line brown-eye (N)	0.03 ± 0.02	0.02 ± 0.02	0.05 ± 0.03

Table 5A-2 (cont.)

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Apamea remissa	Dusky brocade (N) [c]	0.03 ± 0.02	0.02 ± 0.02	0.05 ± 0.03
Graphiphora augur	Double dart (N) [b, c]	0.03 ± 0.02	-	0.06 ± 0.04
Mesoleuca albicillata	Beautiful carpet (G) [b]	0.02 ± 0.01	0.02 ± 0.02	0.03 ± 0.02
Phalera bucephala	Buff-tip (No) [b]	0.02 ± 0.02	-	0.05 ± 0.04
Cidaria fulvata	Barred yellow (G) [b]	0.02 ± 0.01	0.02 ± 0.02	0.03 ± 0.02
Apamea crenata	Clouded-bordered brindle (N)	0.02 ± 0.02	0.03 ± 0.03	0.02 ± 0.02
Mythimna pallens	Common wainscot (N)	0.02 ± 0.01	-	0.05 ± 0.03
Xanthorhoe ferrugata	Dark-barred twin-spot carpet (G) [c]	0.02 ± 0.02	0.02 ± 0.02	0.03 ± 0.03
Alcis jubata	Dotted carpet (G) [b]	0.02 ± 0.01	0.03 ± 0.02	0.02 ± 0.02
Chloroclysta citrate	Dark marbled carpet (G) [b]	0.02 ± 0.02	0.03 ± 0.03	0.02 ± 0.02
Eupithecia pulchellata	Foxglove pug (G)	0.02 ± 0.02	-	0.05 ± 0.04
Thera obeliscata	Grey pine carpet (G) [b]	0.02 ± 0.02	0.05 ± 0.04	-
Arctia caja	Garden tiger (A) [c]	0.02 ± 0.02	-	0.05 ± 0.05
Orthosia gothica	Hebrew character (N)	0.02 ± 0.01	0.03 ± 0.02	0.02 ± 0.02
Eulithis prunata	Phoenix (G)	0.02 ± 0.02	0.02 ± 0.02	0.03 ± 0.03
Schrankia costaestrigalis	Pinion-streaked snout (N)	0.02 ± 0.02	0.05 ± 0.04	-
Hydraecia micacea	Rosy rustic (N) [c]	0.02 ± 0.01	-	0.05 ± 0.03
Euplexia lucipara	Small angle shades (N)	0.02 ± 0.01	0.02 ± 0.02	0.03 ± 0.02
Odontopera bidentata	Scalloped hazel (G) [b]	0.02 ± 0.01	0.05 ± 0.03	-
Abrostola tripartite	Spectacle (N)	0.02 ± 0.01	0.02 ± 0.02	0.03 ± 0.02
Ourapteryx sambucaria	Swallow-tailed moth (G) [b]	0.02 ± 0.01	0.03 ± 0.02	0.02 ± 0.02
Lampropteryx suffumata	Water carpet (G) [b]	0.02 ± 0.01	0.02 ± 0.02	0.03 ± 0.02
Bupalus piniaria	Bordered white (G) [b]	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Mythimna farrago	Clay (N)	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Selenia dentaria	Early thorn (G) [b]	0.02 ± 0.01	0.03 ± 0.02	-
Xanthorhoe fluctuata	Garden carpet (G)	0.02 ± 0.01	-	0.03 ± 0.02
Naenia typical	Gothic (N)	0.02 ± 0.01	-	0.03 ± 0.02

Table 5A-2 (cont.)

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Biston betularia	Peppered moth (G) [b]	0.02 ± 0.01	0.03 ± 0.02	-
Notodonta ziczac	Pebble prominent (No) [b]	0.02 ± 0.01	0.03 ± 0.02	-
Perizoma flavofasciata	Sandy carpet (G) [b]	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
Agrotis segetum	Turnip moth (N)	0.02 ± 0.02	-	0.03 ± 0.03
Camptogramma bilineata	Yellow shell (G)	0.02 ± 0.02	0.03 ± 0.03	-
Eupithecia assimilata [d]	Currant pug (G)	0.02 ± 0.02	-	0.03 ± 0.03
Noctua frimbriata	Broad-bordered yellow underwing (N) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Mythimna conigera	Brown-line bright-eye (N)	0.01 ± 0.01	0.02 ± 0.02	-
Rusina ferruginea	Brown rustic (N) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Agrochola litura	Brown-spot pinion (N) [b, c]	0.01 ± 0.01	0.02 ± 0.02	-
Craniophora ligustri	Coronet (N) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Orthosia cerasi	Common quaker (N) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Scopula floslactata	Cream wave (G) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Hepialus lupulinus	Common swift (H)	0.01 ± 0.01	0.02 ± 0.02	-
Blepharita adusta	Dark brocade (N) [c]	0.01 ± 0.01	0.02 ± 0.02	-
Amphipoea sp.	Ear moth (N) [c, f]	0.01 ± 0.01	0.02 ± 0.02	-
Ectropis bistortata	Engrailed (G) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Macrothylacia rubi	Fox moth (L)	0.01 ± 0.01	0.02 ± 0.02	-
Luperina testacea	Flounced rustic (N)	0.01 ± 0.01	-	0.02 ± 0.02
Hepialus humuli	Ghost moth (H) [c]	0.01 ± 0.01	0.02 ± 0.02	-
Pseudoips prasinana	Green silver-lines (N) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Autographa bractea	Gold spangle (N)	0.01 ± 0.01	-	0.02 ± 0.02
Scoliopteryx libatrix	Herald (N) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Chiasmia clathrata	Latticed heath (G) [c]	0.01 ± 0.01	-	0.02 ± 0.02
Selenia lunularia	Lunar thorn (G) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Amphipyra tragopoginis	Mouse moth (N) [c]	0.01 ± 0.01	-	0.02 ± 0.02
Cryphia domestica	Marbled beauty (N)	0.01 ± 0.01	-	0.02 ± 0.02

Table 5A-2 (cont.)

Latin name	Common name (Family) [a]	Abundance per trap (mean ± SE)	Abundance per trap – interior (mean ± SE)	Abundance per trap – edge (mean ± SE)
Mormo Maura	Old lady (N)	0.01 ± 0.01	-	0.02 ± 0.02
Hepialus sylvina	Orange swift (H)	0.01 ± 0.01	-	0.02 ± 0.02
Pterostoma palpina	Pale prominent (No)	0.01 ± 0.01	-	0.02 ± 0.02
Thyatira batis	Peach blossom (T) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Perizoma affinitata	Rivulet (G) [b]	0.01 ± 0.01	0.02 ± 0.02	-
Xestia c-nigrum	Setaceous Hebrew character (N)	0.01 ± 0.01	0.02 ± 0.02	-
Macaria liturata	Tawny-barred angle (G) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Peribatodes rhomboidaria	Willow beauty (G) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Eupithecia tenuiata [d]	Slender pug (G)	0.01 ± 0.01	-	0.02 ± 0.02
Eupithecia abbreviata [d]	Brindled pug (G) [b]	0.01 ± 0.01	-	0.02 ± 0.02
Eupithecia virgaureata [d]	Golden-rod pug (G)	0.01 ± 0.01	0.02 ± 0.02	-
Eupithecia lariciata [d]	Larch pug (G) [b]	0.01 ± 0.01	0.02 ± 0.02	-

[a] Family codes: Arctiidae (A), Geometridae (G), Hepialidae (H), Lasiocampidae (L), Noctuidae (N), Notodontidae (No), Sphingidae (S), Thyatiridae (T).

[b] Species for which woodland is listed as the main habitat where species occurs and/or for which the larval food is strongly associated with woodland (e.g. woody plants; according to Waring & Townsend 2003).

[c] Species included in the UK Biodiversity Action Plan (BAP) for moths, listed as 'Common and widespread, but rapidly declining moths – Research only'.

[d] Genitalia were examined to confirm species identification.

[e] *H. blanda* is included in the UK BAP list, *H. alsines* is not.

[f] Only *A. oculea* is included in the UK BAP list.

Appendix 5B. Comparisons between models without landscape metrics and models incorporating a landscape metric at several spatial scales to the 'woodland character' models.

Table 5B-1. Comparisons between models without landscape metrics and models incorporating woodland cover % at several spatial scales. The model with the lowest AIC value (in bold if it was significantly better than the model without the landscape metric) was identified as the most parsimonious and the particular spatial scale it incorporated was recognized as the most relevant for a landscape-scale management approach. Standardized parameter estimates (±SE) and model R^2 values are shown for the models with the lowest AIC. Statistical differences between models were based in deviance values (χ^2 tests).

	GLMM (woodland character) AIC	+woodland 250m AIC [a]	+woodland 500m AIC	+woodland 1000m AIC	+woodland 1500m AIC	+woodland 2000m AIC	+woodland 2500m AIC	+woodland 3000m AIC
Micromoth abundance	AIC = 559.4 R^2 = 74.97 %	558.5 ◌̇	**557.2 *** **0.67±0.31** **(75.17%)**	561.2	561.2	561.3	561.1	561.1
Micromoth richness	AIC = 192.5 R^2 = 52.09 %	193.8	192.6 ns (52.61%)	194.4	194.5	194.5	194.5	194.5
Micromoth diversity	AIC = 285.5 R^2 = 32.03 %	**282.6 *** **(0.15±0.07)** **(34.65 %)**	283.0 *	287.2	285.9	285.9	286.3	286.8
Macromoth abundance (all species)	AIC = 862.4 R^2 = 59.85 %	864.2	863.6 ns (59.89%)	864.3	864.3	864.1	864.2	864.3
Macromoth richness (all species)	AIC = 242.0 R^2 = 55.66 %	239.0 *	**236.9 **** **(0.28±0.10)** **(57.11%)**	241.8	241.1 ◌̇	242.8	242.5	242.5
Macromoth diversity (all species)	AIC = 812.3 R^2 = 42.27 %	812.3 ns (42.48%)	813.3	814.5	814.5	814.5	814.5	814.5
Macromoth abundance (woodland species)	AIC = 479.1 R^2 = 64.81 %	**475.1 *** **(1.17±0.45)** **(65.28%)**	475.4 *	480.6	480.8	481.1	481.1	481.1
Macromoth richness (woodland species)	AIC = 190.4 R^2 = 57.29 %	190.3	187.8 *	188.1 *	**186.0 *** **(0.26±0.10)** **(58.97%)**	190.3	189.9	190.1

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '.' $p \leq 0.1$ and 'ns' $p \geq 0.1$.

Table 5B-2. Comparisons between models without landscape metrics and models incorporating semi-natural environment cover % at several spatial scales. Standardized parameter estimates (±SE) and model R^2 values are shown for models with the lowest AIC values (in bold if significantly better than the model without the landscape metric). Statistical differences between models were based in deviance values (χ^2 tests).

	GLMM (woodland character) AIC	+semi-natural 250m AIC [a]	+semi-natural 500m AIC	+semi-natural 1000m AIC	+semi-natural 1500m AIC	+semi-natural 2000m AIC	+semi-natural 2500m AIC	+semi-natural 3000m AIC
Micromoth abundance	AIC = 559.4 R^2 = 74.97 %	**557.3** * **(0.41±0.20)** **(75.16%)**	559.7	560.5	561.2	560.6	560.3	560.3
Micromoth richness	AIC = 192.5 R^2 = 52.09 %	**186.4** ** **(0.34±0.12)** **(54.31%)**	189.0 *	192.5	194.5	193.1	192.4 .	191.9 .
Micromoth diversity	AIC = 285.5 R^2 = 32.03 %	287.3	287.5	287.2	287.1	286.0	285.6	285.3 ns (33.21%)
Macromoth abundance (all species)	AIC = 862.4 R^2 = 59.85 %	**860.7** ◌̇ **(0.16±0.08)** **(60.03%)**	863.2	862.9	864.0	863.6	862.6	862.9
Macromoth richness (all species)	AIC = 242.0 R^2 = 55.66 %	237.4 *	237.0 **	**236.9** ** **(0.18±0.06)** **(57.11%)**	243.5	244.0	243.7	243.7
Macromoth diversity (all species)	AIC = 812.3 R^2 = 42.27 %	814.4	814.2	813.8	812.5	811.8	**811.5** ◌̇ **(-1.27±0.79)** **(42.21%)**	811.9
Macromoth abundance (woodland species)	AIC = 479.1 R^2 = 64.81 %	480.7	481.1	481.0	476.2 *	**474.9** * **(-0.58±0.24)** **(65.28%)**	475.1 *	476.9 *
Macromoth richness (woodland species)	AIC = 190.4 R^2 = 57.29 %	192.3	192.2	192.2	191.2	190.4	189.7 ns (58.00%)	190.5

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '.' $p \leq 0.1$ and 'ns' $p \geq 0.1$.

Table 5B-3. Comparisons between models without landscape metrics and models incorporating urban cover % at several spatial scales. Standardized parameter estimates (±SE) and model R^2 values are shown for models with the lowest AIC values (in bold if significantly better than the model without the landscape metric). Statistical differences between models were based in deviance values (χ^2 tests).

	GLMM (woodland character) AIC	+urban 250m AIC [a]	+urban 500m AIC	+urban 1000m AIC	+urban 1500m AIC	+urban 2000m AIC	+urban 2500m AIC	+urban 3000m AIC
Micromoth abundance	AIC = 559.4 R^2 = 74.97 %	**559.8 ◌̇** **(-0.44±0.24)** **(75.14%)**	561.5	562.3	563.0	563.2	563.3	563.2
Micromoth richness	AIC = 192.5 R^2 = 52.09 %	192.6	192.3 ns (52.69%)	194.5	194.3	194.1	194.1	194.3
Micromoth diversity	AIC = 285.5 R^2 = 32.03 %	286.9	286.1 ns (32.80%)	287.3	287.5	287.4	287.1	286.8
Macromoth abundance (all species)	AIC = 862.4 R^2 = 59.85 %	864.4	863.4	864.2	863.7	863.1	863.1 ns (59.92 %)	863.4
Macromoth richness (all species)	AIC = 242.0 R^2 = 55.66 %	242.6	242.2	**239.9 *** **(-0.15±0.07)** **(56.50%)**	243.0	243.8	243.9	243.9
Macromoth diversity (all species)	AIC = 812.3 R^2 = 42.27 %	813.4	812.9 ns (42.53%)	814.1	814.3	814.2	814.2	814.2
Macromoth abundance (woodland species)	AIC = 479.1 R^2 = 64.81 %	481.1	481.0	480.7 ns (64.84%)	481.1	481.0	481.0	480.8
Macromoth richness (woodland species)	AIC = 190.4 R^2 = 57.29 %	192.4	192.1	189.8 ns (57.97 %)	190.6	191.3	191.7	191.9

[a] Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '.' $p \leq 0.1$ and 'ns' $p \geq 0.1$.

Chapter 6

General discussion

6. General discussion

Drastic population declines of many bat species have occurred in the UK during the 20th century and the main cause if believed to be the loss of roosting and foraging habitat through agricultural expansion and intensification (Harris *et al.* 1995; Walsh & Harris 1996). Nonetheless, no specific actions have been taken to enhance bat populations in agricultural areas. Bat population declines have been linked to a decrease in the abundance of their insect prey. Amongst them, Lepidoptera have also been affected by habitat loss caused by agricultural intensification and have undergone severe population declines (Conrad *et al.* 2004; New 2004). Current agri-environment schemes (AES) introduced in many countries to counteract the negative effects of intensive agriculture on biodiversity, do not take the needs of bats and many of their insect prey into consideration. Whilst such schemes are potentially beneficial to these taxa, the response of either bats, or their prey species, to the implementation of AES prescriptions had not been assessed prior to this study.

6.1. The effectiveness of agri-environment-schemes for the conservation of bats and nocturnal insects

In the first ever assessment of the response of bats and their insect prey to the implementation of four common agri-environmental prescriptions in the UK, we showed that activity levels of Pipistrelle bats and the abundance of their insect prey (mainly Diptera and Trichoptera) were lower (by almost half) on farms participating in AES than on non-participating farms (Chapter 2). Differences in insect prey availability were also noticeable when we compared specific AES management prescriptions with equivalent conventionally-managed features. In general, AES involving management prescriptions for hedgerows, water margins and species-rich grasslands were associated with lower insect prey availability and did not increase bat activity levels. The management of field margins was the only AES prescription which was associated with marginally higher levels of bat activity. Our findings show that these AES prescriptions – as they currently operate – are of little or no value to Pipistrelle bats (and other bat species foraging on similar prey).

Some of these AES prescriptions do benefit moth populations in agricultural environments, and could potentially benefit moth-eating bats such as *P. auritus* and *Barbastella barbastellus* (Vaughan 1997), by increasing their foraging resources (Chapter 3). AES species-rich grasslands and water margins increased micro- and macromoth abundance, whereas AES field margins increased only micromoth abundance. Moth species richness was also enhanced by some of these prescriptions. Hedgerows under AES management enhanced neither micromoth nor macromoth populations. These contrasting results between bats and moths reflect the fact that many AES prescriptions (e.g. species-rich grasslands) were specifically designed to benefit pollinator species rather than bats or their insect prey species. The inclusion of features selected by bats (e.g. tree lines; Walsh and Harris 1996) into AES management recommendations would be a good way to enhance bat populations through these schemes. For instance, linear features (e.g. hedgerows) containing trees are associated with higher incidence levels of *P. pygmaeus* and higher moth abundance than linear features without trees (Merckx *et al.* 2010b; Boughey *et al.* 2011b). Prescriptions for the establishment and maintenance of hedgerow trees have recently been introduced in the English Entry Level Stewardship (ELS); High Level Stewardship (HLS) management options also include the maintenance of ancient trees in arable/pastoral land and the creation, maintenance and restoration of wood pasture and parkland (Natural England 2010). However, the current Scottish LMC relevant option (management of hedgerows and hedgerow trees), has only loose recommendations to "encourage hedgerow trees to develop where possible" (Anonymous 2008). Other hedgerow characteristics, such as width, do not seem to influence the use of these linear features by Pipistrelle bats (Boughey *et al.* 2011b).

6.2. Woodland: a key habitat for the conservation of bats

The implementation of the four common AES management prescriptions assessed in this study did not benefit Pipistrelle bats and is unlikely to benefit other bat species foraging on similar prey. The most important factors associated with bat activity in farmland (regardless of farm participation within AES) were metrics related to woodland configuration in the surrounding landscape. These results, together with the considerable evidence supporting the importance of woodland for British bats (e.g. Walsh & Harris 1996; Vaughan, Jones & Harris 1997; Russ & Montgomery 2002; Altringham 2003), suggest that conservation efforts for bats should focus on this habitat. Currently in the UK, a number of AES aim to increase the amount and quality of woodland on agricultural land. However, the limited knowledge about how woodland character relates to bat abundance and insect prey availability, has resulted in recommendations for the creation and management of woodland without consideration for the needs of foraging bats (although guidelines for creating and maintaining roosting opportunities are more common; e.g. Anonymous 2005).

The lack of information about the influence of woodland character on bats derives in part from the difficulties of surveying and monitoring this taxon. Sampling techniques vary in their efficacy depending on the species involved and the habitats surveyed. For instance, mist nets (and harp traps) set at ground level are ineffective at detecting species which often commute and forage above the forest canopy; in addition, aerial insectivores are able to detect and avoid trapping devices (MacSwiney G., Clarke & Racey 2008). Ultrasonic detectors, on the other hand, often fail to detect species with quiet echolocation calls and to distinguish between species with similar call structures (especially in cluttered environments where bats modify their echolocation calls; Schnitzler & Kalko 2001). The use of both acoustic and capture methods for sampling, significantly increases the number of bat species detected by either method alone (MacSwiney G., Clarke & Racey 2008). Consequently, complete descriptions of bat assemblages generally require the simultaneous use of multiple methods (Meyer *et al.* 2011). In this study, we used two complementary techniques – sound recording and trapping (assisted by an acoustic lure for bats) – to assess bat species presence, abundance and activity in woodland patches. By using both methods we were able to detect species which responded poorly to one of the methods (particularly *P. pipistrellus* which was rarely caught but often recorded, and *P. auritus* which was caught in some sites and recorded in others). In addition, the use of the acoustic lure for bats considerably increased the number of individuals captured during the surveys.

By combining two complementary surveying techniques, we showed that bat populations were influenced by woodland vegetation character (Chapter 4). Habitat associations were species-specific: for example, *Pipistrellus* species responded positively to an open understory and a closed canopy cover, whereas *Myotis* species showed the opposite trend. Non-Lepidoptera insects (mainly Diptera) were not influenced by woodland vegetation. This has implications for *Pipistrellus* and *Myotis* bats, which feed mainly on this group of insects (although the latter have a more varied diet). In contrast, Lepidoptera were strongly associated with vegetation character; in general, woodlands composed of broadleaved trees only, a large number of native tree species and a dense understory cover were related to higher moth abundance and species richness (Chapter 5). The presence of grazing stock in woodlands had strong negative effects on moths. This has important implications for the conservation of moths, and of moth-eating bats such as *P. auritus* and – to a lesser degree – *Myotis* species.

Woodland patch size and configuration also influenced bat populations, but seemed less important than woodland vegetation structure. We observed patterns of higher bat abundance and activity at small and isolated woodland patches, which suggests that bats utilize this habitat more intensively in landscapes where woodland and other good quality foraging areas are limited (Chapter 4). Whereas the abundance of non-Lepidoptera insects (food resources for *Pipistrellus* and *Myotis* bats) was not influenced by woodland configuration, moth abundance (food resources for moth-eating bats) and richness were higher in large and well connected woodland patches. However, small patches still maintained relatively high abundance and richness of moths if they were located close to other woodlands and had a low proportion of edge exposed to the surrounding landscape (Chapter 5). Within a woodland patch, overall insect abundance was higher at woodland edge than at woodland interior, suggesting that woodland edges offer more foraging opportunities for bats. However, activity of *P. pygmaeus* and *Myotis* species was actually slightly higher in woodland interior than in woodland edge (although foraging effort, i.e. number of feeding buzzes emitted when attempting prey capture, was not assessed). Similarly, some moth species (e.g. micromoths and macromoth woodland specialists) were also associated with woodland core habitat.

Findings relating to bats and their insect prey's associations with woodland vegetation character and patch configuration have important implications for agri-environment schemes involving woodland creation and management at the local scale. For instance, the importance of size, plant species composition and tree density are particularly relevant for the design of newly created woodland patches, whereas the importance of a dense understory cover and of the exclusion of grazing stock are relevant for woodland management prescriptions (e.g. to benefit moths and moth-eating bats). The influence of woodland patch configuration on bats and their insect prey is particularly relevant to woodland creation/planting schemes (e.g. importance of the location of a newly created woodland patch relative to other woodlands) and highlight the importance of managing habitats not only at a local-, but also at a wider landscape-scale.

6.3. The importance of a landscape-scale management approach

Numerous studies have highlighted the importance of the surrounding landscape (e.g. heterogeneity, proportion of non-cropped areas and woodland) on farmland biodiversity (e.g. Tscharntke *et al.* 2005; Hendrickx *et al.* 2007; Kleijn *et al.* 2009). It has also been shown that landscape character influences the effectiveness of AES and that prescriptions aimed at enhancing or maintaining landscape complexity are likely to be highly effective at conserving biodiversity in agricultural landscapes (Concepción, Díaz & Baquero 2008; Batáry *et al.* 2011). A species' mobility may influence its response to the surrounding landscape. Many bat species are highly mobile and are, therefore, strongly influenced by the landscape context at relatively large spatial scales (e.g. within 5 km; Boughey *et al.* 2011a; Gorresen, Willig & Strauss 2005; Klingbeil & Willig 2009). Our findings showed that bat species with relatively high dispersal abilities (e.g. *P. pipistrellus* and *Myotis* species) were influenced by the surrounding landscape at large spatial scales (e.g. within 3 km); less mobile species (e.g. *P. pygmaeus*), however, were only influenced by the landscape at smaller spatial scales (e.g. within 1 km).

Woodland related metrics were the most important landscape parameters influencing bat populations; woodland extent within the landscape also had a strong influence on moth communities, but mostly at relatively small spatial scales (within 500 m). A high proportion of semi-natural environment (e.g. rough grassland and scrub) was also associated with high insect prey availability (non-Lepidoptera abundance and moth abundance and species richness); once more, these effects were only noticeable at small spatial scales (e.g. within 500 m). These findings indicate that increasing the percentage cover of woodland and semi-natural environment at a local scale is likely to increase food availability for a wide variety of bat species (e.g. those feeding mainly on moths, and those feeding on other invertebrate groups such as Diptera) and enhance moth communities in agricultural environments.

Whereas a conservation strategy which incorporates management at small spatial scales might be sufficient to protect some species, others require a wider-scale strategy. For instance, macromoth ‘woodland species’ were influenced by the surrounding woodland within 1500 m, while highly mobile bats (such as *P. pipistrellus* and *Myotis* species) were influenced by the surrounding woodland within 3000 m. A landscape-scale management approach, which encompasses low and high mobility species, is therefore necessary in order to protect a larger proportion of local biodiversity.

Taxa with poor dispersal abilities require a well connected network of habitats and even relatively small distances between suitable patches may act as dispersal barriers (Geertsema 2005). For instance, micromoths were more strongly affected by woodland patch isolation than the more mobile macromoths (e.g. negative effects of isolation were noticeable at smaller distances on the former than on the latter group). *P. pygmaeus*, a bat species of relatively low mobility, was also influenced by woodland isolation (woodland patches were more intensively used when they were more isolated). These outcomes emphasize the potential importance of spatial-targeting to optimize the benefits of AES, by ensuring that newly created woodland patches are located in the right areas. Spatial-targeting can be beneficial for woodland de-fragmentation and it is likely to yield higher biodiversity benefits than non-spatially-targeted woodland planting in agricultural areas (van der Horst 2007; Quine & Watts 2009). Previous spatially-targeted woodland creation schemes have been based on map evaluations and scoring systems where higher scores were given to the creation of larger woodlands, in proximity to existing woodland, linking existing woodlands, and/or adjacent to other semi-natural habitats (e.g. the Joining and Increasing Grant Scheme for Ancient Woodland (JIGSAW); Quine & Watts 2009). Whereas this approach fits well with our findings for moths' associations with woodland configuration, it somewhat contradicts the results found for bats; for this group, the more intensive use of woodland patches in isolated sites and in sparsely wooded landscapes suggested that woodland creation is more important (and should be prioritized) in these areas. Other studies support the idea that the benefits bats gain from an increase in woodland extent would be higher in landscapes with little existing woodland cover (e.g. < 20% within 1 km; Boughey *et al.* 2011a). A compromise strategy might be to focus woodland creation in sparsely wooded landscapes, but to ensure that woodland patches are well inter-connected by, for example, tree lines or riparian strips.

It is important to keep in mind that increasing the amount of woodland and/or semi-natural environment on farmland to enhance biodiversity necessarily implies the loss of agricultural land. The need to satisfy the food demands of an expanding human population poses constrains on the extent of agricultural land which can be converted back into woodland (or other semi-natural habitats). Therefore, an adequate design of the character and spatial configuration of newly created woodland (or other semi-natural habitat) patches is essential to maximize the biodiversity gains.

6.4. Contrasting habitat associations of bats vs. moths: are different conservation strategies required for different species?

Throughout this thesis, different (sometimes contrasting) responses of different taxa to the implementation of AES, and to woodland character, were observed. For instance, AES field margins benefited micro- but not macromoths; other AES prescriptions (e.g. water margins and species-rich grasslands), benefited micro- and macromoths but had fewer non-Lepidoptera insects than conventionally-managed features. In addition, whereas bats and their insect prey sometimes showed similar habitat associations (e.g. Pipistrelle bats and non-Lepidopteran insects having higher activity/abundance on conventional than on AES farms), this was not always the case (e.g. non-Lepidoptera abundance was not influenced by woodland character, while Pipistrelle bat activity was). Overall food availability for bats was higher at woodland edges than at woodland interior, but woodland core habitat was essential for many moth species (e.g. macromoth ‘woodland species’ and micromoths) and was preferred by some bat species (e.g. *P. pygmaeus* and *Myotis* sp.). The presence of grazing stock in woodland patches had strong negative effects on moths, but was associated with higher activity levels of *P. pipistrellus* and *Myotis* species. A dense understory seemed to benefit micromoths, but was associated with lower activity levels of some bat species (e.g. *P. pipistrellus*). Different bat species were also influenced by woodland character in different ways. For instance, *Pipistrellus* species were positively related to low tree densities, open understory and a closed canopy cover, while *Myotis* species showed the opposite trend; this reflects differences in these species’ life histories (e.g. some species having short and broad wings which allow them to fly and hunt amongst cluttered vegetation).

Previous studies have pointed out that the outcomes of AES depend on the nature of the taxa under study, and that the one-size-fits-all approach adopted by many AES is not the most efficient way to maximise biodiversity gains (Batáry *et al.* 2011). The design of AES specifically targeted to species (or species groups) might be preferable. Some of the most successful cases of AES at enhancing populations of certain species (e.g. birds) have derived from intensive research of target species and a close supervision of management implementation (e.g. Perkins *et al.* 2011). However, what is beneficial for one species might be disadvantageous for others. For instance, management recommendations for improving woodland quality for wildlife often involve thinning or clearing the understory, and widening rides and glades (Blakesley & Buckley 2010). While this is beneficial for some taxa (e.g. woodland butterflies and moth assemblages associated with open habitats) it is likely to be detrimental for species associated with mature woodland such as woodland specialist moths

(Anonymous 2007; Broome *et al.* 2011), and some bat species which are associated with woodlands with a well-developed understory (e.g. *P. auritus* and *B. barbastellus*; Hill & Greenaway 2008). In contrast, bat species associated with woodland edges and open areas (e.g. aerial hawkers such as *P. pipistrellus*) might benefit from the creation of open areas (e.g. woodland glades). A heterogeneous mosaic of habitats of different character seems, therefore, essential to fulfil the requirements of different taxa. However, priority should be given to managing habitat to benefit species of special conservation concern.

Whereas species-targeted AES are more efficient at increasing species abundance, ‘general’ AES prescriptions still provide some benefits to biodiversity (Perkins *et al.* 2011). In this thesis, we showed that many moth species – even macromoth species considered ‘widespread but rapidly declining’, which are of special conservation concern – gained benefits from simple AES management prescriptions. In addition, ‘general’ management strategies are likely to benefit a wide range of species. For instance, the establishment/maintenance of hedgerow trees benefits not only moths and bats (Merckx *et al.* 2010b; Boughey *et al.* 2011b), but also many bird species (Hinsley & Bellamy 2000). Therefore, a combination of ‘targeted’ (both spatially and to species or species groups) and ‘general’ AES prescriptions is likely to yield greater biodiversity gains. The former would ensure the creation of high quality habitat for species of special conservation concern and in the right areas; the latter would increase the permeability of the surrounding matrix (Donald & Evans 2006) while benefiting a much wider range of species. This approach resembles the one adopted by the English AES, which are divided into ELS – non-competitive schemes which incorporate simple, non spatially-targeted land management prescriptions – and HLS – competitive schemes which incorporate more complex management prescriptions tailored to specific local targets (Natural England 2010).

6.5. Management recommendations

A number of management recommendations can be drawn from this thesis; these are likely to contribute to the conservation of bats and nocturnal insects by improving the benefits that these taxa gain from agri-environment schemes:

1. AES programmes should include a combination of ‘targeted’ (both spatially and to species or species groups) and ‘general’ AES prescriptions. ‘Targeted’ prescriptions would ensure the creation of high quality habitat for species of special conservation concern, in the right areas; ‘general’ prescriptions would increase the permeability of the surrounding matrix while benefiting a wide range of species.

2. The implementation of common AES management prescriptions, such as the creation of species-rich grasslands and the management of water margins and field margins, is an effective method to enhance moths and (potentially) moth-eating bat species in agricultural environments. These relatively simple and commonly applied AES options should be maintained in future AES programmes.

3. Current AES prescriptions involving the management of hedgerows should be improved to ensure they provide benefits to biodiversity. The inclusion of features selected by bats, such as tree lines or hedgerow trees, is likely to benefit a wide variety of taxa, including moths.

4. The extent of semi-natural habitats, such as rough grassland and scrub, should be increased to benefit nocturnal insects (and increase food availability for bats). Although this is constrained by the necessity of agricultural land to produce enough food for human consumption, prescriptions which promote semi-natural environments should be maintained/incorporated in AES. Prescriptions similar to the old set-aside measure (taking land out of agricultural production) might favour the development of this habitat.

5. Woodland cover should be increased to benefit bats and woodland moth species. Because this is limited by the need of agricultural land to produce enough food for human consumption, an adequate design of the character and spatial configuration of newly created woodland to benefit biodiversity is of outmost importance. Large woodland patches of compact shapes, located close to other woodlands will yield the greatest benefits to moths; small patches are still valuable for moths, but shape and proximity to other woodlands are of particular importance. In contrast, bats would gain more benefits from the creation of woodland patches in isolated sites and in sparsely wooded landscapes where good foraging habitat is scarce. New woodland patches planted in sparsely wooded areas, but well connected to other woodlands (e.g. by tree lines or riparian strips) may satisfy these contrasting requirements.

6. In general, woodland patches with a large number of (native) tree species and a dense understory cover will benefit moths and woodland bat species (e.g. gleaning, moth-eating bats such as *P. auritus*). Less cluttered areas with a low tree density will benefit aerial hunters (e.g. Pipistrelle bats). Therefore, habitat heterogeneity within or between woodland patches should be maintained to

fulfil the requirements of different taxa. Priority should be given to manage habitat for species of special conservation concern.

7. The presence of grazing stock in a woodland patch has strong negative effects on moths and is likely to be detrimental for woodland bat species feeding on these insects (e.g. gleaning bats such as *P. auritus*). Grazing could benefit Pipistrelle bats by reducing understory clutter, but it should only be allowed after careful consideration.

8. Whilst local management is important, a landscape-scale management approach, which considers low and high mobility species, will protect a larger number of species and yield greater biodiversity gains. Highly mobile bat species (e.g. *P. pipistrellus* and *M. nattereri*) were influenced by the landscape within up to 3 km, but effects at larger scales (which were not evaluated) could exist.

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