Bat exploitation of Sitka Spruce plantations: Impacts of management on bats and nocturnal invertebrates

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Declaration

I hereby declare that this thesis has been completed by myself, and 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.

…………………………………………………………………….

Lucinda Kirkpatrick

Summary

Plantations are widespread throughout temperate regions, and the area of plantation land cover is predicted to get larger in the future. Interest in ensuring sustainable plantation management is also growing, as it is increasingly recognised that productive areas should play a role in biodiversity conservation. Plantation landscapes can comprise the majority of forested cover in some countries, but taxon-specific guidance can be lacking, due to plantations often being under surveyed. Therefore, despite substantial incentives existing to ensure that plantations meet various ecological criteria, plantation managers lack the information necessary to implement effective management plans. Many bat species have undergone widespread declines in recent decades, attributed to habitat loss and fragmentation, particularly of forested habitat. In many temperate countries, historical deforestation has resulted in very low native tree cover, and subsequently, considerable replanting with non-native commercial coniferous plantations has taken place. Species specific habitat surveys have often demonstrated avoidance of conifer plantations by bats, which has been attributed to a lack of roosts and low invertebrate prey abundance. Furthermore, widespread lepidopteran declines have been partly attributed to afforestation with non-native conifer, but moth associations with commercial coniferous plantations are usually only studied for pest species.

Bats present a particular challenge in plantation landscapes; tree cover is important to many species to a greater or lesser extent, and in the United Kingdom, destruction of a roost site is illegal, regardless of whether it was deliberate or accidental. However, the extent to which bats associate with non-native commercial plantations is relatively unexplored. This is the first study to explicitly test bat associations with *Picea sitchensis* plantations (using acoustic detectors, trapping and radio tracking), and shows that, contrary to expectations, they may be an important habitat for breeding populations of *Pipistrellus* spp*.,* particularly *P. pygmaeus.* High levels of activity were recorded for both *P. pygmaeus* and *P. pipistrellus*, despite little difference in dipteran abundance between different stand types, both species preferentially foraged in felled or less dense stands. This suggests that bats preferentially forage in areas with less acoustic and physical clutter, which will increase foraging efficiency. The impacts of felling in non-native commercial coniferous plantations on foraging activity was tested, for the first time, using a Before – After – Control – Impact experimental design. Bat activity (specifically *P. pipistrellus* and *Nyctalus*) increased after felling, particularly in smaller stands. In contrast felling had significant, negative impacts on moth abundance, species richness and diversity, and these effects remain after constraining for functional trait similarity. Reductions in richness and diversity in response to felling were similarly large for both rare and abundant species. Therefore, while bats may benefit from clear fell practices, albeit as long as the size of patches is small, moth populations could benefit from a shift towards other forestry methods,

such as continuous cover forestry. These results also have implications for the recent, but increasing practice of siting wind turbines in commercial coniferous plantations, as pre-installation preparation involves clearing small patches of forest which may attract foraging bats; post felling monitoring should be carried out to examine potential impacts on bat populations.

The presence of broadleaf trees in and around plantations significantly increased moth richness, mostly through increased occurrence of rare species. Broadleaf woodlands (defined as land spanning more than 0.5 ha, with trees higher than 5m and a combined cover of shrubs, bushes and trees above 10%), also had higher functional redundancy than plantation sites. For a diverse moth population to persist in plantation landscapes, preserving remnant patches of broadleaf trees is essential. There was little difference in bat activity between broadleaf woodlands and plantation sites. However, bat abundance, particularly that of reproductively active females, was greater in broadleaf sites compared to plantations. This was particularly true for *Myotis* and *Nyctalus* spp*.,* very few of which were trapped in commercial plantations. Therefore, although reproductively active female *Myotis* bats are present in the surrounding landscape, they do not appear to associate with plantations themselves. This may reflect a lack of roost availability; both *P. pygmaeus* and *P. pipistrellus* preferentially form large maternity colonies in buildings, but for *Myotis* and *Nyctalus* spp*.* which roost switch regularly and often use trees, it is unlikely many suitable roosts exist within the plantations themselves.

Many substantial *P. pygmaeus* maternity colonies were identified in and around Galloway forest, with some holding more than 500 individuals. All maternity colonies were in buildings, and most inhabited (and one uninhabited) buildings within the plantation contained a roost. Although females occasionally used old or dead deciduous trees as temporary roosts, there was no evidence of roosting in crop trees such as *P. sitchensis*. During this study, the Forestry Commission installed 36 bat boxes; within 6 months over 90% had been used, with a number of harems found inside. This fast uptake compared with bat use of boxes in other locations reflects the paucity of appropriate structures for either roost or harem use in commercial plantations.

Twelve bats were captured while foraging, tagged with small radio transmitters, and followed for between 2 and 6 nights during 2014 and 2015. All but one tagged female preferentially foraged within the plantation, with individuals selecting equally riparian habitats and felled stands. Tagged females which roosted furthest from the plantation had the largest home ranges; one individual flew nearly 40km each night to reach foraging areas distant from her roost, suggesting that the food availability within the plantation was sufficient to render such a long journey energetically viable.

These results have important implications for bat populations in and around commercial coniferous plantations. Far from being avoided by bats, plantation landscapes may constitute an important habitat type for both *P. pygmaeus* and *P. pipistrellus*, likely due to the high abundance of nematoceran diptera in plantation woodlands. Furthermore, plantation forests support a similar richness of moth species to urban and agricultural woodlands, including a number of declining species of special conservation concern. A list of management recommendations to benefit both bat and moth populations in commercial plantations is presented at the end of this thesis.

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Finishing fieldwork. Photo by Lynn Munro, reproduced with permission

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Chapter One

Chapter 1 Introduction

Demonstrating the finest clothing for midge protection while bat catching

1.1 Introduction

Biodiversity, the variety and variability of living organisms and the ecological complexes in which they occur, is a central concept in the study of ecology, including diversity within species, between species and within and between ecosystems (Chao et al 2014). It is now well established that human actions are substantially and negatively influencing biodiversity (Cardinale et al., 2012; Chapin et al., 2000; Newbold et al., 2015; Sala et al., 2000; Vitousek et al., 1997). Over the last 500 years, human activities have triggered a wave of extinctions, population declines and threats that are comparable with both the rate and magnitude of the five previous extinction events (Cardinale et al., 2012; Dirzo et al., 2014), resulting in the naming of a new epoch, the Anthropocene (Zalasiewicz et al., 2011). Declines are occurring across taxonomic groups and regions, although some are more affected than others (Dirzo et al., 2014), for example amphibians and large-bodied vertebrates appear disproportionately impacted by anthropogenic threats (Schipper et al., 2008) although this may reflect the relative ease and human interest in sampling these organisms. A major driver behind these potentially catastrophic losses is land use change (Dirzo et al., 2014; Newbold et al., 2015; Sala et al., 2000) where once pristine landscapes dominated by primary vegetation are replaced by human-dominated mosaic landscapes (Tscharntke et al., 2012).

1.2 Global impacts of anthropogenic change on biodiversity:

Agricultural intensification, urbanisation and deforestation are all contributing to biodiversity loss, altering the resilience of ecosystems to environmental change and impacting ecosystem functioning (Chapin et al., 2000; Newbold et al., 2015). This is likely to have serious consequences for human health and wellbeing; for example between 23 and 36% of birds, animals and amphibians used for medicinal purposes are now threatened with extinction (Dirzo et al., 2014) and increased use of pesticides in intensified agriculture has significantly and negatively impacted biological control organisms (Geiger et al., 2010). Bumble bees and honey bees, vital for crop pollination (the value of which has been estimated at between $5 and $14 billion a year) and honey production are also facing widespread declines in both Europe and North America due to introduced predators, pesticide use and loss of native plant life (Goulson et al., 2008). Rapid urbanisation as a consequence of human population growth and resettlement of rural populations, along with climate change pose a growing challenge both in management of ecosystem resources but also human health (Stephenson et al., 2013). Estimates suggest that localised but significant biodiversity degradation associated with current and future urbanisation is the main driver behind the decline of 8% of red listed imperilled terrestrial vertebrate species (Mcdonald et al., 2008). Urbanisation also promotes the establishment of non-native species by increased importation and by creating new “niche opportunities” through

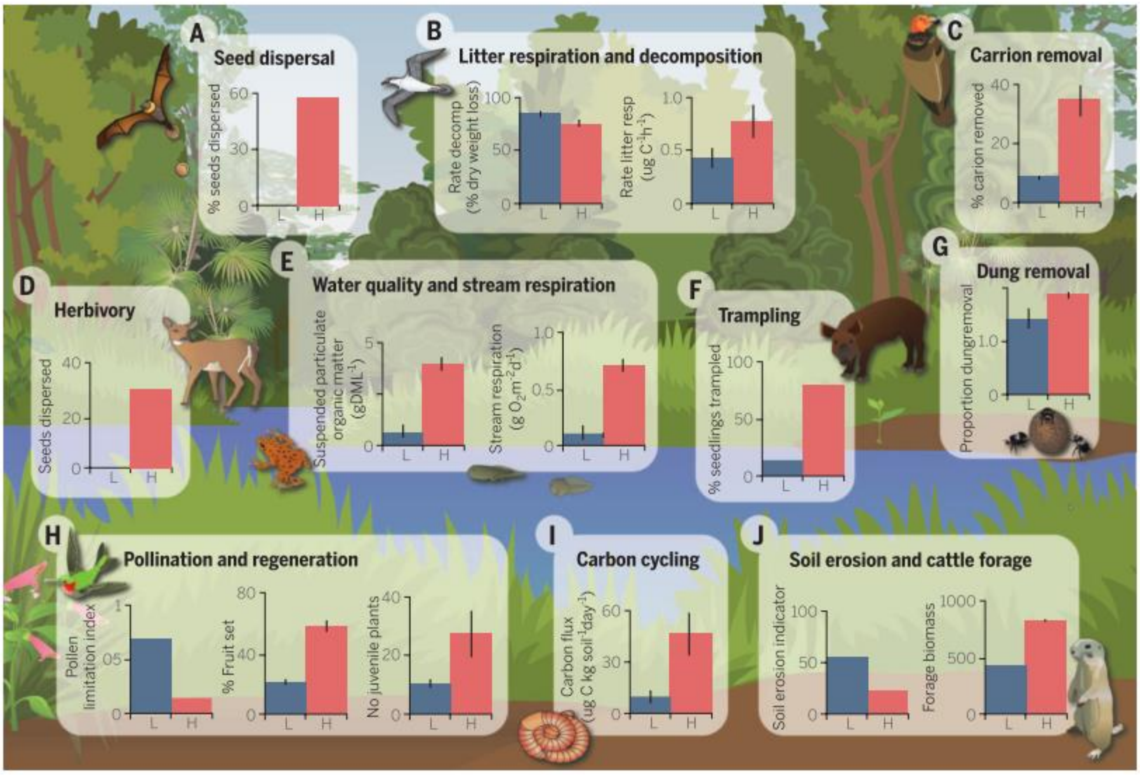

Figure 1.1: Consequences of defaunation on ecosystem functioning and services (Dirzo et al., 2014). *Figure shows changes in annual abundance from low (blue, L) to high (red, H) within a region and affects on a range of ecosystem functioning and services including (A) Seed dispersal (flying foxes). (B) litter respiration and decomposition (sea birds). (C) carrion removal (vultures). (D) herbivory (large mammals). (E) water quality and stream restoration (amphibians). (F) trampling of seedlings (mammals). (G) dung removal (dung beetles). (H) pollination and plant recruitment (birds). (I) carbon cycling (nematodes). (J) soil erosion and cattle fodder (prairie dogs).*

the alteration of habitats (McKinney, 2006). In tropical regions, deforestation has been an area of intense research and interest, with intensive forestry resulting in the highest rates of global forest change (Hansen, 2014).However, boreal and temperate forest regions are also under intensive deforestation pressure, and will be the focus of this thesis.

Deforestation has been implicated in the loss of bird, mammal and invertebrate species across a range of different forest types (Dirzo et al., 2014). During the Holocene, deciduous and coniferous forests covered most of the temperate and boreal landscape (Wallenius et al., 2010). Throughout the previous 5000 years, there has been widespread historical deforestation throughout central and southern Europe (Wallenius et al., 2010) although areas where boreal forest remains (e.g. Canada, northwest United States, Russia) are still under intensive logging pressure (Hansen, 2014). While large declines in deciduous forest cover have been attributed to historical forestry practices (e.g less than 0.2% deciduous cover remains in a natural state in central Europe, Bengtsson et al., 2000; more than 40% of native forest cover lost in Australia, Bradshaw, 2012), coniferous regions of Russia, Sweden and Finland show both loss and gain of forest cover associated with forestry practices (i.e loss due to harvesting and gain due to replanting; Hansen, 2014). The pressure on the world's forests to deliver economic, social and environmental services has now reached unsustainable levels in many places (Paquette and Messier, 2009). Non-concurrent forest clearing in eastern US, which has resulted in a temporally staggered loss of forest cover, has led to more bird species going extinct than predicted based on forest losses alone (Pimm and Askins, 1995) and bird fauna in Ireland lacks many forest specialist species due to historical deforestation (Sweeney et al., 2011). Generally, a movement from primary vegetation to secondary or cleared vegetation results in simplified landscapes and corresponding reductions in both vertebrate and invertebrate richness (Newbold et al., 2015; Tscharntke et al., 2012). Additionally, deforestation and simplification of landscapes has been linked with increased risk of disease transfer between populations (Sehgal, 2010), including the risk of increased transfer of zoonotic diseases between humans and animal reservoir hosts (Daszak et al., 2000; Mills, 2006).

1.3 Initiatives reducing anthropogenic impacts on biodiversity loss

Traditionally, practitioners often attempt to limit biodiversity loss through the use of protected areas (currently 15.4% of terrestrial area is designated a protected area; Gray et al., 2016). In protected areas, core units of land are set aside from human interference in order to maintain intrinsic values such as biodiversity (Chape et al., 2005). There is evidence that sites within protected areas contain a higher species richness and abundance compared to sites from unprotected sites, but there is no evidence of greater species richness or levels of endemicity (Gray et al., 2016). There is debate as to the effectiveness of protected areas; although parks are generally effective at curtailing deforestation within their boundaries, surrounding deforestation can result in isolated fragments of forest (Naughton-Treves et al., 2005) which may fail to provide the necessary landscape components required for species persistence (i.e. components necessary for foraging, resting, reproduction and movement between them; Tscharntke et al., 2012). Population declines can also occur inside protected areas; Laurance et al. (2014) found that for half of the protected areas they surveyed, biodiversity erosion was occurring across a wide array of both taxonomic and functional groups due to hunting and habitat exploitation, often mirroring environmental changes occurring around the protected area (Laurance and KIRSTY, 2014). Protected areas are most effective where they limit human-dominated land use and safeguard primary or secondary vegetation (Gray et al., 2016) which has been linked with higher biodiversity (Newbold et al., 2015). However, simply relying on protected areas will not provide sufficient land cover to preserve even a modest proportion of biodiversity and the use of protected areas is only effective in regions where sufficient primary habitat exists to protect (Gardner, 2012). In areas of extensive defaunation, deforestation and habitat alteration such as much of the western hemisphere, there is arguably little "natural" habitat remaining, and the majority of habitats have been altered by human activity to a greater or lesser extent (Gardner, 2012). Therefore, human-altered habitats have an important role to play in biodiversity conservation (Paquette and Messier, 2009).

Conservation initiatives in human-dominated landscapes are numerous. For example, agri-environment schemes offer financial incentives for environmentally sensitive agricultural management (Knop et al., 2006). However, the extent to which these schemes are effective differs both geographically and between taxa (Albrecht et al., 2007; Fuentes-Montemayor et al., 2011; Kleijn and Sutherland, 2003; Knop et al., 2006). While hoverflies, bees, butterflies and to some extent moths respond positively to a range of agri-environmental prescriptions (Albrecht et al., 2007; Alison et al., 2016; Kleijn and Sutherland, 2003), there is evidence that Diptera, Arachnida, plant, bat and bird species richness were lower on plants with agri-environment schemes (Fuentes-Montemayor et al., 2011; Kleijn and Sutherland, 2003; Knop et al., 2006). A movement away from more intensive farming methods and a switch to organic farming has been suggested to improve biodiversity (Wickramasinghe et al., 2003). Reducing crop field size positively influences a range of different taxa, and diversity at several spatial scales (Fahrig et al., 2015), but schemes are most likely to be effective in intermediately disturbed habitats and will vary depending on the quantity of remaining semi-natural vegetation within the landscape (Tscharntke et al., 2012).

Along with increased awareness of the impacts of intensive agriculture on biodiversity, the last few decades have also seen considerable interest and progress in improving the sustainability of plantation forest management (Brin et al., 2009; Brockerhoff et al., 2008; S. Stephens and Wagner, 2007). In Europe this has been driven by policy change initiated as a result of the Convention of Biological Diversity, requiring explicit consideration of environmental, economic and social objectives and a multi-purpose approach to forestry (Watts et al., 2008). As a result of this, there is growing recognition that plantations need to provide a range of services, not just those of timber production, but also for biodiversity, recreation, carbon sequestration, alternative energy generation, or where appropriate conversion back to the original landscape (Brockerhoff et al., 2008; Carnus et al., 2003).

Forest landscapes pose a different challenge to agricultural landscapes; one third of the world's forest are primarily designated for timber production (Anon, 2015), and in temperate areas, native tree cover often consists of small, highly fragmented and disturbed forest patches, often surrounded by a hostile agricultural or urban matrix (Gardner, 2012). Natural forest systems have been impacted by a range of human activities including hunting and removal of large herbivores and predators, grazing with domestic herbivores, clearance for agricultural, firewood and industrial purposes and conversion to monoculture or non-native plantations (Bengtsson et al., 2000). Despite increased planting of deciduous trees (e.g. an increase of deciduous tree cover from 5% to 13% in the UK; Watts et al., 2008), widespread and severe declines of forest specialist species are still occurring (State of Nature, 2016). In some temperate forest systems changes to forest management such as abandonment and the cessation of coppicing has led to declines in open and edge adapted species (Broome et al., 2011; Horak et al., 2014), but increased richness and diversity of mature forest and saproxylic species due to the increase in coarse woody debris and presence of older trees (Broome et al., 2011; Lassauce et al., 2012). The presence of deadwood is vital for the ecosystem health of forested landscapes; old or dying trees provide roosts for cavity-nesting birds (Spiering and Knight, 2005), bats (e.g. Elmore et al., 2005) and are an important habitat for saproxylic organisms such as fungi, lichens and invertebrates (Horak et al., 2014). Finally, in some regions widespread conversion of native woodland (defined as “land spanning more than 0.5 ha, with trees higher than 5m and a combined cover of shrubs, bushes and trees above 10%“; Anon., 2005) , upland areas such as peat bogs, or areas of degraded agricultural ground to non-native, plantation forests has occurred (Gardner, 2012). These have been traditionally managed for timber production rather than biodiversity benefits and as a consequence, are often considered to contribute little to biodiversity (Brockerhoff et al., 2008).

1.4 Importance of plantation landscapes for biodiversity

Forest landscapes, even those comprising degraded, semi-natural or artificial forest habitat can provide a refuge for species unable to survive in agricultural or urban matrices (Gardner, 2012) and as such may be compatible with biodiversity conservation goals (Brockerhoff et al., 2008). Plantation forests, defined as “cultivated forest ecosystems established by planting and or seeding in the process of afforestation, primarily for wood biomass but also soil and water conservation and wind protection” (Carnus et al., 2003), cover large areas of the Western hemisphere (Anon, 2015; Brockerhoff et al., 2008), currently representing 6% of total global forest cover, and that figure is set to rise (FSC, 2012). Although the largest increases are likely to be in tropical regions rather than temperate regions, there is little evidence that temperate plantation areas will decrease in the future (fig 1.2)

Despite the widespread assumption that plantation forests are less favourable habitats than native forests (Carnus et al., 2003) there is evidence that there may be important opportunities for biodiversity conservation if plantation design and management are sensitive and appropriate (Lantschner et al., 2009). The extent to which plantation forests provide suitable habitat for native

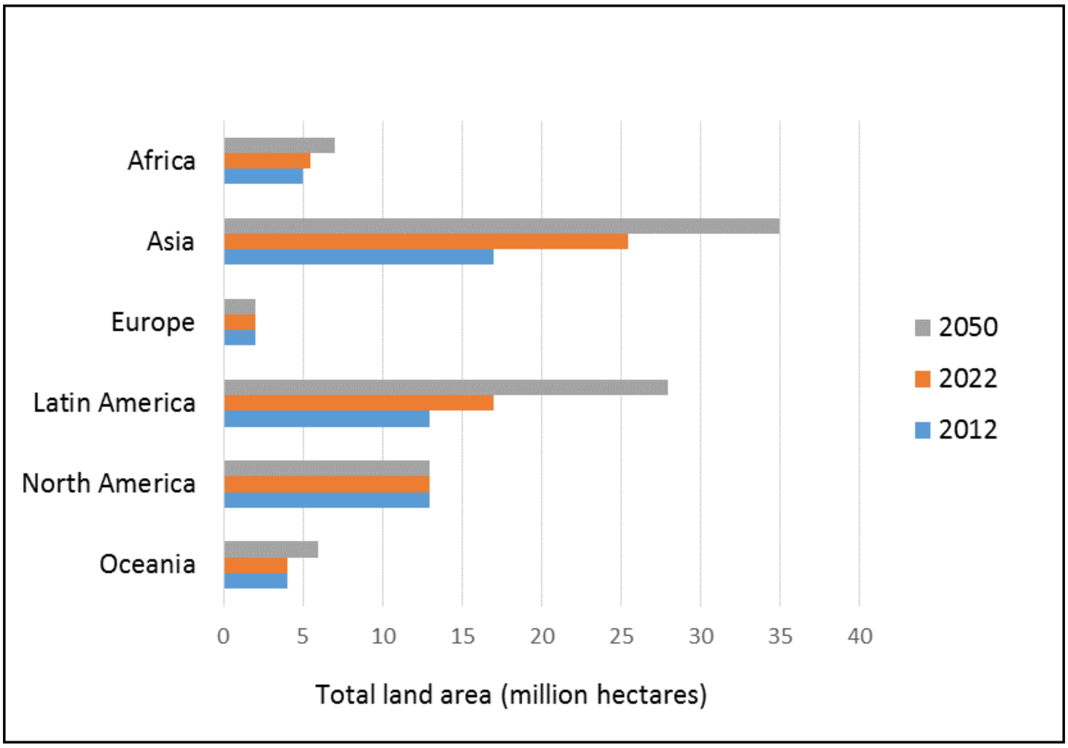

Figure 1.2: Global plantation area forecasts by region alongside current plantation land cover. From FSC, (2012).

flora and fauna will depend on the species composition of the plantation, the intensity of forest management, the surrounding landscape, and the previous land use.

1.5 Influence of species composition on biodiversity in plantations

The most commonly planted tree species in temperate plantations are *Pinus* spp*,* followed by *Eucalyptus* spp, with the majority of plantations formed of single or few species (FSC, 2012)*,* although this varies significantly depending on the region in which the plantation is being established*.* Although non-native species are often used to achieve timber quality goals (Gardner, 2012), plantations of native species generally support higher biodiversity than those of non-native species. For example *Pinus syvestris* (Scots Pine, native to Scotland) supports a greater richness and diversity of arachnid, particularly Opilionid communities compared to *Pinus contorta* (Lodgepole pine, native to North America) plantations in Scotland (Docherty et al 2007) and similar carabid and syrphid diversity to native woodlands (Humphrey et al 1999). If the phenology of non-native trees is not synchronised with the demands of native fauna, then this will also limit the community assemblage that will develop in non-native plantations compared to native plantations (Proenca 2010).

However, some exotic pine forests provide habitat for vulnerable, critically endangered or endemic species (e.g. *Chalinobus tuberculatus* (long-tailed bat), Borkin and Parsons, 2010; *Holcaspis brevicula*

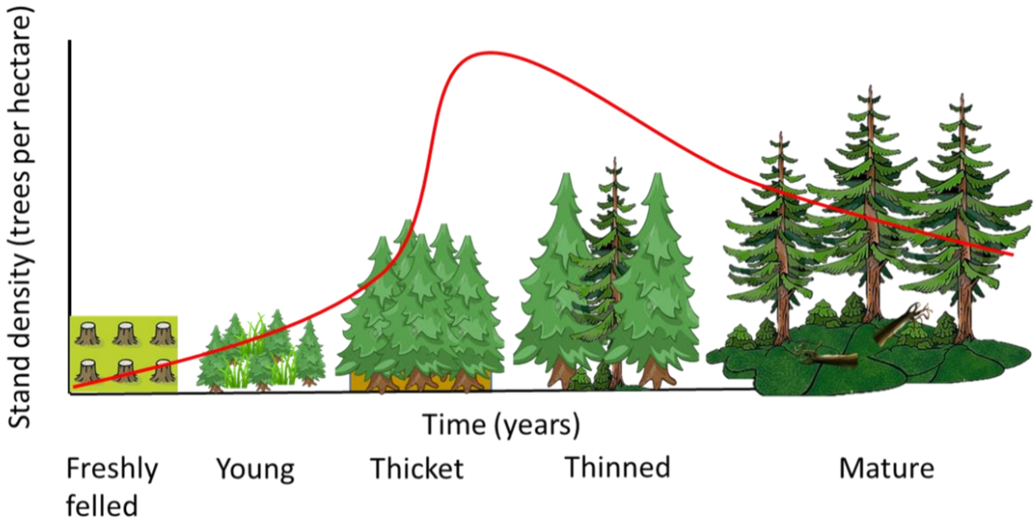

Figure 1.3: Relationship between stand density and stand age. Categories relate to stand descriptions (appendix 2.1).

(New Zealand ground beetle), Brockerhoff et al., 2005; *Streptopelia turtur* (European turtle dove), Paquet et al., 2006), and it is likely that factors other than tree species composition will also influence flora and fauna diversity and abundance.

1.6 Intensity of forest management

There is substantial evidence to suggest that the stand (a forestry unit denoting a distinct area of tree cover that is composed of uniform group of trees in terms of species composition, age class distribution and size class distribution) structure will have a significant impact on both community composition and species richness for a range of taxa (e.g. De Warnaffe and Lebrun, 2004; Donald et al., 1998; Eycott et al., 2006; Oxbrough et al., 2005; Paquet et al., 2006; Sullivan et al., 2009). Stand structural complexity will change greatly throughout the “life cycle” of a plantation (Figure 1.3), with most plantations consisting of a mosaic of different aged stands (Sullivan et al., 2009). Newly felled or planted stands lack the structural complexity of older stands, but have a higher vegetative cover, and many open specialist species preferentially associate with younger stands (Donald et al., 1998; du Bus de Warnaffe and Deconchat, 2009; Eycott et al., 2006; Jukes et al., 2001; Lin et al., 2006; Oxbrough et al., 2010; Paquet et al., 2006) , although in some cases communities are dominated by a few open specialists and overall diversity is low (Haskell et al., 2006).

Open areas such as clear fell are quickly colonised by particularly mobile taxa such as “ballooning” spider species which disperse by wind over relatively long distances (Oxbrough et al., 2010, 2005), but recolonization generally occurs from surrounding areas rather than as a result of persistence through the felling cycle (Oxbrough et al., 2010). Open areas often contain a higher and more diverse ground vegetative layer, for example, migrant bird species are positively associated with both young and mature stands due to the increasing ground vegetation cover (Donald et al., 1998). Similarly, in the Ardennes, clear felled areas with substantial ground vegetative cover, act as refuges for heathland and moorland specialist bird species (Paquet et al., 2006). Felled areas can also support generalist and open specialist spider and carabid species (Oxbrough et al., 2010), possibly as a result of the higher plant species richness found in young plantation stands compared to older stands (Eycott et al., 2006). Clear felled areas can support small mammal populations such as *Microtus agrestis* (field vole) which can become major pests in plantations, causing substantial damage to newly planted trees (Zárybnická et al., 2014), yet also form an important part of *Strix aluco* (tawny owl) diet (Petty, 1999). Therefore, felled and open areas in plantations can support a range of species at differing trophic levels.

As stand density increases and canopy closure occurs, all but the most shade-tolerant plants are unable to persist (Eycott et al., 2006; Paquet et al., 2006). Consequently, community composition and diversity of taxa including Lepidoptera, arachnids, carabidae, and avifauna is substantially reduced (Donald et al., 1998; Oxbrough et al., 2010; Paquet et al., 2006; van Halder et al., 2008). Usually, generalist species persist in dense plantation stands (Oxbrough et al., 2010). However, as stands reach maturity, stand density is reduced and increased reduced canopy closure allows the establishment of increased ground vegetation (Eycott et al., 2006; Oxbrough et al., 2010). Responses to the reduction in stand density are taxon-specific, for example, bird richness and abundance is highest in stands over 50 years of age, especially for migrant species (Donald et al., 1998). Mature stands support a higher proportion of forest specialist avifauna (Barbaro et al., 2007; Lantschner et al., 2009; Seaton et al., 2010), invertebrates (Oxbrough et al., 2010) and carnivorous mammals (Lantschner et al., 2012). Predator presence in commercial plantations is likely to be driven by prey availability; reduced stand densities and increased vegetative cover will support a higher population of potential prey such as *Lepus europaeus* (European hare) and other small mammals (Lantschner et al., 2012). In general, mature stands in plantations more closely resemble native forests than do other stand types (Haskell et al., 2006); they may provide shelter, breeding sites for species reliant on old trees and will have a higher quantity of deadwood, which is important for saproxylic invertebrate (Brin et al., 2009) and fungi communities (Paillet et al., 2010) populations. However, in short rotation systems, mature stands are often felled before the conditions preferred by forest specialists are achieved (Paquet et al., 2006).

1.6.1 Impacts of harvesting practices

1. Clear-felling: The impact of forest modification on biodiversity due to human activities is most likely to be due to logging intensity (Gardner, 2012) which can result in drastic changes to the structural composition of the forest, allowing early successional species to establish,

Figure 1.4: (A) Typical stand of clearfelled Sitka Spruce against a backdrop of mature trees. (B) Thinning in a stand of mature Sitka Spruce. (C) Continuous cover forestry carried out at Clocaenog Continuous Cover Forestry Research area, Wales

or mimics natural disturbance regimes through selective removal of individual trees (figure 1.4; Gardner, 2012). For forest systems using clear fell, the size and shape of the cleared area can also affect biodiversity (Pawson, 2006). Between the forest edge and the interior of the open stand, there is often a more moderate microclimate which may shelter a specific invertebrate community or even mature forest specialists (Baker et al., 2013; Pawson et al., 2006). Despite the popularly held belief employed in forest systems in e.g. Tasmania or British Columbia, that mature forest will influence biodiversity in harvested areas within one canopy tree height of the forest edge, there is little empirical evidence to support or dismiss this (Baker et al., 2013). More realistically, the extent to which the forest edge influences the movement of taxa into harvested areas will depend on species-specific dispersal ability and microclimatic requirements, although Baker et al (2013) found that edge effects only seemed to extend to 100m for most species, excluding larger vertebrates. As the size of the clearcut increases, there will be proportionally less edge, therefore more complex and smaller clear cuts are likely to support a higher abundance and diversity of a range of both forest and open specialist species compared to larger clear cuts (Baker et al., 2013; Grindal and Brigham, 1998).

2. Surrounding forest condition: The condition of the nearby forest may be as important as the size of the felled area; Pawson (2006) found that the greatest beetle richness was in the largest clear cuts, adjacent to species rich mature forest (Pawson, 2006). Early successional specialist species using clear cuts face additional challenges in dispersing to suitable habitat once conditions change due to the ephemeral and shifting nature of felled areas (Acuña and Estades, 2011). Size is also important; if the felled area is too small, microclimatic conditions may be unsuitable for some open adapted specialist species, but if it is too large, and therefore isolated within the landscape, dispersal between clear cuts will be difficult for all but the most dispersive of species (Acuña and Estades, 2011). Finally, clear felling may directly cause mortality due to forest operations, which will primarily affect forest specialist

mammal and bird species such as bats, cavity nesting birds and some small mammal species (Borkin et al., 2011; Escobar et al., 2015; Rosenvald and Lõhmus, 2008).

3. Thinning: Thinning involves the mechanical removal of individual trees, with the aim of reducing stand density, allowing nearby trees to increase in size and therefore timber quality and economic worth. Reducing stand density in mature stands can also be an effective way to increase species richness and abundance of a range of taxa by altering the community structure of understory vegetation to the benefit of a range of taxa (e.g. bats, Blakey et al., 2016; birds, De La MontaÑA et al., 2006; small mammals, Sullivan et al., 2001; bees, butterflies and hoverflies, Taki et al., 2010).
4. Continuous cover forestry: There is considerable evidence that species diversity will be positively influenced if management operations such as felling mimic natural disturbances, for example by creating multi-aged rather than even-aged plantations (Bardat and Aubert, 2007). Multi-aged forest systems can support a higher diversity of species through the provision of different habitats for a wide range of flora and fauna, from those reliant on early successional habitats e.g. some songbirds (Sweeney et al., 2010) to species dependent on mature habitats e.g. canopy dwelling Coleoptera (Ohsawa, 2007). As a result, many forest managers are moving away from practices such as clear felling to more targeted harvesting approaches such as continuous cover forestry (Lindenmayer and Hobbs, 2004; Pawson et al., 2006), which requires the continuous and uninterrupted maintenance of forest cover (Pommerening and Murphy, 2004). Taxa that may particularly benefit from continuous cover include Lepidoptera (Summerville, 2013; Thorn et al., 2015), avifauna (Lefort and Grove, 2009; Lencinas et al., 2011) and mammals (Lantschner et al., 2012; Lindenmayer et al., 2010). Although there is a commitment to converting substantial areas of the plantation estate to continuous cover forestry in the United Kingdom (Mason, 2007), there is active discussion as to whether continuous cover management is suitable for the majority of plantations in the UK (Mason, 2015; but see Macdonald et al., 2009).
5. Rotation length: Lengthening the period between forest rotations increases the potential for stands to develop the features that are important for the persistence of many species such as cavity nesting birds (Spiering and Knight, 2005) or saproxylic beetles (Brin et al., 2009). In particular, increasing rotation length is likely to support an increased diversity of forest specialist beetle species, especially Carabidae (Jukes et al., 2001; Lange et al., 2014; Ohsawa and Shimokawa, 2011). Rotation length varies greatly depending on plantation tree species (e.g. *Eucalyptus* and some *Pinus* spp*.* are harvested 15 – 30 years after planting compared to *Picea sitchensis*, which is harvested between 40 – 60 years; Gardner, 2012)

6. Retention of deadwood: Historically, dead wood was removed from managed plantation systems due to hygiene fears (Ruczyński et al., 2010), However, dead wood often harbours natural predators of many pest species (Paillet et al., 2010), and the volume of coarse woody debris maintained in commercial plantations is important for a range of taxa (Ranius et al., 2014). Saproxylic beetles, bryophytes, lichens, and fungi rely on deadwood microhabitats; unmanaged woodlands with a higher quantity and quality (i.e. size, decay stage) of deadwood support a higher diversity and abundance of these taxa (Brin et al., 2009; Paillet et al., 2010). Both bat and cavity nesting bird species rely on the presence of standing dead wood for roost or nest sites (Arnett et al., 2010; Elmore et al., 2005; Erickson and West, 2003).

1.6.2 Importance of landscape composition on diversity in plantations:

The surrounding landscape can significantly influence the diversity and abundance of a range of taxa in commercial plantations. Maintaining patches of remnant vegetation allows native species to persist in plantation landscapes, particularly forest specialists (Hsu et al., 2010; Oxbrough et al., 2012; Proença et al., 2010). Patches of native broadleaf tree cover increase diversity and abundance of taxa by facilitating recolonization of newly felled plantation stands; few plant species persist through the forest cycle, and plant regeneration after felling mostly occurs through the seed bank (Eycott et al., 2006) or from remnant patches. Remnant patches also support a higher abundance and diversity of lepidopteran species due to the increased richness of plant species (van Halder et al., 2008) and may act as important refugia for predators, arthropods, birds, amphibians, mammals and reptiles (Barbaro et al., 2007; Charbonnier et al., 2016; Felton et al., 2010; Lin et al., 2006; Seaton et al., 2009). Proponents of commercial plantations also suggest that compared to other intensive land use types, commercial plantations may improve landscape connectivity (Brockerhoff et al., 2008) which is vital for the persistence of populations in fragmented landscapes (Lindenmayer and Fischer, 2006). There is evidence that when planted in forest areas plantations may be a low contrast matrix compared to conversion to urban or intensive agriculture (Brockerhoff et al., 2008; Felton et al., 2010; Ferreras and Ferreras, 2015; Wethered and Lawes, 2005), however this may reflect the distribution of semi-natural vegetation retained within the plantation area rather than the effects of the plantation itself (Mortelliti et al., 2014; Wethered and Lawes, 2005).

1.7 Impacts of anthropogenic change on bats

Bats represent one of the largest and arguably the most diverse mammal radiations (Calisher et al., 2006; Kunz et al., 2011); nearly one-fifth of all mammal species worldwide are bats (Kunz et al., 2011). Found on every continent apart from Antarctica, the 18 extant families of bats have existed for between 50 and 30 million years (Teeling et al., 2005). Bats are unique amongst mammals for the use of true self-powered flight, which has contributed to the wide variety of foraging and roosting strategies that bats employ (Teeling et al., 2005). This has resulted in a plethora of dietary, morphological and behavioural adaptations which have contributed greatly to their success (Altringham, 2013), and bats play a key role in pest control and pollination services (Kunz et al., 2011). For example, it has been predicted that bats reduce the number of pesticide applications required for cotton crops (Cleveland et al., 2006), and as a consequence, the loss of bats in North America could lead to agricultural losses estimated at more than $3.7 billion dollars per year (Boyles et al., 2011). Nearly 70% of all bat species are insectivorous (Boyles et al., 2011), but in many systems they are also key pollinators (e.g. of agave; Molina-Freaner and Eguiarte, 2003) seed dispersers (e.g. banana, mango, durian fruit amongst others, Kunz et al., 2011) and can even be responsible for island reforestation (Shilton et al., 1999).

Many bat populations are declining worldwide due to a range of human-induced stressors (Jones et al., 2009). Fifteen percent of all bat species are considered threatened (Jones et al., 2003), with another 7% considered near threatened and nearly 250 species considered data deficient (Voigt and Kingston, 2015). Bat populations are considered stable for less than 1% of bat species, and there are a range of specific threats that have been identified, even for species currently listed as Least Concern (Voigt and Kingston, 2015). The factors contributing to bat population declines and extirpations are numerous; roost destruction or disturbance (e.g. disturbance of underground roost sites, loss of tree roosts or exclusion from buildings), persecution (e.g. culling of bats either due to perceived damage to agricultural crops or hunting for bushmeat), the spread of emerging diseases (e.g. white-nose syndrome in North America) and climate change (e.g. increased frequency of tropical storms, Mickleburgh et al., 2002) all contribute (Voigt and Kingston, 2015). However, possibly the most important factor influencing bat populations is habitat degradation and fragmentation (Mickleburgh et al., 2002; Walsh et al., 1996), with the threats posed by land use change to and human disturbance in forest landscapes particularly pernicious (Voigt and Kingston, 2015).

Bats are vulnerable to human-mediated disturbance in forested landscapes for a variety of reasons. Long-lived, with slow reproductive rates, particularly in relation to body size, bats recover slowly from population declines (Altringham, 2013; Voigt and Kingston, 2015). Due to the evolution of energetically costly flight and their small body size, bats have relatively high metabolic rates and as a consequence must consume a food amount equalling a relatively high proportion of their body weight each night (Voigt and Kingston, 2015). Most species also have particular behavioural or physiological requirements which may involve the need to roost communally, which places constraints on whether or not sufficient appropriate sites exist in an area. For example, some species are specialist tree roosters, preferentially using large, mature trees with features such as cavities and switch roost frequently, therefore there needs to be provision of sufficient trees of a suitable condition to support breeding populations (Burgar et al., 2015). Other species will form large, communal roosts in human dwellings which can result in conflict with human occupiers and subsequent exclusion of colonies from the building (Stone et al., 2015). Due to habitat fragmentation and deforestation, bats may be forced to either travel substantial distances between roosting and foraging sites (Popa-Lisseanu et al., 2009) or use suboptimal habitats (Burgar et al., 2015) which can lead to population declines (Borkin et al., 2011).

The ability of bats to negotiate their environment will differ depending on their morphology, echolocation call structure and their sensitivity to anthropogenic impacts. Bat species vary in size considerably (1.9g – 1.6kg, Norberg and Norberg, 2012), but insectivorous bats are generally small and constrained by both morphology and prey size, particularly aerial insectivores (Brigham and Barclay, 1991). The aspect ratio, wing loading and wing shape of a bat will dictate manoeuvrability and consequently the habitat in which the bat forages (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Schnitzler et al., 2003), and such features have even been used to reconstruct late Pleistocene habitats based on bat fossil remains (Stimpson, 2012).

Bats with a high aspect ratio and a higher wing loading (e.g. *Nyctalus noctula*) tend to be fast, high flying, not particularly manoeuvrable bats who monopolise open spaces and use overlap sensitive, low-frequency narrowband calls, although the FM component of the call increases during foraging flight (Jones, 1995). Low frequencies will attenuate less quickly in air, so travel further before becoming degraded, yet will provide poorer resolution (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Schnitzler et al., 2003). Bats with low aspect ratio and a low wing loading tend to be highly manoeuvrable, slow fliers which can monopolise more cluttered environments, for example, *Myotis nattereri* or *Rhinolophus hipposideros*. Such bats will use either low duty cycling frequency modulated (FM) calls or constant frequency (CF) calls which are adapted for cluttered environments. Their echolocation calls are usually broadband and higher frequency to preserve detail, although they will attenuate faster (Fenton et al., 1995; Jones, 1999; Schnitzler et al., 2003). Bat species are often classified into guilds related to their foraging style, using both the structure of the echolocation calls and morphology. Bats in the “open adapted” guild are those with fast, direct flight and low-frequency calls which frequent open spaces. “Edge adapted” bats are more manoeuvrable, and occupy edge spaces (e.g. open gaps with background clutter), with calls which usually contain a frequency modulated component. Finally, “clutter adapted” bats are slower, highly manoeuvrable species which move in highly cluttered spaces and employ either frequency modulated or constant frequency calls with Doppler shift (Adams et al., 2009; Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Schnitzler et al., 2003). It has been suggested that bats with a low aspect ratio, and therefore a preference for foraging in cluttered environments are at a higher risk of extinction than high aspect ratio species (Jones et al. 2003). It is likely that this reflects the widespread loss of forest habitat worldwide, especially since low aspect ratio species have attained more manoeuvrable flight at the cost of smaller foraging ranges (Jones et al., 2003). Small home ranges increase vulnerability to extinction, as bats may not be able to disperse to more suitable habitat, or fragmentation may result in home ranges which do not contain the necessary landscape features for roosting, foraging and mating behaviour (Borkin et al., 2011).

While bat use of particular habitats is primarily driven by the interplay between hunting style, wing morphology, echolocation characteristics and preferred prey species, species-specific sensitivity to anthropogenically derived disturbance such as light and noise pollution or roads can also influence bat use of landscapes. Although some bat species will actively forage around streetlights due to the congregation of flying invertebrates (Jung and Kalko, 2010), slow flying clutter adapted bats are more sensitive to light pollution due to increased risk from diurnal avian predators (Stone et al., 2009). Similarly, although some bat species may preferentially use roads as linear features while traversing a landscape, roads are also likely to negatively affect bat populations due to increased collision risk, night time lighting, removal of roosts during road development, and severance of critical flight routes used for commuting and migration (Berthinussen and Altringham, 2012; Voigt and Kingston, 2015).

1.8 Bat associations with plantation landscapes:

Due to the potential provision of both foraging and roosting habitats, forests are one of the most important habitat types for insectivorous bats (Law et al., 2015). However, they are also one of the most threatened. In addition, bats are highly mobile and while their use of forested landscapes at the stand level will be constrained by their morphology and echolocation style, it is likely that a landscape level approach will be as, if not more important (Duchamp et al., 2007). Whilst bat associations with native forest is well established (Altringham, 2013; Dietz et al., 2009) relatively little attention has been paid to bat use of temperate commercial plantations, despite their large geographical extent. Work to date indicates substantial and growing evidence that, contrary to previous expectations, bat use of commercial plantations may be more widespread than previously thought (e.g. Europe, Charbonnier et al., 2016; Cistrone et al., 2015; Cruz et al., 2016; Mortimer, 2006; Pereira et al., 2016; Russo et al., 2010; New Zealand and Australia, Borkin and Parsons, 2011;

Borkin et al., 2011; Burgar et al., 2015; North America, Morris et al., 2010; Patriquin and Barclay, 2003).

The abundance and diversity of bats supported by a particular landscape will be influenced by the availability of roosts, the structural complexity of the environment the bat is moving within, and prey and water availability (Hayes and Loeb, 2007). These conceptual models suggest that there are theoretical thresholds beyond which bat abundance will not increase and another factor becomes limiting (Hayes and Loeb, 2007). Low-quality habitat for bats can, therefore, result from a low density of resources (e.g. foraging areas or roost structures), degradation of resources, unsuitable vegetative structure or inhospitable location within the landscape (Duchamp et al., 2007).

1.9 Roost availability

The impact of plantation management on roost availability is two-fold. If trees with roosting features are retained bats will make use of them (Arnett, 2007; Elmore et al., 2005; Mortimer, 2006) although forest practices may necessitate the removal of trees before suitable features for roosting develop (Mortimer, 2006; Russo et al., 2010). Clear felling can result in the removal of all potential roost

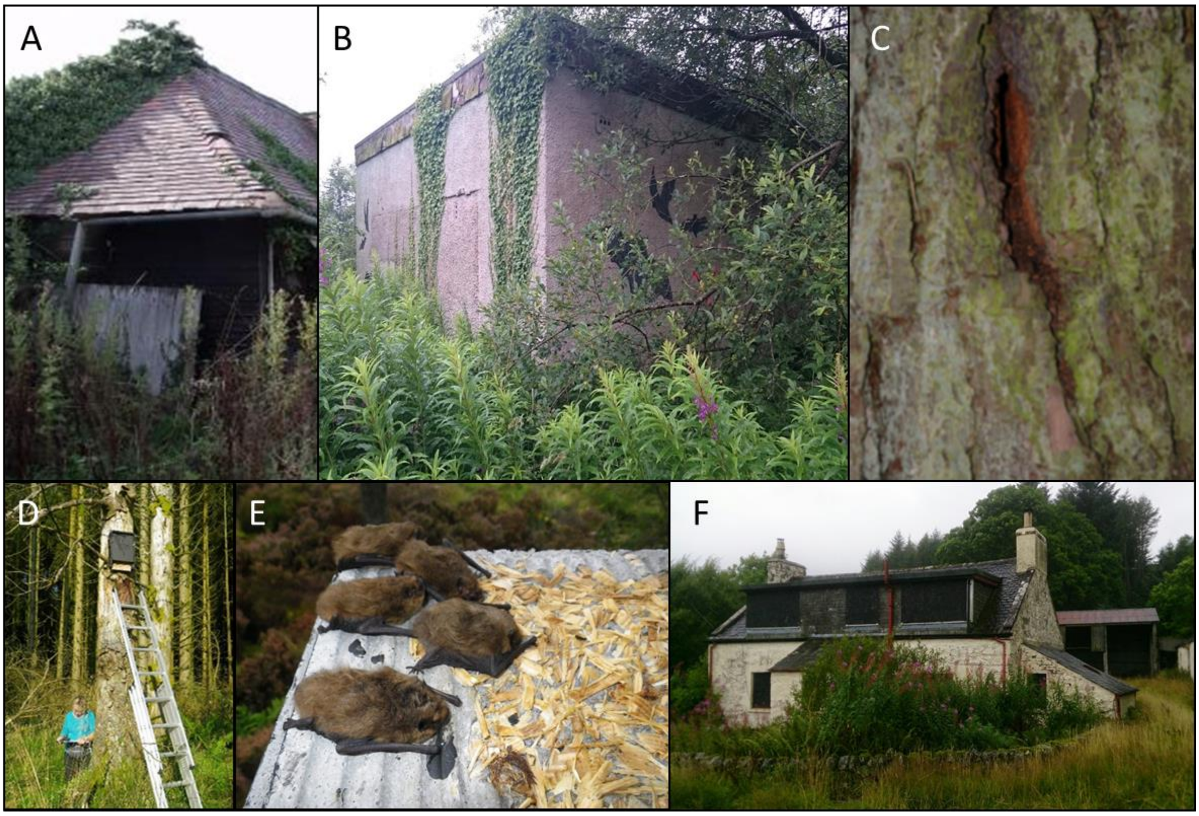

Figure 1.5: *Examples of potential roost sites in plantations. (A) abandoned barn, (B) Converted substation (Galloway), (C) Example of split / double leader in Pinus nigra, (D) Artificial bat box (installed in Galloway Forest as part of this work), (E) Harem of P.pygmaeus bats found in artificial box, (F) boarded up building in the plantations. Large maternity colony found underneath the black boards covering the windows.*

trees within a colonies home range (Borkin et al., 2011). As many bat species show high fidelity to roost areas (Borkin et al., 2011; Elmore et al., 2005), the loss of a number of roost trees can lead to reductions in colony size (Borkin et al., 2011; Farrow and Broders, 2011) and force bats to use less appropriate roosts (Arnett, 2007). Ensuring that large, over-mature or deciduous trees are maintained in plantations will benefit a range of bat species as appropriate roosting features are more likely to have developed in such trees (Charbonnier et al., 2016; Mazurek and Zielinski, 2004). Forestry operations may also cause direct mortality if they result in the felling of trees with a bat roost inside (Borkin et al., 2011). Therefore, further knowledge is required to assess the extent to which bats associate with commercial plantation tree species, in order to avoid potential mortality. For example, although commercial conifer trees are considered unlikely to develop features appropriate for roosting, *Myotis nattereri* use *Pinus nigra* stands in Eastern Scotland (Mortimer, 2006) and both *Nyctalus noctula* and *N. leisleri* roost within managed stands in Bialowieza Forest (Ruczyński et al., 2010), potentially putting bats at direct risk of mortality due to forestry operations. If forestry practices reduce the abundance and quality of potential roost sites within the landscape, bats may adapt by increasing their home range (Popa-Lisseanu et al., 2009), forming larger colonies, become less selective in roost choice or relocate to another area (Borkin and Parsons, 2011; Ciechanowski, 2015; Elmore et al., 2005). However, little is currently known on how plantation forestry influences this.

1.10 Foraging opportunities in plantation forests:

The extent to which bats can forage efficiently within plantations will vary between species and guilds. At the local scale, foraging in plantation forests will be affected by the physical structure of the stand, but the mosaic of different aged stands within a plantation landscape may provide adequate foraging habitat for a range of different bat species. Bats which forage within forests must negotiate a structurally complex environment. This structural forest clutter is both physical clutter and potential acoustic clutter (Jung et al., 2012) which may make it difficult for the bat to differentiate, identify and localise prey against disruption from background echoes (Schnitzler and Kalko 2001). Bat activity in forest stands is positively associated with measures of structural heterogeneity which describe old growth forests with patches of different vegetation height (Jung et al., 2012). However, if stand density, and therefore structural complexity is too high bat activity will be low regardless of invertebrate availability (Adams et al., 2009; Bender et al., 2015; Blakey et al., 2016; Cistrone et al., 2015; Cox et al., 2016; Dodd et al., 2012; Patriquin and Barclay, 2003). Commonly, bat use of commercial coniferous landscapes is considered low due to a lack of invertebrate prey (Boughey et al., 2011; Haupt et al., 2006; Walsh et al., 1996) but both mature and felled stands are important sources of invertebrate prey (see section 3.1). Stand edges provide protection from the wind for weak flying Diptera, act as windbreaks collecting airborne insects blown in from adjacent open or felled areas and provide protection from predators (Baker et al., 2013; Nicholls and Racey, 2006a; Verboom and Spoelstra, 1999). Therefore, patches of clear felling within plantations may provide foraging habitats for both open and edge adapted bat species (Dodd et al., 2012; Elmore et al., 2005; Grindal and Brigham, 1998; Heer et al., 2015; Hein et al., 2009; Loeb and O'Keefe, 2011; Patriquin and Barclay, 2003; Pauli et al., 2015; Rodríguez-San Pedro and Simonetti, 2014), although the size of the clearcut is likely to be important (Grindal and Brigham, 1998; Loeb and O'Keefe, 2011). Finally, linear features through plantations such as roads and tracks are positively associated with bat activity. Linear features combine low structural complexity with prey provision, shelter from predators and high invertebrate abundance (Brigham, 2007; Hein, 2008; Hein et al., 2009; Owen et al., 2004). Riparian corridors are also commonly used both as foraging habitats and navigational aids by commuting bat species, as well as providing water (Buckley et al., 2012; Davidson-Watts et al., 2006; Nicholls and Racey, 2006a; Vindigni et al., 2009; Warren et al., 2000).

1.11 Nocturnal invertebrates and moths

The availability and spatial distribution of invertebrate prey is a key driver of bat abundance and distribution (Dodd et al., 2012; Fukui et al., 2006). Therefore, understanding the factors that influence prey distribution is important for improving plantation management for bat species.

1.11.1 Impact of plantation management on invertebrates:

Invertebrates are important components of ecosystem functioning and play a critical role in pollination, nutrient cycling, and biological control. Three main invertebrate orders form a substantial component of bat dietary requirements, Lepidoptera, Diptera and Coleoptera (Vaughan et al., 1997). Dipteran diversity in plantation landscapes is positively related to vegetation characteristics, for example, a higher diversity and abundance of dipteran detritivores was seen in spruce plantations if *Fagus* (beech) spp. were included in the tree species mixture (Elmer et al., 2004), while overall dipteran diversity was highest in open canopy stands and at stand edges (Allgood et al., 2009). Open areas, especially patches of shrub succession, and increased structural heterogeneity within forest stands will all contribute to increasing dipteran diversity in plantation landscapes (Felton et al., 2010; Jukes et al., 2001; Lin et al., 2006) and also support both open specialist and generalist carabid beetle species (Lin et al., 2006). In contrast, forest specialist species will persist in older forest stands (Lange et al., 2014). In older stands, increased canopy gaps allow the regeneration of the ground vegetative layer, which acts as both a food source and shelter for a wide diversity of invertebrate species (Spake et al., 2016), which is lacking in dense plantations

(Magura et al., 2000). To some extent, invertebrate populations in plantations will reflect the previous land use prior to planting and the wider landscape (Lin et al., 2006; Magura et al., 2000). However, plantations in previously forested areas do not support a similar diversity to native forests, for example, many native forest carabid species are strongly associated with deciduous leaf litter cover which is lacking in plantation stands (Magura et al., 2000; Pedley et al., 2014; Woodcock et al., 2003). Small, fragmented invertebrate populations of native forest species are at greater risk of extinction if patches of native forests are too small to maintain viable populations (Magura et al., 2000), particularly as many forest specialist species are smaller and less dispersive than open specialist species (e.g. Carabidae, Spake et al., 2016). However, if plantations are planted in predominantly heathland or open areas, there is some evidence that open specialist heathland carabid and arachnid communities persist throughout the forestry cycle (Lin et al., 2006; Oxbrough et al., 2010).

Lepidoptera comprise a relatively conspicuous invertebrate group which are easy to both sample and identify. Moths (night active Lepidoptera) have undergone severe, substantial declines in recent decades, both in the United Kingdom (Conrad et al., 2006; Fox et al., 2013; Thomas et al., 2004) and elsewhere in Europe (Franzén and Johannesson, 2007; Mattila et al., 2006; Uhl et al., 2015). Rapid economic development, urbanisation, changes to silvicultural management and agricultural expansion have all been implicated in causing these declines (Conrad et al., 2006; Fox et al., 2013). Taken together, these studies provide overwhelming evidence that moths are facing declines on a large geographic scale, across a range of habitats and mirror similar effects found in fewer species-rich groups such as butterflies and bumblebees (Goulson et al., 2008; Warren et al., 2001). Although changes in silvicultural practices have been suggested as a major driver behind lepidopteran declines very few studies have explicitly explored the impact of commercial coniferous plantation management on moth abundance and diversity (Luque et al., 2007), while to the best of our knowledge no studies have involved non-native commercial plantations. Therefore, little is known about the impacts of timber harvesting in intensively managed non-native plantations. In native forest systems, felling significantly disrupts moth communities (Summerville, 2014; Summerville and Crist, 2002), with impacts persisting for more than 60 years post harvesting (Summerville et al., 2009). Impacts of felling are less severe if less intensive timber extraction methods are used (Summerville, 2013). However, the extent to which this is true for non-native plantations remains to be seen.

1.12 Measurements of biodiversity

In order to assess the impacts of anthropogenic habitat alteration on biodiversity, practitioners need to be able to accurately and effectively assess biological diversity. Comparable measures of diversity are vital to answer crucial questions about how diversity has arisen, and how we may best act to conserve it (Purvis and Hector, 2000). Many measures of diversity rely on the “species concept” (Agapow et al., 2004), which in itself has inherent difficulties. Defining species based on the “biological species concept” is one of the most popular and easily understood approaches, but is fundamentally undermined by the natural and substantial production of fertile hybrids across species boundaries (Agapow et al., 2004). Nevertheless, the assessment of species richness (a count of the number of individual species) is a common, and easily understood approach to assessing diversity (Agapow et al., 2004; Purvis and Hector, 2000) and is widely used in biodiversity assessments, even if it is not always the optimal measure (Mori et al., 2013). Counts of species richness simply assess the number of species present in a habitat (alpha diversity). As the size of the area being assessed increases, it is likely that species richness will increase as a function of the change in sampling effort, as more species are sampled (Hill, 1973). Additionally, rare species are given as much weight as abundant species, rare species may contribute little to ecosystem functioning. Other common metrics partition abundance between different species, and therefore quantify different aspects of diversity, such as Shannon’s entropy (which is a measure of dominance and insensitive to rare species) and Simpson’s index (which is a measure of evenness and wholly insensitive to rare species).

A major problem with both Shannon’s entropy and Simpson’s index, however, is that they are indices, rather than true numbers, and therefore do not accurately reflect changes in diversity and behave as one would intuitively expect (Jost, 2007). This is particularly true in ecosystems of high diversity where cases of mass extinction may barely alter their values (Jost, 2007; Jost et al., 2010). For example, if a continent with 30 million equally common species undergoes a catastrophic event, losing half of its species, the loss of species richness is 15 million, or 50%. However, if the same calculations are done for Shannon’s Entropy, the loss is 4%, and for Simpson’s Index, the loss is 0.000003% (Jost, 2007). Therefore, losses of diversity measured using Shannon’s Entropy or Simpson’s Index do not reflect actual losses, and comparisons between indices are meaningless.

Converting diversity indices to “numbers equivalents” makes them behave intuitively, so that changes in the numbers equivalent of Shannon’s entropy (the exponential of Shannon’s entropy) and Gini – Simpson’s index (subtract from unity and take the reciprocal) reflect actual changes in diversity (Hill, 1973; Jost, 2007). Hill numbers, (first derived in relation to Shannon’s entropy, Hill

1973, but since extended to cover a range of diversity measures, Jost 2006) provide an easily interpreted measure of diversity with differing sensitivity to abundances. If the example above is calculated with numbers equivalents than the commonly used diversity indices, the results are far more intuitively sensible. Species richness is in itself a numbers equivalent, so a change in species richness from 30 to 15 million results in the expected 50% loss in diversity. However, if we calculate the numbers equivalents for both Shannon's Entropy and the Gini – Simpson index, the change in diversity accurately reflects the real life situation. Therefore, where previously diversity calculations could be misleading, as the change in diversity between two habitats could differ as a result of the measure used rather than reflecting actual change, numbers equivalents more accurately represent the actual changes in diversity that have occurred (Chao et al., 2014; Jost, 2007, 2006; Leinster and Cobbold, 2012).

Regardless of which biodiversity metric is used, they all assume meaningful delineations between species, which may not necessarily be true (Hooper et al., 2002). Not all species are equally distinct from each other (Chao et al., 2014; Leinster and Cobbold, 2012); all else being equal an assemblage of species that are highly divergent is more diverse than an assemblage of similar species (Chiu and

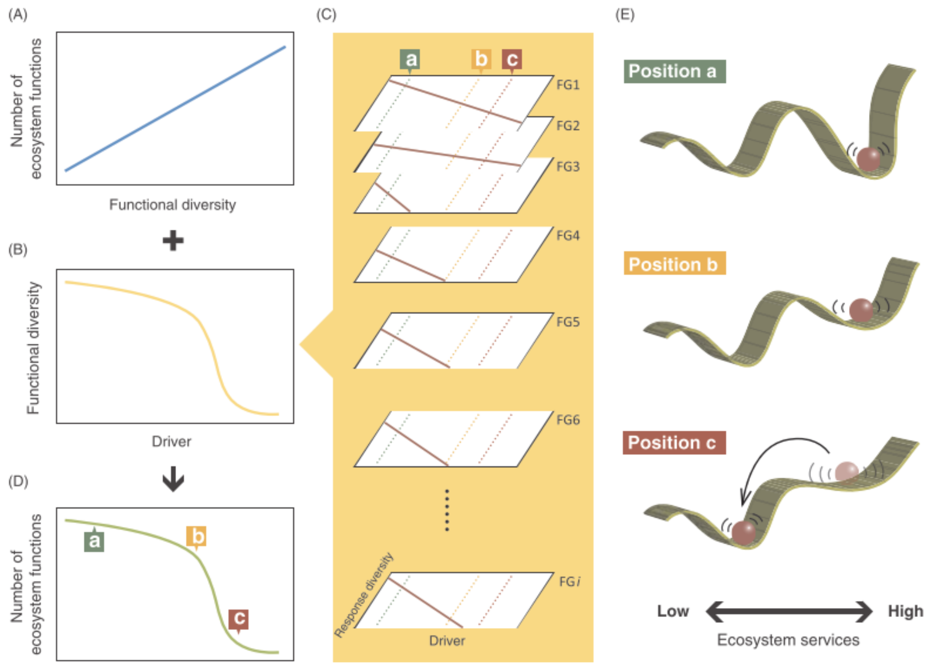

Figure 1.6: Relationship between anthropogenic pressures (driver), functional diversity, response diversity and ecosystem state, showing that accumulated loss of response diversity mediates an abrupt shift in ecosystem state triggered by decreased functional diversity. (A) Relationship between functional diversity and number of ecosystem functions. (B) Non linear change in functional diversity with increasing pressure. (C) Relationship between response diversity and driver intensity for a series of functional groups (FG). (D) Non linear change in number of ecosystem functions with increasing pressures. (E) Basic ball and cup model of ecosystem resilience. Cups represent attractors (right, desirable; left, undesirable into which the ball (ecosystem) is drawn. Positions A – C in E correspond with the same letters in panels C and D. From Mori et al., 2013.

Chao, 2014). Increasingly, attention is turning towards measures of functional, phylogenetic and genetic diversity (Laliberté and Legendre, 2010) which offer a more mechanistic understanding of ecosystems than simply using patterns of species diversity (Hooper et al., 2002). Quantifying genetic diversity is appropriate for communities where species delineations are unclear (e.g. microbial communities; Veresoglou et al., 2014). Using phylogenetic diversity will incorporate evolutionary histories (Chalmandrier et al., 2014), while using functional traits will allow assessments of ecosystem health and functioning (Chao et al., 2014; Hooper et al., 2002). The assumption is that by including a variety of different morphological, phenological, biochemical, morphological and behavioural traits that influence an organism's ability to reproduce, acquire resources, disperse and persist in the environment (Hooper et al., 2005; Spake et al., 2016), it is possible to gain a better understanding of the mechanisms by which communities respond to environmental change and provide ecosystem services (Spake et al., 2016; Standish et al., 2014). While the extinction of a species is important, declines in the number of individuals in local populations and consequently changes to the composition of species in a community will cause the greatest impacts on ecosystem function (Dirzo et al., 2014; Mori et al., 2013). If this occurs, ecosystems can undergo a state change from which recovery to pre-disturbance levels is hard (Figure 1.6; Mori et al., 2013). Functional groups are defined as sets of species which either have similar "responses" to the environment (response traits) or have similar "effects" on their environment (effect traits, Díaz and Cabido, 2001). Different species often have similar effects on ecosystem processes when a single function is considered under one set of environmental conditions (Díaz and Cabido, 2001; Mori et al., 2013). This functional redundancy plays a vital role in sustaining the functionality of ecosystems during environmental perturbation, as the extinction of a particular species can be compensated for by the growth of another species with similar functional effects. However, if disturbance moves beyond a tipping point, with "keystone" species (species whose impact on the ecosystem is large relative to their biomass; Davic, 2003), or too many species in a particular functional group are lost then the functional diversity of that system will decline (Figure 1.6 B). Eventually, if disturbance persists, the loss of ecosystem services will cause the transition from a stable community with high functional diversity to an impoverished community with low diversity and resilience (figure 1.6 E). Measures of functional diversity such as response diversity and redundancy may therefore act as proxy measures of resilience, particularly if multi-trait measures are used, which will capture a more comprehensive view of the complex ecosystem processes maintaining ecosystem states (Elmqvist and Folke, 2003; Laliberté and Legendre, 2010; Mori et al., 2013; Standish et al., 2014). As shown in Figure 1.6, an ecosystem with high functional redundancy and extensive connectivity across multiple scales will be more resilient to habitat degradation and fragmentation than an adjacent ecosystem with low functional redundancy and limited connectivity across scales (landscape insurance hypothesis; Tscharntke et al., 2012).

1.13 Study aims and thesis outlines

There is growing recognition that plantation landscapes have a role to play in conserving biodiversity, although taxon-specific guidance is still lacking in many cases. The area of plantation land cover is predicted to increase substantially in the future (FSC, 2012), and interest in ensuring sustainable plantation management is also growing (Brockerhoff et al., 2008; Maes et al., 2011). Substantial incentives now exist to ensure that plantation management meets various ecological criteria but in order to be effective, plantation managers need information on taxon-specific abundance, diversity, and relationship to stand features. Bats present a particular challenge in plantation landscapes; all bat species are protected in the United Kingdom (Wildlife and Countryside Act 1981 (as amended)), and destruction of a roost site regardless of whether the roost had previously been identified is illegal. Therefore there is a pressing need to determine how bats use plantation landscapes (Russo et al., 2016). Furthermore, the potential contribution of plantation landscapes to lepidopteran diversity is yet to be explored, despite the implication that afforestation of non-native plantations is a likely driver of widespread moth declines (Conrad et al., 2006; Fox et al., 2013). This thesis aims to address these knowledge gaps.

In particular, this thesis aims to:

- Assess bat use of commercial coniferous plantations at both the local and the landscape scale, relating bat activity and abundance to both stand and landscape scale features (Chapter 2). This will inform forest managers of how bat activity varies throughout the life cycle of a plantation.
- Investigate the impact of felling and remnant patches of broadleaf tree cover on moth abundance, richness, and diversity (Chapter 3).
- Extend the findings of chapter 3 by exploring the use of alternative biodiversity metrics when assessing the impacts of disturbance. Moth taxonomic and functional richness and diversity will be compared between broadleaf woodlands and plantation sites to allow comparison of moth species in plantation forest compared to surrounding broadleaf woodland (Chapter 4).
- Investigate the immediate impact of clear fell harvesting on bats in commercial coniferous plantations (Chapter 5).
- Quantify use of plantations by individuals using radiotracking, in order to identify features important for foraging, roosting and social behaviour (Chapter 6). This will provide important

information for forest managers about bat use of predominantly Sitka spruce plantations, and reveal fine-scale associations with plantation features.

- Compare bat abundance, activity and behaviour between plantation and broadleaf sites. This provides the context of bat activity in plantation landscapes compared to the surrounding area (Appendix 1).

Information from each chapter is related to implications for plantation forest and management, with and recommendations for changes to plantation management that will benefit both bat and moth species are made.

Chapter 2 Bat use of commercial coniferous plantations at multiple spatial scales: Management and conservation implications

View from one of the field sites in Galloway showing a range of different stand types

An adapted version of this chapter has been accepted for publication as:

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2.1 Abstract

Commercial plantations are primarily managed for timber production and are frequently considered poor for biodiversity, particularly for mammalian species. Bats, which constitute one-fifth of mammal species worldwide, have undergone large declines throughout Europe, most likely due to widespread habitat loss and degradation. While bat use of modified landscapes such as urban or agricultural environments has been relatively well studied, intensively managed plantations have received less attention, particularly in Europe. I assessed three of the largest, most intensively managed plantations in the UK for the occurrence of bats, activity levels, and relative abundance in response to environmental characteristics at multiple spatial scales, using an information theoretic approach. I recorded or captured nine species; *Pipistrellus pipistrellus* and *P. pygmaeus* were the most commonly recorded species on acoustic detectors and female *P. pygmaeus* were the most commonly captured. The influence of environmental characteristics on bat activity varied by species or genus, although all bat species avoided dense stands. Occurrence and activity of clutter and edge adapted species were associated with lower stand densities and more heterogeneous landscapes whereas open adapted bats were more likely to be recorded at felled stands and less likely in areas that were predominantly mature conifer tree cover. In addition, despite morphological similarities, *P. pipstrellus* and *P. pygmaeus* were found foraging in different parts of the plantation. This study demonstrates that with sympathetic management, non-native conifer plantations may have an important role in maintaining and supporting bat populations, particularly for *Pipistrellus* spp.

2.2 Introduction

Unsustainable exploitation of native forests is considered one of the greatest threats to biodiversity and has led to the fragmentation and degradation of forests worldwide (Anon., 2011). Demand for wood-based products is likely to increase in the future and there is a growing need for this to be met by sources other than primary forests. Plantation forests, defined as cultivated forest ecosystems established by planting and/or seeding in the process of afforestation and reforestation, are economically important worldwide as sustainable sources of wood fibre become more necessary (Carnus et al., 2003). Widespread historical deforestation, post-war planting initiatives and a need for wood products meant many countries established plantations during the 20th Century. Globally, plantation forests cover 54.3 million hectares with regions such as the US, Japan, Oceania, and Europe accounting for more than 50% of plantation areas, and demand for wood products is predicted to increase (FSC, 2012; Honnay, 2004). Due to their lack of structural complexity, intensive management, and often single or low species composition, plantations are often considered to be devoid of biodiversity (Bremer and Farley, 2010) although there is evidence that for some taxa this is not the case (Humphrey et al., 2003).

Maintaining and restoring biodiversity is a key tenet in sustainable ecosystem management, the paradigm currently guiding habitat management practices across Europe, North America and Australasia (Ober and Hayes, 2010; Paquette and Messier, 2009). This is driven by concern about worldwide declines in species and populations across a range of taxa (Dirzo et al., 2014) and recognition that much of this is driven by habitat loss and fragmentation, caused by anthropogenic change (Thomas et al., 2004). In many countries, the timber industry has responded by shifting focus from purely timber production to one which encourages sustainable practices that promote both wildlife conservation and sustainable timber yields (FSC, 2012). In Europe this has been driven by policy change initiated as a result of the Convention of Biological Diversity, requiring explicit consideration of environmental, economic and social objectives and a multi-purpose approach to forestry (Watts et al., 2008)

Previous studies have suggested that species diversity will be positively influenced if management operations such as felling mimic natural disturbances, for example by creating multi-aged rather than even-aged plantations (Bardat and Aubert, 2007). Multi-aged forest systems can support a higher diversity of species through the provision of different habitats for a wide range of flora and fauna, from those reliant on early successional habitats e.g. some songbirds (Sweeney et al., 2010) to species dependent on mature habitats e.g. canopy dwelling Coleoptera (Ohsawa, 2007). As a result, many forest managers are moving away from practices such as clear felling (the removal of all trees within a stand) to more targeted harvesting approaches such as continuous cover forestry (Lindenmayer and Hobbs, 2004; Pawson et al., 2006). Other forest management practices such as retention of stands with longer rotations, leaving dead wood (Humphrey et al., 2003) and restructuring plantations have had positive impacts for a wide range of taxa (e.g. Oxbrough et al. 2010).

Bats have undergone major historical declines across many temperate regions, in part due to widespread habitat loss (Walsh et al., 1996). The majority of temperate bat species rely on forest for at least part of their life cycle (Altringham, 2013), but while bat associations with native woodlands are well established (e.g Boughey et al., 2011; Dietz et al., 2009), less is known about their use of plantation habitats. This paucity of research is perhaps in response to many habitat studies showing active avoidance of plantations by individual species (Boughey et al., 2011; Russo and Jones, 2003; Smith and Racey, 2008; Walsh et al., 1996). However, there is growing evidence from Europe (Charbonnier et al., 2016; Cistrone et al., 2015; Cruz et al., 2016; Mortimer, 2006; Pereira et al., 2016; Russo et al., 2010), New Zealand and Australia (Borkin et al., 2011; Borkin and Parsons, 2011; Burgar et al., 2015) and North America (A D Morris et al., 2010; Patriquin and Barclay, 2003) that suggests that bat use of plantations may be more widespread than previously assumed. While management for biodiversity and protection of European Protected Species is a key requirement for European forestry management (Boye & Dietz 2005), the lack of broad scale studies in European plantation forests means that there is currently insufficient information for forest managers to ensure sufficient and appropriate mitigation is carried out (Russo et al., 2016). Understanding whether there are general patterns that underpin how highly mobile species make use of plantations may be an important strategy for protecting against future species declines.

Here, I examine the extent to which bat species use plantation forests in northern Britain by assessing the influence of various environmental characteristics on bat abundance and activity at multiple spatial scales. Specifically, my objectives were to:

1. Assess the composition of bat populations in commercial coniferous plantations.
2. Identify local and landscape scale variables which influence occurrence, abundance, and activity, and how this varies between species.
3. Compare how two morphologically similar species (*Pipistrellus pipistrellus* and *P. pygmaeus*) respond to plantation characteristics.
4. Use these findings to give appropriate management recommendations.

Nine of the seventeen species resident in Britain occur within the study area, including *Myotis*, *Nyctalus* and *Pipistrellus* spp. These can be categorised into different foraging "guilds", bats with similarities in morphology, hunting technique and echolocation call structure (Schnitzler et al., 2003). Bats in the genus *Nyctalus* forage primarily in open spaces (open adapted) compared to *M. nattereri* (clutter adapted) or *P. pipistrellus* (edge adapted) and are therefore likely to respond differently to both local and landscape-scale characteristics. *Pipistrellus pipistrellus* and *P. pygmaeus* are of particular interest as they are common, sympatric species which share morphological and dietary similarities (Barlow, 1997) and may use habitat selection as a mechanism for resource partitioning.

2.3 Methods

The study was conducted in three plantation forests in Central and Southern Scotland and Northern England (Figure 2.1). I chose forests for their large size (ranging from 30,000 ha in Cowal and Trossachs to 60,000 ha in Kielder and 114,000 ha in Galloway), high productivity and the predominance of *Picea sitchensis* (Sitka spruce), the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each forest, multiple sites

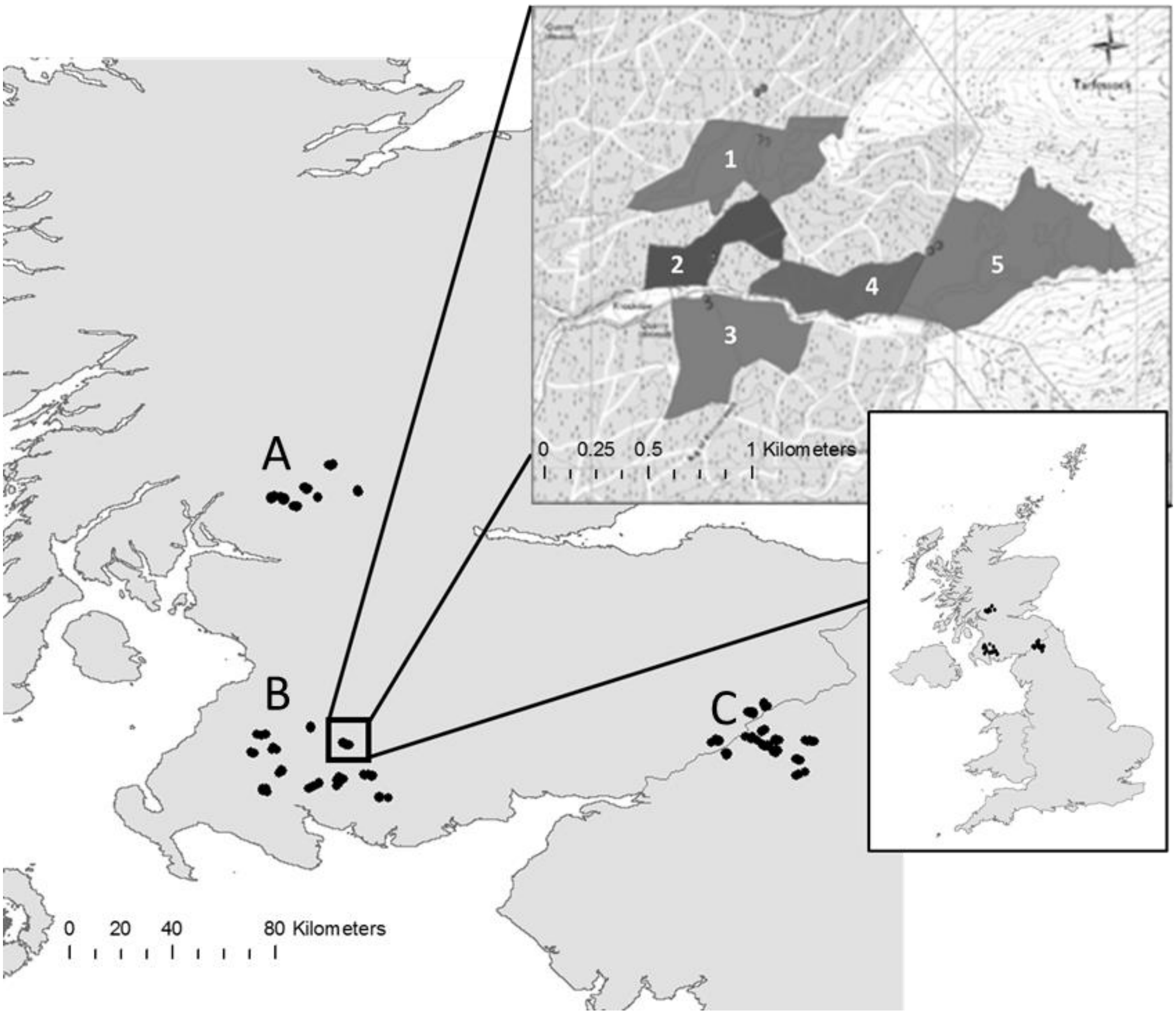


Figure 2.1: Location of field sites at three different study areas in (A) Cowal and Trossachs, South West Scotland, (B) Galloway, South West Scotland and (C) Kielder, Northern England. Stand types were as follows: Clearfell (felled less than 5 years ago, 1), Young (planted between 5 and 10 years ago, 2), Thicket (planted between 10 and 20 years ago, 3), Thin (planted between 20 and 40 years ago, 4), Mature (planted more than 40 years ago, 5).

were selected using a Forestry Commission sub-compartment database within a Geographic Information System (GIS) (ArcMap 10.1, ESRI) based on stand age and species composition (Figure 2.1).

In total, seven sites were surveyed in Cowal and Trossachs, 12 in Galloway Forest and 12 in Kielder Forest. Where possible, a stand of trees at each management stage (from a total of six management stages: see appendix 2.1) were selected in each site, which was a maximum of $2km^2$ in size and at least 4km from another site. Not all sites had all stands of each management stage resulting in an unbalanced design of between four and six stands per site and a total of 285 stands across 31 sites (Figure 2.1).

2.3.1 Bat abundance surveys

For some species identification from echolocation calls is not possible (Schnitzler et al., 2003), therefore capturing individuals for inspection in the hand can be the only way to confirm species occurrence while also allowing confirmation of reproductive status (Hill and Greenaway, 2005). I assessed relative bat abundance (number of captures per site) by placing an Austbat harp trap (2.4 x 1.8m) and three Ecotone mist nets (2.4 x 6m) at one location in each site to trap bats. The location was selected based on ease of access and nets were placed across potential flight lines (e.g. tracks or rides) between either two mature stands or extending from the edge of a mature stand into felled stands. Nets were placed at least 50m from each other, with placement dictated by the plantation structure and deliberately chosen to maximise capture rates. I used an acoustic lure (The Autobat, Sussex University, Brighton, UK) with four different synthesised bat calls (*Pipistrellus* spp mix, a mixture of *Myotis* sp., *Nyctalus leisleri* and *M. nattereri*), which has been demonstrated to greatly improve capture rates (Hill and Greenaway, 2005) and attracts a variety of different bat species present in the study area (following Lintott et al. 2014). Each call was played at each trap for 15 minutes, with the lure moved between traps every 30 minutes. Traps were checked every 15 minutes and any captured bats were identified to species, weighed, measured, aged, sexed, assessed for reproductive status and marked temporarily by fur clipping. All captures were carried out under licences 19584 and 20131093 (Scottish Natural Heritage, Natural England)

2.3.2 Bat acoustic surveys

All surveys were carried out between 12th June and 3rd September 2013. I surveyed all the stands within a site simultaneously and for a single night, starting 30 minutes after sunset ensuring that recorded individuals would be actively foraging rather than commuting from roosts. Surveys finished 4 hours later as this represents the length of the shortest night in this area during summer. Bat activity was quantified using a SongMeter SM2 Bat+ (Wildlife Acoustics, Inc., Concord, MA) using two microphones, at a height of 1m and positioned at a 45 degree angle. One microphone was placed at the stand edge pointing towards adjacent tracks or rides; the other was positioned 20 – 40m into the trees (depending on ease of access) pointing towards the stand interior, allowing simultaneous recording of both the stand edge and interior.

2.3.3 Bat call analysis

All calls were converted using zero crossing and analysed in AnalookW (Corben, 2006). Any calls which were unclear were checked in Batsound (Pettersson Elektronics AB, Upsala) using a sample frequency of 44,100 samples / second, 16 bits/sample and an automatic FFT with a Hanning window. I identified all calls manually to species or genus and counted the number of bat passes (defined as at least 2 echolocation calls within one second of each other) resulting in a measure of activity per four-hour recording period at each stand edge and interior. *Pipistrellus* species can be separated due to differences in the end frequency of the call (Fc = frequency of the right hand end of the flattest part of the call; Russ, 2012) and the call shape. Bats in the genus *Myotis* have a similar call structure and as such were identified only to genus. It can be difficult to distinguish between *Nyctalus* calls in cluttered environments (Schnitzler et al., 2003), so again these were only identified to genus. *Plecotus auritus* have very quiet calls, so their occurrence will be underestimated by using acoustic recordings alone. Due to low activity levels of *Nyctalus* and *Myotis* species I was unable to analyse activity and assessed presence / absence instead.

2.3.4 Local habitat characteristics

I carried out vegetation surveys in two 0.01 ha plots around each microphone point within two weeks of bat surveys. Due to the homogenous nature of stands these plots were considered representative of the stand as a whole. At each plot I recorded the total number of trees with diameter at breast height greater than 7 cm (stand density) and recorded what the dominant ground cover was according to the following structural categories: bare, needle, moss, grass, tussock, bracken, flowering plant. I also recorded the total number of standing dead trees (snags) in each plot as these can be associated with higher species richness and abundance of a variety of taxa in managed forests and provide potential roost sites for bats (Elmore et al., 2005), however it was very rare to see standing dead wood that was appropriate for bat roosts at any of our study sites. I assessed the amount of dead wood on the forest floor using the following scale: 0 – no coarse woody debris, 1 – small twigs, 2 – large twigs and branches over 7cm in diameter, 3 – both large and small branches. Understory vegetation height (defined as all ground vegetation not including trees) was measured at 10 evenly spaced points across the radius of the circle and canopy cover was recorded at each point using a sighting tube with an internal crosshair; if the crosshair intersected with any canopy vegetation presence of canopy cover was recorded and converted to a percentage cover score (Lintott et al., 2015). I also recorded stand age (as years since planting).

2.3.5 Landscape analysis

I used ArcMap 10.1 to determine landscape scale features within 250, 500, 1000, 2000, 3000 and 4000m of the centre point of each site. The smaller scale allows the extraction of site-specific characteristics whereas the larger scale reflects the home range of low and intermediate vagility species such as *P. pygmaeus* (Lintott et al., 2015). Data from the OS Mastermap (EDINA, 2014) was combined with a high resolution Forestry Commission database specific to the study areas to reclassify the landscape within each specified distance into the following eight categories: 1. Human infrastructure (e.g. buildings), 2. Felled (recently felled or conifers < 5 years old), 3. Broadleaf trees, 4. Thicket conifer (between 5 and 20 years old), 5. Closed canopy conifer (> 20 years old), 6. Water (tidal or inland), 7. Open (heathland, upland areas, scree), 8. Tracks and roads. Fragstats 4.2 (Mcgarigal, 2014) was used to calculate the proportion of land covered by each category and Shannon's diversity index (a measure of landscape heterogeneity which increases as the number of different patch types increases) within each buffer. Additionally, the Largest Patch Index (a measure of habitat dominance, LPI is the percentage of the landscape comprising the largest patch of any of the habitats outlined above), Euclidian Nearest Neighbour distance (ENN, mean value of ENN distances between all patches of type in a landscape), and total Edge Density (ED, the sum of the lengths of all stand edge segments divided by the total landscape area) were calculated as previous studies have shown these influence bat foraging activity (Fuentes-Montemayor et al., 2013; Lintott et al., 2015). Additional features were measured as proxies for either water, roost or food availability (Hayes and Loeb, 2007), the full list of local and landscape variables considered in analyses is outlined in appendix 2.2.

2.3.6 Statistical analysis

All analysis was carried out in R Studio using R version 3.2.2 (R core development team) with the lme4, effects, MuMIn, ggplot2, arm and glmmADMB packages. Analysis involved four stages:

1). To select the ***local characteristics*** I constructed species- or genus-specific models which explained variation in bat responses (occurrence, activity or abundance of each species or genus separately) between stands. A generalised linear mixed effect model (GLMM) with site nested in forest as a random effect was used to account for differences due to geographical location, with the error structure dependent on the species or genus being tested (see step 4 for more details). I tested models consisting of either stand type or quantitative descriptors of stand type (e.g. stand density, % canopy cover, supplementary data, appendix 2.2), selecting those with the highest F-statistic to be entered into the maximal model (step 4).

2). To select the ***landscape variables*** to be entered into the maximal model I tested land cover type parameters (e.g. proportion of land cover and LPI, appendix 2.2) at multiple spatial scales (250m – 4km; see section 2.5) on bat response variables (occurrence, activity or abundance of each species or genus separately) using linear regression models as no random factor was required. Individual models for each landscape parameter at each scale were performed and R^2 values calculated to quantify the amount of variation in the data explained; the variables with the highest R^2 at the relevant scale were chosen for inclusion.

3). All predictor variables selected for inclusion in the maximal model were tested for collinearity, retaining those which were not collinear (Pearson's correlation < 0.5). See appendix 2.3 for description of model construction.

4). ***Maximal models***; all continuous predictors included in the maximal models were scaled and centred around a mean of zero with a standard deviation of 1 to allow direct comparisons between the estimates regardless of differences in scale. All possible combinations of variables within the maximal model were ranked using Akaike's Information Criterion adjusted for small samples (AICc) (Burnham and Anderson, 2002). Model fit was assessed using change in AIC and Akaike weights. As there was no single best model (change in AIC greater than 4), I accounted for model uncertainty by computing model averaged predictions and standard errors across the models retained within a 95% Akaike weights confidence set (Burnham and Anderson, 2002). The full model averaged coefficients with shrinkage are presented to reduce model selection bias from parameters which do not appear in all the "best" models (Burnham and Anderson, 2002). Where possible, the marginal R^2 is presented following Nakagawa & Schielzeth 2013, which quantifies the proportion of variance explained by the fixed effects without considering the random effects. Predictions from model outputs are given as means with 95% confidence intervals. Using a mixed effect generalised linear modelling approach allows us to account for a lack of independence between stands within sites, while controlling for other influential variables, and the model averaging approach allows assessment of the influence of variables across multiple models when no single best model is found.

I only modelled abundance for *P. pygmaeus,* as I caught insufficient numbers of other bat species. *Pipistrellus pygmaeus* abundance was modelled using a Poisson distribution, *P. pygmaeus* and *P. pipstrellus* activity using negative binomial distributions, and *Nyctalus* and *Myotis* occurrence using binomial GLMMs (objective 2) as activity was low for these species. R^2 was used as a measure of explanatory power for all models except those with negative binomial error distributions, for which I used F statistics.

I assessed differential responses to plantation management for the two *Pipistrellus* spp. due to an ecological interest in understanding how morphologically similar species may partition resources (objective 3). I used a GLMM with a binomial distribution to determine the relative effects of landscape and local characteristics on *P. pygmaeus* in comparison to *P. pipistrellus.* The model was run with the proportion of *P. pygmaeus* to total identified *Pipistrellus* passes at each stand location. An equal proportion of *P. pipistrellus* and *P. pygmaeus* passes indicates stands where activity was similar and unequal proportions where one species dominates compared to the other. After examining the data, I included an interaction between stand type and distance with water, in addition to other measures as previous work has shown *P. pygmaeus* have a preference for riverine habitats compared to *P. pipistrellus* (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006a). I also included stand age as a quadratic term to allow for a non-linear relationship and an interaction between temperature and altitude as bats may forage at higher altitude in warmer weather. In summary, models were constructed for the following bat responses: *P. pygmaeus* abundance; *P. pygmaeus* and *P. pipistrellus* activity (passes per four hour period); occurrence of *Myotis* and *Nyctalus*; proportion of *P. pygmaeus* to *P. pipistrellus* activity. Finally, I tested the influence of the acoustic lure on our bat capture rates using Wilcoxon's paired test.

2.4 Results

2.4.1 Bat use of commercial coniferous plantations

I caught a total of 85 bats between May and August 2013 (sites = 31, Table 2.1); capture rates were considerably improved by use of an acoustic lure (Wilcoxon's paired test, n= 31, w = 665, p = 0.006). Over 80% of bats were *P. pygmaeus* (41 adults, 28 juveniles). Of the adult bats, the majority (28) were females, of which 84% were either pregnant, lactating or post lactation. I also caught a small number of other species including *P. pipistrellus* and *N. leisleri* lactating females (Table 2.1) and juvenile *N. noctula, N. leisleri, P. pygmaeus* and *M. nattereri.* I recorded a total of 19,222 passes during 1,104 hours of acoustic sampling (Table 2.1); bats were recorded within all stand types and at all sites. The majority of calls were *Pipistrellus* spp. (some could not be identified to species), but I

Table 2.1: Total adult abundance and number of passes recorded for species / genera in three forests. Numbers in parentheses indicate adult females. I was unable to identify some Pipistrellus calls to species and were removed from further analysis. I caught Myotis nattereri, M. daubentoni and M. mystacinus in the plantations but due to echolocation similarities I did not differentiate between their call types. I caught Nyctalus leisleri and N. noctula but again recorded occurrence at the genus level. I caught Plecotus auritus and recorded Pipistrellus nathusii in very low numbers and present them here for interest. Sites at which species were present was determined by both acoustic and capture data.

Species/species group	Total abundance (of which females)	Total passes recorded	% of bat calls	Kielder (%)	Galloway (%)	Cowal and Trossachs (%)	Sites present (total n = 31)
Pipistrellus pygmaeus	42 (26)	6569	34.17	17.59	9.23	7.35	31
Pipistrellus pipistrellus	1 (1)	6333	32.95	28.58	2.47	1.90	30
Pipistrellus spp.	0	4849	25.23	12.22	7.26	5.75	31
Myotis spp.	3 (0)	737	3.83	2.93	< 1 %	< 1 %	30
Nyctalus spp.	1 (1)	540	2.81	< 1 %	2.20	< 1 %	20
Plecotus auritus	2 (0)	117	< 1 %	< 1 %	< 1 %	< 1 %	23
Pipistrellus nathusii	0 (0)	77	< 1 %	< 1 %	< 1 %	0.00	7

also recorded *Myotis* and *Nyctalus.* In addition, both *P. auritus* and *P. nathusius* were recorded in plantations but in very low numbers, and were excluded from further analysis (Table 2.1).

2.4.2 Factors affecting bat abundance and activity in coniferous plantations

Pipistrellus pygmaeus abundance was highest in sites closer to buildings (Figure 2.2D), with mean captures falling from 3.9 (95% Confidence Interval 2.3 – 7.4) in sites within 400m of buildings to 0.8 (0.3 – 1.6) in sites more than 2km from buildings. There was a trend towards higher abundance in sites with a higher landscape heterogeneity but the effect size was small (Table 2.2). Both local and landscape scale factors influenced *P. pygmaeus* activity in coniferous plantations (Table 2.3); activity was highest at stand edges and stands surrounded by a relatively low proportion of open ground, falling by 90% as the percentage of surrounding open space increased from 30 to 65% (Figure 2.2A). Activity of *P. pygmaeus* decreased with increasing stand density falling from 29 (16 – 53) passes in stands of less than 50 trees ha^{-1}, to 7 (3 – 15) passes in stands of 3000 trees ha^{-1} (Figure 2.2B). Activity was also lower (11; 5 – 23 passes) in stands over 50 years old, compared to 25 (14 – 44) passes in clear felled stands (Figure 2.2C).

Pipistrellus pipistrellus was most influenced by stand type, with the highest activity occurring in felled areas and at stand edges compared to stand interiors, apart from at felled stands where *P. pipistrellus* used both stand edges and stand interiors (Table 2.3).

The probability of recording *Myotis* sp. was greater at stand edges compared to interiors (Table 2.4) and was strongly influenced by stand density; there was a 0.7 (0.5 – 0.9) likelihood of recording *Myotis* in stands with fewer than 50 trees ha^{-1} which fell to a 0.3 (0.1 – 0.6) in denser stands (>2750 trees ha^{-1}).

Occurrence of *Nyctalus* in plantations was influenced at both the local and the landscape scale; this group were most likely to be recorded at the edge of felled stands and least likely to be recorded in stand interiors, particularly stands where canopy closure has occurred (“mature” and “thinned” stands; see appendix 2.1). At the landscape scale, as the distance between patches of closed canopy conifer increased, the likelihood of recording *Nyctalus* species also increased from 0.1 (0.0 – 0.3) in stands within 100m of closed canopy cover to 0.7 (0.3 – 0.9) in stands with more than 1km between mature conifer stands (Figure 2.3 A). *Nyctalus* were also less likely to be recorded in stands in which water is the largest patch in the surrounding landscape (Table 2.4).

Table2. 2 Best approximating GLM models (with shrinkage) using an information-theoretic approach based on Akaike's Information Criterion (AICs) adjusted for small sample sizes for P. pygmaeus abundance. Listed are the parameters and their respective influence on P. pygmaeus abundance in commercial plantations. Parameters in bold have a large effect size. $R^2 = 0.27$.

GLM Model	Habitat parameters	Estimate	Error	Z value
Abundance of				
P. pygmaeus spp.	(Intercept)	-29.7	12.6	0.22
(poisson)	**Distance to buildings**	**-0.51**	**0.18**	**-2.74**
	Total buildings within 4km	**0.23**	**0.11**	**2.114**
	Shannon's diversity index (Landscape heterogeneity)	**0.28**	**0.14**	**1.96**
	% ASNW within 4km	-0.15	0.17	0.37
	Date	0	0	0.69
	Temperature	0.18	0.11	0.11

Table 2.3: Best approximating GLMM models (with shrinkage) using an information-theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc) for both Pipistrelle species. Listed are the parameters and their respective influence on (a) P. pygmaeus (intercept is for stand edge), and (b) P. pipistrellus (intercept is stand edge at felled stands). It is not possible to calculate R^2 for negative binomial mixed effects models. Bold indicates parameters where the error of the estimate does not cross zero. ASNW is ancient semi-natural woodland (woodland continuously present since 1700; Anon., 2005)

GLMM Model	Structural parameters	Estimate	Error	Z value
(a)	*Local characteristics*			
P. pygmaeus	**(Intercept)**	**3.06**	**0.28**	**10.79**
activity (negative binomial)	**Stand interior**	**-1.46**	**0.21**	**-6.83**
	Stand density (ha)	**-0.42**	**0.12**	**-3.59**
	Stand Age	**-0.30**	**0.12**	**-2.58**
	Altitude (m)	-0.09	0.16	0.56
	Landscape characteristics			
	% Open land (3km)	**-0.57**	**0.18**	**-3.14**
	Distance to broadleaf tree cover (m)	-0.14	0.19	-0.70
	Distance to water (m)	0.00	0.05	0.07
	% ASNW (4km)	-0.06	0.14	-0.39
	Total buildings	0.21	0.21	1.08
	Environmental characteristics			
	Temperature (°C)	0.10	0.15	0.53
(b)	*Local characteristics*			
P. pipistrellus	**Intercept**	**3.58**	**0.70**	**5.05**
activity (negative binomial)	**Stand Interior**	**-1.64**	**0.21**	**-7.79**
	Stand type: Mature	**-1.88**	**0.33**	**-5.68**
	Stand type: Thicket	**-1.63**	**0.34**	**-4.78**
	Stand type: Thin	**-0.96**	**0.37**	**-2.60**
	Stand type: Young	**-1.12**	**0.32**	**-3.43**
	Altitude (m)	-0.23	0.23	-0.98
	Landscape characteristics			
	Edge density	-0.01	0.11	-0.11
	Distance to water (m)	0.25	0.18	1.36
	Distance to nearest building (m)	0.09	0.07	0.60
	% Felled land (3km)	0.16	0.21	0.76
	% ASNW (4km)	-0.05	0.16	-0.34
	ENN distance to closed canopy conifer (m)	-0.40	0.23	-1.77
	Environmental characteristics			
	Temperature (°C)	**0.54**	**0.25**	**2.14**

Table 2.4: Best approximating GLMM models (with shrinkage) using an information-theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc) for both Myotis and Nyctalus occurrence in commercial coniferous plantations. Listed are the parameters and their respective influence on (a) Myotis spp *(marginal* $R^2 = 0.29$*). (b) Nyctalus (marginal* $R^2 = 0.86$*). Bold indicates parameters where the error of the estimate does not cross zero.*

GLMM Model	Habitat parameters	Estimate	Error	Z value
The occurrence of Myotis spp**.**	*Local scale*			
	Intercept	0.54	0.50	1.09
Presence (binomial)	**Stand interior**	**-1.30**	**0.31**	**-4.22**
	Stand density per hectare	**-0.60**	**0.17**	**-3.45**
	Altitude (m)	0.00	0.10	0.01
	Stand age	-0.05	0.12	-0.40
	Landscape-scale			
	Distance to water (m)	-0.20	0.19	-1.72
	Shannons diversity index	0.08	0.15	0.53
	LPI (open land within 250 m)	0.06	0.14	0.46
	% ASNW (4km)	-0.08	0.20	-0.41
	Environmental variables			
	Mean nightly temperature (°C)	0.02	0.10	0.21
Occurrence of Nyctalus	*Local scale*			
	Intercept	-0.53	0.65	0.82
Presence (binomial)	**Stand interior**	**-1.46**	**0.39**	**-3.73**
	Stand type: Mature	**-2.04**	**0.70**	**-2.90**
	Stand type: Thicket	**-1.39**	**0.65**	**-2.13**
	Stand type: Thin	**-1.71**	**0.67**	**-2.53**
	Stand type: Young	-0.93	0.60	-1.53
	Altitude (m)	-0.03	0.17	-0.19
	LPI (open water within 500m)	**-4.85**	**1.43**	**-3.38**
	Shannon's diversity index	0.26	0.32	0.81
	Distance to water (m)	-0.07	0.17	-0.44
	% ASNW (4km)	-0.09	0.32	-0.27
	Total buildings	**-1.58**	**0.65**	**-2.44**
	ENN distance to nearest patch of closed canopy conifer (m)	**1.00**	**0.31**	**3.21**
	Environmental variables			
	Temperature	**1.66**	**0.40**	**4.12**

Table 2.5: Best approximating binomial distributed generalised linear mixed models (GLMM's) for the differential responses of P. pygmaeus and P. pipistrellus to local and landscape scale habitat parameters. Presented are the best approximating models (with shrinkage) using an information theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc). Listed are the parameters and their respective impact on P. pygmaeus activity proportional to P. pipistrellus activity. Positive estimates predict a higher probability of recording P. pygmaeus, negative estimates predict a higher probability of recording P. pipistrellus. No response does not necessarily indicate that neither species was impacted but could mean both respond in the same way. Marginal R^2 = 0.09. Bold indicates parameters where the error of the estimate does not cross zero.

GLMM Model	Habitat parameters	Estimate	Error	Z value
Proportion of P. pygmaeus to	*Local scale*			
P. pipistrellus	Intercept	0.15	0.45	0.35
Activity (binomial)				
	Mature* stand interior	-0.44	0.44	-1.02
	Thicket* stand interior	-0.28	0.19	-1.45
	Thin* stand interior	**-1.45**	**0.25**	**-5.64**
	Young* stand interior	0.26	0.13	2.12
	Mature* distance to water	**0.55**	**0.07**	**7.15**
	Thicket* distance to water	**0.32**	**0.09**	**3.28**
	Thin* distance to water	**0.23**	**0.08**	**2.58**
	Young* distance to water	**0.40**	**0.08**	**4.89**
	Stand age (quadratic term)	**0.19**	**0.04**	**4.68**
	Landscape scale			
	Distance to nearest building (m)	**-0.32**	**0.06**	**-5.50**
	% felled land (3km)	-0.24	0.17	-1.42
	Distance to broadleaf tree cover (m)	**0.55**	**0.05**	**9.96**
	Environmental variables			
	Temperature*Altitude	-0.36	0.07	-4.25

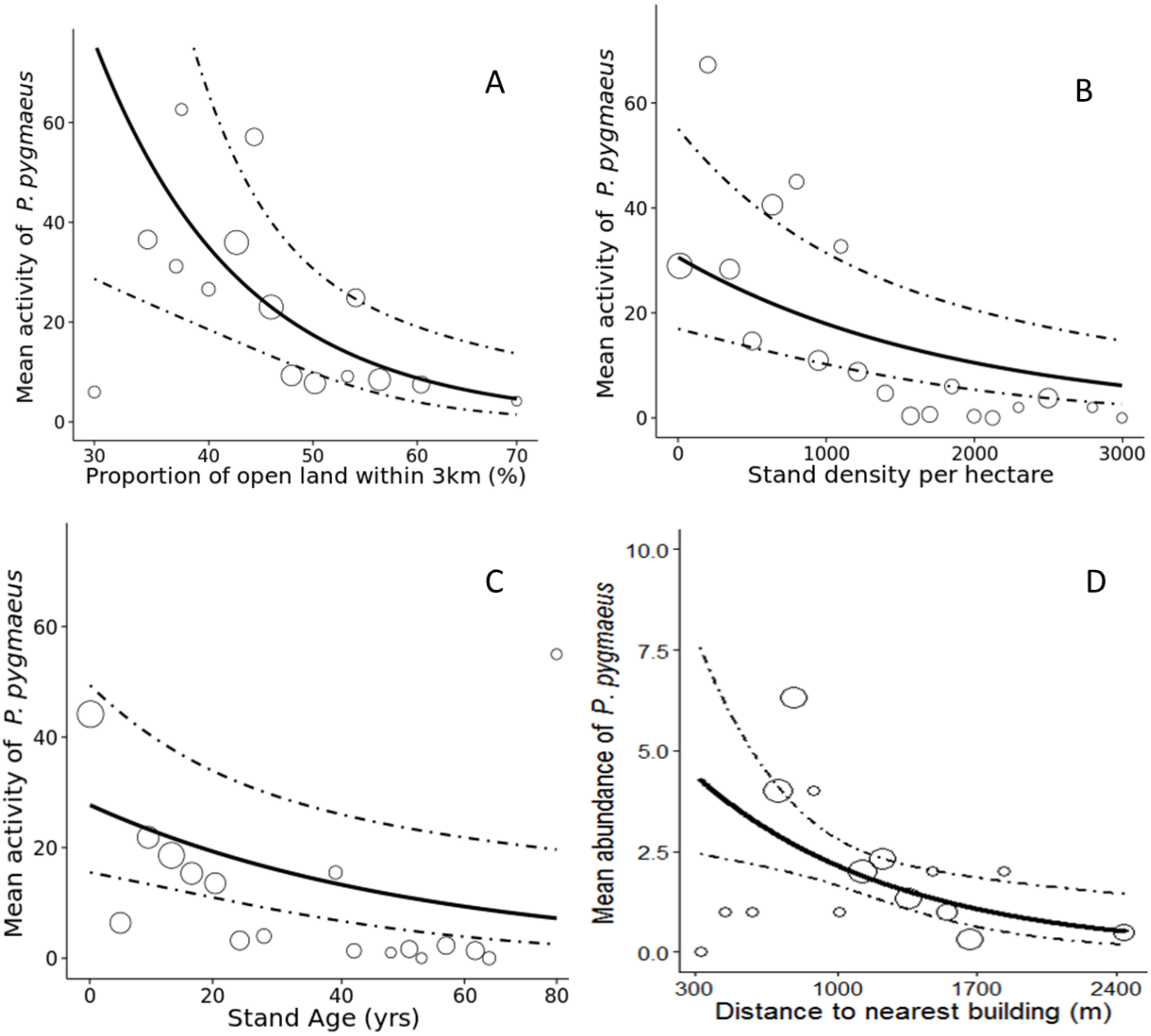


Figure 2.2: A – C. Estimated mean P. pygmaeus *activity against (A) Proportion of open land within 3km radius of sampling point, (B) Stand tree density per hectare and (C) Stand age (years), using model averaged estimates. Original data on activity (number of passes in a four hour sampling period) are superimposed as grey circles with diameter proportional to the number of sampling points where mean activity occurred. Bold line indicates line of best fit from the top model set. Dashed lines represent 95% confidence intervals around the predictions. Figure 2 D. Estimated probability of* P. pygmaeus *abundance in relation to distance to nearest building (m), using model averaged estimates. Original data on abundance (number of individuals caught) are superimposed as grey circles with diameter proportional to the number of sampling points where mean abundance occurred. Bold line indicates line of best fit from the top model set. Dashed lines represent 95% confidence intervals around the predictions.*

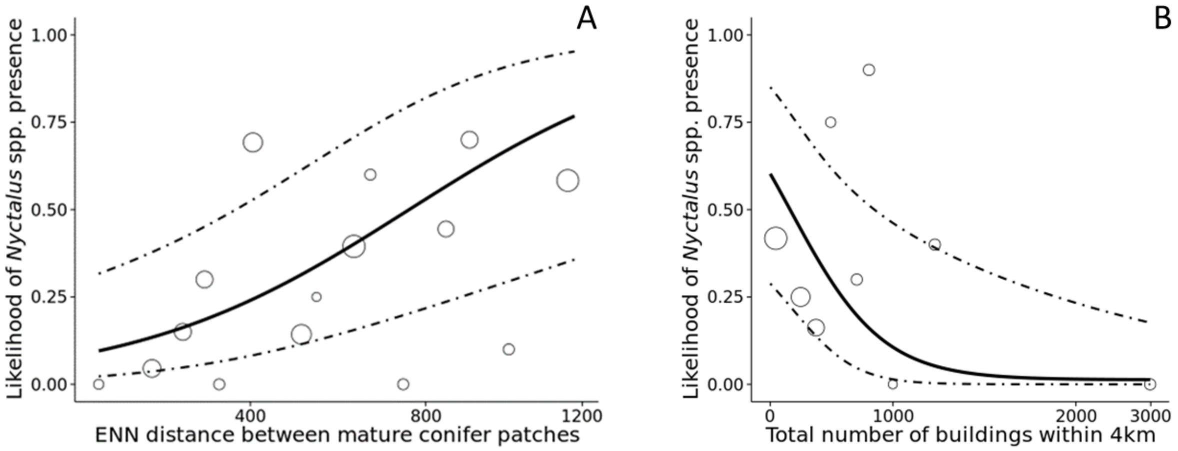


Figure 2.3: *Estimated probability of recording* Nyctalus *with (A) increasing Euclidean distance (ENN) between closed canopy conifer patches, (B) Total number of buildings within 4km. Original data on activity (number of passes in a four-hour sampling period) are superimposed as grey circles with diameter proportional to the number of sampling points where mean activity occurred. Bold line indicates line of best fit from the top model set.*

Nyctalus species responded negatively to the built environment; in less populated areas (fewer than 50 houses within 4km) there was a 60% (28 – 85%) likelihood of recording *Nyctalus* but this fell to 2% (0.2 – 32%) likelihood of recording *Nyctalus* in stands with more than 1500 buildings within 4km (Figure 2.3 B).

2.4.3 Differential use of plantations by *P. pygmaeus* and *P. pipistrellus*

Proximity to broadleaf tree cover was the most influential variable explaining differences in activity between *P. pygmaeus* and *P. pipistrellus* (Table 2.5). At stands close to broadleaf trees (< 1km), approximately 40% (20 – 62) of activity was *P. pygmaeus* compared to *P. pipistrellus,* rising to nearer 80% (60 – 91) in stands further away (~ 4km) from broadleaf trees (4A). A higher proportion of *P. pygmaeus* to *P. pipistrellus* calls was predicted in felled or freshly planted stands (< 5 years) and older (60+ years) stands but was approximately equal for those between 20 to 40 years (Figure 2.4 B). Stands close to buildings had higher *P. pygmaeus* activity (0.68; 0.46 – 0.84) than those over 2.5km from buildings which had higher *P. pipistrellus* activity (0.36; 0.18 – 0.59, Figure 2.4 C). Finally, there was a trend for *P. pygmaeus* to dominate in stands close to water, and *P. pipistrellus* in stands > 1km from water, particularly in felled areas (Table 2.5; Figure 2.4 D).

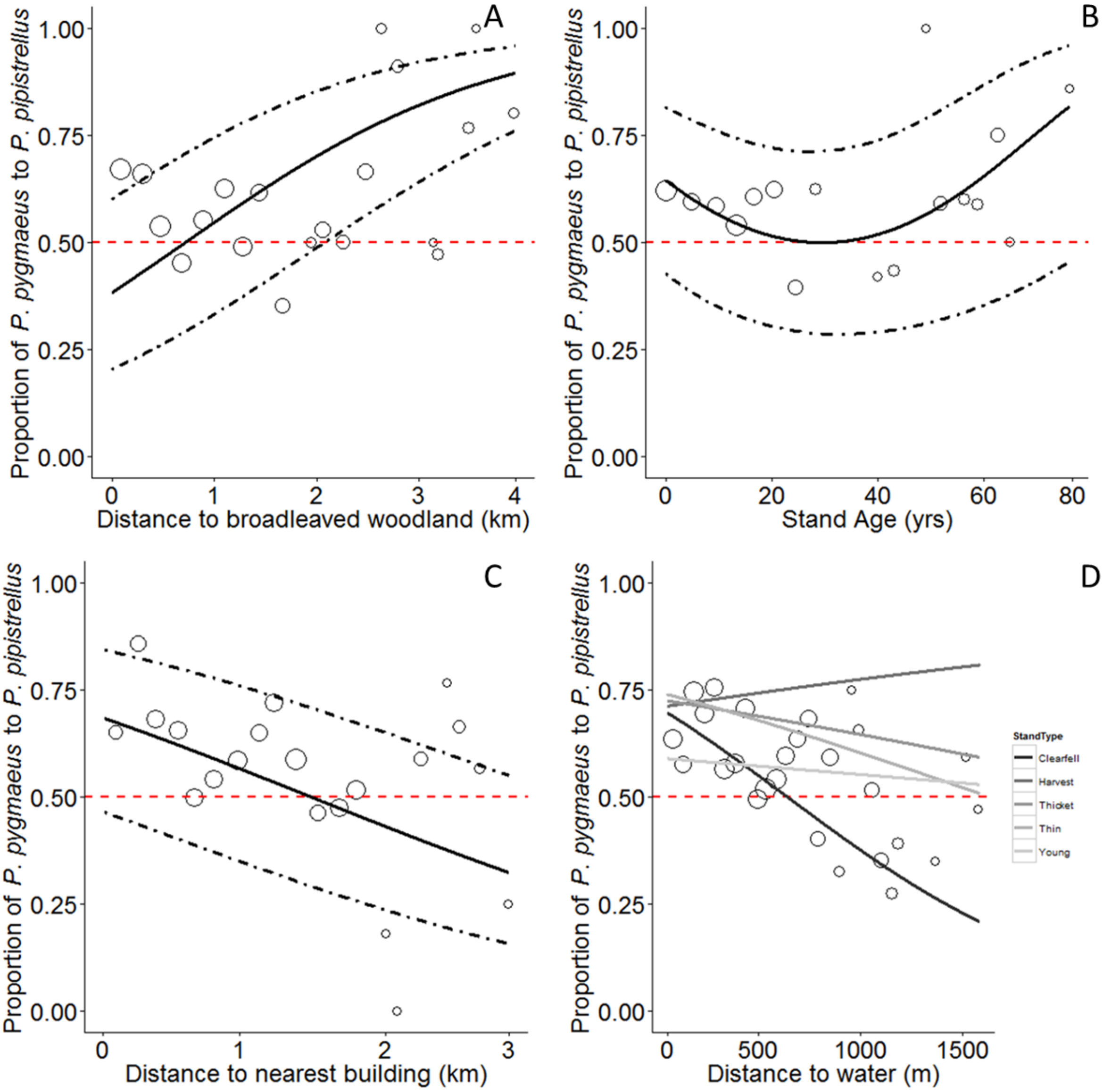


Figure 2.4: A - D Model averaged estimated probability of P. pygmaeus *activity proportional to* P. pipistrellus *activity as (A) Distance to broadleaved, (B) Stand age (quadratic term), (C) Distance to nearest building (D) Stand type and distance to water. Original data on the proportion of* P. pygmaeus *to* P. pipistrellus *are superimposed as grey circles with diameter proportional to number of sampling locations where proportional activity was recorded. Dashed red line indicates the proportion at which* P. pygmaeus *and* P. pipistrellus *activity was equal. Bold line indicates line of best fit from the top model set.*

2.5. Discussion

Plantation forests have been viewed as "green deserts", often presumed to be hostile to wildlife and of little intrinsic value for biodiversity (Gardner, 2012). However, as most bat species rely on forests during their life cycle, understanding how forestry management impacts bat use of plantations is highly important for bat conservation (Russo et al., 2016), particularly as plantation landscapes are receiving growing interest as sites of alternative energy generation. In this study, I found a wide diversity of bat species used commercial plantations, with edge, clutter and open adapted foragers detected. However, the extent of plantation use depended on both local and landscape habitat composition and varied between species and species' guilds.

2.5.1 Composition of bat populations in commercial coniferous plantations:

Relative abundance, assessed through captures, was generally low in comparison to studies in a similar geographical area (Fuentes-Montemayor et al. 2013; Lintott et al. 2015). Despite the fact that levels of activity of *P. pygmaeus* and *P. pipistrellus* were very similar, *P. pipistrellus* was under-represented in the capture records. Lintott et al (2014) found comparable capture rates when using a lure for both *P. pygmaeus* and *P. pipistrellus* in a similar geographical region, therefore, it is unlikely that the difference in capture rate in this study is due to capture bias from the acoustic lure. Rather this may be in part due to higher *P. pipistrellus* activity in felled and open areas which I did not target for catching due to the lack of clearly defined flight lines. Nevertheless, it is evident that I cannot use capture data for *P. pipistrellus* to infer relative abundance. Analyses using the capture data have been restricted to *P. pygmaeus*, as a previous, larger scale, study indicated that measures of abundance using the lure was complementary to activity levels (Lintott et al. 2014). This study indicates that plantation forests support the foraging activities of breeding populations of *P. pygmaeus* (and potentially *P. pipistrellus and N. noctula*), which are likely to roost in nearby buildings (Altringham et al., 1996) as I caught relatively high numbers of lactating females. However, I found no evidence that breeding colonies of forest specialist bats such as *Myotis* and *Plecotus* species are using plantation forests. The lack of forest specialists in plantations has been reported from other studies and has been attributed to the paucity of appropriate natural roost structures such as tree cavities (Bender et al., 2015; Burgar et al., 2015; Pereira et al., 2016; Rodríguez-San Pedro and Simonetti, 2015; Russo et al., 2010). Although standing dead wood is retained as part of forestry operations I saw no evidence of any standing dead wood being appropriate for roosting. In addition, I saw no evidence of any tree holes, rot or damage in (*Picea sitchensis*) which could be used as a potential roost, and found no evidence of lactating female *P. pygmaeus* using (*Picea sitchensis*) as temporary roosts while radio tracking study (chapter 6). *Myotis* species such as *M. nattereri*, *M. daubentoni,* and *M. mystacinus* roost switch regularly and use a combination of tree holes, man-made structures such as bridges, and occasionally bat boxes (Altringham et al., 1996) which were uncommon in the plantations surveyed for this study (pers. obs). Furthermore, dipteran abundance was similar between stand types (Appendix 2.4). Therefore, it is highly likely that the lack of appropriate roosting structures for forest specialist bats is responsible for the sex-specific differences in bat diversity and abundance.

3.5.2 Responses of bats to features at the local scale: In this study, although bat associations with plantation habitat features separated into two broad guilds (those using more complex habitats such as *P. pygmaeus* and *Myotis* spp., and open space foragers such as *Nyctalus* and to some extent *P. pipistrellus*), all species preferentially used stand edges. Edges may allow both clutter-tolerant and clutter sensitive bats access in and around different areas of the plantation (Heer et al., 2015; Hein et al., 2009; Rodríguez-San Pedro and Simonetti, 2014), provide protection from wind for weak flying Diptera or act as windbreaks collecting airborne insects blown in from adjacent open or felled areas and also provide protection from predators (Nicholls and Racey, 2006a; Verboom and Spoelstra, 1999). The exception was at felled stands which were used by both open and edge-space foragers such as *Nyctalus* and *P. pipistrellus*. *Pipistrellus pygmaeus* foraged more near water and in older stands compared to *P. pipistrellus* which more commonly used areas near to broadleaf tree cover, further from buildings or water, particularly felled stands. Whilst there are small differences in the diet of the two pipistrelle species (Barlow 1997), both primarily feed on Nematoceran Diptera; a parallel study not presented here (Kirkpatrick, appendix 2.4) found no difference in the abundance of this group between stand types within plantations, so prey abundance does not appear to be driving the within plantation differences in foraging activity I see here. Rather, a high dipteran abundance may attract *Pipistrellus* spp. to plantations, but within plantations, the two different species segregate based on local stand characteristics and different foraging styles, such as the well-documented association of *P. pygmaeus* with riverine habitats (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006a).

The activity of *P. pygmaeus* and occurrence of *Myotis* spp. decreased with increasing stand density, being highest at felled stands and decreasing at thin and thicket aged stands which are harder to negotiate (Dietz et al., 2009; Jung et al., 2012). Adams and Law (2011) suggested that thinning to a threshold of below 1100 stems ha^{-1} would benefit bat species in Australian plantation forests, with other studies from Australia and America supporting this recommendation (Bender et al., 2015; Blakey et al., 2016; Cistrone et al., 2015; Cox et al., 2016; A D Morris et al., 2010; Patriquin and Barclay, 2003). I was unable to directly test the impacts of thinning as mechanical thinning was rare in our study system but as the average density of mature stands was 1200 stems ha^{-1} and *P. pygmaeus* activity was predicted to fall by a third in stands over 1000 stems ha $^{-1}$, it is likely that thinning would be beneficial.

2.5.2 Responses of bats to features at the landscape scale

In general, bat species or genera had stronger responses to local rather than landscape features. However, *P. pygmaeus* responded strongly and negatively to the proportion of open land within 3 km, which was strongly correlated with increased landscape heterogeneity. Firstly, *P. pygmaeus* distinguished between open ground (i.e. moorland or upland) compared to felled land. Structurally, felled stands and open areas are similar, so access to prey and exposure to predators will be similar in both land cover types. However, felled stands may support different prey abundance and diversity than open areas. Felling causes soil disturbance and results in a boggy environment which may be a better breeding ground for Nematoceran Diptera (Blackwell et al., 1994). Landscapes with a higher proportion of open ground may have a lower proportion of suitable edge habitats and linear features which *P. pygmaeus* may use for commuting into and through plantations (Law et al., 2015). Bender et al (2015) found that most species-specific bat occupancy and activity was related to stand level, rather than landscape-level features, similarly to Erickson et al (2003). The lack of strong associations with landscape at larger spatial scales may reflect the fact that bats do not perceive different management stages in plantations as inhospitable habitat (Bender et al., 2015; Heer et al., 2015) compared to broadleaf forest patches within an agricultural or urban matrix (e.g. agricultural dominated landscape; Fuentes-Montemayor et al., 2013; urban dominated landscape; Lintott et al., 2015). In contrast, the likelihood of detecting *Nyctalus* was higher in stands surrounded by a lower proportion of mature conifer. *Nyctalus* are large, fast flying bats which forage by gleaning in open habitats and will avoid cluttered habitats such as mature conifer (Russ, 2012).

2.5.3 Management implications for commercial coniferous plantations

The lack of information regarding bat use of commercial plantations in Europe means that current management recommendations are sparse and predominantly drawn from research in America and Australia (e.g. Bender et al., 2015; Blakey et al., 2016; Borkin and Parsons, 2011; Heer et al., 2015). Although plantation management regimes can vary markedly between countries resulting in differences in composition and structure, I have outlined a number of recommendations likely to benefit bat species across a range of plantation forests:

1. Increasing roost availability: it is likely that roosts rather than food availability are constraining the use of commercial plantations for many bat species. I saw no evidence of suitable roosting features in stands of *Picea sitchensis*, although other conifer species such as *Pinus nigra* can house maternity colonies of *M. nattereri* (Mortimer, 2006). Therefore, although felling operations have been shown to reduce colony size and available roosting habitat in *Eucalyptus* plantations in New Zealand (Borkin et al., 2011), it is unlikely that felling directly causes roost loss or increased mortality in *Picea sitchensis* plantations. In fact, in the current study *Pipistrellus* and *Nyctalus* species preferentially foraged in these areas. Installing bat boxes in riparian areas, near broadleaf woodland or in stands not included in felling schedules should allow more bat species, particularly lactating females, to make use of plantation areas without impacting forest operations. Other studies have demonstrated accelerated uptake of bat boxes adjacent to plantation forests, probably as a result of the lack of alternative roosting possibilities (Ciechanowski, 2005; López-Baucells et al., 2016; Russo et al., 2010; Smith and Agnew, 2002). It may be unlikely that boxes will be used by *P. pygmaeus*

maternity colonies (e.g McAney and Hanniffy, 2015), although harem formation in late summer and autumn would be expected (McAney and Hanniffy, 2015; Park et al., 1996). However, for forest specialist bats such as *M. nattereri*, bat boxes may be appropriate for the formation of maternity colonies (Mortimer, 2006). Long-term monitoring of mitigation such as installing bat boxes is essential to assess the effectiveness of installing bat boxes in commercial plantations and should be built into any management plan (Russo et al., 2016).

2. Enhancing plantation heterogeneity: I found that the presence and activity of different species or genera were impacted at multiple spatial scales. Plantations can cover huge areas as a contiguous forest; maintaining a variety of stand types and ages will allow species such as *P. pygmaeus* which preferred the edges of mature or felled stands as well as *Nyctalus* species which preferred felled stands to both make use of plantation landscapes.

3. Reducing stand density: In line with various other studies across temperate zone plantations, maintaining and enhancing thinning programs where possible may allow stands to reach similar densities to mature stands at a younger age, which will benefit edge and clutter adapted species (Bender et al., 2015; Blakey et al., 2016; Cox et al., 2016; A D Morris et al., 2010). In addition, felling creates new foraging patches for open and edge adapted species. Studies which have found no effect of thinning may not have thinned sufficiently; Blakey et al (2016) found that felling to densities below 1100 stems ha^{-1} resulted in greater bat activity whereas Patriquin and Barclay (2003) found no impact of thinning to 1250 stems ha^{-1}. Adams et al (2011) recommend thinning to below a threshold of 1100 stems ha^{-1} where appropriate. I found a 30% increase in activity in stands below 1000 stems ha^{-1}, although the mean density of mature stands in our dataset was 1260 stems ha^{-1}, which may still be too dense for even clutter adapted bats to make use of.

4. Improving feeding opportunities: the presence of bats in plantations is likely a reflection of food availability, as Nematoceran Diptera were abundant across all stand types and dominated invertebrate diversity (Kirkpatrick, unpublished data). Shifts in plantation management toward continuous cover forestry and maintaining riparian habitat will support a wider diversity of invertebrates (Kerr, 1999), benefiting species that forage on other invertebrates. In addition, continuous cover forestry may benefit clutter adapted bat species such as *M. nattereri* and even *P. auritus* which are gleaning foragers, while maintaining clear felling will benefit open adapted species. Both *P. pipistrellus* and *Nyctalus* associated strongly with freshly felled areas. Felling operations resulting in a change in land use should be aware that bats may be using these areas in greater numbers post felling and ensure that the new operations are not likely to harm bat species.

Chapter 2 Appendix

Appendix 2.1:

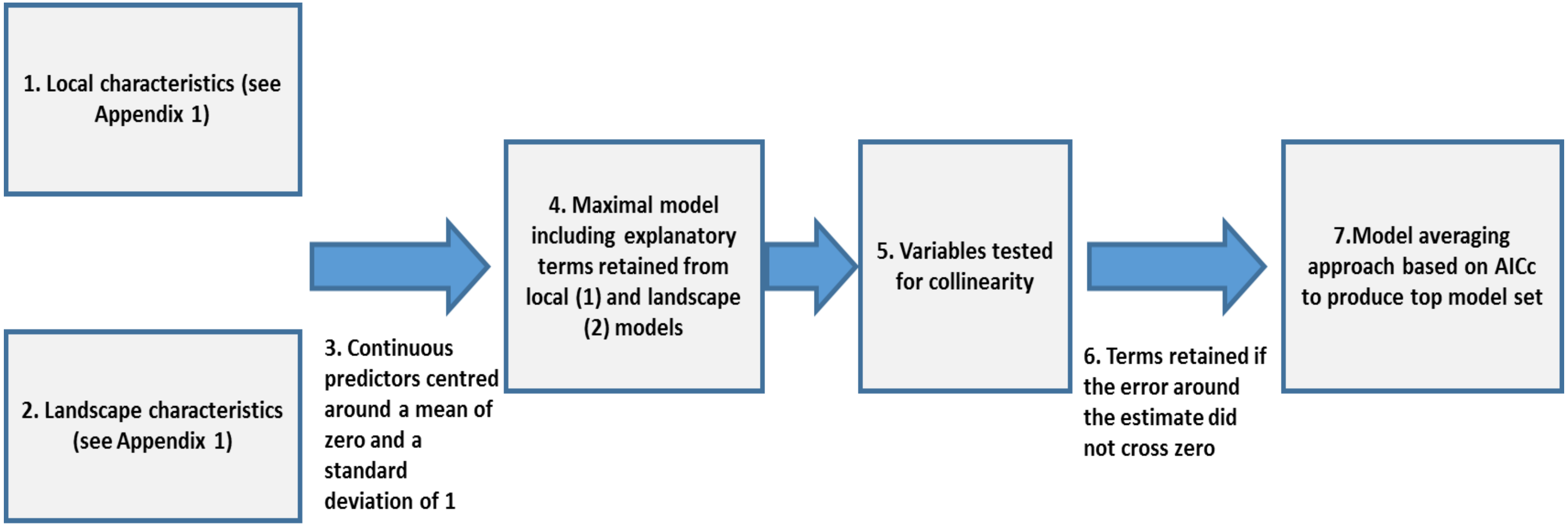
Stand characteristics for each management stage and stand features associated with management. *Diameter at Breast Height – estimate of tree maturity

Stand Age	Management Stage	Key stand features
40 – 60 years	Mature	Occasionally thinned, stand density between 500 and 2200 stems ha^{-1}, average stand density: 1267 stems ha^{-1}, canopy closure between 80 and 100%, average closure 99%
20 – 40 years	Thin	Trees more densely packed, losing midstem branches and some trees dying off (self thinned). Occasionally thinned through management. Stand density between 600 – 2800 stems ha^{-1}, average stand density: 1624 stems ha^{-1}. Canopy closure between 50 and 100%, average closure: 95%
10 – 20 years	Thicket	Very dense, retain midstem branches, no undergrowth. Stand density between 300 – 3000 stems ha^{-1}, average stand density: 1850 stems ha^{-1}. Canopy closure between 16 and 100%, average closure: 69%
5 – 10 years	Young	Small, nearly all trees < 7cm DBH*, no canopy closure, lots of vegetation and ground cover
Clearfell	Felled < 5 years ago	Lots of dead wood and brash, standing water and undergrowth

Appendix 2.2 Description of explanatory variables used in models.

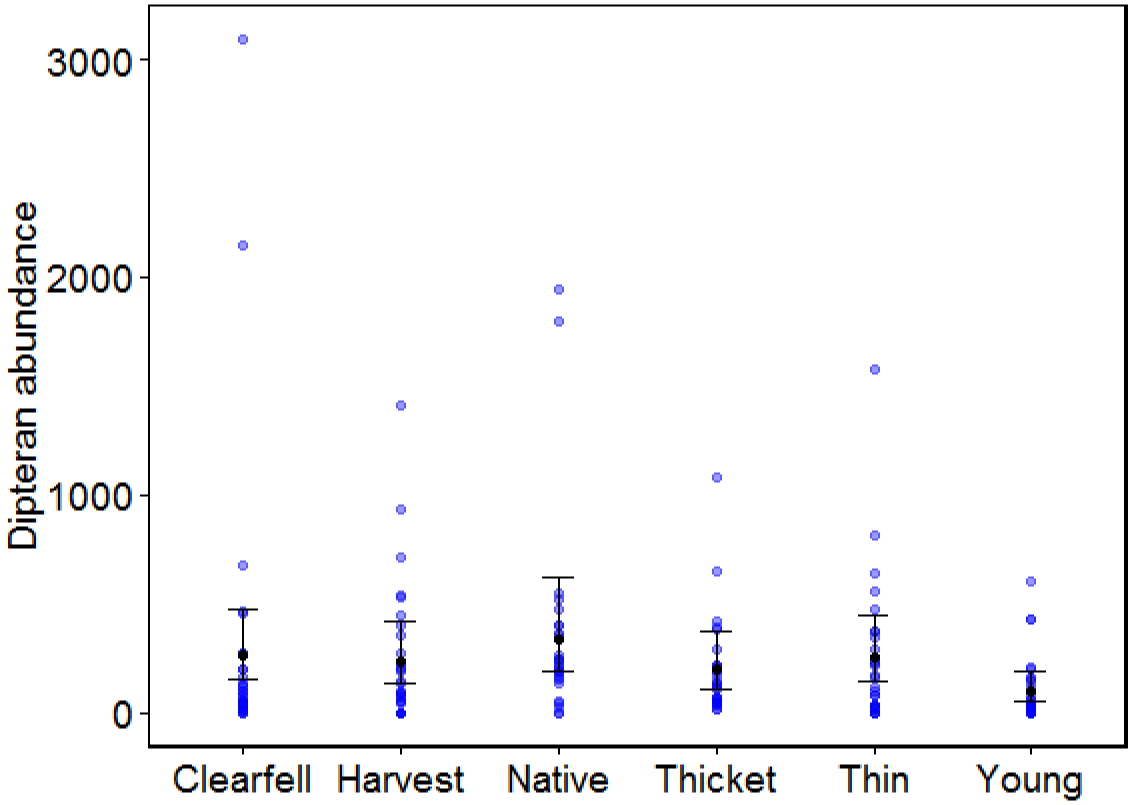
Scale	Metric	Units	Description
Local	Altitude	metres	
Local	Stand edge / interior		Location of detector at stand edge or stand interior
Local	Stand density	trees per ha	Total number of trees with over 7cm diameter at breast height within 0.01ha plot
Local	Canopy cover	%	% canopy cover averaged across 0.01ha plot
Local	Vegetation height	Mm	Vegetation height averaged across a transect
Local	Stand age	years	Years since stand planted
Local	Stand type		Stands categorised by management stage (see appendix 2)
Local	Coarse woody debris		Score of coarse woody debris on stand floor inn 0.01ha plot around detector
Local	Standing dead wood		Count of standing dead wood in 0.01ha plot around detector
Local	Dominant ground cover		Dominant ground cover in 0.01ha plot around detector – categorical. Bare, Needle, Moss, Grass, Tussock, Bracken, Flowering plant"
Landscape	Distance to water	m	Distance to nearest river, stream or loch
Landscape	Distance to nearest building	m	Distance to nearest building or human dwelling
Landscape	Distance to broadleaf tree cover	m	Distance to nearest patch of ancient semi natural woodland
Landscape	Total buildings		Total number of buildings within 4km
Landscape	Track length	m	Total track length within 4km as estimation of available "edge habitat" within plantations
Landscape	Shannon's diversity index		Measure of landscape heterogeneity within 250m - 4km of each site
Landscape	Percentage of land type	%	Percentage of different land cover types within 250m – 4km of each site
Landscape	Edge density		Sum of the lengths of all patch edge segments divided by the total landscape area)
Landscape	Euclidean nearest neighbour (ENN) land cover type		Euclidean distance to the nearest patch of land cover types
Landscape	Largest Patch Index	%	Percentage of landscape comprised of largest patch of each land cover type within 250m – 4km of each site
Landscape	% ASNW	%	Percentage of ancient semi natural woodland within 4km

Appendix 2.3: Flowchart demonstrating process used to construct all GLMMs used in this study.



Appendix 2.4:

Total dipteran abundance between different stand types, showing predicted dipteran abundance (modelled as a glmm with a negative binomial error structure to account for over dispersion and plantation included as a random factor). Blue dots represent the raw data, predicted dipteran abundance plus standard errors is plotted in black.



Chapter Three

Chapter 3 Negative impacts of felling in exotic spruce plantations on moth diversity mitigated by remnants of broadleaf tree cover

Light trap located in mature coniferous stand

3.1 Abstract:

Moths provide a range of ecosystem services and are currently undergoing extensive and severe declines across multiple species, partly attributed to habitat alteration. Despite the majority of remaining forest cover in Europe consisting of intensively managed plantation forests, no studies have examined the influence of management practices on moth communities within plantations. In this study I aimed to do the following: (1) determine species richness, abundance, diversity of macro and micro moths in commercial conifer plantations and responses to management at multiple spatial scales, and (2) determine how priority Biodiversity Action Plan (BAP) species are influenced by plantation characteristics, felling or presence of broadleaf within the landscape. I assessed moth communities in three separate conifer plantations in Northern UK by light trapping, combining stand and landscape level information to predict the impacts of the prevalence of felling and broadleaf on night active, light attracted moths. I found no effect of local factors on moth richness, abundance and diversity but the scale of felling in the surrounding landscape had a strongly negative impact. The prevalence of broadleaf in the surrounding landscape positively impacted macro moth richness and abundance. For six BAP species, abundances were lower close to felled areas but increased with the size of adjacent broadleaf patch. I conclude that clear felling negatively impacts moths, probably through alteration of habitats, the loss of larval host plants, and by limiting dispersal. A shift to continuous cover forestry would benefit a range of moth species, while maintaining broadleaf tree cover within plantations will greatly enhance their value for moth communities.

3.2 Introduction

Maintaining and restoring biodiversity is a key tenet in sustainable ecosystem management, the paradigm currently guiding habitat management practices across Europe and North America (Ober and Hayes, 2010). This is driven by concern about world-wide declines in species and populations across a range of taxa (Dirzo et al., 2014) and recognition that much of this is driven by habitat loss and fragmentation, caused by anthropogenic change (Thomas, 2004). In many countries the timber industry has responded to recognition of the importance of biodiversity by shifting focus from purely timber production to one which encourages sustainable practices that promote both wildlife conservation and sustainable timber yields (Macdonald et al., 2009). In Europe this has been driven by policy change initiated as a result of the Convention of Biological Diversity, requiring explicit consideration of environmental, economic and social objectives and a multi-purpose approach to forestry (Watts et al., 2008). However, efforts to assess the impact of forest practices can be challenging as there is often inadequate knowledge of the current distribution and abundance of many taxa in managed forest systems (Ober and Hayes, 2010).

Plantation forests are generally considered poor for biodiversity as they are primarily composed of non-native tree species, often in monocultures, which are under an intensive management regime (Brockerhoff et al., 2008). However, they usually constitute the largest patches of forest in many European countries and as such may be valuable for preserving biodiversity if managed sympathetically. One of the few studies carried out at a national scale demonstrated that plantations can support diverse invertebrate communities in the UK, and that invertebrate community composition and abundance is most impacted by coniferous tree species planted and geographic location (Humphrey et al., 2003). The structure of the plantation was also important for some groups: floor dwelling Carabid diversity decreased with canopy cover whereas overall Coleopteran richness and abundance in the canopy increased (Humphrey et al., 2003). The effect of stand age on invertebrate communities can also vary between taxa. Whilst higher abundance and diversity of Coleoptera has been associated with older larch (*Larix kaempferi*) and Sitka spruce plantations in Japan and Northern Ireland due to increased heterogeneity and regeneration of native trees (Ohsawa 2005; Oxbrough et al. 2010), the high canopy cover in mature plantations can negatively affect Arachnid diversity due to a loss of species associated with open habitats (Oxbrough et al., 2010). However, despite being a speciose taxonomic group and an important component of the invertebrate community the impacts of plantation forestry on night active Lepidoptera is yet to be explored.

Substantial declines of many moth species have occurred in the last few decades; two thirds of common and widespread species in the UK have suffered rapid population decreases (Conrad et al., 2006) with similar patterns occurring in Finland (Mattila et al., 2006) and Sweden (Franzén and Johannesson, 2007). Rapid economic development, urbanisation, changes to silvicultural management and agricultural expansion have all been implicated in causing these declines (Conrad et al., 2006; Fox et al., 2013). Taken together, these studies provide overwhelming evidence that moths are facing declines on a large geographic scale, across a range of habitats and mirror similar effects found in less species rich groups such as butterflies and bumblebees (Goulson et al., 2008; Warren et al., 2001). Such losses are likely to have substantial effects at both higher and lower trophic levels. Moths are a key component of terrestrial ecosystems, providing ecosystem services through modification of ecosystem functioning by saproxylic species (Merckx et al., 2012), impacting upon plant growth through larval feeding activity, acting as pollinators and providing food for a range of taxa such as birds, small mammals and bats (Fox et al., 2013). Concern about declines of formerly widespread moth species in the United Kingdom has resulted in the designation of 152 Biodiversity Action Plan (BAP) priority species, emphasising the need for further scientific study in order to assess and understand their population declines (Conrad et al., 2006).

Intensified silvicultural practices have been suggested as one major driver of the decline in moth diversity and abundance (Fox et al., 2013). However, most studies have only focussed on the impact the reduction in traditional deciduous forest management practices has had on lepidopteran species, and have not considered non-native plantations at all. Reductions in deciduous forest management techniques such as coppicing and opening up rides have resulted in lower moth diversity by increasing structural complexity and changing botanical communities (Fox et al., 2013; Merckx et al., 2012; Warren and Bourn, 2011). In general, moths associated with deciduous trees have declined throughout Europe, with larval host plant specificity a key factor in extinction likelihood in parts of Scandinavia (Franzén and Johannesson, 2007; Mattila et al., 2006), whilst species associated with conifer trees have increased (Fox et al., 2013). Our current knowledge of moths in non-native coniferous plantations comes largely from studies which have focused on the management of pest species, and to the best of our knowledge no research has explicitly explored moth diversity and the impacts of forest management in exotic plantations.

Whilst little is known about the impacts of timber harvesting on Lepidoptera in non-native plantations, work in native hardwood forests has suggested effects are largely negative. In Indiana, Summerville and Crist demonstrated that clearfelling in native hardwood forests disrupted moth communities beyond the stand being felled, limiting the diversity of species able to persist within the landscape (Summerville, 2014; Summerville and Crist, 2002). Impacts of timber harvest on Lepidoptera can persist for up to 60 years (Summerville et al., 2009), although Summerville (2013) suggests that less intensive practices such as shelterwood harvest (removal of 15% standing wood) may support a higher richness and abundance of moth communities (Summerville, 2013). In native conifer forests in Oregon, moth dominance and diversity was associated with greater canopy cover whereas richness was only impacted by elevation, with higher species richness at lower elevations (Ober and Hayes, 2010). These studies from North America demonstrate that managed native forest systems can support diverse Lepidopteran communities, but the extent to which this is true in managed non-native plantations has not yet been examined. Specifically, in this study I aim to:

1. Assess species richness, abundance and diversity in commercial conifer plantations
2. Determine influential plantation characteristics on moth communities in conifer plantations
3. Assess the impact of clear felling on moth richness, diversity and dominance.
4. Evaluate the importance of broadleaf remnant patches within plantations on measures of moth diversity.
5. Determine whether priority Biodiversity Action Plan (BAP) are influenced by plantation characteristics, felling or presence of broadleaf within the landscape.

3.3 Methods

The study was conducted in three plantation forests in Central and Southern Scotland and Northern England (Figure 3.1). Forests were chosen for their large size (ranging from 30,000 ha in Cowal and Trossachs to 60,000 ha in Kielder and 114,000 ha in Galloway), high productivity and the predominance of *Picea sitchensis*, the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each forest, multiple sites, a minimum of 4 km from each other, were selected using a Forestry Commission sub-compartment database within a Geographic Information System (GIS) (ArcMap 10.1, ESRI) based on stand age and species composition (Figure 3.1).

In total seven sites were surveyed in Cowal and Trossachs, 12 in Galloway Forest and 12 in Kielder Forest. Where possible a stand of trees at each management stage was selected in each site, which was a maximum of 2km^2 in size. Not all sites had all stands of each management age resulting in an unbalanced design of between four and six stands per site and a total of 285 stands across 31 sites.

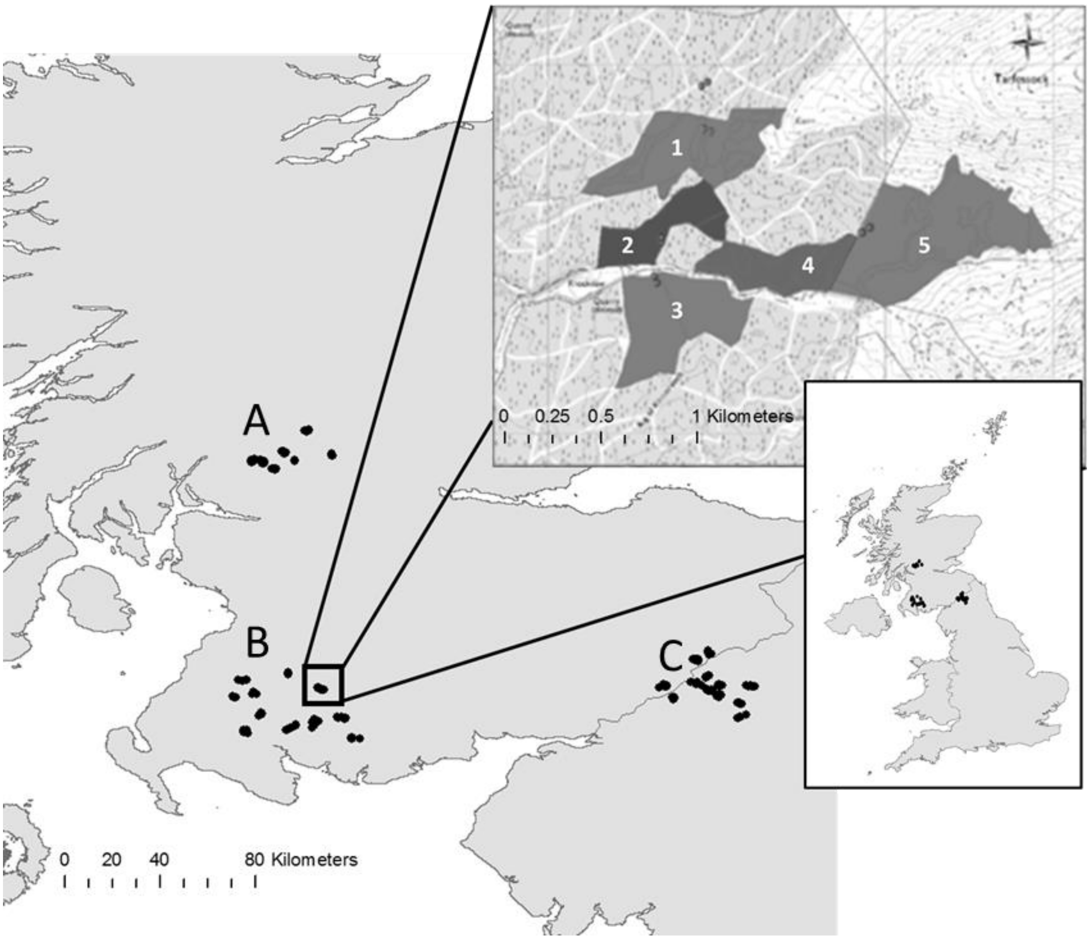


Figure 3.1: Location of field sites at three different study areas in (A) Cowal and Trossachs, South West Scotland, (B) Galloway, South West Scotland and (C) Kielder, Northern England. Stand types were as follows: Clearfell (1), Young (2), Thicket (3), Thin (4), Mature (5). See appendix 3 for stand details.

3.3.1 Invertebrate trapping

Each site was surveyed for one night. Moths were trapped using portable 6W heath light traps using E7586 9'' actinic tube lights, powered with 12V batteries which were activated 15 mins after sunset and switched off after 4 hours (approximating the duration of the shortest night in the study area). This ensured that species flying at dusk and during the night were surveyed regardless of night duration. Species flying at dawn would most likely be missed as traps were often turned off before dawn. Surveys were only conducted on nights that were above 8^{o}c in temperature and wind speed of less than Beaufort 4, and were randomised as far as possible during the survey season between the different geographical areas. I recognise that surveying each site only once provides a coarse estimate of local moth assemblages; however, I am primarily interested in comparisons between stand types in order to identify potentially influential characteristics, which requires a large sample size. This same approach has been used to identify the influence of woodland characteristics on species richness, diversity and abundance of moth populations in both agricultural and urban landscapes (Fuentes-Montemayor et al., 2012; Lintott et al., 2014). In addition, previous studies have suggested that patterns of moth community composition remain consistent despite seasonal turnover (Summerville and Crist 2003).

Within each stand a heath trap was placed 15 metres from the edge, at least 200m from the next nearest trap and the location recorded with a GPS. Traps were selectively positioned in order to ensure that similar light levels were emitted (for example ensuring that vegetation did not obscure the light). In most cases, the traps were not visible from each other, apart from in felled stands. This may introduce a bias in traps at felled sites as the lights were visible from further away, reducing spatial independence (Lacki et al., 2007) although the attraction radii of heath light traps is commonly between 10 – 30m depending on moth family (Truxa and Fiedler, 2012). Any moths attached to the outside of the trap at the end of the trapping session were gently removed and released. A cotton wool ball soaked in ethyl acetate was immediately added to the trap and left overnight to kill trapped invertebrates. Macro moths were removed and pinned to boards for later identification and micro moths were separated for identification by an expert at the National Museum of Scotland. Approval for this work was obtained from the Ethical Review Committee within the Department of Biological & Environmental Sciences at the University of Stirling. Species data were shared with local moth recorders and added to the National Moth Monitoring Scheme (Fox et al., 2010).

3.3.2 Local habitat characteristics

I carried out vegetation surveys in two 0.01 ha plots at each stand type; due to the homogenous nature of stands these plots were considered representative of the stand as a whole. At each plot I recorded the total number of trees with diameter at breast height greater than 7 cm (stand density) and recorded the dominant ground cover (vegetated / non vegetated). Since dead wood is important for saproxylic moths I assessed the amount of dead wood on the forest floor using the following scale: 0 – no coarse woody debris, 1 – small twigs, 2 – large twigs and branches over 7cm in diameter, 3 – both large and small branches. Understory vegetation height was measured at 10 evenly spaced points across the radius of the circle and canopy cover was recorded at each point using a sighting tube with an internal crosshair; if the crosshair intersected with any canopy vegetation presence of canopy cover was recorded and converted to a percentage cover score (Lintott et al., 2015).

3.3.3 Landscape analysis

The GUIDOS toolbox (Soille and Vogt, 2009) was used to determine percentage cover of broadleaf forest cover, closed canopy conifer, felled land (within the previous five years) and open land within 4km of each moth trap by combining data from the OS Mastermap (EDINA, 2014) and a high resolution Forestry Commission database specific to the study areas.

3.3.4 Statistical analysis

All analysis was carried out using R (version 3.4, R core development team) using the following packages: MuMIn, lme4, vegan, ggplot2. I used Margalef diversity to assess species diversity as it is straightforward to interpret and because it can deal with occasions where the number of individuals in a trap is equal to the number of species (Magurran, 1988). Micro and macro moths were analysed separately. Although the distinction between macro moths and micro moths is not taxonomically supported, micro moths typically have lower dispersal distances apart from some migratory species (Nieminen et al., 1999).

Many of the local and landscape variables were collinear so I used principle components analysis (PCA) to remove collinearity and reduce the number of predictors. Three separate PCAs were conducted for local, felling and broadleaf characteristics (See appendix 1 for an explanation of the variables included in the PCA). For each PCA I retained those axes which explained more variation than random using the "broken stick" approach (Jackson, 1993). For the local characteristics (Local PC), the first two axes explained 77% of the variation between stands; Local PC1 mainly explained the change from stands with low canopy cover and high understorey vegetation height to stands with low vegetation cover and high canopy cover, and loosely described different stand types (appendix 2, Figure A). Local PC2 was driven largely by differences in altitude, describing the difference between the three different forests, with Galloway sites primarily at low altitudes, Kielder stands predominantly at high altitudes and Cowal and Trossachs falling in between. For felling characteristics (Felling PC), only the first axis explained more variation (63%) than by chance; stands with low values of Felling PC1 were closer to patches of clearfell and surrounded by greater areas of felling in a 1km radius and those loading high on Felling PC1 were further from felling with less overall felling in a 1km radius (appendix 2, Figure C). For characteristics relating to broadleaf tree cover in the landscape (Broadleaf PC), only the first axis explained more variation (67%) than by chance; stands loading high on Broadleaf PC1 were further from smaller patches of broadleaf tree cover, with less broadleaf tree cover in the surrounding landscape whereas sites loading low on Broadleaf PC1 were closer to larger patches of broadleaf, with more overall broadleaf tree cover in the surrounding habitat (appendix 2, Figure B).

Using an information theoretic approach, I assessed the influence of stand and landscape variables on the **abundance** and **species richness** of macro and micro moths separately, using each metric per stand as the unit of replication. I used generalised linear models with a negative binomial error structure to account for overdispersion, and included an interaction between latitude and longitude as a fixed effect in all models to account for spatial autocorrelation. Models were validated by visual assessment of the residuals (Crawley, 2007). Continuous variables were standardised and centred around a mean of zero and a standard deviation of 1 to allow direct comparisons of estimates, and model fit was assessed by comparing the change in AIC, retaining the best model (change in AIC greater than 2). McFaddens pseudo R^2 (McFadden, 1974) was used to assess the amount of variation explained by each model. Local PC2 was not used, as this mainly described the difference in altitude between the stands and was collinear with date; in all cases simply using date was a better predictor. Models were fitted using either the stand type or the Local PC1, depending on model fit. I assessed the impact of felling and surrounding broadleaf on each response measure using either Felling PC1 or Broadleaf PC1 separately. The same process was followed for **Margalef diversity** and **dominance** using a Gaussian error distribution. For each response measure, if there was no clear "top" model I averaged the coefficients across the top models in the set which accounted for a change in AIC of less than 2, using full averaged models to reduce the bias from explanatory factors which do not appear in every model (Burnham and Anderson 2002). Explanatory variables were considered to have a "significant" effect on the responses if the standard error of the estimate did not cross zero (Burnham and Anderson, 2002).

In addition to moth diversity measures outlined above, I could model the influence of local and landscape characteristics on the occurrence of six of 13 **BAP priority species** recorded in the plantations. The following six species (*Eugnorisma glareosa* (Autumnal Rustic), *Arctia caja* (Garden Tiger), *Celaena haworthii* (Haworths Rustic), *Xestia castanea* (Neglected Rustic), *Ecliptopera silaceata* (Small Phoenix) and *Spilosoma lubricipeda* (White Ermine)) were present at the most sites and represented species which have declined between 70 – 90% over the last ten years (Conrad et al., 2006). I had insufficient data to model abundance at stand-level, so presence of these species was modelled using a binomial mixed effects model with species ID as a random intercept and Local PC1 as a random slope in order to assess species specific responses to stand level changes. I used the same approach as the previous analyses but in this situation visual inspection of the data and subsequent model checking indicated that species occurrence was strongly and similarly associated with distance to felled areas and the size of broadleaf patches, so these were used in preference to the Felled and Broadleaf PC axis.

I graphically present the results for the single best model for each analysis including standardised parameters and standard errors for all explanatory variables, as well as the individual models included in model averaged sets. Inferences were made by comparing each parameters standardised estimate with other predictor variables to assess its relative importance, the upper and lower 95% quantiles of each parameter obtained from N = 2000 simulated draws from the estimated distribution (Lintott et al., 2014) and a comparison of selected models using AIC.

3.4 Results

3.4.1 Composition of moth populations in commercial coniferous plantations

I collected a total of 8074 moths comprising 6464 macro moths belonging to 140 species and 10 families, and 1762 micro moths, belonging to 90 species and 19 families (appendix 4). Of these, 60% were generalist species while only 14% were forest specialists and 26% were associated with open habitats (open specialists). I recorded an average of 38 (± 4.2) macro moth species and 10 (± 1.5) micro moth species per stand. Species composition was dominated by a few, highly abundant species such as the micro moth *Scoparia ambigualis* and the macro moth *Colostygia pectinataria*, with 34% of macro moth species accounting for over 80% of all macro moths, and less than 20% of micro moth species accounted for over 80% of all micro moths collected (Figure 3.2). I recorded 13 BAP priority species, with an average of 3.2 ±0.6 per stand.

3.4.2 Influence of local characteristics on moth communities

After accounting for date and temperature, there was relatively little influence of local characteristics on moth communities (Table 3.1), with associations between Local PC1 and macro moth abundance only. Abundance was highest in stands with a low Local PC1 score (low canopy cover and high vegetation height), falling 53% in older stands with a closed canopy and lower understory vegetation height. Fewer moths of both groups were collected later on in the season, with a similar pattern for species richness and diversity, but not dominance. Finally, the interaction between latitude and longitude influenced richness, abundance and diversity for micro moths but not macro moths (Table 3.1) revealing regional differences in species richness and abundance, with the highest abundance in Galloway plantation (27.0 ± 3) and lower in Kielder (13.0 ± 1.6) and Cowal and Trossachs (8.5 ± 1.3).

3.4.3 Influence of felling on moth communities

There was a negative impact of felling on species richness, abundance and diversity for both macro- and micro moths (Figure 3.3, Table 3.1). Macro moth species richness fell from 13.4 (9.3 – 19.4) in sites furthest from felling and with less felling within 1km to 4.0 (2.5 – 6.6) in sites nearest to felling or surrounded by more felling in 1km. Similarly, micro moth species richness fell from 4.2 (2.9 – 6.2) to 1.5 (0.9 – 2.5) in sites close to felling or with a greater proportion of felling in the surrounding landscape (Figure 3.3 A, D). Both micro and macro moth abundance responded strongly to Felling PC1; macro moth abundance decreased from 68.0 (40.0 – 114.0) moths in sites far from felling or with a low proportion of felling in the surrounding landscape to 10.0 (5. 4 – 18.5) in sites further from felling or with less felling in the surrounding landscape, and micro moth abundance decreased from 25.0 (14.0 – 42.0) individuals to 2.5 (1.3 – 4.9) individuals (Figure 3.3 B, E). There was little response of diversity of either group to felling (Figure 3.3 C, F).

3.4.4 Effects of the presence of broadleaf on moth communities

In general, an increase in the amount of broadleaf tree cover within 4km of the site and a decrease in the distance from broadleaf forest cover are associated with higher species richness, abundance and diversity for both macro and micro moths, although the effect was smaller than the impact of felling (Table 3.1, Figure 3.4). The effect is clearest for species richness, with richness of macro moths in stands nearest to the largest patches of broadleaf double that of stands furthest from smaller patches of broadleaf, increasing from 7.0 (5.0 – 9.0) species to 15.0 (8.0 – 29.0) species per stand (Figure 3.4A). Similarly, micro moth richness increased from 2.5 (1.3 – 3.1) species in stands far from broadleaf and with a low proportion of broadleaf in the surrounding area to 5.0 (3.0 – 10.0) species richness in stands closest to broadleaf or with a high proportion of broadleaf in the surrounding landscape (Figure 3.4D). Whilst the influence of broadleaf tree cover on abundance of both groups is similar, the relationship appears to be weaker (Figures 3.4B, E), and for macro moths appears to be driven by high abundance at one particular site (Figure 3.4B). Neither local variables, felling nor broadleaf characteristics had any impact on macro or micro moth dominance. The interaction between felling PC1 and broadleaf PC1 was not supported as it was not retained in any top model.

Table 3.1. Best approximating GLM's assessing influence of local, felling and broadleaf parameters on moth richness, abundance, diversity and dominance, conducted using an information theoretic approach with model averaging to assess importance of parameters. NA's indicate parameters not included in the top model sets. Dominant ground cover, coarse woody debris and the interaction between Felling PC1 and Broadleaf PC1 was never included in any top models and are not presented here. Parameters in bold are those which have a significant effect on response values, determined by whether the standard error of the estimate crosses zero (Burnham and Anderson, 2002). *Akaikes weight is the total weight explained by all models. Averaged estimates are presented ± the standard error.*

		No. models averaged across	Intercept	Local PC1	Felling PC1	Broadleaf PC1	Date	Temp	Lat:Long	Akaike's weight
Macro moths	Sp. Richness	7	**264.9 ± 177.6**	**-0.70 ± 0.20**	**0.27 ± 0.08**	**-0.10 ± 0.00**	**-0.35 ± 0.11**	0.01 ± 0.05	0.27 ± 0.34	0.62
	Abundance	5	**3.21 ± 0.17**	**-0.26 ± 0.11**	**0.49 ± 0.12**	**-0.38 ± 0.17**	**-0.61 ± 0.19**	0.16 ± 0.16	0.21 ± 0.39	0.63
	Marg. Diversity	6	**2.01 ± 0.18**	-0.11 ± 0.12	**0.34 ± 0.11**	**-0.33 ± 0.14**	**-0.39 ± 0.15**	0.02 ± 0.07	0.30 ± 0.42	0.64
	Simp. diversity	9	**1.22 ± 0.19**	-0.04 ± 0.12	-0.03 ± 0.10	NA	0.08 ± 0.21	0.04 ± 0.11	NA	0.27
Micro moths	Sp. Richness	4	**1.23 ± 0.15**	-0.02 ± 0.06	**0.24 ± 0.09**	**-0.28 ± 0.11**	**-0.10 ± 0.13**	**0.33 ± 0.10**	**1.54 ± 0.40**	0.77
	Abundance	2	**2.28 ± 0.20**	NA	**0.47 ± 0.12**	**-0.45 ± 0.17**	**-0.32 ± 0.25**	**0.42 ± 0.15**	**1.93 ± 0.50**	0.73
	Marg. Diversity	4	**1.07 ± 0.10**	-0.01 ± 0.03	**0.13 ± 0.06**	**-0.14 ± 0.10**	**-0.13 ± 0.10**	**0.30 ± 0.07**	**0.86 ± 0.24**	0.65
	Simp. diversity	13	**0.75 ± 0.17**	-0.04 ± 0.11	NA	0.01 ± 0.05	-0.03 ± 0.11	0.10 ± 0.16	NA	0.43

Table 3.2: Best approximating GLM's assessing influence of local, felling and broadleaf parameters on BAP moth species probability of being detected. These were conducted using an information theoretic approach with model averaging to assess importance of parameters. NA's indicate parameters which were not included in the model. Dominant ground cover, coarse woody debris and the interaction between Felling PC1 and Broadleaf PC1 was never included in any top models and is not presented here. Parameters in bold are those which have a significant effect on response values, determined by whether the standard error of the estimate crosses zero (Burnham and Anderson 2002). Akaikes weight is the total weight explained by all models. Estimates for the full averaged model are presented ± the standard error. Estimates provided for the top 7 models, with a change in AIC of less than 2. The same variables as for the overall moth communities were originally used but inspection of the broadleaf and felling PC output showed that the main relationships were with specific components of the principle components

	Intercept	Size of nearest broadleaf patch	Altitude	Distance to felled stand	Lat:Long	Local_PC1	AICc	Akaikes weight
Averaged Model	**-2.88 ± 0.25**	**0.22 ± 0.09**	-0.04 ± 0.10	**0.16 ± 0.14**	0.02 ± 0.09	-0.44 ± 0.35		0.50
1	-2.95	0.22	NA	0.22	NA	-0.59	479.90	0.13
2	-2.92	0.22	NA	NA	NA	-0.53	480.92	0.08
3	-2.97	0.23	-0.13	0.24	NA	-0.59	480.96	0.07
4	-2.67	0.21	NA	0.21	NA	NA	481.17	0.07
5	-2.96	0.23	NA	0.20	0.09	-0.59	481.53	0.06
6	-2.98	0.27	-0.22	0.21	0.18	-0.59	481.56	0.05
7	-2.67	0.21	NA	NA	NA	NA	481.82	0.05

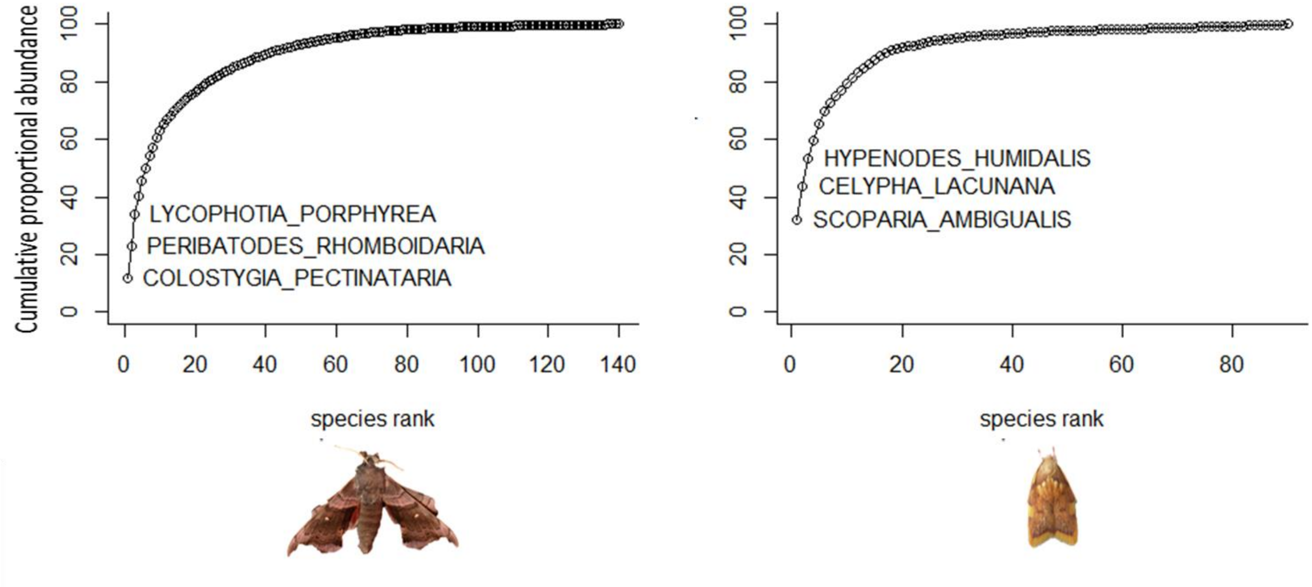


Figure 3.2: Species rank abundance curves for macro and micro moths considered separately. The three most abundant species are named. Rank abundances are given as cumulative proportions of total abundance.

3.4.5 Influence of local characteristics, felling and broadleaf tree cover on BAP priority species

The likelihood of catching a BAP species increased further from felled areas, and as the size of the nearest patch of broadleaf increased, with all six species having very similar response to both

Variables (Table 3.2). However, the influence of Local PC1 differed between the BAP priority species. The Autumnal Rustic (Figure 3.5 A) and the Small Phoenix (Figure 3.5 E) responded relatively strongly to Local PC1, and were more likely to be recorded in open stands with taller vegetation whereas there was relatively little change in the probability of capture for the Garden Tiger (Figure 3.5B).

3.5 Discussion:

Lepidoptera are one of the most abundant and diverse insect orders, but are currently undergoing widespread declines across Europe (Fox et al., 2013). Loss of habitat and changes to silvicultural practices in native woodlands have been cited as drivers of these losses, but so far the value of coniferous plantations for moths has been ignored due to their perception as being a poor habitat for biodiversity. This study demonstrates that plantations can support large communities of moths, including several BAP priority species, although I was only able to assess light attracted, night active Lepidoptera.

Macro moth abundance was highest in relatively low density stands with vegetation cover, which are more likely to support appropriate larval host plants, compared to dense stands with predominantly bare or moss as dominant ground cover.

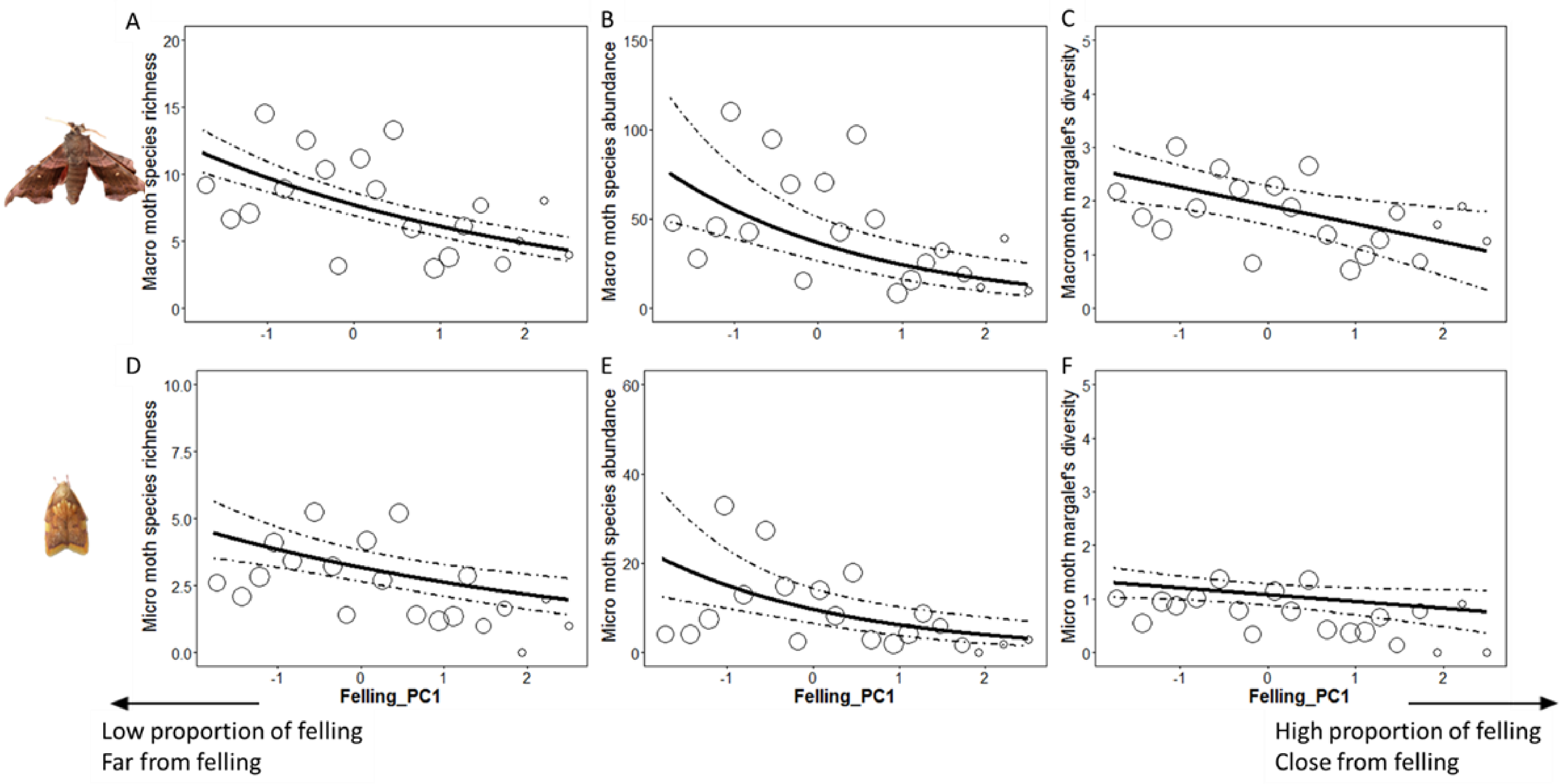


Figure 3.3: Impacts of felling on (A – C) Macro moth species richness, abundance and diversity and (D – F) Micro moth species richness, abundance and diversity per site. Different scales are used for abundance and richness due to higher richness and abundance in macro moths compared to micro moths. Original data on richness, abundance and diversity are superimposed as grey circles with diameter proportional to the number of sampling points where mean values occurred. Dashed lines represent 95% confidence intervals around the predictions (solid line).

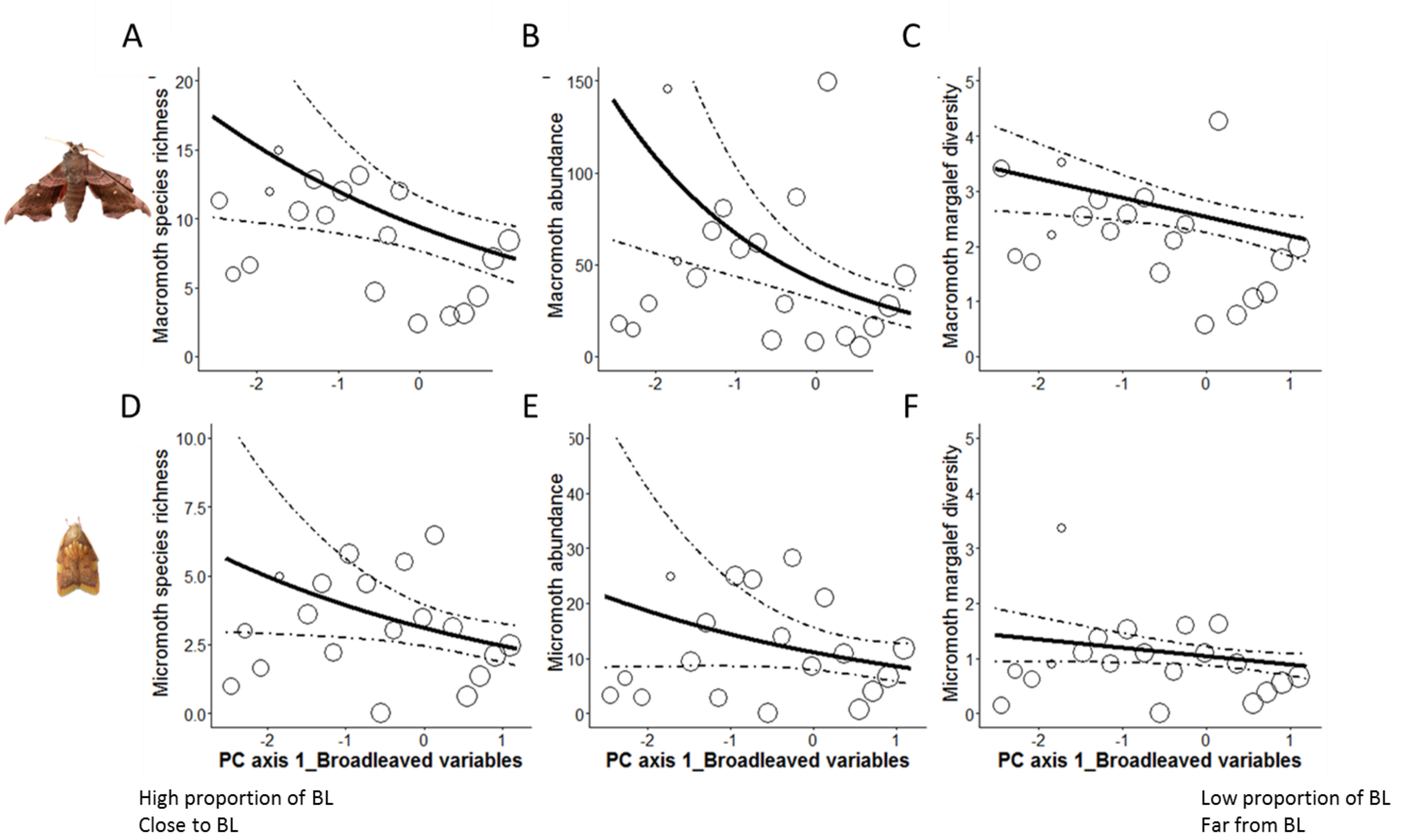


Figure 3.4: Impacts of the amount and proximity of broadleaved woodland (BL) on (A – C) Macro moth species richness, abundance and diversity, and (D – F) Micro moth species richness, abundance and diversity per stand. Different scales are used for abundance and richness due to higher richness and abundance in macro moths compared to micro moths. Original data on richness, abundance and diversity are superimposed as grey circles with diameter proportional to the number of stands where mean values occurred. Dashed lines represent 95% confidence intervals around the predictions

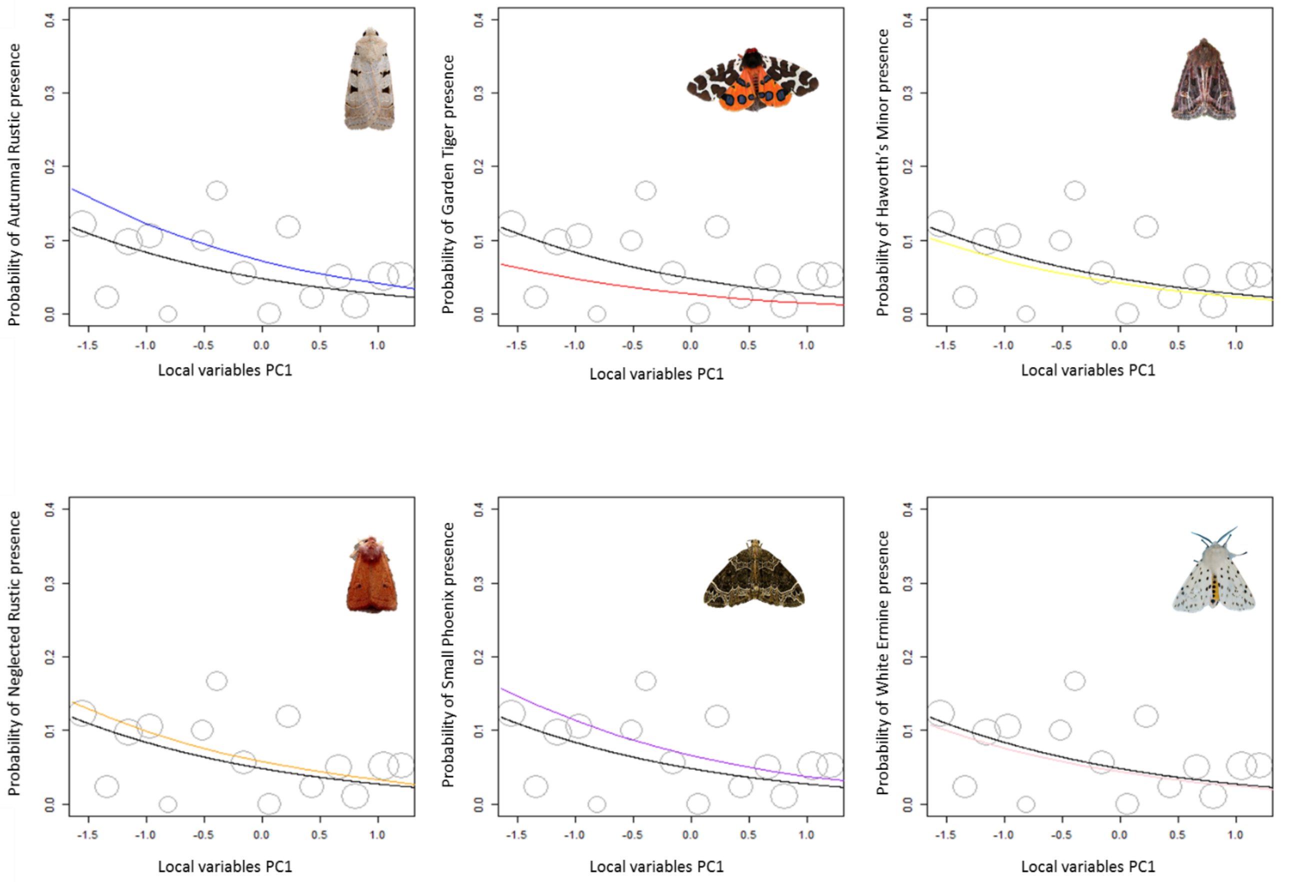


Figure 3.5: Probability of recording priority BAP species by Local PC1 scores (associated with a shift from stands with low canopy cover and taller vegetation height to stands with high canopy cover and low vegetation height). Sites low on PC1 are predominantly clearfell and young, moving to thin and mature aged stands loading high on PC1. Coloured lines are species specific, whilst the black line shows the trend across all six BAP species.

In addition, sites loading low on Local PC1 were often recently felled and young stands with large amounts of dead wood remaining which would benefit saproxylic species (Thorn et al., 2015). However, I saw no effect of stand characteristics on species richness or diversity in macro moths or for any micro moth response metric, possibly because I captured a high proportion of generalist moth species which have less strict habitat associations.

Felling had a substantial negative impact on both macro- and micro moth species richness, abundance and diversity. Macro and micro moth species richness was three times higher in sites furthest from felling, and with fewer felled patches in the immediate landscape, whereas abundance for macro and micro moths was between 7 and 10 times higher further from felling and with less felling in the surrounding landscape. This reflects patterns reported from managed native broadleaf forests in Indiana, which found that clear felling significantly reduced moth species richness compared to either no management or selective felling (Summerville and Crist, 2002). Clear felling causes substantial changes in the floristic composition of the forest habitat and through substantial changes in microclimate, herbaceous ground cover and host plant availability (Summerville, 2011). Summerville (2011, 2013) found that species richness of moths was 40% lower after timber removal, with the impacts of felling persisting up to 200m from the cleared site itself. The nature of the landscape matrix stands are embedded in may impede or facilitate dispersal between habitat types (Tscharntke et al., 2012); if there is too much felling in the surrounding landscape it may impede moth movements. Felled stands themselves may still be attractive to particular moth species due to intermediate levels of disturbance allowing pioneer and to some degree specialist species to coexist (Hamer et al., 2003). Indeed, in simplified landscapes, characterised by high disturbance, dynamics in habitat patches are likely to be determined by the availability of landscape wide remnant communities, particularly for species able to disperse over wide distances (Tscharntke et al., 2012).

Disturbed habitats are often characterised by a high abundance of a few generalist species, with the same subset of taxa dominating local stands and at the regional level. The majority of the moths I trapped were generalist species (appendix 4), this may reflect the fact that moths using the plantations are those which can persist in a disturbed environment, as generalist species are more resilient to disturbance (Franzén and Johannesson, 2007). For example, although 14% of all the moths I recorded are deciduous specialist feeders, the tree species they specialise on are very common. It is not possible to tell from our study whether moth populations in plantations differ significantly from those in native broadleaf woodlands. However, due to the levels of disturbance caused by felling and the potential lack of host plants, as well as the predominance of generalist species I found in our plantation sites, it would be expected that plantation forests support a less diverse moth population than broadleaf woodlands do. Macro moth species richness in the plantations was similar to that found in agricultural broadleaf woodlands, although abundance was lower, while micro moth richness was 25% higher than in agricultural woodlands (Fuentes-Montemayor et al., 2012). Micro moth richness was similar to that reported from urban woodlands, but macro moth richness was 40% higher in plantations (Lintott et al., 2014). It is therefore surprising that similar species richness and abundance was found in urban (Lintott et al., 2014) and agricultural woodlands (Fuentes-Montemayor et al., 2012) and it would be interesting to determine whether this is due to geographical differences (sites surveyed by Fuentes-Montemayor et al. 2012, and Lintott et al. 2014 were in Scotland but further north than the majority of sites surveyed for this study) or whether woodlands surrounded by agricultural and urban land are similarly disturbed habitats due to a more hostile matrix (Tscharntke et al., 2012), although the drivers of disturbance may differ.

Continuous cover forestry, which involves the continuous and uninterrupted maintenance of forest cover and avoids clear felling (Pommerening and Murphy, 2004), has been advocated as an alternative forest management system. The UK forest standard requires managers to identify areas "which can be managed under a continuous cover forestry system and build them into forest design" (Mason et al., 1999). Despite not being appropriate for widespread use in all plantation forests due to the potential risk of wind damage to stands, there is evidence to suggest that multi aged systems may be more resilient to impacts of wind (O'Hara and Ramage, 2013) and the potential forest health and yield benefits are increasingly recognised, with over 10% of Forestry Commission forests now under continuous cover management (Macdonald et al., 2009; O'Hara and Ramage, 2013). Switching to continuous cover forestry may benefit moth communities; in Indiana (USA) Summerville et al (2009) found that shelterwood harvesting (removal of 15% biomass and similar in concept to continuous cover forestry) did not reduce functional and compositional resilience of Lepidopteran communities compared to group selection harvesting and clear felling which had a significant negative impact. Additionally, moth communities showed signs of recovery within three years compared to other studies showing impoverished moth communities up to 60 years after clearfelling (Summerville, 2013; Summerville et al., 2009)

I found that moth species richness, and to some extent abundance, was greater in stands closer to larger patches of broadleaf tree cover, and those with a larger proportion of broadleaf within 4km. I found no evidence of an interaction between the proximity or size of broadleaf patches with the proximity or extent of felling, indicating that the presence of broadleaf tree cover is beneficial in both heavily felled and non felled areas, and as such may act as valuable mitigation for disturbance caused by felling. Many native tree species such as *Betula*, *Quercus* and *Salix* have large numbers of moth species associated with them (Tallamy and Shropshire, 2009) and are commonly planted in conifer plantations as broadleaf regeneration trees. Fuentes-Montemayor et al (2012) found that species richness was highest in woodland with no conifers, so patches of broadleaf tree cover within the plantation landscape may be invaluable islands allowing moth species to persist within the plantation matrix despite felling disturbance.

I recorded 13 BAP priority species using plantation forests. Of these, seven were present in fewer than 10 sites and were removed from further modelling. Of the six remaining species, all are habitat generalists or conifer and moorland habitat specialists. These species responded to stand type characteristics (separated by local PC1) differently. The Autumnal Rustic (*Eugnorisma glareosa*) and the Small Phoenix (*Ecliptopera silaceata*) were most likely to be detected in open stands with low canopy cover and stand density; the Autumnal Rustic is a generalist species often associated with moorland habitats which constitute a large proportion of the surrounding landscape and the Small

Phoenix is a conifer specialist, and therefore likely to thrive in conifer plantations. All BAP species were significantly less likely to be recorded in stands closer to felled areas regardless of the size of the felled area or the proportion of felling in the surrounding area, which considering two species' preference for open stands is somewhat surprising. All BAP species also responded equally positively to the size of the nearest patch of broadleaf. Broadleaf areas within plantations are not part of active harvesting programs, and are maintained or increased to meet biodiversity and restructuring guidelines (Watts et al., 2008), so may provide a potential source from which moth species can disperse.

3.5.1 Management recommendations:

Worldwide, forest managers increasingly recognise the importance of sustainable forest management to improve biodiversity but exotic pine plantations have received relatively little attention for potential contribution to moth diversity above and beyond the potential impacts of pest moth species. However, I found similar or higher levels of abundance and diversity compared to fragmented urban and agricultural woodlands in nearby regions (Fuentes-Montemayor et al., 2012; Lintott et al., 2014), and more BAP priority species in conifer plantations than urban woodlands (Lintott et al., 2014). I found that moth richness, abundance and diversity were directly impacted by plantation management and consider that the following should be taken into account when considering how plantation management may impact moth communities:

1. Switching to continuous cover forestry:

   Similar to other studies in native forests under felling pressure (Summerville, 2014, 2013, 2011; Summerville et al., 2009; Summerville and Crist, 2002), felling significantly affected moth populations in our study sites, reducing species richness and abundance. Since clear felling was the only timber extraction technique used at our sites I was not able to compare with other lower-intensity methods. However, Summerville et al (2013) and Thorn et al. (2015) showed that felling regimes which removed 15% or less tree volume, and allowed some dead wood to remain (analogous to continuous cover forestry), had a lower impact on moth populations than clear felling or salvage logging. Switching to continuous cover forestry where appropriate will benefit moth communities and in turn the small mammal, bird and bat species which rely on them as a prey source while not negatively impacting forest productivity (Macdonald et al., 2009). As logging significantly reduces both moth species richness and abundance, this may reduce both the breadth and the magnitude of the ecosystem services provided by moths in commercial plantations (Fox et al., 2013; Merckx et al., 2012). Furthermore, it is highly likely that susceptibility to invasion by alien pest species is lower with increasing species richness; as there are many examples of moth species which are serious economic pests for plantation managers, an increased species richness of native moth species reduces the risk of invasion and widespread damage by invasive moth species (Hooper et al., 2005).

2. Maintaining broadleaf tree cover:

Moth abundance and richness was far higher close to broadleaf tree cover; continued replanting of broadleaf stands and reduced intensity of management where possible near broadleaf stands should benefit both micro and macro moth richness and abundance. Most moth species can only disperse over relatively short distances (Merckx et al., 2012), therefore increasing the amount and connectivity of broadleaf tree cover may allow moth species to persist within and disperse throughout plantations. All BAP priority species responded strongly to the size of the nearest patch of broadleaf, so reducing forestry operations near large areas of broadleaf tree cover is likely to benefit moth communities in general and BAP species in particular.

3. Monitoring BAP priority species in plantations:

Of all the BAP priority species, the Garden Tiger moth was of particular interest as it is a conspicuous species that has declined widely across the UK, possibly due to climatic changes such as warmer wetter winters (Conrad 2002). More northerly habitats may be essential for the persistence of this species, and low density plantation stands may be an important refuge for this species in the face of future climate change. In addition, the Autumnal Rustic which was abundant in plantation sites, has undergone substantial declines throughout the UK, thought to be related to pesticide use. Plantation sites should be included in long term monitoring programs to understand further how BAP priority species are using plantation forests.

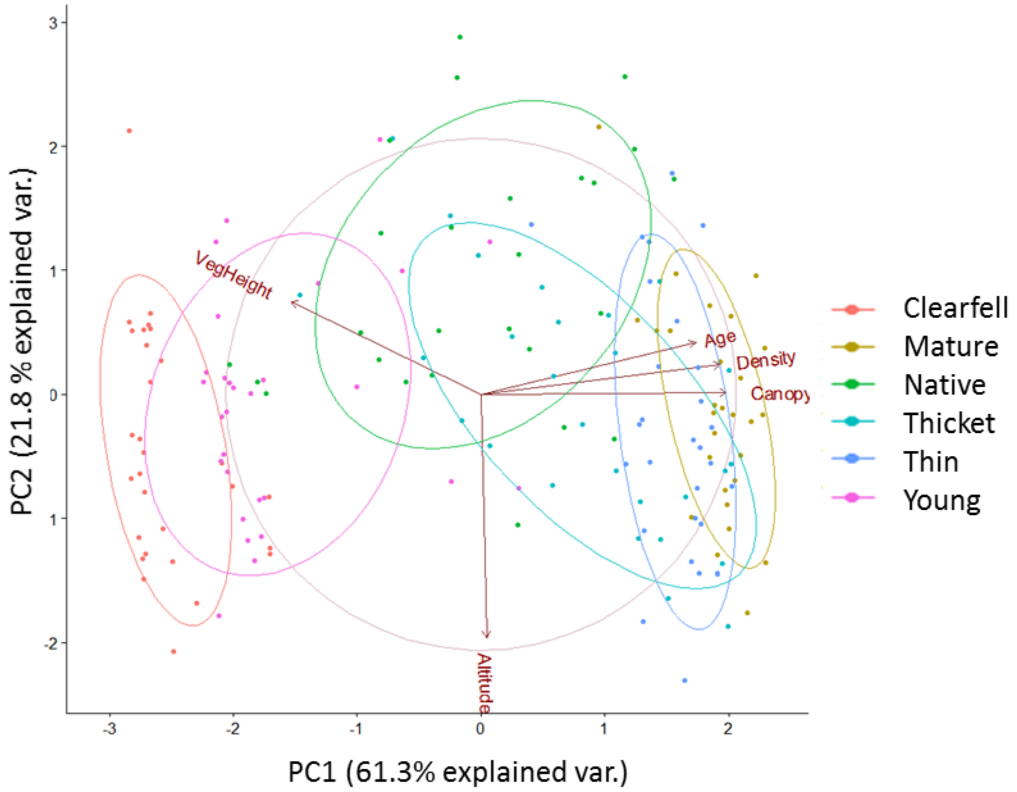
Moth communities in Sitka spruce plantations appear to be predominantly generalist species, which may imply a disturbed community (Summerville et al., 2009). However, some BAP species are present, and with sympathetic management plantation forests may have a role to play in preserving and improving moth populations particularly as climate change may cause species to extend their range northward.

Appendix 3.1:

Table 1: Variables included in Principle Components Analysis.

PC axis	Measure	Unit	Minimum	Maximum	Median	Description
Local PC1	Altitude	m	83.8	466	230.7	Height above sea level
Local PC1	Density	trees per ha	0	3000	600	Number of trees per hectare
Local PC1	Vegheight	mm	0	1744.1	156.6	Height of vegetation measured at 10 points across plot
Local PC1	Canopy cover	%	0	1	0.67	Total canopy cover as a percent
Local PC1	Stand Age	years	0	133	14	Stand age calculated from year of planting
Broadleaf PC1	BL_distance	m	0	3934	682	Distance in metres to nearest patch of mature broadleaf
Broadleaf PC1	BL_area	m2	0.1	163.2	1.3	Size of nearest mature broadleaf patch
Broadleaf PC1	Tot_BL_4000	%	0	11.3	0.8	Total broadleaf cover as a % of a 4km2 circle
Broadleaf PC1	Edge_BL_4000	%	0	2.9	0.2	Edge broadleaf cover as % of a 4km2 circle
Broadleaf PC1	Core_BL_4000	%	0	4.9	0.05	Core broadleaf (at least 10m from an edge) as a % of a 4km2 circle
Broadleaf PC1	Com_BL_4000	%	0	2.1	0.3	Total area / Edge area - complexity of cover within the landscape
Felled PC1	FE_distance	m	0	2670	527	Distance in metres to nearest felled stand
Felled PC1	FE_area	m2	0.04	92	13.9	Size of nearest felled stand
Felled PC1	Tot_FE_4000	%	0	35	5.1	Felled cover as a % of a 4km2 circle
Felled PC1	Edge_FE_4000	%	0	8	1.9	Edge felled cover as % of a 4km2 circle
Felled PC1	Core_FE_4000	%	0	26.5	2.4	Core felled (at least 10m from an edge) as a % of a 4km2 circle
Felled PC1	Com_FE_4000	%	0.8	2.1	1.5	Total area / Edge area - complexity of cover within the landscape

Appendix 3.2. Output from principle components analysis:



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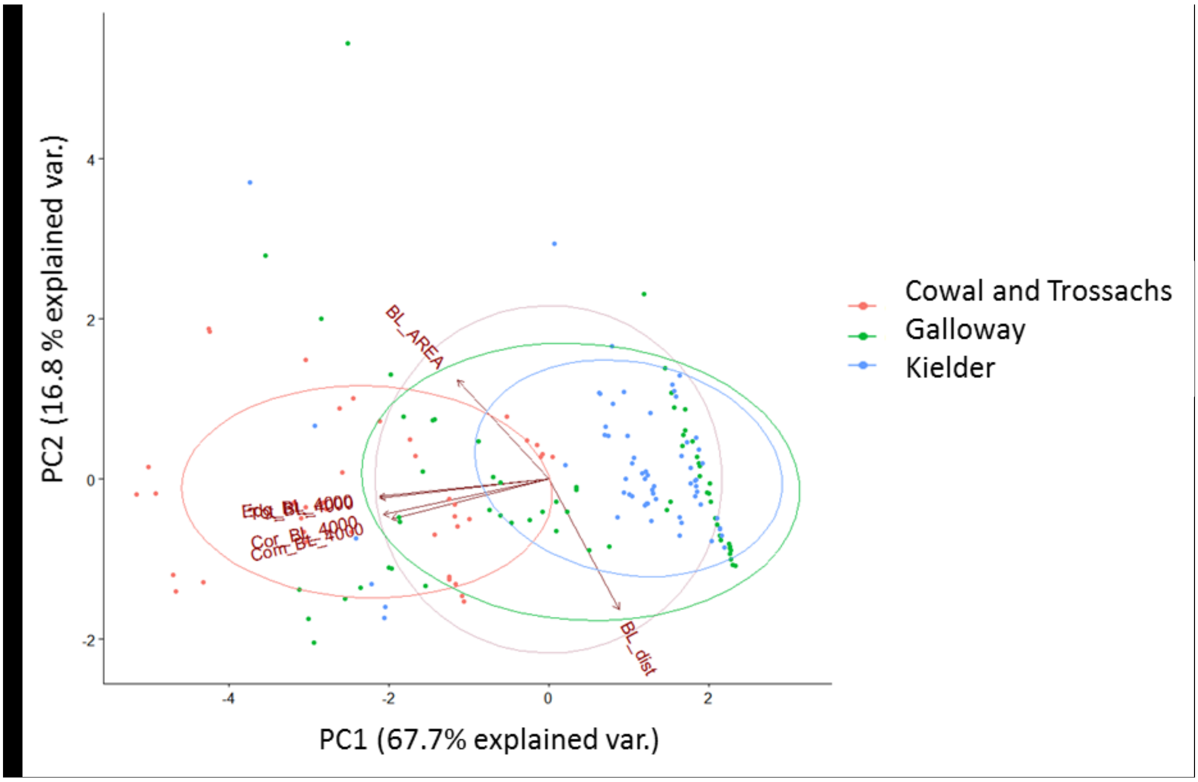


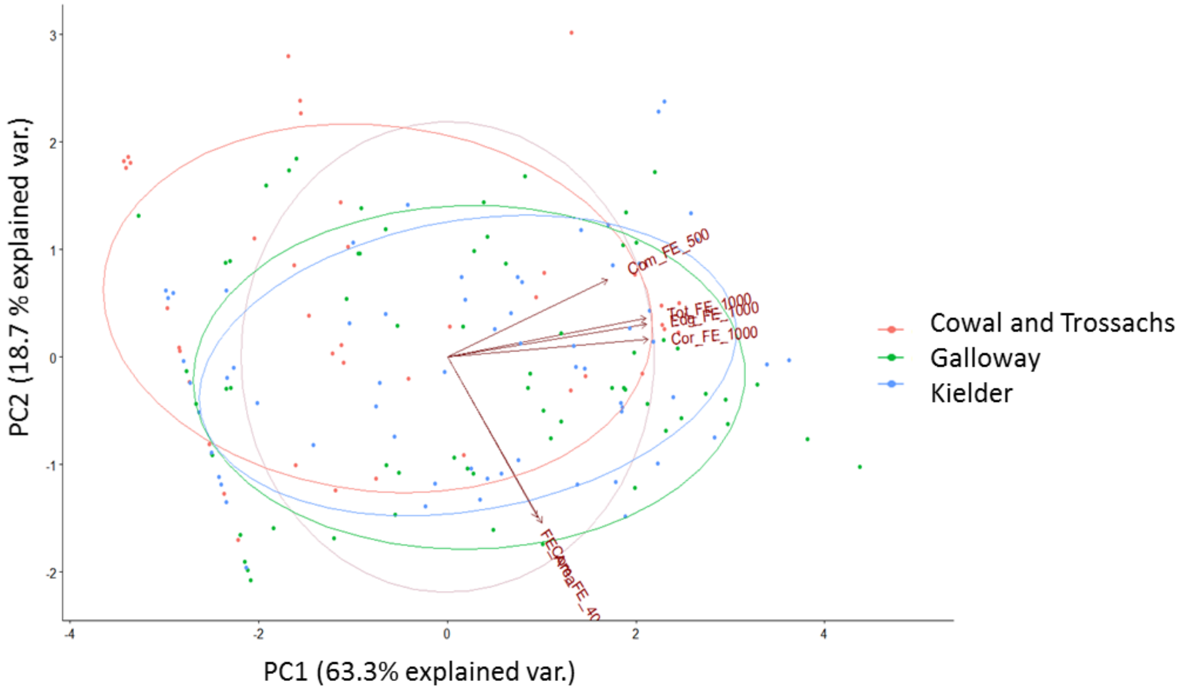


Figure 1. Principle components loadings for A) Local variables, B) Broadleaf variables and C) Felling variables. (see appendix 1). Sites are coloured by stand type (Local PC) and by plantation (Broadleaf PC and Felling PC). Coloured ellipses delineate sites within each plantation that are similar to each other based on a normal probability distribution of 0.68. Dark red ellipsoid encompasses sites across all three plantations within a normal probability distribution of 0.68. Arrows indicate direction and magnitude of relationship, variables that are close together or directly opposite are highly correlated.

Appendix 3.3:

Stand characteristics for each management stage and stand features associated with management.

*Diameter at Breast Height – estimate of tree maturity

Stand Age	Management Stage	Key stand features
40 – 60 years	Mature	Occasionally thinned, stand density between 500 and 2200 stems ha^{-1}, average stand density: 1267 stems ha^{-1}, canopy closure between 80 and 100%, average closure 99%
20 – 40 years	Thin	Trees more densely packed, losing midstem branches and some trees dying off (self thinned). Occasionally thinned through management. Stand density between 600 – 2800 stems ha^{-1}, average stand density: 1624 stems ha^{-1}. Canopy closure between 50 and 100%, average closure: 95%
10 – 20 years	Thicket	Very dense, retain midstem branches, no undergrowth. Stand density between 300 – 3000 stems ha^{-1}, average stand density: 1850 stems ha^{-1}. Canopy closure between 16 and 100%, average closure: 69%
5 – 10 years	Young	Small, nearly all trees < 7cm DBH*, no canopy closure, lots of vegetation and ground cover
Clearfell	Felled < 5 years ago	Lots of dead wood and brash, standing water and undergrowth
Native	Unmanaged	Broadleaf stand, planted as part of plantation restructuring

Appendix 3.4: Full list of moth species recorded as part of study. [a] signifies BAP species.

Table 1: Macro moth species:

Common name (Family)	Latin Name	Abundance per trap (± SE)	Habitat preference
Antler Moth (Noctuidae)	*Cerapteryx graminis*	0.24 ± 0.08	Grassland
Autumnal Rustic (Noctuidae)[a]	*Eugnorisma glareosa*	0.47 ± 0.17	Generalist
Barred Chestnut (Noctuidae)	*Diarsia dahlii*	0.01 ± 0.01	Deciduous
Barred Red (Geometridae)	*Hylaea fasciaria*	1.21 ± 0.33	Conifer
Barred Straw (Geometridae)	*Gandaritis pyraliata*	0.34 ± 0.13	Generalist
Barred Umber (Geometridae)	*Plagodis pulveraria*	0.01 ± 0.01	Deciduous
Beautiful Carpet Moth (Geometridae)	*Mesoleuca albicillata*	0.04 ± 0.02	Deciduous
Beautiful Golden Y (Noctuidae)	*Autographa pulchrina*	0.39 ± 0.10	Generalist
Bordered Beauty (Geometridae)	*Epione repandaria*	0.01 ± 0.01	Deciduous
Bordered Gothic (Noctuidae)	*Sideridis reticulata*	0.01 ± 0.01	Open ground
Bordered Pug (Geometridae)	*Eupithecia succenturiata*	0.01 ± 0.01	Generalist
Bordered Sallow (Noctuidae)	*Pyrrhia umbra*	0.02 ± 0.01	Grassland
Bordered White (Noctuidae)	*Bupalus piniaria*	0.07 ± 0.03	Conifer
Bright Line Brown Eye (Geometridae)	*Lacanobia oleracea*	0.02 ± 0.01	Generalist
Brimstone Moth (Noctuidae)	*Opisthograptis luteolata*	0.04 ± 0.03	Generalist
Broom Moth (Crambidae)	*Ceramica pisi*	0.12 ± 0.05	Moorland
Brown Rustic (Arctiidae)	*Elophila nymphaeata*	0.17 ± 0.11	Deciduous
Buff Ermine (Erebidae)	*Spilosoma lutea*	0.08 ± 0.03	Generalist
Buff Footman (Notodontidae)	*Eilema depressa*	0.19 ± 0.13	Wood generalist
Buff Tip (Noctuidae)	*Phalera bucephala*	0.01 ± 0.01	Deciduous
Burnished Brass (Geometridae)	*Diachrysia chrysitis*	0.12 ± 0.04	Open ground
Chevron (Arctiidae)	*Eulithis testata*	0.01 ± 0.01	Open ground
Clouded Border (Noctuidae)	*Tyria jacobaeae*	0.11 ± 0.05	Deciduous
Clouded Bordered Brindle (Erebidae)	*Apamea crenata*	0.06 ± 0.03	Grassland
Clouded Buff (Geometridae)	*Diacrisia sannio*	0.02 ± 0.01	Moorland
Clouded Magpie (Geometridae)	*Abraxas sylvata*	0.04 ± 0.03	Grassland
Common Carpet (Erebidae)	*Epirrhoe alternata*	0.23 ± 0.06	Generalist
Common Footman (Drepanidae)	*Eilema lurideola*	0.01 ± 0.01	Generalist
Common Lute String (Geometridae)	*Ochropacha duplaris*	0.01 ± 0.01	Deciduous
Common Marbled Carpet (Noctuidae)	*Dysstroma truncata*	0.01 ± 0.01	Wood generalist
Common Rustic (Hepialidae)	*Mesapamea secalis*	0.11 ± 0.07	Generalist
Common Wainscot (Geometridae)	*Korscheltellus lupulina*	0.42 ± 0.22	Grassland
Common Wave (Geometridae)	*Cabera exanthemata*	0.8 ± 0.22	Deciduous
Coxcomb Prominent (Noctuidae)	*Cabera pusaria*	0.07 ± 0.03	Deciduous
Dark Arches (Geometridae)	*Apamea monoglypha*	0.27 ± 0.09	Generalist
Dark Brocade (Geometridae)[a]	*Xanthorhoe ferrugata*	0.17 ± 0.10	Generalist
Dark Marbled Carpet (Noctuidae)	*Dysstroma citrata*	0.54 ± 0.14	Generalist
Dark Tussock (Noctuidae)	*Abrostola triplasia*	0.01 ± 0.01	Open ground
Dotted Carpet (Noctuidae)	*Aporophyla lutulenta*	0.01 ± 0.01	Wood generalist
Dotted Clay (Noctuidae)	*Xestia baja*	0.22 ± 0.10	Generalist

Double Dart (Noctuidae)[a]	*Graphiphora augur*	0.02 ± 0.01	Wood generalist
Double Square Spot (Geometridae)	*Xestia triangulum*	0.27 ± 0.13	Deciduous
Double Striped Pug (Lasiocampidae)	*Gymnoscelis rufifasciata*	0.04 ± 0.02	Generalist
Drinker Moth (Noctuidae)	*Euthrix potatoria*	0.36 ± 0.09	Generalist
Dusky Brocade (Noctuidae)[a]	*Apamea remissa*	0.02 ± 0.02	Generalist
Dwarf Pug (Geometridae)	*Eupithecia tantillaria*	0.02 ± 0.01	Conifer
Ear Moth (Geometridae)[a]	*Amphipoea oculea*	0.08 ± 0.04	Generalist
Flame Carpet (Noctuidae)	*Selenia dentaria*	0.53 ± 0.14	Generalist
Flame Shoulder (Noctuidae)	*Ochropleura plecta*	0.58 ± 0.14	Generalist
Four Dotted Footman (Geometridae)	*Luperina testacea*	0.1 ± 0.05	Generalist
Foxglove Pug (Geometridae)	*Eupithecia pulchellata*	0.01 ± 0.01	Generalist
Frosted Orange (Noctuidae)	*Gortyna flavago*	0.01 ± 0.01	Generalist
Garden Carpet (Geometridae)	*Xanthorhoe fluctata*	0.13 ± 0.10	Generalist
Garden Tiger (Erebidae)[a]	*Arctia caja*	0.33 ± 0.12	Generalist
Gold Spangle (Noctuidae)	*Autographa bractea*	0.01 ± 0.01	Generalist
Gold Swift (Hepialidae)	*Phymatopus hecta*	0.02 ± 0.02	Generalist
Golden Rod Pug (Geometridae)	*Eupitheca virgaureata*	0.02 ± 0.01	Generalist
Golden Y (Noctuidae)	*Autographa jota*	0.09 ± 0.04	Generalist
Gothic (Noctuidae)	*Naenia typica*	0.01 ± 0.01	Deciduous
Green Arches (Noctuidae)	*Anaplectoides prasina*	0.01 ± 0.01	Generalist
Green Carpet (Geometridae)	*Colostygia pectinataria*	4.44 ± 0.86	Deciduous
Green Pug (Geometridae)	*Pasiphila rectangulata*	0.01 ± 0.01	Deciduous
Grey Arches (Noctuidae)	*Polia nebulosa*	0.01 ± 0.01	Generalist
Grey Dagger (Noctuidae)[a]	*Acronicta psi*	0.01 ± 0.01	Deciduous
Grey Mountain Carpet (Geometridae)[a]	*Entephria caesiata*	0.13 ± 0.05	Generalist
Grey Pine (Geometridae)	*Thera obeliscata*	0.03 ± 0.03	Moorland
Haworths Minor (Noctuidae)[a]	*Celaena haworthii*	0.18 ± 0.08	Conifer
Heath Rustic (Noctuidae)[a]	*Xestia agathina*	0.15 ± 0.13	Moorland
Ingrailed Clay (Noctuidae)	*Diarsia mendica*	2.36 ± 0.50	Open ground
July Highflyer (Geometridae)	*Hydriomena furcata*	1.54 ± 0.44	Generalist
Knotgrass (Noctuidae)[a]	*Acronicta rumicis*	0.03 ± 0.01	Wood generalist
Larch Pug (Geometridae)	*Eupithecia lariciata*	0.05 ± 0.03	Conifer
Large Emerald (Geometridae)	*Geometra papilionaria*	0.09 ± 0.04	Generalist
Large Yellow Underwing (Noctuidae)	*Noctua pronuba*	1.66 ± 1.01	Generalist
Latticed Heath (Geometridae)[a]	*Chiasmia clathrata*	0.01 ± 0.01	Generalist
Lempkes Gold Spot (Noctuidae)	*Plusia putnami*	0.14 ± 0.05	Generalist
Lesser Swallow Prominent (Notodontidae)	*Pheosia gnoma*	0.01 ± 0.01	Open ground
Lesser Yellow Underwing (Noctuidae)	*Noctua comes*	0.36 ± 0.15	Generalist
Light Emerald (Geometridae)	*Campaea margaritaria*	0.15 ± 0.07	Generalist
Map Winged Swift (Hepialidae)	*Korscheltellus fusconebulosa*	2.09 ± 0.39	Wood generalist
Marbled Minor (Noctuidae)	*Oligia strigilis*	0.11 ± 0.06	Generalist
Middle Barred Minor (Noctuidae)	*Oligia fasciuncula*	0.39 ± 0.14	Generalist
Mouse Moth (Noctuidae)[a]	*Amphipyra tragopoginis*	0.01 ± 0.01	Generalist
Muslin Footman (Arctiidae)	*Nudaria mundana*	0.09 ± 0.03	generalist

Narrow Winged Pug (Geometridae)	*Eupithecia nanata*	0.21 ± 0.09	Generalist
Neglected Rustic (Noctuidae)[a]	*Xestia castanea*	0.04 ± 0.02	Open ground
Northern Arches (Noctuidae)	*Apamea exulis*	0.91 ± 0.31	Open ground
Northern Spinach (Geometridae)	*Eulithis populata*	0.01 ± 0.01	Open ground
Pale Eggar (Lasiocampidae)[a]	*Trichiura crataegi*	0.02 ± 0.01	Generalist
Peach Blossom (Drepanidae)	*Thyatira batis*	0.04 ± 0.02	Generalist
Pebble Prominent (Notodontidae)	*Notodonta ziczac*	0.05 ± 0.02	Deciduous
Pine Carpet (Geometridae)	*Pennithera firmata*	0.01 ± 0.01	Deciduous
Pink Barred Sallow (Noctuidae)	*Xanthia togata*	0.04 ± 0.02	Conifer
Poplar Grey (Noctuidae)	*Subacronicta megacephala*	0.02 ± 0.01	Generalist
Poplar Hawk Moth (Sphingidae)	*Laothoe populi*	0.01 ± 0.01	Deciduous
Pretty Pinion (Geometridae)	*Perizoma blandiata*	0.29 ± 0.07	Generalist
Purple Bar (Geometridae)	*Cosmorhoe ocellata*	0.56 ± 0.15	Moorland
Purple Clay (Noctuidae)	*Diarsia brunnea*	0.09 ± 0.03	Open ground
Red Carpet (Geometridae)[a]	*Xanthorhoe decoloraria*	0.01 ± 0.01	Generalist
Red Twin Spot Carpet (Geometridae)	*Xanthorhoe spadicearia*	0.01 ± 0.01	Generalist
Riband Wave (Geometridae)	*Idaea aversata*	0.01 ± 0.01	Moorland
Rosy Minor (Noctuidae)	*Litoligia literosa*	0.01 ± 0.01	Generalist
Rustic (Noctuidae)[a]	*Hoplodrina blanda*	0.01 ± 0.01	Grassland
Sallow (Noctuidae)[a]	*Cirrhia icteritia*	0.01 ± 0.01	Generalist
Satyr Pug (Geometridae)	*Eupithecia satyrata*	0.01 ± 0.01	Moorland
Saxon (Noctuidae)	*Hyppa rectilinea*	0.28 ± 0.14	Generalist
Scalloped Hazel (Geometridae)	*Odontopera bidentata*	0.01 ± 0.01	Generalist
Scalloped Hooktip (Drepanidae)	*Falcaria lacertinaria*	0.04 ± 0.02	Wood generalist
Scalloped Oak (Geometridae)	*Crocallis elinguaria*	0.01 ± 0.01	Generalist
Scalloped Shell (Geometridae)	*Hydria undulata*	0.08 ± 0.04	Wood generalist
Scarce Silver Y (Noctuidae)	*Syngrapha interrogationis*	1.25 ± 0.43	Deciduous
Shoulder Striped Wainscot (Noctuidae)[a]	*Leucania comma*	0.01 ± 0.01	Moorland
Silver Ground Carpet (Geometridae)	*Xanthorhoe montanata*	0.01 ± 0.01	Generalist
Sixstriped Rustic (Noctuidae)	*Xestia sexstrigata*	0.17 ± 0.04	Generalist
Small Angleshades (Noctuidae)	*Euplexia lucipara*	0.01 ± 0.01	Generalist
Small Dotted Buff (Noctuidae)	*Photedes minima*	0.07 ± 0.03	Generalist
Small Fanfoot (Erebidae)	*Herminia grisealis*	0.09 ± 0.04	Generalist
Small Phoenix (Geometridae)[a]	*Ecliptopera silaceata*	0.07 ± 0.02	Deciduous
Small Rivulet (Geometridae)	*Perizoma alchemillata*	0.01 ± 0.01	Generalist
Small Square Spot (Noctuidae)[a]	*Diarsia rubi*	0.07 ± 0.04	Generalist
Small Wainscot (Noctuidae)	*Denticucullus pygmina*	0.21 ± 0.14	Generalist
Smokey Wainscot (Noctuidae)	*Mythimna impura*	0.01 ± 0.01	Generalist
Snout (Erebidae)	*Hypena proboscidalis*	0.08 ± 0.04	Generalist
Spruce Carpet (Geometridae)	*Thera britannica*	0.01 ± 0.01	Generalist
Square Spot Rustic (Noctuidae)	*Xestia xanthographa*	0.05 ± 0.03	Conifer
Square Spotted Clay (Noctuidae)	*Xestia stigmatica*	0.22 ± 0.10	Generalist
Straw Dot (Noctuidae)	*Rivula sericealis*	0.22 ± 0.11	Deciduous
Striped Twin Spot Carpet (Geometridae)	*Coenotephria salicata*	0.01 ± 0.01	Open ground
Swallow Prominent (Notodontidae)	*Pheosia tremula*	0.34 ± 0.10	Generalist

Tawny Barred Angle (Geometridae)	*Macaria liturata*	0.01 ± 0.01	Deciduous
The Clay (Noctuidae)	*Mythimna ferrago*	0.02 ± 0.02	Conifer
Treble Bar (Geometridae)	*Aplocera plagiata*	0.01 ± 0.01	Open ground
Triple Spotted Clay (Noctuidae)	*Xestia ditrapezium*	4.09 ± 0.82	Generalist
True Lovers Knot (Noctuidae)	*Lycophotia porphyrea*	0.07 ± 0.07	Deciduous
Twin Spot Carpet (Geometridae)	*Mesotype didymata*	0.01 ± 0.01	Moorland
Water Carpet (Geometridae)	*Lampropteryx suffumata*	0.04 ± 0.02	Open ground
Welsh Wave (Geometridae)	*Venusia cambrica*	0.05 ± 0.02	Generalist
White Ermine (Erebidae)[a]	*Spilosoma lubricipeda*	0.02 ± 0.01	Generalist
White Wave (Geometridae)	*Cabera pusaria*	4.07 ± 1.03	Generalist
Willow Beauty (Geometridae)	*Peribatodes rhomboidaria*	0.05 ± 0.03	Wood generalist
Wormwood Pug (Geometridae)	*Eupithecia absinthiata*	0.01 ± 0.01	Generalist

Table 2: List of micro moth species recorded:

Common name (Family)	Latin Name	Habitat preference	Abundance per trap (± SE)
Water Veneer (Crambidae)	*Acentria ephemerella*	Water	0.05 ± 0.03
Caledonian Button (Tortricidae)	*Acleris caledoniana*	Moorland	0.01 ± 0.01
Notched winged Tortricid (Tortricidae)	*Acleris emargana*	Deciduous	0.04 ± 0.02
Dark-triangle Buttion (Tortricidae)	*Acleris laterana*	Open ground	0.01 ± 0.01
Rhomboid Tortrix (Tortricidae)	*Acleris rhombana*	Generalist	0.01 ± 0.01
Thistle Conch (Tortricidae)	*Aethes cnicana*	Grassland	0.04 ± 0.03
Burdock Conch (Tortricidae)	*Aethes rubigana*	Open ground	0.01 ± 0.01
Hook-marked Straw Moth (Tortricidae)	*Agapeta hamana*	Open ground	0.01 ± 0.01
Hemlock Moth (Depressariidae)	*Agonopterix alstromeriana*	Open ground	0.01 ± 0.01
Angelica Flat-body (Depressariidae)	*Agonopterix angelicella*	Generalist	0.01 ± 0.01
Brindled Flat-body (Depressariidae)	*Agonopterix arenella*	Generalist	0.01 ± 0.01
Gorse Tip Moth (Depressariidae)	*Agonopterix nervosa*	Generalist	0.02 ± 0.01
Coastal Flat-body (Depressariidae)	*Agonopterix yeatiana*	Generalist	0.01 ± 0.01
Barred Grass Veneer (Crambidae)	*Agriphila inquinatella*	Grassland	0.02 ± 0.01
Pearl Veneer (Crambidae)	*Agriphila straminella*	Grassland	0.68 ± 0.18
Common Grass Veneer (Crambidae)	*Agriphila tristella*	Grassland	0.01 ± 0.01
Broken Barred Roller (Tortricidae)	*Ancylis unguicella*	Moorland	0.01 ± 0.01
Birch Marble (Tortricidae)	*Apotomis betuletana*	Deciduous	0.05 ± 0.03
Rush Marble (Tortricidae)	*Bactra lancealana*	Open ground	0.22 ± 0.07
(Blastobasidae)	*Blastobasis decolorella*	Wood generalist	0.01 ± 0.01
Dark Groundling (Gelechiidae)	*Bryotropha affinis*	Generalist	0.01 ± 0.01
(Gelechiidae)	*Bryotropha boreella*	Generalist	0.01 ± 0.01
Cinereous Groundling (Gelechiidae)	*Bryotropha terrella*	Grassland	0.01 ± 0.01
Pearl-band Grass Veneer (Crambidae)	*Catoptria margaritella*	Moorland	0.21 ± 0.10
Pearl Grass Veneer (Crambidae)	*Catoptria pinella*	Moorland	0.01 ± 0.01
Dark Strawberry Tortrix (Tortricidae)	*Celypha lacunana*	Generalist	1.23 ± 0.30
Garden Grass Veneer (Crambidae)	*Chrystoteuchia culmella*	Grassland	0.14 ± 0.06
Flax Tortrix (Tortricidae)	*Cnephasia asseclana*	Generalist	0.01 ± 0.01
Hedge Case-bearer (Coleophoridae)	*Coleophora striatipennella*	Deciduous	0.01 ± 0.01
Hook-streaked Grass Veneer (Crambidae)	*Crambus lathoniellus*	Grassland	0.01 ± 0.01
Grass Veneer (Crambidae)	*Crambus pascuella*	Grassland	0.31 ± 0.09
Grey Gorse Piercer (Tortricidae)	*Cydia ulicetana*	Open ground	0.23 ± 0.07
Northern Tubic (Oecophoridae)	*Denisia similella*	Deciduous	0.01 ± 0.01
Little Grey (Crambidae)	*Dipleurina lacustrata*	Deciduous	0.01 ± 0.01
(Crambidae)	*Donacaula micronellus*	Moorland	0.04 ± 0.02
Dotted Shade (Tortricidae)	*Eana osseana*	Open ground	0.01 ± 0.01
Brown China Mark (Crambidae)	*Elophila nymphaeata*	Water	0.01 ± 0.01
Knapweed Bell (Tortricidae)	*Epiblema cirsiana*	Deciduous	0.01 ± 0.01
Thistle Bell (Tortricidae)	*Epiblema scutulana*	Open ground	0.01 ± 0.01
Bramble Shoot Moth (Tortricidae)	*Epiblema uddmanniana*	Deciduous	0.01 ± 0.01
Square Barred Bell (Tortricidae)	*Epinotia fraternella*	Conifer	0.01 ± 0.01
Common Birch Bell (Tortricidae)	*Epinotia immundana*	Deciduous	0.16 ± 0.09

Grey Poplar Bell (Tortricidae)	*Epinotia nisella*	Deciduous	0.03 ± 0.03
Small Birch Bell (Tortricidae)	*Epinotia ramella*	Deciduous	0.01 ± 0.01
Variable Bell (Tortricidae)	*Epinotia solandriana*	Deciduous	0.01 ± 0.01
Common Spruce Bell (Tortricidae)	*Epinotia tedella*	Conifer	0.01 ± 0.01
White Blotch Bell (Tortricidae)	*Epinotia trigonella*	Wood generalist	0.11 ± 0.04
Bright Bell (Tortricidae)	*Eucosma hohenwartiana*	Grassland	0.02 ± 0.02
Two-coloured Bell (Tortricidae)	*Eucosma obumbratana*	Open ground	0.04 ± 0.02
Pied Grey (Crambidae)	*Eudonia delunella*	Deciduous	0.01 ± 0.01
Small Grey (Crambidae)	*Eudonia mercurella*	Deciduous	0.01 ± 0.01
Brassy Tortrix (Tortricidae)	*Eulia ministrana*	Deciduous	0.25 ± 0.16
Lilac Leafminer (Gracillariidae)	*Gracillaria syringella*	Generalist	0.01 ± 0.01
Small Fanfoot (Erebidae)	*Herminia grisealis*	Deciduous	0.02 ± 0.01
Marsh Oblique-barred (Erebidae)	*Hypenodes humidalis*	Open ground	0.99 ± 0.44
Red Piercer (Tortricidae)	*Lathronympha strigana*	Wood generalist	0.01 ± 0.01
Rust-blotch Cosmet (Momphidae)	*Mompha lacteella*	Grassland	0.01 ± 0.01
Little Cosmet (Momphidae)	*Mompha raschkiella*	Grassland	0.01 ± 0.01
Carrion Moth (tineidae)	*Monopis weaverella*	Generalist	0.01 ± 0.01
Heather Groundling (Gelechiidae)	*Neofaculta ericetella*	Moorland	0.01 ± 0.01
Beautiful China Mark (Crambidae)	*Nymphula stagnata*	Water	0.08 ± 0.03
Sorrel Bent-wing (Opostegidae)	*Opostega salaciella*	Grassland	0.01 ± 0.01
Woodland Marble (Tortricidae)	*Orthotaenia undulana*	Generalist	0.01 ± 0.01
Barred Fruit Tree Tortrix (Tortricidae)	*Pandemis cerasana*	Deciduous	0.04 ± 0.03
White-faced Tortrix (Tortricidae)	*Pandemis cinnamomeana*	Deciduous	0.01 ± 0.01
Dark Fruit Tree Tortrix (Tortricidae)	*Pandemis hepararia*	Deciduous	0.03 ± 0.01
Large Marble (Tortricidae)	*Phiaris schulziana*	Moorland	0.01 ± 0.01
Small Clouded Knot-horn (Pyralidae)	*Phycitodes saxicola*	Open ground	0.01 ± 0.01
Light Streak (Oecophoridae)	*Pleurota bicostella*	Moorland	0.01 ± 0.01
Diamondback Moth (Plutellidae)	*Plutella xylostella*	Generalist	0.01 ± 0.01
Ash Bud Moth (Praydicae)	*Prays fraxinella*	Deciduous	0.01 ± 0.01
White Plume Moth (Pterophoridae)	*Pterophorus pentadactyla*	Generalist	0.01 ± 0.01
Common Purple and Gold (Crambidae)	*Pyrausta purpuralis*	Grassland	0.01 ± 0.01
Holly Tortrix Moth (Tortricidae)	*Rhopobota naevana*	Generalist	0.04 ± 0.02
Pinion Streaked Snout (Hypenodinae)	*Schrankia costaestrigalis*	Open ground	0.57 ± 0.15
Common Grey (Crambidae)	*Scoparia ambigualis*	Deciduous	3.26 ± 0.62
Meadow Grey (Crambidae)	*Scoparia pyralella*	Open ground	0.05 ± 0.02
Brown Plume (Pterophoridae)	*Stenoptilia pterodactyla*	Generalist	0.01 ± 0.01
Fulvous Clothes Moth (tineidae)	*Tinea semifulvella*	Generalist	0.01 ± 0.01
Birds-nest Moth (tineidae)	*Tinea trinotella*	Generalist	0.01 ± 0.01
Pale Straw Pearl (Crambidae)	*Udea lutealis*	Generalist	0.17 ± 0.07
Olive Pearl (Crambidae)	*Udea olivalis*	Generalist	0.02 ± 0.01
Dusky Pearl (Crambidae)	*Udea prunalis*	Generalist	0.01 ± 0.01
Spindle Ermine (Yponomeutidae)	*Yponomeuta cagnagella*	Deciduous	0.01 ± 0.01
Bird-cherry Ermine (Yponomeutidae)	*Yponomeuta evonymella*	Deciduous	0.44 ± 0.43
White-shouldered Smudge (Ypsolophidae)	*Ypsolopha parenthesella*	Deciduous	0.01 ± 0.01
Larch Tortrix (Tortricidae)	*Zeiraphera griseana*	Conifer	0.15 ± 0.12
Spruce Bud Moth (Tortricidae)	*Zeiraphera ratzeburgiana*	Conifer	0.17 ± 0.06

Chapter Four

Chapter 4 Felling alters functional but not taxonomic diversity of moths in conifer plantations

Some moths trapped as part of the study. Photo reproduced with permission by Lynn Munro

4.1 Abstract:

Widespread concerns about the impact of human activities on ecosystems, and consequently ecosystem functioning, has made quantifying biodiversity important, but difficulties remain in deciding what to measure. The use of functional diversity, a measure which does not rely on species delineations, has been proposed as a suitable approach for providing a more mechanistic understanding of ecosystems, rather than traditional biodiversity metrics such as species richness. Functional diversity, which quantifies the range and relative abundance of particular functional traits within a given community, could therefore provide new insight into how anthropogenic pressure will affect diversity, and ecosystem processes. Moths are currently undergoing widespread declines, with habitat loss and anthropogenic impacts implicated as major drivers of species loss. Specifically, I aimed to determine whether particular functional groups were disproportionately vulnerable to felling pressure, or responsive to remnant patches of broadleaf in plantation landscapes, and whether diversity (including constraining for similarity due to shared taxonomy or functional traits) and redundancy (the degree to which species share the same functional traits) differs between plantation and broadleaf sites. I also investigated how remnant patches of broadleaf, and commercial felling, impact diversity using the same response measures. Finally, I assessed whether there was any evidence that abiotic factors (environmental filtering) were limiting species persistence or occurrence. I found that felling significantly decreased naïve and functional richness and diversity, but had no impact on taxonomic richness and diversity. The presence of broadleaf tree cover in the surrounding landscape was associated with moth communities with a greater range of larval host plants and habitat specialism, and primarily driven by the presence of rare species in stands closer to remnant broadleaf patches. There was little difference in functional richness and diversity between broadleaf and plantation sites, but higher redundancy in broadleaf woodlands, which may therefore be more resilient to environmental perturbations. Moth communities in plantation dominated landscapes may reflect historical deforestation pressure, which has resulted in the persistence of species which are relatively tolerant of disturbance. However, a high prevalence of clear felling in the surrounding landscape clearly significantly reduces moth functional diversity, particularly for species which over winter as an egg or a pupa. Switching to continuous cover forestry, and preserving and expanding remnant broadleaf patches where possible is likely to benefit moth communities, and overall functional diversity.

4.2 Introduction:

Widespread concerns about the impact of human activities on ecosystems have made the accurate measurement and assessment of biodiversity increasingly important. Species richness has long been the most commonly employed measure of biological diversity, yet this stems from the premise that species delineations are distinct (Hooper et al., 2002). Additionally, in most measures of species diversity all species are treated as equally different from each other, whereas this is clearly not the case (Chao et al., 2014; Leinster and Cobbold, 2012). For example, a community comprising distantly related species has more evolutionary diversity than a community with only closely related species. Likewise, an assemblage in which species share similar functional traits is less diverse than an assemblage with a range of functional traits, and may correspondingly result in reduced ecosystem functioning.

Measures of functional diversity (the range and relative abundance of particular functional traits within a given community), offer a more mechanistic understanding of ecosystems than using simple patterns of species diversity and evenness (Hooper et al., 2002). As such, they can inform on the effects that anthropogenic pressures have on the suite of functional traits in a community, rather than by taxonomic identity, and thereby on ecosystem processes (Hooper et al., 2005; Tilman, 2000). While species richness may act as a suitable surrogate for functional diversity, this will depend on patterns of species assemblage; if functional diversity increases linearly with species richness, then environmental filtering (the process by which abiotic factors limit the establishment or persistence of species with particular functional traits in a particular location) is unlikely to be occurring (Hooper et al., 2002). However, in systems characterised by disturbance and recovery, environmental filtering may result in reduced functional richness compared to species richness as specific functional traits may disproportionately unable to persist through disturbance (Mori et al., 2013). Alternatively, functional and species richness may be collinear as species assemblages may occur at random due to stochastic colonisation post disturbance events (Hooper et al., 2002). Functional traits also allow an alternative perspective on conservation. While the loss of a single species is serious from a conservation perspective, from a functional perspective a resilient ecosystem with high functional redundancy will be sustained through environmental perturbations despite a loss of individual species (Mori et al., 2013). Measures of functional redundancy and diversity can therefore be used to assess the vulnerability of ecosystems to changes of state from a functioning system to one with a reduced number of ecosystem services (Mori et al., 2013), when measures such as species richness or diversity may not detect that loss of a key functional trait is occurring.

Moths have undergone substantial declines in recent decades; two thirds of common and widespread species have suffered rapid population decreases (Conrad et al., 2006) with similar patterns occurring elsewhere in Europe (Franzén and Johannesson, 2007; Mattila et al., 2006). Rapid economic development, urbanisation, changes to silviculture, and agricultural expansion have all been implicated (Conrad et al., 2006; Fox et al., 2013) although there is little information on the impacts of forest management on moth communities in temperate plantations. Moths are a key component of terrestrial ecosystems providing ecosystem services through modification of ecosystem functioning by saproxylic species (Merckx et al., 2012), impacting upon plant growth through larval feeding activity, are pollinators and provide food for a range of taxa such as birds, small mammals and bats (Fox et al., 2013). Previous work (Chapter 3) demonstrated that clear felling significantly reduced moth abundance, species richness and diversity in commercial coniferous plantations, while the occurrence and close proximity to large stands of broadleaf had the opposite effect. While plantation management practices clearly influence moth abundance and diversity, the extent to which this affects functional diversity, and the ability of moth communities to persist through the felling cycle is unclear. This is key to understanding how moth communities may respond and recover from disturbance in order to continue performing key ecosystem functions.

Many plantation forests are even aged, with simplified forest structure through the loss of horizontal (spatial heterogeneity) and vertical (stratification) structural diversity (Sullivan et al., 2009). This is likely to support a lower invertebrate diversity than native or uneven aged forests due to a lack of old growth conditions and suitable understory habitat for a variety of species (Sullivan et al., 2009). For example, Spake et al (2016) found that carabid functional diversity was lower in stands with a high canopy cover, primarily driven by the loss of open habitat specialists. Overwintering style is a key response trait behind moth extinctions and distribution declines, with species overwintering as eggs or adults declining less than individuals overwintering as larvae or pupa (Mattila et al., 2006). Additionally, specificity either in larval feeding habits or habitat preferences has been linked with increased vulnerability to extinction and disturbance events (Betzholtz and Franzén, 2013; Mattila et al., 2006; Summerville and Crist, 2002). In Chapter 3, I demonstrated that clear felling negatively affected moth species richness and abundance. However, it was unclear whether this adversely impacted particular functional groups compared to others, or how this might compare to native broadleaf woodland, a higher quality habitat for most forest specialist moths. In this study, I aimed to build on our previous findings to determine the following:

1. Are functional groups similarly affected by clear felling of plantation forestry?
2. To what extent does the proximity and size of broadleaf tree cover in plantation landscapes reduce the impacts of clear felling on functional diversity?
3. How does moth functional richness and diversity differ between plantation stands and surrounding broadleaf woodlands?
4. Is there higher redundancy (i.e. more species filling the same functional niche) in broadleaf woodlands than in plantation forests?

4.3 Methods

Two different studies were carried out; one was conducted across three plantation forests during 2013 (late May until early September), comparing different stand types based on plantation management (Study 1). The other, comparing semi native broadleaf woodlands with paired plantation sites was carried out in 2014 and 2015 (late May until early September, Study 2).

4.3.1 Study 1: Within plantation comparison:

Three plantation forests in Central and Southern Scotland and Northern England (Figure 4.1A) were surveyed; these were chosen for their large size (30,000 ha in Cowal and Trossachs; 60,000 ha in Kielder;114,000 ha in Galloway), high productivity and the predominance of *Picea sitchensis*, the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each forest, multiple sites, a maximum of 2km^2 in size and at least 4 km from each other, were selected using a Forestry Commission sub-compartment database within a Geographic Information System (GIS) (ArcMap 10.1, ESRI) based on stand age and species composition (Figure 4.1 A).

In total seven sites were surveyed in Cowal and Trossachs, 12 in Galloway Forest and 12 in Kielder Forest. Where possible, a stand of trees at each management stage (from a total of six management stages: see supplementary data, appendix 4.1) were selected in each site. Not all sites had all stands of each management stage resulting in an unbalanced design of between four and six stands per site and a total of 285 stands across 31 sites.

4.3.2 Study 2. Broadleaf woodland and plantation forest comparison:

Fifteen paired broadleaf and plantation sites were selected in Galloway Forest Park, south west Scotland (Figure 4.1B). Previous to planting much of the Galloway area consisted of open upland and moorland habitat with low deciduous woodland cover due to historical deforestation. For comparison with plantations, I identified broadleaf woodlands which have existed since at least 1840, all of which were over 20ha in size. Most of these woodlands are publically owned and under conservation management although a few are privately owned. All broadleaf woodland sites were paired with felled plantation areas adjacent to mature stands (there appears to be little difference in moth richness and diversity between stand types; Chapter 3).

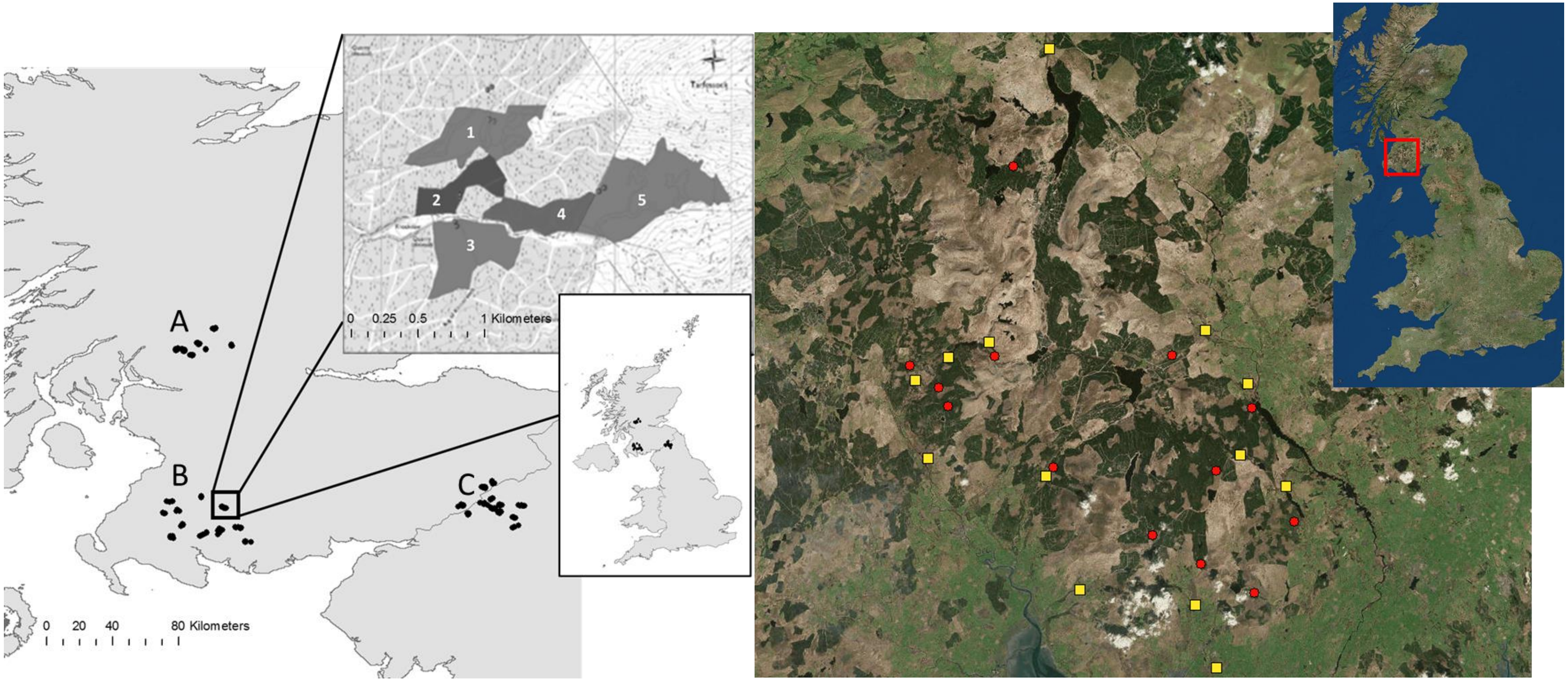


*Figure 4.1*A Location of field sites at three different study areas in (A) Cowal and Trossachs, South West Scotland, (B) Galloway, South West Scotland and (C) Kielder, Northern England. Stand types were as follows: Clearfell (felled less than 5 years ago, 1), Young (planted between 5 and 10 years ago, 2), Thicket (planted between 10 and 20 years ago, 3), Thin (planted between 20 and 40 years ago, 4), Mature (planted more than 40 years ago, 5). Figure 4.1B. Map showing sites (broadleaf woodlands are displayed as squares, plantations as circles. Colours indicate woodland types) and distribution around Galloway Forest Park.

Plantation sites were selected by identifying areas of plantation forest which were within at least 6km of the selected broadleaf site and at a similar altitude.

4.3.3 Invertebrate sampling protocol:

Each site was surveyed for one night. Moths were trapped using portable 6W heath light traps using E7586 9'' actinic tube lights, powered with 12V batteries which were activated 15 mins after sunset and switched off after 4 hours (approximating the duration of the shortest night in the study area). This ensured that species flying at dusk and night were surveyed regardless of night duration. Species flying at dawn would most likely be missed as traps were often turned off before dawn. Nights were only surveyed that were above 8 ^{o}C in temperature and wind speed of less than Beaufort 4. At the end of the surveying period, any moths attached to the outside of the trap were gently removed and released. A cotton wool ball soaked in ethyl acetate was immediately added to the trap and left overnight to kill trapped invertebrates. Macro moths were removed and pinned to boards for later identification including consultation with local recorders, and although micro moths were separated for identification by an expert they are not included in this study as there is insufficient information available about functional traits.

Study 1: Within each stand, the heath trap was placed 15m from the edge, and was at least 200m from the next nearest trap in order to reduce possible interference between traps. In most cases, the traps were not visible from each other, apart from in felled stands. This may introduce a bias in traps at felled sites as the lights were visible from further distances, reducing spatial independence (Lacki et al., 2007) although the attraction radii of heath light traps is commonly between 10 – 30m depending on moth family (Truxa and Fiedler, 2012).

Study 2: Woodland and forest pairs were surveyed within seven days of each other, and I randomised whether broadleaf or plantation sites were surveyed first. Within each site two heath traps were used, placed at least 30m from the wood edge and at least 50 m from each other and results from both traps were pooled. In plantations a heath trap was placed in a felled stand with another placed within 5m of the edge of a mature stand. Traps were positioned in such a way that the light was not visible from one trap to another.

4.3.4 Local and landscape analysis:

Study 1: I assessed the impact of the same local and landscape scale variables related to plantation management (following chapter 3) on a variety of different moth response metrics related to functional diversity as well as functional redundancy. Vegetation surveys in two 0.01 ha plots at each stand type were considered representative of the stand as a whole due to the homogenous nature of stands. At each plot I recorded the following: stand density (the total number of trees with diameter at breast height greater than 7 cm); understory vegetation height at 10 evenly spaced points across the radius of the circle; canopy cover at each point using a sighting tube with an internal crosshair (chapter 3). Stand age was recorded as years since planting and altitude as metres above sea level. At the landscape level, I determined the percentage cover of various aspects of broadleaf woodland and felled stands within a 4km radius of the light trap using the GUIDOS toolbox (Soille and Vogt, 2009). The distance to, and size of the nearest broadleaf patch and felled stand were also recorded.

Study 2: In this study the primary interest was whether moth communities differed between plantation stands and broadleaf woodlands so local and landscape variables were not included in the analysis.

4.3.5 Functional trait identification:

To understand the variation in abundance, spatial distribution of moth species and the impact of forest management on moths across all sites, I selected six traits which have been previously implicated as potential predictors of moth extinction (Franzén and Johannesson, 2007). Of these, the moths that I captured only showed sufficient variation for analysis in four traits (see appendix 4.1 , table 2): larval host plant preference, larval specialism (whether the larvae specialised on a single plant family or multiple families), overwintering stage (egg, cocoon, pupa, na) and wingspan (tentatively linked with dispersal ability, Sekar, 2012). Trait values were obtained from Waring and Townsend (2009). As I mostly used categorical traits defined from the literature, and had a small sample set for measured traits, I was only able to measure between-species variation, ignoring within-species variation.

All analysis was carried out in R (R core development team) using the following packages: FD, Vegan, rDiversity (currently under development; pers. comm Sonia Mitchell) and ggplot. In order to quantify how the moth communities differed between “treatments” I used the rDiversity package. rDiversity extends the framework of Hills numbers (Hill, 1973) to incorporate not only a parameter q, which allows practitioners to include information about abundance of species, but also a similarity matrix Z (Leinster and Cobbold, 2012). This allows researchers to also incorporate similarity between species due to e.g. phylogeny, functional traits or genetics into diversity measures, making it possible to determine alpha, beta and gamma diversity within the effective numbers framework (Reeve et al 2014).

4.3.6 Calculating diversity measures:

Hill Numbers (Hill, 1973) provide a framework unifying species richness, Shannon’s entropy and Simpson’s index into a diversity measure which is based on effective numbers, and sensitive to abundance (Hill 1973). Comparisons of species richness, evenness and dominance are now possible, as diversity is expressed as the number of effective species present, rather than an index (Hill 1973). Hill defines a sensitivity parameter "q" which takes into account the difference between rarer and more common species; as a range of different q values are produced (e.g. q = 0 is equivalent to species richness, q = 1 to Shannon's entropy and q = 2 to Simpson's index) it is possible to plot these values as a diversity profile (Leinster and Cobbold, 2012). This allows visual assessment of ecosystem or community diversity across a range of values. In recognition of the fact that species are not always equally different, Leinster and Cobbold 2012 extended these measures to take into account species similarity as distance matrices. Therefore, it is now possible to assess changes in diversity across a range of measures graphically, as effective numbers which are comparable, and constrained by species similarity (Leinster and Cobbold). This approach has been implemented in the "R" environment, using the package "rDiversity".

rDiversity requires the construction of a population abundance matrix, a normalised similarity matrix and a range of user determined sensitivity parameters ("q"). I used the "gowdis" function in FD to calculate the functional similarity matrices, which can handle a variety of different data types including categorical traits and missing data. A similarity matrix was constructed for each functional trait separately, then one including all functional traits. Therefore, species which share several functional traits are more similar than species which have only a few functional traits in common (see appendix 4.1, tables 3A - C for examples of unconstrained (naïve), taxonomic and functional similarity matrices).

Since there is insufficient phylogenetic resolution for moths, I constructed taxonomic similarity matrices by determining taxonomic level information to genus for each species, and used the taxa2dist function in the R package "Vegan" to create a taxonomic similarity matrix. Species which are in the same genus or family will be more similar than species in different families (See appendix 4.1, 3B for example of taxonomic similarity matrix). Henceforth, situations where all species are assumed to be equally different will be referred to as "naïve" compared to "taxonomic" (taxonomic similarity incorporated) or "functional" (similarity due to functional trait values included) diversity. All matrices were normalised before further analysis in rDiversity.

4.3.7 Statistical analysis

Study 1: Similar to Chapter 3, I assessed the impact of stand composition, felling and broadleaf cover in the surrounding landscape on moth naïve and constrained diversity, functional redundancy and the extent to which this was driven by the presence of rare species. Many of the local and landscape variables were collinear so I used Principle Components Analysis (PCA) to remove collinearity and reduce the number of predictors, as in chapter 3. Three separate PCAs were conducted for local, felling and broadleaf characteristics (See Appendix 4.1, table 4 for an explanation of the variables included in the PC analysis). For each PCA I retained those axes which explained more variation than random using the "broken stick" approach (Jackson, 1993). For all PCAs only the first axis explained more variation than expected by chance (Jackson, 1993) and was used in subsequent modelling. The local PC1, which explained 61% of the variation in stand composition loosely described different stand types, explaining the change from stands with low canopy cover and high understorey vegetation height to stands with low vegetation cover and high canopy cover, (Appendix 4.1, Figure 1A). For felling characteristics (Felling PC), only the first axis explained more variation (63%) than by chance; stands with low values of Felling PC1 were closer to patches of clear fell and surrounded by greater areas of felling in a 1km radius and those loading high on Felling PC1 were further from felling with less overall felling in a 1km radius (Appendix 4.1, Figure 1C). For characteristics relating to broadleaf tree cover in the landscape (Broadleaf PC), only the first axis explained more variation (67%) than by chance; stands loading high on Broadleaf PC1 were further from smaller patches of broadleaf tree cover, with fewer trees in the surrounding landscape whereas sites loading low on Broadleaf PC1 were closer to larger broadleaf patches, with more overall broadleaf forest cover in the surrounding habitat (Appendix 4.1, Figure 1B).

Using an information theoretic approach, I assessed the influence of stand (Local PC1) and landscape (Felling PC1, Broadleaf PC1) variables on measures of macro moth naïve, taxonomically and functionally constrained richness, diversity and dominance (see appendix 4.1, table 3 for description of all measures), using the value of each metric per stand as the unit of replication. I used linear models with a Gaussian error structure and an interaction between latitude and longitude to account for spatial autocorrelation. Models were validated by visual assessment of the residuals (Crawley, 2007). Continuous variables were standardised and centred around a mean of zero and a standard deviation of 1 to allow comparisons of estimates, and model fit was assessed by comparing the change in AIC, retaining the best model (change in AIC greater than 2). The conditional R^2 (variance explained by both the fixed and the random effects (Nakagawa and Schielzeth, 2013) was used to assess the amount of variation explained by each model. For each response measure, since there was no clear "top" model I averaged the coefficients across the top models in the set which accounted for a change in AIC of less than 2, using full averaged models to reduce the bias from explanatory factors which do not appear in every model (Burnham and Anderson 2002). Explanatory variables were considered to have a "significant" effect on the responses if the standard error of the estimate did not cross zero.

I graphically present the results for the single best model for each analysis and standardised parameters and standard errors for all explanatory variables, as well as the number of individual models included in model sets. Inferences were made by comparing each parameter's standardised estimate with other predictor variables to assess its relative importance, the upper and lower 95% quantiles of each parameter obtained from N = 1000 simulated draws from the estimated distribution (Lintott et al., 2014) and a comparison of selected models using AIC.

Finally, I used a null model approach to test the effects of the occurrence or proximity to clear-felled areas or broadleaf patches on patterns of trait values (Crawley, 2007). Null models allow the comparison of the observed communities with randomly assembled communities of equal species richness (Swenson, 2014). To generate random communities, I randomly permuted (n=999) moth abundance across stands. For each randomisation I calculated functional diversity measures, using the standardised effect size (SES) to compare the deviation of observed values relative to the null model assemblage (Rolo et al., 2016). The SES is calculated as the ratio of the difference between the observed value and the mean of the null distribution to the standard deviation of the null distribution. The null hypothesis is that the average SES is zero; significantly higher values indicate niche complementarity whereas lower values indicate environmental filtering. I used linear models including an interaction with latitude and longitude to account for spatial autocorrelation and excluded the intercept to determine whether mean SES values significantly deviated from zero.

Study 2: Differences in naïve, taxonomic and functional richness, diversity and evenness between plantation and broadleaf woodlands were tested using generalised linear mixed effects models with a gaussian error distribution. Site nested in year was included as a random effect to account for the paired design, and the fact that sampling occurred across two years. Models were validated by visual assessment of the residuals (Crawley, 2007). The conditional R^2 (variance explained by both the fixed and the random effects (Nakagawa and Schielzeth, 2013) were used to assess the amount of variation explained by each model. Explanatory variables were considered to have a "significant" effect on the responses if the standard error of the estimate did not cross zero. The standardised effect size was calculated as above to determine whether communities in broadleaf woodlands and plantation forests showed evidence of environmental filtering in measures of functional richness and diversity.

4.4 Results:

4.4.1 Study 1: Influence of local and landscape scale variables on naïve, taxonomic and functional diversity and redundancy.

A total of 6464 macro moths belonging to 140 species and 10 families were collected from the plantation sites, recording an average of 38 (± 4.2) macro moth species per stand. Naïve species richness was lower in stands loading high on Local PC1, with number of species in stands with high canopy cover and stand density two thirds that of in patches of with lower cover and density. In contrast, there was no association between stand level variables and naive measures of evenness and dominance, or for any constrained measures of richness, diversity (Table 4.1) and dominance (Table 4.2). Larger areas of felling or proximity of felling in the surrounding landscape had a negative effect on functional richness, diversity and dominance but no impact on taxonomic richness, diversity (Table 4.1) or dominance (Table 4.2). For example, after constraining for functional similarity, both naïve and raw species richness fell by 50% in stands adjacent to clear-felled areas (Figure 4.2). Functional redundancy, in the larval host plant preference trait fell from 2.4 (2.0 – 2.8) to 1 (0.4 – 1.5) as the proximity and quantity of felling in the surrounding landscape increased (Table 4.2). Similarly, functional redundancy for larval specialism was halved in stands surrounded by a high proportion of felling in the landscape, as was redundancy in overwintering stage (Table 4.2).

A high proportion of broadleaf tree cover in the surrounding landscape positively influenced functional richness, particularly larval host plant preference and larval specificity (Figure 4.3). Larval host plant preference richness increased from 3.2 (2.6 – 3.9 95% CI) in stands further from broadleaf or with a lower proportion of broadleaf in the surrounding area to 5 (3.7 – 6.1) in stands closer to broadleaf or with a higher proportion of broadleaf in the surrounding area. Similarly, species richness constrained by larval specialism increased from 2.7 (2.1 – 3.3) species per stand in stands further from broadleaf or with a lower proportion of broadleaf to 4.2 (3.1 – 5.2) species per stand in stands closer to, or with a higher proportion of, broadleaf tree cover in the surrounding landscape. The presence of broadleaf tree cover had no impact on naïve or constrained diversity or dominance (Table 4.1, 4.2), however, it did positively impact functional redundancy for over wintering stage; redundancy increased from 2.6 (2.0 – 3.2) to 4.0 (2.9 – 5.1; Table 4.2) as the amount of nearby broadleaf tree cover increased (Table 4.2).

Table 4.1: Best approximating GLM's assessing influence of local, felling and broadleaf parameters on naïve and constrained measures of species richness and diversity. Information theoretic approach using model averaging to assess importance of parameters. NA's indicate parameters which were not included in any of the top models. The interaction between Felling PC1 and Broadleaf PC1 was never included in any top models and is not presented here. Parameters in bold are those which have a significant effect on response values, determined by whether the standard error of the estimate crosses zero (Burnham and Anderson). Akaikes weight is the total weight explained by all models. Estimates for the full averaged model are presented ± the standard error.

Alpha diversity measures	Constraint	No. models	Intercept	Local_PC1	Felling PC1	Broadleaf PC1	Date	Temp	Lat:Long
Species richness (Naïve = poisson, others = gaussian) (q = 0)	Naïve	4	**264.9 ± 177.6**	**-0.7 ± 0.2**	**-0.2 ± 0.0**	-0.1 ± 0.0	**-0.0 ± 0**	**0.0 ± 0.0**	1.2 ± 0.3
	Taxonomic	4	**939.8 ± 310.8**	0.1 ± 0.1	0 ± 0.1	0 ± 0.1	0 ± 0	NA	NA
	Host Plant	3	**1589 ± 527.3**	NA	**-0.5 ± 0.2**	**-0.5 ± 0.2**	0 ± 0	0 ± 0.1	**2.3 ± 1.7**
	Larval Specialism	4	**1196.3 ± 434.4**	0 ± 0	**-0.5 ± 0.1**	**-0.4 ± 0.2**	0 ± 0	0 ± 0	0.4 ± 1
	Overwintering stage	5	**922.1 ± 218.2**	NA	**-0.4 ± 0.1**	0 ± 0.1	0 ± 0	0 ± 0	NA
	WingSpan	4	**643.5 ± 113.1**	NA	**-0.2 ± 0.1**	-0.1 ± 0.1	0 ± 0	0 ± 0	NA
Shannon's entropy (gaussian) (exp SE, q = 1)	Naïve	14	**1421.1 ± 979.9**	-0.2 ± 0.2	**-0.9 ± 0.3**	-0.5 ± 0.5	0 ± 0	0.1 ± 0.1	0.8 ± 2
	Taxonomic	3	**847.7 ± 276.4**	0.1 ± 0.1	0 ± 0.1	0 ± 0.1	0 ± 0	NA	NA
	Host Plant	7	**1406.6 ± 345.3**	NA	**-0.4 ± 0.1**	-0.1 ± 0.1	0 ± 0	0 ± 0	0.5 ± 0.9
	Larval Specialism	5	**350.8 ± 171.8**	NA	**-0.3 ± 0.1**	0 ± 0.1	0 ± 0	0 ± 0	NA
	Overwintering stage	7	**884.7 ± 319.9**	NA	**-0.4 ± 0.1**	-0.2 ± 0.2	0 ± 0	0 ± 0	0.1 ± 0.5
	WingSpan	4	**630.2 ± 112.3**	NA	**-0.2 ± 0.1**	-0.0 ± 0.1	0 ± 0	0 ± 0	NA

Table 4.2: Best approximating GLM's assessing influence of local, felling and broadleaf parameters on naïve and constrained measures of species dominance and functional redundancy. Information theoretic approach using model averaging to assess importance of parameters. NA's indicate parameters which were not included in any of the top models. The interaction between Felling PC1 and Broadleaf PC1 was never included in any top models and is not presented here. Parameters in bold are those which have a significant effect on response values, determined by whether the standard error of the estimate crosses zero (Burnham and Anderson). Akaikes weight is the total weight explained by all models. Estimates for the full averaged model are presented ± the standard error.

Alpha diversity measures	Constraint	No. models	Intercept	Local_PC1	Felling PC1	Broadleaf PC1	Date	Temp	Lat:Long
Simpson's Index (gaussian) (Inverse SI, q = 2)	Naïve	12	**551.4 ± 646.5**	-0.1 ± 0.1	**-0.6 ± 0.2**	-0.2 ± 0.3	0 ± 0	0 ± 0	0.2 ± 0.9
	Taxonomic	4	**770.3 ± 246**	0.1 ± 0.1	0 ± 0.1	0 ± 0.1	0 ± 0	NA	NA
	Host Plant	5	**1218.8 ± 253.7**	0 ± 0	**-0.3 ± 0.1**	0 ± 0.1	0 ± 0	0 ± 0	0.1 ± 0.4
	Larval Specialism	9	**722.1 ± 281.4**	NA	**-0.3 ± 0.1**	-0.1 ± 0.1	0 ± 0	0 ± 0	0.1 ± 0.5
	Overwintering stage	12	149.1 ± 172.2	NA	**-0.2 ± 0.1**	0 ± 0.1	0 ± 0	0 ± 0	NA
	WingSpan	4	**619.1 ± 111.6**	NA	**-0.2 ± 0.1**	-0.1 ± 0.1	0 ± 0	0 ± 0	NA
Functional and taxonomic redundancy (gaussian) (q = 0)	Taxonomic	4	**2403.9 ± 1127.2**	**-0.4 ± 0.2**	-1.2 ± 0.4	-0.2 ± 0.4	-0.1 ± 0	0.4 ± 0.2	2.6 ± 3.3
	Host Plant	11	**526.6 ± 292.6**	-0.1 ± 0.1	**-0.4 ± 0.1**	-0.1 ± 0.1	0 ± 0	0 ± 0	0.2 ± 0.5
	Larval Specialism	7	**808.9 ± 345.9**	-0.1 ± 0.1	**-0.3 ± 0.1**	-0.1 ± 0.1	0 ± 0	0.1 ± 0	**1.4 ± 1**
	Overwintering stage		**995.5 ± 461.7**	-0.1 ± 0.1	**-0.4 ± 0.1**	-0.4 ± 0.2	0 ± 0	0.1 ± 0.1	**2.6 ± 1.3**
	WingSpan	5	**1894.5 ± 850.8**	-0.2 ± 0.1	**-1.0 ± 0.2**	-0.3 ± 0.3	-0.1 ± 0	0.2 ± 0.1	2.8 ± 2.6

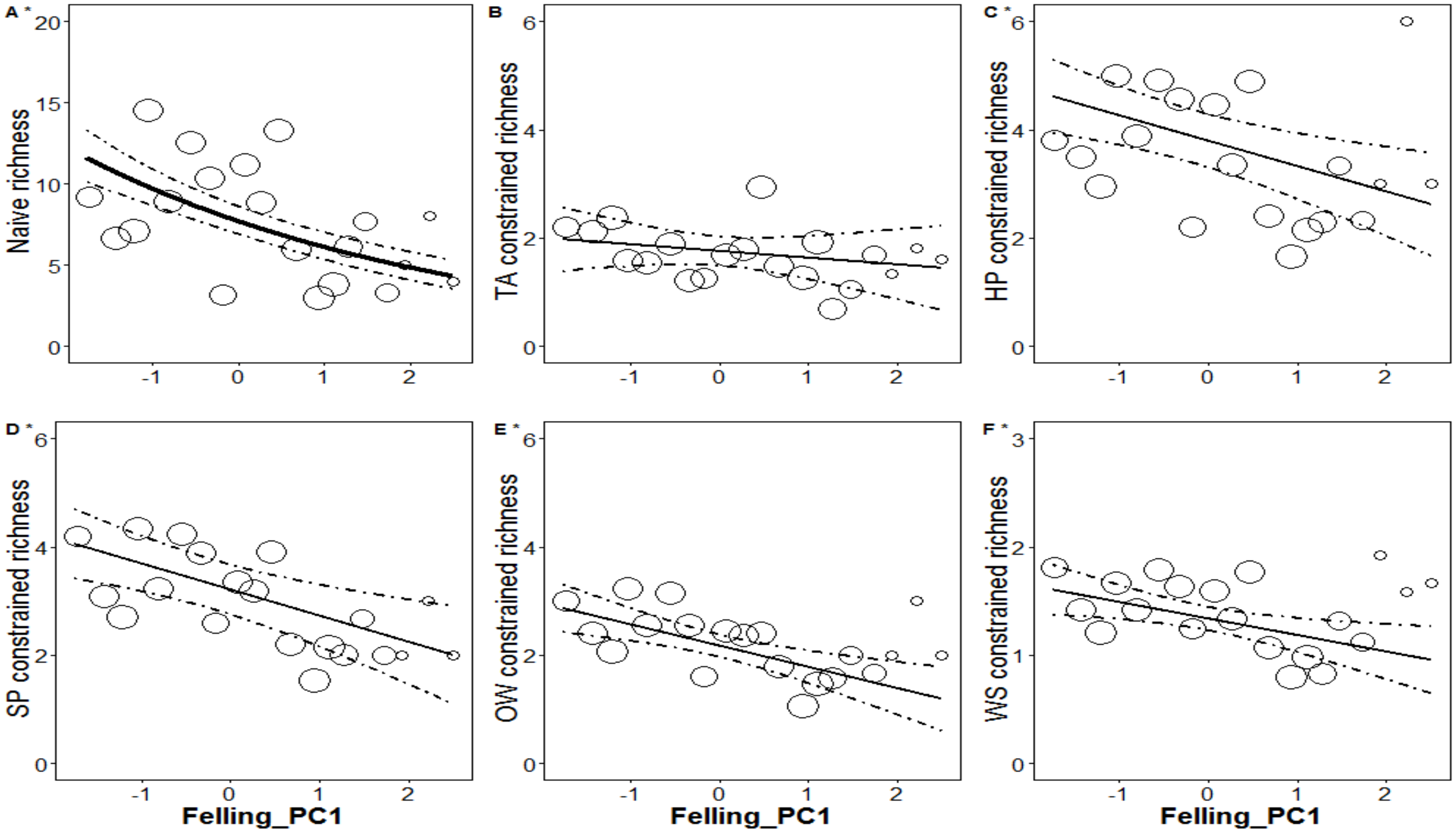


Figure 4.2: Impacts of felling on moth species richness (Naïve, A), taxonomic richness (TA, B), richness constrained by functional similarity in host plant preference (HP, C), larval specialism (SP, D), overwintering stage (OW, E) and average wingspan (WS, F) Original data on naïve, taxonomic and functional richness are superimposed as grey circles with diameter proportional to the number of sampling points where mean values occurred. Dashed lines represent 95% confidence intervals around the predictions (solid black line). Sites low on PC1 are those with a higher proportion of felling within 1km and nearer to felled areas whereas sites high on PC1 are those with a lower proportion of felled areas within 1km and are further from felled areas.

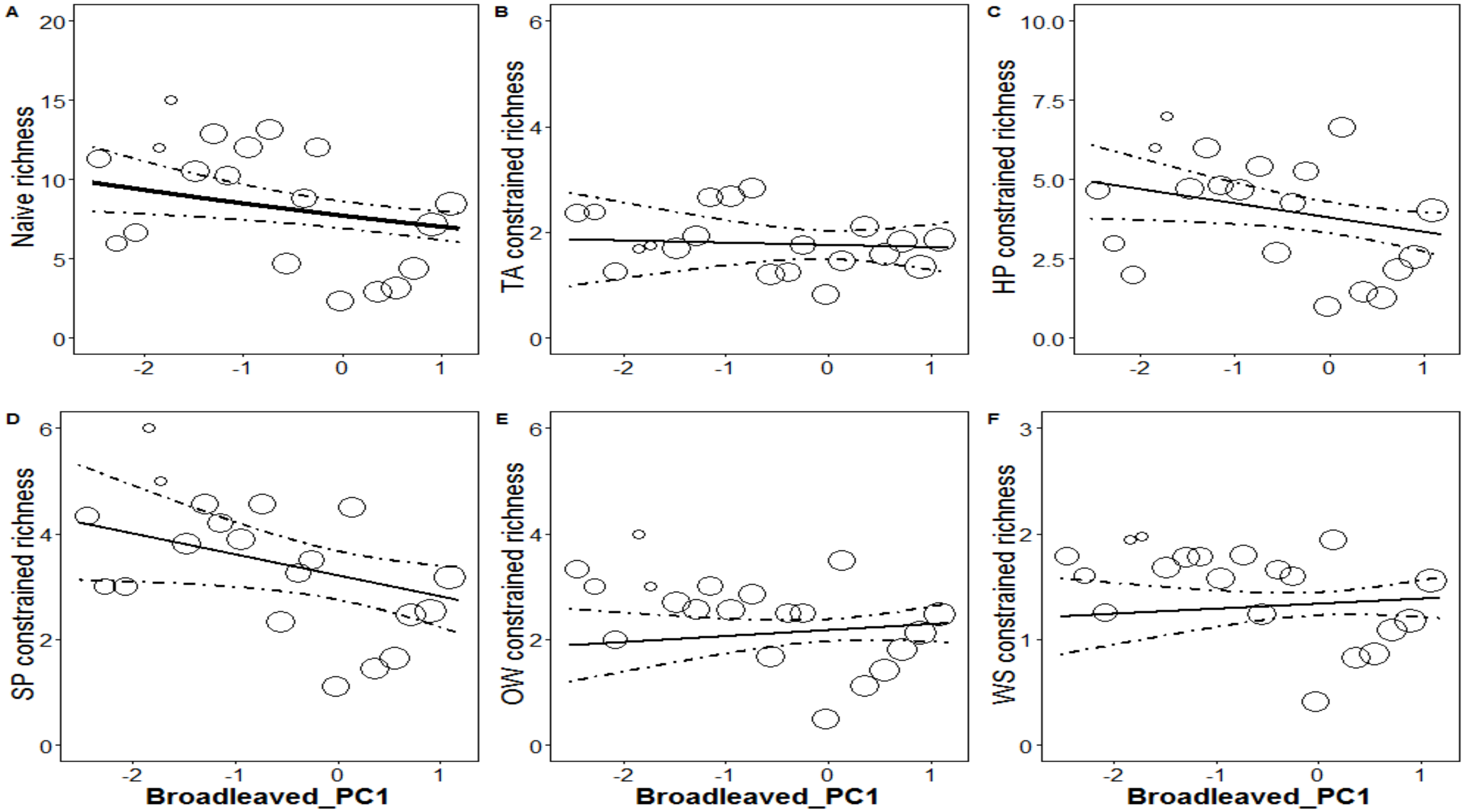


Figure 4.3: Impacts of broadleaf on moth species richness (Naïve, A), taxonomic richness (TA, B), richness constrained by functional similarity in host plant preference (HP, C), larval specialism (SP, D), overwintering stage (OW, E) and average wingspan (WS, F) Original data on naïve, taxonomic and functional richness are superimposed as grey circles with diameter proportional to the number of sampling points where mean values occurred. Dashed lines represent 95% confidence intervals around the predictions (solid black line). Sites low on PC1 are those with a higher proportion of felling within 1km and nearer to broadleaf tree cover whereas sites high on PC1 are those with a lower proportion of broadleaf tree cover within 1km and are further from broadleaf tree cover.

4.4.2 Study 2: Differences in naïve, taxonomic and functional diversity and redundancy between plantation and ancient woodland sites:

An average of 27 (±5) moth species were recorded in plantation forest compared to 63 (±3) species in broadleaf sites. However, after constraining for taxonomic and functional similarity species richness was similar between woodland types (Table 4.3). Similarly, I found no difference in diversity or dominance between plantation broadleaf sites, particularly after constraining for functional similarity (Table 4.3). The conditional R^2 was high for measures of diversity and dominance constrained by functional similarity, particularly larval host plant preference. This indicates greater variation between years or sites than woodland type per se (Table 4.3). Broadleaf woodland sites had greater functional redundancy than plantation sites, although there was little difference in functional richness, diversity or dominance. Broadleaf woodland sites also had significantly more species sharing the same larval host preferences and overwintering stage (Table 4.3, Figure 4.4) although there did not appear to be any difference in larval specialism between broadleaf and plantation sites (Table 4.3).

4.4.3 Patterns of trait based values:

Using null models allowed us to investigate how the prevalence of both felling and broadleaf tree cover influenced measures of functional richness and diversity (study 1). There was no evidence of a relationship between functional richness and either local (stand level) features or the surrounding landscape for any trait apart from after constraining for functional similarity due to overwintering guild (Table 4.4). Stands further from broadleaf tree cover or with less broadleaf cover in the surrounding area had a SES significantly smaller than zero (Table 4.4) compared to those with greater amounts nearby, indicating that moth species in these stands shared a limited and similar range of overwintering stages. This suggests that environmental filtering is occurring; species which overwinter as a pupa or an egg were negatively impacted compared to species which overwinter as a larva. There was no evidence that functional richness and diversity deviated significantly from zero for either broadleaf or plantation paired sites (study 2).

Table 4.3: Best approximating GLMM's assessing the difference between paired broadleaf and plantation sites for naïve and constrained measures of species richness, diversity, dominance and functional redundancy. Parameters in bold are those which have a significant effect on response values, determined by whether the standard error of the estimate crosses zero (Burnham and Anderson). Akaikes weight is the total weight explained by all models. Estimates for the full averaged model are presented ± the standard error. Marginal (R^2 explained by fixed effects) and conditional (R^2 explained by both fixed and random effects) as calculated by (Nakagawa and Schielzeth, 2013) presented.

Alpha diversity measures	Constraint	Intercept (Broadleaf woodland)	Plantation	F Statistic	Marginal R2	Conditional R2
Species richness (gaussian) (q = 0)	Naïve	22.1 ± 3	**-6.7 ± 3.1**	-2.1	0.08	0.49
	Taxonomic	5.3 ± 0.5	-0.6 ± 0.4	-1.3	0.03	0.58
	Host Plant	5.9 ± 0.6	0.1 ± 0.5	0.2	0	0.58
	Larval Specialism	4.9 ± 0.3	-0.3 ± 0.4	-0.9	0.02	0.21
	Overwintering stage	1.6 ± 0.0	0.0 ± 0.1	0.1	0	0
	WingSpan	1.2 ± 0.0	0.0 ± 0.0	-0.4	0	0
Shannon's entropy (gaussian) (exp SE, q = 1)	Naïve	20.9 ± 2.8	-6.2 ± 3	-2.1	0.08	0.49
	Taxonomic	4.3 ± 0.3	-0.1 ± 0.3	-0.4	0	0.61
	Host Plant	4.7 ± 0.6	0.3 ± 0.4	0.7	0.01	0.57
	Larval Specialism	4.2 ± 0.3	-0.3 ± 0.3	-1.1	0.02	0.29
	Overwintering stage	1.6 ± 0.0	0 ± 0.1	0	0	0
	WingSpan	1.2 ± 0.0	0.0 ± 0.0	-0.4	0.01	0.13
Simpson's Index (gaussian) (Inverse SI, q = 2)	Naïve	19.7 ± 2.6	-5.6 ± 2.8	-2	0.07	0.49
	Taxonomic	3.9 ± 0.3	0 ± 0.3	0	0	0.58
	Host Plant	4.1 ± 0.6	0.3 ± 0.4	0.9	0	0.61
	Larval Specialism	3.8 ± 0.3	-0.3 ± 0.3	-0.9	0.02	0.34
	Overwintering stage	1.6 ± 0	0 ± 0	-0.1	0	0.12
	WingSpan	1.2 ± 0.0	0.0 ± 0.0	-0.4	0.01	0.19
Functional and taxonomic redundancy (gaussian) (q = 0)	Taxonomic	3.9 ± 0.4	-0.8 ± 0.5	-1.7	0.08	0.21
	Host Plant	3.6 ± 0.4	**-1.2 ± 0.4**	**-2.8**	0.17	0.38
	Larval Specialism	4.4 ± 0.5	-1.2 ± 0.6	-1.9	0.08	0.31
	Overwintering stage	13.7 ± 1.8	**-4.3 ± 1.9**	**-2.3**	0.08	0.49
	WingSpan	17.9 ± 2.4	**-5.1 ± 2.6**	**-1.9**	0.07	0.43

Table 4.4: Standardised effect sizes (SES ± SE) and P *values regressed against Study 1: Felling PC1 (prevalence of felling in the surrounding landscape), Broadleaf PC1 (prevalence of broadleaf in the surrounding landscape) and Local PC1 (local measures of stand composition) and Study 2: per habitat type of ancient semi natural broadleaf woodland or plantation woodland for all trait values as compared to a null model.*

	Study 1					
Constraint	Felling_PC1		Broadleaf_PC1		Local_PC1	
	SES	P value	SES	P value	SES	P value
Host Plant	-0.1 ± 0.1	0.348	0.1 ± 0.1	0.254	0 ± 0	0.297
Larval Specialism	0.1 ± 0.1	0.149	0.1 ± 0.1	0.293	0 ± 0	0.741
Overwintering stage	0.1 ± 0.1	0.273	**-0.1 ± 0.1**	**0.038**	0 ± 0	0.431
WingSpan	-0.1 ± 0.1	0.099	0.0 ± 0.0	0.878	0 ± 0	0.220

	Study 2			
Constraint	Broadleaf		Plantation	
	SES	P value	SES	P value
Host Plant	0.2 ± 0.3	0.589	-0.3 ± 0.3	0.358
Larval Specialism	0.1 ± 0.3	0.617	-0.3 ± 0.3	0.325
Overwintering stage	0.2 ± 0.3	0.570	-0.3 ± 0.3	0.335
WingSpan	0.0 ± 0.2	0.894	0.2 ± 0.2	0.333

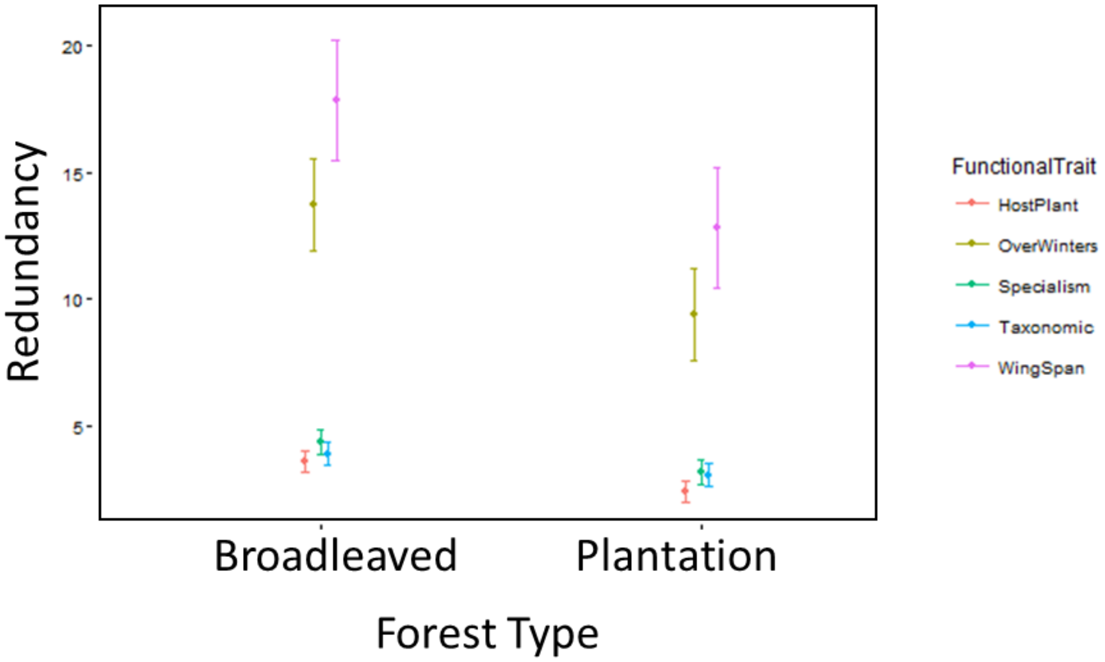


Figure 4.4: Mean functional and taxonomic redundancy recorded in broadleaf and plantation sites. Error bars give the standard error.

4.5 Discussion:

How to best limit and mitigate diversity loss due to anthropogenic practices is currently a key question for conservation (Sutherland et al., 2006). Research on the impacts of environmental change on diversity often traditionally adopts a “naïve” approach, by focussing on the composition and diversity of particular taxonomic groups without taking into account similarities between species due to functional, genetic or phylogenetic relationships (Spake et al., 2016). However, the usefulness of these approaches will depend on species assemblages (Chiu and Chao, 2014) and provides little information on mechanistic links between taxa and their environment (Hooper et al., 2002). Using functional diversity measures allows conclusions to be drawn about drivers behind diversity loss (Mori et al., 2013). For example, previously I demonstrated that the proximity and size of surrounding broadleaf tree cover had a positive impact on species richness (Chapter 3). Results presented in the current chapter suggest that this is because stands close to broadleaf tree cover support moths with a wider range of larval host plant preferences and habitat specialisms. Using Hill numbers, it is possible to determine whether rare or abundant species are driving different patterns in functional diversity. While the prevalence of clear felling in the surrounding landscape negatively impacts lepidopteran functional richness when both rare and abundant species are considered, the presence and proximity of broadleaf woodland mitigates this somewhat by increasing the number of rare species found at a site.

Lepidoptera are currently undergoing substantial declines across Europe, although relatively little is known about the potential drivers of this (Conrad et al., 2006; Fox et al., 2014). Changes to silvicultural practices and consequently habitat loss and fragmentation have been identified as potential causes of these falls in population with evidence that intensification of agriculture (Gámez-Virués et al., 2015) and fragmentation of broadleaf woodland (Slade et al., 2013) all negatively impact lepidopteran populations. Despite the recognition that moth species are a key priority research area in the United Kingdom (Sutherland et al., 2006) and the fact that over half of all forest area in the UK is plantation forestry, the potential contribution of plantation forests to moth conservation has received very little attention. I show here that despite plantations supporting a wide diversity of moth species, the impacts of management processes such as felling on functional richness and diversity are decoupled from those on taxonomic richness and diversity, and affect both rare and common species similarly.

4.5.1 Impacts of felling on lepidopteran richness and diversity:

I found no evidence of stand level differences in functional richness and diversity, although more open stands with a greater vegetation cover (young, felled and native stands) had a higher naïve species richness. Native planting, felled and young stands have a greater diversity of vegetation cover compared to denser, closed canopy stand (Parrish and Summerville, 2015) and may also have greater amounts of dead wood which benefit a range of moth species (Parrish and Summerville, 2015; Thorn et al., 2015). However, it is unclear whether increased host plant availability or dead wood availability is driving this difference in species richness.

Felling negatively affected naïve and functional diversity, but not taxonomic diversity. The scale of such environmental disturbance was apparent up to 1500 m, in contrast to the small scale impacts of environmental stressors described by Uhl et al. 2015 for micro-moths. Felling may reduce richness and diversity via a range of mechanisms including the removal of host plants (Summerville and Crist, 2002), changes in microclimate and disturbance to forest understory vegetation (Parrish and Summerville, 2015). Using effective numbers allows comparisons of changes in richness or diversity in relation to abundance. For example, I found that a higher prevalence of felling in the surrounding landscape reduced functional richness, diversity and dominance for all the functional traits investigated. Therefore, the reduction in functional diversity occurred for both rare and abundant species, although there was no evidence that particular families or genera were impacted more than others. Losses in functional richness and diversity were strongly mirrored with losses in naïve richness and diversity, and there was little evidence of environmental filtering. Intensive management can act as an environmental filter by removing entire functional groups and creating biotic homogeneity by shifting towards reduced communities with a smaller number of shared, more generalist traits (Gámez-Virués et al., 2015). These effects have been demonstrated most often in response to increasing agricultural intensity, resulting in landscape simplification and reduced capacity to support a large species pool (Gámez-Virués et al., 2015). In general, losses appeared to be across all functional groups rather than concentrated within particular groups for all functional traits with the exception of overwintering stage. Moth communities in stands with a high prevalence of broadleaf in the surrounding landscape consisted predominantly of species which overwinter as larvae compared to stands with less broadleaf in the surrounding landscape ; many moth species which overwinter as larvae do so underground (Mattila et al., 2006) and may be better protected, or find more appropriate, less exposed overwintering sites in or near remnant broadleaf patches.

4.5.2 Remnant patches of broadleaf mitigate loss of functional richness

The prevalence of broadleaf woodland in the surrounding landscape mitigated the impacts of felling to some extent, with a greater functional richness for host plant preference guilds and larval specialism, although this was primarily driven by the presence of rare species. Restricting analyses to abundant species (e.g. with a sensitivity parameter q of 1 or higher), there was no influence of the prevalence of broadleaf tree cover on functional diversity. Patches of broadleaf tree cover in the surrounding area may act as a source for moth species, allowing persistence of species vulnerable to disturbance in the plantation landscape (Scalercio et al., 2012).

4.5.3 Difference in functional richness and diversity between plantation and broadleaf sites

With study 2, I aimed to compare moth populations in commercial plantations with those in broadleaf woodlands in the Galloway area. Given that the size and proximity of broadleaf patches surrounding plantation stands had marked positive effect on functional richness, a difference in functional richness and diversity was expected between plantation and broadleaf sites. Surprisingly, although naïve richness was lower in plantation sites compared to broadleaf sites, I found no difference in functional richness, diversity and dominance. This is in contrast to previous work in native woodlands managed for logging, which found that particular functional guilds were negatively impacted by felling, and were therefore less diverse than in unmanaged woodlands (Summerville 2003). However, plantations differ from native woodlands in that open specialist species may persist in early successional stands (Spake et al., 2016), increasing the functional diversity. Alternatively, the paired design which ensured that plantation stands were no more than 5km from broadleaf woodland sites may be sufficiently small enough to allow dispersal between both forest types

(Lewis, 2001). Wingspan and larval host plant preference have both been tentatively linked to dispersal ability in Lepidoptera (Sekar, 2012). I found no difference in functional richness and diversity between broadleaf woodlands and plantation woodlands after constraining for similarity due to wing span, habitat specialism or host plant preference, which suggests that moths may be able to readily disperse between broadleaf and plantation sites. Broadleaf patches in the landscape may provide habitats from which species spill over can occur (Tscharntke et al., 2012). Summerville et al (2009) found that the signal of disturbance due to felling in old growth woodlands persisted for over 60 years. Potentially the lack of difference between plantations and broadleaf woodlands may also reflect historical disturbance pressure such as the widespread removal of deciduous woodland and the consequent post war planting of coniferous forests (Conrad et al., 2006). This may have led to a reduction in, or local extinction of, species with specific functional attributes (Lewis, 2001) as remaining woodland fragments may be too small for some moth species to persist. Soga et al (2015) found that woodland specialist lepidopteran species were influenced at large spatial scales, which I did not investigate in our study, potentially the surrounding landscape is more important that the woodland type for conserving lepidopteran diversity.

There was no evidence of environmental filtering or niche complementarity occurring between plantations and broadleaf sites, as SES scores did not differ significantly from zero. This implies that the functional composition of moth communities in broadleaf and plantation sites does not differ significantly from random, with functional groups similarly represented in the two woodland types. I did however find lower redundancy in plantations, particularly after constraining for similarity in host plant preference, overwintering stage and wing span. Potentially moth populations in plantations represent a reduced subset of moth populations compared to the surrounding area which are more vulnerable to disturbance pressures such as felling due to low resilience (Elmqvist and Folke, 2003; Soga et al., 2015).

4.5.3 Importance of spatial scale:

I found little impact of stand level measures on moth functional richness and diversity, with local variables rarely retained in the top model sets. Landscape scale features such as felling and presence of broadleaf tree cover were always retained in the top model set, and the prevalence of felling consistently had a negative impact on functional richness, diversity and dominance. The higher richness of moth species in felled and young stands (Chapter 3) seems counterintuitive considering the impact of felling on moth richness and diversity. However, this could support the landscape moderated insurance hypothesis (Tscharntke et al., 2012); increased landscape compositional heterogeneity provides insurance in the face of intense management by supporting more biodiversity (Tscharntke et al., 2012), and stands with a low proportion of felling in the surrounding matrix may be embedded in a more heterogeneous landscape, resulting in higher functional richness and diversity (Gámez-Virués et al., 2015; Scalercio et al., 2012), even in felled stands. Hamer et al (2003) also showed that reductions in lepidopteran diversity in logged forests was the result of lower environmental heterogeneity. It has been proposed that higher diversity should be found in areas of intermediate disturbance, where both climax and pioneer species can coexist (Hamer et al., 2003). Felled stands with a low proportion of felling in the surrounding landscape may represent intermediate disturbance whereas a high proportion of felling the surrounding landscape may result in levels of disturbance which only certain species can tolerate (Hamer et al., 2003). Increased felling in the surrounding landscape may limit dispersal between different habitat types, with low dispersal moths most vulnerable to disturbance impacts (Scalercio et al., 2012).

4.5.4 Management recommendations

With these results in mind I recommend reducing the size felling coupes where possible, avoiding felling stands close to each other, to reduce the impacts of felling on moth communities caused by low landscape heterogeneity (Hamer et al., 2003; Scalercio et al., 2012). Maintaining areas of undisturbed, broadleaf stands within the production matrix may act as stepping stones for Lepidoptera to move through the plantation matrix (Slade et al., 2013) and buffer the impacts of felling to some extent as has been demonstrated for butterflies in tropical systems (Hamer et al., 2003). Since clear felling was the only timber extraction technique used at plantations in this study I was not able to compare its effects with those of other lower-intensity methods. However, Summerville et al (2013) and Thorn et al. (2015) showed that felling regimes which removed 15% or less tree volume, and allowed some dead wood to remain (analogous to continuous cover forestry), had a lower impact on moth populations than clear felling or salvage logging, while Hamer et al 2003 found little evidence that selective logging impacted butterfly diversity in tropical forestry systems. Switching to continuous cover forestry where appropriate will benefit moth communities and in turn the small mammal, bird and bat species which rely on them as a prey source while not negatively impacting forest productivity (Macdonald et al., 2009).

Chapter 4 Appendix:

Appendix 4.1

Table 1: Stand characteristics for each management stage and stand features associated with management for study 1. *Diameter at Breast Height – estimate of tree maturity

Stand Age	Management Stage	Key stand features
40 – 60 years	Mature	Occasionally thinned, stand density between 500 and 2200 stems ha^{-1}, average stand density: 1267 stems ha^{-1}, canopy closure between 80 and 100%, average closure 99%
20 – 40 years	Thin	Trees more densely packed, losing midstem branches and some trees dying off (self thinned). Occasionally thinned through management. Stand density between 600 – 2800 stems ha^{-1}, average stand density: 1624 stems ha^{-1}. Canopy closure between 50 and 100%, average closure: 95%
10 – 20 years	Thicket	Very dense, retain midstem branches, no undergrowth. Stand density between 300 – 3000 stems ha^{-1}, average stand density: 1850 stems ha^{-1}. Canopy closure between 16 and 100%, average closure: 69%
5 – 10 years	Young	Small, nearly all trees < 7cm DBH*, no canopy closure, lots of vegetation and ground cover
Clearfell	Felled < 5 years ago	Lots of dead wood and brash, standing water and undergrowth

Table 2: Description of traits used in analysis.

Measure	Description
Naïve	No similarity matrix is provided, assumes that all species are equally different
Taxonomic	Distance matrix describing differences in genera, family or suborder
Host Plant	Difference in larval host plant preferences. Species catagorised as preferentially foraging on the following plant groups: Bracken, coniferous trees, deciduous trees, detritus, flowering plants, grasses, moss and lichen, shrubs and trees, both deciduous and coniferous trees, generalist
Larval Specialism	Difference in larval specialisms based on habitat preferences. Species catagorised as follows: Herb generalist, herb specialist, Lichen specialist, lichen and wood specialist, wood generalist or wood specialist
Overwintering Stage	Difference in overwintering stage between moth species. Species catagorised as follows: Cocoon, egg, larva, pupa, various, na
Wing Span	Moth wing span as reported from the literature. Average wing span 32.8 (15.0 - 77.5) mm

Table 3A: Example of naïve similarity matrix (all species are considered equally different from each other)

	Antler_Moth	Autumnal_Rustic	Barred_Chestnut	Barred_Red	Barred_Straw	Barred_Umber	Beautiful_Carpet_moth	Beautiful_Golden_Y	Bordered_Beauty
Antler_Moth	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Autumnal_Rustic	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Barred_Chestnut	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00
Barred_Red	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00
Barred_Straw	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00
Barred_Umber	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00
Beautiful_Carpet_moth	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00
Beautiful_Golden_Y	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00
Bordered_Beauty	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00

Table 3B: Example of taxonomic constrained similarity matrix – SWAP THERse

	Antler_Moth	Autumnal_Rustic	Barred_Chestnut	Barred_Red	Barred_Straw	Barred_Umber	Beautiful_Carpet_moth	Beautiful_Golden_Y	Bordered_Beauty
Antler_Moth	0.00	1.00	1.00	1.00	0.33	1.00	1.00	1.00	0.33
Autumnal_Rustic	1.00	0.00	0.33	0.67	0.33	0.67	0.33	0.33	1.00
Barred_Chestnut	1.00	0.33	0.00	0.33	0.33	1.00	0.33	0.33	0.33
Barred_Red	1.00	0.67	0.33	0.00	0.33	0.33	0.33	0.33	1.00
Barred_Straw	0.33	0.33	0.33	0.33	0.00	1.00	1.00	0.67	1.00
Barred_Umber	1.00	0.67	1.00	0.33	1.00	0.00	0.67	1.00	1.00
Beautiful_Carpet_moth	1.00	0.33	0.33	0.33	1.00	0.67	0.00	1.00	0.33
Beautiful_Golden_Y	1.00	0.33	0.33	0.33	0.67	1.00	1.00	0.00	1.00
Bordered_Beauty	0.33	1.00	0.33	1.00	1.00	1.00	0.33	1.00	0.00

Table 3C: Example of functional constrained similarity matrix

	Antler_Moth	Autumnal_Rustic	Barred_Chestnut	Barred_Red	Barred_Straw	Barred_ Umber	Beautiful_Carpet_ moth	Beautiful_Golden _Y	Bordered_Beauty
Antler_Moth	0.00	0.59	0.59	1.00	1.00	1.00	1.00	0.59	1.00
Autumnal_Rustic	0.59	0.00	0.35	1.00	1.00	1.00	1.00	0.59	1.00
Barred_Chestnut	0.59	0.35	0.00	1.00	1.00	1.00	1.00	0.59	1.00
Barred_Red	1.00	1.00	1.00	0.00	0.59	0.35	0.59	1.00	0.35
Barred_Straw	1.00	1.00	1.00	0.59	0.00	0.59	0.35	1.00	0.59
Barred_Umber	1.00	1.00	1.00	0.35	0.59	0.00	0.59	1.00	0.35
Beautiful_Carpet_moth	1.00	1.00	1.00	0.59	0.35	0.59	0.00	1.00	0.59
Beautiful_Golden_Y	0.59	0.59	0.59	1.00	1.00	1.00	1.00	0.00	1.00
Bordered_Beauty	1.00	1.00	1.00	0.35	0.59	0.35	0.59	1.00	0.00

Table 4: Variables included in Principle Components Analysis for study 1

PC axis	Measure	Unit	Minimum	Maximum	Median	Description
Local PC1	Altitude	m	83.8	466	230.7	Height above sea level
Local PC1	Density	trees per ha	0	3000	600	Number of trees per hectare
Local PC1	Vegheight	mm	0	1744.1	156.6	Height of vegetation measured at 10 points across plot
Local PC1	Canopy cover	%	0	1	0.67	Total canopy cover as a percent
Local PC1	Stand Age	years	0	133	14	Stand age calculated from year of planting
Broadleaf PC1	BL_distance	m	0	3934	682	Distance in metres to nearest patch of mature broadleaf
Broadleaf PC1	BL_area	m2	0.1	163.2	1.3	Size of nearest mature broadleaf patch
Broadleaf PC1	Tot_BL_4000	%	0	11.3	0.8	Total broadleaf cover as a % of a 4km2 circle
Broadleaf PC1	Edge_BL_4000	%	0	2.9	0.2	Edge broadleaf cover as % of a 4km2 circle
Broadleaf PC1	Core_BL_4000	%	0	4.9	0.05	Core broadleaf (at least 10m from an edge) as a % of a 4km2 circle
Broadleaf PC1	Com_BL_4000	%	0	2.1	0.3	Total area / Edge area - complexity of cover within the landscape
Felled PC1	FE_distance	m	0	2670	527	Distance in metres to nearest felled stand
Felled PC1	FE_area	m2	0.04	92	13.9	Size of nearest felled stand
Felled PC1	Tot_FE_4000	%	0	35	5.1	Felled cover as a % of a 4km2 circle
Felled PC1	Edge_FE_4000	%	0	8	1.9	Edge felled cover as % of a 4km2 circle
Felled PC1	Core_FE_4000	%	0	26.5	2.4	Core felled (at least 10m from an edge) as a % of a 4km2 circle
Felled PC1	Com_FE_4000	%	0.8	2.1	1.5	Total area / Edge area - complexity of cover within the landscape

Chapter Five

Chapter 5 Responses of bats to clear fell harvesting in Sitka Spruce plantations

Image from GoogleEarth showing typical patches of clear fell in the study area, Galloway

An adapted version of this chapter has been accepted for publication as:

Lucinda Kirkpatrick, Isobel F. Oldfield, Kirsty J. Park (in press). Responses of bats to clear fell harvesting in Sitka Spruce plantations, and implications for wind turbine installation. *Forest Ecology and Management*

5.1 Abstract

Commercial coniferous plantations are often assumed to be poor habitats for bats. As a result, the impact of forest management practices such as clear felling on bats has received little attention, particularly in Europe. However, there is growing evidence from multiple regions that bats do make use of plantation landscapes, and as interest in siting onshore wind turbines in upland conifer plantations grows, there is an urgent need to address this knowledge gap. In this study, we use a "before – after – control - impact" study to explore the short-term impacts of clear fell harvest on bat activity in commercial plantations. To the best of our knowledge, this is the first study of its kind carried out into the immediate impact of felling on bats in commercial plantations. Thirty-one mature stands of Sitka Spruce were surveyed in three large, upland Sitka Spruce plantations. Eleven stands were felled between 2013 and 2015, and 26 of the original 31 stands were resurveyed in 2015. Bat activity was monitored with acoustic detectors. The change in total bat activity and species / genus specific bat activity was modelled before and after felling occurred at both felled and control stands using generalised linear models. There was no change in overall bat activity at felled sites compared to control sites, but the activity of *Nyctalus* species was significantly higher following felling. Both *P. pygmaeus* and *P. pipistrellus* activity increased slightly but non-significantly and was mainly driven by increased activity at a few felled sites. The size of the felled area was influential with activity (for bats overall and *Pipistrellus* spp.), and highest in smaller felled areas. For *P. pipistrellus* activity in felled areas decreased with the duration since harvesting. Higher activity for some groups following felling may occur due to the creation of more edge habitat which is preferred by both *Pipistrellus* species we recorded. An increase in activity following the small-scale felling required for the installation of turbines could put foraging bats at risk from collisions with turbines. Further investigation of the impacts of both size of the clear fell patch, timing of felling and changes in invertebrate abundance due to felling are required to establish the potential impact of turbine installation.

5.2 Introduction:

Large scale clear felling is a controversial forest management process which has been heavily criticised for its perceived impacts, particularly on forest dependent flora and fauna (Borkin and Parsons, 2014; Lindenmayer et al., 2006). However, there is little consistency in the literature about the impacts of clear felling on biodiversity, with responses to clear felling being highly taxon-specific. Felling may negatively affect organisms by isolating populations, decreasing resources, increasing predation or changing climatic conditions (Grindal and Brigham, 1998). For example, forest specialists may be negatively affected due to increased predation risk from the lack of cover (e.g.

arboreal sciurids; Fisher 2005). However, felling may be beneficial for open and edge adapted species, particularly successional species, which respond positively to the changes in vegetation structure and composition caused by harvesting and preferentially use clear-cuts (e.g. some early successional birds; Loeb and O'Keefe, 2011; Oxbrough et al., 2010; Paquet et al., 2006). Plant species richness is 60% lower in stands with full canopy closure and increases in the first few years post-harvest as regeneration occurs (Eycott et al., 2006), which may be positive for some invertebrate taxa (Lin et al., 2006), but not for canopy specialists (Humphrey et al., 2003). In general, generalist and open specialist species benefit from clear felling, while forest specialist abundance and diversity decreases (Humphrey et al., 2003; Ohsawa and Shimokawa, 2011; Oxbrough et al., 2010). Therefore, while species richness may not change in response to felling pressure, community composition can be altered. Indeed, for moth species, I found that the size and proximity of felled areas had a negative impact on both taxonomic and functional diversity, although species richness was not affected (Chapter 3).

Many habitat selection studies have found that bats avoid commercial coniferous plantations (Boughey et al., 2011; Russo and Jones, 2003; Smith and Racey, 2008; Walsh et al., 1996), which is often attributed to low invertebrate diversity, amongst other factors (Boughey et al., 2011; Haupt et al., 2006; Russo and Jones, 2003; Smith and Racey, 2008). However, often these studies are carried out in areas of extremely low conifer cover which may be too low to detect any association (e.g. conifer cover of less than 3%, Davidson-Watts and Jones, 2005; Davidson-Watts et al., 2006) and there is growing evidence that certain bat species are able to make use of intensively managed non-native plantations in plantation dominated landscapes (Charbonnier et al., 2016; Cistrone et al., 2015; Mortimer, 2006; Russo et al., 2010, Chapter 2, Chapter 6). While the impacts of logging forests have been investigated for a number of different bat species worldwide (e.g New Zealand: Borkin and Parsons, 2010a, 2010b; USA: Grindal and Brigham, 1998; Australia: Law and Law, 2011), much of the previous work has concentrated primarily on landscapes in which logging is occurring in old growth or native forests (Dodd et al., 2012; Grindal and Brigham, 1998; Loeb and O'Keefe, 2011; Loeb et al., 2006; Menzel et al., 2002; Patriquin and Barclay, 2003). The impact of forest management practices in non-native commercial plantations has received far less attention (Borkin et al., 2011; Borkin and Parsons, 2014), and focuses on the impacts management may have on forest specialist bats which rely on tree roosts for much of their life cycle (Borkin et al., 2011; Borkin and Parsons, 2014). However, for bat species which are adept at utilising anthropogenically disturbed habitats and rely on building roosts rather than tree roosts, these plantations may represent an opportunity.

If individual home ranges are fully within plantation forests, bats, particularly tree-roosting bats, are likely to come into contact with felling operations (Borkin and Parsons, 2011). Features such as standing dead wood, snags, tree damage such as double leaders, and peeling bark all form key roosting habitats for bats and other taxa (Altringham et al., 1996; Arnett, 2007; Russo et al., 2010). However, in some plantation systems, trees are removed before these features develop due to reaching economic maturity, safety concerns, damage, fire risk or to limit the spread of parasites (Russo et al., 2010). Felling may therefore directly cause direct mortality by removal of a roost that is currently occupied by a bat colony or indirect mortality through impacting reproductive fitness and success as the number of roost trees within a colony home range is reduced (Borkin and Parsons, 2014).

Felling causes an immediate and substantial change to stand structural complexity, which may benefit edge and open adapted bats (Chapter 2; Adams, 2012; Elmore et al., 2005). In stands with substantial vegetative clutter, bat activity will be reduced due to constraints on both echolocation and manoeuvrability (Dodd et al., 2012; Adam D Morris et al., 2010; Patriquin and Barclay, 2003), and bat activity is likely to increase once clear felling has occurred. Felled stands may support a similar invertebrate abundance compared to mature forest (Dodd et al., 2012; Lacki et al., 2007; Ohsawa, 2005; Oxbrough et al., 2010), particularly in non-native plantations. Edge habitats often provide protection from wind and predators (Nicholls and Racey, 2006a), while invertebrates may accumulate passively due to wind (Law and Law, 2011; Verboom and Spoelstra, 1999). Even when invertebrate availability is lower in felled stands compared to mature stands, bat activity may be higher, suggesting that the structure of the habitat may be more important than prey abundance in determining the spatiotemporal foraging patterns of bats (Adams et al., 2009; Dodd et al., 2012).

Previously (Chapter 2, 7) I found evidence of *P. pipistrellus* and *P. pygmaeus* making widespread use of three large, predominantly Sitka Spruce (*Picea sitchensis*) plantations in Scotland and Northern England, and all other species in this geographic range were also detected, albeit in low numbers (Chapter 2). We also found little difference in activity between plantations and nearby broadleaf woodland (Appendix 1). This, coupled with the findings that half of the lactating female *P. pygmaeus* I radio-tracked (Chapter 6) preferentially associated with felled areas (Chapters 2,5, 6), suggests that certain bat species may increase their foraging activity as a result of harvesting operations. Therefore, felling, if roost structures are not removed or damaged in the process, may benefit some bat populations in commercial plantations. To our knowledge, the impact of clear felling on foraging activity of bats in commercial plantations has not been experimentally tested (but see Grindal and Brigham (1998) for a similar study in native forest, and Cistrone et al. (2015) for the impacts of selective logging on bat activity). In this study I used a before – after – control – impact (BACI) design to quantify the effect of felling on bat activity in the short term (between 1 and 16 months post-felling).

Specifically, we aimed to answer the following questions:

1. How does bat activity change in response to felling in the short term?
2. What influence does the size of the felled area have on bat activity?
3. How does time elapsed since felling influence bat activity in the short term?

5.3 Methods:

The study was conducted in three large, intensively managed plantation forests in Central and Southern Scotland, and Northern England. All three forests were chosen because of their large size (between 30,000 – 114,000 ha), high productivity and predominance of *Picea sitchensis*, which is the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each plantation, multiple sites (total n=31) were selected, each with a range of different stand ages including mature stands of harvestable age. Sites were at least 4 km from another site to reduce potential impacts from autocorrelation (Bellamy et al., 2013). Bat activity was surveyed pre- and post-harvesting at a total of 26 mature stands (11 harvested between Autumn 2013 and Spring 2015; 15 control stands which were not felled). Access to the remaining five sites was not possible due to changes in ownership or deterioration of access routes into the plantation area.

5.3.1 Bat surveying:

Data on pre-harvesting activity were collected in the summer of 2013, and post-harvesting activity in the summer of 2015. Stands were surveyed for a single night, starting 30 minutes after sunset ensuring that recorded individuals would be actively foraging rather than commuting, and continuing for four hours (the length of the shortest night in our study area). Bat activity was quantified using a SongMeter SM2 Bat+ (Wildlife Acoustics, Inc., Concord, MA) as described in chapter 2. Microphones were positioned at both the stand edge and interior; I pooled activity for this study due to low activity. Surveying was repeated after treatment sites were felled in the same way, with microphones placed at the same location as previously used. I tried to keep sampling dates as similar as possible between years but this was not always possible (date difference between pre and post felling sampling = 15 (4 – 33)).

5.3.2 Bat call analysis:

Calls were analysed as described in Chapter 2. We identified all calls manually to species or genus, counting the number of bat passes per night (four hour period), which was used as a measure of activity. Analyses were conducted for total bat activity and also separately for bats in the genera *Myotis* and *Nyctalus,* and for *Pipistrellus pygmaeus* and *P. pipistrellus*. Bats in the genus *Myotis* have a similar call structure and as such were also identified only to genus. It can be difficult to distinguish between *Nyctalus* calls in cluttered environments (Schnitzler et al., 2003), so again these were only identified to genus. *Pipistrellus* species can be differentiated between due to differences in end call frequency (Fc = frequency of the right-hand end of the flattest part of the call; Russ, 2012) and the call shape, so where possible passes were identified to species level. For passes where it was not possible to assign to either *Pipistrellus* species, I assigned them to genus. We recorded a very small number of *Plecotus auritus* calls and did not carry out further analysis. *P. auritus* have very quiet calls, so their occurrence will be underestimated by using acoustic recordings alone.

5.3.3 Statistical analysis:

All analyses were carried out in R studio using R version 3.3.1 (R core development team) using the following packages: MASS, lme4, ggplot2. All activity is expressed as passes per night. To assess the effect of felling on foraging activity (objective 1), total or species / genus specific activity was modelled with sampling time ("period"; pre / post), treatment ("treatment"; felled / control), and plantation (Cowal and Trossachs, Galloway or Kielder) as fixed factors. In order to determine if activity changed at harvested sites compared with control sites post-felling, an interaction between pre / post periods and treatment was also included. Models used either a negative binomial (total bat activity, *P. pygmaeus* activity, *P. pipistrellus* activity, all *Pipistrellus* activity and *Myotis* activity) or Poisson (*Nyctalus* activity) error distribution. Residuals were checked to ensure normality (Crawley, 2007). Two sites with much higher activity than all other sites were found to be strongly influencing the results, so analyses were carried out both with and without these sites.

To determine whether the size of the felling area (objective 2) or the time elapsed since felling (objective 3) influenced bat activity, I used a generalised linear regression model with a negative binomial error distribution for the 11 harvested sites only. Total bat activity, *Pipistrellus* spp activity and the two *Pipistrellus* species separately were response variables, with the size of the felled area (ha), months since felling and plantation as explanatory variables. I was unable to model the influence of the size of the felling area or time elapsed since felling for *Myotis* and *Nyctalus* due to the low activity we recorded for these genera. One site was found to be heavily influencing the results, so the analysis was carried out both with and without.

5.4 Results:

5.4.1 Influence of felling on bat activity:

In the first set of analyses, total activity increased significantly at treatment compared to control stands after felling had taken place, after controlling for forest and temperature (F= 3.10, p<0.005; Control: Pre 17.4 (12.1 – 25.2), Post 22.4 (15.6 – 32.3); Felled: Pre 22.0 (12.7 – 29.5), Post 96.4 (63.4 – 146.9). However, after removing the two sites with unusually high activity, this difference was no longer significant (F = 0.59, p = 0.56; Control: Pre 17.7 (12.5 – 25.0), Post 21.2 (15.0 – 29.9); Felled: Pre 19.3 (12.7 – 29.5), Post 29.1 (19.10 – 44.2); Table 5.1A, B, Figure 5.1A, 6.2 A).

At the species level, the impact of felling on bat activity was less marked. *Nyctalus* activity was 23 times higher post felling, which was unaffected by removal of outliers (Table 5.1A, B, Figure 5.1E, 5.2E). Overall, *Pipistrellus* activity more than doubled post felling, but only if the outlying sites were included. (Table 5.1A, 5.1B, Figure 5.1F). When both *Pipistrellus* spp. were considered separately, *P. pipistrellus* activity increased slightly post felling, but only if outlying sites were included (Table 5.1A, Figure 5.1C, 5.2C). Although from Figure 5.1B it appears that *P. pygmaeus* activity increases post harvesting, this is the influence of an outlying site, and once removed there was no significance difference in *P. pygmaeus* activity (Table 5.1A, B, Fig 5.2B). Finally, *Myotis* spp. activity was similar before and after felling at control and treated sites, both with and without outliers (Table 5.1A, 5.1B, Figure 5.1D, 5.2D).

5.4.2 Influence of size of the felled area and time since felling:

Overall bat activity, consisting largely of *Pipistrellus* species, declined significantly with the size of the clearfell (Figure 5.3E, Table 5.2A). This effect persisted after outliers were removed (Table 5.2B, Figure 5.3A. Total bat activity was 97% lower in the largest stands (40 ha) compared to smaller stands (3 ha), and similar reductions in activity were seen when *P. pygmaeus* and *P. pipistrellus* were modelled separately (Figures 5.3B, C, F, G). There was no effect of the time elapsed since felling (which ranged from 1 month – 18 months) on bat activity with the exception of *P. pipistrellus*, where activity was 90% higher in the stands which were newly felled (Table 5.2A, 5.2B).

5.5 Discussion

Maintaining and enhancing biodiversity in plantations is a key aim for forest managers (Ober and Hayes, 2010; Paquette and Messier, 2009), particularly as interest in alternative land uses such as renewable energy generation is growing. Currently, there is little information available for managers on how management and harvesting operations affect biodiversity in non-native conifer plantations.

Table 5.1: Change in bat activity at control and felled sites after harvesting occurred. Presented are model estimates plus standard error for activity night, including outliers (A) and excluding outliers (B). Bold indicates parameters with a significant effect (standard error does not cross zero) on predicted activity. Models are presented both with (A, n = 26) and without (B, n = 24) two outlying sites.

Model A (with outliers)	(Intercept)	Treatment Felled	Activity Post felling	Temperature	Galloway	Kielder	Felled: Post felling	R^2
All bat activity	0.66 ± 0.87	0.23 ± 0.28	0.25 ± 0.27	0.24 ± 0.06	-2.14 ± 0.31	-0.42 ± 0.29	1.23 ± 0.4	0.22
P. pygmaeus	2.09 ± 1.53	0.21 ± 0.5	0.37 ± 0.47	0.17 ± 0.11	-2.07 ± 0.55	-0.64 ± 0.52	0.94 ± 0.7	0.27
P. pipistrellus	-1.7 ± 1.6	0.44 ± 0.5	0.61 ± 0.48	0.32 ± 0.11	-2.51 ± 0.56	0.69 ± 0.5	1.03 ± 0.7	0.59
Myotis	-2.69 ± 1.69	-0.01 ± 0.53	-0.15 ± 0.51	0.22 ± 0.12	0.72 ± 0.65	1.85 ± 0.61	0.19 ± 0.74	0.2
Nyctalus	-2.94 ± 0.99	-1.14 ± 0.39	-0.24 ± 0.29	0.13 ± 0.05	2.66 ± 0.72	0.28 ± 0.79	1.67 ± 0.48	0.54
All pipistrellus activity	1.39 ± 1.35	0.32 ± 0.44	0.34 ± 0.41	0.26 ± 0.1	-2.36 ± 0.49	-0.49 ± 0.45	1.16 ± 0.61	0.44
Model B (without outliers)								
All bat activity	0.74 ± 0.84	0.09 ± 0.27	0.18 ± 0.25	0.23 ± 0.06	-1.81 ± 0.29	-0.63 ± 0.27	0.23 ± 0.38	0.1
P. pygmaeus	2.18 ± 1.51	-0.25 ± 0.5	0.32 ± 0.44	0.17 ± 0.11	-1.62 ± 0.52	-0.93 ± 0.49	0.24 ± 0.7	0.16
P. pipistrellus	-1.55 ± 1.46	0.58 ± 0.46	0.47 ± 0.42	0.31 ± 0.1	-2.17 ± 0.5	0.51 ± 0.44	-0.59 ± 0.65	0.49
Myotis	-2.04 ± 1.81	0.01 ± 0.58	-0.19 ± 0.53	0.18 ± 0.13	0.87 ± 0.67	1.76 ± 0.64	-0.2 ± 0.82	0.17
Nyctalus	-2.83 ± 0.99	-1.4 ± 0.44	-0.26 ± 0.29	0.12 ± 0.05	2.68 ± 0.72	0.17 ± 0.82	1.97 ± 0.52	0.55
All pipistrellus activity	1.54 ± 1.29	0.18 ± 0.43	0.25 ± 0.38	0.25 ± 0.09	-2.04 ± 0.45	-0.72 ± 0.42	0.22 ± 0.6	0.26

Table 5.2: Change in total bat activity and P. pygmaeus / P. pipistrellus /*all* Pipistrellus *activity felled sites after felling occurred by the size of felled area and time elapsed since felling. Presented are model estimates plus standard error for activity per four hour sampling period excluding outliers. Models are presented both with and without two outlying sites.*

Model	Term	Estimate ± std error (with outliers)	F-statistic		R2	Estimate ± std error (without outliers)	F-statistic		R2
Total bat activity	(Intercept)	2.55 ± 1.02	2.50	**	0.83	2.08 ± 1.04	2.00	*	0.72
	Size of felled area	-0.10 ± 0.02	-4.57	***		-0.09 ± 0.03	-3.46	***	
	Months since felling	-0.04 ± 0.04	-0.99	ns		-0.01 ± 0.04	-0.31	ns	
	Galloway	3.34 ± 0.97	3.46	***		3.30 ± 0.96	3.42	***	
	Kielder	5.38 ± 1.05	5.13	***		5.08 ± 1.09	4.65	***	
Pipistrellus pygmaeus	(Intercept)	2.16 ± 1.34	1.62	ns	0.68	1.82 ± 1.43	1.28	ns	0.54
	Size of felled area	-0.11 ± 0.03	-3.53	***		-0.10 ± 0.04	-2.71	**	
	Months since felling	-0.03 ± 0.06	-0.55	ns		-0.01 ± 0.06	-0.18	ns	
	Galloway	2.96 ± 1.26	2.34	*		2.94 ± 1.31	2.25	*	
	Kielder	4.77 ± 1.38	3.45	***		4.57 ± 1.50	3.05	***	
Pipistrellus pipistrellus	(Intercept)	2.40 ± 1.45	1.65	ns	0.85	2.10 ± 1.52	1.38	ns	0.75
	Size of felled area	-0.09 ± 0.03	-3.20	***		-0.08 ± 0.03	-2.41	*	
	Months since felling	-0.14 ± 0.05	-2.64	**		-0.12 ± 0.06	-2.11	*	
	Galloway	1.59 ± 1.42	1.12	ns		1.58 ± 1.45	1.09	ns	
	Kielder	4.99 ± 1.48	3.38	***		4.82 ± 1.56	3.08	***	
All Pipistrellus	(Intercept)	2.62 ± 1.12	2.34	*	0.80	2.20 ± 1.17	1.88	*	0.67
	Size of felled area	-0.11 ± 0.03	-4.23	***		-0.09 ± 0.03	-3.20	***	
	Months since felling	-0.04 ± 0.05	-0.94	ns		-0.02 ± 0.05	-0.39	ns	
	Galloway	3.15 ± 1.06	2.97	***		3.11 ± 1.08	2.90	***	
	Kielder	5.38 ± 1.15	4.67	***		5.12 ± 1.23	4.17	***	

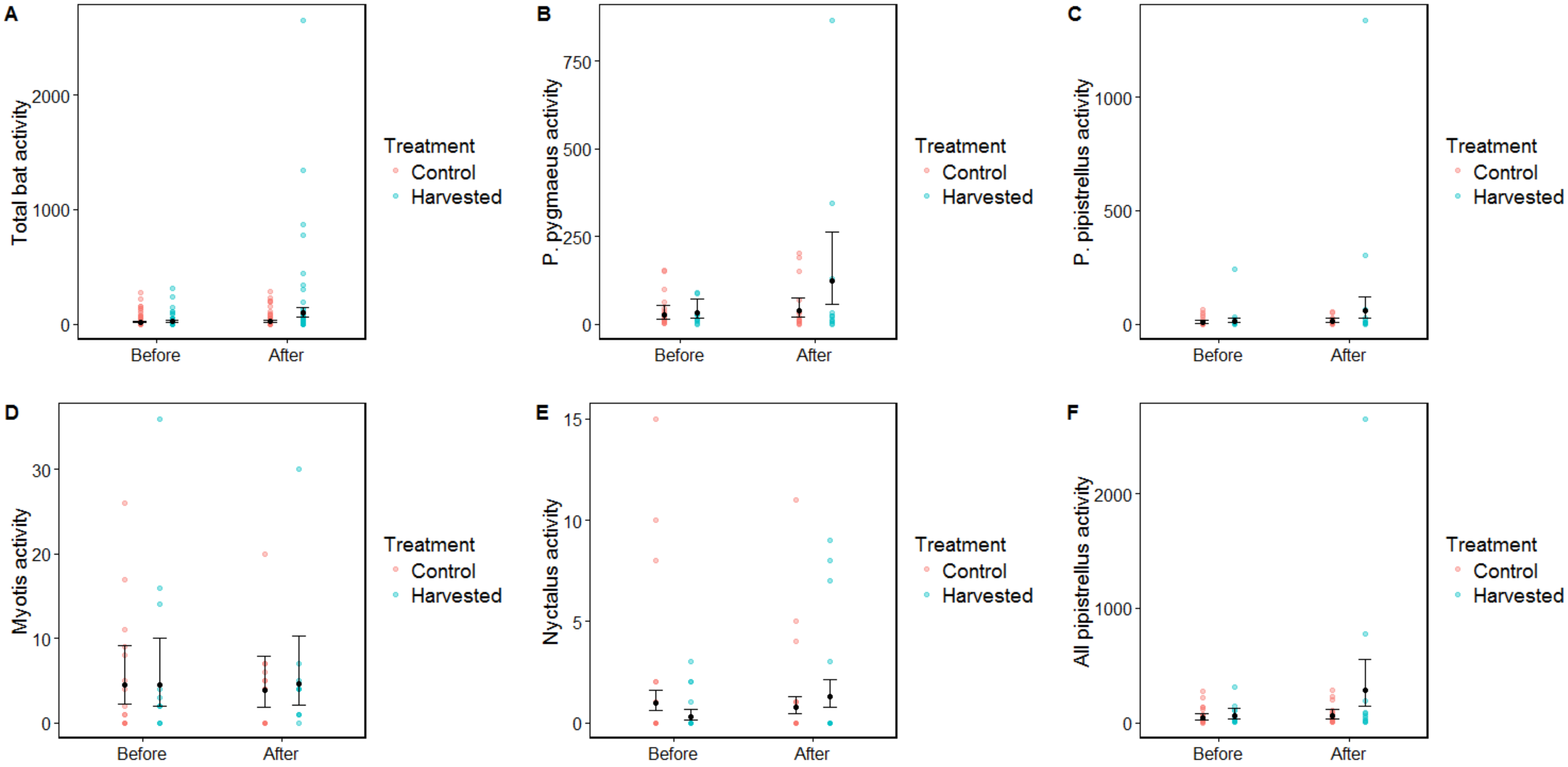


Figure 5.1: Change in bat activity at control and felled sites before and after harvesting occurs for total and species / genus specific activity. Outlying sites are included (n = 26). Coloured dots depict raw data on bat activity, black dot shows model predicted activity and error bars show 95% confidence intervals.

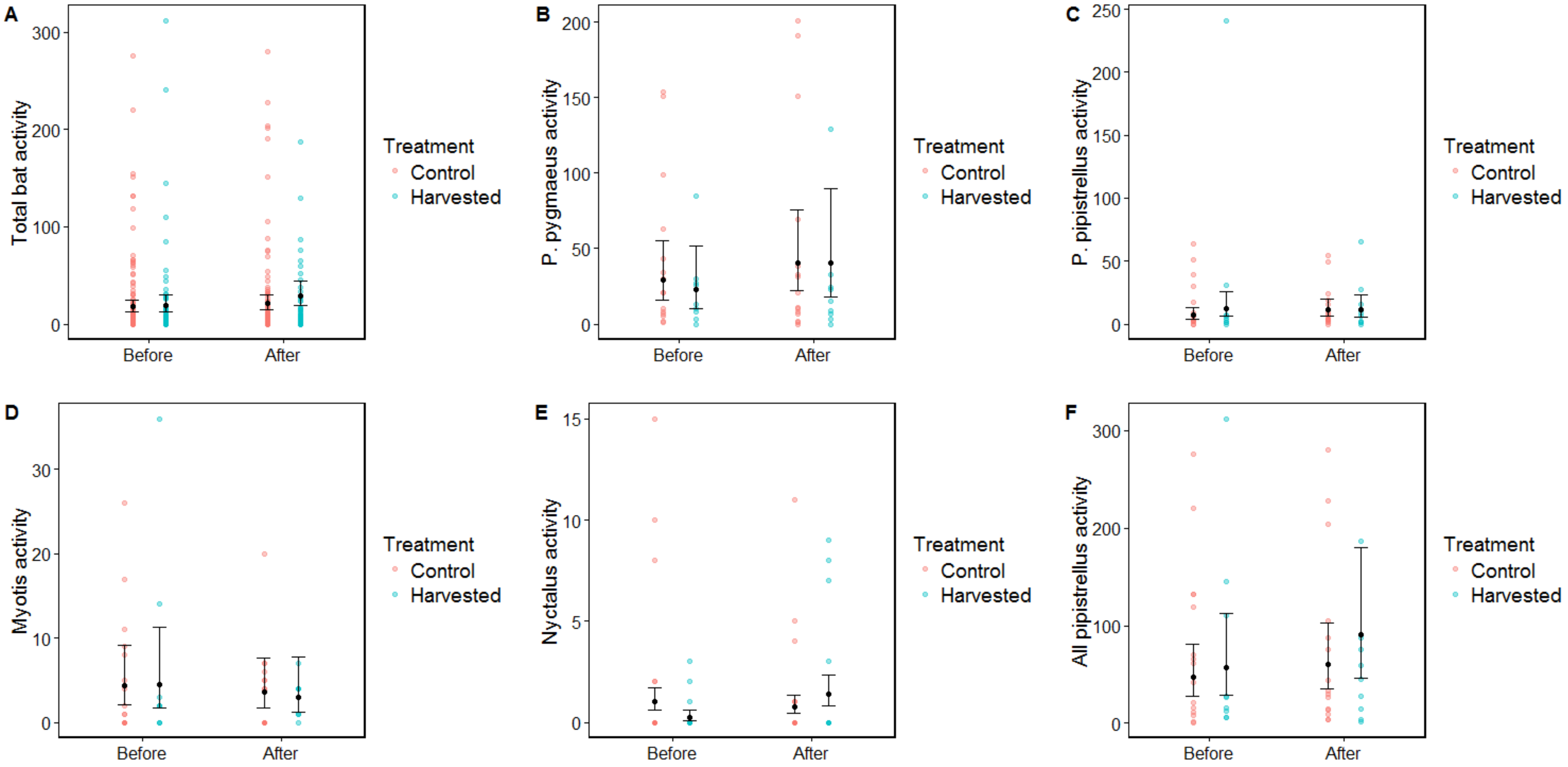


Figure 5.2: Change in bat activity at control and felled sites before and after harvesting occurs for total and species / genus specific activity. Outlying sites are excluded (n = 24). Coloured dots depict raw data on bat activity, black dot shows model predicted activity and error bars show 95% confidence intervals

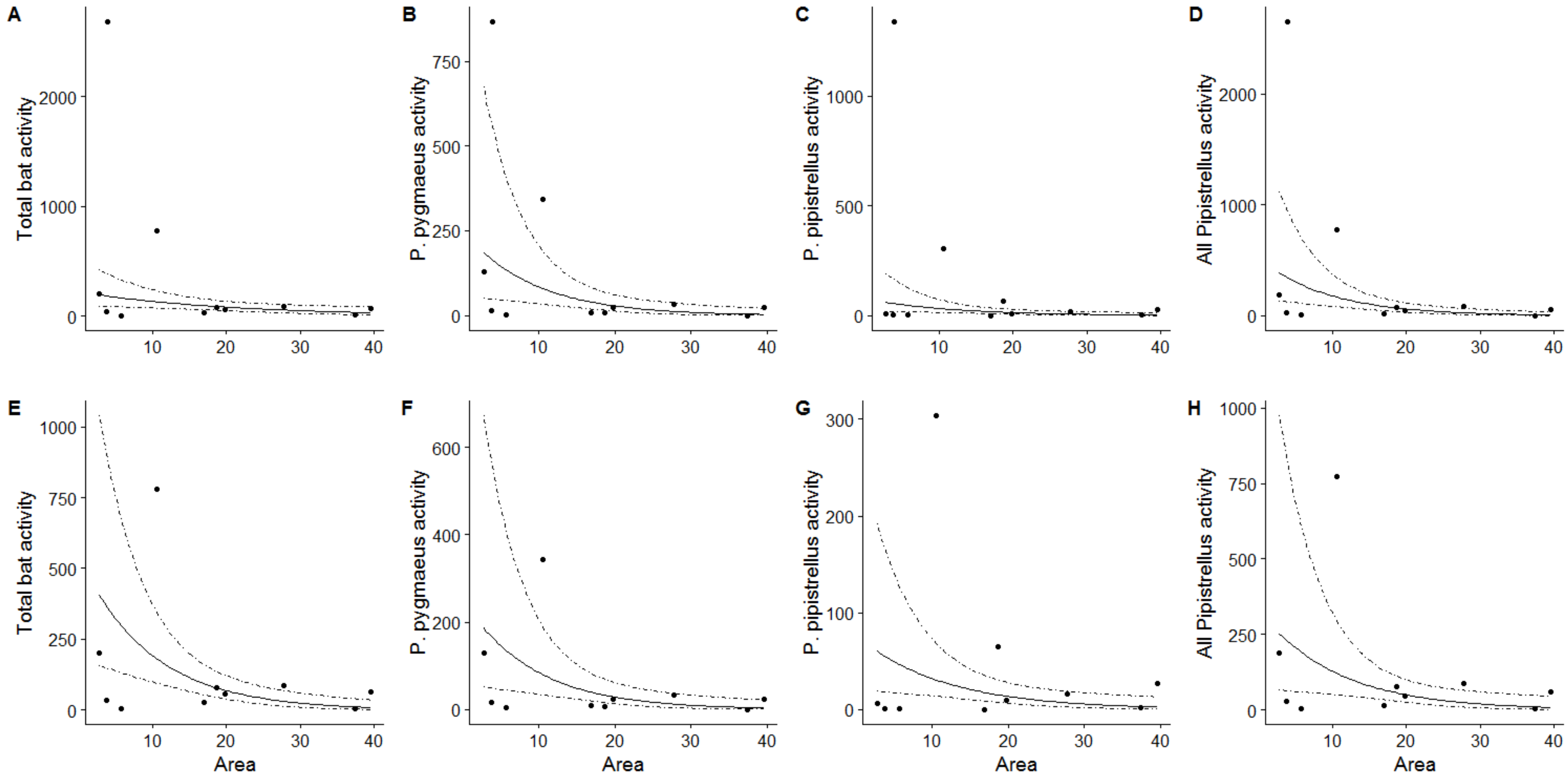


Figure 5.3: Change in total, P. pygmaeus, P. pipistrellus *and all* Pipistrellus *activity in response to felled stand area (n =11). Black dots are raw data, the solid black line is the model prediction for change in activity, the dashed lines are the 95% confidence intervals. Graphs A – D include outlying site (n = 11), graphs E – H exclude outlying site (n = 10).*

To our knowledge, this is one of only a few studies to explicitly test the immediate impact of clear felling on bat activity using a BACI study (e.g. Grindal and Brigham, 1998), and is the only one conducted in commercially managed plantations rather than native woodland (but see Cistrone et. al (2015) for a study investigating the impacts of thinning on bat activity in commercial plantations). Previous studies investigating timber felling on bats have largely focussed on impacts in old growth and boreal forests (Dodd et al., 2012; Grindal and Brigham, 1998; Hogberg et al., 2013; Patriquin and Barclay, 2003) or have concentrated on the effects of roost loss due to harvesting on forest specialist or tree roosting bats (Arnett, 2007; Borkin et al., 2011; Borkin and Parsons, 2014; Elmore et al., 2005).

Conclusions from these studies may not be completely transferable to plantation forest systems common across much of Europe, where production forestry involves non-native coniferous stands felled before old growth conditions are achieved, rather than the removal of old growth or native forest (FSC, 2012). Here, we found that bat activity did not fall after harvesting, and for some species, there was an increase in activity. However, this was dependent on the size of the clear cut, with an increase in bat, and particularly *Pipistrellus* spp*.,* activity at smaller clear cuts compared to larger clear cuts. There is little evidence that felling impacts bats through the loss of potential roost trees. Both *Pipistrellus* species preferentially roost in buildings, and I found no evidence of breeding females using Sitka Spruce trees (Chapter 6). Furthermore, Sitka Spruce reach economic maturity and are harvested before suitable roost features form, reducing the likelihood of *Myotis* or *Nyctalus* breeding colonies being present. It is likely that Sitka Spruce plantations may be important primarily as foraging habitat, with felling causing little in the way of mortality due to roost loss or reduction in reproductive potential (Borkin et al., 2011)

5.5.1 Impacts of felling on bat activity

I found no evidence that bat activity in post-harvesting sites fell in response to felling, and some evidence that for certain species, activity may increase (Dodd et al., 2012; Grindal and Brigham, 1998; Loeb and O'Keefe, 2011; Patriquin and Barclay, 2003; Pauli et al., 2015). Bat responses to felling were species specific and consistent with predictions from ecomorphology (Aldridge and Rautenbach, 1987; Schnitzler and Kalko, 2001). Open adapted bats, such as *Nyctalus* spp*.* which have long thin wings, a high aspect ratio and low-frequency calls, are less manoeuvrable in cluttered conditions, and as expected, increased in activity at felled stands. Similarly, both *Pipistrellus* species, which are typical edge foragers, had a non-significant trend towards higher activity post-harvest at felled stands compared to control stands, although the extent of the response varied with stand size. Alternatively, small changes in bat activity could be due to increased commuting along new access roads constructed to allow machinery access into felling areas (Grindal and Brigham, 1998; Hein et al., 2009; Law and Law, 2011). Finally, bat activity could be occurring above the canopy of the mature stands that were not harvested (control sites), which is beyond the detection range of our detectors (Grindal and Brigham, 1998). Creating new tracks and felled areas may change the location of the edge used by bats from horizontal to vertical in these areas (Grindal and Brigham, 1998).

My results contrasted with those of Law and Law (2011), who found that bat activity was reduced in *Eucalyptus* plantations in Tasmania, particularly at the stand centre. However, their study focussed on longer term effects, as it was conducted more than five years after felling, during which time substantial changes in stand structure and plant species composition are likely to have occurred. In contrast, I carried out all sampling within two years of felling, and as such my results reflect felled stands rather than stands in which substantial vegetative regrowth has occurred (Law and Law, 2011).

In Appendix 1 we found a strong correlation between echolocation passes and feeding buzzes suggesting that areas of high activity are areas in which increased foraging is occurring. However, the mechanism behind increased activity for some species at felled stands does not appear to be driven by increases in invertebrate abundance. While we did not compare invertebrate activity before and after felling in this study, a previous study in the same study area (Chapter 2) found no difference in invertebrate activity between stand types, including felled stands. However, we did not explicitly model the influence of time since felling on invertebrate abundance. It may be that the increased ground disturbance, prevalence of deadwood and stagnant groundwater that remains immediately after clear felling results in a short-lived but substantial increase in Nematoceran diptera abundance (Blackwell et al., 1994), providing an ephemeral food source which bats are able to exploit (Fukui et al., 2006). Further investigation of the changes in invertebrate abundance and diversity post felling would be interesting to understand fully the mechanism driving these relationships.

5.5.2 Changes in bat activity in relation to time since felling

Pipistrellus pipistrellus activity decreased as time since felling increased, perhaps in response to changing invertebrate abundance, but *P. pygmaeus* and total bat activity was unaffected. Previous studies have found that the two closely related and morphologically similar *Pipistrellus* species (*P. pipistrellus* and *P. pygmaeus*), whilst similar in foraging ecology, have habitat and dietary differences (Barlow, 1997; Davidson-Watts et al., 2006; Nicholls and Racey, 2006a). Both species were commonly recorded in the three Sitka Spruce plantations surveyed as part of this study, and have previously been found to preferentially forage at felled stands (Chapter 2, Chapter 6). Potentially the two species avoid interspecific competition through *P. pipistrellus* targeting more recent clear fell, which is structurally less complex (Haupt et al., 2006). Longer term analysis of changing invertebrate diversity and abundance post felling alongside concurrent acoustic recording would be necessary to understand how invertebrate populations may change post felling. However, the change in structural complexity may be more important in driving bat activity than invertebrate availability (Dodd et al., 2012; Adam D Morris et al., 2010). Physical clutter may impede flight efficiency and be harder to negotiate as dense vegetation will result in increased acoustic clutter (Jung et al., 2012; Adam D Morris et al., 2010; Patriquin and Barclay, 2003). Therefore freshly felled areas in Sitka Spruce plantations may represent a patchy and ephemeral food resource in the landscape, with minimal physical and acoustic clutter, which is thereby easier to negotiate and hunt in (Patriquin and Barclay, 2003; Pauli et al., 2015).

5.5.3 The influence of the size of the felled area on bat activity

The size of the felled area had a significant, negative impact on bat activity for total bat activity, driven by *P. pygmaeus* and *P. pipistrellus* activity, similar to other studies (Law and Law, 2011; Patriquin and Barclay, 2003). It is possible that the large differences in cut block size in this study (2.7 – 39ha) may be responsible for the somewhat equivocal species-specific responses to felling. The size of clear-felled areas investigated here was far greater than in previous studies (e.g. 0.5 - 1.5ha; Grindal and Brigham, 1998) and more representative of current clear fell forestry practices. Edge adapted bats are likely to benefit most from felling in commercial plantations (Borkin and Parsons, 2011) due to the relatively high proportion of edges compared to that found in other woodland types such as native woodlands which are not traditionally managed for timber extraction. However, larger felled areas will not offer an increased foraging area through the provision of proportionately larger edges (for example a 750% increase in felled area resulted in a 200% increase in edge perimeter habitat in this study), but may be avoided by bats due to increased perceived predation risk (Grindal and Brigham, 1998), or because exposure to climatic conditions in larger clear fells is not conducive to supporting large invertebrate populations (Baker et al., 2013). Again, further comparisons of both felling techniques and extent would be necessary to fully understand the impacts of felling in a commercial forestry context on bat species.

5.5.4 Management implications:

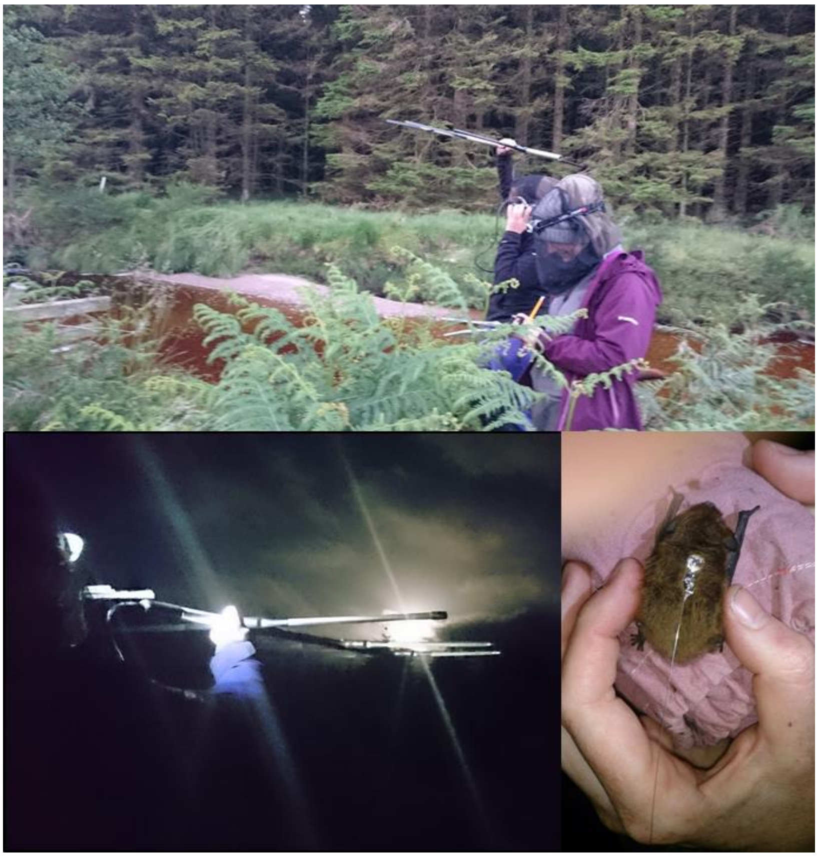
This work has implications for our understanding of how habitat management prior to installing turbines may influence bat activity in plantations. This often involves felling small areas of trees (50m beyond turbine blade tip, Anon., 2015), along with constructing access roads into newly felled areas. Roads are important flyways for bats, allowing access into different plantation areas (Chapter 6; Grindal and Brigham, 1998; Hein et al., 2009) and may potentially guide bats towards newly installed turbines, particularly *Nyctalus* and *P. pipistrellus*. This may create a patchwork of attractive foraging patches within which turbines have been installed, acting as an ecological trap (Tscharntke et al., 2012), particularly as low structural clutter is maintained in these areas. Since it is assumed that bat activity in upland plantations is low, there are currently no requirements for monitoring post felling and post construction and no guidance on the potential impacts on bats (Mathews et al., 2016). My results tentatively suggest that some bat species could be at far greater risk from the installation wind turbines in commercial plantations than previously thought. Further investigation of both short and long term responses of bats to keyholing is an urgent priority, particularly for *Nyctalus* species (Mathews et al., 2016).

From this study, it appears that felling in Sitka Spruce plantations does not appear to directly destroy bat roosts. However, felling does influence bat activity levels, although this appears to be species specific, and related to both extent of and time elapsed since felling. Overall, bat activity is either the same or higher post-felling, with the greatest increase at smaller felled stands, similar to studies from native forest systems (Grindal and Brigham, 1998; Patriquin and Barclay, 2003). Plantation forests are receiving increased interest as sites of alternative energy generation, but currently, guidance on the impacts of installing wind turbines in upland plantations on bats is lacking, which has recently been highlighted as a key priority for further research (Mathews et al., 2016). Here we present initial evidence that bat activity may increase in response to the initial felling activity, with a suggestion that activity is greatest immediately after felling, and decreases as time since felling increases. However, this would need further investigation with an increased sample size, repeated sampling for more years and targeted invertebrate monitoring to assess whether the higher bat activity in newly felled sites is in response to a sudden increase in invertebrate abundance. Further investigation of the size of different clear fell patches on bat activity will be necessary in order to determine the effect of keyholing on bat activity. Due to the small number of sites surveyed here, it is not possible to determine the optimal size of clearing for bat activity, but in stands over 20ha activity was far lower. Finding optimal stand sizes can be useful for two reasons. Firstly, finding the optimal stand size and using a patchwork of these across the plantation landscape would be possible in larger plantation forests, resulting in a more “bat friendly” forest landscape. Alternatively, finding the optimal stand size beyond which bat activity in the stand centre is very low could be used to guide how wind turbines are installed within the plantation landscape.

This study is the first of its kind to investigate the impact of felling on bats in Sitka Spruce plantations and demonstrates not only that upland commercial coniferous plantations are not devoid of bats, but that there is an urgent need for further studies, especially in light of changing land use in upland plantations.

Chapter Six

Chapter 6 Sitka spruce plantations: A land of opportunity for *Pipistrellus pygmaeus*?



Radio tracking female *P. pygmaeus* in Galloway Forest Park.

6.1 Abstract:

Plantation forests are a widespread land use type across the temperate zone, yet information on the impact that management has on both abiotic and biotic environments for certain taxa can be sparse. Although there is growing recognition that, with sympathetic management, plantation forests may be able to support more biodiversity than previously thought, the extent to which they may support bat populations has been contentious. Many studies have demonstrated active avoidance of coniferous plantations and attributed this to the lack of available roost sites and low invertebrate diversity. However, studies carried out in plantation dominated landscapes have shown that bats are able to exploit these areas to some extent. In Chapter 2 I found evidence of high bat activity in commercial plantations, with a high proportion of captured individuals were lactating female *Pipistrellus pygmaeus.* In this study, female *P. pygmaeus* were radio tracked over two summers in order to establish the extent to which individual bats use plantations for foraging, locate roost sites and assess the implications for felling operations on bats. All maternity roosts identified (n=17) were in dwellings, with most holding in excess of 500 individuals. I found no evidence of bats roosting in mature Sitka Spruce, although several bats used roosts in old or dead beech and oak trees as an alternative to their main maternity roost. Home ranges and to some extent core areas were much larger than those reported from other studies (an average of 9.6 compared to 0.6 – 1.6 km^2 home range area), and it is likely that roost availability rather than foraging availability constrains bat use of Sitka Spruce plantations. Protecting maternity roosts identified in buildings and installing bat boxes to reduce pressure on maternity roosts may benefit bat populations and will also enable use for alternative functions such as harem formation. Home ranges were larger for individuals in maternity roosts further from plantations. At a landscape scale, the majority of individuals selected coniferous habitats over other habitat types, whilst at a local scale, areas of felling or broadleaf trees were most commonly used, using forest tracks to move around the plantation. The association with felled stands has implications for forest management as plantations are increasingly being used for wind turbines, associated with high bat mortality in some countries, following small-scale felling operations. Decisions about siting wind turbines in upland plantations should take into account the likelihood of increased bat activity post felling.

6.2 Introduction

In landscapes where we lack a thorough understanding of the interactions and relationships between organisms and their environment, it can be difficult to manage anthropogenic environmental change for the benefit of biodiversity. For example, plantation forests are a widespread land use type yet information on the impact that management has on both abiotic and biotic environments, and consequently the organisms which are present, can be sparse for certain taxa. They are usually large in size, intensively managed and, perhaps due in part to the perception of plantations as poor for biodiversity, often under surveyed, resulting in insufficient information to determine the impact of management on organisms (Brockerhoff et al., 2008; Russo et al., 2010). However, there is growing evidence that changing forest management practices will allow social and ecological benefits without impacting economic performance (Brockerhoff et al., 2008; Humphrey, 2005; Russo et al., 2016; S. S. Stephens and Wagner, 2007).

Commercial plantations in Europe are generally considered poor habitat for bats (Boughey et al., 2011; Russo et al., 2010) which may have resulted in their potential contribution to bat conservation being under explored (Russo et al., 2016). However, a growing body of research suggests that such plantations may be a suitable habitat for bats if roosting and foraging requirements are met (Borkin and Parsons, 2011; Law et al., 2015). For example, extensive bat use of commercial plantation forests has been reported from Australia (Adams et al., 2009; Blakey et al., 2016; Law et al., 2015), New Zealand (Borkin and Parsons, 2010a, 2010b), North America (e.g. Patriquin and Barclay, 2003), Italy (Cistrone et al., 2015), France (Charbonnier et al., 2016) and the UK (Chapter 2; Mortimer, 2006). Although these plantations differ greatly in terms of tree species and management style, bats appear to respond broadly similarly to certain management prescriptions such as increased bat activity in response to reduced stand density (Bender et al., 2015; Blakey et al., 2016; Cistrone et al., 2015; A D Morris et al., 2010; Patriquin and Barclay, 2003). Despite this, forest management plans currently lack appropriate information to ensure management for bats is effective and meets legislative requirements (Russo et al., 2016). In addition, as plantations are increasingly being used for the installation of wind turbines, which have been associated with bat mortality, understanding their use by bats is essential for informing forest management plans and ensuring that appropriate mitigation is carried out.

Bats rely on forest habitats for foraging, provision of roosts for maternity colonies and mating behaviour (Altringham et al., 1996). In addition, forest habitats often harbour large populations of invertebrate prey, provide protection from predators and forest edges provide linear features to allow easier negotiation around the landscape (Heer et al., 2015; Rodríguez-San Pedro and Simonetti, 2014; Verboom and Spoelstra, 1999). Conifer plantations are primarily planted with non-native, fast growing tree species which are harvested before reaching maturity, rarely developing features appropriate for bat roosts (Burgar et al., 2015). However, suitability as roosts varies between different tree species. For example both *Pinus nigra* and *P. sylvaticus* were used as maternity roosts by a colony of *M. nattereri* in Scotland (Mortimer, 2006). Felling may directly cause mortality through the removal of roost trees if occupied by bats, or indirectly by reducing the reproductive potential of a population (Borkin et al., 2011; Borkin and Parsons, 2014, 2010a). In addition, the practice of clear felling (the removal of all the trees of harvestable age within a single stand, a forestry unit denoting an area of even aged trees, usually planted at the same time) can result in extreme habitat alteration and the creation of new, large gaps can limit bat movement around plantation landscapes (Grindal and Brigham, 1998). Finally, while plantations may support substantial invertebrate populations, the increased structural complexity in densely planted plantation forests may limit the accessibility of invertebrate prey for all but the most manoeuvrable bat species (Dodd et al., 2012; Jung et al., 2012).

Many bat species occurring in Western Europe have undergone severe population declines in the previous decades (Walsh et al., 1996) although monitoring programs have shown that some populations are beginning to recover as a result of increased legislation (Barlow et al. 2015). In the United Kingdom, seven of the 16 resident bat species have been designated Biodiversity Action Plan (BAP), one of which is *Pipistrellus pygmaeus* (Joint Nature Conservation Committee, 2011). Previously I found evidence of high bat activity, primarily *P. pygmaeus* and *P. pipistrellus* in commercial plantations (Chapter 2), and this was similar to activity levels in semi natural ancient woodlands, a habitat considered higher quality for bats (Appendix 1). For *P. pygmaeus* at least, a large proportion of individuals captured in or around plantation areas were lactating females (Chapters 2, 5), indicating that *P. pygmaeus* use plantation forests to some degree during an energetically expensive period. *Pipistrellus pygmaeus* preferentially feeds on nematoceran Diptera with aquatic larvae (Barlow, 1997) which are abundant in plantation areas (Appendix 1), and form large maternity colonies in buildings, so are less dependent on tree cavity roosts. Previous studies have found that *P. pygmaeus* associate strongly with riparian habitats (Davidson-Watts et al., 2006; Nicholls and Racey, 2006a; Sattler et al., 2007), and an avoidance of coniferous plantations which was attributed to lower invertebrate densities (Davidson-Watts and Jones, 2005). However, these studies were not carried out in plantation dominated landscapes, and in these areas it is unclear to what extent *P. pygmaeus* associate with particular habitats within plantations, and whether *P. pygmaeus* also use tree cavities in mature conifer as roosts and may therefore be directly at risk from felling operations. Specifically, in this study, I aimed to:

1. Identify maternity roosts for *P. pygmaeus* in plantation landscapes
2. Characterise bat habitat associations within plantation landscapes at multiple spatial scales
3. Identify key foraging habitats
4. Use the findings to make management recommendations

6.3 Methods

6.3.1 Study area, colonies and capture method

The study was conducted between early June and late August across both 2014 and 2015 in Galloway Forest Park in South west Scotland. Galloway forest park is a large (114,000 ha), upland, coniferous plantation dominated by *Picea sitchensis* (Sitka Spruce) and managed primarily for timber extraction. Bats were trapped at foraging sites within the plantation (see Appendix 1 for a description of field sites) as part of another study comparing activity between paired broadleaf and plantation stands. Prior to planting in 1925, Galloway consisted of open uplands with a few, isolated broadleaf fragments. The current landscape is one of stands of conifer, primarily *Picea sitchensis,* at various ages and densities interspersed with open uplands and small patches of fragmented broadleaf woodlands. As a result of damming rivers several large lochs also exist.

All trapping sessions began 30 minutes after midnight to reduce the likelihood of trapping commuting bats as I wanted to target bats foraging within plantation areas. Individual bats were trapped by placing mist nets and a harp trap across potential flight-lines in plantation sites. I used an acoustic lure with four different synthesised calls played for 15 minutes at each net. After capture bats were held in bags before biometric data was recorded. I recorded mass to an accuracy of 0.1g and forearm to 0.1mm. Individuals were aged based on ossification of the phalangeal joints and sexed (Kunz et al., 1996). I assessed the reproductive status of the females I trapped by the presence of hairless, large nipples and whether they were palpably parous. I stopped trapping during late June when individuals are likely to be heavily pregnant to reduce the stress of catching. Only females were used for the tracking study as I was primarily interested in how *P. pygmaeus* uses plantations during pregnancy and lactation, an energetically costly period. I selected females for trapping based on a minimum weight of 6.0 g (Aldridge and Brigham 1998) and reproductive status (avoiding heavily pregnant bats). One female juvenile was tagged in the first year as adult females began to disperse out of the plantation area earlier than anticipated. I did not catch any juveniles in the second year.

6.3.2 Transmitters and tracking methods

Bats were tagged with Holohil LB-2X (Holohil Systems, Carp, Ontario, Canada) transmitters, which are between 0.22 – 0.31g in weight and are the smallest tags currently available. The fur on the back of the bats between the scapulae was trimmed and transmitters were attached using a surgical latex cement (Torbot Ostomy and Medical Supplies, Rhode Island, US) which provides a flexible hold and limits disturbance to the bat. Transmitter batteries had a minimum life span of 7 days although several lasted 14 days. One tagged failed shortly after application, all others detached before battery failure. Bats were tracked using a combination of Sika (Biotrack, UK) and Australis (Titley, Australia) receivers with hand held Yagi aerials. The topography of the area, the density of plantation stands and the limited range of the tags meant that bats were located by “homing in” (technique by which fieldworkers follow a signal’s increasing strength until the animal is observed, or circling a small area under the assumption that the animal is within the area, White and Garrott, 1990). Field workers worked in pairs, homing in on bat locations while another fieldworker used higher altitude positions to locate bats when they were lost. If contact with the bat was lost for more than half an hour then the night was not considered a full session; only full sessions were used for further analysis. Locations were assigned an accuracy based on confidence in the location of the bat, whether field workers were able to see the bat, and on the quality of the signal. The accuracy bands were determined by carrying out field experiments with a transmitter in different habitats. Tags were set at known points, and the strength of the signal at distances from this point were recorded. Fieldworkers were trained with these tags to ensure familiarity with the process of tracking before bats were tagged. Areas of dense conifer reduced the transmitter range considerably. I only retained points with an accuracy of 100m or less for further analysis. Bearings were recorded as frequently as necessary to ensure continuous contact with the bat, dependent on whether the bat was foraging (moving consistently within a small area, many bearings) or commuting (moving quickly from one area to another, bearings were taken as frequently as possible but bats moved quickly between locations and as a consequence fewer bearings were recorded). Bearings were subsequently subsampled to every 5 minutes to reduce temporal autocorrelation.

I recorded time, location of observers (ten figure grid reference), GPS waypoint, bearing on the bat, accuracy information, description of the location and notes about the bats behaviour and location (e.g. flight height, whether other bats were foraging nearby, habitat over which bats were foraging). Climatic conditions such as temperature, rain and cloud cover were recorded where possible. The positions of the bats were calculated from their bearing and estimated distance and re-projected as estimated locations using R (R core development team, version 3.3.1; Donnell, 2015).

6.3.3 Analysis of habitat

All analysis was carried out in R (R core development team, version 3.3.1) using the following packages: AdehabitatHS, AdehabitatHR, rgeos, raster, sp, rgdal, ggplot2. Habitat was assessed on two scales. First, using the Centre for Ecology and Hydrology 2007 Land Cover Map (Morton et al., 2011) and a forestry commission specific database I created a *broad scale* map by categorising the landscape according to the following variables: Buildings, Broadleaf, Conifer, Open (upland or moorland), Tracks, Mixed woodland (both broadleaf and conifer), Water, Grassland (including improved pasture). Secondly, I created a *fine scale,* forest management specific map which categorised the plantation habitat into finer detail, distinguishing between stand types according to management. Stands were classified into felled (felled within 3 years of the sampling), young conifer (stands less than 10 years old) and closed canopy conifer (stands more than 25 years old, appendix, table 6.1). I included patches of broadleaf at a finer scale than that of the land cover map, capturing remnant patches remaining within the conifer plantation and mapped waterways

Ranges of tagged bats were calculated using two methods. Home range was determined by using a 95% minimum convex polygon (MCP) around all locations, and core areas were determined using an 80% kernel density estimate (density estimate of 80% of activity, KDE) with a smoothing factor of 83 (the standard deviation of the estimated accuracy) and the same grid for all animals (Harris et al., 1990). Least squares cross validation LCSV (Reiter et al., 2013) was unsuitable in this case as different animals required different smoothing parameters, which render comparisons between individuals meaningless.

Habitat associations were assessed on two scales. At the landscape scale the proportion of each habitat in the individual bats MCP was compared to the available habitat, which was determined by calculating an MCP around all tracking locations for all bats (second order habitat selection; Johnson and Prairie, 1980). On the local scale I compared the selection of habitats within each individual bat's home range to the selection of habitat within their core area (third order habitat selection; Johnson and Prairie, 1980). I used χ squared tests to assess whether habitat selection was consistent across individuals, and as it was not, used selection ratios (Manly et al., 2007) to assess individual associations with habitat types. Eigenanalysis of selection ratios (Calenge and Dufour, 2006) provided further clarification on the direction and magnitude of habitat selection by allowing graphical exploration of habitat selection. This approach was applied to habitat selection using both the *broad scale* map and the more detailed forest management *fine scale* map at both spatial scales. Manly selection ratios were used to investigate individual bat selectivity. A Manly selection ratio of close to 1 indicates no selection, below 1 indicates avoidance of the habitat and above 1 indicates selection of the habitat in relation to its availability (Manly et al., 2007).

6.4 Results

Eleven individual female *P. pygmaeus* were radio tracked successfully for between 3 and 6 consecutive calendar days (Table 6.1). Five bats were tracked during the summer of 2014, six bats during the summer of 2016 (late June to late August to avoid trapping heavily pregnant bats or tagging bats which then dispersed out of the tracking area). I collected a total of 9050 telemetry locations, which was reduced down to 2371 after subsampling by five minute intervals to reduce the effect of autocorrelation, only retaining locations with an accuracy of 100m or less.

I identified 17 new maternity roosts from 11 tagged bats (Figure 6.1). Bats foraging in a similar area were often roosting in separate roosts, and switching between maternity roosts was low. The majority of roosts were in human dwellings, although there was some diurnal use of tree roosts and one individual regularly roosted at a derelict hut in the plantation interior. All tree roosts were in old or dead deciduous trees and I found no evidence of any roosting in Sitka Spruce despite this being the dominant tree species in the area.

A two way ANOVA indicated that there was no statistically significant difference in core area between the two sample years ($F_{1,9} = 0.76$, $p = 0.41$) or between bats of differing reproductive status ($F_{2,8} = 0.46$, $p = 0.64$). The same was true for the home range (Year: $F_{1,9} = 0.73$, $p = 0.41$; Reproductive status: $F_{2,8} = 1.724$, $p = 0.23$). Therefore I pooled telemetry data to calculate means of home range area and core area (Bonaccorso et al., 2015).

Table 6.1: Reproductive status, biometric details, tracking information and home range / core area details for individual Pipistrellus pygmaeus.

Animal ID	Study year	Reproductive status	Forearm (mm)	Mass (g)	Number of nights	Number of locations	Home range area (km2 MCP)	Core foraging area (km2)
3	2014	Lac	32.4	6.4	5	585	0.58	1.72
4	2014	Lac	32.5	6.0	3	627	32.38	13.36
6	2014	Lac	33.0	6.1	5	673	19.56	12.40
8	2014	Plac	33.0	6.4	5	974	9.58	7.55
9	2014	NA (Juvenile)	32.8	6.6	3	405	0.28	1.59
10	2015	Preg	32.0	6.7	4	910	7.36	5.41
11	2015	Preg	30.8	7.0	4	751	3.63	5.98
12	2015	Preg	31.3	7.2	4	649	4.24	6.12
14	2015	Lac	31.9	6.3	4	740	21.06	6.83
15	2015	Lac	32.5	6.4	6	1887	3.62	2.70
16	2015	PLac	31.9	6.5	5	849	2.29	4.57

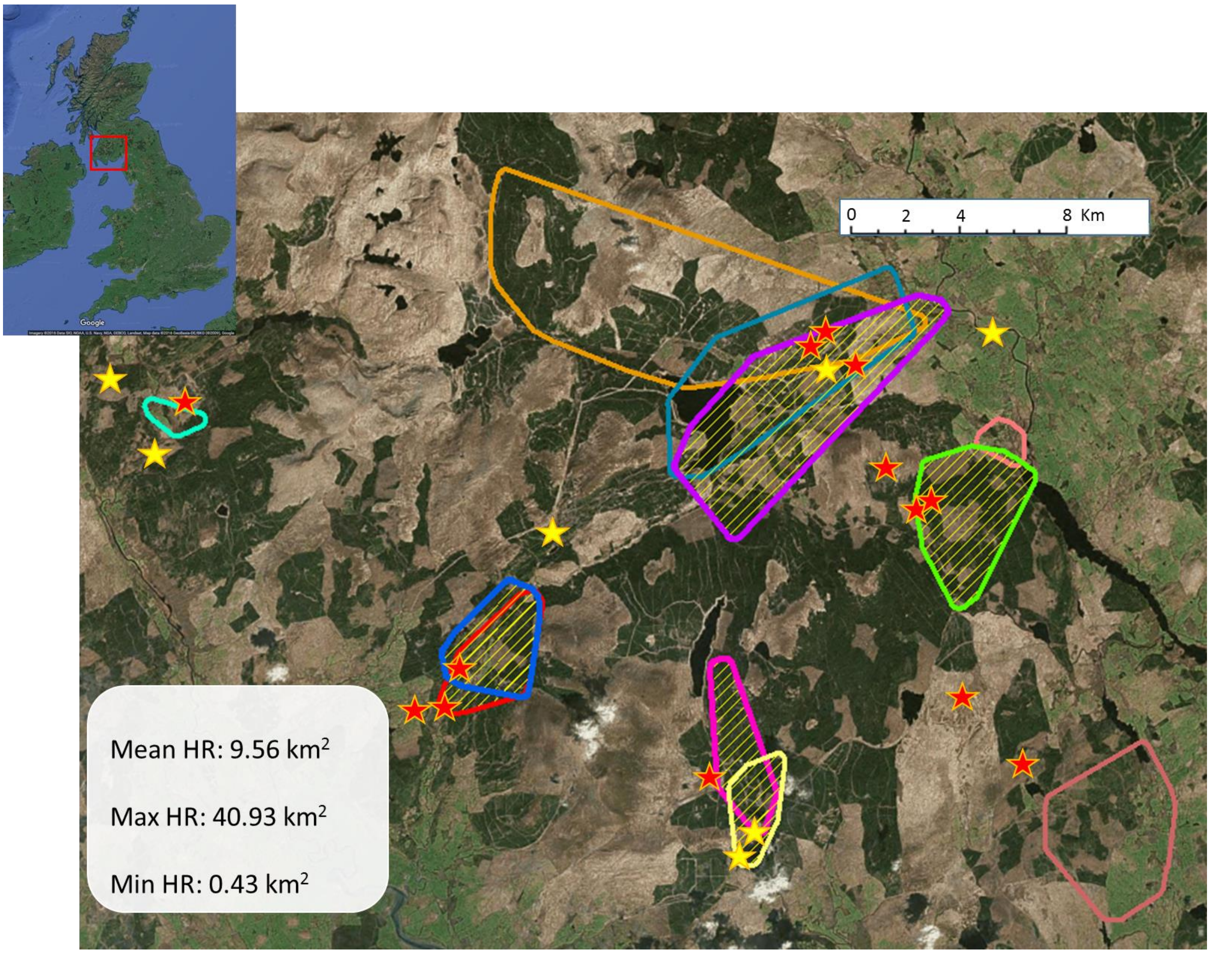
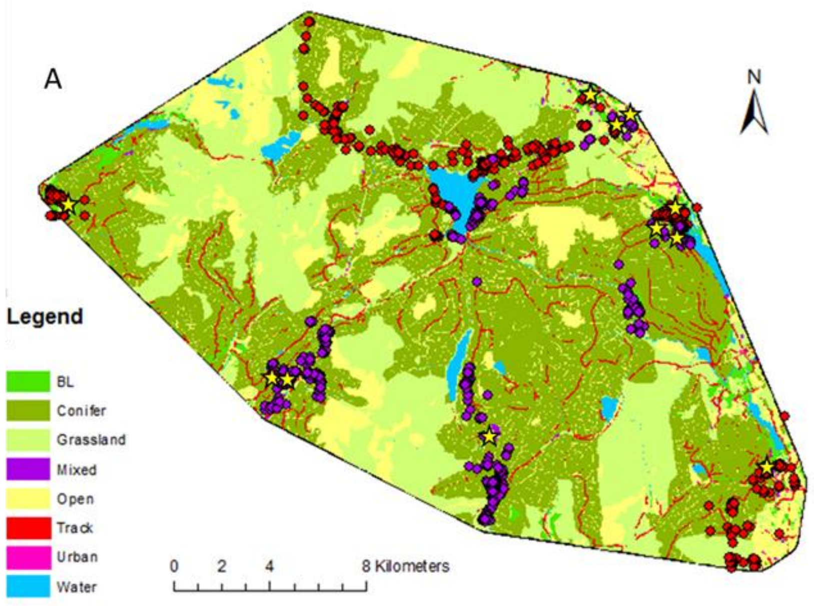


Figure 6.1: Map showing the home ranges of individual bats (hashed interior of home range indicates bats tracked in the second year) and maternity colonies used by individual bats. Red stars show colonies used by bats which were included in the analysis, yellow stars show roosts which were either identified separately as part of tracking or used by bats for which we did not get sufficient data to include in the analysis. Other roosts were identified through conversations with home owners but were not surveyed so the species composition and size of the roost was unknown. These roosts are not displayed



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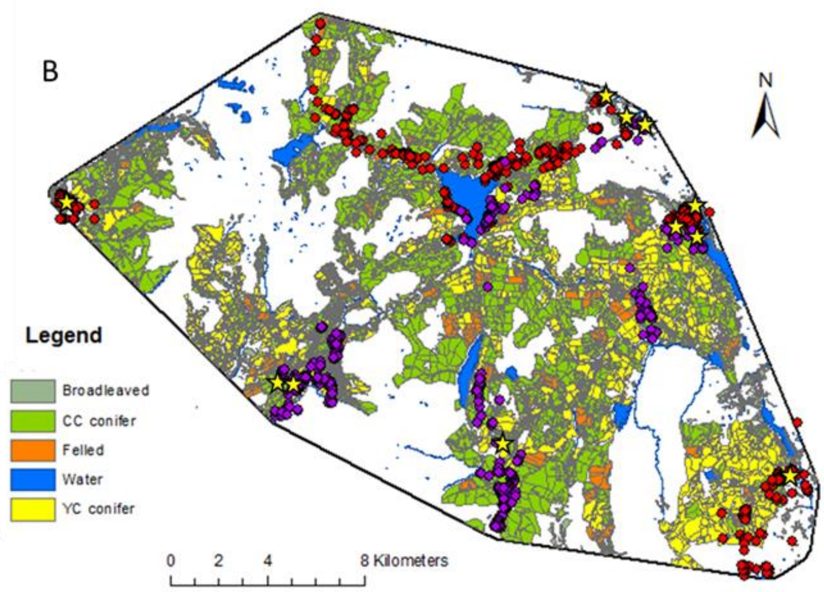

Figure 6.2: *Total available habitat for P. pygmaeus (area inside minimum convex polygon formed around all relocations) and available habitat within individual bat HR's for (A) broad scale habitat map and (B) fine scale forest management. The white spaces on the fine scale map indicate areas are upland, open areas which were not included in the analyssi as bats rarely used those area, and I was primarily interested in how bats used plantation areas. Main maternity roost location for each bat indicated by a star. Relocations indicated by points. Red points are bats surveyed in the first year, purple points are bats surveyed in the second year. CC conifer is Closed canopy conifer, YC conifer is young conifer.*

6.4.1 Spatial behaviour:

Mean home range (HR) area was 9.51 ± 3.75 km^2 and was highly variable across individuals, ranging from 0.28 to 32.38 km^2 (Table 6.1). However, foraging was focussed in substantially smaller core areas (CA, mean 2.9 ± 0.5 km^2) which ranged from 0.97 – 5.82 km^2 per individual (Table 6.1). There was no difference in home range or core area between bats who were highly selective in habitat choice (and therefore may commute further to access favoured sites) compared to bats which used a greater variety of different habitat types (over 70% of the home range encompasses a single habitat type; HR: $F_{1,9} = 0.02$, $p = 0.87$; CA: $F_{1,9} = 0.48$, $p = 0.53$). However, bats which roosted in buildings further from the plantation had a significantly larger HR and CA than bats which roosted in buildings at the edge or interior of the plantation (HR: $F_{2,8} = 10.21$, $p = 0.006$; CA: $F_{2,8} = 3.76$, $p = 0.07$). The total distance flown in a night varied between individuals, with one individual regularly completing a 40km round trip, while another individual flew 10km from the roost to her foraging site and back twice within a night (Figure 6.1), substantially larger than those reported from other studies. Foraging bouts varied between individuals and with temperature and rainfall; low temperatures or heavy rainfall resulted in diurnal foraging for some individuals (see Appendix 1, occurred more frequently in 2015 compared to 2014), while other individuals foraged throughout the night, often briefly using night roosts. Individuals tracked in 2014 foraged on average nearly twice as long as individuals in 2015 in a single session, reflecting the better weather conditions recorded in 2014 compared to 2015 (Appendix A1). Night roosting usually occurred as a result of inclement weather conditions (Appendix 6.3).

6.4.2 Foraging area overlap:

Overlap between individual core areas was low, only occurring for 6 out of 55 potential dyads (Table 6.2). The average core area overlap was 11.7%. A high degree of overlap was seen between two pairs of bats (11 and 12; 15 and 16; Table 6.2), all of whom were highly selective in their habitat choice. Most overlap occurred in similar commuting routes bats were using to move around the plantation, with little overlap in core areas. Frequent antagonistic interactions such as chasing behaviour were recorded by fieldworkers while tracking.

6.4.3 Compositional analysis:

Habitat use by bats was non random and although individual bats were consistent in their use of core areas, there was little consistency between bats ($\chi^2 = 855$, $p<0.001$), therefore averaging across habitat types was not appropriate. Instead I present and discuss individual Manly selection ratios (SR; Manly et al., 2007) and results of the eigenanalysis (see figure 6.2 for examples of bat home ranges with both the *broad scale* and *fine scale* maps). I ranked habitats by the number of bats positively selecting that habitats, with rankings for the landscape scale as follows for the *broad scale* map: Conifer>>Tracks>>Mixed>>Broadleaf>>Water>>Open>>Urban>>Grassland (Table 6.3A). Nine of the 11 tagged bats showed some preference for conifer, and somewhat surprisingly only four bats showed a preference for water (Table 6.3A, Figure 6.3A, 6.5A). Bat 3 was unusual, at the landscape scale she showed a strong preference for both broadleaf and mixed woodland habitat (Broadleaf: SR = 7.7; Mixed: SR = 11.6) but demonstrated clear avoidance of conifer and grassland habitats (Conifer: SR = 0.09; Grassland: SR = 0.03).

Table 6.2: Percent overlap in core area (CA) for all 11 tracked bats. *^{n} *denotes individuals trapped at the same trapping section. Values to the left of the black cells represent overlap of the individual from the left border of the matrix with the bat from the top row of the matrix, values to the right represent the opposite comparison of dyads.*

Bat ID	3	*4	*6	8	9	10	*11	*12	14	*15	*16
3	--	0	0	0	0	24	0	0	0	0	0
*^{1}4	0	--	14	0	0	0	0	0	2	0	0
*^{1}6	0	14	--	0	0	0	0	0	12	0	0
8	0	0	0	--	0	0	0	0	0	0	0
9	0	0	0	0	--	0	0	0	0	0	0
10	9	0	0	0	0	--	0	0	0	0	0
*^{2}11	0	0	0	0	0	0	--	62	0	0	0
*^{2}12	0	0	0	0	0	0	58	--	0	0	0
14	0	4	23	0	0	0	0	0	--	0	0
*^{3}15	0	0	0	0	0	0	0	0	0	--	68
*^{3}16	0	0	0	0	0	0	0	0	0	30	--

Table 6.3: Broad scale: Individual bat associations with each habitat type at (A) the landscape scale comparing habitat availability within each HR compared to overall availability and (B) the local scale comparing habitat availability in CA compared to HR for the broad scale land cover habitat descriptions. Selection ratios are represented as follows: --- SR <0.25; -- 0.25< SR < 0.50; - 0.50 < SR <0.75; ns 0.75 < SR < 1.25; + 1.25 < SR < 1.50; ++ 1.50 < SR < 2.5; +++ SR> 2.5

(A) Bat associations at the landscape scale

Bat ID	Human infrastructure	Broadleaf	Conifer	Open	Tracks	Mixed	Water	Grassland
3	+++	+++	----	++	++	+++	+++	----
4	----	----	+	--	--	----	----	ns
6	-	-	+	--	ns	ns	+++	ns
8	+	+	+	ns	++	++	ns	--
9	ns	+++	++	-	--	--	ns	----
10	----	ns	+++	----	ns	----	----	----
11	----	ns	++	-	+	++	ns	----
12	----	--	++	--	+++	----	--	----
14	-	----	+	--	+	ns	+++	ns
15	----	----	+++	--	+	----	--	----
16	--	----	++	--	ns	++	----	-

(B) Bat associations at the local scale

Bat ID	Human infrastructure	Broadleaf	Conifer	Open	Tracks	Mixed	Water	Grassland
3	ns	ns	++	ns	ns	ns	ns	ns
6	+++	+++	-	ns	+++	+++	+++	ns
4	ns	--	++	++	++	++	----	--
8	++	ns	ns	ns	ns	++	--	+
9	+	ns	-	ns	++	+	+	NA
10	+++	+++	-	+++	++	+++	+++	++
11	ns	ns	ns	ns	++	ns	ns	++
12	+	+	ns	ns	-	----	+	++
14	+++	+++	-	ns	++	+++	++	-
15	++	NA	ns	-	++	NA	ns	+++
16	+++	----	ns	ns	++	----	++	ns

Table 6.4: Fine scale: Individual bat associations with each habitat type at (A) the landscape scale comparing habitat availability within each HR compared to overall availability and (B) the local scale comparing habitat availability in CA compared to HR for the fine scale forest management habitat descriptions. Selection ratios are represented as follows: --- SR <0.25; -- 0.25< SR < 0.50; - 0.50 < SR <0.75; ns 0.75 < SR < 1.25; + 1.25 < SR < 1.50; ++ 1.50 < SR < 2.5; +++ SR> 2.5

(A) Bat associations at the landscape scale

BatID	Felled	Broadleaf	Closed canopy conifer	Young conifer	Water
3	----	+++	----	----	++
4	ns	----	+	-	----
6	----	--	ns	-	+++
8	-	ns	-	+++	-
9	-	+++	-	ns	-
10	----	--	ns	++	----
11	----	--	ns	++	--
12	----	----	ns	++	----
14	--	----	ns	++	++
15	ns	----	ns	ns	----
16	-	----	+	ns	----

(B) Bat associations at the local scale

BatID	Felled	Broadleaf	Closed canopy conifer	Young conifer	Water
3	----	ns	NA	NA	----
4	+	+++	ns	++	+++
6	+++	+++	ns	ns	-
8	ns	ns	+	ns	--
9	+	++	-	--	++
10	ns	+++	ns	--	+++
11	+++	ns	ns	ns	ns
12	+++	+	ns	ns	ns
14	--	+++	-	ns	+++
15	+++	NA	ns	--	+++
16	++	+++	ns	-	----

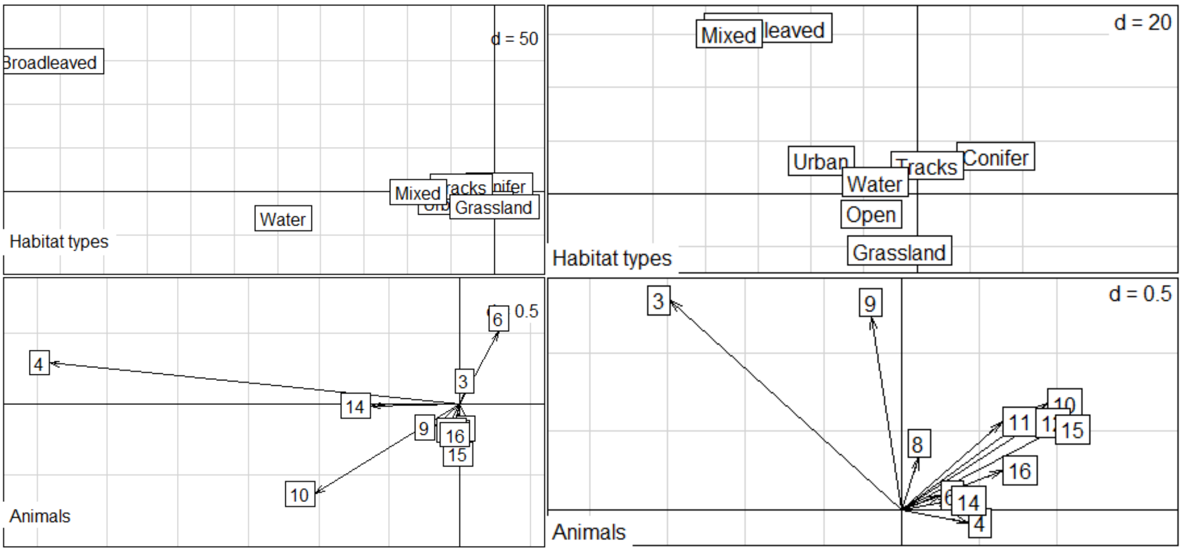

Figure 6.3: *Results of eigenanalysis using the broad scale land cover map performed on individual selection ratios for (A) Second order habitat associations comparing habitat composition in bat home ranges compared to its availability and (B) Third order habitat associations comparing habitat composition in individual core areas compared to their home ranges. Numbers indicate individual bats, the direction and magnitude of the arrows show the direction and strength of the bats assocation with different habitat types and the clustering of the bats in space shows similarity between habitat selection. For example in A bat 4 is strongly associating with broadleaf, and is very different from the majority of other bats.*

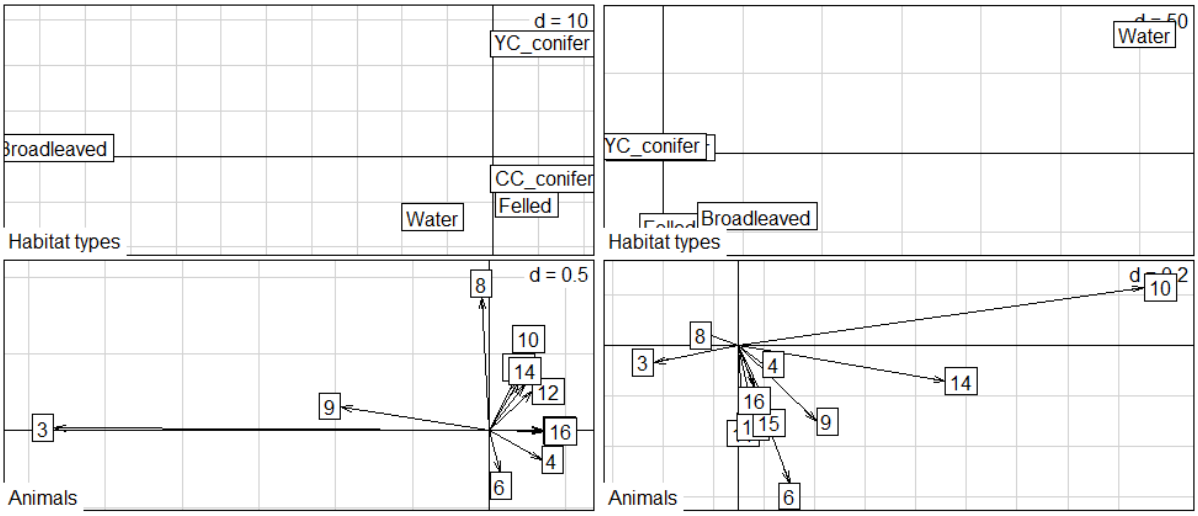

Figure 6.4: *Results of eigenanalysis using the fine scale forest management map performed on individual selection ratios for (A) Second order habitat associations comparing habitat composition in bat home ranges compared to its availability and (B) Third order habitat associations comparing habitat composition in individual core areas compared to their home ranges. Numbers indicate individual bats, the direction and magnitude of the arrows show the direction and strength of the bats assocation with different habitat types and the clustering of the bats in space shows similarity between habitat selection. For example in A bat 3 is strongly associating with broadleaf, and is very different from the majority of other bats which appear to avoid broadleaf.*

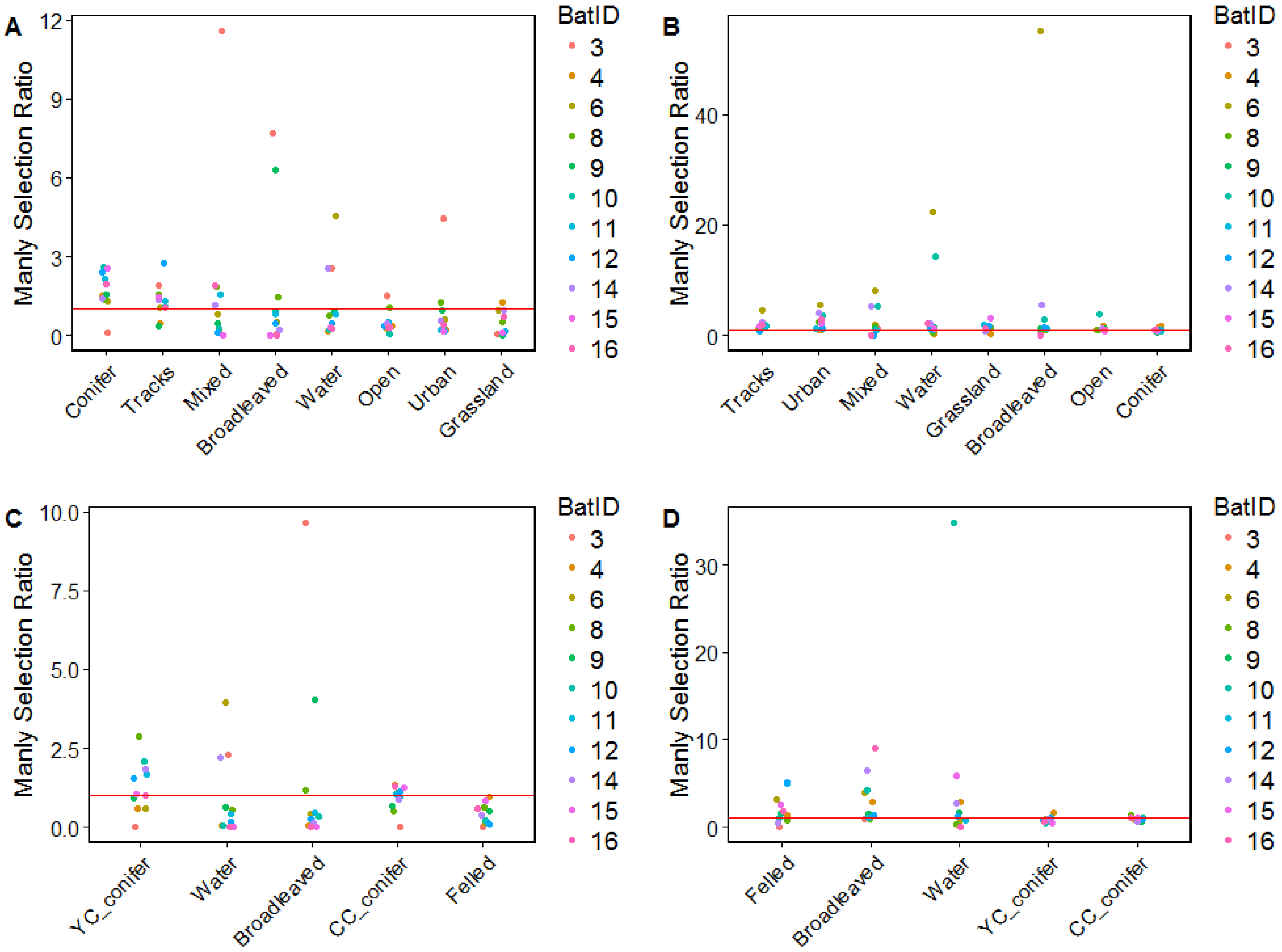

Figure 6.5: Individual Manly selection ratios for all bats at both the landscape (A, C) and local (B, D) scale. Habitats are ranked from left to right according to the number of individuals which positively selected that habitat type. Points are coloured by bat ID.

At the local scale habitats were ranked as following for the *broad scale* habitat classification: Tracks>>Urban>>Mixed>>Water>>Grassland>>Broadleaf>>Open>>Conifer (Table 6.3B). Three out eleven bats show a strong selection for broadleaf within core areas compared to its overall availability within their home ranges, while three show little selection between habitat types and a further three selected mixed woodlands. Two bats preferentially selected water in their core areas, while bat 15 selected grassland over other habitat types (SR = 2.3) and bat 16 preferred urban and water habitats while avoiding broadleaf and mixed woodland habitats (Table 6.3B, Figure 6.3B, 6. 5C).

Using the *fine scale* forest management map and looking at second order habitat selection, habitat preferences were ranked as following: Young conifer>>Water>>Broadleaf>>Closed canopy conifer>>Felled. There was little consistency between bats, but in general habitat selection is fairly weak (Table 6.4). Again, two individuals strongly favour broadleaf areas while three favour water, two prefer closed canopy conifer and six show some selection for young conifer when comparing home ranges to available habitat (Table 6.4A, Figure 6.4A, 6.5C).

Using the *fine scale* classification at the local scale, half of the bats I tracked preferentially foraged over water compared to its availability in the core area, with four using water over all other habitat types. Bats 6, 11 and 12 preferentially foraged over felled stands compared to all other habitat types, while bat 9 foraged mostly over young conifer and bat 16 showed little association with any habitat feature. The habitat rankings had changed compared to selection in the home range: Water>>Felled>>Broadleaf>>Closed canopy conifer>>Young conifer (Table 6.4B, Figure 6.4B, 6.5D).

6.5 Discussion

These results demonstrate that, further to what was shown in chapters 2 and 5, *P. pygmaeus* makes widespread use of a commercial Sitka Spruce plantation during an energetically demanding period. There was little evidence that bats primarily foraged in optimal broadleaf habitats compared to plantation habitats, although the sample of bats is very small. All individuals were trapped in the plantation so I do not know what proportion of the colonies located use plantation areas. *Pipistrellus pygmaeus* is distributed patchily throughout continental Europe (Sattler et al., 2007) although it reaches locally high densities in the UK (Davidson-Watts et al., 2006; Russ and Montgomery, 2002). Hence UK populations are substantial, and may be important for overall persistence of *P. pygmaeus* populations. Boughey et al (2011) used information from the National Bat Monitoring Program to assess bat habitats surrounding roosts across the UK. However, few roosts in plantation dominated areas were included, and as such the importance of this habitat type may have been ignored. Davidson-Watts et al (2005) found that *P. pygmaeus* avoided coniferous plantations, but in their study area the proportion of available coniferous forest was below 1%. For *P. pygmaeus* and *P. pipistrellus* avoidance of commercial plantations may reflect sampling bias rather than habitat preferences (indeed, Nicholls and Racey (2006) found that a commercial coniferous plantation was an important foraging site for *P. pipistrellus* in North East Scotland).

6.5.1 Roost use in the plantation

All individuals roosted primarily in houses, and although I was unable to carry out roost counts due to time constraints, at least two incomplete counts were carried out at all buildings I found bats roosting. In all but one case the roosts held in excess of 500 bats with some roosts appearing to house far greater numbers of bats. Barlow and Jones (1999) hypothesized that the large number of bats in *P. pygmaeus* roosts is due to the low number of suitable roosts near preferred foraging sites. It is likely that roost availability is limiting in the study area and although *P. pygmaeus* has been recorded to form large maternity roosts elsewhere, the high density of large roosts in Galloway implies a substantial population of bats resident in the area during the summer. A study in North East Scotland involved a single colony of ca. 250 individuals, and surrounding buildings were surveyed to ensure no other roosts were present (Nicholls and Racey, 2006a). From discussions with home owners and personal observations the majority of houses in our study area contained a bat roost, including houses in close proximity to another roost. Despite individuals being tagged in fairly close proximity to each other, they rarely roosted in the same building. It is therefore possible that the density of bats in the Galloway plantation area is much higher than the population density in the area surveyed by Nicholls and Racey (2006a, 2006b) and may explain differences in home ranges and habitat associations I found. No bats made use of coniferous trees of any species, although several individuals used deciduous tree roosts as night roosts and occasional day roosts. All tree roosts identified have been recorded to ensure ongoing protection. One tree roost was a dead oak, two others were old beech trees near the main maternity roosts. Low numbers of bats exited tree roosts, and bats were observed moving from maternity colonies to tree roosts after dawn, maybe suggesting that space in the maternity roost was limiting. Boughey et al. (2011) found that *P. pygmaeus* roosted in buildings nearer water and broadleaf woodland than would be expected by chance; in our study area 53 % of broadleaf tree cover in the landscape was within 200m of a building and 89% of broadleaf tree cover was within 1km of a building, and all the houses I found bats roosting in were within 100m of a watercourse. *Pipistrellus pygmaeus* also made use of abandoned buildings within the plantations including a small, derelict hut, which may indicate a lack of roosts and the importance of ensuring surveys are undertaken if buildings need to be removed. Lack of appropriate roost space is a common feature of plantations managed for timber extraction as trees are removed before they reach an age where features appropriate for bat roosts form

(Burgar et al., 2015). Studies have demonstrated that in areas where existing roost availability is low, bat uptake of artificial bat boxes is often substantial (Smith and Agnew, 2002).

6.5.2 Home range and core area size, overlap in ranges and antagonistic behaviour

Species habitat relationships are dependent on scale, with selection occurring at multiple spatial scales (Chambers et al., 2016). For highly mobile species such as bats, effective habitat management requires understanding of habitat associations at both the landscape (second order) scale and local (third order) scale (Chambers et al., 2016). In this study, home ranges varied considerably in size between bats with the largest belonging to bats roosting furthest away from the plantation and were much larger than home ranges reported from other studies (e.g. Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006b; Sattler et al., 2007). Large foraging ranges could be a response to low food availability (travelling further to find more food), inter or intraspecific competition from other bats or low roost availability (Ciechanowski, 2015; O’Donnell, 2015). Bats in areas with an abundance of both potential roosts and foraging areas tend to have smaller home ranges and greater overlap of individual ranges (August et al., 2014), indeed individuals roosting inside the plantation had smaller home ranges than those roosting outside the plantation. In this study, it is likely that the large difference in home range sizes I recorded compared to the above studies exist as a result of the distribution and abundance of available roosts, with bats roosting further from the plantation expending more energy to access profitable foraging sites (O’Donnell, 2015). As flight is energetically expensive, individuals must have benefited from being active over such large areas (O’Donnell, 2015). I recorded a mean HR of 9.51 km^2, although mean CA was much smaller at 2.9 km^2. In contrast Davidson-Watts and Jones (2005) recorded a mean HR of 1.63 km^2 whereas Nicholls and Racey (2006a) reported a mean HR of less than 0.6 km2 and a mean CA of less than 0.25 km^2. Clearly, *P. pygmaeus* is less constrained by behavioural or ecomorphological factors than other, rarer species (eg *Rhinolophus hipposideros*, Reiter et al., 2013) and the energetic cost of accessing plantation areas from more distant roosts is offset by the quality of available foraging areas. Commuting over large distances can even be a foraging strategy within itself when linked to the continuous intake of “aerial plankton”(Haupt et al., 2006).

Individual bats consistently behaved the same way each night of tracking, suggesting that female *P. pygmaeus* may use space in a structured way; individual bats may either focus on particular profitable habitats or adopt a filter feeding approach. In a concurrent study *P. pygmaeus* feeding buzz rate increased with the rate of social calling (Appendix 1), this coupled with fieldworkers frequently observing chasing behaviour while tracking may suggest that antagonistic behaviour is occurring between foraging bats. However, I was only able to track a small number of bats for a few nights across the season due to technological limitations concerning tag lifespan and it is likely that bat behaviour will change seasonally, particularly once young are weaned (Swift, 1980).

6.5.3 Habitat associations

Bats across both years consistently used a few commuting routes to access plantations which consisted of both rivers and forest tracks. Linear landscape features such as forest tracks are known to be important features for bats for navigation, provision of invertebrate prey and shelter as they provide low structural complexity with high invertebrate abundance (Ciechanowski, 2015; Grindal and Brigham, 1998; Hein, 2008; Schnitzler et al., 1988). In plantation forests, where stands can be structurally complex, tracks may provide important flyways that allow bats to access foraging areas (Law et al., 2015), as well as providing a suitable foraging habitat for edge adapted bats such as *P. pygmaeus* (Ciechanowski, 2015; Verboom and Spoelstra, 1999). The vast majority of tracks in this study went through the plantation, therefore the strong association of all but two bats with tracks also reflects use of conifers. At the local scale using the fine scale forest management map, bats showed little association with either young or closed canopy conifer. Previous work demonstrated that conifer between 10 and 20 years had the lowest levels of activity (Chapter 2), activity alongside these stand types is likely to reflect bat movement along forest tracks which are used by bats to access preferred foraging areas scattered within the plantation (Hein, 2008). Identifying these is key to target management practices towards preserving access to foraging sites.

Individual bats were highly consistent within the core areas that they used, but there was little consistency in habitat selection between bats at either the local or the landscape scale. Previous studies have identified high levels of habitat specificity for *P. pygmaeus*, particularly riparian and broadleaf habitats (Boughey et al., 2011; Davidson-Watts et al., 2006; Nicholls and Racey, 2006a; Russ and Montgomery, 2002). In this study, half of the bats tracked associated with both broadleaf and to some extent water in a greater proportion than its availability. However, the majority of remaining broadleaf patches within the plantation landscape are associated with river margins or buildings which often contained a roost, so it is not possible to disentangle the relative effects of these habitats. More surprising was the high degree of selection of felled stands at the local scale, despite most bats appearing to avoid felled stands at the landscape scale. This may be an artefact of plantation management; at the landscape scale bats are likely to be selecting based on roost locations, which are patchily distributed within the landscape. While felled stands are also scattered throughout the landscape, they are ephemeral, which may explain the far larger home ranges I found in this study compared to others (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006b; Sattler et al., 2007). Six bats preferentially selected felled stands in core areas compared to their availability within individual home ranges and only two bats showed any avoidance at the local scale.

The difference between association with felled patches at different spatial scales suggests that bats are responding to fine scale patchiness within superficially homogenous units (i.e. conifer plantations), and demonstrates the importance of investigating fine scale variations at the microhabitat level (Arrizabalaga-Escudero et al., 2013). Felled patches may represent an easily accessible and abundant food supply, with large populations of *Culicoides impuctatus* (Chapter 2) and low structural complexity.

6.5.4 Implications for conservation

This study shows that far from not supporting bat populations, Sitka spruce plantations may actually provide an opportunity for lactating female *P. pygmaeus*, but roost availability is likely to be limiting. The high density of bats within each roost suggests that there is a substantial *P. pygmaeus* population present in the area. Although I found no evidence of bats roosting in Sitka spruce or other coniferous trees, bats did use old or dead deciduous trees. Felling operations should preserve these trees where possible. Retaining and expanding broadleaf patches, particularly in riparian areas will benefit bats by providing potential roosting areas important for harem formation in late summer (Park et al., 1998). However, as natural roosts are sparse in plantation landscapes, installing bat boxes along riparian zones, in remnant broadleaf patches and commuting routes into plantation areas will reduce pressure on maternity colonies and provide alternative roosts. There is evidence from both Australia and Europe that installing bat boxes in habitats with low roost availability often results in swift uptake (Flaquer et al., 2006; López-Baucells et al., 2016). As part of this study, 50 bat boxes were erected in February 2016 in various locations around the study area, concentrating on known commuting routes and areas near well used foraging patches. A survey was carried out to assess uptake of the boxes in the first year (September 2016); 131 bats (all *P. pygmaeus*, several mixed sex harems) were found in the boxes, over 90% of which had evidence of bat use. The large number of harems found, even in boxes adjacent to each other is testament to the lack of suitable features for harems in plantation landscapes. However, the extent to which these boxes will be suitable for maternity roosts remains to be seen. It is highly unlikely that *P. pygmaeus* maternity colonies will form in boxes installed as part of this study (see appendix 7.2 for details of boxes used), and bats are likely to continue to preferentially use building roosts (Park et al., 1998). Nevertheless, in Mediterranean wetlands *P. pygmaeus* formed maternity colonies in bat boxes on posts and houses, but avoided boxes mounted on trees. As roost availability is so low in plantation landscapes, further exploring the installation of different bat box types which may be appropriate for maternity roosts in plantation dominated landscapes is likely to benefit *P. pygmaeus* (Flaquer et al., 2006).

One of the more surprising elements to come from the study was the strong preference for foraging in felled stands, which has implications for the increasing installation of wind turbines in plantations.

Establishing wind farms in plantation areas currently requires guidance for species such as hen harriers, but the preferred management of phased felling and restocking up to keyholes (typically permanent open areas 50m from trees to turbine tip are retained while restocking occurs over the rest of the stand ; Anon., 2015) This is likely to result in a patchwork of felled areas linked by tracks which would be attractive foraging habitat for bats, but to the best of our knowledge this has not yet been studied. In this study bats were commuting longer distances than has been previously reported (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006b), potentially to access preferred foraging sites. Due to the perception of plantations being poor for bats, and the likelihood of bats not being so numerous before felling takes place, it is likely that pre felling surveys would underestimate bat activity likely to be present post felling. Installing wind turbines in Sitka Spruce plantations could pose a considerable risk to the bat population. Previous work (Chapter 2) also found that *P. pipistrellus* also associated strongly with felled areas. Rather than assume bats are not present in plantation areas, decisions about siting wind turbines in upland plantations should also assess pre and post felling bat populations and take into account the likelihood of increased bat activity post felling.

6.5.5 Conclusions:

Sitka spruce plantations may support a high density of *P. pygmaeus* during an energetically costly period, with this study finding many new, large bat roosts in buildings in and around Galloway Forest. In landscapes dominated by Sitka Spruce plantations, plantations may form an important foraging habitat for a high density of individuals, particularly in areas with a high abundance of nematoceran Diptera. This study demonstrates that *P. pygmaeus* is an adaptable bat, capable of flying much further distances than previously reported to reach foraging areas and able to adapt its foraging style to exploit opportunities offered by alternative habitats.

Appendix

Appendix table 6.1: Description of stand types

Stand characteristics for each management stage and stand features associated with management. *Diameter at Breast Height – estimate of tree maturity

Stand Age	Management Stage	Key stand features
40 – 60 years	Mature	Occasionally thinned, stand density between 500 and 2200 stems ha^{-1}, average stand density: 1267 stems ha^{-1}, canopy closure between 80 and 100%, average closure 99%
20 – 40 years	Thin	Trees more densely packed, losing midstem branches and some trees dying off (self thinned). Occasionally thinned through management. Stand density between 600 – 2800 stems ha^{-1}, average stand density: 1624 stems ha^{-1}. Canopy closure between 50 and 100%, average closure: 95%
10 – 20 years	Thicket	Very dense, retain midstem branches, no undergrowth. Stand density between 300 – 3000 stems ha^{-1}, average stand density: 1850 stems ha^{-1}. Canopy closure between 16 and 100%, average closure: 69%
5 – 10 years	Young	Small, nearly all trees < 7cm DBH*, no canopy closure, lots of vegetation and ground cover
Clearfell	Felled < 5 years ago	Lots of dead wood and brash, standing water and undergrowth

Appendix 6.2: Description of bat boxes installed in Galloway forest park (August 2015 and February 2016). Pictures reproduced with permission from John Martin.

All boxes installed as part of this work were Schwegler 1FF's and a further 9 2F Schwegler boxes were installed as part of mitigation for removal of an old hide. Bat use of the old hide was identified due to tracking work carried out as part of this project. Boxes were installed in august 2015 (2F) and February 2016 (1FF). Boxes were checked in September 2016. All box checks were carried out under license

Figure 1 A. Schwegler 1FF box with harem of *P. pygmaeus* inside. B. Location of one of the boxes installed as part of this study. Boxes were put on trees in stands not included in felling schedules. Photos courtesy of John Martin

Appendix 6.3: Summarised details of bat foraging sessions. Maximum and minimum temperatures are given in degrees celcius, and are the average maximum and minimum temperatures recorded during all foraging sessions for that bat.

Animal ID	Study year	Reproductive status	Number of nights	Total No Foraging sessions	Average foraging session length (mins)	Average maximum temperature	Average minimum temperature
3	2014	Lac	5	11	169	12	10
4	2014	Lac	3	4	290	15	14
6	2014	Lac	5	6	309	15	12
8	2014	Plac	5	6	277	14	12
9	2014	NA (Juvenile)	3	4	94	12	9
10	2015	Preg	4	6	132	12	11
11	2015	Preg	4	8	97	14	12
12	2015	Preg	4	9	87	12	9
14	2015	Lac	4	7	134	12	8
15	2015	Lac	6	10	182	12	9
16	2015	PLac	5	8	142	11	8

Chapter Seven

Chapter 7 General discussion

Example of some of the diversity captured in commercial plantations. Some photos reproduced with permission (John Haddow, James Shipman, John Martin), others my own.

7.1 General Discussion

Despite their large size, and predominance in some landscapes, commercial coniferous plantations, are probably one of the least studied bat habitats. This is despite the fact that bats, and their roosts, are protected by law. However, whilst it is clear that some bats do make use of plantations to some extent, forest managers have little information about the effects of management on the provision of foraging and roosting resources for bats. In this thesis, three large, intensively managed *Picea sitchensis* (Sitka Spruce) plantations in Northern England and Central and Southern Scotland were surveyed for bats using a range of approaches. The species composition, reproductive status and fine scale habitat associations of bats in *P. sitchensis* dominated landscapes was assessed. For the first time, direct comparisons of bat activity in broadleaf and commercial plantations have been carried out. Furthermore, to the best of my knowledge, this is the first time that a before – after – control – design (BACI) study has been used to assess the short-term (i.e. 1 -18 months) impacts of clear felling on bat populations in non-native plantations. The results and recommendations from this thesis are relevant for both forest management and bat conservation. Similar to Mortimer (2006), my findings challenge the classically held position that plantations are a poor habitat for bats. Rather, with sympathetic management, Sitka Spruce plantations may be an important and as yet, unrecognised habitat for breeding populations of *Pipistrellus* spp*,* particularly *P. pygmaeus.*

As part of this work, I also surveyed for potential invertebrate prey, including night active Lepidoptera. Lepidoptera are undergoing significant declines worldwide (Conrad et al., 2002; Fox et al., 2013), but again, commercial plantations are under-surveyed for moth species. Micro moth richness was higher than that reported from broadleaf woodlands embedded within the plantation matrix (Fuentes-Montemayor et al., 2012), and macro moth richness was nearly double that reported from urban broadleaf woodlands (Lintott et al., 2014). While the underlying causes driving these differences are unclear, plantation sites, particularly those with low levels of clear felling in the surrounding landscape, and a higher prevalence of broadleaf woodland, may constitute a less disturbed habitat than both urban and agricultural broadleaf woodlands. Intensive management, such as forestry operations, can act as an environmental filter by removing entire functional groups and creating biotic homogeneity by shifting towards reduced communities with a smaller number of shared, more generalist traits (Gámez-Virués et al., 2015). These effects have been demonstrated most often in response to increasing agricultural intensity, resulting in landscape simplification, and consequently, a reduced capacity to support a large species pool, and a lack of opportunity for spillover between complementary resources (Gámez-Virués et al., 2015). In contrast, complex landscapes are characterised by a high level of immigration of organisms from remnant semi-natural or natural habitat, masking any positive impacts (Tscharntke et al., 2012). These results are encouraging in that it suggests that intensively managed *P. sitchensis* landscapes may represent a landscape under intermediate disturbance, which is the most likely to see positive changes through effective management (Tscharntke et al., 2012).

7.1.1 Influence of survey method and measures on assessing abundance and diversity

Quantifying bat abundance and diversity is challenging; most capture methods are biased to a certain extent as species with high frequency echolocation calls are more likely to detect nets, and some species are better at detecting both nets and harp traps (Berry et al., 2004). Nets and harp traps are most effective when placed along flight lines, alongside rivers, or across forest tracks (Hill and Greenaway, 2005), therefore bats moving in open habitats will be under-sampled. Although the use of an acoustic lure does boost capture rates (Hill and Greenaway, 2005), responses to the lure can vary both temporally and between species and will depend on the type of call being broadcast (Lintott et al., 2013). Despite this, trapping is often necessary to enable practitioners to confirm species identity and collect detailed information about body condition, morphometrics, gender and reproductive state (Lintott et al., 2013). Advances in acoustic detectors means that passive acoustic sampling is now inexpensive, non-intrusive, and, due to improvements in battery life, automated to allow for long periods of remote sampling (Lintott et al., 2013). However, again, detectability differs between species; so-called “whispering bats” either emit very quiet echolocation calls or use passive listening to detect prey (e.g. *Plecotus auritus*; Schnitzler and Kalko, 2001), so will be underestimated by acoustic surveys alone. The position and orientation of the microphone will influence the extent to which bats are detected; bats moving above the canopy cover or beyond the range of the microphone will not be sampled, and increased structural complexity will reduce microphone sensitivity (Britzke et al., 2004). Sampling using acoustic detectors only provides a relative index of activity, rather than abundance, as a single bat may be detected repeatedly, although, for some species, relative activity is a reliable predictor of abundance (Lintott et al., 2013). Finally, acoustic sampling provides no information about populations or individuals such as sex, age or reproductive status, and due to similarities in some bat species echolocation call structures, identification to species level is not always possible (Russ, 2012). Using complementary techniques where possible provides the most detailed information about bat associations with a particular habitat. For example, the low number of *P. auritus* calls recorded in plantation sites could be a result of under-recording due to the low volume of their echolocation calls. However, it probably also reflects the low number of individuals which are likely to be present; *P. auritus* were rarely caught in plantation sites (chapter 2). Without capture data I would not have been able to identify that plantations appear to be an important habitat for lactating *P. pygmaeus* during an energetically costly period, or that three different species of *Myotis* use plantations, the majority of which are likely to be male (chapter 2). However, using acoustic monitoring allowed a large-scale assessment of bat habitat associations across three plantations. Furthermore, identifying social calls and feeding buzzes enabled a greater understanding of the differences in how bats use broadleaf and plantation sites (Appendix 1). Finally, radio tracking is expensive, both in monetary terms and in the effort required to track a small number of bats, and potentially stressful for tagged individuals. However, without it, I would not have identified the high density of large *P. pygmaeus* maternity roosts which exist in and around Galloway plantation (chapter 6). In addition, the discovery that individual bats roosting 5km out of the plantation are commuting long distances to access foraging sites emphasises the potential importance of *P. sitchensis* dominated plantations for *P. pygmaeus*. Furthermore, radio tracking enabled me to identify the location of key roosts and commuting routes used by bats in the plantation (chapter 6). This knowledge has been used to site bat boxes in key areas, over 90% of which had evidence of bat use within a single season. Combining the results of both the BACI and the radio tracking revealed that *P. pygmaeus, P. pipistrellus* and *Nyctalus* spp preferentially forage above felled stands, particularly smaller ones, highlighting a potential conflict with the use of plantations to install wind turbines (chapter 5, 7; Mathews et al., 2016). Using a range of approaches has resulted in a thorough assessment of bat, and particularly, *P. pygmaeus* use of plantation landscapes.

We were only able to survey for light attracted, night-active moths in this study, due to constraints on both time and equipment. Therefore, this study focusses on a subset of moth species. However, the responses I found for both felling and remnant patches of broadleaf tree cover reflect results from studies in other regions on a wide range of Lepidopteran species (Slade et al., 2013; Summerville, 2013; Summerville et al., 2009; Summerville and Crist, 2002; Thorn et al., 2015). Changes to forestry practices (Summerville, 2013; Thorn et al., 2015), preservation of broadleaf tree cover (Slade et al., 2013) and maintaining a heterogeneous landscape (Merckx et al., 2012) is likely to benefit a range of moth species. The structural complexity of different habitats will influence the attractiveness of the trap light (Merckx and Slade, 2014); for example, the heath trap light was far more visible in felled stands than in all other stand types (Lacki et al., 2007). However, the attraction radii of heath light traps are commonly between 10 – 30m depending on moth family (Merckx and Slade, 2014), and traps in felled stands were placed at least 50 m away from the stand edge to ensure that trapped individuals represent moth species composition of those stands.

In chapter 4, I extended the results of chapter 3 to show that, despite plantations supporting a wide diversity of moth species, the impacts of management processes such as felling on functional richness and diversity are decoupled from those on taxonomic richness and diversity, and impact both rare and common species similarly. Using functional trait measures allows a greater understanding of the mechanisms by which disturbance impacts moth richness and diversity. Remnant patches of broadleaf tree cover are an important feature in plantation landscapes for preserving moth richness, regardless of moth habitat specialism. Using Leinster Cobbold indices allows practitioners to simultaneously investigate the influence of both rare and abundant taxa on functional richness or diversity profiles. For example, I found that a higher prevalence of felling in the surrounding landscape reduced functional richness, diversity and dominance for all the functional traits I investigated, but particularly moths overwintering as pupa or eggs.

7.1.2 Are Picea sitchensis plantations an "ecological desert"?

This study adds to this growing pool of knowledge to suggest that, far from being an "ecological desert" (Brockerhoff et al., 2008), plantations support viable populations of bats, although composition is dominated by two common species (Chapter 2, 5, 7). Both *P. pygmaeus* and *P. pipistrellus* are widespread and common, and although populations have undergone historic declines (Hutson et al., 2001), there is evidence that populations are beginning to increase (Barlow et al., 2015). Previous studies in the UK have found that bats, including both *P. pygmaeus* and *P. pipistrellus*, often avoid coniferous forest for foraging (Davidson-Watts et al., 2006; Nicholls and Racey, 2006a; Walsh et al., 1996) and roosting (Bellamy and Altringham, 2015; Boughey et al., 2011; Jenkins et al., 1998), which has been attributed to a low invertebrate diversity and abundance (Walsh et al., 1996). To some extent, this may reflect sampling bias. For example, Boughey et al (2011) used a long-term database of known roost sites which are assessed for occupancy during the summer breeding period and concluded that bats preferentially roost near broadleaf woodland and avoid coniferous forest. However, very few *P. pygmaeus* and *P. pipistrellus* roosts assessed as part of their study were in plantation dominated landscapes, although I show in Chapter 6 that substantial roosts of *P. pygmaeus* do exist near *P. sitchensis* plantations. This may reflect the lower human population density, and therefore volunteers willing to count roosts in these areas. Furthermore, in studies investigating *P. pygmaeus* and *P. pipistrellus* habitat associations, the proportion of coniferous forest within the landscape is typically very low (e.g. 0.6 - 3.2%, Davidson-Watts et al., 2006), and bats may adjust their behaviour in landscapes with different dominant habitat types. Here, I add to the current understanding of *P. pipistrellus* and *P. pygmaeus* habitat associations with riparian and deciduous habitats (Davidson-Watts et al., 2006; Nicholls and Racey, 2006a; Russo and Jones, 2003; Sattler et al., 2007; Walsh et al., 1996), by showing that in plantation dominated landscapes, both *P. pygmaeus* and *P. pipistrellus* make widespread use of coniferous plantations. Such differences in responses of bats to coniferous plantations suggests that there is geographical variation in bat habitat associations related to landscape composition (Chapter 2, 6, 7). Bat associations with commercial plantations, including those consisting of non-native tree species, have been reported from a variety of different regions (e.g. Europe; Charbonnier et al., 2016; Cistrone et al., 2015; Cruz et al., 2016; Mortimer, 2006; Pereira et al., 2016; Russo et al., 2010, New Zealand and Australia; Borkin and Parsons, 2011; Borkin et al., 2011; Burgar et al., 2015 and North America; Morris et al., 2010; Patriquin and Barclay, 2003), emphasising the importance of surveying areas which may appear poor for biodiversity.

Potentially, *P. pygmaeus* females associate with large, commercial coniferous plantations during pregnancy and lactation due to a high abundance of *Culicoides impuctatus* (the Highland midge, a highly abundant dipteran species which reaches pest proportions in all three study areas; Marsh, 1986). Bats will adjust their spatiotemporal foraging behaviour in response to invertebrate abundance (Fukui et al., 2006; Gonsalves et al., 2013), and dietary studies have found that *P. pygmaeus* and to some extent, *P. pipistrellus* feed on nematoceran diptera, such as *C. impuctatus* (Barlow, 1997). *Pipistrellus pygmaeus* home ranges recorded during radio tracking were much larger than those reported from other studies (Davidson-Watts et al., 2006; Nicholls and Racey, 2006b; Sattler et al., 2007), with the largest home ranges found in bats roosting furthest from the plantation edge (chapter 6). Bats were flying considerable distances to access plantation areas; one individual regularly flew nearly 40km each night to access preferred foraging areas, suggesting that the abundance of the food supply may outweigh the energetic cost of flight. Furthermore, nights with very high bat activity in both plantation and broadleaf sites were associated with high dipteran abundance (which was almost exclusively *C. impuctatus,* Appendix 1). Only a small number of bats were tagged, and all were initially captured in plantations, so it is unknown whether the behaviour of these bats reflects behaviour in the wider population. It should be noted however that all but one habitable building (and one uninhabited) within the forest park housed a bat colony, many of them substantial, and it is unlikely that these individuals are commuting long distances out of the plantation to forage. Tagged individuals that shared a roost were both roosting within plantations and had a high degree of overlap in home range and core area overlap, and usually the smallest home ranges (Chapter 6).

Towards the end of the first tracking season, at the beginning of August, tagged females dispersed out of the plantation area and I was unable to locate them. *Pipistrellus pygmaeus* is migratory in continental Europe (Fornu, 2009; Sztencel-Jabłonka and Bogdanowicz, 2012), and there is some evidence of migratory movement in the U.K (Racey et al., 2007), although the extent of movement depends on geographical location (Sztencel-Jabłonka and Bogdanowicz, 2012). Migratory movement appears to be modest in the U.K. compared to Central and Northern Europe (Racey et al., 2007; Sztencel-Jabłonka and Bogdanowicz, 2012), possibly reflecting the milder, maritime climate. Very little is known about *P. pygmaeus* hibernation behaviour, although females are known to join males in harems before hibernation (Park et al., 1996), which may result in some of the population structuring evident in genetic studies (Sztencel-Jabłonka and Bogdanowicz, 2012). The movement of *P. pygmaeus* out of the study area towards the end of summer, coupled with the predominance of reproductively active female *P. pygmaeus*, suggests that *P. sitchensis* dominated commercial plantations may be an important habitat for *P. pygmaeus* during an energetically costly period (Kurta et al., 1987), but lack structures necessary for mating or hibernation. This results in the use of plantations during a period coinciding with a reliable and abundant prey source (Fukui et al., 2006; Gonsalves et al., 2013). *Picea sitchensis* plantations may also be important for *p. pipistrellus;* although abundance for this species was low, it may reflect capture bias as activity was equal to that of *P. pygmaeus*, and the two individuals which were trapped in plantation sites were both reproductively active females (Chapter 1, 4). Lintott et al (2013) found that relative abundance is correlated with activity for both *P. pygmaeus* and *P. pipistrellus*, suggesting that acoustic activity can be used as a surrogate for abundance. If this holds true for commercial plantations, then *P. sitchensis* dominated plantations support substantial populations of *P. pipistrellus* as well as *P. pygmaeus* bats. Further study is required to understand associations with commercial plantations by *P. pipistrellus* populations.

Plantation forests also supported a surprising diversity of moth species, with both taxonomic and functional diversity in plantation forests similar to broadleaf sites (Chapter 3, 4). In general, moths associated with deciduous trees have declined throughout Europe, while those associated with conifer have increased due to plantation expansion (Fox et al., 2013; Mattila et al., 2006). The conversion of open heathland to arable and plantations has significantly impacted upon species reliant on open, low nitrogen habitats (Fox et al., 2014). Therefore, while there is a relatively high diversity of moths in plantations, this may be a subset of the former, specialist, heathland and upland community which existed pre-planting. The presence of specialist species in plantations is likely to be due to landscape features and reflect moth dispersal abilities (Scalercio et al., 2012); for example felled and open areas may support early successional specialists, while mature stands may support forest specialist species (Ohsawa and Shimokawa, 2011; Oxbrough et al., 2010). However, the presence of moth species depends on the availability of larval host plants (Franzén and Johannesson, 2007), and that in turn relies on colonisation by suitable plant species, which often come from remnant patches of native habitat (Eycott et al., 2006). Proximity to, and size of the nearest patch of broadleaf tree cover positively influenced both naïve and functional richness (chapter 3, 4), and, although diversity did not differ between broadleaf and plantation sites, functional redundancy was greater in the former. This suggests that remnant patches of broadleaf support rarer species and act as a source, allowing dispersal into other areas of the plantation (Scalercio et al., 2012).

Thirteen biodiversity action plan (BAP) species were identified in plantation sites. BAP species are those which were formally widespread and common but have undergone extremely large declines in the last few decades (70 – 90% reductions, Fox et al., 2013). *Eugnorisma glareosa*, the autumnal rustic, and *Arctia caja*, the garden tiger, were fairly abundant in plantation sites (Chapter 3, appendix 4). Climate change, resulting in milder, warmer winters, is detrimental to *A. caja*, resulting in a northward expansion of its range in the UK (Conrad et al., 2002). Changes in species distribution due to global warming may result in more moth species moving into upland, plantation dominated areas. Increased monitoring within plantation areas will be useful to determine changes in moth species composition and develop sympathetic management practices for moth diversity.

7.1.3 Impact of felling practices on bat roosting ecology and behaviour:

A key concern of forestry managers regarding bat populations in commercial plantations is whether forestry practices will cause direct bat mortality, or result in the destruction of a roost, which would contravene European legislation. I found little evidence of tree roosting by bats in *Picea sitchensis* plantations. Although a very small number of *Nyctalus leisleri* or *N. noctula* reproductive females and juveniles were trapped in plantation areas, three of these were caught in broadleaf patches, which are remnants of ancient woodland (defined as sites with constant woodland presence since 1750, Goldberg et al., 2007) that were mostly planted over with crop trees as part of 20th century forestry initiatives. If a maternity colony is present, it is likely that bats are using old deciduous trees with appropriate features, rather than crop trees (Ruczynski and Bogdanowicz, 2008). Indeed, while radio tracking, female *P. pygmaeus* used trees in these remnant broadleaf patches as both night and day roosts but never Sitka spruce. A small number of other forest specialists such *Myotis nattereri*, *M. mystacinus*, and *Plecotus auritus* were also captured in plantation sites, and, apart from a juvenile *M. mystacinus*, all were male. Female forest specialist species were more abundant at broadleaf sites, suggesting that they are present in the area, but do not use plantations extensively. Differing energetic demands can result in sex or age class-specific differences in distribution (Barclay, 1991); males are under reduced energetic constraints compared to females, which cannot use torpor during pregnancy and lactation to avoid periods of low food availability (Kurta et al., 1987), and therefore are constrained by the availability of roosts appropriate for communal roosting.

The low abundance of *M. mystacinus* is somewhat surprising; its habitat associations and roosting behaviour vary greatly geographically, and has been associated with mixed forest (Buckley et al., 2013), riparian areas (Buckley et al., 2013; Walsh et al., 1996), open areas and pasture (Berge 2007), suggesting that it responds flexibly to habitat type, and it has similar requirements to *P. pygmaeus*, which was abundant in the study area. *Myotis mystacinus* also preferentially use both tree roosts and buildings, preferably close to both water and broadleaf woodland, for maternity colony formation (Bellamy and Altringham, 2015; Buckley et al., 2013), roost switching frequently to access new foraging areas (Buckley et al., 2013). *Myotis nattereri*, another slow flying and manoeuvrable bat, typically found in broadleaf woodlands, has been shown to roost and forage in pine plantations in Scotland (Mortimer, 2006), but was rarely caught at spruce plantations in this study. Similar to *M. mystacinus*, *M. nattereri* will roost in trees and buildings (and occasionally bat boxes, Mortimer, 2006) but avoids roosting near roads and built up areas, possibly due to increased collision risk with vehicles, and predation risk due to artificial lighting (Bellamy et al., 2013). Smaller populations of *Myotis* spp. may reflect a low availability of roosts, and a low availability of suitable foraging areas close to suitable roosts (Buckley et al., 2013). Furthermore, the low numbers of *Myotis* species may also reflect interspecific competition from *P. pygmaeus* and possibly *P. pipistrellus.*

Both *P. pygmaeus* and *P. pipistrellus* preferentially roost in buildings (Jenkins et al., 1998), and have adapted to manmade structures to the extent that they are rarely found in natural roosts (Bartonička et al., 2008; Stone et al., 2015). In addition, they are more tolerant of anthropogenic disturbance such as roads and light pollution than *M. mystacinus* and *M. nattereri* (Bellamy and Altringham, 2015). Radio tracking reproductively active female *P. pygmaeus* revealed a high density of bats in the Galloway Forest area; in total 20 new roosts were identified from either following a tagged female or from speaking to members of the public. At a subset of these roosts informal counts (carried out while waiting for tagged bats to emerged) revealed in excess of 500 bats at a number of roosts, substantially larger than roost densities reported elsewhere for *P. pygmaeus* (e.g. mean 200 bats; Barlow, 1999; mean 158 bats; Stone et al., 2015). In the United Kingdom, *P. pygmaeus* often forms large maternity colonies (the largest recorded *P. pygmaeus* colony, located near Galloway Forest park, exceeds 2000 individuals, J. Martin, pers. comm; two roosts identified while radio tracking held in excess of 1000 individuals). I found that switching between roosts was rare, although *P. pygmaeus* forms smaller colonies, and roost switches more frequently in central Europe (Bartonicka et al., 2008). *Pipistrellus pygmaeus* preferentially roosts in buildings with a higher proportion of deciduous woodland, water (Bellamy and Altringham, 2015; Boughey et al., 2011; Jenkins et al., 1998) and coniferous forest (Jenkins et al., 1998) within 0.5km. Within the study area, 53% of broadleaf tree cover was within 200m of a building and nearly 90% was within 1km, as the majority of broadleaf woodland is either maintained around dwellings or privately owned. Therefore, the association between presence of maternity colony and broadleaf tree cover in the study area is biased, as broadleaf tree cover has preferentially been maintained near buildings. Tagged bats did occasionally use old or damaged deciduous trees as day roosts, therefore buildings surrounded by deciduous tree cover likely offer alternative roosting opportunities (Bartonicka et al., 2008). Conserving deciduous trees within the wider plantation landscape is likely to benefit *P. pygmaeus*, and possibly *Myotis* spp. as well (Bellamy and Altringham, 2015; Buckley et al., 2013; Charbonnier et al., 2016). Good tree cover adjacent to the roost may also offer protection from predators such as diurnal raptors, allowing bats to emerge earlier, and provide linear features along which bats may commute to foraging sites (Jenkins et al., 1998). There was little evidence of *P. pygmaeus* using crop trees (e.g. *Picea* spp. or *Pinus* spp.) for night or day roosts, apart from one individual who day roosted alone in a stump during a period of particularly inclement weather. Therefore, in contrast to other plantation systems (e.g. Arnett, 2007; Borkin et al., 2011; Mortimer, 2006), it is highly unlikely that felling in *Picea sitchensis* dominated plantations poses a direct threat to bat populations.

Despite recording similar activity levels for *P. pipistrellus*, abundance was low. This may reflect our trapping regime, but while assessing buildings for roosts, no *P. pipistrellus* roosts were found. In Central Europe, *P. pipistrellus* is more abundant than *P. pygmaeus*, with *P. pygmaeus* often attaining locally high densities (Sattler et al., 2007). Furthermore, *P. pipistrellus* roost switch more frequently, and form smaller maternity colonies than *P. pygmaeus* (Racey et al., 2007), so may, therefore, remain undetected by home owners. Further research to identify *P. pipistrellus* roosts near *Picea sitchensis* plantations would be interesting, especially as *P. pipistrellus* are considered to be more sedentary than *P. pygmaeus* (Racey et al., 2007; Sztencel-Jabłonka and Bogdanowicz, 2012). As I recorded similar activity levels to *P. pygmaeus,* this suggests that plantations may also support large breeding populations of *P. pipistrellus*. However, further investigation would be necessary to confirm this.

7.1.4 Impact of forest management practices on bat foraging ecology

Clear felling was the only management technique commonly carried out across all the study sites, reflecting current forestry practices in *Picea sitchensis* dominated plantations in the UK (Andrew Jarrott, pers.comm). Similar to studies in native managed forest systems, activity increased post felling for some species (Dodd et al., 2012; Grindal and Brigham, 1998; Loeb and O'Keefe, 2011; Patriquin and Barclay, 2003; Pauli et al., 2015). *Nyctalus* spp. and to some extent *P. pipistrellus* and *P. pygmaeus* activity increased in felled compared to control stands, particularly where the area of clear fell was small (chapter 5). I also recorded higher activity, and a higher probability of occurrence at felled stands compared to other stand types for both *P. pipistrellus* and *Nyctalus* spp (chapter 2). It is likely that increased activity reflects selection of these areas for foraging (Appendix 1; Dodd et al., 2012). Based on wing morphology, the increase in *Nyctalus* activity was expected, as both species in this genus in the UK are fast, high flying, open adapted bats (Aldridge and Rautenbach, 1987). Both *P. pygmaeus* and *P. pipistrellus* are edge adapted bats, increased activity may reflect their ability to exploit forest edges created by clear felling which allow easier flight and prey capture (Dodd et al., 2012). It is likely that bats are responding to reduced physical and acoustic clutter rather than increased invertebrate abundance (Dodd et al., 2012; Jung et al., 2012; Titchenell et al., 2011), especially as I found no difference in non-Lepidoptera invertebrate abundance between different stand types (appendix 2.4). Furthermore, felled patches were positively selected by the majority of radio-tracked bats at the local level, suggesting that bats move between felled patches to forage on accessible and reliable dipteran populations (chapter 6).

Activity of both *P. pygmaeus* and *P. pipistrellus* was lower with larger areas of recently felled stands (chapter 5), similar to findings from other studies (Law and Law, 2011; Patriquin and Barclay, 2003). Although Grindal and Brigham (1991) found no effect of the size of the cut block on bat activity, it is likely that the felled patches in their study were too small to detect any differences (0.5 – 1.5ha). In contrast, in this study, where the size of felled areas reflects common forestry practice, cut blocks were far larger (2.9 – 39ha). Overall bat activity was higher at stand edges rather than stand interiors, regardless of stand type (chapter 2). Higher activity in smaller felled areas is likely due to the increased provision of edge habitats which are structurally simple compared to forest interior (Hogberg et al., 2013; Jung et al., 2012), provide shelter from predators (Grindal and Brigham, 1998), and may harbour a larger invertebrate prey population due to microclimatic variables (Baker et al., 2013; Verboom and Spoelstra, 1999). Larger stands have proportionally less edge compared to interior than smaller stands, and may be more exposed to predation risk and adverse microclimatic effects (Baker et al., 2013).

Knowledge of how bats respond to felling practices is important in understand the potential implications of siting wind turbines in plantations, a practice which has greatly increased in recent years. There is overwhelming evidence to suggest that wind turbines cause both direct and indirect mortality through barotrauma, collision, and avoidance resulting in changes to habitat use (Voigt and Kingston, 2015), although the extent to which such effects can exert population level impacts is likely to vary greatly between regions. Current practices involve the felling the area in which turbines are to be installed, and then replanting up to around 50m beyond the turbine blade tip (Anon., 2015), a process known as keyholing. This may create a patchwork of attractive foraging patches within which turbines have been installed, acting as an ecological trap (Tscharntke et al., 2012). Since it is assumed that bat activity in upland plantations is low, there are currently no requirements for monitoring post felling and post construction and no guidance on the potential impacts on bats (Mathews et al., 2016). Results from this thesis suggest that some bat species could be at far greater risk from the installation wind turbines in commercial plantations than previously thought.

In line with other studies, all species responded negatively to stand density, with decreased activity or a reduced probability of recording certain species as stand density increased (Bender et al., 2015; Blakey et al., 2016; Cistrone et al., 2015; Cox et al., 2016; A D Morris et al., 2010). Again, this is likely to reflect the increased structural, and therefore physical and acoustic clutter in dense stands (Jung and Kalko, 2010; Patriquin and Barclay, 2003). Thinning is not common in the study areas examined in the thesis, and even in mature stands, the average stand density was 1250 trees ha^{-1}. Recommendations of thinning to below 1100 trees ha^{-1} (Adams et al., 2009) are likely to be effective, Blakey et al (2016) found increased bat activity in stands which were thinned to below this level, and in this study bat activity increased by 30% in stands in which density was below 1000 trees ha^{-1} (Chapter 2).

As a result of forest restructuring, U.K. forest guidelines now require a proportion of the plantation landscape to be broadleaf tree cover and surviving remnant patches of broadleaf trees are protected from forestry practices (Pommerening and Murphy, 2004). Preserving broadleaf patches in the environment is likely to benefit bat species by alternative roost provision (Altringham et al., 1996) or due to increased invertebrate diversity (Felton et al., 2010; van Halder et al., 2008). Of the two Pipistrellus species recorded in this study, *P. pygmaeus* was more common close to broadleaf woodland. Since the majority of broadleaf woodland was within 200m of a building, and most of these buildings contained a *P. pygmaeus* roost (Appendix 1, chapter 6), associations with broadleaf woodland in our study area are therefore conflated with the locations of roost. However, the presence of deciduous trees in commercial coniferous plantations has been linked with increased bat activity (Charbonnier et al., 2016), and as lactating female *P. pygmaeus* did use deciduous trees as both night and day roosts, preserving them in the plantation landscape is likely to benefit bats, particularly tree roosting dependent species. Although dipteran abundance was not significantly greater in native stands within the plantations (appendix 2.4), preserving broadleaf woodland is likely to support a greater diversity of invertebrate species.

7.1.5 Impacts of forest management on night active Lepidoptera

Despite the widespread decline in abundance for multiple moth species across the UK being attributed to changes to silvicultural practices such as afforestation with non-native conifers (Conrad et al., 2006), the impacts of forestry practices on moth abundance have rarely been explored (but see Luque et al., 2007). To the best of my knowledge, chapters 3 and 4 are the first time *P. sitchensis* plantations have been surveyed for night active lepidopteran abundance and diversity.

Felling significantly and negatively impacted moth richness and diversity, including functional diversity. Moth species richness and abundance was higher in more open, native and felled stands, although after constraining for functional similarity there were no stand level differences in richness and diversity (chapter 3, 4). This emphasises the importance of spatial scale when considering the impacts of anthropogenic disturbance on biodiversity, with moths impacted at landscape (Jew et al., 2015; Parrish and Summerville, 2015; Summerville and Crist, 2002) rather than the local scale (Uhl et al., 2015). Plantation areas which have undergone substantial and widespread felling may represent extremely simplified landscapes, which can only sustain a few surviving populations (Tscharntke et al., 2012). If the landscape is too structurally homogenous, as could be the case in areas with a large proximity of felling in the surrounding landscape, it is unlikely to support a large enough species pool to produce effective results from environmental management schemes (Tscharntke et al., 2012). Increased landscape compositional heterogeneity provides insurance in the face of intense management by supporting more biodiversity (Tscharntke et al., 2012), and stands with a low proportion of felling in the surrounding matrix may be embedded in a more heterogeneous landscape resulting in higher functional richness and diversity (Gámez-Virués et al., 2015; Scalercio et al., 2012). Hamer et al (2003) also found reductions in lepidopteran diversity in logged forests due to reduced environmental heterogeneity and found that sampling had to occur at large enough spatial scales to account for the impacts of disturbance on forest heterogeneity. It has been proposed that higher diversity should be found in areas of intermediate disturbance, where both climax and pioneer species can coexist (Hamer et al., 2003). Felled stands with a low proportion of felling in the surrounding landscape may represent intermediate disturbance whereas a high proportion of felling the surrounding landscape may result in levels of disturbance which only certain species can tolerate (Hamer et al., 2003).

I hoped to find that using functional traits would reveal the mechanism by which felling reduces moth richness, diversity and abundance. Felling may reduce richness and diversity via a range of mechanisms; removal of host plants (Summerville and Crist, 2002), changes in microclimate, and disturbance to forest understory vegetation (Parrish and Summerville, 2015). However, moth communities in landscapes showed no signal of environmental filtering (chapter 4). There was no clear impact of felling on particular host plant or habitat preferences, so potentially the practice of clear felling may reduce survival through a range of mechanisms such as host plant removal or disturbance during overwintering period. Overwintering underground as larvae may provide protection from cold, desiccation, predators or felling disturbance compared to moths overwintering as eggs or pupa (Mattila et al., 2006). I found that distance from broadleaf tree cover significantly reduced trait diversity in moth overwintering style, broadleaf patches may provide more appropriate shelter for moths during the winter.

7.1.6 Enhancing plantations for bats and nocturnal invertebrates

1. The presence of BAP moth species in plantation sites, including *A. caja*, which has undergone widespread declines elsewhere emphasises the importance of surveying a range of habitats, even ones usually considered poor for biodiversity. As declines of *A. caja* are in part attributed to climate change and warmer, wetter, winters, upland plantations may be an important refuge for this species. Sites in plantation dominated landscapes should be included in long-term monitoring programs. Surveys of *P. sitchensis* in other geographical regions such as North Wales will also be beneficial, to assess whether rarer bats such as *Rhinolophus hipposideros* also associate with commercial plantations. Conflicting anecdotal evidence reports both low bat activity and regular sightings of bats in commercial plantations (pers. comm H. Schofield, G. Billington, M. Shewring), especially as bat habitat associations can vary geographically. At wind farm sites, monitoring should be instigated, particularly after felling and prior to installation
2. Structures for both maternity roosts and harem formation appear limiting in *P. sitchensis* plantations. I found no evidence of bats using *P. sitchensis* for day roosting, or reproductive behaviour. While deciduous trees were used by bats, trees of the appropriate age and quality were rare in the study area. Installing artificial bat boxes in areas where felling operations will not occur will benefit bats. Bat box uptake in areas of low roost availability is often swifter than in other areas (Flaquer et al., 2006; López-Baucells et al., 2016) and provides alternative locations for both maternity colonies (Flaquer et al., 2006) and harem formation (Park et al., 1996). During this study, 41 Schwegler 1FF and nine Schwegler 2F boxes were erected throughout Galloway Forest (on August 2015 and February 2016) along flight routes and in areas where high *P. pygmaeus* activity was recorded (chapter 2, 7). Box checks carried out in September 2016 found that 90% of the boxes had evidence of bat use, and 131 *P. pygmaeus* were recorded, many of which were in harem groups (Park et al., 1996). The large number of harems found, often in bat boxes adjacent to each other reflects the low roost density in plantations. However, whether these boxes will be adopted as matenity colonies remains to be seen; surveys carried out in Ireland found that, although *Myotis* spp. used boxes for maternity colonies, *Pipistrelle* spp. never did (McAney and Hanniffy, 2015). Other, custom built, standalone structures have had considerable success

however (e.g. unheated bat boxes which hold maternity colonies of *P. pygmaeus,* J. Martin, pers. comm). If boxes are installed, regular monitoring should occur to determine the success of uptake, and whether species other than *P. pygmaeus* use the boxes

3. Reducing stand density: In line with various other studies across temperate zone plantations, maintaining and enhancing thinning programs where possible may allow stands to reach similar densities to mature stands at a younger age, which will benefit edge and clutter adapted species (Bender et al., 2015; Blakey et al., 2016; Cox et al., 2016; A D Morris et al., 2010). Thinning also reduces canopy closure by creating gaps, which will allow regeneration of ground vegetation (Eycott et al., 2006), providing a greater diversity of host plants for moth species. Switching to continuous cover has been shown to positively influence moth diversity and abundance in native managed woodlands(Summerville, 2013; Thorn et al., 2015), but has not yet been assessed in non-native systems.
4. Management of plantations should occur at the landscape scale as well as the local scale wherever possible. For small, private forest managers this may not be realistic, but for larger forests, management that ensures a heterogeneous mix of stand ages, smaller clear cuts and patches of broadleaf tree cover will support a higher diversity of both moth and bat species. The presence of broadleaf tree cover in the landscape significantly increased moth richness and abundance, while reducing the size and extent of felling should also have positive benefits for both moth and bat species. *Pipistrellus pygmaeus* preferentially forages in felled stands, at remnant patches of broadleaf and in riparian habitats, and will roost in deciduous trees where the appropriate features exist. Preserving broadleaf and riparian habitats, and reducing clear-cut sizes will benefit *P. pygmaeus,* during an energetically costly part of their life cycle.

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Appendix

Comparison of bat abundance and activity in native woodlands and Sitka Spruce plantations.

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Typical broadleaf and plantation sites surveyed in Galloway Forest plantation.

A1.1 Abstract

Most bats species, which are highly mobile, depend on forest for some or all of their life cycle. However, native forests are under growing anthropogenic pressure worldwide, and the majority of temperate forest land cover now consists of non-native, intensively managed production plantations, which are thought to contribute little to bat conservation. To the best of my knowledge, the extent to which bat activity in non-native plantations differs from nearby broadleaf areas has not been explicitly investigated, although habitat studies suggest that coniferous plantations are generally avoided by bats. Here, I compare 14 paired broadleaf woodlands and plantation forests over two years to determine whether bat abundance, activity and behaviour differs between two habitat types. Overall there were similar levels of activity in the two woodland types but a large difference between sampling years, which varied considerably in weather conditions. *Pipistrellus pygmaeus* and *P. pipistrellus* were the most commonly recorded species, while *P. pygmaeus* was the most frequently captured. Activity of *P. pygmaeus* was similar between years but higher in plantation sites in 2014 and higher in broadleaf sites 2015. *Pipistrellus pipistrellus* activity was low and similar in both broadleaf and plantation sites in year one but much higher in broadleaf sites in 2015. There was also a trend of higher *Myotis* and *Nyctalus* activity in broadleaf sites in 2015. In 2015 it was substantially cooler and wetter than 2014. Whilst it is unclear if the differences in weather conditions are responsible for the apparent switch in habitat preference, at least for *Pipistrellus* spp., as small, endothermic mammals, bats are sensitive to low temperatures and may change their behaviour in response to adverse weather conditions. As different sites were sampled in year one compared to year two, it is not clear whether differences in bat activity and abundance reflect site level differences, variation in habitat use, or are due to the different meteorological conditions between the two sampling years. Repeated monitoring of all sites across multiple years should reveal whether differences in bat activity are due to habitat differences or bats changing their behaviour due to adverse weather conditions.

Plantation forests and broadleaf woodlands may fulfil different habitat requirements for bats, for example, bats may roost in broadleaf woodlands but forage in plantations. Differences in rates of social calling or feeding buzzes may reflect these different habitat uses. *Pipistrellus pygmaeus'* rate of social calling was higher closer to buildings, whereas *P. pipistrellus* social calling increased in sites with lower invertebrate abundance. The majority of buildings in the study area house *P. pygmaeus* maternity colonies, and increased social calling near buildings may be due to intraspecific communication when foraging close to roost sites, or reflect social communication between females and volant offspring. Increased social calling as invertebrate abundance decreases is likely a reflection of increased antagonistic interactions as competition for food resources increases.

A1.2 Introduction

The ability of a particular habitat to support a diverse range of taxa depends on whether it provides resources necessary for food provision and shelter from elements, as well as sufficient connectivity between these resources to support a viable population. Habitats such as native woodland can support high levels of biodiversity, yet native forested landscapes are under growing anthropogenic pressure (Anon., 2011). Increasingly, as plantation land cover is predicted to expand (FSC, 2012) productive landscapes may play a greater role in supporting biodiversity. The contribution these landscapes may make to biodiversity conservation is receiving growing attention worldwide (Brockerhoff et al., 2008; Quine and Humphrey, 2010; Russo et al., 2016; Stephens and Wagner, 2007). Species assemblages are driven by both local scale, fine grained habitat composition and structure and regional composition, which influences resource availability and niche opportunity (e.g. at the landscape level; Charbonnier et al., 2016), management of which can be built into plantation forestry plans. For example, the majority of native woodland in the UK is small, fragmented and often surrounded by agriculture or urban land which can be relatively hostile, and limit dispersal between fragmented patches (Watts et al., 2016). Plantation forests are much larger and consist of a mosaic of different habitat types which may support a range of different species providing they can recolonise different areas through the plantation management cycle (Stephens and Wagner, 2007). However, plantations are often even aged systems which reduce structural and compositional heterogeneity, limiting the taxa which are able to exploit them (Lindenmayer and Hobbs, 2004).

Highly mobile, but with slow reproductive rates, Chiroptera are one of a few orders of mammal which associate with both human modified landscapes and forest / woodland, although the strength of association is species specific depending on mobility and specific requirements for roosting, foraging or hibernation (Altringham et al., 1996; Law et al., 2015; Lintott et al., 2015). Numerous habitat studies have demonstrated avoidance of conifer habitats (Boughey et al., 2011; Davidson-Watts et al., 2006; Walsh et al., 1996), but *Myotis mystacinus, Pipistrellus pygmaeus* and to some extent *Plecotus auritus* have all been found to prefer mixed woodlands to broadleaf (Buckley et al., 2012; Fuentes-Montemayor et al., 2013). Forest specialist species such as *M. nattereri* have also been recorded making use of a commercial plantation in East Scotland despite normally being associated with broadleaf woodland (Mortimer, 2006), and *Barbastella barbastelle* has been found to associate with commercial plantations in Italy (Russo et al., 2010). In this example, bats preferentially associated with Corsican pine despite Scots Pine being the commonest tree species in that plantation. To the best of our knowledge however, direct comparisons of bat communities in native broadleaf woodland and coniferous plantations are rare. Previously, (chapter 2), I found substantial bat activity in plantation woodlands for both *P. pygmaeus* and *P. pipistrellus,* and radio tracking revealed that individuals were travelling from roosts in buildings on the edge of a Sitka Spruce plantation into plantation areas to forage (chapter 6). However, it is not known how activity within plantation forests reflects activity in the wider landscape. For example bat activity in plantation forests may be spill over from broadleaf woodlands, where non breeding individuals are forced into suboptimal areas (e.g non lactating *Nyctalus noctula* used marginal habitats such as moorland or conifer more frequently than lactating individuals; Mackie and Racey, 2007). Alternatively, activity may increase as the proportion of deciduous land cover increases Charbonnier et al. (2016); although I found no evidence of this in chapter 2, the proportion of broadleaf in the landscape was very low and I did not survey broadleaf remnants surrounding the plantation. Differential responses to habitats based on energetic costs have also been shown in response to altitudinal gradients; for example, female *Myotis daubentoni* preferentially use low altitude habitats whereas males, who have lower energetic demands and can use torpor to minimise energetic costs on nights with low invertebrate availability, use sub-optimal higher altitude foraging areas (Angell et al., 2013; Nardone et al., 2015). If plantations are sub optimal habitat compared to surrounding broadleaf woodland I would expect to find lower abundance, species richness and activity in plantations, and would be primarily used by males, rather than lactating females or juveniles.

Use of different woodland types may differ depending on invertebrate prey availability, with seasonal, temporal or even meteorologically driven differences in habitat use (Andreas et al., 2012; Razgour et al., 2011); insectivorous bat abundance and activity is often strongly associated with arthropod abundance (Kunz et al., 2011). For example, individuals may target foraging activity based on particular invertebrate emergence events (eg. invertebrate pest species; Cleveland et al., 2006, aquatic insects; Fukui et al., 2006). However, invertebrate availability alone is unlikely to be the sole influence on choices of foraging areas; Dodd et al. (2012) found that foraging activity was greatest in stands with low structural complexity which did not necessarily have the highest insect abundance, and bat activity is greater in the canopy (Adams et al., 2009; Dodd et al., 2012), along tree lines and edge habitats which may be easier for bats to negotiate within (Verboom and Spoelstra, 1999). As bats differ in morphology, echolocation style and foraging strategy (Altringham et al., 1996), this will influence the extent to which they are able to exploit commercial plantations. *Plecotus auritus*, a gleaning woodland specialist with slow, manoeuvrable flight and very quiet echolocation calls avoids conifer plantations and forages almost exclusively in mixed and broadleaf woodland and around deciduous trees, a behaviour attributed to greater availability of its invertebrate prey in these habitats but may also reflect the paucity of available roosts in plantations. *Pipistrellus pygmaeus* and *P. pipistrellus,* which are aerial hawking edge specialist bats, have also been found to use commercial plantations (Chapter 2) probably due to the locally high abundance of *Nematoceran* Diptera, their primary food source (Barlow, 1997). Previously, I demonstrated spatial partitioning of bats into areas of low tree density in plantations, particularly mature and freshly felled stands, despite relatively similar levels of invertebrate abundance between denser and more open stand types, probably due to reduced acoustic and physical clutter in less dense stands (Chapter 2; Kirkpatrick et al. in press).

Bat abundance in Sitka Spruce (*Picea sitchensis*) plantations in Scotland and Northern England was dominated by lactating *P. pygmaeus,* and juveniles later in the season, and activity was dominated by both *P. pipistrellus* and *P. pygmaeus* (Chapter 2). There was little evidence of breeding populations of *Myotis* spp. using these plantations. Most coniferous plantations are unlikely to contain many tree roosts since the trees are typically harvested before suitable features form (Mortimer, 2006; Russo et al., 2010). Perhaps as a reflection of the lack of alternative roosts in non-native commercial plantations, bat box uptake can be higher than has been found in broadleaf woodlands or near urban centres (López-Baucells et al., 2016; Smith and Agnew, 2002). It is likely that foraging opportunities may be more plentiful than roosting opportunities in plantation forests (Elmore et al., 2005), while broadleaf woodlands may provide habitat for both roosting and foraging (Boughey et al., 2011). However, high levels of activity do not necessarily reflect particular behaviour such as foraging or social interactions. Specific echolocation calls emitted during pursuit of invertebrate prey (“feeding buzzes”) can be used as an indication of foraging activity, while other calls related to communication rather than orientation (“social calls”) are emitted as either intraspecific antagonistic interactions, or possibly between mothers and offspring (Russ, 2012). For example Russ et al. 2004 found that *Pipistrellus* spp*.* responded to both conspecific and congeneric distress calls resulting in mobbing behaviour. Most social call types I recorded were either Type D (thought to be involved in antagonistic interactions) or Type C (information transfer between mother and offspring). Identifying these calls provides additional information about bat behaviour as well as bat activity in both woodland types. This may reveal whether bats are actively foraging in plantation areas, or if bats are using plantation forests to commute between different remnant patches of broadleaf woodland.

Although I found evidence of widespread bat foraging activity in plantation landscapes (Chapter 2), this did not enable a comparison with broadleaf woodlands, which is generally considered of higher habitat quality. I address this here, by assessing the following in paired broadleaf and plantation sites:

1. Differences in species specific bat activity between broadleaf woodlands and plantations

2. How bat abundance, diversity and population composition differs between plantations and broadleaf woodlands
3. How the rate of social calling and feeding buzzes varies between broadleaf woodlands and plantation forests.
4. The extent to which invertebrate abundance drives differences between broadleaf and plantation forests.

A1.3 Methods

The study was conducted in Galloway Forest Park in 14 paired semi natural woodlands and plantation forests (South west Scotland, Figure A1). Galloway is a very large, intensively managed plantation (114,000 ha) in south west Scotland, predominantly planted with *Picea sitchensis*, a common and widespread commercial tree species. Previous to commercial planting, much of Galloway forest consisted of open upland and moorland habitat with low deciduous woodland cover due to historical deforestation. I identified 14 broadleaf woodlands which had a constant presence

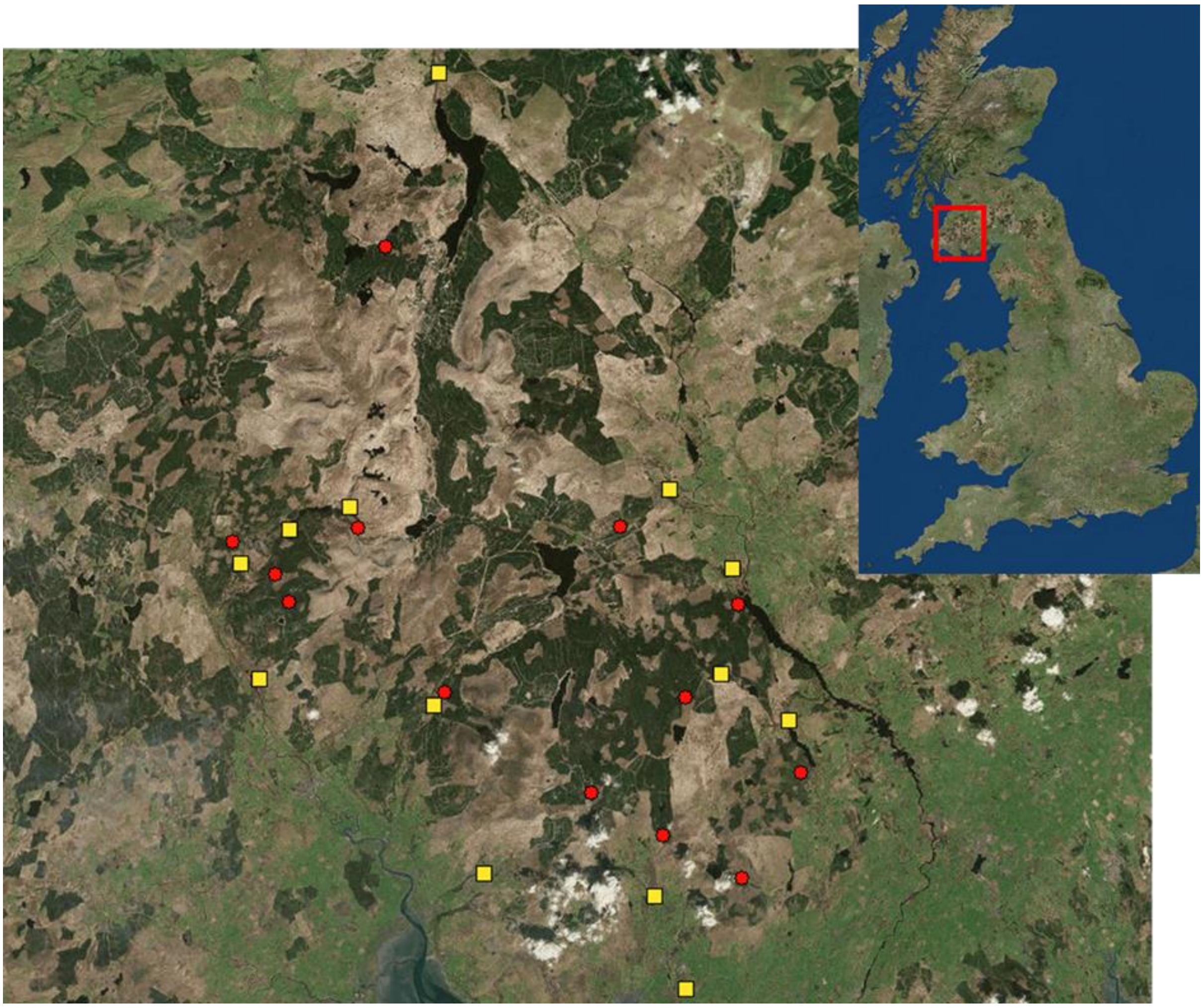

Figure A1: Map showing sites (broadleaf sites are displayed as squares, plantation sites as circles. Colours indicate paired sites) and distribution around Galloway Forest Park.

on maps going back to at least 1840, all of which were over 20ha in size.
Most of these woodlands are now publically owned and under conservation management. All broadleaf woodlands were paired with nearby (< 6 km) plantations. A Geographic Information System (GIS) was used to select felled stands adjacent to mature stands, as results from Chapter 2 suggest that this is where bat activity in plantations is highest. Selected sites were ground-truthed for access and permissions to survey secured from landowners.

A1.3.1 Bat acoustic surveys:

All surveys were carried out between 20th June – 21st August 2014 and 13th June – 8th August 2015. Each pair of sites were surveyed simultaneously for five nights starting 30 minutes after sunset, ensuring that recorded individuals would be actively foraging rather than commuting from roosts. Surveys finished four hours later as this represents the length of the shortest night in this area during the summer. At each site, bat activity was assessed using a SongMeter SM2 Bat+ (Wildlife Acoustics, Inc., Concord, MA) using two microphones at a height of 1m and positioned at a 45 degree angle. One microphone was placed at the stand edge pointing towards adjacent tracks or rides; the other was positioned 20 – 40m into the trees (depending on ease of access) pointing towards the stand interior, allowing simultaneous recording of both the stand edge and interior.

A1.3.2 Bat ***abundance*** *surveys*

For some species, identification from echolocation calls alone is not possible (Schnitzler et al., 2003). Therefore capturing individuals for inspection in the hand can be the only way to confirm species occurrence and to determine sex and breeding status (Hill and Greenaway, 2005). Number of captures can also provide a measure of relative abundance. I assessed relative bat abundance by placing an Austbat harp trap (2.4 x 1.8m) and three Ecotone mist nets (2.4 x 6m) at one location in each site. Nets were placed across potential flight lines (e.g. tracks or rides) between either two mature stands or extending from the edge of a mature stand into felled stands, at least 50m from each other and chosen deliberately to increase capture rates. I used an acoustic lure (The Autobat, Sussex University, Brighton, UK) with four different synthesised bat calls (*Pipistrellus* spp mix, a mixture of *Myotis* sp., *Nyctalus leisleri* and *M. nattereri*), which has been demonstrated to greatly improve capture rates (Hill and Greenaway, 2005) and attracts a variety of different bat species present in the study area (Lintott et al. 2014). Each call was played at each trap for 15 minutes, with the lure moved between traps every 30 minutes. Traps were checked every 15 minutes and any captured bats were identified to species, weighed, measured, aged, sexed, assessed for reproductive status and marked temporarily by fur clipping.

A1.3.3 Bat call analysis

Activity was quantified by counting the number of bat passes (defined as at least 2 echolocation calls within one second of each other) per night and identifying all calls manually to species or genus. *Pipistrellus* species can be separated due to differences in the characteristic frequency of the call (Fc = frequency of the right hand end of the flattest part of the call (Russ, 2012) and the call shape. Bats in the genus *Myotis* have a similar call structure and as such were identified only to genus. It can be difficult to distinguish *Nyctalus* calls in cluttered environments (Schnitzler et al., 2003), so again these were only identified to genus. *Plecotus auritus* have very quiet calls, so their presence will be underestimated by using acoustic recordings alone. I also counted feeding buzzes and social calls as measures of bat behaviour. Feeding buzzes are a specific change in call speed, shape and frequency as an individual bat homes in on and then potentially captures invertebrate prey (Russ, 2012). This is commonly seen in aerial hawking bats which capture prey on the wing (Russ, 2012). I inspected each sound file for evidence of a feeding buzz, recording whether it was present or absent, then divided the number of feeding buzzes per site by the overall activity per site for each species. I followed the same protocol to quantify social calling behaviour. Social calling can be hugely variable between and within different species depending on the context in which the bat is calling and the potential information the bat may portray, intentionally or otherwise (Middleton et al., 2014). However, as information is scarce regarding the different types of social call, analysis was carried out with all social calls treated as a single category.

A1.3.4 Invertebrate collection and identification

Each site was surveyed for invertebrates for one night, concurrently with bat abundance, using two portable 6W heath light traps with E7586 9'' actinic tube lights, powered with 12V batteries which were activated 15 mins after sunset and switched off after 4 hours. This ensured that invertebrates flying at dusk and during the night were surveyed regardless of night duration, although species flying at dawn may have been missed as traps were often turned off before this time. Surveys were only conducted on nights that were above 8 ^{o}C with a wind speed of less than Beaufort 4, and were randomised as far as possible during the survey season between the different geographical areas. Within each site the two traps were placed 15 metres from the tree cover edge, at least 100m from the next nearest trap and the location recorded with a GPS. Traps were selectively positioned in order to ensure that similar light levels were emitted (for example ensuring that vegetation did not obscure the light) and that traps were not visible from each other. Following surveys, a cotton wool ball soaked in ethyl acetate was added to the trap and left overnight to kill captured invertebrates. Macro moths were removed and pinned to boards for later identification, whilst micro moths were separated for identification by an expert at the National Museum of Scotland. Other invertebrates were stored in 80% ethanol solution for identification and counting.

A1.3.5. Roost identification and meteorological information

A parallel radio tracking study (Chapter 6) found that the majority of habitable buildings within the plantation housed maternity colonies of *P. pygmaeus.* Therefore I used distance to the nearest building, and the total number of buildings within a 500m radius, as a measure of roost availability as both *P. pygmaeus* and *P. pipistrellus* have similar roost requirements (Dietz et al., 2009). *Nyctalus* bats will also form maternity colonies in buildings (Dietz et al., 2009). There was no local weather station which collected both rain and daily temperature information so meteorological data was retrieved from the MIDAS database, with rainfall data retrieved from Forrest Lodge (BADC id: 13290 and temperature data from Threave Castle (BDAC id: 1035). We used temperature at 21.00 to calculate a seasonal average minimum and average maximum temperature for both spring and summer periods.

A1.3.6 Statistical analysis

I tested for correlations between feeding buzzes and activity using Spearmans Rank correlations to account for non normally distributed data, in order to test whether bat activity was correlated with foraging activity. I modelled differences in abundance (1) initially for all bats, then for *P. pygmaeus*, *Myotis mystacinus, M. nattereri* and *Nyctalus* spp*.* separately, using generalised linear mixed effects models as I caught sufficient individuals of these species. Enough *P. pygmaeus* were trapped to model the interaction of year and habitat with male or female abundance. I excluded juveniles from these analyses as juveniles are disproportionately abundant as they become volant. Despite representing a large proportion of activity data, I caught insufficient *P. pipistrellus* individuals to assess the association of abundance with habitat type. I used generalised linear mixed effect models to assess (2) the influence of forest type, roost availability and food availability on *P. pygmaeus, P. pipistrellus, Myotis* and *Nyctalus* passes per night (4 hour sampling period), which were logged to reduce over dispersion in the residuals (Crawley, 2007). The proportion of *P. pygmaeus* to *P. pipistrellus* calls were also modelled in response to the aforementioned variables. Site was included as a random effect to account for the paired sampling design, with a year*habitat interaction as inspection of the data suggested differences in habitat use between the different years. I had sufficient data to (3) model the impacts of habitat type and year on the rate of social calling (pooling social call type; Middleton et al., 2014) for both *P. pygmaeus* and *P. pipistrellus* as a proportion of total activity, including (4) proxies for food and roost availability.

A1.4 Results

Due to equipment failure or poor weather conditions, the total number of complete nights per site varied between 1 and 4 (mean = 2.3). Overall, 2014 was a warmer, drier year compared to 2015. There was no difference in spring rainfall between the two sampling years, but there was significantly more rain in summer 2015 compared to summer 2014 (T. test: Summer: F_{520} = 8.4, p<0.01; Table 5.1). Maximum spring and summer temperatures were both significantly lower in 2015 compared to 2014, as was the minimum spring and summer temperature (T. test; Maximum Spring: F_{179}2.64; p<0.01; Maximum Summer: F_{180} = 3.74, p<0.001; Minimum Spring: F_{179}=4.08; p<0.001; Minimum Summer: F_{168}=3.36; p<0.001; Table 5.1).

A1.4.1 Bat species composition and abundance

A total of 223 bats were captured, 142 in broadleaf sites and 81 in plantation sites. These comprised eight species in broadleaf, and six species in plantation sites, with *Plecotus auritus* and *Nyctalus noctula* only captured in broadleaf woodlands (Table A1.2). *Pipistrellus pygmaeus* was the most numerous species captured in both woodland types comprising 72% of all captures. The majority of non *Pipistrellus* individuals captured in plantation sites were male, although two female *Myotis mystacinus* were captured at plantation sites, one of which was a juvenile (Table A1.2). Male *P. pygmaeus* were captured in significantly greater numbers than females in 2015, rising from 27 to 82, with the greatest increase occurring in broadleaf sites (Table A1.3). No juvenile bats were captured in

2015, compared to 19 in 2014. Numbers of *P. pipistrellus* and *Nyctalus* were also low (Table A1.2). Overall there was little difference in the number of species between year or woodland type, with similar species richness in plantation and broadleaf sites (Table A1.2, Figure A1.2 B). Total abundance, however was lower in plantation sites (Table A1.2). There was no difference in abundance for either *M. nattereri* or *M. mystacinus* between plantation and broadleaf sites, or between either year (Table A1.3). *Nyctalus* abundance was low in both broadleaf and plantation sites, but our capture protocol would be unlikely to trap *Nyctalus* bats as they are fast flying bats that preferentially move in open spaces (Dietz et al., 2009).

5.4.2 Bat activity

Based on the fitted means, in 2014 *P. pygmaeus* activity in plantations was approximately double that in the broadleaf sites. However, in 2015 the opposite was true (Figure A1.3A). This was also the case for *P. pipistrellus*; activity was slightly higher in plantations in 2014 but was much higher in broadleaf sites in 2015 (Figure A1.3 B).

Table A1.1: Bat abundance and composition in broadleaf and plantation sites over two years of sampling. Numbers in parentheses are adult female totals. Pipistrellus nathusius *is another relatively rare and cryptic* Pipistrellus spp.; *these captures have not been confirmed with DNA testing, and it is possible that some of these are* P. pipistrellus.

Species	Age	2014		2015	
		Broadleaf	Plantation	Broadleaf	Plantation
Myotis daubentoni	Adult	5 (4)	0	3 (3)	0
Myotis daubentoni	Juvenile	1	3	0	0
M. mystacinus	Adult	3 (2)	3 (1)	1 (0)	3 (0)
M. mystacinus	Juvenile	0	1	0	0
M. nattereri	Adult	7 (7)	2 (0)	5 (0)	4 (0)
M. nattereri	Juvenile	0	0	0	0
Nyctalus leisleri	Adult	2	1 (0)	4 (1)	0
Nyctalus leisleri	Juvenile	0	0	0	0
N. noctula	Adult	1 (0)	0	1 (0)	0
N. noctula	Juvenile	0	0	0	0
Plecotus auritus	Adult	4 (3)	0	1 (0)	0
Plecotus auritus	Juvenile	0	0	0	0
*Pipistrellus nathusius**	Adult	0	0	2 (1)	0
*Pipistrellus nathusius**	Juvenile	0	0	0	0
P. pipistrellus	Adult	0	0	4 (2)	1 (1)
P. pipistrellus	Juvenile	0	0	0	0
P. pygmaeus	Adult	30 (20)	16 (10)	63 (19)	31 (13)
P. pygmaeus	Juvenile	6	15	0	0
Total bat abundance	Adult	51 (35)	22 (11)	84 (27)	39 (14)
Total bat abundance	Juvenile	7	19	0	0

Table A1.2: Differences in weather between the two sampling years during spring (March - May) and summer (June - August)

Variable	2014	2015
Spring mean minimum temperature (°C)	7.3 ± 0.3	5.6 ± 0.3
Spring mean maximum temperature (°C)	12.7 ± 0.3	11.5 ± 0.3
Spring mean rain (mm)	4.5 ± 0.4	5.2 ± 0.5
Summer mean minimum temperature (°C)	13.3 ± 0.2	12.2 ± 0.2
Summer mean maximum temperature (°C)	19.1 ± 0.3	17.6 ± 0.3
Summer mean rain (mm)	3.1 ± 0.3	5.0 ± 0.6
Nights above 6 °C (Summer)	92	61
Nights without rainfall (Summer)	51	27

Table A1.3: Model estimates ± standard error for measures of abundance (based on capture data) for all bats and for individual species and species composition (male: female). The parameters are listed Model estimates ± standard error for measures of abundance (based on capture data) for all bats and for individual species and species composition (male: female). The parameters are listed with their respective influence on measures of abundance. Site was included as a random effect in all models; date was included in all models but did not improve model fit in any case and not presented here. Estimates in bold indicate parameters with a significant effect (standard error of the estimate does not cross zero, Burnham and Anderson, 2002).

	Model	Intercept	Forest Type:Year	Distance to nearest building	Dipteran abundance	Min temperature
Activity	*P. pygmaeus*	5.1 ± 0.9	**-1.8 ± 0.6**	**-0.7 ± 0.2**	-0.1 ± 0.1	0 ± 0.1
	P. pipistrellus	2.7 ± 1.4	**-2.6 ± 0.8**	0.5 ± 0.4	-0.1 ± 0.2	0 ± 0.1
	Myotis	1.8 ± 0.8	**-1.4 ± 0.5**	0.4 ± 0.2	0.0 ± 0.1	0 ± 0.1
	Nyctalus spp	0.9 ± 1.3	-0.4 ± 0.6	**1.0 ± 0.4**	0.2 ± 0.2	0 ± 0.1
Rate of social calling	*P. pygmaeus*	-1.6 ± 0.3	**-0.5 ± 0.2**	**-0.5 ± 0.1**	-0.1 ± 0.1	NA
	P. pipistrellus	-1.6 ± 0.4	**-1.7 ± 0.4**	-0.1 ± 0.2	**-0.3 ± 0.1**	NA
Proportion of activity	*P. pygmaeus: P. pipistrellus*	1.5 ± 0.4	0.3 ± 0.1	**-0.9 ± 0.1**	0.0 ± 0.0	NA

Table A1.4: Model estimates ± standard errors for potential explanatory variables influencing measures of activity, social calling and dipteran abundance (based on invertebrate trapping data) for species / genus specific relative activity and behaviour. Site was included as a random effect in all models; date was included in all models but insignificant in every case and not presented here. Estimates in bold indicate parameters with a significant effect (standard error of the estimate does not cross zero, Burnham and Anderson, 2002)

	Model	Intercept	Forest Type	Year	Sex male: Year	Sex male: Forest Type
Species richness	*Species Richness*	**1 ± 0.2**	-0.2 ± 0.3	0.0 ± 0.2	NA	NA
Abundance	*All bats*	**2.2 ± 0.2**	**-0.6 ± 0.1**	0.4 ± 0.4	NA	NA
	P. pygmaeus	**1.4 ± 0.3**	**-0.5 ± 0.2**	**0.7 ± 0.4**	NA	NA
	P. pygmaeus (proportion male: female)	**0.7 ± 0.3**	**-0.5 ± 0.2**	0.3 ± 0.4	**1.3 ± 0.4**	-0.3 ± 0.4
	M. nattereri	-0.4 ± 0.5	-0.5 ± 0.5	0.3 ± 0.6	NA	NA
	M. mystacinus	**-1.1 ± 0.7**	0.3 ± 0.8	-0.9 ± 1.2	NA	NA
	Nyctalus spp	-0.7 ± 0.5	**-2.1 ± 1.1**	-0.4 ± 0.7	NA	NA

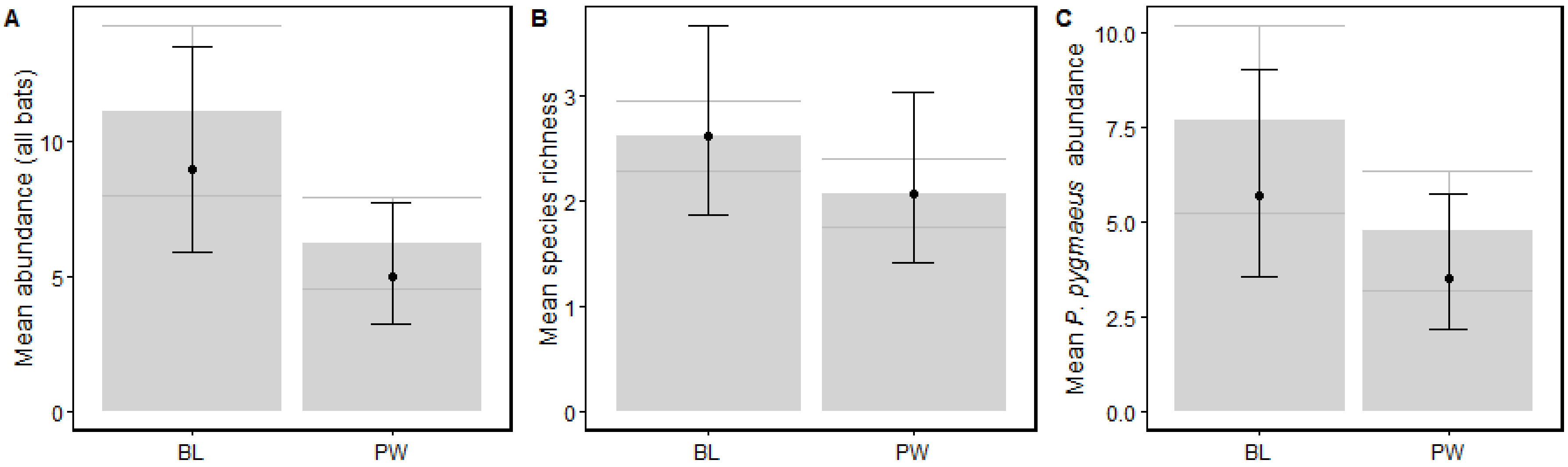

Figure A1.2: Mean abundance of all bats (1A), mean species richness (1B) and mean P. pygmaeus abundance (2C). Grey bars and errors indicate mean abundance and standard errors whilst black points and errors give the mean and 95% confidence intervals predicted by the model (Table 3). Only P. pygmaeus is presented as mean abundance and model accuracy was low for other species.

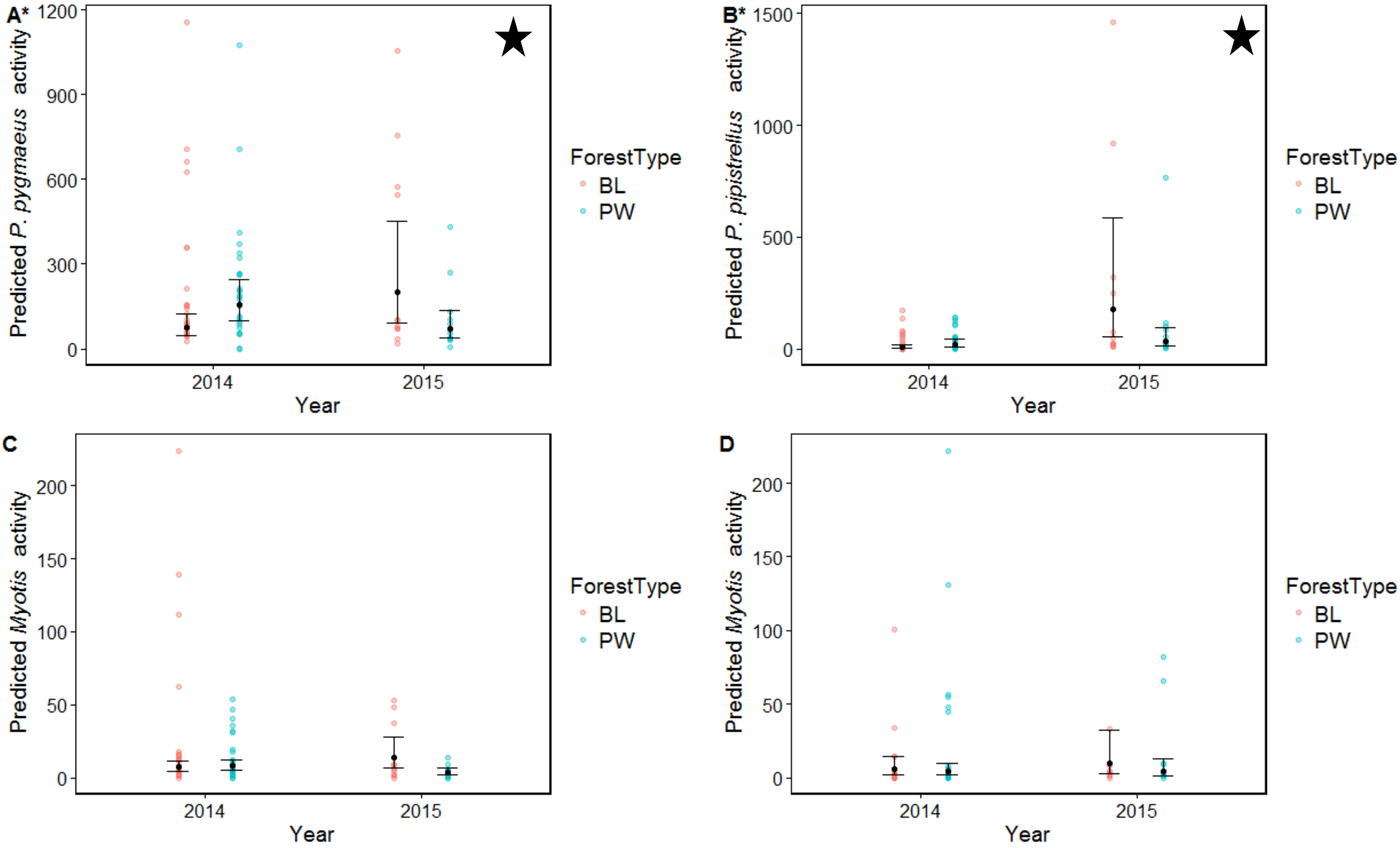

Figure A1.3: Predicted species and genus specific activity in different forest types in different years. Black points and error bars are model predictions plus 95% confidence intervals. Raw data is indicated by red (broadleaf sites) and blue dots (plantations). Star indicate significant interactions between year and forest type.

Myotis and *Nyctalus* activity was similar between woodland in 2014 (and for *Nyctalus* in 2015; Figure A1.3D, Table A1.4), but *Myotis* activity was higher in the broadleaf woodlands in 2015 (Table A1.4, Figure A1.3 C).

The proportion of *P. pygmaeus* to *P. pipistrellus* passes also differed significantly between forest type and year (Table A1.4); in 2014, 81% of *Pipistrellus* activity was *P. pygmaeus* in both forest types reducing to 63% in 2015 (Figure A1.4 A). *Pipistrellus pygmaeus* activity was greater near potential roosts; at sites within 500 m of a building mean predicted passes per night was 170 (116 – 248) but this fell to 50 (27 – 93) passes in sites more than 2.5 km from a building. In sites more than 2.5 km from a building the proportion of *P. pygmaeus* to *P. pipistrellus* was more equal, with 57 (44 – 62) % of *P. pygmaeus* activity compared to *P. pipistrellus* (Figure A1.4 B). In contrast, *Nyctalus* spp. predicted activity was 2 (1 – 6) passes per night in sites within 500 m of a building rising to 19 (5 – 69) passes per night in sites more than 2.5 km from a building.

A1.4.2 Bat social calling and foraging behaviour

For both *Pipistrellus* species, the number of feeding buzzes was highly negatively correlated with social calling (Spearmans Rank test: *P. pygmaeus* df = 74, t = 14.9, p<0.001; *P. pipistrellus*: df = 74, t = 8.4, p<0.001), and with overall activity for both species (Spearman's Rank test; *P. pygmaeus*; df = 74, t=27.8, p<0.001; *P. pipistrellus*: df = 74, t = 27.8, p<0.001). I recorded insufficient feeding or social activity for *Myotis* or *Nyctalus* spp for further analysis.

For both *P. pygmaeus* and *P. pipistrellus* rates of social calling were considerably higher in 2015 compared to 2014. The rate of social calling for *P. pygmaeus* was higher in plantations in 2014, whereas in 2015 it was similar between plantation and broadleaf sites (Table A1.4, Figure A1.5 A). For *P. pipistrellus* there is a reversal in patterns between years with a higher rate of social calling in plantations in 2014, switching to broadleaf woodlands in 2015 (Figure A1.5 D). Whilst the rate of *P. pipistrellus* social calling did not vary with distance to the nearest building, it was higher in sites with a lower abundance of Diptera (Table A1.4, Figure A1.5 B,E). the rate of social calling for *P. pygmaeus* was highest close to buildings and fell by half in sites further from a building (Table A1.4, Figure A1.5 C, F).

A1.4.3 Diptera abundance

Dipteran abundance was higher in 2015 than in 2014, with the largest increase in abundance observed in plantations. Abundance increased from 355 (127 – 989) in 2014 to 615 (127 – 1924) per night in broadleaf sites in 2015 and from 419 (152 – 1154) in 2014 to 837 (268 – 2616) per night in plantation sites in 2015.

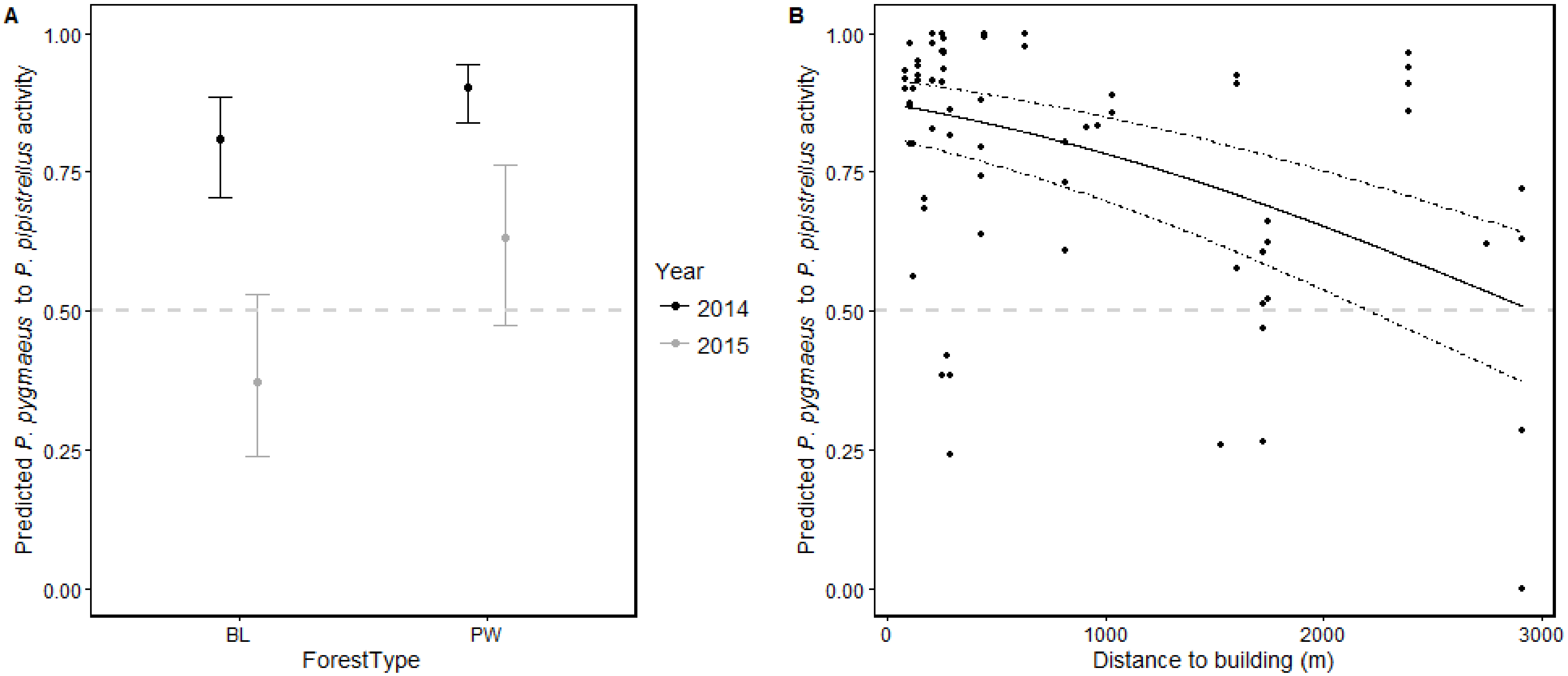

Figure A1.4: Probability of P. pygmaeus activity proportional to P. pipistrellus activity as a function of (A) Forest type and year and (B) distance to potential roost site. (A) Points show mean predicted activity of P. pygmaeus to P. pipistrellus, error bars show 95% confidence intervals. Dashed grey line indicates the proportion at which activity was equal between both species. (B) Raw data on P. pygmaeus activity proportional to P. pipistrellus activity is plotted as black points. Predicted change in the proportion of activity of both species in response to increasing distance from potential roost sites is plotted as the solid black line, the dashed black line represents 95% confidence intervals. The dashed grey line indicates the proportion at which activity was equal between both species.

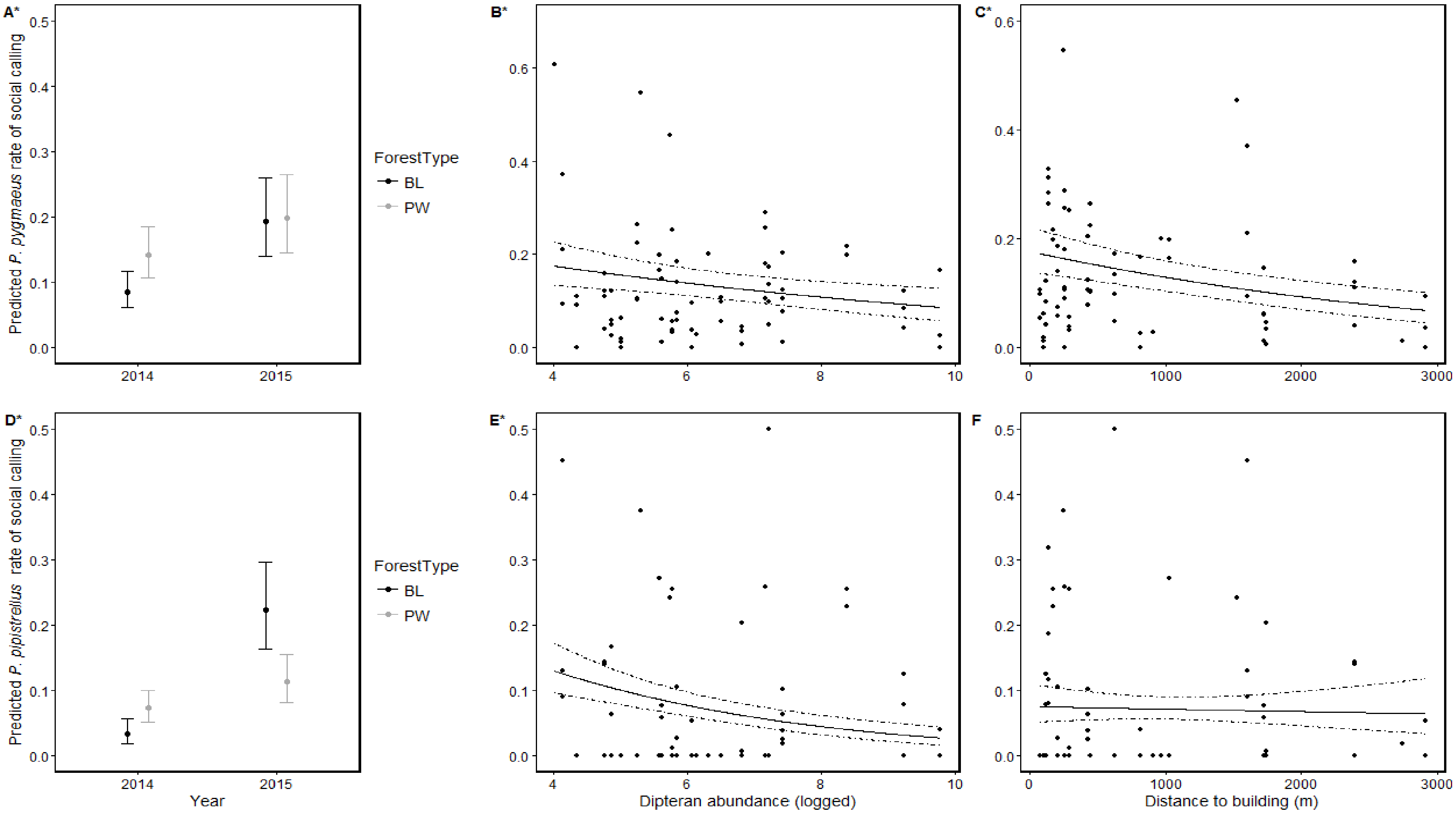

Figure A1.5: Predicted difference in rate of social calling for P. pygmaeus and P. pipistrellus between habitat type (A, D), and the influence of Dipteran abundance (B,E) and distance to potential roost sites (C, F). Black indicates predicted rate of social calling for broadleaf sites, grey indicates predicted rate of calling for plantation sites, points are mean predicted rates, error bars are 95% confidence intervals (A,D). Original data (passes per night) is plotted as black points, black line gives the predicted change in rate of social calling as a function of proxies for food or roost availability. Dashed lines indicate 95% confidence intervals (B,C,E,F).

A1.5 Discussion

Both spring and summer 2015 had lower temperatures than in 2014, with summer 2015 having fewer nights over 8 ^{o}C and more nights with rainfall than in 2014. Unfavourable weather conditions such as rain and low temperatures impose additional energetic costs on bats by increasing thermoregulatory stress (Erickson and West, 2002) particularly for pregnant or lactating females (Racey and Swift, 1981). Bat activity is negatively impacted by precipitation and cool temperatures (Erickson and West, 2002); temperature may determine whether bats forage or not and invertebrate activity (which is reduced at lower temperatures) may determine the length of time which bats forage (Syme et al., 2001). As weather conditions in 2015 were less favourable for bat foraging, this is likely to have affected bat activity and behaviour. No juveniles were captured in 2015 in either broadleaf or plantation sites. Female bats in temperate areas may abort pregnancies or abandon young in unfavourable years (Barclay et al 2004), leading to low juvenile survival for that year, which may explain these results.

A1.5.1 Differences in bat diversity, abundance and composition

Bat species richness did not differ significantly between broadleaf woodland and plantation forest although relative abundance was, on average, 44% higher in broadleaf sites. This may be partly due to capture bias, as flight lines are much harder to identify and block in plantations (pers. obs). The difference in bat abundance between woodland types in 2015 was mainly driven by a large increase in the number of male *P. pygmaeus*. Lintott et al. (2013) found that later in the breeding season male *P. pygmaeus* respond more to the use of an acoustic lure than female *P. pygmaeus,* which may result in capture bias between sexes. However, the same sampling procedure was followed at all sites in both years, which suggests that the change in the composition of the *P. pygmaeus* population between 2014 and 2015 is more likely to be driven by external factors. Males may use suboptimal habitats while females rely on high quality foraging habitats due to increased energetic demands of pregnancy and lactation (Angell et al., 2013; Mackie and Racey, 2007; Nardone et al., 2015). If fewer pregnant or lactating females are present, then lower intraspecific competition may allow male bats to use habitats that are dominated by female *P. pygmaeus* in better years. In cooler, wetter years temperate bats will cluster together in fewer roosts to reduce thermoregulatory costs (Syme et al., 2001). In less optimal habitats more males are tolerated in maternity roosts, possibly because the increased thermoregulatory benefits of more bats in the roost outweigh the cost to lactating females of higher levels of intraspecific competition (Nardone et al., 2015). Therefore, a higher abundance of *P. pygmaeus* males in particular in 2015 may be as a result of reduced intraspecific competition from lactating *P. pygmaeus* females.

The majority of female *Myotis* bats were trapped in broadleaf woodlands although numbers per site were low in both years. Abundance of Diptera was dominated by a single small species, *Culicoides impuctatus,* and numbers of larger prey were similar between both woodland types, suggesting than differences in invertebrate availability did not drive the differences in population composition for *Myotis* species. The lack of suitable roosts near to foraging grounds may be more limiting for *Myotis species; M. nattereri* and *M. mystacinus* usually forage within 3km of roosts and, for *M. nattereri* at least, avoid dense conifer plantations (Bellamy et al., 2013; Buckley et al., 2012; Smith and Racey, 2008). Mortimer (2006) found that *M. nattereri* roosted and foraged in a mixed, lowland pine plantation but these are structurally less complex than Sitka Spruce plantations. Corsican and Scots pine will also form features suitable for roosting bats, something I have found no evidence of in Sitka Spruce (Chapter 6). Both *M. nattereri* and *M. mystacinus* roost switch frequently (Buckley et al., 2012; Smith and Racey, 2008) and the low proportion of broadleaf woodland in the wider geographic area, coupled with the seemingly low likelihood of finding appropriate roost structures in Sitka Spruce, is likely to result in a low abundance of appropriate roost structures for these species. As they have been recorded using bat boxes (Buckley et al., 2012; Mortimer, 2006; Smith and Racey, 2008), increasing bat box provision in plantations may benefit these species, at least for some parts of their life cycle. Furthermore, differences in foraging style (e.g. gleaning; *M. nattereri* compared to aerial hawking; *P. pygmaeus / P. pipistrellus*) may account for these differences as the understory in broadleaf woodlands is more developed than that of coniferous plantations (Ferris et al., 2000)

A1.5.2 Variability of bat activity between habitat types and sample year

Bat activity was highly variable between the two years, particularly in broadleaf woodlands in 2015. In general bat activity was similar or slightly higher in plantations in 2014, and there was less variation between sites. In contrast, activity levels in 2015, particularly for *Pipistrellus* species was higher, and more variable in broadleaf woodlands. In order to maximise the number of sites surveyed, paired sites were only surveyed in one year and it is possible that by chance I may have surveyed high-activity plantations in 2014 and high-activity broadleaf sites in 2015. Further sampling across multiple years would greatly strengthen the results of this comparison.

Alternatively, as suggested for differences in abundance, these patterns in foraging activity may be due to differences in meteorological conditions between the two years. There is evidence from Europe to suggest that *P. pygmaeus* is a migratory bat, which is less sedentary than *P. pipistrellus* (Racey et al., 2007). Individuals have been recorded feeding at offshore wind turbines and light houses (Ahlén et al., 2009), and movements up to 70km have been recorded in Britain (Racey et al., 2007). I recorded nightly movements of up to 40km from foraging, lactating female *P. pygmaeus* (chapter 6), therefore it does not seem unfeasible that *P. pygmaeus* may travel long distances to access favourable foraging sites, possibly responding to locally abundant invertebrate populations (Gonsalves et al., 2013). In years of poorer weather, individuals may use alternative, nearer foraging areas, reducing interspecific competition. Nicholls and Racey (2006) observed radio tagged *P. pipistrellus* foraging a coniferous plantation, while *P. pygmaeus* preferentially used riparian woodland close to their roosts, and concluded that this use of a perceived suboptimal habitat was to avoid interspecific competition with *P. pygmaeus*. Although *P. pipistrellus* appears to have more generalist habitat requirements compared to *P. pygmaeus* (Davidson-Watts et al., 2006; Nicholls and Racey, 2006a), it forages preferentially on pollution sensitive invertebrates (Barlow, 1997) which may be patchy and ephemeral in the landscape. In this study abundance of Diptera was dominated by a single species and it is unlikely that *P. pygmaeus* and *P. pipistrellus* use different habitat types due to dietary differences, as numbers of Psychodidae and Anisopodidae were low even in sites where *P. pipistrellus* activity was high. Differences in habitat use between *P. pygmaeus* and *P. pipistrellus* may be reflect historical interspecific competition ("Ghost of competition past"; Connell, 1980), as I surveyed different sites in the two years, sites surveyed in 2015 may have been those with a locally greater population of *P. pipistrellus* by chance, although this seems unlikely. There is insufficient monitoring in commercial coniferous plantations to determine whether *Pipistrellus* populations of either species are resident year round, and little is known about *P. pipistrellus* / *P. pygmaeus* hibernacula, particularly in the UK. Indeed, the National Bat Monitoring Program (NBMP), a long term bat monitoring scheme in the UK, only has information on summer activity and roost occupancy for both *P. pygmaeus* and *P. pipistrellus* (Barlow et al., 2015). Activity for both *Myotis* and *Nyctalus* spp. was similar between plantations and broadleaf sites in 2014, although there was an increase in *Myotis* activity in the latter in 2015. Again, it is hard to determine whether this is a site level difference or due to different weather conditions between the two sampling years. Because of the marked differences in weather between years, the effect of site identity and weather are confounded, and further sampling across all sites in a single year is required to determine whether the incongruous results are due to spatial differences in the sites surveyed between the two years or a result of changed behaviour in response to weather conditions.

A1.5.3 Differences in social behaviour and foraging behaviour:

I found higher rates of social calling for *P. pipistrellus* at sites with low invertebrate abundance, which is expected if social calling is defensive and territorial over foraging patches (Barlow and Jones, 1997; Middleton et al., 2014). At sites with high invertebrate availability the energetic costs of defending foraging resources is unnecessary compared to sites with few invertebrate (Barlow and Jones, 1997).The high proportion of social calling near roosts for *P. pygmaeus* may be contact calling between females and their newly volant offspring, especially as a radio tracking study in the same area identified a large proportion of buildings within the wider plantation area that contained a substantial (>500 individuals) *P. pygmaeus* nursery colony (Chapter 6). Alternatively, it may be that *P. pygmaeus* preferentially forage closer to the roost, which increases intraspecific competition in these areas.