



Landscape-scale habitat requirements of flower-visiting insects in the
Nene Valley Nature Improvement Area

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Abstract

Recorded population declines of flower visiting insects are a cause for concern. The presence of an abundant and diverse community of insects is essential for ecosystem stability and continued agricultural prosperity. As human populations continue to increase so do the pressures on the natural environment, therefore it is important to ensure pollinator services for the future. Landscape structure may influence the resilience of pollinators in the face of environmental change.

In 2012 a pilot scheme of twelve Nature Improvement Areas (NIA) in England (UK), was created seeking to improve ecological networks through increased landscape connectivity. The Nene Valley NIA follows the course of the River Nene from its source in west Northamptonshire through to Peterborough and covers an area of 41,350 hectares. This thesis evaluates the effects of landscape context on pollinator communities in grasslands within the Nene Valley NIA. Furthermore, the influence of local variables such as floral cover, management and site maturity on insect pollinator abundance and species richness are analysed.

At present landscape-scale studies on insect pollinators, whilst limited, generally fall into two categories: those analysing drivers of distribution in landscape or entirely theoretical models with little overlap of the two. This thesis aimed to address this gap, using statistical analysis of field data to produce spatially explicit models of pollinator distribution. A modelling framework is outlined, applying the Generalised Linear Model (GLM) to abundance and species richness data collected in grasslands within the Nene Valley NIA, ultimately producing habitat suitability maps within a Geographical Information System (GIS).

This study examines data collected from 34 grassland sites between 2013 and 2015 in the Nene Valley NIA. Overall 1692 individuals were recorded, and 103 species observed, analysis revealed a nested community structure. Abundance and species richness of flower visiting insects was significantly correlated with floral cover. Analysis of local scale habitat factors indicated that day-flying Lepidoptera are sensitive to agri-environment schemes, indicating a need to review the current recommendations and systems.

This thesis presents a methodology for producing spatially explicit habitat suitability models for flower visiting insects. This research provides a timely contribution to current methodology, particularly in the context of the emerging ecosystem services framework. The results of the landscape modelling highlight the difficulty in encapsulating resource utilisation and distribution in landscapes and a need for a standardised recording network and open access to data, both ecological and environmental.

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Chapter 1 Introduction

1.1 Introduction

In this chapter the diversity and importance of insect pollinators will be discussed. Causes of decline will be explored and the potential of habitat suitability modelling as a method for examining the landscape-scale requirements for these organisms and its application in conservation outlined. The latter part of this chapter will introduce the project's aims and objectives, and the thesis structure.

1.1.1 Insect diversity

Class Insecta is highly diverse, with early estimates of ~30 million insect species (Erwin, 1982); however, recent estimates give more conservative estimates of 1-10 million (Stork, 2018; Gaston, 1991). Consisting of between 26-29 orders (varying as new classifications and taxonomy come to light), the diversity of insects derives largely from four insect orders: Coleoptera, Diptera, Lepidoptera and Hymenoptera (see Table 1.1) (Gaston, 1991).

Bees, butterflies and hoverflies have been identified as flower visiting insects key to pollination services within the UK and north western Europe (Garratt *et al.*, 2014b; Carvalheiro *et al.*, 2013). In addition, some pollination may be undertaken by moths and some fly (non-Syrphid), beetle and wasp species, although these taxa are generally understudied (Mobbs, 2015). At present in Britain there are 25 species of bumblebee, over 200 described species of solitary bee, over 250 species of hoverfly, 57 (and two vagrant) species of butterfly and 2,500 species of moth (Butterfly Conservation, 2014; Royal Entomological Society, 2014a; 2014b).

Table 1.1 Number of estimated species described per insect Order globally and nationally.

Order*	Described species	Source
Coleoptera	290, 000-370,000	Arnett, 1985; Lawrence, 1982; Southwood, 1978; Hammond, 1974; Arnett, 1967
Coleoptera (GB)	4,100	Amateur Entomological Society, 2014
Diptera	98,000-120,000	Evenhuis, 1989; Arnett, 1985; Southwood, 1978
Diptera (UK)	7,000	The Dipterists Forum, 2014
Lepidoptera	112,000-165,000	Holloway <i>et al.</i> , 1987; Arnett, 1985; Southwood, 1978; Laithwaite <i>et al.</i> , 1975
Lepidoptera (GB)	2559	Butterfly Conservation, 2014
Hymenoptera	100,000-130,000	Arnett, 1985; Brown, 1982; Southwood, 1978
Hymenoptera (GB, aculeate species only)	692	Natural History Museum, 2014

*Great Britain (GB) refers to England, Scotland and Wales and United Kingdom (UK) refers to England, Scotland, Wales and Northern Ireland.

See Appendix 1.1-1.6 for life histories of main groups of bees, hoverflies and day-flying Lepidoptera.

1.2 Insects as pollinators

Insects are believed to pollinate around 78% of wildflowers in temperate regions, providing habitat and resources for a vast number of species (Ollerton *et al.*, 2011). Restricting exposure to flower visiting insects reduces seed set in both wild and crop plant species (Bartomeus *et al.*, 2014; Jacobs *et al.*, 2009). Declines in insect pollinators are likely to lead to declining abundance and diversity of wildflower species (Biesmeijer *et al.*, 2006).

Decreased numbers of insect pollinators may not only cause reduced seed set, but may lead to an increase in self-pollination, which could result in a reduced gene pool and therefore lower fitness (Kearns and Inouye, 1997). Concurrently, a decline in wildflowers may lead to lower pollinator abundance and diversity (see Section 1.3).

1.2.1 Ecosystem services

The dependency and fragility of the relationships between humans and the environment has long been recognised (Costanza *et al.*, 2016; Boyd and Banzhaf, 2007; De Groot *et al.*, 2002). The term “ecosystem services” has been used to describe these relationships and “...are the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. They maintain biodiversity and the production of ecosystem goods such as seafood, forage, timber, biomass fuels...” (Daily, 1997). Ecosystem services have seen a surge in interest in the past decade, with an increasing desire to assign economic values to the various services (e.g.; Costanza *et al.*, 2014; Bagstad *et al.*, 2013; Crossman *et al.*, 2013). The Millennium Ecosystem Assessment (MEA) was set up by the United Nations in 2001 with the aim of assessing how changes in ecosystems may affect human health and well-being (Millennium Assessment, 2014). This led to the creation of the UK National Ecosystem Assessment (UKNEA), which aimed to assess ‘the UK’s natural environment in terms of the benefits it provides to society and the nation’s continuing prosperity’ (UKNEA, 2011). The Economics of Ecosystems and Biodiversity (TEEB) initiative was launched by the European Union in 2007. It intended to compare the economic costs of declining ecosystem services (through the loss of biodiversity) against the costs of better conservation and sustainable land-use (European Commission, 2014). The term ecosystem services represents four broad categories: supporting, provisioning, cultural and regulating services (see Table 1.2) (Mace *et al.*, 2011). As a regulating service, pollination by insects is not only important for crop pollination but also for maintaining plant diversity and abundance (Ollerton *et al.*, 2011). The broad scope of the regulating service highlights the need for a holistic approach to pollinator and ecosystem conservation.

Table 1.2 Ecosystem services by category, products in italics (Mace *et al.*, 2011)

Ecosystems processes		Final ecosystem services (<i>example of goods</i>)	
Supporting services	<ul style="list-style-type: none"> • Primary production • Soil formation • Nutrient cycling • Water cycling 	Provisioning services	<ul style="list-style-type: none"> • Crops, livestock, fish (<i>food</i>) • Trees, standing vegetation, peat (<i>fibre, energy, carbon sequestration</i>)
	<ul style="list-style-type: none"> • Decomposition • Weathering • Climate regulation • Pollination • Disease and pest regulation • Ecological interactions • Evolutionary processes • Wild species diversity 	Cultural services	<ul style="list-style-type: none"> • Wild species diversity (<i>recreation</i>) • Environmental settings (<i>recreation, tourism, spiritual/religious</i>)
		Regulating services	<ul style="list-style-type: none"> • Climate regulation (<i>equable climate</i>) • Pollination • Detoxification and purification in soils, air and water (<i>pollution control</i>) • Hazard regulation (<i>erosion control, flood control</i>) • Noise regulation (<i>noise control</i>) • Disease and pest regulation (<i>disease and pest control</i>)

Pollination of crops by insects was estimated to be worth around £603 million in 2010 in the UK (Vanbergen *et al.*, 2014). Dependency on insects for pollination services varies widely between crop plants. For instances, dessert apples are 85% dependent on insects for their pollination, a service which was valued at £44 million for 2007 (Smith *et al.*, 2011). Oilseed rape, which is only 25% dependent on insect pollination services, was valued at £106 million in 2007 (Smith *et al.*, 2011; see Table 1.3). It is evident that even where low levels of dependency exist, the availability of pollinators is highly important if the market value of the crop is high. In contrast to self-pollination, pollen transfer by insects increases the genetic diversity of plant species, ensuring a more resilient population (Faegri and van der Pijl, 1979). Economics aside, global human nutrition is also highly reliant on insect pollination, crop plants largely or partially dependent on insect pollination accounting for 90% of dietary vitamin C as well as a large proportion of vitamin A, calcium and folic acid (Eilers *et al.*, 2011).

Table 1.3 Estimated crop dependencies on insect pollinators and value from pollination for the UK in 2007 (Smith *et al.*, 2011)

Crop	Dependence on pollinators (%)	Value per annum (£ millions)
Oilseed rape	25	106
Strawberries	45	72
Dessert apples	85	44
Culinary apples	85	43
Raspberries	45	39
Cucumbers	65	22
Tomatoes	25	21
Runner beans	85	16
Plums	65	6
Pears	65	5
Others	5-85	54

It is important to note that the efficacy of individual flower visiting insect species as pollinators varies dramatically and is a relatively new focus of study, particularly in relation to commercial plant species. Garratt *et al.* (2014b) found that bumblebees were significantly more effective at pollinating *Vicia faba* (field bean) than other studied insects (honey bees, mason bees and a hoverfly species -*Episyrphus balteatus*). In the same study, however, it was found that oilseed rape was most efficiently pollinated by all studied species except the hoverfly, *Episyrphus balteatus*. Similarly, Woodcock *et al.* (2013), found that 71.3% of visitations of solitary bees to oilseed rape could result in pollen transfer to the stigma, whilst this was only 34% and 35.1% for honey bees and bumblebees respectively. It follows that presence of a diverse pollinator community may significantly affect yield (Garibaldi *et al.*, 2013; Klein *et al.*, 2003), and the size and quality of fruit. Garratt *et al.* (2014a) found that Gala apples were significantly larger and heavier on trees open to pollination than those hand-pollinated or excluded from pollination.

1.3 Population decline of insect pollinators

There is a growing body of evidence that suggests that the diversity and abundance of UK pollinator populations is in decline (Potts *et al.*, 2010; Biesmeijer *et al.*, 2006). Twenty-three solitary bee, bumblebee and flower visiting wasp species (Ollerton *et al.*, 2014) are now extinct, whilst a further eight bumblebee species are declining rapidly (Goulson, 2003). A 10-year citizen science study indicated that 72% of UK butterflies declined at the monitored sites

(Fox *et al.*, 2011a). The International Union for the Conservation of Nature (IUCN) red list criteria was applied to the 62 species of butterflies, either resident to or regularly breeding in Britain, of which 37% were classified as either Regionally Extinct or Threatened (Fox *et al.*, 2011b).

Despite some indication that the declines in pollinator species richness are slowing (Carvalho *et al.*, 2013), it is important that complacency is avoided due to the importance of pollinators both for biodiversity and for regulating services. Surprisingly little is currently known about insect pollinators, their habitats and dependencies and their interactions with other organisms, and this is often a barrier to appropriate conservation measures (Senapati *et al.*, 2016; Dicks *et al.*, 2015; Bommarco *et al.*, 2013).

1.3.1 Causes of decline: i) Loss of semi-natural habitats

Loss of habitat, in terms of both nesting/oviposition and species rich forage, may be the most significant causative factor in decline of insect populations (Potts *et al.*, 2010). Utilised Agricultural Area makes up 71% of the UK's land cover (Defra, 2015) and therefore changes in agricultural practice can be highly influential.

Increasing human populations inevitably leads to an increased pressure on agriculture to produce food (Vanbergen and The Insect Pollinators Initiative, 2013). The Enclosure Acts 1604-1914 (Parliament, 2017) allowed people to apply (to Parliament) for private ownership/use of land, a move away from the Open Field system where land was used communally, largely for agriculture and grazing. Enclosure resulted in large areas of land being divided among private owners and being hedged/fenced to demonstrate ownership, these smaller plots allowed higher productivity through more intensive farming (Sharman, 1989). Advances in technology led to reduced transportation costs and the introduction of nitrogen fertilisers in the early 20th century, furthering both the profitability and intensification of the enclosures (Thompson, 2008). Surpluses of produce generated capital, and an excess of cheap labour due to enclosures, enabled the industrial revolution, which in turn led to a steep increase in population, creating yet further demands on agriculture (Thompson, 2008).

Modern pressures have vastly exceeded those of the past leading to an agricultural revolution at the cost of native species. Post-war expansion, starting after WWI, led to a desire for greater food security culminating after WWII in the introduction of the 1947 Agricultural Act, offering British farmers guaranteed market price for stock, with the aim of increasing productivity and lowering dependence on imports (Robinson and Sutherland *et al.*, 2002). Mechanisation of agriculture allowed larger field sizes, leading to the removal of hedgerows and the reduction of field margins, in turn reducing plant diversity and creating more homogenous landscapes (Stoate *et al.*, 2009). A move away from traditional practices such as low density grazing and hay making has led to further reduction in grasslands (Robinson and Sutherland, 2002). These significant changes in agricultural practices have been associated with declines in British bee and wasp species, such as a peak of bee and wasp extinctions between 1929-1959 associated with post war intensification (Ollerton *et al.*, 2014).

Through urban expansion, agricultural intensification and other land-use change many areas of habitat have been lost, leading to a reduction in suitable forage and nesting areas for pollinators (Vanbergen and The Insect Pollinators Initiative, 2013). The agricultural revolution of the 19th and 20th centuries, has changed and continues to change, the landscape significantly. From 1930 to 1984, around 97% of species-rich grassland was lost in England and Wales (Fuller, 1987) and in some areas this decline has continued (Lawton *et al.*, 2010). Loss of habitat has not only affected size of patches, but also increased isolation of patches within the agricultural matrix, reducing the chance of recolonization events following extinction within patches (Summerville and Crist, 2001). The existence of small isolated patches of semi-natural habitat, also increases the likelihood of inbreeding depression and a reduced gene pool, resulting in vulnerability to disease and environmental factors (Keller and Waller, 2002). Warzecha *et al.* (2016) found body size of two *Andrena* species to increase with habitat fragmentation. As body size has been positively correlated with dispersal ability it may be inferred that fragmented or isolated habitats select against individuals with lower dispersal ability (Warzecha *et al.*, 2016).

1.3.2 Causes of decline: ii) Pesticides

Pesticides can have many sub-lethal effects on non-target organisms, altering navigational ability, changing feeding behaviours and reducing fecundity and longevity (Desneux *et al.*, 2007). Pesticide usage has increased globally, with the majority of use in developed areas

such as the UK (Wilson and Tisdell, 2001). Whilst for some crops in the UK pesticide usage has declined or levelled off, others have seen large increases such as oil seed rape which has increased from 84% to 190% (as percentage of crop area sprayed: values over 100% indicate multiple pesticide applications) (Defra, 2007). Method of application has also changed with increase of pesticide concentration and quantity, along with the number of applications and the number of pesticides used (Wilson and Tisdell, 2001). Often the full effects of pesticides to the environment are unknown, for example neonicotinoid pesticides, which have been featured heavily in the UK media in recent years (e.g. Johnston, 2016; Carrington, 2016). Neonicotinoids are believed to cause nerve damage in honey bees, reducing their ability to forage and to return to the hive; evidence also suggests that exposure to neonicotinoid pesticides can cause declines of queen production in bumblebee colonies (e.g. Whitehorn, *et al.*, 2012; Cresswell, 2011; Yang *et al.*, 2008; Morandin and Winston, 2003). Uncertainty of the effects of neonicotinoids on pollinators resulted in an EU wide restriction of three neonicotinoid pesticides in 2013 (Zhang *et al.*, 2017); as current pesticide guidelines are inadequate (Decourtye *et al.*, 2013) it is possible that pesticides used in place of neonicotinoids may also have detrimental effects on pollinators.

1.3.3 Causes of decline: iii) Climate change

At present the effects of climatic warming on insect pollinators are unclear (Dormann *et al.*, 2008). Rising mean temperatures could lead to a northward shift of invertebrate populations; evidence suggest this has already impacted some butterfly species. In a study based on existing insect records, Parmesan *et al.* (1999) discovered that of the 35 European species of butterflies investigated, 63% had shifted their range northwards. This range expansion is particularly notable in *Pararge aegeria* (speckled wood), which has shown a considerable range expansion northward since 1915 (see Figure 1.1).

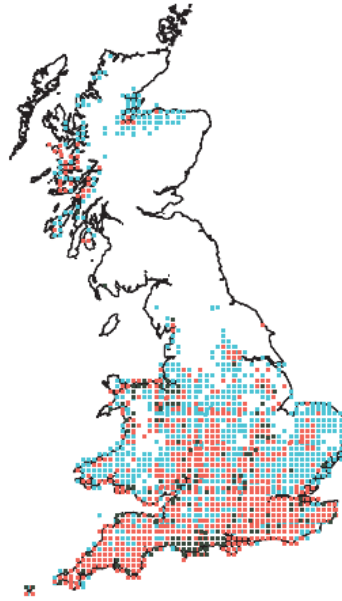


Figure 1.1 Presence of *Pararge aegeria* within 10km x 10km squares, black squares show records between 1915-1939, red 1940-1969 and blue 1970-1997 (Parmesan *et al.*, 1999).

The success of northward shifts of populations is dependent on the availability of suitable habitat for them to move into. Species which are already at their northernmost limit, such as the northern coast of the UK, could face population instability and potential extinction due to increased environmental pressure on the species and its habitats (Parmesan *et al.*, 1999). Similarly, montane species are especially vulnerable to climatic warming, rising temperatures could cause populations to inhabit higher and higher altitudes ultimately leading to extinction, a sequence of events known as the ‘escalator effect’ (Marris, 2007). Another potential effect of climate change is the decoupling of plant-pollinator phenologies. Warming temperatures could lead to a shift in plant or insect life cycles, either: coming out of hibernation, hatching or flowering earlier in the year due to mild winters. It is possible that these temporal shifts may not be synchronised depending on organisms' differing ability to adapt which could lead to misalignment of plant-pollinator interactions (Memmott *et al.*, 2007). For example, if an insect food plant flowers much earlier, when its associated pollinator emerges or comes out of dormancy there may be no suitable forage available. The effects of climates on phenology are currently largely unknown (Hegland *et al.*, 2009), though a study suggests that North American bee species are managing to adapt to changing host plant phenology (Bartomeus *et al.*, 2011).

1.3.4 Causes of decline: iv) Parasites

The parasites of *Apis mellifera*, the honey bee, are relatively well known including *Varroa destructor*, *Nosema ceranae*, *Melissococcus plutonius* and deformed wing virus (e.g. Becher *et al.*, 2014; Forsgren, 2010; Bowen-Walker *et al.*, 1999). Originally a parasite of *Apis cerana*, *Varroa* mites have become ubiquitous with *A. mellifera* (Rosenkranz *et al.*, 2010). It is believed these mites transferred host when *A. mellifera* were transported to the Far East in the early 1900's (Rosenkranz *et al.*, 2010). Through the transportation of colonies and movement of the insects themselves, *Varroa* mites spread rapidly and are found in all parts of the world, except Australia (Rosenkranz *et al.*, 2010). When parasitising *A. mellifera* larvae and pupae, *V. destructor* can significantly reduce the resulting longevity of the adult bee (Rosenkranz *et al.*, 2010). Mites on adults may reduce their body weight, reduce life span and decrease foraging ability (Evison *et al.*, 2012). They also act as vectors for many *A. mellifera* viruses, including: Sac Brood Virus (SBV) and Deformed Wing Virus (DWV), and fungi such as *Nosema apis* (Evison *et al.*, 2012; Rosenkranz *et al.*, 2010).

A recent study in Evison *et al.* (2012) suggests that *Wolbachia*, *Ascospaera*, microsporidians and DWV are likely to be common across many pollinator groups such as solitary bees, bumblebees and hoverflies. This study also highlights that the potential effects of these shared parasites are unknown, the pathologies of these parasites and the ability of species to act as vectors is unobserved (Evison *et al.*, 2012). Graystock *et al.* (2015) found flowers could aid dispersal of parasites, with flowers acting as transmission hot spots, both to parasite hosts and to non-host vectors.

Butterflies may also be affected by parasites, for instance, populations of *Aglais urticae* (small tortoiseshell) declined dramatically between 2003 and 2008, following the introduction of the parasite *Sturmia bella* (Gripenberg *et al.*, 2011). Gripenberg *et al.* (2011) found that survival rates of *A. urticae* larvae were 25-48% lower when *S. bella* was present.

Changes in climate, habitat suitability and general species fitness may also cause individuals to become more susceptible to parasitism. Introduction of further parasite populations or new parasite species also poses a threat, 77% of commercial bumblebee colonies in one study carrying microbial parasites despite being 'parasite free' (Graystock *et al.*, 2013).

1.4 Landscape scale approach to understanding ecological patterns

Key topics in landscape ecology that have been highlighted include: pattern, scale, connectivity, historical land-use and land-use change, sustainability and landscape modelling (Wu, 2013). Understanding how the composition and configuration of habitat within a landscape matrix affects community composition, abundances and temporal dynamics is of vital importance within a conservation context.

Early research into how insect pollinators interact with landscapes mostly focussed on how patch size affects population dynamics (Kareiva and Wennergren, 1995; Rathcke, 1993). Several studies showed that larger patches hosted higher abundances and diversities of the study organisms and that continuous landscapes are better than fragmented ones (e.g. Jennersten, 1988; Bowers, 1985; Shreeve and Mason, 1980). Westrich (1996) elegantly illustrated the problems of fragmented landscapes with the example of *Andrena agilissima*. In southern Germany *A. agilissima* is dependent on the steep, exposed earth sides of old track ways (or hollow ways) for nest sites, yet depends on *Sinapis arvensis* (wild mustard), almost entirely as a food source. *S. arvensis* can only be found in untreated agricultural fields and ruderal habitats, and in landscapes including hollow ways. Hollow ways surrounded by intensively managed farmland do not, therefore, provide for the nutritional demands of *A. agilissima*. Similarly, landscapes where large amounts of forage are provided by extensively managed farmlands, but otherwise do not feature hollow ways, do not provide for the nesting needs of *A. agilissima* (Westrich, 1996). A further example from Williams and Kremen (2007), demonstrated that populations of *Osmia lignaria* isolated from areas of semi-natural habitats are likely to produce fewer offspring and have lower larval survival rates, than those in more connected landscapes. This was of particular importance for populations nesting in farmland compared to those nesting in semi-natural habitat, likely to be explained by the preference of *O. lignaria* for pollen from native plant species.

Steffan-Dewenter *et al.* (2002) produced a seminal paper on the subject, recording the effect of proportion of semi-natural habitat at differing spatial scales for honey bees, bumblebees and solitary bees. The study found that there was a significant positive relationship between

proportion of semi-natural habitat and solitary bee abundance at a 250m scale, whilst honey bees demonstrated a significant negative relationship with the proportion of semi-natural habitats at the 3,000m scale. Bumblebees showed no significant relationships at any of the scales in the study. A similar study found that species richness of hoverflies was positively correlated with landscape diversity at a scale of 250m, yet abundance was negatively correlated with diversity at the 750m scale (Meyer *et al.*, 2009).

Other studies focus on landscape structures rather than composition, such as linear features, patchiness, connectivity, and specific traits such as urban-rural gradients and agricultural management (e.g. Lander *et al.*, 2013; Cranmer *et al.*, 2012; Bates *et al.*, 2011; Jauker *et al.*, 2009).

1.5 Habitat suitability modelling

Habitat suitability modelling is strongly linked to ecological niche theory, the idea that species or individuals will occupy specific areas within a habitat due to resource provision and mutualist, predator and competitor relationships (Hirzel and Le Lay, 2008). If an individual's resource requirements are known, then it follows that where these resource requirements are met one will find suitable habitat for the species in focus. Grinnell (1917) first used the term 'niche' to describe the environmental conditions within which *Toxostoma redivivum* (California thrasher) can exist and the behavioural adaptations which enable it to do so. This was further developed by Salisbury (1926) who explored the climatic influence on the distribution of several plant species including lesser celandine, *Ranunculus ficaria*.

The introduction and popularisation of Geographical Information Systems (GIS) and advanced satellite imagery has enabled the scope of ecological modelling to expand enormously, meaning large areas can be mapped without the need for extensive field work (Guisan and Thuiller, 2005). This means that large-scale studies are now much more viable in terms of time and funding, thus increasing the influence and utility of modelling. Perhaps the most studied area within ecological modelling is predicting the impacts of climatic change, in particular on plant and vertebrate species (e.g. Thomas *et al.*, 2004; Bakkenes *et al.*, 2002; Zimmermann and Kienast, 1999) though invertebrates have received some attention (e.g. Roberts *et al.*, 2011; Fleishman, *et al.*, 2001).

GIS can be used to predict species distributions within a landscape. There are two main approaches, statistical and theoretical (Krueger *et al.*, 2012; Guisan and Thuiller, 2005). The first uses existing species and environmental records; the model will plot the species records and extract the environmental data for that point. The model will then match up areas that hold the same or similar environmental data as the species records and assume that these areas will also be suitable for the species. The second is the reverse approach to the first; where known, the environmental requirements of the species are modelled, where areas carrying more suitable requirements are deemed more suitable habitat. This second approach allows habitat suitability predictions in areas where there are fewer useful records available, or for under-recorded taxonomic groups. The latter is also less demanding on resources as the first approach requires extensive data collection in the field before modelling (e.g. Guisan and Thuiller, 2005; Yamada *et al.*, 2003; Guisan and Zimmermann, 2000).

Tomlinson *et al.* (2018) used a thermoenergetic approach to habitat suitability modelling for a select group of bee species. Fine resolution topoclimatic models were produced from temperature data logged at 960 points, extrapolated across the landscape in relation to habitat information and elevation data. Habitat suitability was inferred through understanding of the thermoenergetic requirements of the study species, that is the maximal temperature at which flower visiting activities will take place and an understanding of energetic expenditure at varying temperatures. This approach has strong potential but was limited by study resource.

Often models are produced but not tested, however, habitat suitability modelling has proven applicable for instance in: grizzly bears (Apps *et al.*, 2016), fish communities (Lamouroux and Oliver, 2015), chin-strap penguins (Warwick-Evans *et al.*, 2018) and the mosquito species *Anopheles arabienis* (Gwitira *et al.*, 2018).

1.6 Taxonomic vs functional traits approach

Across ecology two main approaches are used to group species, either through the taxonomic approach or the functional traits approach. The taxonomic approach traditionally groups species by physical characteristics or morphology, latterly advanced by DNA sequencing allowing groupings to be refined to reflect evolutionary processes. The functional traits approach groups by shared characteristics, such as dispersal distance, clutch size, larval habitat, which effect the fitness and dynamics of the group (McGill *et al.*, 2006). Hoehn *et al.* (2008) for instance grouped bees into functional groups based on flower height preference,

time of day of visitation and body size, to study the effects on functional diversity on crop yield. Eskildsen *et al.*, (2015) grouped butterflies based on overwintering stage, habitat openness, migratory behaviour, habitat specialisation, host plant distribution, body size, host plant specialisation and voltinism. The functional traits approach has strong merits with the potential to reveal biological drivers for the relationship between organisms and environment, however, it is dependent on having extensive information on species biology (Kearney *et al.*, 2010). Frequently studies taking the functional approach will look at a single broad taxonomic group such as bees or butterflies e.g. Eskildsen *et al.* (2015), Martins *et al.*, (2015) Bell *et al.* (2008). Even where the study reviews the main flower visiting insects groups are reduced by functional traits in separation from each other, effectively reducing sample size (Aguirre-Gutiérrez *et al.*, 2016). With a well-established literature for comparison and less restrictive requirements for both existing species literature, and sample size, the taxonomic approach is more appropriate for resource limited studies such as this.

1.7 Grasslands

In the UK grasslands are largely a product of management through livestock grazing and cutting for hay. Species-poor improved grasslands exist where grasslands are managed for high productivity by seeding areas with dominant species such as *Lolium perenne* (perennial ryegrass), managed with selective herbicides and fertilisers for intensive grazing, frequent cutting for silage or amenity use (Crofts and Jefferson, 1999). This thesis focuses on semi-natural grasslands which are less intensively managed and often species-rich due to their ability to support pollinators (see Section 1.6.1) and their conservation priority through decline (see Section 1.3.1 and Section 2.2).

1.7.1 Importance of pollinators within grasslands and surrounding agricultural landscapes

The importance of grassland as habitat for insect pollinators is two-fold, providing habitat for both larvae and adults. Many bee species require grassland for nesting; utilising exposed areas of soft soils, neighbouring hedgerows and trees or exposed banks. As central place foragers it is important that nest sites are within close proximity of floral provisions, for species with small foraging ranges located within highly fragmented landscapes this becomes

even more significant (Bommarco *et al.*, 2010). *Bombus pascuorum* in particular depends on grassland habitats for nesting (Falk and Lewington, 2015; Goulson *et al.*, 2010).

Whilst hoverflies do not demonstrate provisioning behaviours, grasslands may provide both larval and adult habitats, both of which should be considered separately (Jonsson *et al.*, 2015). This presents some difficulty within the landscape ecology framework as records are more likely to represent individuals ‘passing through’ rather than as a strict habitat association (Jonsson *et al.*, 2015). Hoverflies display a diverse range of larval habits, many associated with grassland (Ball and Morris, 2015). Hoverfly larvae have strong associations with herbaceous plants with 54% of UK species living either on or within living plant tissues as many species are phytophagous (Speight, 2015; Meyer *et al.*, 2009). Several species are associated with the nests of aculeate insects although these relationships are poorly understood (Ball and Morris, 2015; Speight, 2015). Several species of the genus *Eristalis* and *Helophilus pendulus* are associated with cow dung in pasture (Speight, 2015). All adult hoverflies require nectar as an energy source and females utilise pollen as a protein source for egg development (Stubbs and Falk, 2002). There is conflicting evidence as to whether adults are selective in their food plant choice, but aphidophagous individuals will show oviposition preferences based on plant host (Alhmedi *et al.*, 2008; Branquart and Hemptinne, 2000; Colley and Luna, 2000).

Similarly, butterflies may utilise grasslands within agricultural landscapes in a number of ways, providing both forage and oviposition habitat. Butterflies show clear plant host preferences, both for larval and adult food sources (Curtis *et al.*, 2015). This is particularly evident in the larval associations between *Maniola jurtina* and grasses, *Pieris brassicae* and *P. rapae*, and cruciferous species and the preferences of thistle species as a nectar source for adult butterflies of the species *P. rapae*, *Aglais io* and *Polygonia c-album* (Thomas and Lewington, 2011). From mark-recapture and harmonic radar studies it is suggested that butterflies have short flight ranges (~100-200m) and are thus heavily dependent on either large areas of habitat to sustain populations or patches within close proximity to enable dispersal within the landscape (Cant *et al.*, 2005; Schneider, 2003; Ricketts, 2001).

Grasslands are thought to act as sources of pollinators within agricultural settings, providing stability to pollination services in otherwise poor landscapes (Öckinger and Smith, 2007). Several studies reveal that bumblebee and butterfly density and species richness decrease with

distances from semi-natural grassland (Ekroos *et al.*, 2013; Öckinger and Smith, 2007). Other studies suggest a positive correlation between seed-set of wildflowers and proximity to semi-natural grassland, although this may be counteracted by higher levels of seed predation in these settings (Jakobsson and Agren, 2014). Provision of semi-natural habitat could be of particular importance in intensive landscapes of mass flowering crops such as oilseed rape and sunflowers. During the flowering period these crops can act as abundant resource and are associated with high densities of bumblebees and *Osmia bicornis* (Holzschuh *et al.*, 2013; Westphal *et al.*, 2003). *Osmia bicornis* nesting in intensive oilseed rape landscapes have been associated with greater brood mortality caused by higher levels of parasitism (Jauker *et al.*, 2012). Furthermore, bumblebee colonies, which initially benefit from high densities of oilseed rape do not show greater reproductive success (Westphal *et al.*, 2009). Riedinger *et al.* (2014) suggest agricultural landscapes should support a combination of both early and late mass flowering crops and semi-natural habitats to ensure support of pollinator life cycles.

1.7.2 Context of lowland grasslands within Northamptonshire

Northamptonshire has one of the fastest growing populations in the UK and is part of the Milton Keynes and South Midlands Growth Area (Centre for Cities, 2016; Northamptonshire BAP, 2009). This growth is expected to continue, putting increasing pressures on the natural environment. Northamptonshire is characterised by mainly agricultural land use, resulting in highly fragmented areas of semi-natural habitats. Whilst in 1928 permanent pasture accounted for 90% of land use in the Nene Valley, by 2000, this reduced to 43% and is likely to be of much lower conservation interest through more intense management (McCollin *et al.*, 2000). Three grassland types were identified by the Northamptonshire Biodiversity Action Plan (LBAP) as conservation priorities: Lowland Dry Acid Grassland, Lowland Calcareous Grassland and Lowland Meadow (Northamptonshire BAP, 2009; see Figure 1.2). Calcareous and acid calcareous grasslands are poorly represented in the NIA as such this thesis focuses on neutral grasslands.

Lowland meadow is a habitat associated with mesotrophic soils and including flood plain meadows. Lowland meadows are characterised by high potential diversity of plant species include rare species such as: *Orchis morio* (green winged orchid), *Platanthera chlorantha* (greater butterfly orchid), *Silene silaus* (pepper saxifrage) (JNCC, 2008). Within Northamptonshire this habitat has been estimated at 300 ha including remnants within local

wildlife sites, SSSIs and other protected areas (Northamptonshire BAP, 2009). This habitat type is found throughout the study area, largely following the River Nene (see Figure 1.2). NVC communities found in the region include: MG4 *Alopecurus pratensis*-*Sanguisorba officinalis* floodplain meadow, MG5 *Cynosurus cristatus*-*Centaurea nigra* grassland and MG8 *Cynosurus cristatus*- *Caltha palustris* flood pasture (Northamptonshire BAP, 2009).

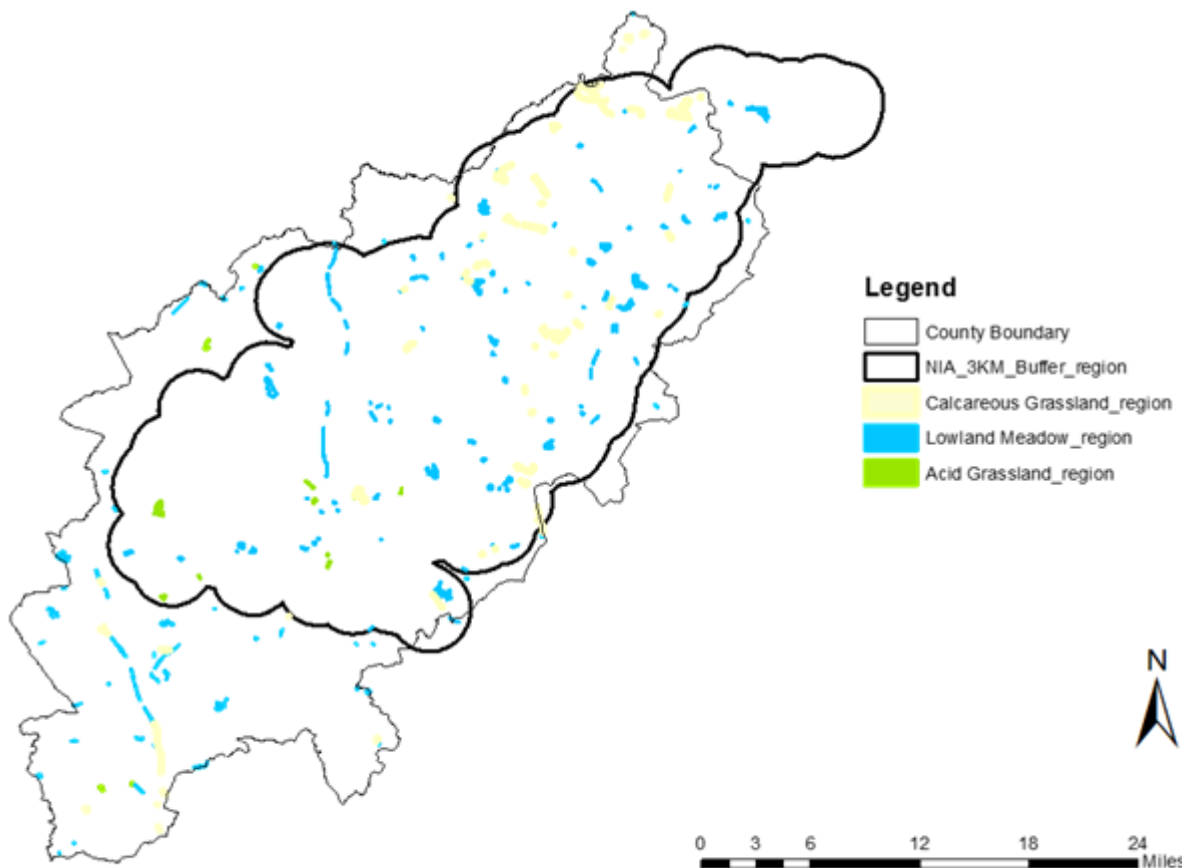


Figure 1.2 Distribution of LBAP grasslands within the Nene Valley NIA 3km buffer zone and the Northamptonshire County boundary (Natural England, 2010).

1.8 Ecosystem service provision in Northamptonshire

Wind-pollinated cereal crops, including wheat, oats and barley, make up the large part of arable land use within Northamptonshire; the County does however host significant areas of crops highly dependent on insect pollination, such as oilseed rape (31,725 hectares in 2013) and field beans (4,362 hectares in 2013) (Defra, 2015). Within the Nene Valley NIA a

preliminary valuation of pollination services has been estimated at £7,764,000 per annum (based on Figures 2010-2014) (Rouquette, 2015b). This value was estimated on the basis of the major insect pollinated crops grown in the region: oilseed rape, field beans, linseed and orchard fruits, and thus does not include all agricultural output or domestic output (from gardens and allotments). Similarly, the value does not take into account the potential added value of crops should optimal pollination services be reached (Rouquette, 2015b).

1.9 The Nene Valley Nature Improvement Area

In 2011 the concept of Nature Improvement Areas (NIA) was introduced in a governmental White Paper (Defra, 2011), based on the Ecological Restoration Zones proposed in Lawton *et al.* (2010). Lawton *et al.* (2010) proposed that these NIAs should be:

- “a shared vision for an enhanced, resilient natural environment exists among local communities, landowners, local authorities, NGOs and government agencies;
- significant enhancements of the ecological network over large areas are planned (and subsequently implemented) by enlarging and enhancing existing wildlife sites, improving the ecological connectivity between sites and/or creating new wildlife sites;
- the surrounding land use is better integrated with the management of the network, so that businesses remain profitable while reducing the pressures upon sites and improving the ability of wildlife to move between them;
- wildlife habitats and underpinning ecosystem processes are restored, so that the ecological network is both better able to cope with pressures and change, and can help to reduce climate change and its impacts; and
- people are inspired by their enhanced experience of the natural world.”

In 2011 a bidding competition was opened by the Department for Environment, Food and Rural Affairs (Defra) for the designation of 12 NIA with a total funding of £7.5 million. A bid for funding was put forward by the Nene Valley NIA Partnership, made up of 22 partners including The University of Northampton, The Wildlife Trust BCN, and Northampton Borough Council. The bid was successful and the Nene Valley was designated an NIA in

February 2012 by Defra. The NIA follows the course of the River Nene from its source in West Northamptonshire through to East Peterborough and covers an area of 41,350 hectares (see Figure. 1.3).

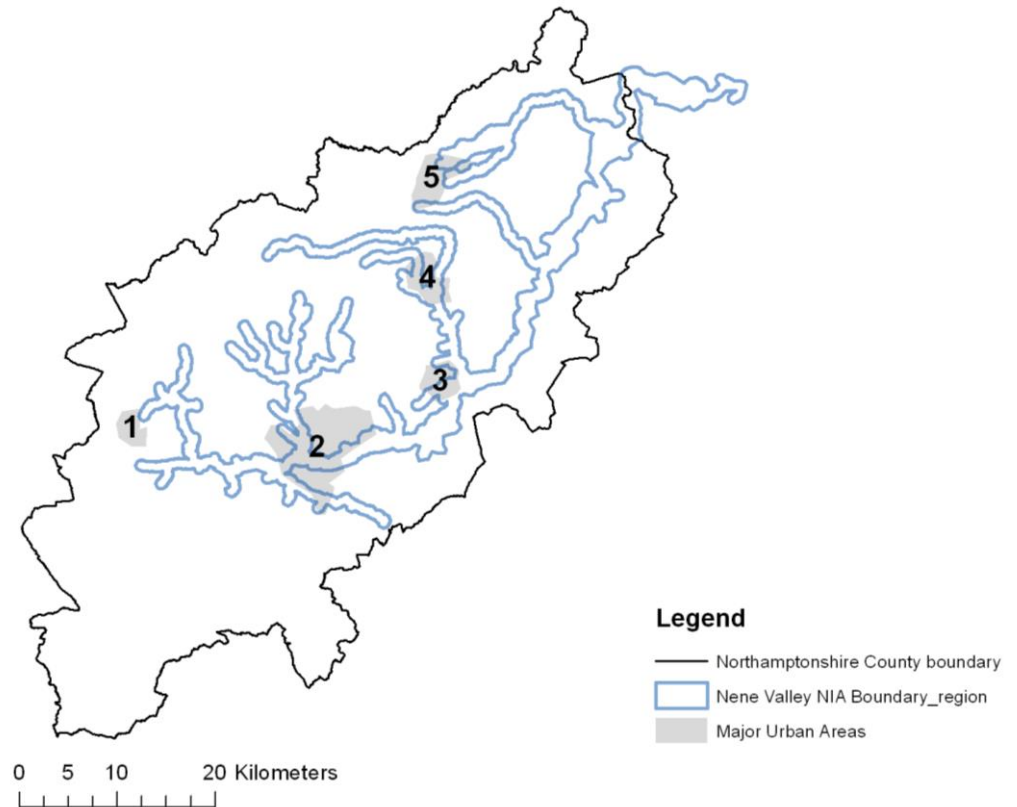


Figure 1.3 Nene Valley NIA boundary with major urban areas in Northamptonshire marked (1= Daventry, 2= Northampton, 3= Wellingborough, 4= Kettering and 5= Corby).

The Nene Valley NIA sought to address five objectives (Natural England, 2014):

- "Objective 1: Growth and development will support, value and benefit the natural environment resulting in a net gain in biodiversity by 2020.
- Objective 2: Enhance public awareness, access and benefits of the NIA in a sustainable and sympathetic way.
- Objective 3: Improve ecological status of the river and enhance ecosystem service provision

- Objective 4: Strengthen the ecological network through effective engagement with farmers and landowners.
- Objective 5: Investigate the potential to market the ecosystem services provided by the Nene Valley."

The University of Northampton achieved funding to work on Objective 5 of the NIA project, with the main foci being:

- Mapping biodiversity
- Exploring ecosystem services
- Investigating potential for payment of ecosystem services within the Nene Valley

As part of the University of Northampton's commitment to the Nene Valley NIA, this project was developed to explore how pollinators are affected by different landscapes within the NIA; ultimately to understand how to improve resilience of pollinator populations within the NIA on the basis of local and landscape factors.

1.10 Aims and objectives

The overall aims and objectives for this thesis are outlined below:

Objective 1: To investigate how floral cover and weather variables effect abundance and species richness of pollinating insects.

- Exploring how season variation in floral cover effects insect pollinators in grasslands.
- Observing the effects of survey conditions on records.

Objective 2: To explore how invertebrate phenologies vary between survey years.

- To gain insight in emergence and flight periods of invertebrates in the NIA

Objective 3: To explore the effects of landscape and local factors on insect pollinators abundance and species richness.

- To gain greater understanding of the effects of both site management and landscape matrix on insect pollinators and the mechanics of these relationships.

Objective 4: To create and explore hot spot mapping for insect pollinators in the Nene Valley NIA.

- To create predictive mapping for pollinating insects in the Nene Valley and explore the effectiveness and applications of these models.

1.11 Thesis structure

Chapter 1 Introduction

The ecological background to the study covering the broad issues within pollinator conservation and introducing the geographical area of study.

Chapter 2 General methodology

A discussion of the data collection and extraction methods both within the field and for landscape and local variables. The field study sites are introduced and the major statistical methods are reviewed in this chapter.

Chapter 3 Investigating species richness and abundance of insect pollinators in the Nene Valley NIA

The structure and composition of flower visiting insects in the NIA are explored through species abundance distribution curves and nestedness analysis. Environmental gradients describing differences between study sites are explored using Principal Components Analysis. Pollinator phenologies are reviewed in the context of the expected patterns.

Chapter 4 Exploring the influence of landscape and local variables on insect abundance and species richness

The effects of both landscape and local variables on flower-visiting insect abundance and species richness are explored through Generalised Linear Modelling (GLM) and multi model inference.

Chapter 5 Modelling pollinator abundance and species richness using GIS

Models are produced within GIS to give heat maps of pollinator abundance and species richness. The models are explored and the applications discussed

Chapter 6 Conclusion

Results from all chapters are summarised and the potential applications of project findings discussed. Any limitations within the study are addressed and future avenues of research presented.

Chapter 2 General methodology

2.1 Introduction

This chapter will outline the field, Geographic Information Systems (GIS) and statistical methods used in this study which will be discussed in further detail in the relevant results chapters. Ethics and health and safety will also be addressed in this chapter.

2.2 Lowland grasslands

The funding of this project required study of lowland habitats within the Nene Valley Nature Improvement Area (NIA). Sites needed to be comparable, in terms of the pollinator assemblages they may support, and cover a broad geographical range within the NIA to permit modelling of the landscape variables. Grasslands were chosen due to their conservation priority status and their geographical spread within the NIA (Nene Valley, 2012). Semi-natural grasslands are a conservation priority within Northamptonshire; identified due to their reduction and degradation in the area (see Section 1.7.2), largely through agricultural practice. Lowland meadow, acid grassland and calcareous grasslands are identified as Local Biodiversity Action Plan habitats, covering 820ha within Northamptonshire County (Northamptonshire BAP, 2009; see Section 1.7.2).

2.3 Study site selection

Grassland sites were identified within the NIA with potential for this study and included a combination of Rockingham Forest Trust, Wildlife Trust, Local Authority, and privately-owned sites. As it was not possible to obtain contact information for all landowners in Northamptonshire this initial identification came through pre-existing lists, local knowledge and research. These sites were then shortlisted based on access, landowner permissions, area of the grassland and geographical location. The sites were selected to try and cover a broad geographical range of the NIA and to reflect typical range of habitat quality in lowland meadows. Once shortlisted sites all sites were visited to review access and suitability, at this stage some sites were excluded due to exhibiting strong wetland habitat features. Detailed habitat data was not available prior to commencement of the study, as such initial site visits prior to the field season were used to guide site selection.

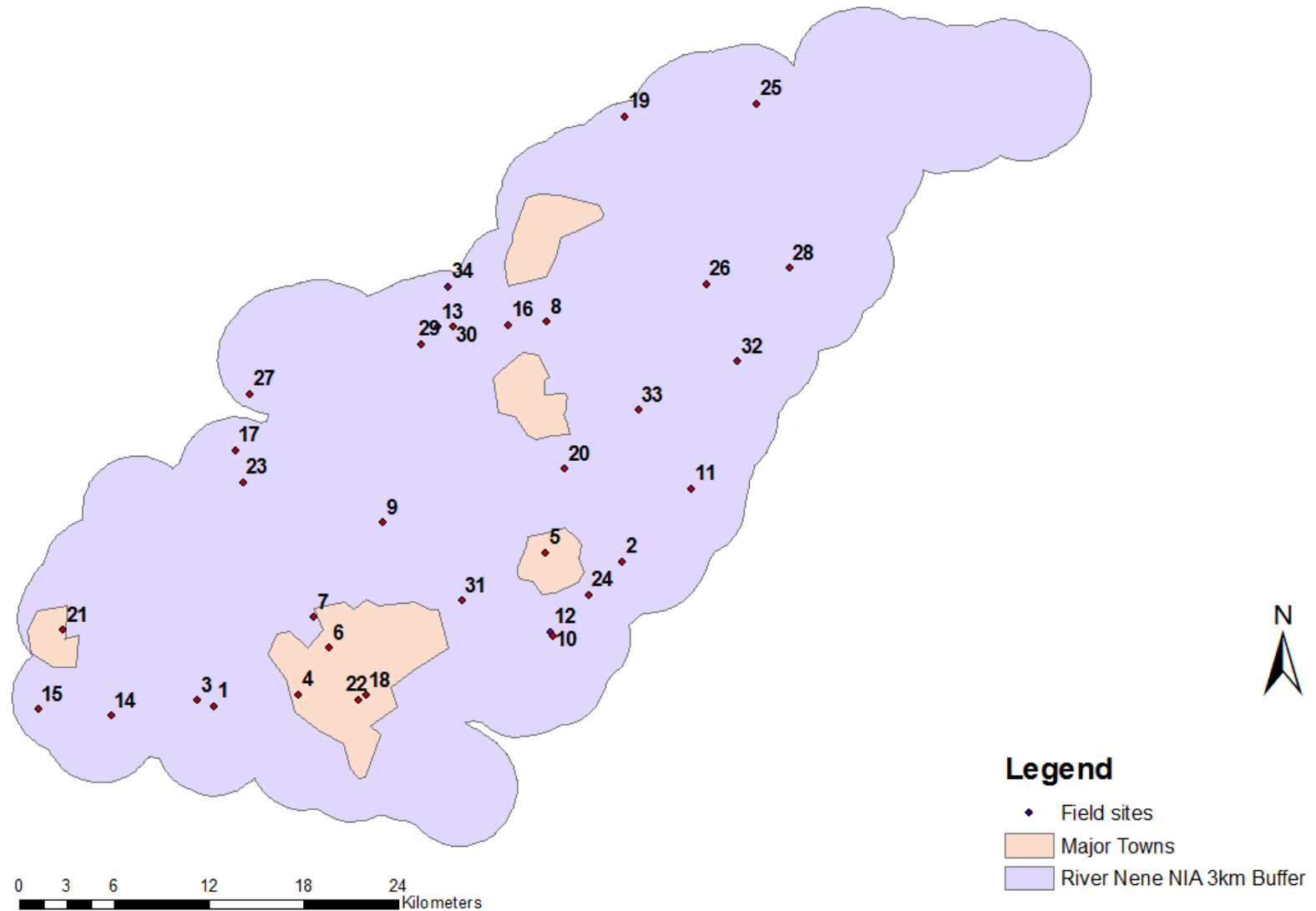


Figure 2.1 Location of field sites within the NIA 3km buffer (see Table 2.1 and 2.2 for map references)

2.3.1 Study sites 2013

Figure 2.1 shows the location of the 34 sites selected for study. Table 2.1 details the 14 sites visited in 2013. Insect surveys were carried out from early April through until late September 2013, with each site receiving a minimum of three surveys throughout the season.

Table 2.1 Field site vegetation, management and locality data for 2013.

Site name	Map reference	Description	Ownership/management	Grid reference
Bugbrooke Meadow	1	Species-rich floodplain meadow.	Owned privately, managed by The Wildlife Trusts	SP672587
Ditchford Meadow	2	Large species-poor meadow.	Owned and managed by The Wildlife Trusts	SP931678
Dovecote Farm	3	Flower dominated floodplain meadow.	Owned and managed privately	SP662590
Duston Meadow	4	Species-poor meadow with low sward.	Owned and managed privately	SP726593
Glamis Meadow	5	Species-poor urban meadow. Wildflower dominated in patches.	Owned and managed by Wellingborough Borough Council	SP881684
Kingsthorpe Meadow	6	Grass dominated urban floodplain meadow.	Owned and managed by The Wildlife Trusts	SP744623
Kingsthorpe North Meadow	7	Grass dominated urban floodplain meadow.	Owned and managed by the Kingsthorpe North Meadows Charitable Trust	SP735643
Newton Field Centre	8	Species-poor floodplain meadow with long flower dominated sward.	Owned privately managed by the field centre	SP884831
Pitsford Water	9	Species-poor meadow with grass dominated sward.	Owned by Anglian Water managed by The Wildlife Trusts	SP779703

Table 2.1 (continued) Field site vegetation, management and locality data for 2013.

Site name	Map reference	Description	Ownership/management	Grid reference
Ryeholmes meadow	10	Species-poor grassland with a short, grass dominated sward.	Owned and managed privately	SP887631
Stanwick Lakes	11	Species-poor grassland with long, grass dominated sward.	Owned and managed by the Rockingham Forest Trust	SP974724
Summer Leys	12	Small species rich grassland area showing signs of early succession.	Owned and managed by The Wildlife Trusts	SP885634
Tailby Meadow	13	Species-poor grassland with long grass dominated sward.	Owned and managed by The Wildlife Trusts	SP814827
Weedon Lodge Meadow	14	Small meadow with long, flower dominated sward.	Owned and managed privately	SP606581

2.3.2 Study sites 2015

After the initial data collection in 2013, a second data collection period was planned for 2015. The intervening period between the two data collection periods was used to identify specimens from the first season, obtain and process GIS datasets, carry-out initial analysis of data and identify and obtain permissions for the 2015 field season. Twenty sites were selected for study in 2015 (see Table 2.2 for descriptions and Figure 2.1 for locations). Insect surveys were carried out on these sites from April-August 2015.

Table 2.2 Field site vegetation, management and locality data for 2015.

Site	Map ref.	Description	Ownership/management	Grid reference
Badby Meadow	15	Species-rich meadow with high floral cover.	Owned and managed privately.	SP560585
Barford Meadow	16	Meadow with a short sward, dominated by grasses and large patches of <i>Sanguisorba major</i> .	Owned and managed by The Wildlife Trusts.	SP858828
Barlow Meadow	17	Species-rich meadow with high floral cover.	Owned and managed privately.	SP685749
Barnes Meadow	18	Large area of rough grassland with long sward.	Owned and managed by The Wildlife Trusts.	SP768593
Bulwick Meadow	19	Large meadow dominated by grasses.	Owned and managed privately.	SP933961
Burton Latimer Meadow	20	Species rich meadow intersected by drainage ditch.	Owned and managed privately.	SP894737
Daventry Country Park	21	Grass dominated species-poor meadow.	Owned and managed by Daventry District Council.	SP576635
Delapre Country Park	22	Grass dominated species-poor meadow.	Owned and managed by Northampton Borough Council.	SP764590
Hollowell Reservoir	23	Short sward, species poor.	Owned and managed by Anglian Water.	SP690729
Irchester Country Park	24	Short sward, species poor grassland.	Owned and managed by Northamptonshire County Council.	SP909657
Kings Cliffe Meadow	25	Grassland with low sward and floral density.	Owned and managed privately.	TL016969

Table 2.2 Field sites for 2015 continued.

Site	Map ref.	Description	Ownership/management	Grid reference
Lyveden New Bield	26	Meadow with high floral density.	Owned and managed by The National Trust.	SP984855
Naseby Meadow	27	Species poor grassland with patchy areas of wildflowers.	Owned and managed privately.	SP694785
Oundle Meadow	28	Species-rich flood plain meadow.	Owned and managed privately.	TL037864
Rothwell Meadow	29	Species-rich dry meadow.	Owned and managed privately.	SP803816
Rushton Meadow	30	A floodplain meadow with a mosaic of wet and dry habitats.	Owned and managed privately.	SP823827
Sywell Reservoir	31	Species-poor grassland with long sward.	Owned and managed by Northamptonshire County Council.	SP829653
Titchmarsh Meadow	32	Grass dominated meadow adjacent to lakes.	Owned and managed by The Wildlife Trusts.	TL004805
Twywell Hills and Dales	33	Grassland formed on limestone quarry spoils. Low floral cover with high density of anthills.	Owned and managed by The Wildlife Trusts.	SP941775
West Lodge Meadow	34	Small area of rough grassland adjacent to planted saplings.	Owned and managed privately.	SP820853

2.4 Field methods

Data were collected on the study groups identified in Chapter One, bees (Apoidea), hoverflies (Syrphidae) and day-flying Lepidoptera. To collect data on insect abundance and richness transect walks were carried out. Transects were 200m in length and 3m wide, covering a total area of 600m² of each site. Transects were split into 10 sub-transects each 20m in length. Each subsection was surveyed for five minutes, in a single timed walk end to end of the sub-transect. Any flower-visiting insects seen on the reproductive parts of the plant were recorded, as well as the species name of the plant. This method was adapted from Kleijn and van Langevelde (2006), broadening the transect width from 2m to 3m to enable greater chance of recording day-flying Lepidoptera (butterfly transects are normally 5m wide - Pollard, 1977), whilst still allowing a narrow enough field of view to record hoverflies and bees. Initial site walkovers revealed few observations of day-flying Lepidoptera on flowers, therefore in the data collection period all day-flying Lepidoptera (on flowers or not) within the transect were observed and their behaviour noted. The transect length was reduced due to the small size of several of the field sites. Points were randomly generated on GIS within the sites to give the transect routes and these were adapted to fit the required transect size (200m) and to represent as much of the site length as possible. Each transect was marked using GPS, enabling reestablishment of the transect on each visit, easily allowing the same area to be surveyed each time as per Pollard (1977). Surveys were carried out between 10am to 5pm as in Steffan-Dewenter *et al.*, (2002) and Pollard and Yates (1993), reflecting the activity period for most individuals. Transects were carried out a minimum of three times (see Appendix 1.6) over the field season (March-September), dependent on weather conditions and access. Sunny days (with temperatures of 15°C or above) with little cloud cover, no rain and low winds were chosen for transect walks (Jauker *et al.*, 2009; Kleijn and Langevelde, 2006; Steffan-Dewenter *et al.*, 2002; Pollard and Yates, 1993). Temperature, wind speed and general conditions were recorded on each visit. Any species that could not be identified in the field were captured and taken to the laboratory for identification.

2.5 Landscape-scale factors

Landscape features were measured and analysed using ArcGIS 10.1. Landscape features were selected based on evidence from the literature demonstrating their influence on pollinator richness and abundance. An information theory approach was taken to assess the effect and magnitude of the landscape variables on species richness and abundance. Data collected in the field was used to assess the effectiveness of this method and to fine tune the model where appropriate.

2.5.1 Spatial scale and resolution

When considering mobile organisms, the spatial scale at which their habitats are studied is important (e.g. Kohler *et al.*, 2008; Kremen *et al.*, 2007; Steffan-Dewenter *et al.*, 2002). Insect pollinators utilise many differing resources within their range for shelter, nesting/egg laying and food sources. Such resources may be widely distributed within the landscape, and therefore it is unlikely that individuals will be restricted to just the immediate area. Bees are ‘central place foragers’, returning to the nest several times in a day to provide provisions for their offspring and thus are often relatively restricted in their dispersal; conversely hoverflies and butterflies do not provide for their larvae but dispersal may be restricted in other ways (Cresswell *et al.*, 2000). Three scales were chosen for this study, to reflect small to large dispersal ability, 250m, 1000m and 3000m and data within these radii were sampled. These scales were chosen on the basis of previous studies, taking into account the mobility of the organisms in question and the limitations of the study (e.g. Meyer *et al.*, 2009; Sjödin *et al.*, 2008; Westphal *et al.*, 2003; Gathmann and Tscharnkte, 2002; Steffan-Dewenter *et al.*, 2002).

GIS layers had to be resampled such that they all held the same cell size for processing. All raster layers were resampled within ArcMap to a cell size of 10m, a compromise between the coarse scale data (25m in Land Cover 2007 (CEH, 2011)) and fine scale (25cm in OS Mastermap (2013)) as a finer resolution dataset would limit processing ability and be beyond the technology available for this project.

2.5.2 Habitat heterogeneity

In landscape ecology the term heterogeneity refers to the composition of a landscape; a heterogeneous landscape is one which is made up of many different habitats or features, a homogenous one being made up of one or a few. As discussed in Chapter 1, land use in the UK has changed dramatically in the last 200 years. This has resulted in a much more homogenised landscape, with large areas of intensively managed agriculture and huge reductions in natural habitats. Previous work has indicated this homogenisation has been linked chronically with a decline in biodiversity, specifically that of pollinators (Meyer *et al.*, 2009; Steffan-Dewenter *et al.*, 2002). It is likely that more diverse landscapes support higher diversity and abundance due to the greater supply and diversity in food and nesting resources (Meyer *et al.*, 2009). In this study the Shannon-Wiener diversity index was used to assess habitat heterogeneity as indicated in Steffan-Dewenter *et al.* (2002). The index (H') is adapted from the Shannon-Wiener diversity index for species diversity:

$$H' = -\sum P_i(\ln P_i)$$

Where P_i is the proportion of each broad habitat area in the study area calculated from the Land Cover 2007 dataset within ArcMap (CEH, 2011).

2.5.3 Proportion of man-made habitat

Generally, urbanisation is perceived to have a wholly negative impact on bee diversity and abundance (Bates *et al.*, 2011; Ahrne *et al.*, 2009; Dauber *et al.*, 2003). Bates *et al.*, (2011) found significantly lower abundance and diversity of bees and hoverflies in urban habitats in Birmingham, UK than in rural areas, most likely limited by availability of floral resources. However, there is indication for some species, particularly cavity nesting bees, that there is a positive association with urban areas, likely due to the presence of suitable nesting habitat in urban walls (Baldock *et al.*, 2015; Sirohi *et al.*, 2015). It is likely that, if a lack of floral resources is the limiting factor of bee diversity and abundance in urban centres, butterfly diversity and abundance may also be limited for the same reason, however, no literature was found to support this hypothesis. Conflicting findings indicate this area requires further study. Information on urban habitats was taken from the Land Cover 2007 data (CEH, 2011),

proportion of urban habitat (the sum of the broad habitat sub classes: Bare, Urban, Urban-industrial and Urban-suburban divided by total area of study radius) was calculated at the 250m, 1000m and 3000m scales.

2.5.4 Habitat connectivity

Connectivity is a term for habitat distribution that gives an organism the ability to travel through a landscape; this may be through linear features or through neighbouring habitat patches within the organisms range (Tischendorf and Fahrig, 2000; Taylor *et al.*, 1993). Regarding the connectivity of habitat patches, two main methods of measurement have been highlighted: Euclidean distance, that is, the measurement of shortest distance between habitat patches; and the more rigorous approach of cost-distance analysis, where habitats are given a weighting based on the permeability of that habitat for a chosen organism/group of organisms (Zeller *et al.*, 2012). For example, a cost distance analysis may lower the connectivity score for two neighbouring patches of woodland if they are bisected by a busy road. Whilst cost-distance analysis best represents how organisms travel through landscapes, there is currently insufficient information on the permeability of differing habitats to pollinators to make the required assumptions (Zeller *et al.*, 2012). To calculate the overall connectedness of grasslands within the landscape distance weighted area value was calculated for the study sites at the three study spatial scales. The formula used was:

$$\sum \frac{p}{\log d}$$

Where p is patch area and d is the distance from the site centre to the patch centre and patches are semi-natural grasslands identified from the Landcover 2007 dataset (CEH, 2011).

Distance from site to patch and patch area were calculated from the Land Cover 2007 dataset within ArcMap (CEH, 2011) for all patches within the sample radii and the sum of the formulae used as a measure of landscape connectivity.

2.5.5 Green linear features

In the context of ecology, a linear feature can be anything from the non-organic e.g. canals, roads, fences, to semi-natural features such as tree lines, hedgerows, ditches, field margins. This study will focus on green linear features, specifically hedgerows. Research indicates that linear features produce both food and nesting resources and potentially act as a visual cue for organisms to navigate (Cranmer *et al.*, 2012; Osborne *et al.*, 2008). The methods of extrapolating green linear features from the Land Use/Cover Area frame statistical Survey database (LUCAS) as proposed in van der Zanden *et al.* (2013) were considered too low resolution for this study. For this research, green linear features are defined as hedgerows and were digitised by overlaying aerial photography with Mastermap boundary data and deleting lines not representing hedgerows, creating a line map of the hedgerows in the study area. Digitisation of hedgerows was carried out by Nicholas Head (University of Northampton). It was not viable within the scope of the project to digitise urban hedgerows due to the density and the inherent difference between species-rich rural hedgerows and species-poor urban hedgerows.

2.5.6 Freshwater habitats

Apis mellifera is dependent on water for the production of honey and the regulation of nest temperature and humidity; this water comes largely from nectar, but the species may also collect water directly (Nicolson, 2009; Haydak, 1970). Sjödin *et al.* (2008) found that bees were significantly affected by proportion of water in the landscape dependent on species, but this link may be due to usage of flowers in riparian habitats rather than presence of water (Sjordin *et al.*, 2008). No literature was found on collection of water by bumblebees and solitary bees in this review, however, there is some anecdotal evidence that bumblebees may collect water (Ferry and Corbet, 1996). Hoverflies are often associated with water, and of the 888 European species, 267 exhibit larval adaptations to allow them to survive inundation by water (Speight, 2015). Larvae of the Eristalini tribe, *Chrysogaster* spp. and *Melanogaster hirtella* develop in water, the larvae of *Eristalis tenax* having developed a long projection or breathing tube, enabling it to breath underwater (Rotheray and Gilbert, 2011; Stubbs and Falk, 2002). On this basis, the possible effects of water at the landscape-scale and insect pollinator

abundance and species richness was measured. OS Mastermap data was sampled at the 250m, 1000m and 3000m scales and the proportion of water calculated.

2.5.7 Proportion of semi-natural habitats

Availability and configuration of semi-natural habitats in landscapes is frequently the basis of landscape pollinator ecology: as providers of pollinators in agricultural landscapes (Beduschi *et al.*, 2018; Nayak *et al.*, 2015; Ockinger and Smith, 2007), as providers of stability in face of climatic change (Papanikolaou *et al.*, 2017) and as an influencer in pollinator movements in landscapes (Cranmer *et al.*, 2012). Several studies have shown that crops in landscapes with higher proportions of semi-natural habitat receive more visits from insect pollinators and/or resulting in a higher seed set (Nayak *et al.*, 2015; Klein *et al.*, 2012). Additionally, presence of semi-natural habitats in agricultural landscapes can improve pollinator population stability in areas where high levels of mass-flowering crops are grown (Beduschi *et al.*, 2018; Riedinger *et al.*, 2014). As the focus habitat of this study, semi-natural grasslands were identified from Landcover 2007 (CEH, 2011) and calculated within ArcGIS at the 250m, 1000m and 3000m scales. In addition, proportion of all semi-natural habitats were identified from the Landcover 2007 dataset (CEH, 2011) and the proportion of these habitats calculated within ArcGIS at the 250m, 1000m and 3000m scales.

2.6 Local factors

Site level data was collected through floral cover surveys, GIS and landowner interviews. Floral cover, site shape, agri-environment scheme, site maturity, restoration and conservation designation were investigated as local scale factors. Binary or dummy variables were used to present information on management, agri-environment scheme, site maturity, restoration, and site designation.

2.6.1 Site Area

Patch area can influence populations in a multitude of ways, effecting: migration rates, extinction rate, overall carrying capacity and species persistence (Hanski and Gaggiotti, 2004). Large patches may support higher numbers, in both species richness and abundance, through a greater availability of resources (although this may be countered by low habitat

quality) and therefore have a higher carrying capacity and attract greater immigration rates (Hanski and Gaggiotti, 2004). In addition larger patches may be subject to passive migration, increased immigration through increased chance of interception (Hanski and Gaggiotti, 2004). Whilst seemingly straightforward, the relationship between area and species richness is still unclear, with conflicting results in the literature (Ewers and Didham, 2006). For instance, Franzén and Nilsson (2010) found patch size did not explain any additional variation in metapopulation dynamics in contrast with the independent effects of local population size (both plants and bees) and habitat quality. At a local scale, patch size has been shown to be positively correlated with visitation rates (Dauber *et al.*, 2010). The effects of site area are investigated in this study, site area was measured using satellite imagery and Ordnance Survey Mastermap (2013).

2.6.2 Floral cover

Floral cover was estimated by recording the number of flowers of each species within each sub-transect. The sizes of flower heads were estimated by averaging that reported in the literature according to Rose and O'Reilly (2006) and Blamey *et al.* (2004). The flower head size and number of flower heads were then multiplied to produce an estimate of floral cover (Tarrant *et al.*, 2013; Meyer *et al.*, 2009; Potts *et al.*, 2006). Floral cover was used in this study as a proxy of forage provision. There is some evidence in the literature that flower head size is positively correlated to nectar provision, suggesting sites with greater floral cover are therefore providing more resources (Harder and Cruzan, 1990).

2.6.3 Grassland management

Grasslands in Britain are largely a man-made habitat, a product of deforestation or drainage for agriculture. As such, management is essential for maintaining both the structure and species composition. Most commonly in a conservation context, aftermath grazing (after a hay cut is taken) is carried out, however other sites will be grazed all year round. Grazing can be important for maintaining plant species diversity, and thus in turn pollinator species richness (Tälle *et al.*, 2016). However, increased grazing intensity can have a detrimental effect through reducing sward height, forage availability and destruction of larval habitat (Van Klink *et al.*, 2016; Börschig *et al.*, 2013). UK grasslands are cut primarily for silage (Withers *et al.*, 2001) and are therefore cut regularly throughout the year. This is the most productive

management but detrimental for conservation (Potts *et al.*, 2009). Grasslands cut for silage are often seeded with productive, and competitive, grass species such as *Lolium perenne* and as such tend to have low diversity. The more traditional hay production method involves a single cut in June/July. This enables flower production and, when clippings are removed from the site after cutting keeps nutrient levels low, thus promoting floral diversity (Crofts and Jefferson, 1999). Information on site management was gathered through landowner interviews and whether the site was mown or grazed was recorded as dummy variables.

2.6.4 Agri-environment stewardship status

There is some indication that agri-environment schemes influence insect pollinator abundance and diversity, but the science remains inconclusive (Kleijn and Sutherland, 2003). This varies dependent on the specific scheme and insect guild in question. Andersson *et al.*, (2013), demonstrated that species richness of bees and hoverflies is more strongly negatively affected on conventional farms in homogenous landscapes than organic farms. Schemes including grassy field margins have been shown to enhance dispersal of *Maniola jurtina* (meadow brown butterfly), suggesting that agri-environment schemes can provide corridors for movement (Delattre *et al.*, 2013). Whether the site was managed under an agri-environment scheme or not was recorded as a dummy variable based on landowner interviews. This is used as a measure of the effects of agri-environment at the local scale.

2.6.5 Conservation status

Within the UK there are several designations of protected areas for wildlife conservation, often aimed at specific target species or habitats. Sites are very rarely designated for their invertebrate fauna, and as such site management specifically for pollinators is likely to be a low priority. Exploring the effectiveness of habitat protection on insect pollinators may indicate that management techniques are currently unsuitable for pollinators or that designation for other organisms in turn has an umbrella effect on these invertebrates. The following designations are considered:

Local Wildlife Sites (LWS): These are designated and protected locally; within Northamptonshire this selection is through a partnership of the Bedfordshire, Cambridgeshire and Northamptonshire Wildlife Trust, local authorities and private landowners. At present

there are approximately 800 LWS within Northamptonshire. Often these sites are privately owned and managed with limited public access. Sites are chosen on the basis of their biodiversity, national priorities, scarcity within the region and threats (Northamptonshire Biodiversity Partnership, 2007).

Local Nature Reserves (LNRS): These are created through application of Local Authorities to Natural England, and sites are selected on the basis of the importance to local: wildlife, geology, environmental education, and leisure (Natural England, 2016c). There are 18 LNR sites within Northamptonshire (Natural England, 2016a).

Site of Special Scientific Interest (SSSI): These are designated by Natural England, SSSIs are sites of national importance on the basis of either exceptional biodiversity, rare species or habitats. Within Northamptonshire there are 57 SSSIs (Natural England, 2016a).

Special Protection Area (SPA): These are protected under Article 4 of the EU Birds Directive. Much of the Nene Nature Improvement Area is part of the Upper Nene Valley Gravel Pits, designated for its population of wintering birds including *Podiceps cristatus* (European Golden Plover) and *Vanellus vanellus* (Northern Lapwing) (Natural England, 2016b). Management of the SPA seeks to maintain the grassland, reed beds, fen and open water habitats and reduce pressures from both planning and disturbance (Natural England, 2016b).

Protected areas are a key tool in terrestrial conservation and are broadly proven as effective, however, their effectiveness and how they deliver their conservation aims is frequently poorly understood (Gray *et al.*, 2016; Geldmann *et al.*, 2013). Site designation was obtained from Natural England (2013) and coded as a dummy variable designated "1" or not designated "0".

2.6.6 Shape

Previous investigation of the effects of habitat shape on plant and invertebrate populations has revealed the influence of edge effect and microclimatic conditions controlled by site shape (Evans *et al.*, 2012). Sites with greater area to edge ratios were found to present higher temperatures in the central areas and in turn host greater grasshopper abundance and foraging activity (Evans *et al.*, 2012). It may follow that a similar relationship could be expected

within other invertebrate groups. However, depending on in-site diversity, the opposite may be true, with hedgerows and margins providing greater forage than field centres with low diversity of floral abundance. As such the effect of site shape on abundance and species richness of pollinating insects was investigated using a measure of shape from Faeth and Kane (1978). Sites were measured in ArcGIS and the following equation applied, where S is shape, P is patch perimeter and A is area:

$$S = \frac{P}{2\sqrt{A\pi}}$$

This index measures how circular a site is and thus in turn indicates edge interactions.

2.6.7 Restoration

Restoration of grasslands may be required due to a change in land use or previous inappropriate management. Research currently indicates that restoration through management (grazing and mowing) may alone be sufficient to create species-rich grassland, however availability of seed may be a limiting factor and as such grasslands may benefit from being sown with wildflower mixes (Pywell *et al.*, 2002). Appropriate restoration has been seen to result in comparable plant and insect assemblages between restored and non-restored grassland sites on landfill sites (Tarrant *et al.*, 2013). Restoration was recorded as dummy variable either restored "1" or not restored "0".

2.6.8 Site maturity

Site maturity may have an impact on both plant species composition and structure within grassland sites (Pywell *et al.*, 2002). The effects of habitat maturity on invertebrate assemblages in woodlands and hedgerows have attracted some research (Deeming *et al.*, 2010; Isaia *et al.*, 2015) but are still poorly understood within grasslands. To investigate the potential effects of habitat maturity on pollinator abundance and species richness, information regarding the site maturity (years since restoration) was gathered from landowners and coded as a dummy variable, restored in the last 5 years or not.

2.7 Statistical methods

Statistical methods were carried out using R: The R Project for Statistical Computing (R Core Team, 2016), unless stated otherwise. The specific statistical methods used are discussed in the appropriate results chapters.

2.7.1 Generalised linear model

Generalised linear modelling was used in this study to explore how the study variables affect the species richness and abundance of insect pollinators in the Nene Valley NIA.

The linear model:

$$y = a + bx$$

describes the relationship between the dependent variable (y) and the independent variable (x) where a and b are parameters. The parameter a describes the intercept and b the degree x changes comparatively with y (Matthiopoulos, 2011). To take account for the stochastic nature of relationships, a stochastic component ϵ is often added to the equation:

$$y = a + bx + \epsilon$$

This approach is dependent on the residuals of the model, the difference between the measured and predicted value of y , being normally distributed. This poses problems for certain types of data, for instance count data, where negative values of y are impossible.

The Generalised Linear Model (GLM) negates the issue of the assumption of residual normality by introducing a link function (h):

$$y = h(a + bx + \epsilon)$$

The link function transforms the mean of y enabling it to be modelled by a linear predictor. The link chosen is dependent on the distribution of the data to be analysed. Common link functions and their indications are shown in Table 2.3.

Table 2.3 Common link functions and their indications.

Distribution	Indication	Link function
Normal	Linear data	Identity
Poisson	Count data	Log
Binomial	Proportion data	Logit
Gamma	Exponential response data	Reciprocal

Count data was used for this study and therefore the Poisson distribution was assumed, using a Log link function (Matthiopoulos, 2011).

2.7.2 Collinearity

Multicollinearity occurs when two or more independent variables are correlated with each other. This collinearity can cause unreliability within the selected models parameter estimates (Zuur *et al.*, 2009; Crawley, 2007). Variance Inflation Factor (VIF) is a measure of how collinearity in a dataset increases the standard errors of a parameter (Zuur *et al.*, 2009). Covariates with a VIF of >3 implies collinearity (Zuur *et al.*, 2009), variables with a VIF of >3 were removed from the model sequentially and the VIFs recalculated until the highest value was <3 .

2.7.3 Spatial autocorrelation

A key assumption of GLM modelling is that the samples are independent of each other. Within landscape ecology, spatial autocorrelation occurs where neighbouring samples occur under such similar conditions as to be considered not true independent samples. Spatial autocorrelation may result in over estimation of the degrees of freedom within the statistical analysis and as such may reduce the reliability of the analysis. The possibility of spatial autocorrelation within the data should be investigated and acknowledged when analysing the results (Hawkins *et al.*, 2007). The package “ape” (Paradis *et al.*, 2004) was used within the R Statistics programme to detect spatial autocorrelation within the residuals of the GLMs investigated in this study.

2.7.4 AIC and model selection

Akaike Information Criteria (AIC) is based on the theory that the Kullback-Liebler distance, that is the measure of distance between the true data values and those predicted by a model, can be used to select the model that has the closest fit (Akaike, 1973). The AIC value is calculated using likelihood:

$$\text{AIC} = -2\log(L(\hat{\theta}|y)) + 2K$$

Where k is the number of estimable parameters and $\log(L(\hat{\theta}|y))$ is the maximum log-likelihood of a model. The AIC does not require knowledge of the true data and parameters and thus holds an advantage over the Kullback-Liebler divergence (Burnham and Anderson, 2003). Calculating AIC values for all possible models allows us to select a model that is believed to fit closest to the truth, based on having the lowest AIC value (Matthiopoulos, 2011).

The AIC value loses its power as a model selection tool when datasets have a small sample size and a large number of parameters. To improve the ability of this method to select models in this instance a second- order information criteria was developed adjusting for the bias created by small sample sizes (Sugiura, 1978; Burnham and Anderson, 2003). This criterion, known as AICc, corrects AIC value based on the number of samples (n):

$$\text{AICc} = \text{AIC} + \frac{2K(K+1)}{n-K-1}$$

Datasets where $n/k < 40$ should use the AICc value rather than the AIC for model selection (Burnham and Anderson, 2003). For this reason, AICc values were used to validate model selection for this project.

2.7.5 Glmulti

The package “glmulti” (Calcagno, 2013) was used within R to carry out automated model selection. The package runs through all possible models based on the variables provided, generating a ranked list based on the specified selection criteria (in this case AICc).

Interaction terms were excluded from the automation and models were limited to a maximum of 4 independent variables to account for the small sample size.

A global model is one which contains all the possible independent variables. The sub-global model (one which contains a reduced number of variables) was used to calculate model fit. This model contained all the independent variables going into the model selection process after collinear variables have been removed. Model fit was assessed through the calculation of $c\text{-hat}$, a measure of model dispersion, that is, how much larger the variance is than the mean. Models are expected to have a $c\text{-hat}$ value of 1, otherwise the model can be considered to be demonstrating over or under-dispersion or lacking fit entirely. This calculation was carried out in the “AICcmodavg” package in R (Mazerolle, 2016). The top model for each model set were further assessed for model fit using diagnostic plots produced in the “boot” package within R.

2.7.6 Restriction of number of independent variables in model

Wisn *et al.* (2008) found a minimum sample size required for accurate predictive habitat suitability modelling to be 30, with datasets falling under this threshold being recommended only for exploratory research. Harrell (2015) recommended a minimum of 10 samples per parameter in a regression model, whilst Austin and Steyerberg (2015) found a minimum requirement of two samples to be sufficient. For this reason, the models were limited to four independent variables.

2.7.7 Model averaging

Model averaging accounts for some model selection uncertainty, that is, the probability that a different model within the top model set would be considered best should model selection be carried out using a different dataset. Models within 2 AICc of the top model are considered to be mathematically equivalent and as such will be considered as part of the top model set. Full-model averaging or “zero method” was used over subset or “natural average method” as a more conservative method to account for model selection bias (Geoghegan *et al.* 2016; Grueber *et al.*, 2011; Burnham and Anderson, 2003). Model averaging was undertaken over the top model set for each dependent variable in the MuMIn package with R (Barton, 2016).

2.8 Ethics & health and safety

A full risk assessment was carried out before surveys began and was approved by the University; all possible measures were carried out to reduce the risk to survey participants. Permission was obtained from landowners/managers prior to surveying and where necessary Natural England was contacted and consent obtained.

Regarding field collecting, where possible, specimens were identified in the field, particularly easily identifiable groups such as butterflies. Where in-field identification was not possible, specimens were collected as per the Invertebrate Link (JCCBI) (2002) taking care to avoid the collection of rare/endangered species. The data from this collection was used both within this project and records were submitted to the local records centre, Northamptonshire Biodiversity Records Centre (NBRC).

Chapter 3 Investigating species richness and abundance of insect pollinators in the Nene Valley NIA

3.1 Introduction

This chapter will explore general seasonal patterns in floral cover and insect pollinator species abundance and richness. Phenology of species within the NIA will be compared with national figures. The effects of weather variables on survey results will be reviewed. Composition of grassland pollinating communities will be examined.

3.1.1 Conservation context of lowland grasslands

An estimated 97% of unimproved grassland was lost between 1930-1984, largely due to conversion of grasslands into high productivity land through post-war pressures for food security and technological advances in agricultural production (Fuller, 1987). Land use change and change in agricultural practice have been associated with declines of a number of taxa and with declines and extinctions of insect pollinator populations within Britain and Europe (Ollerton *et al.*, 2014; Wickramasinghe *et al.*, 2003; Robinson and Sutherland, 2002). Recent evidence suggests that resource provision for insect pollinators stabilized from the 1990s onwards and this is associated with a similar trend in pollinator numbers (Baude *et al.*, 2016; Carvalheiro *et al.*, 2013). A number of threats to lowland grasslands were identified by the JNCC in the national Biodiversity Action Plan: modification of agricultural practice, under-management, fragmentation, air pollution, urban development and inappropriate water management (JNCC, 2008).

3.1.2 Understanding phenologies and population resilience

The term phenology describes the timing of biological events and has piqued the interest of natural historians since the 18th century, with observations of first flowering, first croaking of frogs and toads and first calls of nightingales recorded by Robert Marsham in 1789 (Petanidou *et al.*, 2014; Sparks and Carey, 1995; Marsham, 1789). An understanding of

phenology can give key information about plant-pollinator interdependencies and give insight into potential environmental cues which trigger these events (Forrest, 2015). Temperature is considered to be the most important environment cue affecting plant-pollinator phenologies, however, photoperiodicity, snow melt and carbon dioxide levels have also been indicated as potential drivers (Scaven and Rafferty, 2013; Hegland *et al.*, 2009). Climatic change may cause a plant pollinator phenological mismatch if the species involved do not share a similar speed of response, leading to plants without pollination services or pollinators without food sources or host plants. To date mismatch has been considered through exploration of historical records (Forrest, 2015; Bartomeus *et al.*, 2013; 2011) and through simulations (Rafferty and Ives, 2011) but the area requires further research as findings are conflicting.

3.1.3 Weather conditions and flight activity

Wikström *et al.* (2009) found no significant relationship between wind speeds below five on the Beaufort scale and butterfly species richness and abundance. Furthermore, they found butterfly species richness to be associated with higher temperatures. Gilbert (1985) found a positive relationship between hoverfly activity and temperature. Couvillon *et al.* (2014) found no significant relationship between temperature and honey bee flight distance. Rogers *et al.* (2013) found a negative relationship between wind speed and *Apis mellifera* abundance, whilst solitary bees and *Bombus* sp. showed greater resilience. Kühnel and Bluthgen (2015) found a significant association between temperature and pollinator activity, with species occurring in more intensively managed habitats exhibiting broader thermal tolerances than those in extensive habitats. It may be expected that the effects of temperature and wind speed have differing effects in varying habitats due to the tolerances of communities and species associated with them and the effects of habitat structures on microclimate (Kühnel and Bluthgen, 2015).

3.1.4 Pollinator assemblages and pollination potential

Garibaldi *et al.* (2013) found that wild insects provide a greater contribution to agricultural ecosystem services through increased seed set than honey bees which may only supplement rather than replace this effect. Conversely, Memmott *et al.* (2004) in a network study on bees found honey bees, bumblebees and a limited number of solitary bees to show high numbers of linkages, indicating greater plasticity and potential resilience. Bartomeus *et al.* (2014)

suggests sheer abundances of honey bees may account for losses in pollinator species richness in regards to pollination services.

When plotted, species abundance distributions (SADs) of a community invariably follow a hollow-curve pattern, with few abundant and many rare species (McGill *et al.*, 2007). SADs are of interest for two primary reasons; the ecological drivers behind them and the subsequent effects of them (Matthews and Whittaker, 2014; Morlon *et al.*, 2009; McGill *et al.*, 2007). Species richness has been positively correlated with functional diversity, in turn ensuring the temporal stability of ecosystem service/pollination in grassland pollinator communities (Orford *et al.*, 2016). Winfree *et al.* (2015) found that ecosystem services are more greatly affected by fluctuations in common species (those found to the left of the SAD) than species richness (contributed by the tail of the SAD). Greater understanding of the SADs present in NIA habitats could give insight into both ecosystem service provision, ecological drivers and better targeting of species of importance for conservation.

3.2 Aims and objectives

The aim of this chapter is to explore the data collected within the Nene Valley NIA regarding the abundance, species richness and community structure of pollinators within grasslands and provide context for further study. The following objectives are considered:

3.2.1 Objectives

- **To identify differences in pollinator assemblages between sites**

Differences in field sites, weather conditions and other factors are likely to influence the structure of insect communities between the two years. Species composition and abundances will be explored through species assemblage distributions (SADs) and nestedness analysis. Additionally, Principal Components Analysis (PCA) will be used to identify environmental drivers of differences between sites.

- **To analyse the relationship between floral cover and pollinator abundance**

It is expected that floral cover will have a positive association with pollinator abundance and diversity, with floral cover peaking around midsummer.

- **To ascertain how weather conditions affect survey results**

It is expected that wind speed will negatively affect pollinator abundance whilst temperature will have a positive effect.

- **To identify how insect abundance and richness change throughout the field season**

It is expected that species abundance will increase throughout the field season, peaking around midsummer. Species richness is likely to vary depending on the guild in question, solitary bees are associated with early-late spring, whilst butterflies are more associated with peak summer times.

3.3 Methods

Data was collected at a total of 34 sites, 14 in 2013 and 20 in 2015. Site descriptions and information can be found in Chapter 2. Surveys consisted of 200m x 3m transect walks split into ten 20m sub-sections, each sub-section was surveyed for five minutes. Bees and hoverflies were recorded feeding on flowering plants whilst all day-flying Lepidoptera (DFL) were recorded within the transect and their behaviour recorded. Surveys were carried out under specific conditions (see Chapter 2) and inclement weather delayed survey start dates in both survey years. Surveying started on 13th April in 2013 and 18th April in 2015, concluding on 22nd September in 2013 and 22nd August in 2015. In both years a break from surveying occurred between 19th July- 12th August 2013 and 25th June-1st August 2015 due to the hay cut carried out on field sites. Floral cover within each transect was also estimated (see Chapter 2). Bee records were split into three groups: honey bee, bumblebee and solitary bees, considering the major differences in life history of the groups (see Chapter 1).

3.3.1 Rank abundance curves

Rank abundance distribution plots (otherwise known as Whittaker plots) are frequently used to explore Species Abundance Distributions (SADs) giving insight into evenness and patterns of species abundance (McGill *et al.*, 2007; Magurran, 2005). These plots always display a hollow curve, that is few abundant and many rare species, discussion of the causative factors of this relationship form a large basis of ecological theory (Tokeshi, 1993). A logarithmic scale was used to present relative abundance of species due to the presence of disproportionality high species records for a small number of species (Magurran, 2013).

3.3.2 Nestedness analysis

Analysis was carried out to test for nestedness in the flower-visiting communities recorded in this study. Unlike many commonly used metrics to measure nestedness (Beckett *et al.*, 2014), JDM nestedness analysis (Johnson *et al.* 2013) does not make assumptions on how the input matrices are ordered, input matrices are also binary, more appropriate when considering uneven samples. JDM nestedness analysis and was carried out on a presence-absence species/site matrix using the FALCON package (Beckett *et al.*, 2014) within R, this package

was also used to produce a graphical output to illustrate the network. The resulting normalised temperature compares the resulting temperature output of the matrix against a null model, in JDM a normalised temperature greater than one indicates higher than expected nestedness (Beckett *et al.*, 2014; Johnson *et al.*, 2013).

3.3.3 Flight periods

The field season was divided into equal sections (of nine days), with the diversity and abundance records for each section compiled. To enable comparison only species recorded in both 2013 and 2015 were tabulated. Abundance of each species recorded in each nine-day section were tabulated to help explore the data in terms of sampling strategy and identify trends. Expected flight periods were extracted from key texts for each of the three pollinator groups studied: bees, day-flying Lepidoptera and hoverflies.

3.3.4 Weather records

Weather data was obtained from the Pitsford Weather Station (SP757677) and the mean daily temperature and wind speed during survey times (10:00-17:00 April-September) were recorded. These data were then plotted, and the relationship tested between the abundance and species richness data collected in the field using a Spearman's rank correlation.

3.3.5 Principal Components Analysis

Principal Components Analysis (PCA) was used as a preliminary analysis to identify environmental drivers of inter-site differences. This is in compliment to the more detailed analysis in Chapters Four and Five, which focus on modelling flower-visiting insect abundance and richness using landscape scale variables and local scale variables. Principal Components Analysis was carried out on the landscape and local scale continuous variables (See Table 3.1 and Chapter 2 for details on how landscape data were obtained). R Statistics Programme (R Core Team, 2016) was used to carry out the PCA (variables were scaled and centred within this analysis to aid interpretation). The packages ggplot2 (Wickham, 2016) and ggfortify (Tang *et al.*, 2016) were used to produce biplots. Spearman's Rank analysis was used to test the relationship between the Principal Components and the flower visiting insect abundance and species richness data.

Table 3.1 Abbreviation and corresponding variable description for environmental used in Principal Components Analysis

Vectors/variables
SITEAREA-Area of site
HE-Hedgerow density
SR-Solar radiation
SNH-Semi-Natural habitats
BU-built-up/urban area
WA-weighted area
SNG-Semi-natural grassland
SW-Shannon-Wiener index
FLOCOV-Floral cover
SHAPE- Shape index
W- Water

3.4 Results

3.4.1 Preliminary results

A total of 114 field surveys were carried out over the two field seasons (2013 and 2015), with 1692 individuals recorded and 103 species observed. Overall, hoverflies contributed the greatest species richness over the two field seasons, followed by bees and then day-flying Lepidoptera (Figure 3.1).

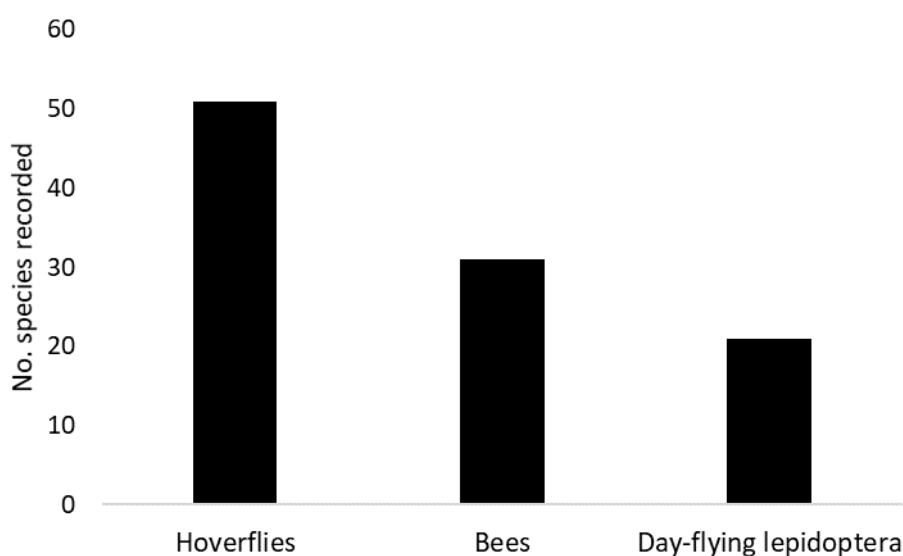


Figure 3.1 Relative richness of species recorded by study group. This figure represents all species recorded throughout the two recording seasons (2013 and 2015)

3.4.2 Insect abundance and composition

Total abundance of insect records and how these records were distributed between the study groups (hoverflies, day-flying Lepidoptera, bumblebees, honey bee and solitary bee) varied greatly between sites in both years (see Figure 3.2). In 2013 the highest abundances of pollinators were found at Pitsford Reservoir and Summer Leys, where records were largely made up of day-flying Lepidoptera (see Figure 3.2). At Glamis, bumblebees made up a greater proportion of the total abundance over the other study insect groups (day-flying Lepidoptera, hoverflies, honey bee and solitary bees). Bugbrooke had the greatest number of recordings of hoverflies in 2013, however no bumblebees or solitary bees were recorded at this site (see Figure 3.2).

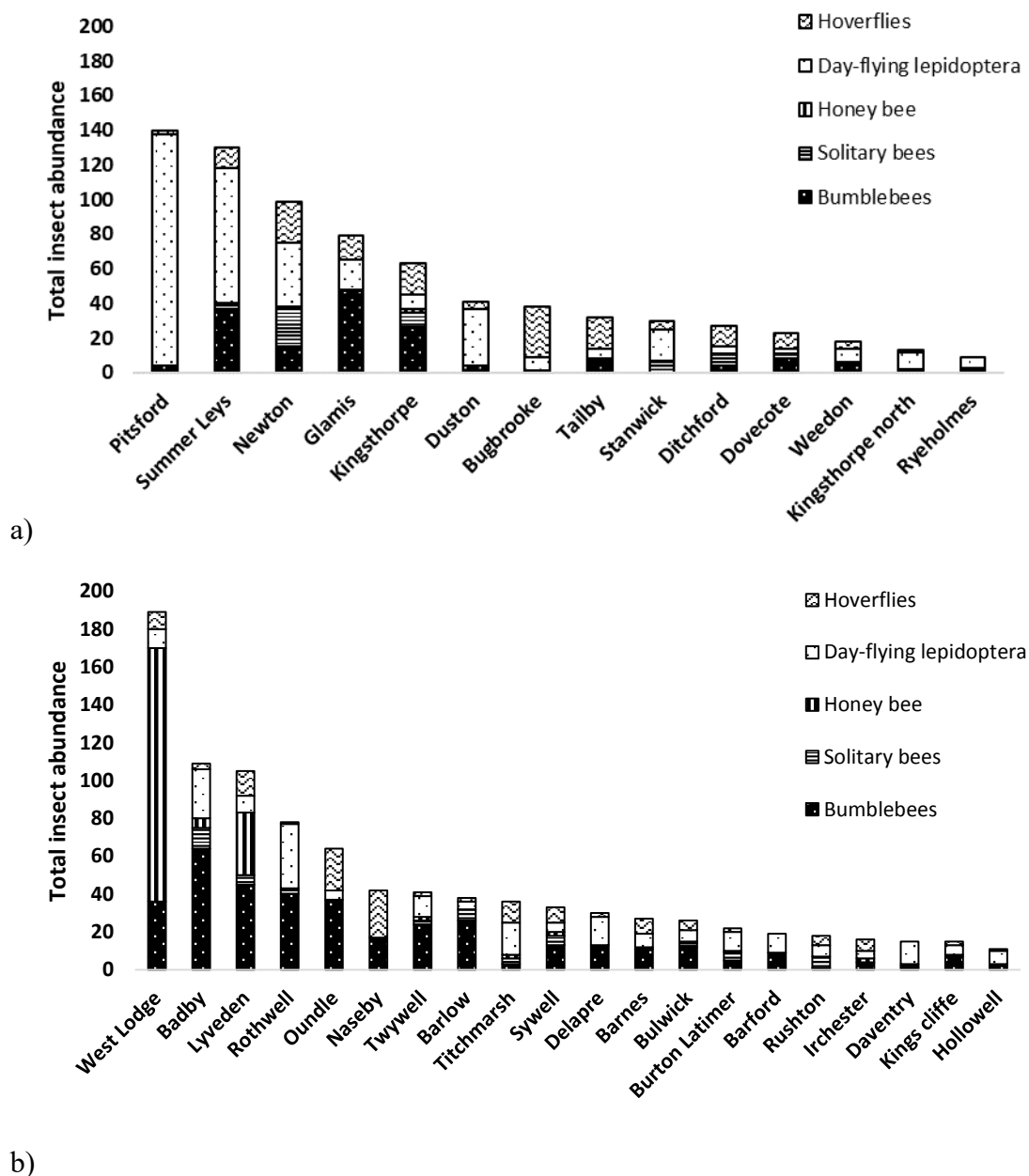


Figure 3.2 Total insect abundance in broad insect groups at each field site recorded in: a) 2013 and b) 2015.

In 2015 the greatest total insect abundance of pollinators was found at West Lodge, Badby and Lyveden (see Figure 3.2). At West Lodge most of the records were of honey bees, similarly at Lyveden there were high numbers of honey bee. Bumblebees made up a high proportion of total insect abundances for several sites including: Badby, Barlow, Oundle, Rothwell and Twywell. Hoverflies and solitary bees can be seen to be making a smaller contribution to total abundances at all the field sites.

3.4.3 Floral cover and floral species richness

In both survey years, 2013 and 2015, Spearman's Rank Correlation showed floral cover was significantly strongly correlated with flower species richness (see Table 3.2)

Table 3.2 Spearman's Rank Correlation of floral cover and flower species richness in 2013 and 2015

Year	Correlation statistic	Species richness
2013	r	0.73
	P	4.79e-10
2015	r	0.75
	P	5.03e-12

3.4.4 Floral cover and insect species abundance and richness

In both years floral cover peaked in early-mid July, hay cutting regimes led to very low cover in late July-early August before reaching a second, lower peak, mid-August. Figure 3.3 shows a strong positive relationship between floral cover and number individual insect records per site visit. A similar relationship can be seen in Figure 3.4, which shows a strong positive relationship between floral cover and number of species recorded per site visit.

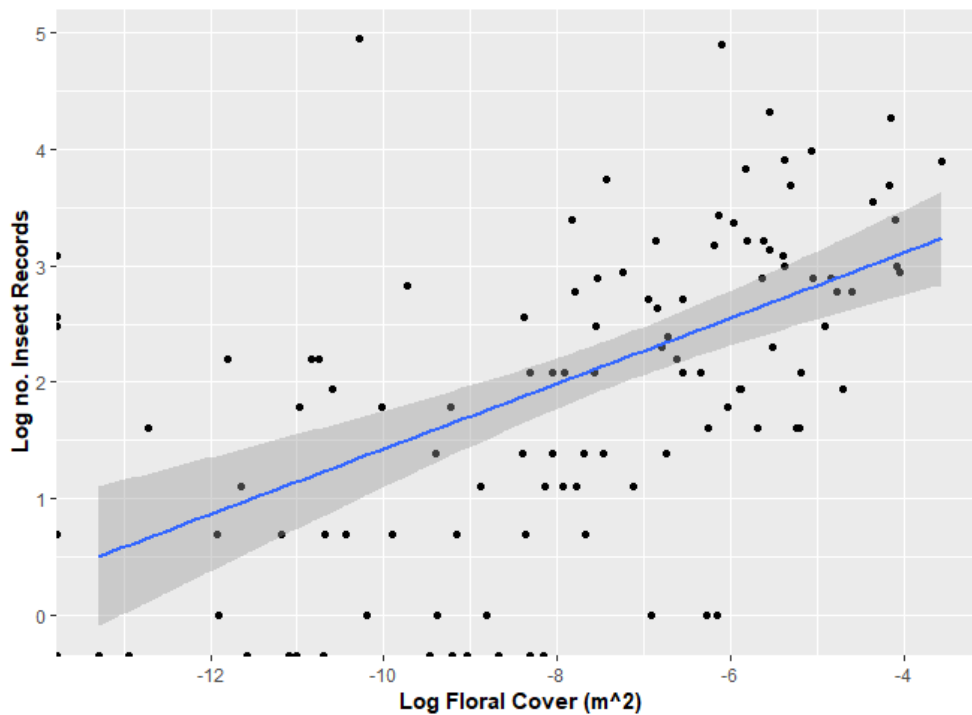


Figure 3.3 Flower visiting visitor counts against floral cover for all transects carried out in 2013 and 2015. Line of best fit represents linear regression and confidence is provided by standard error (Linear regression model, adjusted $r^2 = 0.12$ $P = <0.01$).

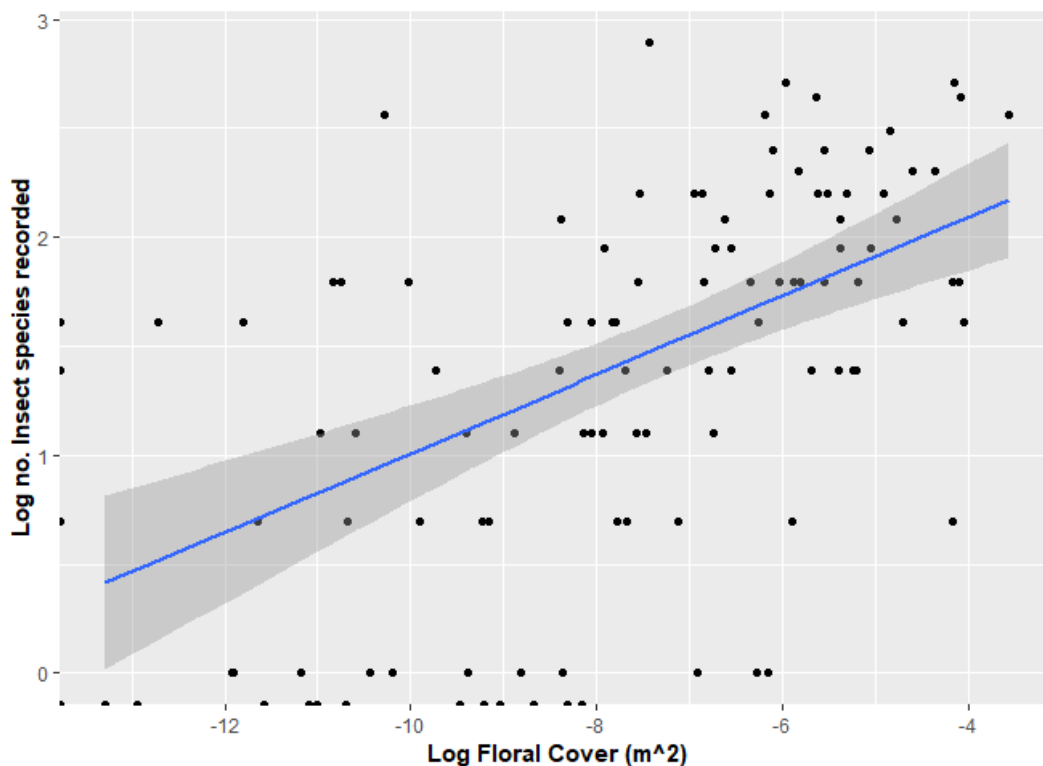


Figure 3.4 Flower visiting insect species richness against floral cover from site all site visits in 2013 and 2015. Line of best fit represents linear regression and confidence is provided by standard error (Linear regression model, adjusted $r^2 = 0.20$ $P = <0.01$).

Spearman's Rank Correlation was carried out between the floral cover data and flower visiting insect abundance and species richness at all site visits. Floral cover was found to positively correlated with both abundance ($r= 0.62$) and species richness ($r=0.64$) at the 0.01 confidence level (Table 3.3).

Table 3.3 Spearman's Rank Correlation of floral cover and flower visitor abundance and richness values from all site visits (2013 and 2015)

Measure	r	P
Abundance	0.62	<0.01
Species richness	0.64	<0.01

3.4.5 Weather records and species abundance and richness

The Spearman's Rank Correlation showed no significant relationship between temperature and wind speed with abundances and species richness recorded in 2013 and 2015 (see Table 3.4).

Table 3.4 Spearman's Rank Correlation of weather variables and abundance and species richness 2013 and 2015.

	Correlation statistic	Abundance	Species richness
2013			
Temperature	r	0.369	0.247
	P	0.145	0.340
Wind speed	r	-0.344	-0.324
	P	0.177	0.205
2015			
Temperature	r	0.165	-0.262
	P	0.574	0.365
Wind speed	r	-0.093	0.102
	P	0.752	0.729

3.4.6 Environmental gradients

Principal Components Analysis was used to explore the variation in the environmental variables between sites. Table 3.4 provides a key to aid interpretation of the PCA biplots in Figures 3.5, 3.6 and 3.7. The PCA analysis on in-site continuous variables and landscape variables recorded at the 250m scale indicates that 43.2% of inter-site variation is described by the first two principal components (Figure 3.5). The first principal component is most strongly associated with floral cover, semi-natural grassland, semi-natural habitat, distance weighted area and Shannon-Wiener Index (Figure 3.5). The biplot indicates that semi-natural grassland, semi-natural habitat and Shannon-Wiener Index are highly collinear and that areas which score highly in these variables may be expected to have lower levels of floral cover. The second principal component is characterised by positive relationship with site area, hedgerow density, solar radiation and proportion of urban area and a negative relationship with proportion of water and shape index. The biplot indicates high similarity between urban area and hedgerow and between site area and solar radiation.

Table 3.5 Descriptors for vector and point data in figures 3.5, 3.6 and 3.7

Vectors/variables	Points/sites		
SITEAREA-Area of site	1-Badby	13-Naseby	25-Kingsthorpe North
HE-Hedgerow density	2-Barford	14-Oundle	26-Kingsthorpe
SR-Solar radiation	3-Barlow	15-Rothwell	27-Summerleys
SNH-Semi-Natural habitats	4-Barnes	16-Rushton	28-Ditchford
BU-built-up/urban area	5-Bulwick	17-Sywell	29-Tailby
WA-weighted area	6-Burton Latimer	18-Titchmarsh	30-Glamis
SNG-Semi-natural grassland	7-Daventry	19-Twywell	31-Newton
SW-Shannon-Wiener index	8-Delapre	20-West Lodge	32-Stanwick
FLOCOV-Floral cover	9-Hollowell	21-Weedon	33-Pitsford
SHAPE- Shape index	10-Irchester	22-Bugbrooke	34-Ryeholmes
W- Water	11-Kingscliffe	23-Dovecote	
	12-Lyvedon	24-Duston	

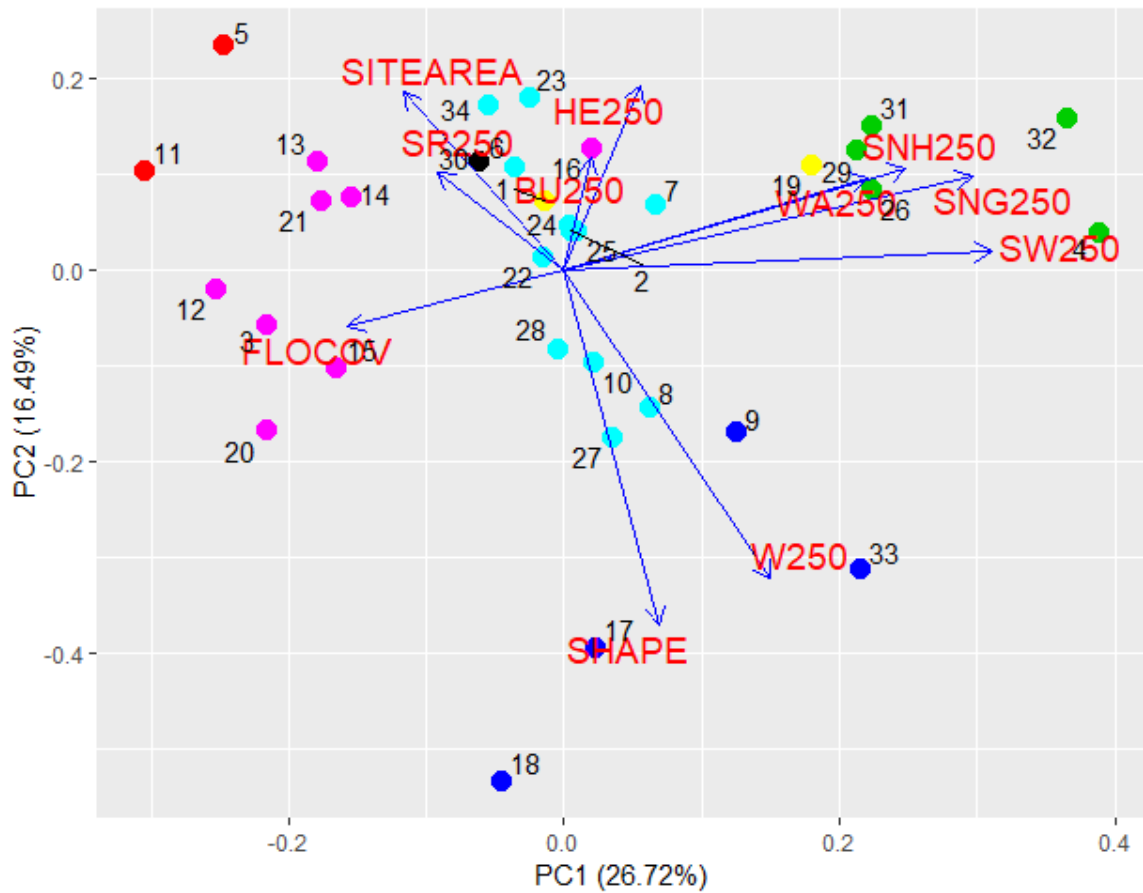


Figure 3.5 PCA Biplot showing first two principal components. Vectors represent environmental variables (in-site and landscape variables at 250m) and points represent field sites. Groupings of sites are colour coded and group membership was determined by UPGMA clustering of Euclidean distances between the loadings on the first seven PCA components

PCA analysis on the in-site and landscape variables recorded at the 1000m (Figure 3.6) scale explained 36.07% of inter-site variation on the first two principal components. Hedgerow density, weighted area, shape, water, Shannon-Wiener and proportion of semi-natural habitat were most closely related with the first principal component in a positive direction. Proportion of urban area, semi-natural grassland and solar radiation were positively associated with the second principal component. Site-area and floral cover were negatively associated with both the first and second principal components.

At the 1000m scale Shannon Wiener Index explained the greatest amount of inter-site variation on principal component one, this variable was closely aligned with the weighted area value, again both of which were calculated from the LandCover 2007 dataset. The proportion of water at this scale was aligned with the proportion of semi-natural habitats indicating that landscapes with higher surface water, such as the gravel pits within the Nene Valley are associated with higher availability of semi-natural habitats.

Proportion of semi-natural grassland was opposite to site area and floral cover at this scale, again this may reflect the relationship observed at the 250m scale, that flower rich habitats occur in isolation of other grassland areas.

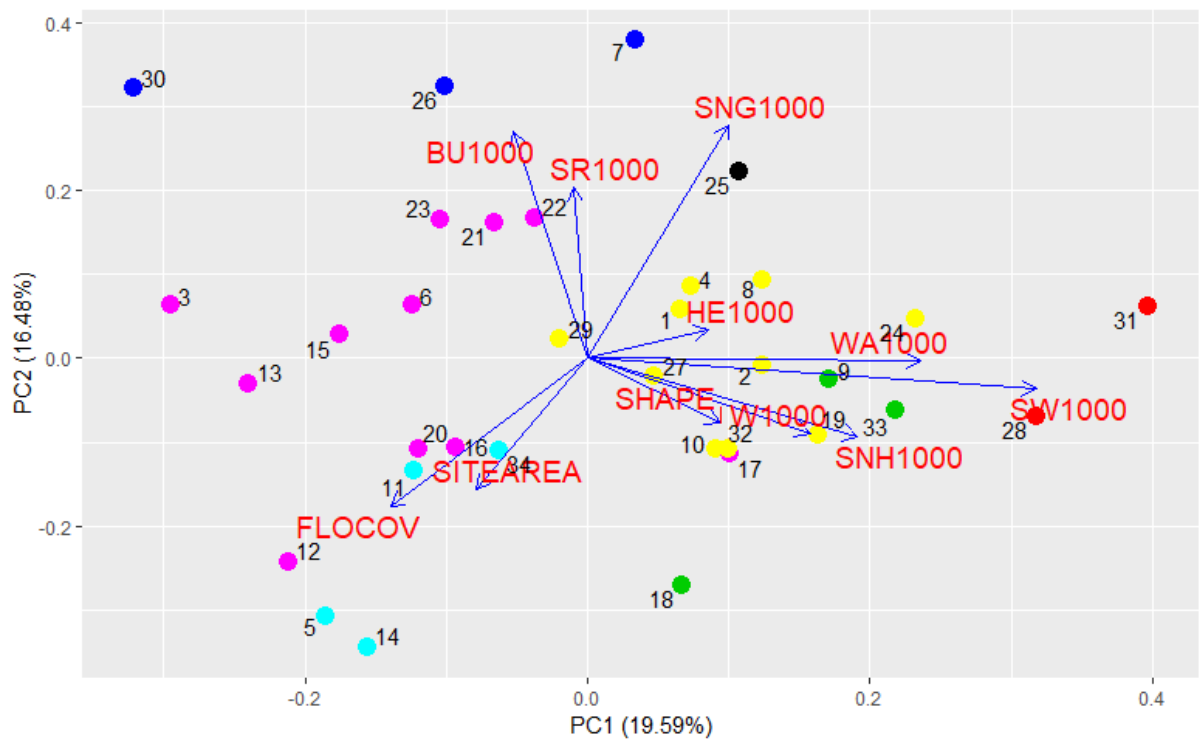


Figure 3.6 PCA Biplot showing first two principal components. Vectors represent environmental variables (in-site and landscape variables at 1000m) and points represent field sites. Groupings of sites are colour coded and group membership was determined by UPGMA clustering of Euclidean distances between the loadings on the first seven PCA components

PCA analysis on in-site and landscape factors recorded at the 3000m scale described 43.11% of inter-site variation in the first two principal components (Figure 3.7). The first principal component was associated with proportion of water and urban area in the positive direction

and hedgerow density and semi-natural habitat in the negative direction. Solar radiation and floral cover were described negatively by component one and positively by component two. Weighted area, semi-natural grassland and site area were negatively associated with principal component one and two. Shannon-Wiener Index was positively associated with principal component one and negatively associated with principal component two. The shape index was positively associated with both principal component one and two (Figure 3.7).

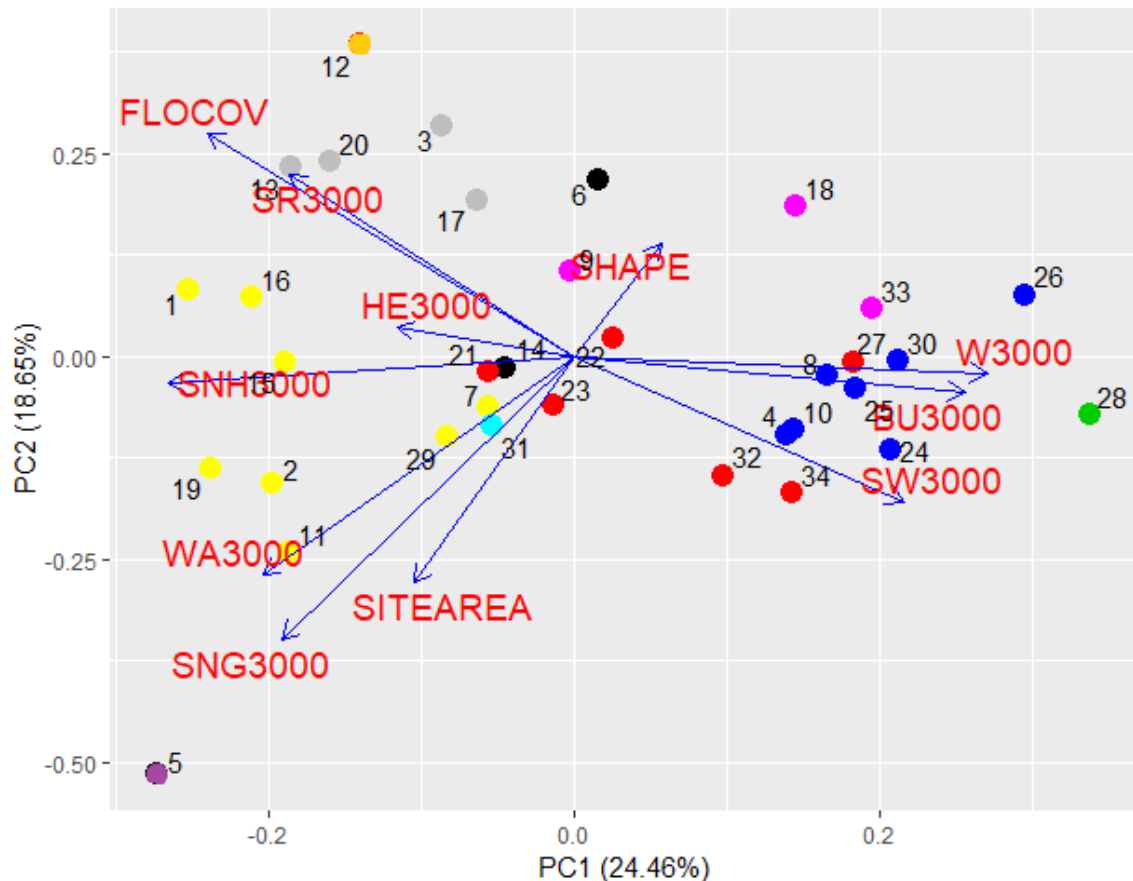


Figure 3.7 Vectors represent environmental variables (in-site and landscape variables at 3000m) and points represent field sites. Groupings of sites are colour coded and group membership was determined by UPGMA clustering of Euclidean distances between the loadings on the first seven PCA components

The principal component scores (components one and two) for each spatial scale were correlated against the abundance and species richness values for the flower-visiting insect groups recorded (bees, hoverflies and day-flying Lepidoptera) (Appendix 1.9). Principal component one, at the 1000m scale, was found to be significantly correlated with the bee abundance data ($r=0.399$, $P=0.019$). Principal component two, at the 3000m scale was found to be significantly correlated with the bee abundance data ($r=0.343$, $P=0.047$). No other

significant correlations between PC1 and PC2 were observed across the differing scales, species groups or recording metric (see Appendix 1.9).

3.4.7 Species abundance distributions

Plotting total observations against species ordered from highest frequency recorded to lowest as in the Whitaker plot (Figure 3.8) demonstrates a distinct curve. The most frequently observed species included: *Bombus lapidarius*, *Maniola jurtina*, *Apis mellifera*, *Bombus pascourum* and *Thymelicus sylvestris*. The tail to the right of Figure 3.8 is largely made up of individual species recorded only once, species here include: *Nomada ruficornis*, *Eristalis hybridus* and *Tyria jacobaeae*.

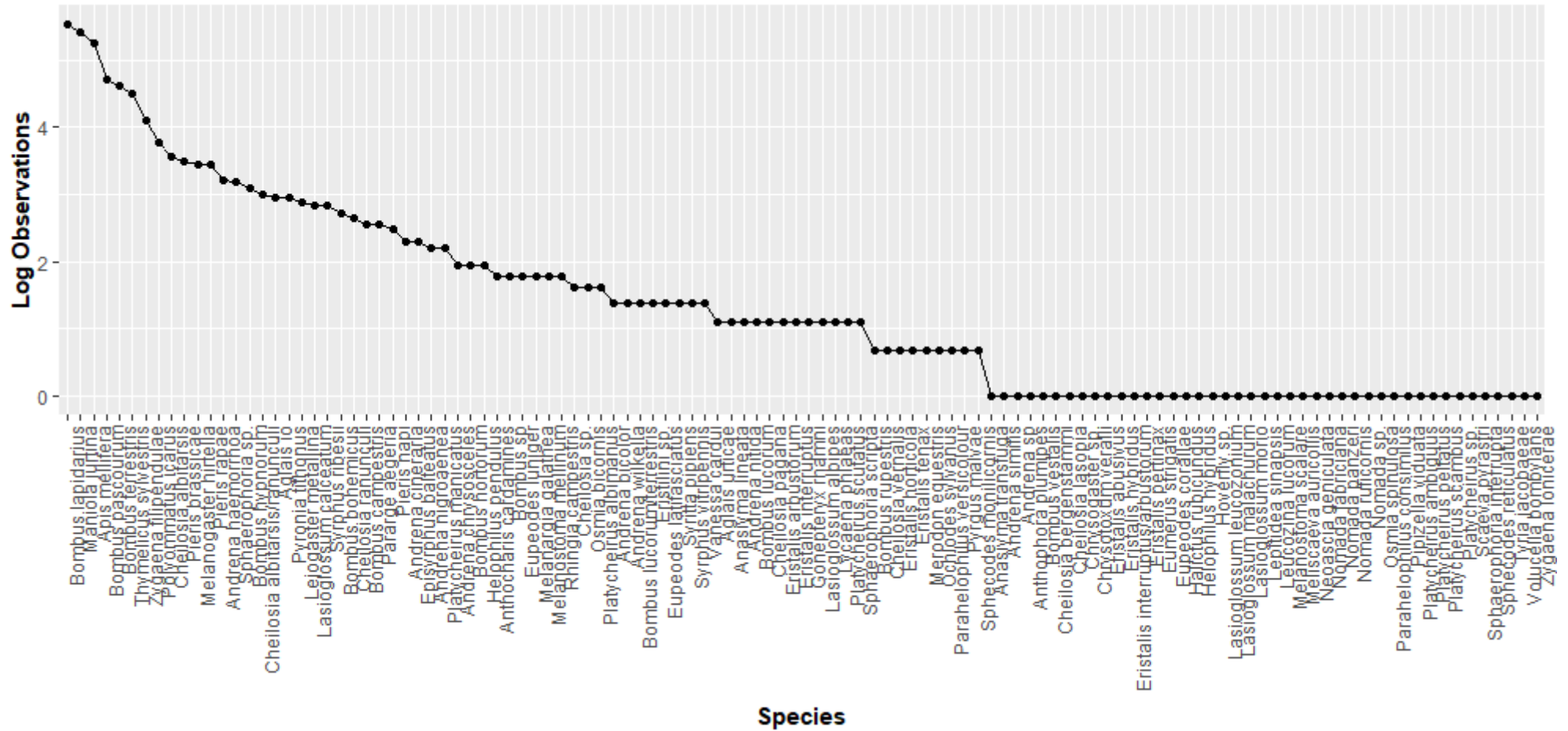


Figure 3.8 Whittaker plot of all flower visitor data collected in 2013 and 2015.

3.4.8 Nestedness

JDM analysis of nestedness carried out revealed higher than expected nestedness (JDM Normalised Temperature= 1.159603, P-Value = 0.01) in the flower-visiting insect communities recorded at sites. The site-species matrix (Figure 3.9) ranks sites based on number of species and ranks species on the number of sites they have occurred at. The matrix demonstrates the 'top-left' curve associated with nestedness, where sites with many species occur at the top of the figure and sites with fewer species generally represent a subset of the more diverse sites.

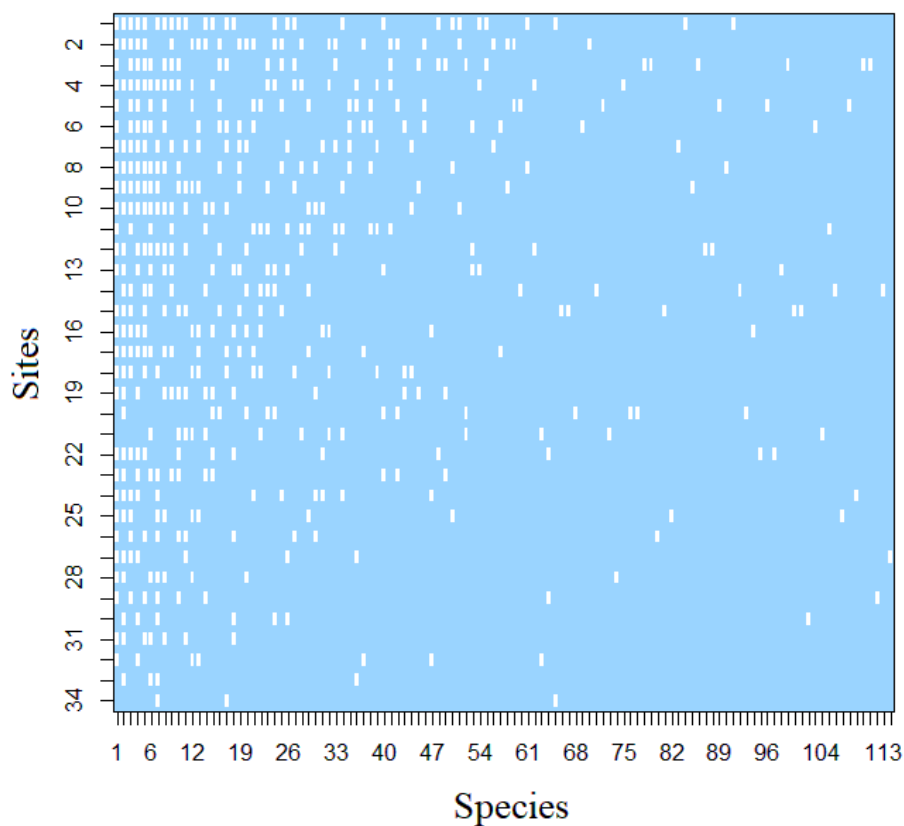


Figure 3.9 Site-species matrix from JDM nestedness analysis on flower-visiting insect data at the 34 field study sites

3.4.9 Flight periods of common species

Flight periods of hoverflies recorded in the first and second field season of the study were compared with the expected flight periods from the literature. In general, flight periods from both years fell within the expected range (see Table 3.6). *Eristalis nemorum/arbustorum*, *E.*

tenax, *Merodon equestris*, *Platycheirus scutatus* and *Sphaerophoria scripta* were recorded infrequently over both survey seasons and show close similarity in date of first record between the two years. *Eupeodes latifasciatus* and *Sphaerophoria* sp. were both recorded earlier than expected from the literature in 2015.

Flight periods of day-flying Lepidoptera recorded in the study with expected flight periods from the literature. Two generations can be seen in the bivoltine species *Aglais io*, *Pieris brassicae*, *P. napi* and *Polyommatus icarus*, with the second occurring in August for most species, as predicted from the literature. All species records fell within the expected range from the literature (see Table 3.7).

Bee flight periods fall within the expected ranges from the literature however *Andrena cineraria*, *Andrena nitida*, *Bombus rupestris* and *Osmia bicornis*, show shorter flight periods over the two years combined than expected, due to lack of records. In the well recorded species *Bombus lapidarius*, a six-week difference between first record for 2015 and 2013 was seen (see Table 3.8).

Table 3.6 Flight periods of hoverflies recorded at field sites in 2013, 2015 and from Ball & Morris (2015).

	Source	4th-13th Mar	14th-23rd Mar	24th Mar-2nd Apr	3rd-12th Apr	13th-22nd Apr	23rd Apr- 2nd May	3rd-12th May	13th-22nd May	23rd May - 1st Jun	2nd-11th Jun	12th-21st Jun	22nd Jun-1st Jul	2nd -11th Jul	12th-21st Jul	22nd-31st Jul	1st-10th Aug	11th-20th Aug	21st-30th Aug	31st Aug- 9th Sep	10th-19th Sep	20th-29th Sep	30th-8th Oct	8th-17th Oct	18th-26th Oct
<i>Eristalis nemorum/arbustorum</i>	2013																								
	2015																1								
	Expected																								
<i>Lejogaster metallina</i>	2013									12	1	1													
	2015							2	1	1															
	Expected																								
<i>Melanogaster hirtella</i>	2013										21	4	0	1											
	2015									1	3	1													
	Expected																								
<i>Merodon equestris</i>	2013										1														
	2015										1														
	Expected																								
<i>Platycheirus albimanus</i>	2013									1	2	0	0	0	0	0	0	2	0	1					
	2015				1	0	0	0	0	0	0	1													
	Expected																								
<i>Syrphus ribesii</i>	2013														6	0	0	0	0	1					
	2015										1	2	0	0	0	0	1	6							
	Expected																								
<i>Cheilosia pagana</i>	2013								1	0	0	0	0	0	0	0	0	0	0	0	1				
	2015				1																				
	Expected																								
<i>Platycheirus scutatus</i>	2013										1														
	2015								2																
	Expected																								
<i>Cheilosia albitarsis</i>	2013									5	1	1	0	1	0	0	0	1							
	2015								13	10	1	1													
	Expected																								
<i>Cheilosia ranunculi</i>	2013									6															
	2015								6	0	1														
	Expected																								
<i>Cheilosia albitarsis/ranunculi</i>	2013									1	0	0	0	1											
	2015								4	4	4	4	1												
	Expected																								
<i>Eupeodes luniger</i>	2013																			1					
	2015											3	0	0	0	0	0	2							
	Expected																								
<i>Helophilus pendulus</i>	2013										2	0	0	0	1	0	0	0	2						
	2015										1	1													
	Expected																								
<i>Melanostoma mellinum</i>	2013									1	1	0	0	0	0	0	0	2							
	2015								1	0	1														
	Expected																								
<i>Rhingia campestris</i>	2013								1	0	0	2													
	2015								1	0	0	0	0	0	0	0	0	0	2						
	Expected																								
<i>Episyrphus balteatus</i>	2013																	5	2						
	2015												1	0	0	0	0	2							
	Expected																								
<i>Eristalis tenax</i>	2013																			1					
	2015											1													
	Expected																								
<i>Eupeodes latifasciatus</i>	2013										1	0	0	0	0	0	0	0	0	1					
	2015								1	0	0	0	0	0	1										
	Expected																								
<i>Sphaephoria scripta</i>	2013								1																
	2015								1																
	Expected																								
<i>Sphaephoria sp.</i>	2013														1	0	0	5	5						
	2015								1	0	0	0	1	0	0	0	0	1	10						
	Expected																								

Table 3.7 Flight periods of day-flying Lepidoptera recorded in 2013, 2015 and from Thomas & Lewington (2011)

Source		4th-13th Mar	14th-23rd Mar	24th Mar-2nd Apr	3rd-12th Apr	13th-22nd Apr	23rd Apr-2nd May	3rd-12th May	13th-22nd May	23rd May - 1st Jun	2nd-11th Jun	12th-21st Jun	22nd Jun-1st Jul	2nd -11th Jul	12th-21st Jul	22nd-31st Jul	1st-10th Aug	11th-20th Aug	21st-30th Aug	31st Aug- 9th Sep	10th-19th Sep	20th-29th Sep	30th-8th Oct	8th-17th Oct	18th-26th Oct
<i>Aglais io</i>	2013						2	0	0	0	0	0	0	0	1	0	0	0	2						
	2015				6	0	0	0	0	1	0	1	0	0	0	0	0	3	5						
	Expected																								
<i>Gonepteryx rhamni</i>	2013						1	0	1																
	2015								1																
	Expected																								
<i>Pieris brassicae</i>	2013						1	0	0	1	0	0	0	7	0	0	5	1	2	0	1				
	2015						1	0	1	1	0	0	0	0	0	14									
	Expected																								
<i>Pieris napi</i>	2013						2	0	0	0	0	0	0	0	0	4	1	1							
	2015						2	0	0	0	0	0	0	0	1										
	Expected																								
<i>Pieris rapae</i>	2013																7	5	4						
	2015						2	1	1	0	0	0	0	0	0	7	1	2							
	Expected																								
<i>Polyommatus icarus</i>	2013									1	0	2	0	0	0	0	6	5							
	2015									1	2	9	2	0	0	0	8	7							
	Expected																								
<i>Maniola jurtina</i>	2013												25	113											
	2015											3	28	0	0	0	55								
	Expected																								
<i>Thymelicus sylvestris</i>	2013													3	71	0	0	0	1	1					
	2015													1	0	0	0	11							
	Expected																								
<i>Pyronia tithonus</i>	2013													1	8										
	2015																8	1							
	Expected																								

Table 3.8 Flight periods of bees recorded in 2013 and 2015 (Falk and Lewington, 2015).

	Source	4th-13th Mar	14th-23rd Mar	24th Mar-2nd Apr	3rd-12th Apr	13th-22nd Apr	23rd Apr-2nd May	3rd-12th May	13th-22nd May	23rd May - 1st Jun	2nd-11th Jun	12th-21st Jun	22nd Jun-1st Jul	2nd -11th Jul	12th-21st Jul	22nd-31st Jul	1st-10th Aug	11th-20th Aug	21st-30th Aug	31st Aug- 9th Sep	10th-19th Sep	20th-29th Sep	30th-8th Oct	8th-17th Oct	18th-26th Oct	
<i>Andrena cineraria</i>	2013						1																			
	2015											2	7													
	Expected																									
<i>Apis mellifera</i>	2013					1	1	0	0	0	0	0	0	0	3	0	0	0	0	1						
	2015					1	0	0	1	0	1	16	3	0	0	0	0	2	160							
	Expected																									
<i>Bombus lucorum/terrestris</i>	2013					2	0	0	0	0	0	1	0	11	2	0	0	6	1							
	2015					2	1	0	0	0	14	35	13	0	0	0	10	3								
	Expected																									
<i>Bombus pascourum</i>	2013					2	0	0	0	0	1	0	18	8	0	0	0	4	2	4						
	2015									1	1	1	28	13	0	0	0	8	18	1						
	Expected																									
<i>Lasioglossum calceatum</i>	2013					6	0	0	1	0	2	0	0	0	0	0	0	0	0	1						
	2015					1	1	3	1																	
	Expected																									
<i>Osmia bicornis</i>	2013																									
	2015																									
	Expected																									
<i>Andrena chrysoceles</i>	2013					1	1	0	0	0	1															
	2015					1	2	0	0	1																
	Expected																									
<i>Andrena nigroaenea</i>	2013					2	2																			
	2015																									
	Expected																									
<i>Bombus lapidarius</i>	2013																									
	2015																									
	Expected																									
<i>Andrena haemorrhoa</i>	2013																									
	2015																									
	Expected																									
<i>Andrena nitida</i>	2013																									
	2015																									
	Expected																									
<i>Bombus hortorum</i>	2013																									
	2015																									
	Expected																									
<i>Bombus hypnorum</i>	2013																									
	2015																									
	Expected																									
<i>Bombus campestris</i>	2013																									
	2015																									
	Expected																									
<i>Bombus rupestris</i>	2013																									
	2015																									
	Expected																									

3.5 Discussion

3.5.1 Variation throughout the season & phenology

Mean insect abundances were generally higher from the middle to latter part of the recording period (late June-August) coinciding with the peak flowering period. Departures from the general assumed pattern could reflect the differences caused by site-to-site variation and weather events. Sampling of further habitats could provide information on how habitat utilisation and food plant preference varies throughout the season. Oilseed rape features strongly in the Northamptonshire landscape and has been seen to attract insect pollinators over their usual wild food plants (Holzschuh *et al.*, 2011). Similarly, sudden loss of floral resources due to the hay cut in July must force pollinators to utilise other species and habitats such as hedgerows and field boundaries.

Flight periods generally fell within the expected ranges suggested by the literature. For many species, records were sparse and peak abundance, emergence and timing of second brood (in bivoltine species) cannot be inferred. Time of first record was generally earlier for species in 2015 than in 2013, which may relate to milder temperatures and flowering times of plant species. As phenology is largely deemed to be controlled by weather conditions, it is likely for flight periods to differ between regions and indeed sites due to microclimatic controls (Checa *et al.*, 2014). Indeed, as phenologies can differ at both a regional and site-based level, the findings indicate a need for robust seasonal recording in the region, with an understanding of how the landscape context may affect patterns or mediate the effects of weather events.

3.5.2 Differences in taxonomic groups between sites

For two sites, Lyveden and West Lodge, considerable numbers of honey bees were recorded raising the total abundances remarkably. Managed honey bee hives were kept around 400m from the recording area at Lyveden, whilst at West Lodge honey bee records were most likely to be associated with a wild hive which colonised a nearby tree around the time of the third survey. Competition for resources between honey bees and wild bees such as *Bombus* spp. are not yet fully understood (Elbgami *et al.*, 2014; Steffan-Dewenter and Tscharnkte, 2000). It is possible that the high levels of honey bees at these sites could affect both the species

richness and abundance of wild pollinators, thus should be considered when analysing the relationships to both local and landscape-scale data in Chapters 4 and 5.

It is widely considered that more diverse pollinator communities are more effective at pollinating floral communities (e.g. Albrecht *et al.*, 2012; Biesmeijer *et al.*, 2006; Klein *et al.*, 2003). Understanding of the functional traits of insect groups can help us understand their efficacy at pollen transfer and resulting seed set (Fründ *et al.*, 2013; Fontaine *et al.*, 2006). Previous studies have identified functional traits such as: length of mouth parts, phenology, feeding heights (driven by microclimates) and differing nutritional requirements and it is important to consider diversity of these traits as well as taxonomic diversity (Blüthgen and Klein, 2011; Fontaine *et al.*, 2006). The foraging habits of insect species and their efficacy as pollinators is poorly understood at present, this paucity of knowledge causes problems when trying to quantify pollination in the ecosystem service framework.

3.5.3 Strong relationship with floral cover

The strong correlation with both insect abundance and species richness and floral cover is supported by other studies (Tarrant *et al.*, 2013; Carrie *et al.*, 2012; Hegland and Boeke, 2006). Availability of food resources are considered the main limiter on pollinator populations, with plant species richness further contributing to visitation frequency in bumblebee and honey bees and species richness in bumblebees, hoverflies and solitary bees (Roulston and Goodell, 2011; Ebeling *et al.*, 2008;). Similarly, more research is required to understand how presence of species-rich grasslands may affect crop yields. Species-rich habitats could provide a food resource to pollinators throughout the flight season and thus ensure population security (Ebeling *et al.*, 2008). Blaauw and Issaacs (2014) found that blueberry yields were significantly higher in fields adjacent to wildflower plantings.

Dicks *et al.* (2015) highlight the need for further research into how agri-environment schemes may best deliver food resources for effective policy making. At present UK agri-environment schemes may not be providing suitable habitats for bees (Kleijn *et al.*, 2006), although some pollinator targeted schemes have been proven to have value (Lye *et al.*, 2009; Wood *et al.*, 2015). Current agri-environment research is largely centred on the effects of wildflower strips and field margins on pollinators, yet these findings highlight the importance of flower cover and indicate a need for better understanding of grassland habitats in agricultural

matrices (Guiller *et al.*, 2016; Wood *et al.*, 2015; Garibaldi *et al.*, 2014). Field margin habitats are considered short term providers of pollinator forage, with longevity of quality of 3-4 years even under strict management conditions (Pywell *et al.*, 2011). On this basis, well managed grasslands should be considered as a more cost-effective approach to conserving pollinators within landscapes.

3.5.4 Environmental gradients

The PCA analyses for all spatial scales (250m, 1000m, 3000m) showed the first two principal components explained a relatively small (36.1-43.2%) amount of variation between the field sites. This indicates the drivers of variation between sites are complex and not fully described by the variables recorded.

The analysis carried out at the 250m scale indicated a gradient on principal component one between floral cover and weighted area, semi-natural habitat, semi-natural grassland and Shannon-Wiener Index. The latter variables are very closely aligned, indicative of collinearity, some similarity is expected in these variables as they are derived or calculated from the Landcover 2007 dataset. These data should not be dismissed though as this effect of collinearity is not so well observed at the larger scales (1000m or 3000m). The observed gradient indicates that grassland sites in this study that are relatively isolated from other semi-natural habitats at this small scale are likely to have higher levels of floral cover. This may indicate that grasslands in isolated (in the immediacy) occur in agricultural landscapes and may either be high in floral cover due to their persistence in the landscape or due good management. Additionally, the sites associated with the floral cover vector were, as a general observation, more recently restored, isolated sites may be more likely to attract grants for habitat restoration projects.

A further gradient was observed on the 250m PCA, proportion of water was opposed to site area and solar radiation on the second principal component. Site area and solar radiation were closely aligned suggesting collinearity, this is in part explained by the opposing effect of proportion of water. At such a small spatial scale it is logical that a higher proportion of water within a 250m radius leaves a reduced space for grassland. Higher levels of surface water are more likely to occur in flatter landscapes, thus sites with high presence of surface water receive a reduced amount of solar radiation.

The PCA at the 3000m scale is perhaps the most difficult to interpret, with floral cover, proportion of semi-natural grassland and proportion of surface water exerting the most influence on the axis. Water and urban area opposed hedgerow density and proportion of semi-natural habitats on the first principal component. Put simply, this axis represents an urban-rural gradient, however, at the 3000m scale points/sites along this axis do not readily classify as either an 'urban' or a 'rural' site. For instance, point 28 (Ditchford Meadow) (Figure 3.7) falls on the 'urban' end of the gradient, but is not associated with the urban area variable on the 250m and 1000m plots (Figures 3.5 and 3.6). Whilst this site is not 'urban', a three-kilometre catchment from site centre includes the outskirts of Wellingborough, Irthlingborough, Higham Ferrers, Irchester and Rushden, significant towns within the NIA. A similar relationship seen at a smaller scale would demonstrate a clearer urban rural gradient, however, at this scale this relationship is more nuanced.

Spearman's Rank Correlation between the dependent variables and the principal components revealed a significant positive relationship between bee abundance and principal component one at the 1000m scale and principal component two at the 3000m scale. This indicates that the observed differences in the recorded environmental factors follow similar differences observed in the bee abundance. The strongest effect on principal component one at the 1000m scale was Shannon-Wiener index. The analysis at the 3000m scale was more difficult to interpret, however, there were two strong relationships on this axis with floral cover and proportion of semi-natural grassland. The relationship between the environmental variables and dependent variables will be analysed and discussed in greater detail in Chapters 4 and 5 of this thesis.

3.5.5 Nestedness

The flower-visiting insect assemblages recorded in this study were found to exhibit significant nestedness. This indicates that the assemblages found at sites with lower species-richness were effective subsets of the assemblages found at sites with higher species-richness. Use of the JDM measure of nestedness allowed for unevenness in sampling and gain an overview of all the site species data. Significance in this analysis provides support to combine the two years of field data (2013 and 2015) as there is commonality across the site samples.

Multiple hypotheses exist for the causes of nestedness in assemblages including: passive sampling, neutrality, selective colonisation, selective extinction, nested habitats, selective environmental tolerances and habitat quality (Ulrich *et al.*, 2009). Passive sampling, based on an assumption that regionally abundant species have a higher probability of colonising patches (Ulrich *et al.*, 2009). In addition, passive sampling effects can be caused where larger patches are effectively sampled more than smaller ones as abundant species are more likely to be sampled than rare species (Mcabendroth *et al.*, 2005; Connor and McCoy, 1979).

Selective colonisation describes nestedness through shrinking subsets with increasing isolation mainland or source habitat, with the assumption that communities most isolated can persist due to having the most generalist needs (Lomolino, 1996). Selective extinction theory may be distinct or complimentary to selective colonisation, where species become sequentially extinct, for instance along a habitat area gradient (Wethered and Lawes, 2005; Lomolino, 1996).

Nested habitat theory consists of two strands; nested habitats and nested habitat quality (Hylander *et al.*, 2005). The nested habitats strand proposes nestedness as product of a gradient along which sites are made up of nested habitats (Hylander *et al.*, 2005). Nested habitats theory expect sites consisting of one habitat type to host few species and sites made up of multiple, nested habitats to host the most species richness (Hylander *et al.*, 2005). The nested habitat quality strand implies that nestedness occurs when sites represent a gradient of habitat quality, the highest quality habitat represents a diverse community and, along the gradient, subsets of the species of this community occur dependent on their tolerance to the habitat quality (Hylander *et al.*, 2005).

Perhaps complimentary to nested habitat quality, selective environmental tolerances explains nestedness through sites occurring along a gradient of environmental stress. Where sites with higher environmental stress contain fewer, more stress tolerant, species and sites with low stress may be populated with a more diverse community of both stress tolerant and intolerant species (Ulrich *et al.*, 2009).

The PCA analysis (see Section 3.4.6.) did not indicate any significant relationship between the environmental gradients described by the principal components and species-richness of the insect groups recorded. Significant relationship between species richness and an

environmental gradient for instance: isolation, site-area, floral cover etc may have readily been attributed to the nestedness theories described above. Analysis in Chapter Four will explore the landscape and local factors driving species-richness in greater detail. This analysis may reveal a gradient along which nestedness could occur e.g. connectivity or patch area.

3.5.6 Species abundance distribution

Species common in both years of survey included: *Maniola jurtina*, *Bombus lapidarius*, *Bombus pascourum*, *Cheilosia albitarsis*, *Pieris brassicae*, *Thymelicus sylvestris* and *Lasioglossum calceatum*. These species are common throughout the British Isles and several have strong associations with grasslands. As the common name meadow brown suggests, *Maniola jurtina* is strongly associated with lowland grasslands and, like *Thymelicus sylvestris*, oviposits on grass species (Thomas and Lewington, 2011). Similarly, *Cheilosia albitarsis* utilises members of the genus *Ranunculus* as both larval host and adult food plant and as such is common in grasslands (Ball and Morris, 2015).

Some species were found in low numbers, including: *Scaeva pyrastris*, *Melanostoma scalare*, *Lasioglossum morio*, *Andrena wilkella* and *Aglais urticae*. *Scaeva pyrastris* is a migratory species and as such numbers can vary greatly between years. The species is known to utilise a number of habitats, as such low numbers may be due to low migration or use of other habitats.

Absence of records of even common species such as *Bombus terrestris* in the region on the National Biodiversity Network gateway suggest low recording or submission of records in the area (NBN Gateway, 2017). This absence of comparative data makes it difficult to interpret whether species with low abundances are infrequent due to regional factors or due to other factors on a smaller spatial or temporal scale.

3.6 Chapter summary

- Floral cover was positively correlated with both species richness and abundance of flower-visiting insects
- Species abundance distribution followed a hollow curve distribution: *Bombus lapidarius* and *Maniola jurtina* were amongst most abundant species whilst *Volucella bombylans* and *Sphaerophoria interrupta* were amongst the singletons.
- Principal components analysis revealed a significant positive relationship between bee abundance and a principal component dominated by Shannon-Wiener index.
- Flight periods recorded fell within the expected range but highlighted the need for a more structured and resourced recording network.
- Nestedness analysis revealed the communities sampled in this study are significantly nested.

Chapter 4 Exploring the influence of landscape and local variables on insect abundance and species richness

4.1 Introduction

In this chapter the effects of both landscape and local scale variables on insect pollinator abundance and species richness are explored. Data collected in 2013 and 2015, both in the field and extracted from GIS datasets, are analysed using Generalised Linear Modelling (GLM). The coefficients from model averaging are discussed in the context of pollinator habitat requirements.

4.1.1 Local scale research

Understanding how pollinators utilise resources at the local scale is essential for habitat management and restoration. Thorough research lead to greater success in reintroduction programmes, for example the short-haired bumblebee *Bombus subterraneus* in Dungeness, Kent in 2012 (Vaughan-Higgins *et al.*, 2016; Goulson *et al.*, 2008) and the large blue butterfly *Maculinea arion* in Polden Hills, Somerset in 1992 (Andersen *et al.*, 2014). Habitats provide several functions depending on the organism: nesting and/or oviposition habitat, forage, shelter/predator avoidance, roosting and overwintering sites.

Flowers act as a forage resource, providing both pollen and nectar for bees, butterflies and hoverflies. Previous studies have shown that floral species richness is positively associated with pollinator functional diversity and pollinator abundance (e.g. Orford *et al.*, 2016; Potts *et al.*, 2003). Floral abundance is also positively correlated with pollinator abundance (Nayak *et al.*, 2015, see also Chapter 3).

Sites bounded by hedgerows may have a greater provision of nesting habitat or provide shelter from predators (Morandin and Kremen, 2013). Similarly, flower rich strips at the outside edges of crop fields have been found to hold higher abundance and diversity of insect

pollinators than the crop fields themselves or than simple grass strips at the edges of fields (Haaland *et al.*, 2011).

4.1.2 Landscape scale research

Landscape ecology focuses on the composition and configuration of habitats within an area and their effects on the distribution and abundance of an organism(s). This geographical scale of research is of particular interest considering highly mobile organisms, in this instance insect pollinators, who often require a number of resources to fulfil their life cycles. Current research indicates different strategies for landscape utilisation amongst the pollinator groups of interest within this study: bees (e.g. Jauker *et al.*, 2009), butterflies (e.g. Sweaney *et al.*, 2014) and hoverflies (e.g. Halder *et al.*, 2017). There are, however, still large gaps in this area of research.

The scale at which processes occur is dependent on the mobility of the organisms of focus. Current knowledge indicates that bees may be affected by landscape at larger scales due to their flight distances and need for heterogeneous habitats for nesting (Kennedy *et al.*, 2013). Patterns of habitat use are more likely to be detectable in bees due to their central-place foraging behaviours. The proportion of semi-natural habitats within 1km of a site was shown to increase bee visitation and, subsequently, seed-set within a cherry orchard (Holzschuh *et al.*, 2012). Furthermore, the proportion of impervious surfaces within the 500m scale have been shown to be negatively associated with bee abundance and richness, indicative of the effects of urbanisation (Geslin *et al.*, 2016).

Hoverflies are not central place foragers and therefore can move linearly through landscapes and utilise different habitats for both forage and oviposition. Habitats used for oviposition vary widely, including aquatic environments, animal dung and plant stems; they can also depend on an abundance of prey for example in the instance of aphidophagous species (Speight, 2015; Sadeghi and Gilbert, 2000). Meyer *et al.* (2009) found that hoverfly species richness was positively correlated with both the diversity of habitats and the availability (proportion) of larval habitats within 250m; however, abundance was affected at much larger spatial scales, up to 1500m. Kleijn and Van Langevelde (2006) found that the proportion of semi-natural habitat at the 500-1000m scales had a positive impact on hoverfly species richness in areas of high floral cover.

Butterflies do not exhibit nest provisioning behaviours but may otherwise be restricted to habitats through their tendency to select specific plant hosts for oviposition. Habitat heterogeneity within 1km was positively associated with butterfly species richness (Perović *et al.*, 2015). Lepidoptera have been shown to use green linear features such as grassy field margins and hedgerows, for both navigation and forage within landscapes (Coulthard *et al.*, 2016; Delattre *et al.*, 2013).

Greater knowledge of how pollinators utilise landscapes and resources could enable more effective conservation through the targeting of areas for habitat conservation and restoration in the most financially beneficial areas. Similarly, centrally governed schemes such as agri-environmental stewardship could be more strategically placed, to ensure greater stability and quality of ecosystem service on the basis of ecological knowledge.

4.2 Aims and objectives

The aim of this chapter is to explore the abundance and species richness data, described in Chapter 3, in the context of the wider landscape. The following objectives are considered:

- **To identify at which spatial scales landscape features influence insect pollinator abundance and species richness.**

The literature indicates that the scales at which landscape variables influence pollinators are closely linked to the flight distance abilities and oviposition behaviours of the study organisms. However, some research indicates that even insects that do not exhibit central place foraging may otherwise be restricted in their movements. This chapter will explore this through Spearman's Rank Correlation and univariate modelling.

- **To analyse how local-scale variables effect insect pollinator abundance and species richness.**

The effects of management practice, site maturity, floral cover, conservation status and site shape on insect pollinator abundance and species richness will be investigated.

- **To analyse how landscape-scale variables influence insect pollinators abundance and species richness.**

The effects of proportion of semi-natural habitat, built-up area, and water, hedgerow density, isolation, habitat diversity and solar radiation on insect pollinator abundance and species richness will be investigated.

- **To model insect species richness and abundance using landscape and local scale factors**

Model selection and multi-model inference will be used to explore how the local and landscape-scale factors influence pollinator abundance and species richness. The model fit, coefficients and variance will be reviewed.

4.3 Methods

4.3.1 Field methods

Timed transect walks were carried out at 14 sites in 2013 and at 20 sites in 2015. Bees, day-flying Lepidoptera (DFL) and hoverflies were hand-netted along the transect and identified either in the field or taken to the laboratory for identification. The location and description of these sites, along with the full field methodology can be found in Chapter 2.

4.3.2 Spatial scale

For the purposes of this study, grain was defined as the smallest resolution of data available, whilst extent, the study area, has been considered as the distance at which an individual may perceive habitat resources (Mayer and Cameron, 2003; Turner *et al.*, 1989). The resolution (grain) considered in this research is 10m (see Section 4.3.3). Three spatial scales (extent); 250m, 1000m, and 3000m were selected for this investigation based on the present scientific literature on pollinator flight distances (see Chapter 2).

4.3.2 Landscape and local scale factors

The full justification for the landscape and local scale variables examined in this thesis can be found in Chapter 2.

All GIS layers were resampled at a 10m x 10m resolution, to enable processing in ArcGIS. This reflects a compromise between the highest resolution dataset (Mastermap) 25cm and lowest (Land Cover 2007) at 25m, allowing processing within the computational constraints of the project. Table 4.1 summarises the landscape-scale factors explored in this chapter.

Table 4.1 Summary of landscape factors explored with both the 2013 and combined dataset in this study.

Variable	Data	Data source	Units
SNH	Proportion of semi-natural habitat	Land Cover 2007, extracted by radius	Proportion
BU	Proportion of built up area	Land Cover 2007, extracted by radius	Proportion
W	Proportion of water	Mastermap (2012)	Proportion
SNG	Proportion of semi-natural grassland	Land Cover 2007, extracted by radius	Proportion
SR	Solar radiation	Solar radiation calculated from a DEM using Solar Radiation tools within ArcGIS.	Mean WH/m ²
SW	Shannon-Wiener habitat diversity index	Land Cover 2007, Calculated using modified Shannon-Wiener	-H (see text)
HE	Hedgerow density	Digitised from aerial photography using Mastermap line layer (2013)	m/m ²
WA	Distance to grasslands (weighted)	Land Cover 2007, Calculated from patch size and distance to site (see text)	See text

The Land Cover 2007 dataset was used to calculate a number of the landscape factors (see Table 4.1). It is a readily available (via www.edina.digimap.ac.uk) dataset produced by the Centre for Ecology and Hydrology, which characterises land cover using 23 habitat classifications. Data were generated through automated classification of habitats from satellite imagery, a subset of which was then corroborated in the field (with a mean 83% identification accuracy) (Morton *et al.*, 2011). This dataset was chosen for this study as it has national coverage and is easily accessible, thus increasing the reproducibility of the research.

Adapted Shannon-Wiener diversity index was used as a measure of landscape heterogeneity:

$$H = -\sum P_i(\ln P_i)$$

where P_i was proportion of each habitat in the study area (Steffan-Dewenter *et al.*, 2002). Habitat information was extracted from the Land Cover 2007 dataset.

Solar radiation (WH/m^2), a metric accounting for both land elevation and aspect, was calculated using the solar radiation toolbox within ArcGIS using the OS Terrain 5 DTM dataset.

At present there is insufficient information on landscape permeability for insect pollinators, so a least-cost path analysis was not appropriate. Connectivity, or isolation, was instead presented as distance area weighted by distance:

$$WA = \sum \frac{P}{\ln D}$$

where P is patch area and D is distance from patch centroid to site centroid.

Aerial photography (Natural England) was overlain with Mastermap (Ordnance Survey) line data the latter of which was then edited to represent hedgerows within the study area. Due to time constraints, and dominance of non-native species, urban hedgerows were not digitised (see Chapter 2). Hedgerow density was calculated as the number of metres of hedgerow per m^2 .

A shape index based on that used by Faeth and Kane (1978) was used as a measure of the site shape, a measure of how circular the site is independent of area (see Section 2.4.5). Sites were measured in ArcGIS and the following equation applied, where S is shape, P is patch perimeter and A is area:

$$S = \frac{P}{2\sqrt{A\pi}}$$

Floral cover was recorded during surveys (see Chapter 2), the area of floral cover was then calculated and presented as a proportion.

Dummy variables were generated for a number of local scale variables based on information from landowner/land manager interviews (see Chapter 2 and Table 4.2).

Table 4.2 Summary of local factors explored with the combined dataset in this study.

Variable	Data	Data source	Units
FLOCOV	Floral cover	Total proportion of floral cover across surveys	
SHAPE	Shape index	Faeth and Kane (1978)	S (see text)
RESTORED	Site has had restoration works carried out	Landowner interview	1= Restored 0= Not restored
NEW	Restored within the last 5 years	Landowner interview	1= Restored in the last 5 years 0=Not restored /not restored in the last 5 years
AGRI	Land is under agri environment scheme	Landowner interview	1=Site under agri-environment scheme 0=Site not under agri-environment
DESIGNATION	Site has a wildlife site designation	Landowner interview	1=Site has designation 0= Site without a designation
HAY CUT	The meadow is cut once a year	Landowner interview	1=Site is cut once a year 0=Site is not cut
GRAZED	The meadow is grazed (usually winter)	Landowner interview	1=Site is grazed 0= Site is not grazed
SITEAREA	Area of field site	Mastermap (2012)	m ²

4.3.3 Statistical methods

For full statistical methodology see Chapter 2. Abundance data were averaged across all surveys for each site and rounded to the nearest whole number to produce a metric of insect abundances. Rarefaction of species richness data collected in the field was carried out in EstimateS, with species richness estimates being taken at 25 samples (the lowest number of subsamples taken at a site) (Colwell *et al.*, 2012). Spearman's Rank Correlation was carried out between all continuous variables to explore the potential relationships in the data. Alternatively, the Mann-Whitney U test was carried out between the binary local scale variables and the continuous variables. Model selection process was adapted from Burnham and Anderson (2003) and conducted using R (R Development Core Team, 2008).

Figure 4.1 outlines the model selection process used in this study. Data were standardised or scaled in R subtracting the mean and dividing by the standard deviation for each variable allowing meaningful comparison of coefficients in the models. Models were checked for collinearity using Variance Inflation Factor (VIF), with variables being removed until the models held a VIF <3, indicating no collinearity (Zuur *et al.*, 2007; Zuur *et al.*, 2009).

Suitable sample size to number of variables within a regression framework has been suggested to be between 2- 10 samples per variable (Austin and Steyerberg, 2015; Harrell, 2015), in this study automated model selection was used, stipulating that models may only contain a maximum of 4 explanatory variables and using AICc to account for small sample size (see Chapter 2). A top model set was produced and those within 2 AICc were selected for model averaging and inference (Burnham and Anderson, 2003).

The residuals of the top model for each taxonomic grouping was tested for spatial auto-correlation using Moran's I (see Chapter 2).

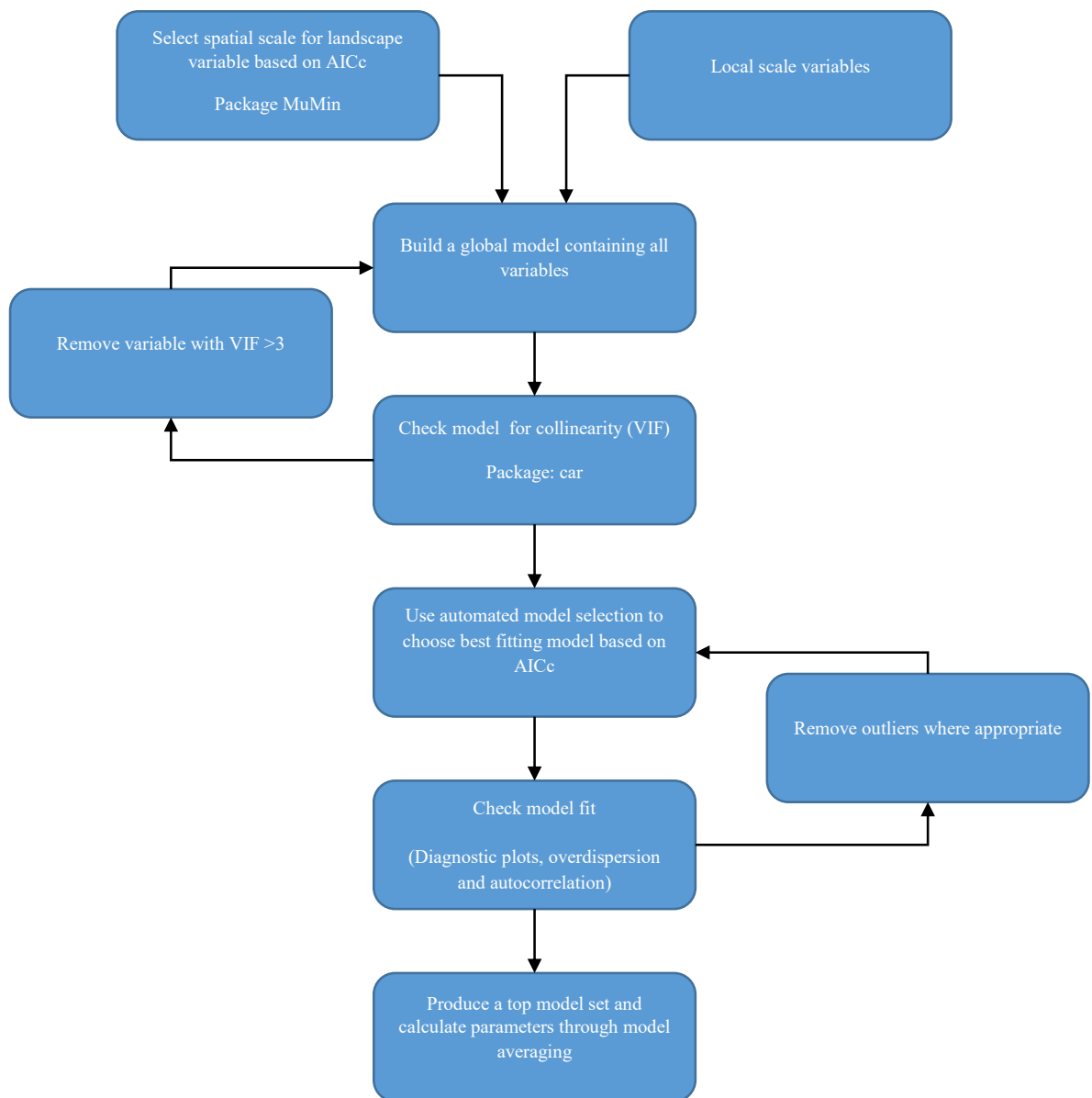


Figure 4.1 Generalised Linear Model selection process (See Chapter 2.7 and Section 4.3.4 for details)

4.4 Results

4.4.1 Preliminary analysis

Combining the data from 2013 and 2015 allowed for greater predictive power in the modelling and for a greater number of terms to be included in the model selection process. Spearman's Rank Correlation was carried out between the dependent variables (measures of insect abundance and richness) and the continuous variables (landscape and local factors and the dependent variables) (see Table 4.). The Mann-Whitney U test was carried out on binary independent variables and continuous variables. Correlations accepted at the 95% confidence level are discussed below (see Table 4.4).

Mean bee abundance was negatively correlated with: the proportion of water sampled at the 1000m and 3000m scales, the Shannon-Wiener habitat diversity index sampled at the 250m scale, proportion of semi-natural grassland at the 250m scale and the proportion of hedgerows sampled at the 3000m scale. Positive correlations were recorded between mean bee abundance and semi-natural habitats recorded at the 3000m scale, weighted area at the 3000m scale and in site floral cover. Rarefied bee species richness was positively correlated with floral cover (see Table 4.).

Hoverfly abundance and richness was negatively correlated with the weighted area variable at the 3000m scale (see Table 4.).

Day-flying Lepidoptera abundance was positively correlated with proportion of semi-natural grassland at the 1000m scale and negatively correlated with solar radiation at 250m and site area. Rarefied day-flying Lepidoptera species richness was negatively correlated with both hedgerows recorded at the 1000m scale and site area (see Table 4.). The Mann-Whitney U test showed higher mean rank values between day-flying Lepidoptera abundance and sites that were not under agri-environment schemes or had not been grazed (see Table 4.4). In addition, the Mann-Whitney U test for day-flying Lepidoptera richness showed higher ranks on sites that had not been grazed.

Table 4.3 Spearman's Rank correlation for dependent and independent variables (95% confidence, see Appendix 1.9 for all results)

	Bee abundance	Hoverfly abundance	Day-flying Lepidoptera abundance	Species richness bee	Species richness hoverflies	Species richness day-flying Lepidoptera
Water (1000m)	-0.47					
Water (3000m)	-0.38					
Shannon-Wiener diversity index (250m)	-0.34					
Semi-natural grassland (250m)	-0.34					
Semi-natural grassland (1000m)			0.37			
Semi-natural habitats (3000m)	0.39					
Hedgerow density (250m)						
Hedgerow density (1000m)						-0.37
Hedgerow density (3000m)	-0.37					
Solar radiation (250m)			-0.35			
Weighted area (3000m)	0.45	-0.38			-0.5	
Floral cover	0.55			0.38		
Site area			-0.46			-0.42

Table 4.4 Mann-Whitney U test for dependent and independent variables (95% confidence, see Appendix 1.9 for full results)

		U	P	Mean rank	
				0	1
Day-flying Lepidoptera abundance	AES	72.5	0.031	25.67	14.56
	Grazed	60	0.041	23.33	15.40
Day-flying Lepidoptera richness	Grazed	39	0.003	25.67	14.56

4.4.2 Variable selection for generalised linear modelling combined years

Univariate models were carried out between the landscape variables and the abundance and species richness data to identify the most appropriate scale to select for the models. AICc was used as a measure of relative model quality, for each landscape metric the model/sample scale with the lowest AICc was chosen as the most suitable for multivariate modelling. Through this process the scales were selected as in Table 4.5 (See Appendix 1.11 for full results of univariate modelling).

Table 4.5 Spatial scales selected for modelling based on univariate modelling.

	Mean abundance				Rarefied richness		
	Bees	Hoverflies	Day-flying Lepidoptera	Bees	Hoverflies	Day-flying Lepidoptera	
Water	3000	1000	250	3000	3000	250	
Shannon wiener	250	250	1000	1000	3000	250	
Built up	3000	250	1000	250	250	3000	
Semi-natural habitats	3000	1000	3000	3000	1000	3000	
Semi-natural grassland	250	1000	250	1000	3000	250	
Hedgerows	3000	250	1000	3000	3000	250	
Solar radiation	3000	1000	250	250	1000	250	
Weighted area	3000	3000	1000	3000	3000	250	

4.4.3 Addressing collinearity within the combined dataset

Global models were checked for collinearity through variance inflation factors with variables being removed step-wise until the variance inflation factor for all variables returned <3 (see Chapter 2). Table 4.6 provides a key to abbreviations for the variables used in the modelling in this thesis. Table 4.7 shows the factors removed from the sub-global models for each of the abundance and species richness data.

Table 4.6 Abbreviations of variables used in modelling

Landscape variables	Local variables
HE-Hedgerow density	FLOCOV-Floral cover
SR-Solar radiation	SHAPE- Shape index
SNH-Semi-Natural habitats	SITEAREA-Area of site
BU-built-up/urban area	AGRI-Agri-environment scheme
WA-weighted area	NEW-Restored in last 5 years
SNG-Semi-natural grassland	DESIGNATION-Site has a conservation designation
SW-Shannon-Wiener index	HAYCUT-Site is mown once a year
W- Water	GRAZED-Site is grazed
	RESTORED-Site has been restored

Table 4.7 Parameters dropped from the global model due to collinearity (Variance Inflation Factor in parentheses) (see Table 4.1 and Table 4.2 for parameter abbreviations).

Mean abundance			Rarefied richness		
Bees	Hoverflies	Day-flying Lepidoptera	Bees	Hoverflies	Day-flying Lepidoptera
BU3000 (10.98)	AGRI (7.51)	W250 (11.17)	W3000 (5.45)	SNG3000 (7.28)	W250 (5.5)
FLOCOV (7.99)	W1000 (5.29)	SNH3000 (4.56)	SITEAREA (3.63)	AGRI (6.35)	AGRI (5.35)
AGRI (4.4)	HE250 (3.93)	NEW (3.13)	AGRI (3.57)	BU250 (3.39)	SNG250 (4.45)
SW250 (3.74)			BU250 (3.17)		

4.4.4 Generalised linear modelling combined data

Table 4.8 shows the sub-global models for the pollinator groups studied based on the combined data from 2013 and 2015. The assumptions of Poisson distribution were assessed both with the overdispersion statistic \hat{c} (see Table 4.8 and Chapter 2) and using diagnostic

residual plots. All models with \hat{c} values over two were discarded due to lack of fit, whilst those falling under this cut-off value were explored using residual diagnostic plots (see Appendix 1.17 for an example residual plot). On this basis, the species richness models for all groups were retained for further analysis and model selection. Negative spatial autocorrelation was detected in the bee species richness model and therefore should be considered in the interpretation of results (see Appendix 1.18).

Table 4.8 Summary of multivariate models from both sampling seasons and the overdispersion statistic (C-hat) (see Table 4.3 for abbreviations)

	Sub-global model terms	C-hat value
Bee abundance	W3000+SNH3000+HE3000+SR3000+SNG250+WA3000+SHAPE+RESTORED+NEW+DESIGNATION+HAYCUT+GRAZED+SITEAREA	4.99
Hoverfly abundance	SW250+BU250+SNH1000+SR1000+SNG1000+WA3000+FLOCOV+SHAPE+RESTORED+NEW+DESIGNATION+HAYCUT+GRAZED+SITEAREA	2.4
Day-flying Lepidoptera abundance	SW1000+BU1000+HE1000+SR250+SNG250+WA1000+FLOCOV+SHAPE+RESTORED+AGRI+DESIGNATION+HAYCUT+GRAZED+SITEAREA	3.68
Species richness bees	SW1000+SNH3000+HE3000+SR250+SNG1000+WA3000+FLOCOV+SHAPE+RESTORED+NEW+DESIGNATION+HAYCUT+GRAZED	1.29
Species richness hoverflies	W3000+SW3000+SNH1000+HE3000+SR1000+WA3000+FLOCOV+SHAPE+RESTORED+NEW+DESIGNATION+HAYCUT+GRAZED+SITEAREA	1.43
Species richness day- flying Lepidoptera	FLOCOV+SHAPE+RESTORED+NEW+DESIGNATION+HAYCUT+GRAZED+SITEAREA+SW250+BU3000+SNH3000+HE250+SR250+WA250	0.76

4.4.5 Model averaging combined data

Bee species richness

The model selection process revealed 11 models within 2 AICc of the top model (see Appendix 1.15 for example). The top model explained 39% of the variance in the data, indicating a moderate explanatory power. Hedgerow density (3000m) (-0.21) and floral cover (0.18) had a relatively strong influence within the model, the other variables had a weaker relationship with high standard errors (see Table 4.9, Figure 4.2 and Figure 4.3).

Table 4.9 model averaged parameter estimates for bee species richness. Independent variables are scaled to allow comparison.

	Parameter estimates	Adjusted standard error
(Intercept)	1.4903	0.0873
Hedgerow density (3000m)	-0.21467	0.08949
Semi-natural grassland (1000m)	0.09639	0.1044
Floral cover	0.17791	0.0892
Haycut taken	0.06784	0.10593
Site restored	-0.05515	0.08934
Solar radiation (250m)	-0.04388	0.08078
Site grazed	0.02213	0.06579

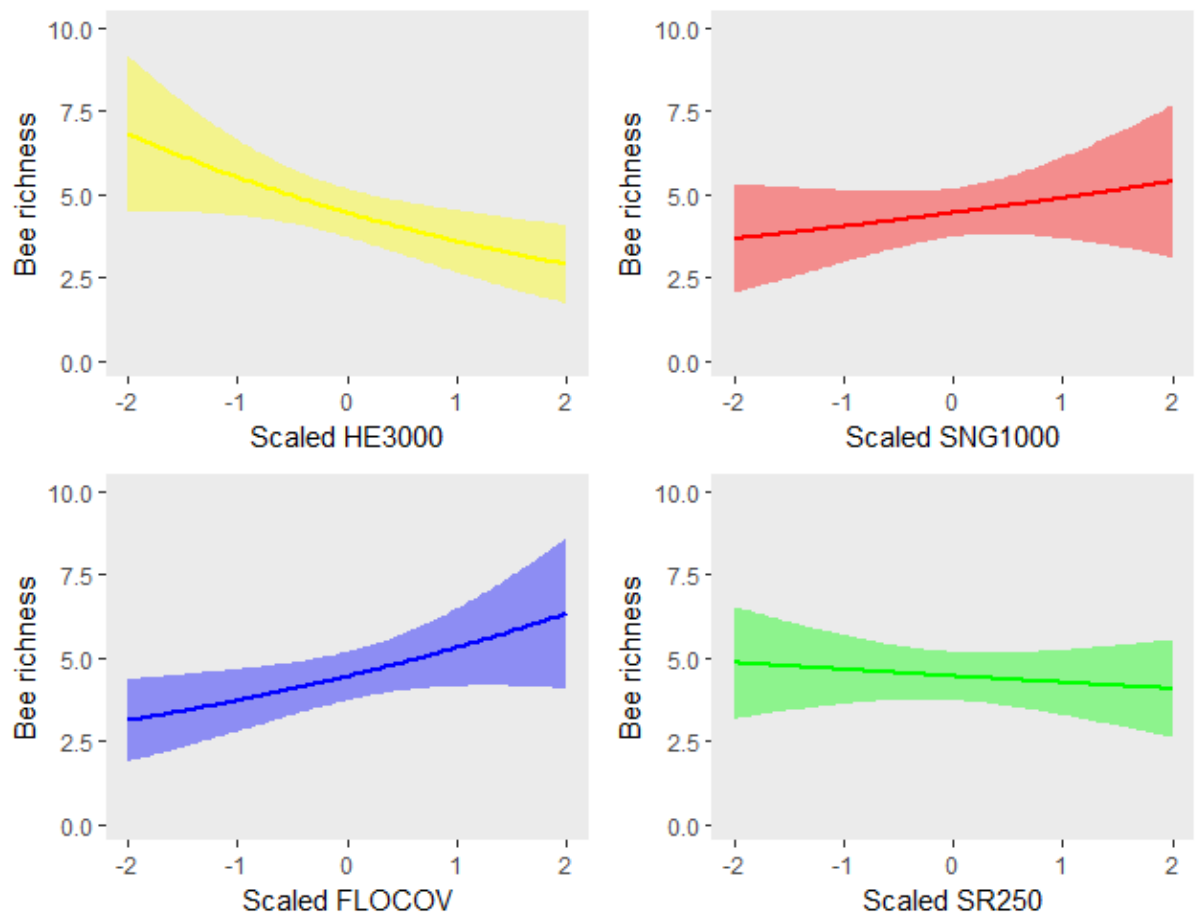


Figure 4.2 Partial effects of independent variables within averaged model of bee species richness (95% CI).

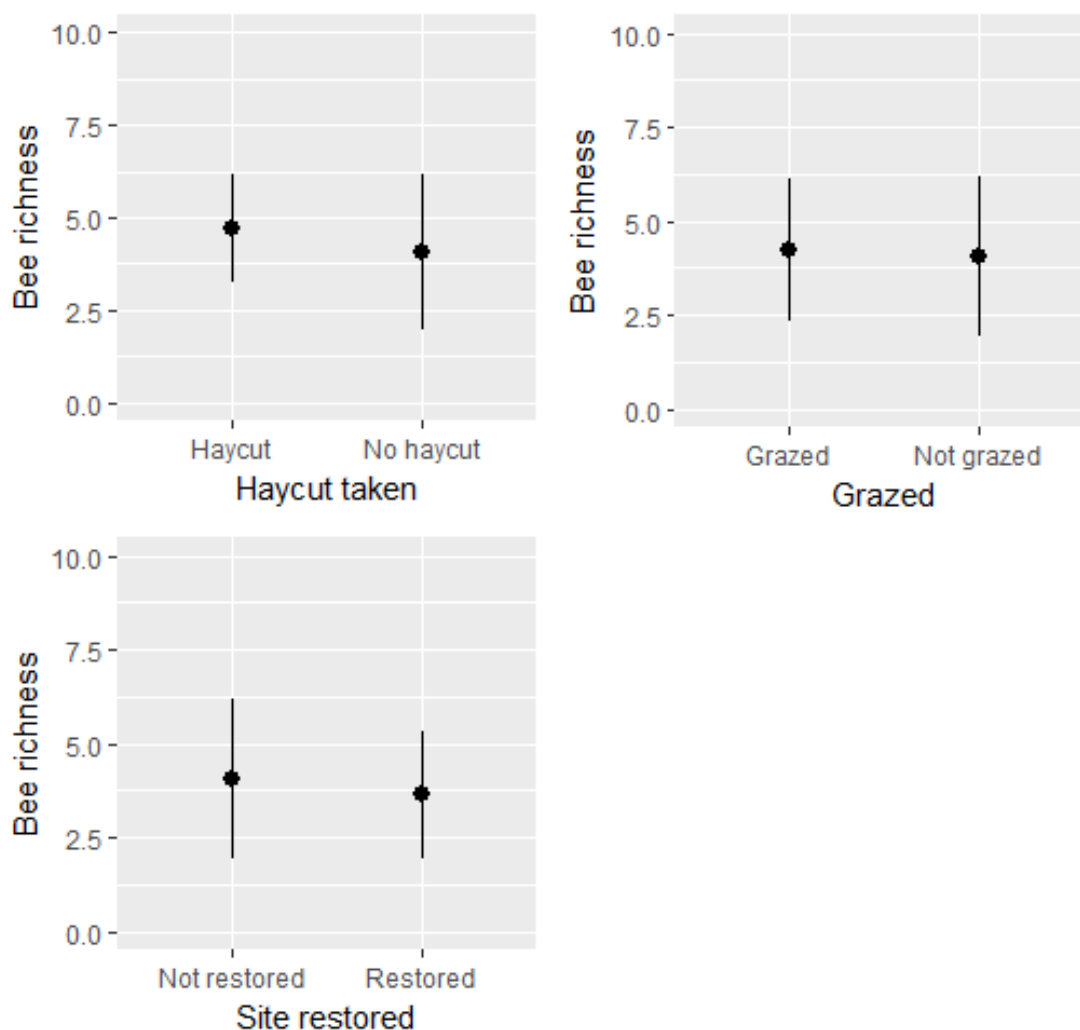


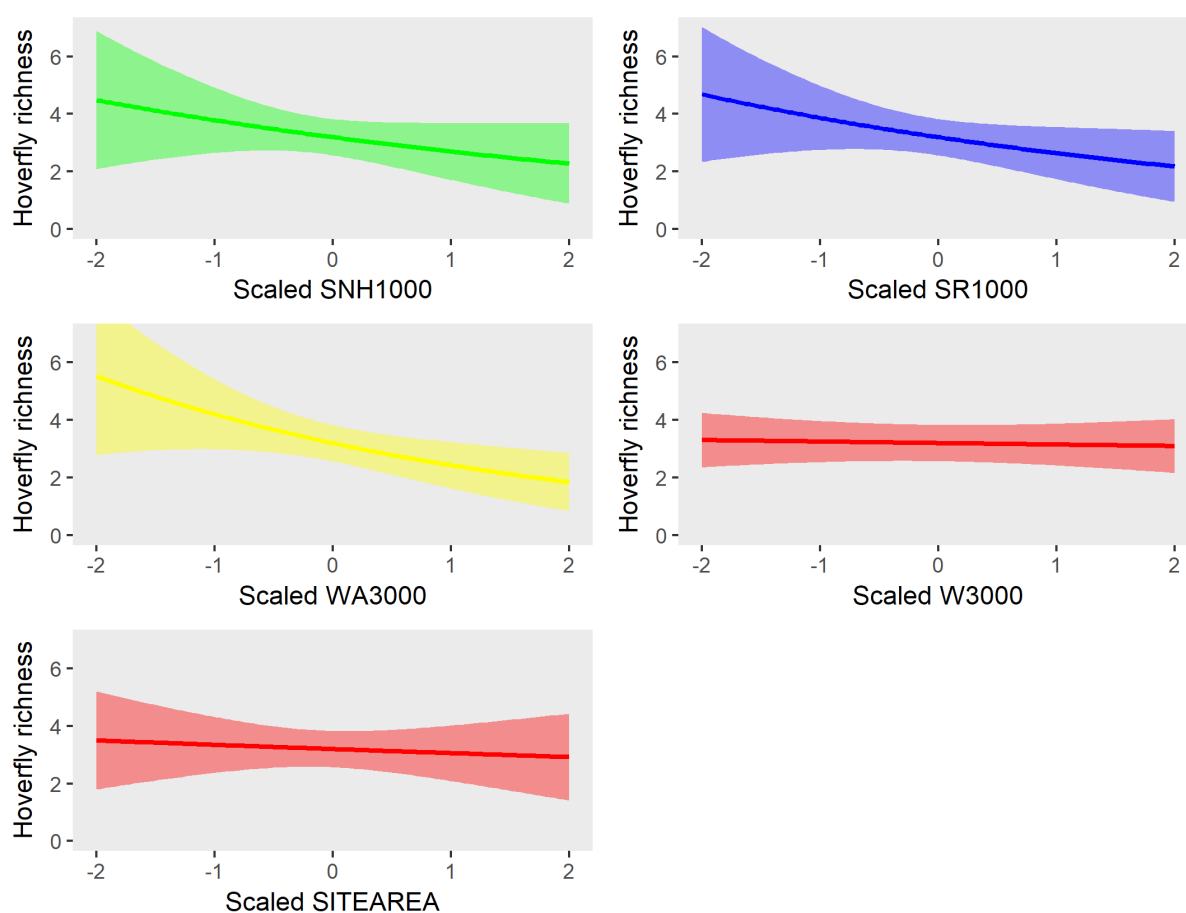
Figure 4.3 Partial effects of independent variables within averaged model of bee species richness (95% CI).

Hoverfly species richness

The model selection process returned 11 models within 2 AICc of the top model. The D^2 value indicated 35% of the variance in the data is explained by the top model. Weighted area (3000m), solar radiation (1000m) and semi-natural habitat (1000m) had the greatest influence within the hoverfly species richness averaged model (see Table 4.10, Figure 4.4 and Figure 4.5). The averaged model also included: water (3000m), site area, haycut, grazing and restoration.

Table 4.10 Model averaged parameter estimates for hoverfly species richness.**Independent variables are scaled to allow comparison**

	Parameter estimates	Adjusted standard error
(Intercept)	1.16169	0.10511
Semi-natural habitat (1000m)	-0.1692	0.14057
Solar radiation (1000m)	-0.19092	0.12909
Weighted area (3000m)	-0.27357	0.12583
Water (3000m)	-0.0162	0.05646
Site area	-0.04525	0.11866
Haycut taken	0.02646	0.07811
Site grazed	0.02513	0.07917
Site restored	0.01652	0.05786

**Figure 4.4 Partial effects of independent variables within averaged model of hoverfly species richness (95% CI).**

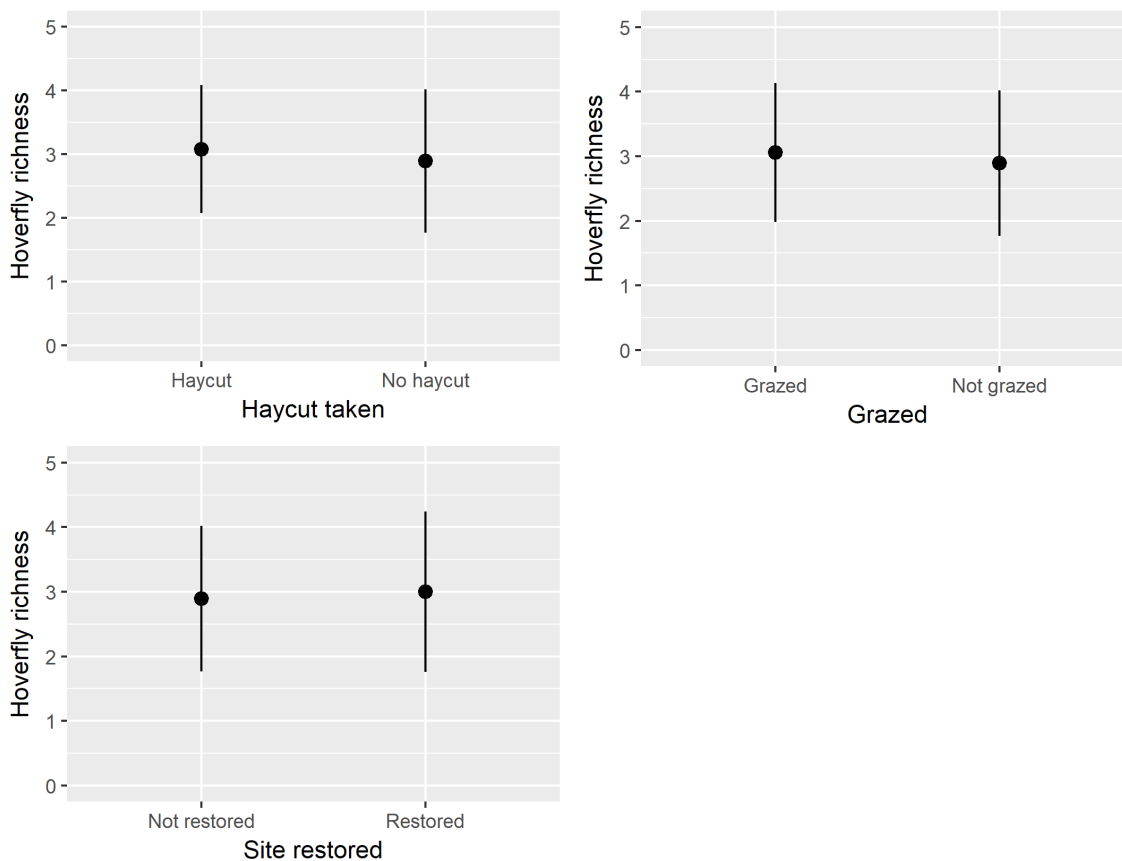


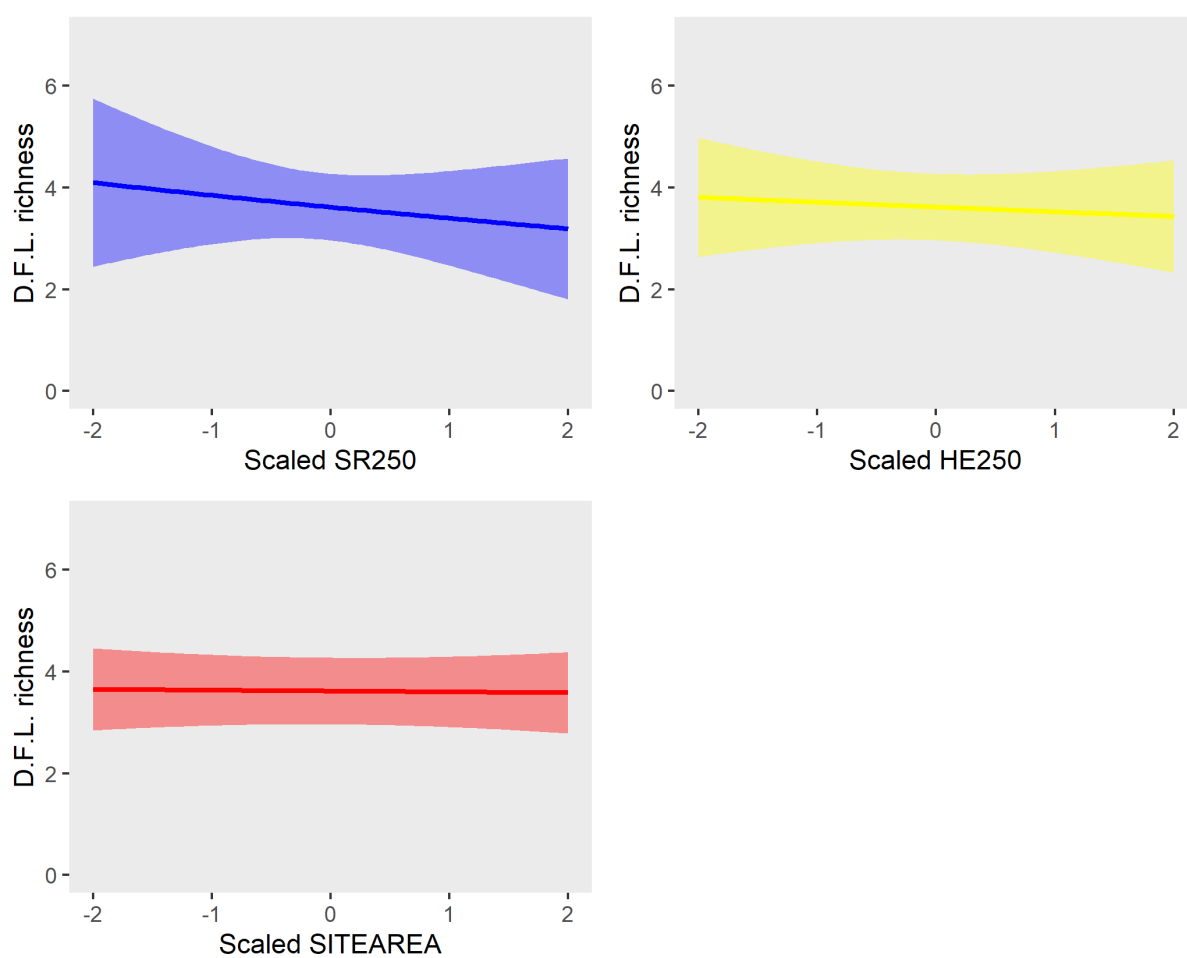
Figure 4.5 Partial effects of categorical independent variables within the averaged model of hoverfly species richness (95% CI).

Day-flying Lepidoptera species richness

The model selection process returned models within 2 AICc of the top model, with the top model explaining 35% of variance in the top model. Grazing (-0.26) had the greatest influence within the day-flying Lepidoptera species richness. Solar radiation (250m), site restoration, haycut and hedgerow density (250m) were also in the model (see Table 4.11 and Figure 4.6 and Figure 4.7)

Table 4.11 Model averaged coefficients for day-flying Lepidoptera species richness.**Independent variables are scaled to allow comparison**

	Coefficients	Adjusted standard error
(Intercept)	1.285214	0.096015
Site grazed	-0.26255	0.08762
Solar radiation (250m)	-0.06247	0.098143
Site restored	-0.03892	0.079761
Haycut taken	-0.02936	0.066967
Hedgerow density (250m)	-0.02601	0.066726

**Figure 4.6 Partial effects of independent variables within averaged model of day-flying Lepidoptera species richness (95% CI).**

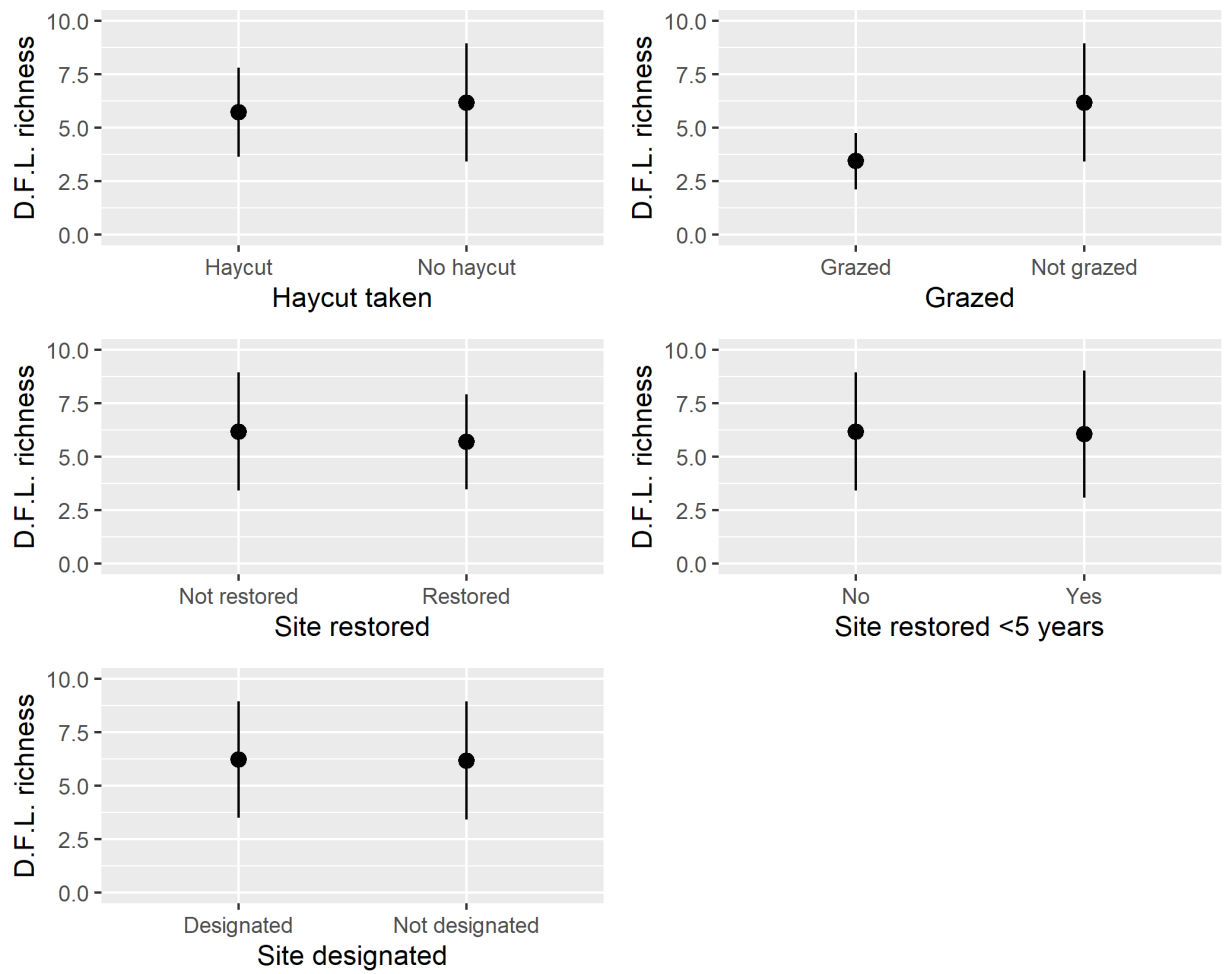


Figure 4.7 Partial effects of categorical independent variables within the averaged model of day-flying Lepidoptera species richness (95% CI).

4.5 Discussion

4.5.1 Combined dataset correlations

Bee abundance was negatively correlated with: water (1000m & 3000m scale), Shannon-Wiener habitat diversity index (250m scale) and hedgerow (3000m scale) (see Table 4.3). Within the NIA areas of high surface water are often associated with artificial water bodies; either reservoirs or remnants from gravel extraction. It may follow that these sites occur in younger, more anthropogenically influenced landscapes. Additionally, landscapes with higher proportion water were negatively correlated with in-site floral cover. This is further supported by the positive correlation between bee abundance and floral richness a relationship observed in previous studies (e.g. Nayak *et al.*, 2015).

Landscape heterogeneity has previously been positively linked to bee diversity, but not abundance (Holzschuh *et al.*, 2016). Heterogeneous landscapes are likely to provide greater nesting opportunity (Steffan-Dewenter, 2002), however the analysis found a negative correlation between bee abundance and Shannon-Wiener habitat diversity index at the 250m scale. At this small scale it may represent the importance of larger patches of semi-natural habitat.

Hedgerows were negatively correlated with bee abundance at the 3000m sampling scale (see Table 4.3). Previous studies have supported hedgerows as part of conservation management for insect pollinators, as such this is converse to expectations (Coulthard *et al.*, 2016; Morandin and Kremin, 2013; Cranmer *et al.*, 2012). This may be indicative of The Circe Principle as posited by Lander *et al.* (2011), which states that favourable habitats may act as a sink to pollinators rather than enabling movement through the landscape; so hedgerows may act as a barrier to insect pollinators in agricultural landscapes. Hedgerows, particularly those which are species rich, can provide high floral density, shelter and nesting/oviposition habitat, and enable navigation in landscapes, which could therefore attract species (Coulthard *et al.*, 2016). However, this theory is contested and conflicted by other published research and thus should be examined in future research (Morandin and Kremin, 2013; Bartomeus and Winfree, 2011). The utilisation of hedgerows by pollinators is poorly understood, this relationship could reflect a preference for non-enclosed habitats, indicative of hedgerows as a barrier to movement across landscapes. Digitisation of hedgerows within urban areas was not within

the scope of this study, 10 of the field sites in this study were within or on the boundary of urban areas, which may have influenced the results.

Negative correlation with semi-natural grassland at the 250m scale is contrary to expectations (Nayak *et al.*, 2015). At such a small scale this may be an influence of in-site edge effect, however this is not supported by a correlation between semi-natural grassland and site area or indeed between site area and bee abundance. This relationship may reflect a need for greater heterogeneity at smaller scales to provide diverse resource needs e.g. nesting, foraging, shelter.

The proportion of semi-natural habitat (3000m scale) was found to be positively correlated with bee abundance (see Table 4.), indicating the importance of semi-natural habitat to bees as a source of both forage and nesting opportunities. This is supported by the literature (Carrié *et al.*, 2017; Nayak *et al.*, 2015; Steffan-Dewenter *et al.*, 2002). Increased areas of semi-natural habitat may also be important in supporting temporal resilience of populations in areas of mass flowering crops, such as oilseed rape (Holzschuh *et al.*, 2016; Diekötter *et al.*, 2010).

Bee abundance was positively correlated with the weighted area variable at 3000m. This measure weights the area of grassland patches within the study radius by their distance to the study site, such that a higher value for this measure indicates larger, closer patches of habitat. A positive relationship between bee abundance and the weighted area variable indicates a preference for landscapes with high connectivity. Jauker *et al.* (2009) found that bee abundance declined with distance from semi-natural habitat within agricultural landscapes, add support to the correlation in this thesis, that is that bees are more abundant in more joined up landscapes.

Bee species richness was positively correlated with floral cover, supporting existing research (Potts *et al.* 2009). This follows the logical argument that larger forage resource supports bigger communities.

Hoverfly abundance and richness was negatively correlated with the weighted area variable at the 3000m scale indicating a relationship with less connected landscapes. Whilst, in contrast to some of the published literature, hoverflies have shown greater ability to utilise agricultural

landscapes than other taxa and many species have close relationships with arable land, which may explain this finding (Öckinger *et al.*, 2012; Jauker *et al.*, 2009).

Day-flying Lepidoptera abundance was negatively correlated with solar radiation, which may reflect differing land uses depending on slope aspect (Singh and Dhillon, 2004) or a correlation with a variable not recorded within this study.

Day-flying Lepidoptera abundance was positively correlated with proportion of semi-natural grassland within 1000m. Most likely this relationship represents a higher availability of resources at the landscape level. Öckinger and Smith (2007) found a positive relationship between butterfly species richness and grassland area at the landscape scale. They posited that landscapes with higher proportions of grassland also held great diversity regarding microhabitats, thus supporting a larger suite of butterflies. There were no correlations between proportion of semi-natural grassland and the other variables in this study suggesting unrecorded resource and opportunity for further research.

The Mann-Whitney U test revealed higher mean rank of Day-flying Lepidoptera abundance on sites without agri-environment schemes or grazing. Additionally, species richness was also higher on un-grazed sites. This indicates a preference for more extensively managed sites. This finding is supported by previous research (Potts *et al.*, 2009) where unfertilised, ungrazed sites with low cutting frequency were shown to have the greatest benefit for butterfly populations. More likely this is an indication of mismanagement or overstocking. Whilst grazing and/or cutting are important for maintaining floral diversity and a heterogenous sward structure, overgrazing or ill-timed grazing can have negative impacts on invertebrate communities (Kormann *et al.*, 2015; van Noordwijk *et al.*, 2012).

Contrary to expectation, day-flying Lepidoptera abundance was negatively correlated with site area. Previous studies have shown a positive relationship between site area and butterfly species richness (Öckinger *et al.*, 2010; Öckinger *et al.*, 2006), however no relationship between site size and butterfly abundance. Öckinger *et al.* (2010) found larger sites were associated with greater species richness and host more specialist species. Site area was not correlated with any of the other variables in this study but may reflect a relationship with site area and a measure of site quality for instance sward structure. This finding presents an opportunity for future research.

Day-flying Lepidoptera species richness was negatively correlated with hedgerow density, a relationship observed in Burgio *et al.*, (2015). This is contrary to expectation from previous literature that has highlighted the importance of hedgerows to both butterflies and moths (Coulthard *et al.*, 2016; Dover and Sparks, 2000). Coulthard *et al.* 2016 found that in arable fields, moth abundance was reduced with distance away from the hedgerow, additionally that like butterflies (Dover and Sparks, 2000), the moths were largely travelling parallel to the hedgerows. As the transects undertaken in this survey were largely central within the site, it may be that areas with higher density of hedgerow overall have a higher abundance of butterflies, but that these individuals are clustered along the linear components.

These correlations do not align with proposed causation of nestedness within the samples (see Chapter 2). For instance, it may be expected to see a positive correlation between species richness and the connectivity metric (weighted area) if isolation were a causative factor. Bee species richness was correlated with floral cover (Section 4.4.1) and on a sample-by-sample basis this study found a significant relationship between floral cover and species richness (Section 3.4.4). This relationship may indicate a gradient of habitat quality, which could create nestedness in samples. Nestedness is a common phenomena in ecology (Valdovinos *et al.*, 2016) and both the drivers, effects of, and even methodologies for assessment, are diverse and not without criticism (Johnson *et al.*, 2013; James *et al.*, 2012; Ulrich *et al.*, 2009).

Whilst no firm conclusions can be drawn from these results it provides opportunity for future research into the community structure seen in this study.

4.5.2 Spatial scale selection

The effects of spatial scale or landscape extent were examined at three scales, based on assumptions of flight distances from the literature (see Chapter 2 and Section 4.3.3). Below, the findings of the univariate models (see Section 4.4.5) are discussed in the context of the current literature.

The species richness and abundance of bees was better modelled at the large (3000m) and moderate (1000m) spatial scales (see Table 4.7). The effect of semi-natural habitat and

grassland and proportion of built up/urban areas on species richness at smaller spatial scales may reflect the shorter flight distances of solitary bees. For example, Zurbuchen *et al.*, (2010) found that the solitary bees *Hoplitis adunca* and *Chelostoma ranunculi* demonstrated reduced reproductive fitness at increasing distance from forage to nest, with negative impacts being felt at as little as 150m. Indication of the importance of larger scales to abundance may reflect the flight distances of social species, particularly bumblebees, which contribute most the bee records (see Section 3.4.1). Osborne *et al.* (2008) found that bumblebees frequently travelled distances of 1.5 km from their nest to a forage field to collect floral resources, however, as this was the maximal distance at which data was collected, it is highly likely that flight distances are often longer. Body size has been positively correlated with flight distance, for instance *Xylocopa flavorufa*, a large carpenter bee associated with coastal habitats in Kenya, has had flight distances of 10km recorded (Pasquet *et al.*, 2008), as such we may expect bumblebees to perceive landscapes at a greater scale.

Hoverfly abundance was best modelled at the 250m and 1000m scales (see Table 4.7), whilst richness was more closely modelled at the 3000m scale. Previous studies have shown hoverflies to move only small distances from source habitats within inhospitable/agricultural landscapes, therefore the selection of variables sampled at the 250m scale is as expected (Kohler *et al.*, 2008; Wratten *et al.*, 2003).

Day-flying Lepidoptera abundance and richness demonstrated best model fit with most variables sampled at the smaller spatial scales (250m and 1000m) (see Table 4.7). Krauss *et al.* (2003) found butterfly species richness to be affected by landscape factors at a scale of 250m. Conversely, some species are seen to fly 1211m in non-linear movements (Cant *et al.*, 2005), therefore the potential for larger scale impacts should not be entirely discounted.

4.5.3 Modelling interpretation combined dataset

Bees

Within the averaged model for bee species richness hedgerow density (3000m) and floral cover were shown to have the strongest effects. To a lesser extent, semi-natural grassland, haycut, site restoration, solar radiation and grazing also effected the model.

The negative relationship with hedgerow density is contrary to expectation (see Section 4.5.1.).

The strong positive association seen in the model with floral cover follows expectation. Higher levels of floral cover are associated with greater provision of both nectar and pollen resources and as such are expected to attract greater pollinator abundances (Ebeling *et al.*, 2008). Ebeling *et al.*, (2008) found solitary bee, bumblebee and butterfly species richness to be positively linearly correlated with blossom cover, however, this relationship becomes saturated at approximately 15% blossom cover, suggesting other limiting factors. There is a developing literature examining the pollen and nectar loads (Hicks *et al.*, 2016; Dicks *et al.*, 2015), furthermore the protein quantity and amino acid composition between differing pollen sources is being considered (Weiner *et al.*, 2010). With these developments and the relationship with floral cover observed we may expect future analyses to have opportunity to consider nutritional benefit of floral resources at a finer scale.

Hoverflies

The averaged model for hoverfly species richness showed greatest effects from semi-natural habitat (1000m), solar radiation (1000m) and the distance weighted area variable (3000m). Site area, haycut, water, grazing and restoration were also in the model but had much weaker influence.

Solar radiation was negatively associated with species richness; this is surprising considering the poikilothermic nature of hoverflies. Land use is likely to differ in landscapes of different aspects, which could affect the response (Singh and Dhillon, 2004), however, the Nene Valley is relatively flat throughout and as such great solar radiation/temperature extremes are unlikely to be experienced. Therefore, this metric provides opportunity for future research.

The negative association with semi-natural grassland and distance weighted area may be reflective of the contribution of aphidophagous species to the hoverfly richness in this study. Jauker *et al.*, (2009) found that hoverfly abundance increased with distance from a semi-natural habitat into agricultural matrix and richness was unaffected. Raymond *et al.*, (2014) found that cultivated fields and field margins provided an important resource for

overwintering immature hoverflies, the negative relationship with semi-natural grassland may reflect this relationship.

Day-flying Lepidoptera

Grazing had the largest overall effect within the day-flying Lepidoptera species richness model, showing a negative effect. As discussed in section 4.5.1 it is likely that this reflects overstocking or poorly timed grazing and the subsequent effects on sward height and increased disturbance.

4.5.4 Spatial autocorrelation

A low level of negative spatial autocorrelation was detected in the residuals of the GLM of bee species richness. This indicates that neighbouring samples were significantly more dissimilar than expected (Gettis and Ord, 1992), although the levels of autocorrelation were overall low. Negative spatial autocorrelation is uncommon within ecology, with positive autocorrelation a more common phenomenon (Griffith, 2006). Whilst positive autocorrelation may result in the artificial inflation of sample size and result in over reporting of significant results, the opposite may be true in the case of negative autocorrelation (Legendre and Legendre, 2012). The study of negative autocorrelation has received little attention (Griffith, 2006); although here we may assume spurious autocorrelation as an effect of spatial scale. The grain and extent of a study may introduce spurious negative spatial autocorrelation for example at a fine scale, neighbouring sites may demonstrate a high degree of variability or dissimilarity, whilst conversely broad scale analysis may exhibit clustering or positive autocorrelation (Overmars *et al.*, 2003). Independent variables within the GLM models in this study were of differing spatial scales; however, where parameters with the greatest relative importance are either in site (local) or fine landscape-scale (e.g. 250m or 1000m) we may expect dissimilarity in neighbouring sites. Negative spatial autocorrelation may be a result of high unexplained variance within the model, indicating that other environmental factors not recorded within this study are affecting variation in the abundance and species richness, furthermore this may highlight the relative importance of local scale variables over landscape.

Sampling strategy may also introduce some spatial autocorrelation, the sequence of site surveys was randomised to reduce recorder bias and the risk of positive autocorrelation (through measurement of neighbouring sites on the same day). This may have introduced some negative autocorrelation by chance e.g. if further apart field sites were surveyed under the same weather conditions or same point within the field season. The spatial autocorrelation seen in these models was low and as such likely to be of minimal influence, however, for future studies a larger sample size, study at a greater number of spatial scales and stratified sampling may address issues of spatial autocorrelation.

4.5.5 Resolution of data

Processing required each raster dataset to have the same cell size for calculation. For this study a cell size of 10m was used, reflecting a compromise between the finest (25cm) and coarsest (25m) grain of data available and considered the computational limitations when using high resolution datasets. Absence of fine scale land cover data may mean that nuances of landscape dynamics are missed. For instance, the water map was produced from 25cm resolution Mastermap data, resampling could mean that smaller water bodies, of perhaps greater importance for terrestrial invertebrates, such as drainage ditches and ponds are not picked up in the final raster.

4.6 Chapter summary

- Bee abundance was found to be positively correlated with proportion of semi-natural habitat and floral cover and negatively correlated with proportion of water, Shannon Weiner index and hedgerow density.
- Hoverfly abundance was negatively correlated with the weighted area variable.
- Day-flying Lepidoptera abundance was negatively correlated with solar radiation, agri-environment scheme and grazing and positively correlated with proportion of semi-natural habitat.
- Bee richness was positively correlated with floral cover.
- Hoverfly richness was negatively correlated with the weighted area variable.
- Day-flying Lepidoptera richness was negatively correlated with hedgerows, grazing and site area.
- There was a high level of over dispersion in the abundance models for bees, hoverflies and day-flying Lepidoptera. Abundance was therefore excluded from the modelling.
- The bee richness model had negative associations with hedgerow density, site restoration and solar radiation and positive associations with semi-natural grassland, floral cover, haycut and grazing.
- The hoverfly richness model had negative association with semi-natural habitat, solar radiation, water, site area and the weighted area variable.
- The day-flying Lepidoptera richness model had negative associations with site grazing, solar radiation, site restoration, haycut and hedgerow density.

The next chapter will explore these findings as predictive models within GIS and view the potential applications of such spatially explicit modelling.

Chapter 5 Modelling pollinator abundance and species richness using GIS

5.1 Introduction

In this chapter GIS models will be produced based on the influence of landscape variables on the abundance and species richness of bees, day-flying Lepidoptera and hoverflies. The subsequent models are tested using a test dataset to assess the ability of the models to predict pollinator abundance and species richness.

5.1.1 Ecosystem service modelling

Mapping is essential within an ecosystem service framework, enabling the identification of both service sources and sinks (Zulian *et al.*, 2013). By modelling ecosystem services, we have opportunities to both assign economic values to landscapes, but also optimise conservation, targeting landscapes where habitat creation will have the most significant impact or return on investment (Stürck *et al.*, 2014). Here two approaches for mapping pollination services are discussed:

InVEST is an interdisciplinary collaborative project researching and developing software to map and model several ecosystem services. Based on the models of Lonsdorf *et al.* (2009), InVEST uses a series of equations to predict crop pollination and demand, using parameters including estimated availability of nesting and forage resources, and species foraging distances. This approach was adapted and applied to pollinators at the European scale in Zulian *et al.* (2013); based on this method it was calculated that a deficit of 25-32% would occur in crop production through the loss of insect pollination, reducing to 2.5% when only examining a single guild of solitary bees with a short flight range.

EcoServ, a UK based project focussed on nine ecosystem services, aims to map ecosystem services at a local or regional scale. EcoServ maps pollination demand and provision and includes a model that predicts provision based on distance from potential bee nesting habitat based on three broad habitat types defined in Schulp *et al.*, (2014) and Winn *et al.* (2015).

Both approaches have limitations, a key one being that the models and model weightings produced are dependent on having sound ecological knowledge. Whilst InVEST requires knowledge of both the habitat requirements and foraging ranges of the species within a study area, EcoServ makes broad assumptions applying both the same habitat requirements and foraging ranges to all species. Whilst the algorithms behind InVEST have tested well against observed data (Lonsdorf *et al.*, 2009), the models are dependent on expert knowledge and theory and may not transfer well between different geographical regions or within different ecological communities. Secondly, these models can only have value if they are verified in the field.

5.1.2 Climatic envelope models

The term Anthropocene was coined in the 1970s, referring to the current era in which humans have the predominant effect on both climate and environment (Steffen *et al.*, 2011).

Modelling the potential effects of anthropogenic climatic change has since become a major focus of modern science, in terms of both the abiotic impacts and how this could affect ecosystems. Of particular interest are the potential effects on species range distributions, especially in organisms of limited dispersibility or restrictive habitat requirements. For example, Aguirre-Gutiérrez *et al.* (2016) have detected northward range expansions in European bees, hoverflies and butterflies.

Due to their nature, predictive modelling of range shifts under differing climatic change scenarios are usually at large international scales. A growing number of studies explore the potential effects of anthropogenic climatic change on invertebrate communities including: butterflies, beetles, insect pest species and bumblebees (e.g. Menéndez *et al.*, 2014; Bebber *et al.*, 2013; Schweiger *et al.*, 2012; Roberts *et al.*, 2011). Broad-scale habitat requirements are extracted from data on the basis of existing distributions, these are then extrapolated under different climatic change scenarios to present visual representation of potential range expansion, a method called climatic envelope modelling (Roberts *et al.*, 2011; Hijmans and Graham, 2006). Such models are dependent on a sufficient amount of non-biased presence data, with a good geographical spread; similarly, they are also likely to overlook important environmental factors or interacting factors (Hijmans and Graham, 2006). As studies are

generally carried out at extremely large scales, landscape and local scale factors, ability to disperse, barrier effects and population dynamics are likely to be overlooked.

5.1.3 Habitat suitability modelling

Data collection for habitat suitability consists of two main routes, either using pre-existing data such as that found in museum records or recording sources such as the NBN Gateway or generating new data for analysis. Whilst using pre-existing data reduces the resources required for a study, this mode has its pitfalls as it is unlikely that data has been collected systematically. Data is often collected by multiple recorders using different methods or may represent token records and thus cannot provide information on absences or abundances. Similarly, data points may represent a number of years, invalidating the environmental data if there is a large disparity in year of recording. Collecting new data for a study negates these issues, ensuring that data collection is systematic and representative with the downside of being limited in terms of amount of data.

Several approaches to modelling and mapping species richness have been developed, including:

Maximum Entropy modelling (MaxEnt): a species distribution model, using environmental data to explain the distributions of species based on presence-only data (Yackulic *et al.*, 2013). MaxEnt functions by comparing the sites environmental conditions where species presence is known compared to those which are unknown (pseudo-absences) (Merow *et al.*, 2013). Research indicates the method is equivalent, in terms of predictive power to GLM but, due to its relative modernity lacks model diagnostics and is frequently used uncritically (Renner and Warton, 2013).

Ecological Niche Factor Analysis (ENFA): Is a method dependant on presence-only data, for which marginality and specialisation within environmental variables are calculated for a species. Marginality is how the mean of the presence-records environmental variable data lies in relation to the global mean of that environmental variable; whilst specialisation is the breadth of the environmental variable within which the species is found (Basille *et al.*, 2008).

Artificial Neural Networks (ANN): Are complex models based on machine learning, where training data are repeatedly fed into an ANN algorithm; once the linkages are learned the environmental data from which a prediction is to be made can be used. These models can have high predictive power but interpretation of parameter contributions is difficult. Until recently this was considered a ‘black box’ method and, as such, made interpretation of the ecological mechanisms behind the model impossible (Giam and Olden, 2015).

The above methods are examples of species distribution models which may be stacked to infer predictions of species richness. However, this is dependent on sufficient availability of presence data for each species to be modelled, which is problematic especially when considering infrequent species (Dubuis *et al.* 2011; Guisan and Rahbek, 2011).

In application, the Forestry Commission produced the Biological and Environmental Evaluation Tools for Landscape Ecology (BEETLE) (Watts *et al.*, 2005). These tools apply landscape ecology principals to predicting species diversity within a landscape using GIS techniques. The models produced through BEETLE are dependent on three components:

- Landcover module: A base layer made up of a habitat classification map.
- Focal Species module: The habitat type, a species (or group of species) requires plus the minimum area of that habitat which is required.
- Connectivity module: Connectivity based on the dispersal ability of the focal species and landscape permeability.

Whilst developed by the Forestry Commission for broader species use and application this method has severe disadvantages due to the assumptions required by BEETLE. The model is dependent on:

- A strong association with a broad habitat type, this modelling approach may not be suitable for species dependent on a matrix of habitat types.
- A clear understanding of the area of habitat required to support a sustainable population of the focal species.
- A good understanding of the ability of the dispersal distance of a focal organism. Similarly, when used for a group of species are being studied the assumption is they have the same ability to disperse.
- Understanding of how the focal species travel through the landscape and how the habitat type effects the ability for that species to permeate.

For well-studied organisms with known, specialist habitat requirements this method provides a cheap and relatively easy way to predict potential ranges/suitable habitat for species and to model the effects of potential landscape change, for instance in the case of the Forestry Commission the effect of timber production or reforestation. However, such stringent dependencies on prior sound ecological knowledge on the requirements of a species or a species group may not be appropriate for invertebrate groups which are often poorly understood.

For this research a method akin to the macroecological approach was taken, addressing the difficulties of missing species data and enabling the production of GIS models (Dubuis *et al.* 2011). Whilst this approach cannot predict individual species distributions it can provide insights into general patterns of distribution.

Traditional approaches such as linear modelling and analysis of variance have been largely superseded by more complex methods such as Generalised Linear Modelling (GLM), enabling the handling of different statistical distributions of data such as count data. Collecting of standardised presence-absence data allowed for a more statistically robust and transparent approach to modelling, therefore GLM was chosen for this study both due to its flexibility and for reasons of practicality, being able to produce a GIS model. This method has been used for numerous taxa: dung beetles (Lobo and Martín-Piera, 2002), plant species richness (using GLM Luoto *et al.*, 2002a and with linear modelling Wohlgemuth, 1998), birds (Cherkaoui *et al.*, 2009) and butterflies (Luoto *et al.*, 2002b).

This chapter compliments the modelling techniques used in Chapter 4, but has been restricted to landscape factors alone to enable the development of GIS hotspot maps.

5.2 Aims and Objectives

- **To produce GLM models exploring the relationship between abundance and species richness of insect pollinators based on landscape variables.**

Models will be produced using the information theoretic approach, finding the landscape variables that explain the most variance in the abundance and species richness data.

- **To produce GIS models predicting the abundance and species richness of pollinator groups in the Nene Valley NIA.**

Maps of the abundance and species richness of the four pollinator groups (bees, day-flying Lepidoptera, hoverflies and combined pollinators) will be produced. General geographic distributions will be discussed.

- **To test the resulting predictive models with a test dataset to explore model predictive power.**

The ability for the models to be used in a conservation setting will be explored.

5.3 Methods

Timed transect walks were carried out at 14 sites in 2013 and 20 sites in 2015. Bees, day-flying Lepidoptera (DFL) and hoverflies were hand-netted along the transect and identified either in the field or taken for identification. The location and description of these sites, along with the full field methodology can be found in Chapter 2.

Three spatial scales, 250m, 1000m and 3000m were selected for this investigation, these distances were considered to best reflect the range of movement of the group of study organisms (see Chapter 2).

Abundance data was averaged across all surveys for each site and rounded to the nearest whole number to produce a metric of insect abundances. Rarefaction of species richness data collected in the field was carried out within EstimateS, with species richness estimates being taken at 25 samples (the lowest number of subsamples taken at a site) (Colwell *et al.*, 2012).

Data were standardised or scaled in R subtracting the mean and dividing by the standard deviation for each variable allowing meaningful comparison of coefficients in the models. Models were produced using the landscape variables alone as data on the local scale variables were not available for the entire study area. The weighted area variable was also excluded at this stage as this was a manual calculation and it was not possible to apply this to the entire study area. The model selection process follows Chapter 4 and was adapted from Burnham and Anderson (2003) and carried out in R (R development core team, 2016).

The residuals of the top model for each taxonomic grouping was tested for spatial autocorrelation using Moran's I (See Chapter 2).

Predictive GIS models were produced using the raster calculator function in ArcGIS. The GLM models produced from the model selection procedure were applied to the GIS layers (see Chapter 2 for layer creation methodology). Averaged model coefficients (β) and the GIS layers representing the parameters (x) were applied to the equation (see Figure 5.1 for example):

$$\text{Exp}(\beta_0 + \beta_1x_1 + \beta_2x_2 \dots)$$

For an example of a GIS layer used in these analyses see Appendix 1.19.

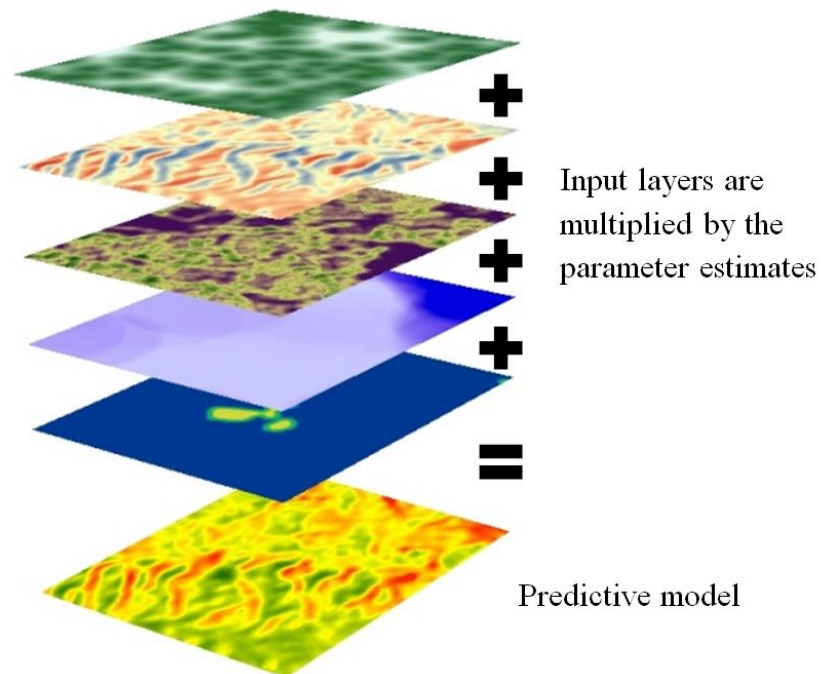


Figure 5.1 Illustration of model production within a GIS. The GLM formula is applied to input layers, resulting in a predictive GIS model.

GIS models were restricted to the study area, the Nene Valley NIA plus a 3km buffer, and were clipped to represent grassland habitats found in the Land Cover 2007 dataset, to reflect the data used to build the statistical models. The resulting model had a cell size of 10m. Models produced should be interpreted as relative abundance or richness rather than an explicit prediction, maps were coloured such that red would highlight areas of higher abundance or species richness and green areas of lower abundance or species richness.

The models were tested using data collected in Northants by a former PhD student, Sam Tarrant (Tarrant *et al.*, 2013; Tarrant, 2010), using a Spearman's Rank correlation to explore the relationship between the values predicted by the model and pollinator richness observed in the field.

5.4 Results

Models were checked for collinearity between variables, and the resulting sub-global models are presented in Table 5.2. The c-hat values indicate overdispersion in the abundance models (see Table 5.2). The species richness models were not considered to demonstrate significant overdispersion and were taken forward for further analysis.

Table 5.1 Abbreviations for landscape variables used in models

Landscape variables
HE-Hedgerow density
SR-Solar radiation
SNH-Semi-Natural habitats
BU-built-up/urban area
WA-weighted area
SNG-Semi-natural grassland
SW-Shannon-Wiener index
W- Water

Table 5.2 Sub-global models for flower visiting insects (abundance and species richness) and overdispersion parameter (see Table 5.1).

	Model terms	C-hat
Mean abundance		
Bees	W3000+SW250+SNH3000+HE3000+SR3000+SNG250	7.16
Hoverflies	W1000+SW250+BU250+SNH1000+HE250+SR1000+SNG1000	2.29
D.F.L.	W250+SW1000+BU1000+SNH3000+HE1000+SR250+SNG250	4.36
Rarefied species richness		
Bees	W3000+SW1000+BU250+SNH3000+HE3000+SR250+SNG1000	1.9
Hoverflies	W3000+SW3000+BU250+SNH1000+HE3000+SR1000	1.53
D.F.L.	W250+SW250+BU3000+SNH3000+HE250+SR250+SNG250	0.96

5.4.1 Bee species richness

The model selection process revealed four models within two AICc of the top model, the top model itself explaining 27% of the variation in the data.

Water, hedgerow density, solar radiation and Shannon wiener diversity were negatively associated, whilst semi-natural grassland were positively associated with bee species richness (Table 5.3). Hedgerow density, solar radiation and water were shown to have the strongest independent effects within the averaged model (Figure 5.7).

Table 5.3 Model averaged parameter coefficients for bee species richness.

	Parameter estimate	Adjusted SE
(Intercept)	1.50285	0.08627
W3000	-0.11778	0.11968
HE3000	-0.19785	0.084
SR250	-0.19264	0.08819
SW1000	-0.08358	0.09915
SNG1000	0.02126	0.06004

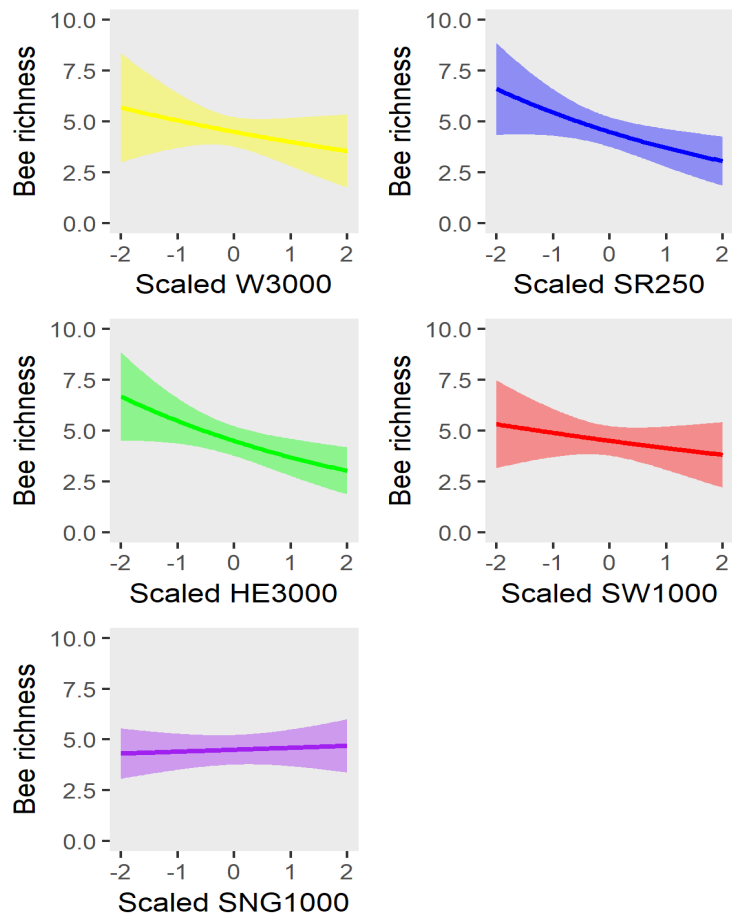


Figure 5.2 Partial effects of parameters in averaged model of bee species richness (95% CI).

The predictive model for bee species richness depends on hedgerows recorded at the 3000m scale, hence the resulting GIS model had to be 3km within the NIA border to represent data availability (see Figure 5.3). The map shows higher predicted species richness in the East of the NIA, with particularly rich areas around the Rockingham forest area (see Figure 5.3).

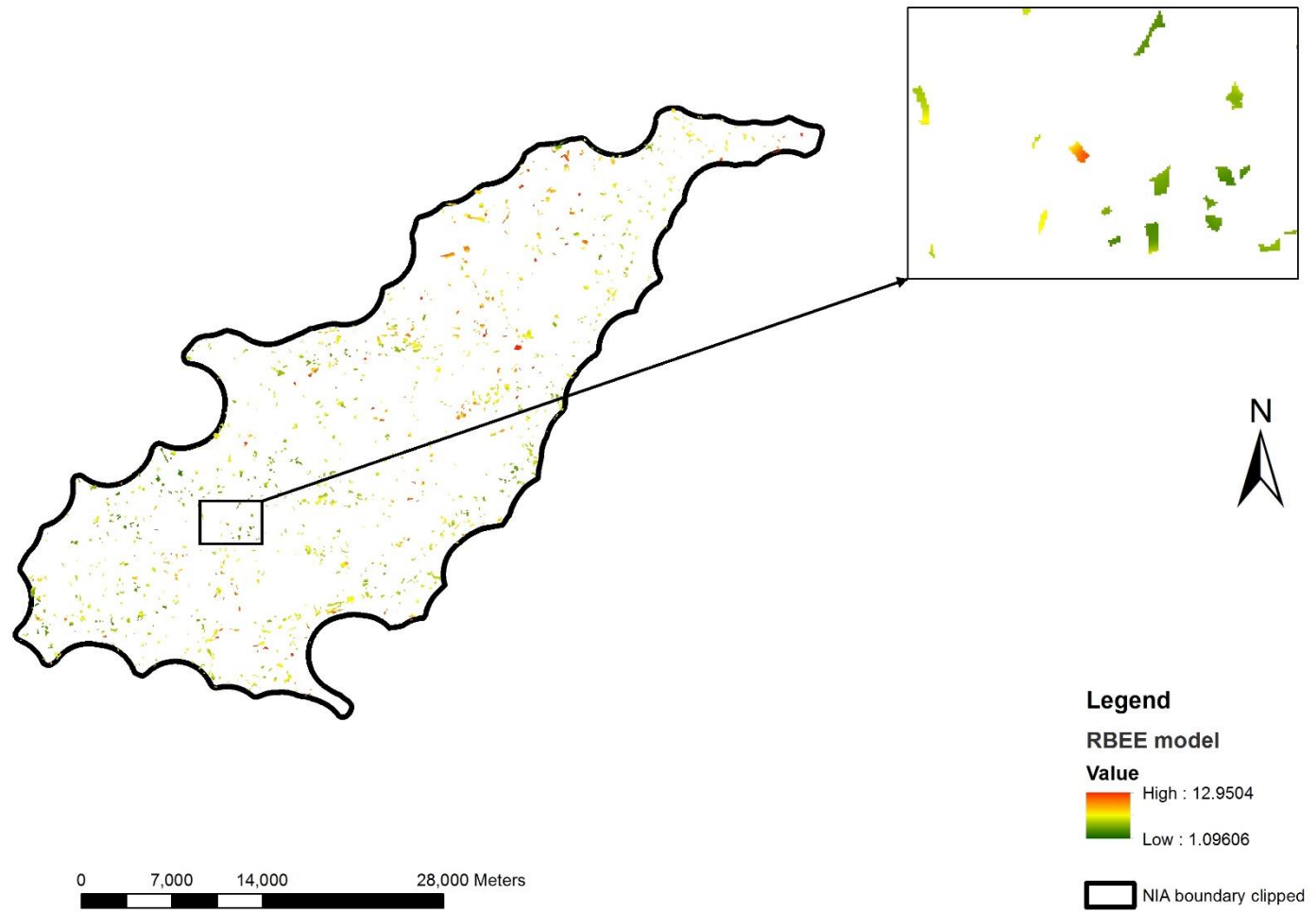


Figure 5.3 Map of predicted bee species richness in grasslands in the Nene Valley NIA. The box shows an expanded view of part of the area.

5.4.2 Hoverfly species richness

There were four models within the top model set for hoverfly species richness, the top model accounting for 21% of the variance in the data.

Semi-natural habitat and solar radiation and water were negatively associated, whilst the Shannon-Wiener index was positively associated with hoverfly species richness (see Table 5.43). Semi-natural habitat and solar radiation were shown to have the strongest independent effects (see Figure 5.9).

Table 5.4 Model averaged parameter coefficients for hoverfly species richness.

	Parameter estimate	Adjusted standard error
(Intercept)	1.19646	0.10138
SNH1000	-0.29219	0.10989
SR1000	-0.24603	0.09828
W3000	-0.02405	0.06572
SW3000	0.01537	0.05253

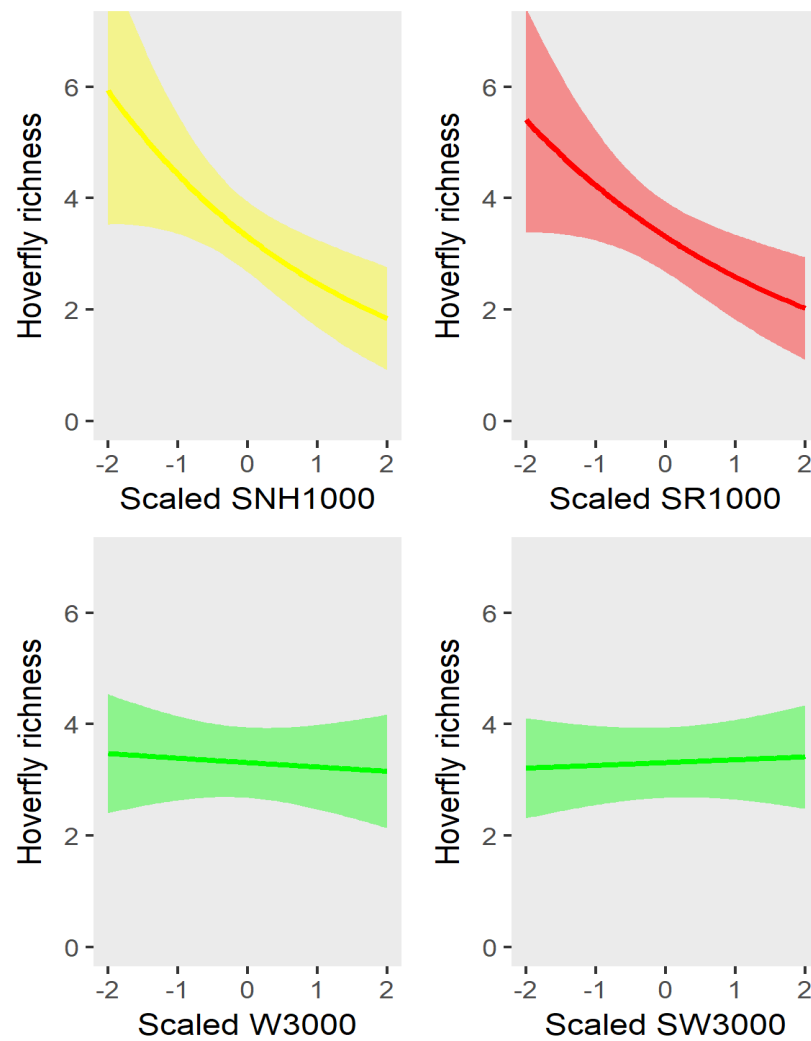


Figure 5.4 Partial effects of parameters in averaged model of hoverfly species richness (95% CI)

The map of predicted hoverfly species richness indicated a strong positive west to east and south to north gradients in hoverfly species richness (see Figure 5.5).

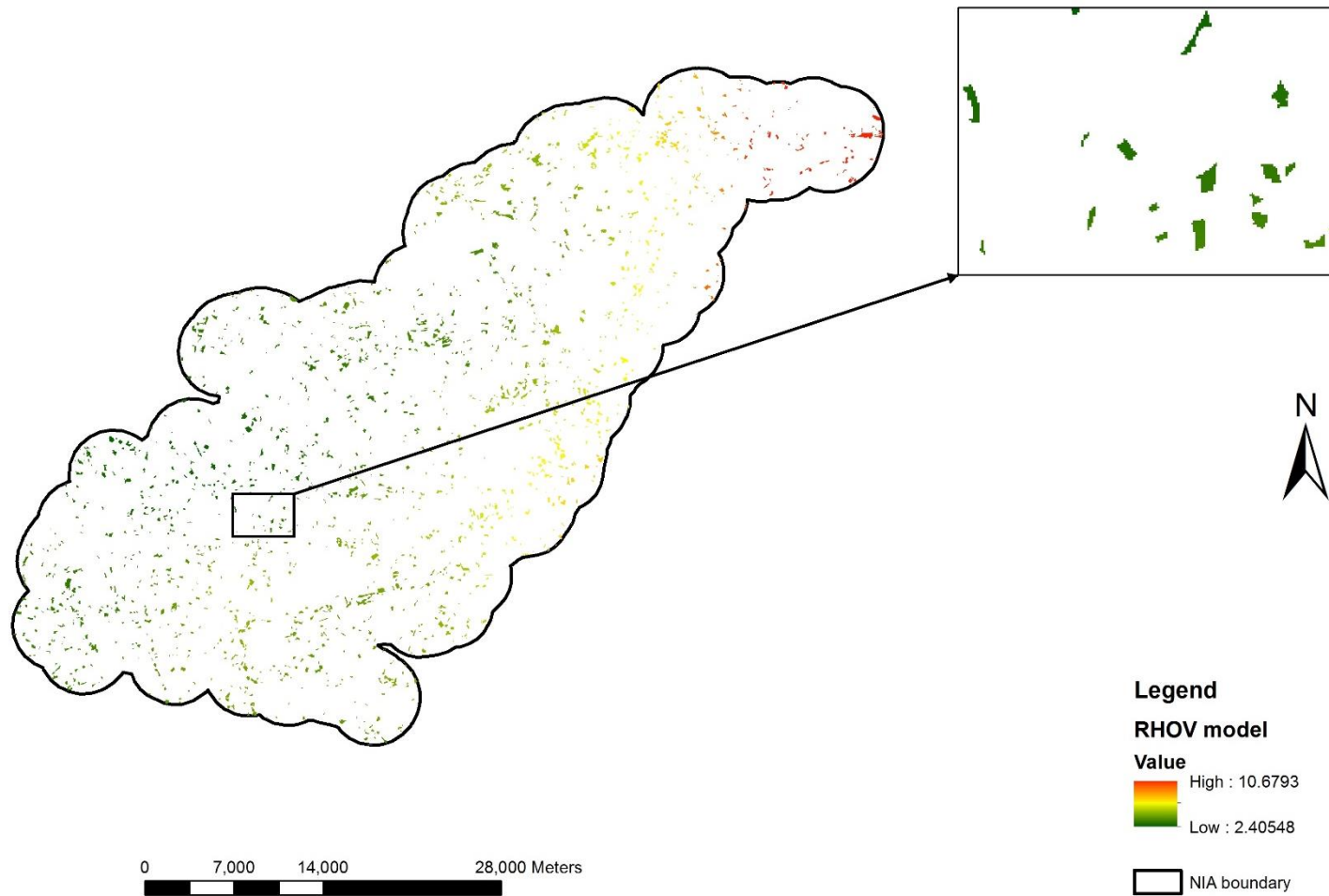


Figure 5.5 Map of predicted hoverfly species richness in grasslands in the Nene Valley NIA. The box shows an expanded view of part of the area.

5.4.3 Day-flying Lepidoptera species richness

The model selection process found 18 models in the top model set, the top model explaining 20% of variation. Water and solar radiation have the strongest independent effects on day-flying Lepidoptera species richness in the averaged model (see Figure 5.6). Proportion of surface water within 250m was found to be positively associated with day-flying Lepidoptera richness whilst solar radiation, hedgerow density, Shannon-Wiener diversity and proportion of semi-natural grassland were negatively associated (see Table 5.4).

Table 5.5 Model averaged coefficients for day-flying Lepidoptera species richness.

	Parameter estimate	Adjusted SE
(Intercept)	1.30928	0.093958
W250	0.128556	0.100014
SR250	-0.11108	0.112722
HE250	-0.04213	0.0802
SW250	-0.00687	0.03824
SNG250	-0.00743	0.037837

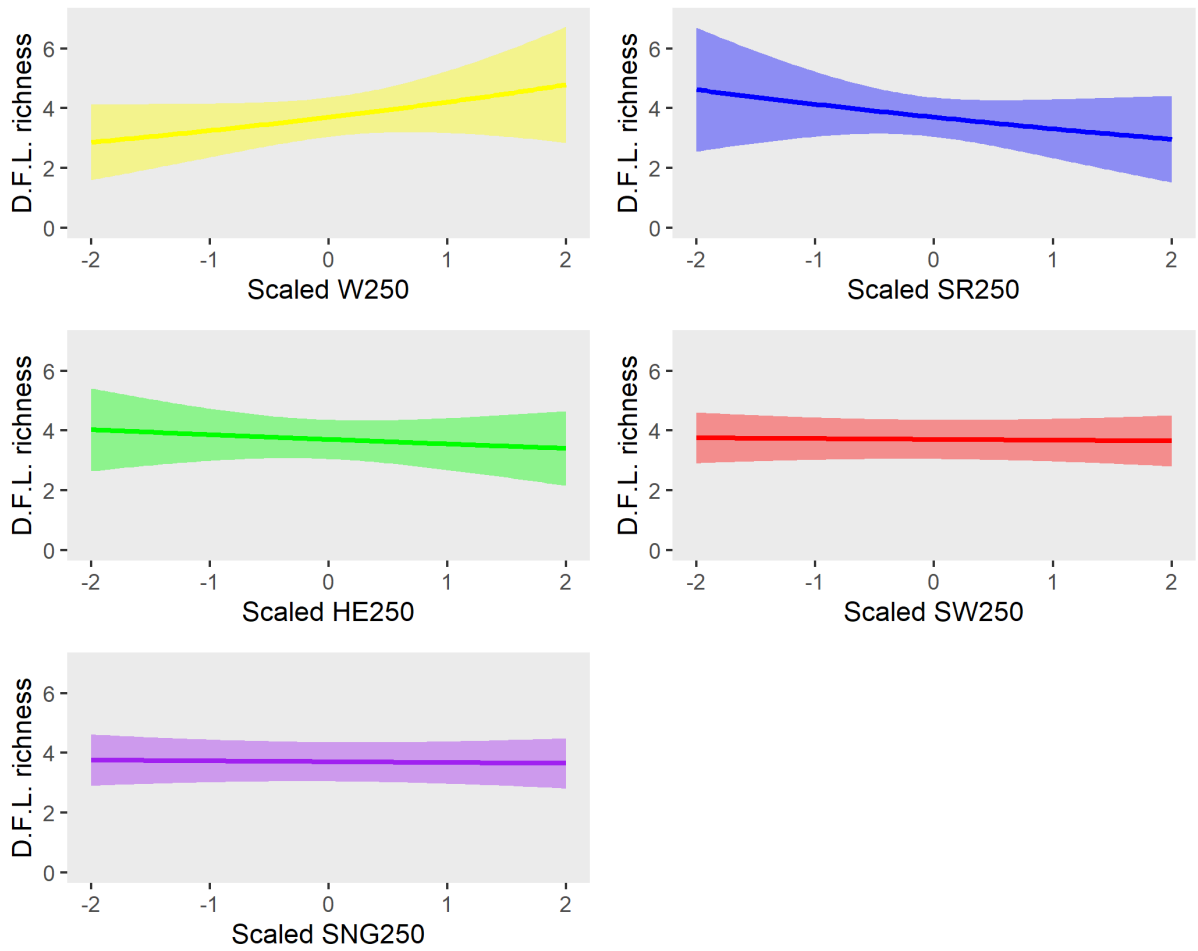


Figure 5.6 Partial effects of averaged day-flying Lepidoptera species richness (95% CI).

Figure 5.7 shows areas of higher day-flying Lepidoptera species richness along the river and lower richness to the north west of the Nene Valley NIA.

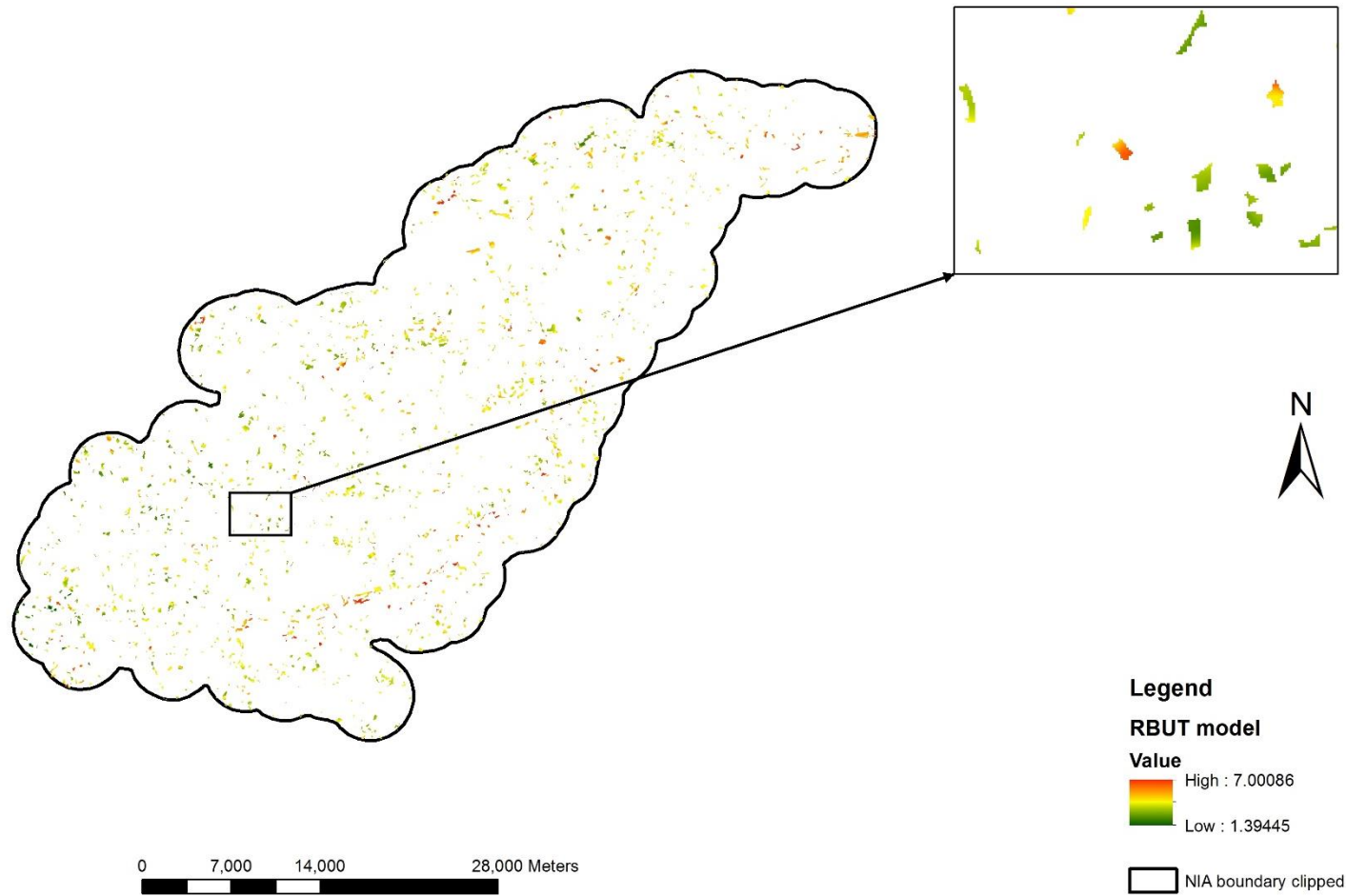


Figure 5.7 Map of day-flying Lepidoptera species richness in grasslands in the Nene Valley NIA. The box shows an expanded view of part of the area.

5.4.4 Testing the models

The test data set consisted of six data points from within the Nene Valley NIA recorded in 2007 in Tarrant *et al.* (2013). Analysis of the observed species richness from Tarrant *et al.* (2013) and the predicted species richness for each flower visiting insect group was analysed using Spearman's Rank correlation. The results showed no significant correlation between the predicted and expected values indicating that the models do not sufficiently predict species richness of flower visiting insect richness, or that sampling was insufficient to reflect full diversity (see Table 5.5).

Table 5.6 Spearman's Rank Correlation of predicted and observed pollinator species richness

Species richness	r	P
Bees	-0.70	0.13
Hoverflies	-0.39	0.44
Day-flying Lepidoptera	0.46	0.36

5.5 Discussion

5.5.1 Bee species richness

Model averaging for bee species richness revealed strong associations with hedgerows and solar radiation. Hedgerow density was negatively associated with bee species richness, which may indicate that hedgerows in high densities work as barriers to dispersal or as a sink due to the high forage density they provide (Lander *et al.*, 2011). Furthermore, this may reflect the absence of urban hedgerows in this study, with urban sites with high species richness likely to skew results. This is discussed further in Chapter 4 (see Section 4.5.1).

The negative association with solar radiation may be explained by differing land use on slopes of different aspects (Singh and Dhillon, 2004). Furthermore, it should be reiterated that the study area is relatively flat and so this relationship does not necessarily represent extremes. This metric may be correlated with other factors not studied in this research and therefore provides opportunity for future research.

The negative association between proportion of surface water and bee species richness may be reflective of the heavy anthropogenic influence in the Nene Valley where water bodies are largely a byproduct of aggregate extraction industries and water storage reservoirs. In turn, landscapes with high surface water may support lower diversity through more immature vegetation communities. In addition, correlations between the independent variables (see Section 4.5.1 and Appendix 1.9) showed a significant negative correlation between proportion of water and in-site floral cover (a variable that was positively correlated with bee species richness (see Table 4.3).

5.5.2 Hoverfly species richness

The averaged model of hoverfly species richness indicated strong associations with solar radiation, semi-natural habitat. Negative association with solar radiation, is unexpected but may be due to differing land-use (see Section 5.5.1). The negative association with proportion of semi-natural habitat may reflect hoverflies greater tolerance to more intensely managed agricultural landscapes, particularly as many species are associated with crop species (Jauker *et al.*, 2009; Meyer *et al.*, 2009).

5.5.3 Day-flying Lepidoptera species richness

The day-flying Lepidoptera species richness indicated a strong positive association with proportion of water and a negative association with solar radiation. In addition, there were weak negative associations with hedgerow density, Shannon Wiener Diversity Index and proportion of semi-natural grassland.

The positive association with water within the landscape and day-flying Lepidoptera species richness may be due to the diverse habitats provided by waterside vegetation. Cole *et al.* (2015) highlighted the importance of conservation sensitive management of riparian habitat to butterfly species richness. The aggregates industry is often held to conservation agreements (Department for Communities and Local Government, 2014), ensuring that gravel pits are suitably managed to enhance the environment after extraction has ceased. This may also reflect the importance of undisturbed areas of vegetation surrounding smaller water bodies such as ponds and ditches which requires further investigation.

Whilst it was expected that warmer sites support abundant and diverse populations of day-flying Lepidoptera the species richness model and the significant correlation between day-flying Lepidoptera abundance and solar radiation observed in Chapter four indicate otherwise. Whilst it was not possible to model fluctuations in solar radiation, areas with higher total solar radiation may be prone to more extreme high temperatures. Research has indicated negative responses to extreme high levels of solar radiation and a preference for sites with high heterogeneity in solar radiation through structural diversity (Suggitt *et al.*, 2015). Suggitt *et al.* (2015) used NEXTMap Digital Elevation Models as their base mapping from which solar radiation values were calculated. This dataset has a resolution of 5m and shows ground level topography, LiDAR data (not used by Suggitt *et al.* (2015) provides information not only on

ground elevation but also vegetation structure, providing an accurate (5cm error margin) structure providing better opportunity for microclimatic studies. Whilst LiDAR data is becoming more readily available it remains expensive and requires high level of processing power, but has been shown to provide significant insight into relationships between butterfly diversity and vegetation structures (Aguirre-Gutiérrez *et al.*, 2017)

5.5.4 Testing the models

Lack of significant correlation and, in the case of bee species richness negative correlation (see Section 5.4.4), between the predicted values and the test data is indicative of shortcomings either in the data used for testing or the predictive power of the model and will be discussed in this section.

Test data

Within the time constraints of this study it was not possible to collect an additional dataset to test the models produced, therefore an existing test dataset was used. It was necessary that a consistent data collection method had been used between the test sites to enable rank comparison. This requirement could not be met simply through widely available data sets such as NBN Gateway where sampling may be inconsistent or represent token records. The test data was obtained from Tarrant (2010) and Tarrant *et al.* (2013) a study looking at the conservation value of restored landfill sites for insect pollinators. In the study, restored landfill sites were paired with reference (grasslands not restored from landfill) grassland sites and differences in species richness and abundance explored. Test data was taken from the reference sites which fell within the NIA, resulting in only 6 data points for comparison. Such limited data significantly reduces the statistical power of the test.

This issue is exacerbated by the temporal gap between the two datasets. The models were produced from datasets in 2013 and 2015 whereas Tarrant (2010) sampled his sites in 2007. Inter-annual variation in pollinator abundances and richness can be expected, caused by differences in weather conditions in those years, particularly influenced by species' life histories (Lebuhn *et al.*, 2013). This highlights the importance of long term systematic sampling and recording schemes.

Predictive modelling

The top models for the four taxonomic groups explained between 8 and 25% of the variation in the data, indicating a high level of unexplained variation. Some models that included the local variables (see Chapter 4) explained a greater amount of variation (such as bee species richness 30%), indicating the importance of local factors. This is supported by the literature for instance in bumblebees (Hatfield and Lebuhn, 2007) and hoverflies (Schweiger *et al.*, 2007); and butterflies may be especially sensitive to local scale factors, especially in species with restricted movements (Sjödin *et al.*, 2008). Lack of local-scale data on a landscape level reduces the potential for accurate predictive modelling of pollinators.

Predictive modelling is often linked to niche theory (Hirzel and Le Lay, 2008), explaining the fitness of species in geographical space based on the environmental variables that permit their life histories. Expert knowledge may be able to shed light on the ecological dependencies of pollinators, however current understanding is restricted to a limited number of species (Senapathi *et al.*, 2017; Dicks *et al.*, 2013). Lonsdorf *et al.* (2009) produced a predictive model based on the life histories of 12 bee species. Production of the model was dependent on the ability to quantify habitats based on their ability to supply both nesting and forage resources, requiring deep existing knowledge of the species ecology. Furthermore, knowledge of the distances and direction of movement were required to predict the scale at which these factors operated. This model was highly successful at predicting movement, predictions accounting for 80% of variation in model validation.

The data collected on landscape factors was from widely available sources, enabling reproducibility of models in other geographical areas. This has a trade off in either the age, or potentially, the accuracy of the dataset. GIS datasets that require any kind of large volume processing, and therefore time to process, introduce the possibility of reduced accuracy. For instance, the Land Cover dataset was published in 2011, based on data collected in 2007, meaning by date of publication the information it contains is already four years old and is now close to a decade out-of-date (Morton *et al.*, 2011). Similarly, the dataset is produced through automated land classification based on satellite imagery, the resulting map being ground-truthed to determine accuracy (Morton *et al.*, 2011). Based on this process the data is given an overall accuracy of 83%, however, this varies greatly between habitat classifications, for instance acid grassland at 43% and rough grassland at 63% (Morton *et al.*, 2011). This

creates additional uncertainty in the production of the models. Similarly, computational limitations may restrict the resolution or grain of a study, which in turn can make samples appear falsely homogenous (Mac Nally *et al.*, 2004; see also Section 4.5.7)

5.5.5 Modelling broad niche organisms

A study comparing modelling of two invasive plant species, one specialist and one generalist found models to perform significantly better for the specialist than the generalist (Evangelista *et al.*, 2008). Cowley *et al.* (2000) modelled distribution of 26 species of butterfly based on 16 coarse habitat categories, and the study found that the models were less effective for mobile species than sedentary species. Furthermore, Brotons *et al.* (2007) modelled habitat occupancy of 99 bird species and found model predictive power to be negatively correlated with species niche breadth and range size.

The species recorded in this study are largely generalist species and the taxonomic groups approached (bees, butterflies and hoverflies) cover a large range of life history traits, we therefore may expect overall a broad niche for each group. This is likely to reduce model fit and increase the influence of local scale factors.

Most UK solitary bees are polylectic, foraging on many different flower species (Falk and Lewington, 2015), and as such are not so restricted in forage habitat. Mass flowering crops have been seen to act as a sink, attracting large numbers of bees and distracting them from semi-natural habitats, this could act to distort landscape influence on species richness on a temporal basis (Riedinger *et al.*, 2014; Jauker *et al.*, 2012).

Hoverflies are not central place foragers and little is known about their flight distance or directional movements. It has been suggested that a hoverfly's foraging range, provided there is no barrier to movement, is around 200m (Wratten *et al.*, 2003); however, Kleijn and van Langevelde (2006) found hoverfly species richness in areas of high floral abundance to be positively affected by the proportion of semi-natural habitat within 500-1000m indicating a greater dispersal ability than expected. In contrast, Meyer *et al.* (2009) found hoverfly species richness most likely to be influenced at a small scale, within 250m (Meyer *et al.*, 2009). Pöyry *et al.* (2009) demonstrated the greater importance of local-scale habitat quality for butterfly species richness and densities over landscape-scale variables. Landscape factors

such as connectivity may be particularly important for specialist species or species with low dispersal ability (Brückmann *et al.*, 2010). For these two taxonomic groups the lack of small scale, fine resolution data could present an additional challenge to modelling landscapes.

5.5.6 Absence of fitted abundance models.

Noise within abundance models has two main sources: demographic stochasticity (random drivers of births and deaths of individuals) and environmental stochasticity (the influence of random environmental variables such as weather) (Bjornstad and Grenfell, 2001). Sites with lower species richness often show greater variation in abundance (Rogers *et al.*, 2013). Inter-annual variation in species abundance is a commonly noted phenomenon in pollinator communities (e.g. Alarcón *et al.*, 2008; Williams *et al.*, 2001; Herrera, 1988). Similarly, seasonal variations are common, with large fluctuations even within a week-long period (Burkle and Alarcon, 2011; Traveset and Sáez, 1997; Cane and Payne, 1993; Herrera, 1988). Emergence events in the spring and for bivoltine species may distort abundances. Noise in data is likely to be amplified in smaller datasets highlighting a need for long-term studies in population fluctuations. Abundance and species richness are influenced by different environmental variables on differing scales (e.g. Flick *et al.*, 2012; Rundlöf *et al.*, 2008; Potts *et al.*, 2003) and the dissonance between predictors and model fit seen in this study may reflect this.

5.6 Chapter summary

- The model of bee species richness showed a negative association with hedgerows, solar radiation, water and Shannon-Wiener index and a positive association with proportion of semi-natural grassland.
- The model of hoverfly species richness showed a negative association with solar radiation, proportion of water and proportion of semi-natural habitat and a positive association with Shannon-Wiener diversity index.
- The model of day-flying Lepidoptera species richness showed a negative association with solar radiation, hedgerow density, Shannon Wiener diversity index and proportion of semi-natural grassland and a positive association with water.
- A process for producing GIS models of pollinator insect species richness was outlined and demonstrated for the study organisms (bees, day-flying Lepidoptera, hoverflies).
- Overall there was no significant correlation between the predicted values from the models and those from a test dataset, except for the bee species richness model which demonstrated a strong negative correlation. This may result through a lack of test data and low predictive power in the models.

Chapter 6 Conclusion

6.1 Introduction

This chapter will review the findings of this thesis, discuss the limitations of the research and suggest future avenues of research with a particular focus on the NIA. This thesis explored pollinator dynamics within grassland habitats in the Nene Valley NIA. Seasonal variations in pollinator abundance and species richness were examined. Local and landscape habitat requirements of pollinators were analysed. The over-arching theme of the thesis was exploring the application of GLM models with a GIS to produce predictive models of insect abundance and species richness (see Section 1.9).

6.2 Overview of findings

Data analysis showed significant strong positive relationships between floral cover and mean species richness and abundance of flower visiting insects (see Chapter 3). This finding supports the need for more sensitive management of grasslands within the NIA and promotes restoration of further potential habitats. Reducing the intensity at which amenity grasslands are mown could provide a cost-effective way of improving the availability of floral resources for flower visiting insects. Floral cover and floral species richness was strongly correlated (significant at the 95% confidence level), as such, sites should also be managed to maintain floral species richness, a factor which is known to improve temporal stability of habitats for pollinators (Proulx *et al.*, 2010).

Whilst the relationship between floral cover and richness and flower visiting insects is as expected from the literature the mechanisms are not fully understood. Both the nutritional quality and diversity of pollen has been shown to effect honey bee development (Di Pasquale *et al.*, 2013). Bumblebees have been shown to forage specifically on the basis of the nutritional quality of pollen (Vaudo *et al.*, 2016; Cook *et al.*, 2003; Rasheed and Harder, 1997). Similarly, the fecundity of the hoverfly *Episyrphus balteatus* was shown to be strongly affected by pollen

from different plant species (Laubertie *et al.*, 2012). Currently nutritional composition of pollen is poorly documented (Roulston and Cane, 2000), although understanding of volume of both pollen and nectar production by flowering plants is emerging (Potts *et al.*, 2003; Hicks *et al.*, 2016). Better understanding of this relationship could enable more strategic restoration of grasslands, improving seed mixtures on the basis of flower visitor nutrition.

In the context of the importance of stability of populations of common species for ecosystem service provision (Winfree *et al.*, 2015), the pollinator assemblages observed in Chapter 3 provide an insight into continued stability of services within the NIA. Similarly, common species are often under recorded or represented, with broad scale geographical distribution masking population fluctuations (Thomas and Abery, 1995). Figure 6.1 illustrates this with the distribution of *Maniola jurtina* (meadow brown) records for a ten-year period (2007-2017) within Northamptonshire and surrounding areas (NBN Gateway, 2017), this distribution is much more likely to reflect recorder bias than true absence or distribution. Frequently the importance of monitoring common species is overlooked, despite abundant species providing the majority of biomass and ecosystem services (Winfree *et al.*, 2015; Gaston and Fuller, 2008). Selection of common species also improves the accessibility of ecological recording to the public, in turn generating opportunity for citizen science projects (Devictor *et al.*, 2010). Common species are more likely to be affected by land use at the landscape-scale, whilst rarer, more specialised species are often more restricted to isolated habitat patches (Shreeve and Dennis, 2011). Whilst nestedness indicated that populations at sites were effective subsets, simply recording the most frequently recorded species in this study overlooks accessibility in identifying cryptic species. Whilst most species of butterfly are readily identifiable in the field, solitary bees and hoverfly species are more difficult, often impossible, to identify in the field. For these groups it may be more appropriate to select distinct species or take a morphospecies approach to assess richness. Morphospecies approach is not without criticism (Derraik *et al.*, 2010) but has been used to overcome resource demands and demand for specialist knowledge (Luder *et al.*, 2018).

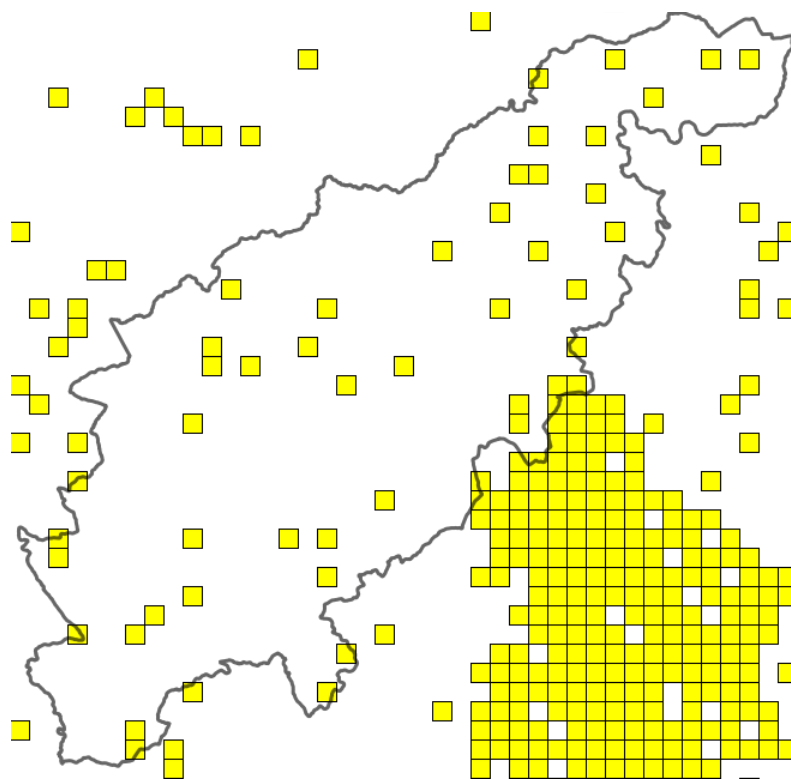


Figure 6.1 *Maniola jurtina* records (2km squares) 2007-2017 (NBN Gateway, 2017)

This research highlights the importance of long term restoration and management planning for grasslands. Opportunity should be taken to understand the long-term cost effectiveness of grassland restoration in terms of both ecosystem services and biodiversity value and how this compares with the more temporary approach of flower strips, which are only effective for 3-4 years (Pywell *et al.*, 2011; Whittingham, 2007). Restoration of grasslands within homogenous agricultural landscapes may be more appropriate than field boundary wildflower strips within AES schemes. Restored grasslands have been shown to be more effective than wildflower strips in landscapes which already have persisting pollinator populations (Winfree, 2010).

The findings of this thesis reflect the sensitivity of day-flying Lepidoptera to traditional grassland management techniques (see Chapter 4), as such approach to management should be considered,

particularly at sites with high species richness of day-flying Lepidoptera. On this basis, site by site assessment of butterfly populations would be appropriate, subsequently writing this into the conservation aims and management. Kruess and Tscharnkte (2002) found an absence of grazing to be much more effective at promoting butterfly abundance than reduced grazing. Rotational management may provide the best conservation solution within agricultural landscapes, fallows being associated with butterfly species richness and nectar rich flowers (Kuussaari *et al.*, 2011; Balmer and Edhardt, 2000), with a subsequent sowing of nitrogen fixing plants (also good for bumblebees) to restore soils for agriculture (Ollerton *et al.*, 2014; Zhang *et al.*, 2007). Rotation depends on the availability of large areas of suitable agricultural land and cooperative land users, as such this may not be viable in most cases. Alternatively, late grazing by cattle or horses could be the most appropriate for maintaining both plant and butterfly diversity (Öckinger *et al.*, 2006).

Whilst the predictive modelling was inconclusive (see Chapter 5), the research demonstrated how GLMs can be used to explore landscape-scale requirements of invertebrates within a GIS. The methods used within this thesis were designed to be replicated by using landscape data that is readily available and a transparent model selection process. Application within GIS in this way shows an opportunity to visualize ecological data, providing a more accessible interface between scientists and decision makers. GIS models can highlight areas of paucity or richness of pollinator communities in a geographical area and as such can be used for the targeting of conservation or influencing planning processes. A transparent modelling system enables exploration of the drivers of species richness and abundance and how differing scenarios of land use change may influence populations. GIS models can be used to focus restoration projects in areas where they are more likely to succeed, ensuring a better outcome for investment and more resilient landscapes. Similarly, from the ecosystem service perspective hot spot mapping enables identification of areas of high or low, species richness and abundance which may possibly be used as a proxy for pollination service provision.

At present, data is largely available at a low resolution; however, Chapter 4 highlighted the importance of local variables, as some models that included local scale parameters explained more variation than their landscape only counterparts. Integrating local scale parameters in a GIS is dependent on the availability of fine scale data and this is discussed further in Section 6.3.

The models revealed some spurious relationships between the environmental variables and the abundance and species richness of flower visiting insects (see Chapter 4 and 5). Negative associations with solar radiation and hedgerows are contrary to expectations and require further investigation (see Chapters 4 and 5). Large amounts of unexplained variance were demonstrated in the models, highlighting the challenges of obtaining sufficient amount of field data, and the possibility of more significant drivers of pollinator distribution that haven't been examined by this study. The modelling also highlighted potential limitations of data available for landscape-scale studies (see Section 6.3) and future research opportunities (see Section 6.4).

6.3 Challenges

The River Nene NIA plus the 3km buffer covers an area of 1,700 km². Extrapolating information for an area this size will always be complex and require a significant amount of data. It was only possible to survey 34 sites for this study due to time and weather constraints. As a consequence, this data can only provide a limited representation of variability in pollinator communities in grasslands. Furthermore, due to the nature of Generalised Linear Modelling, sample size can limit the number of explanatory variables in the final models (to prevent over fitting) as such, a greater dataset would enable greater investigatory power and enable the introduction of quadratic and interaction terms, frequent in ecological relationships (Austin, 2002).

As discussed in Chapter 4 and 5, the availability of accurate, up-to-date, high resolution land-use data is limited and may be highly expensive. Light Detection and Ranging (LIDAR) data enables fine scale mapping of surface structure, which opens up the possibility of research into the effects of habitat structure at the landscape-scale on microclimates, and in turn, the ecological assemblages those landscapes host. At present this dataset is incomplete and the sheer size of the data makes manipulation and exploration difficult at large scales. Land Cover data has been released by CEH on a 7-10 year cycle, with data often being published two years after imagery is captured. Improved data collection by the Sentinel satellites and new processing techniques will hopefully enable faster delivery of service and accuracy to reduce the disparities created due to differences in age of landscape data and field data (CEH, 2017). Furthermore, new Land Cover

datasets intend to map crop types, enabling a further avenue of research into the effects of agriculture on pollinators on a landscape-scale.

Field data collection was restricted to two years, which may affect results through intra-annual and inter-annual fluctuations of pollinator populations. Petanidou *et al.* (2008) found significant variability in plant-pollinator interactions in a four-year study, finding that species that appear to be specialist in a one-year study may actually utilise a number of plant species in other years.

Long-term data collection projects at fixed sites can help address the issues of noise within data sets due to inter and intra-annual population fluctuations. Santamaria *et al.*, (2018) found significant variability in inter-annual pollinator visitation rates and plant-pollinator interactions, this variation adds significant noise when investigating landscape scale effects on communities. Additionally, both species phenologies, weather and in-site microclimate contribute to intra annual fluctuations in species richness, visitation rates and community composition (Valverde *et al.*, 2016; Forrest, 2015; Rollin *et al.*, 2015; Herrera, 1995). Efforts were taken to ensure an even spread of surveys through the field season, however, weather fluctuations inevitably increased time between surveys creating a potential source of additional variation. Surveys were carried out according to the requirements laid out in chapter 2 to reduce the influence of weather variation on pollinator abundance and species richness.

It was noted during the surveys that many sites were cut for hay on or around the 15th July, in accord with HLS agreements. This date has been set to ensure continued diversity of plant species within meadows, as an earlier cut may prevent flowers from setting seed, however, little consideration seems to be made for the realised growing/flowering season. For instance, it was noted that a cold spring in 2013 pushed back the flowering period, such that many species had only just come into flower at the time of the hay-cut. Inevitably, hay-cutting has a drastic impact on pollinator visitation rates, if floral resource is limited in the surrounding landscape this could cause emigration or extinction of the local population. More sensitive grassland management could allow for better timing of hay-cutting, providing greater resources for pollinators whilst not compromising on maintenance of plant species richness. Buffer strips and species-rich hedgerows may also provide forage for insects after hay-cutting. A landscape sensitive cropping

matrix may also provide a practical solution, extending the flight season through provision of complimentary early and late flowering crops and existing semi-natural habitats.

Due to time and resource demands it was only possible to collect data over two field seasons. This was a significant limitation as data could not reflect inter-annual fluctuations and additionally, resulted in a smaller sample size. A multi-year study could potentially reduce noise in generalised linear modelling created by inter-annual and intra-annual fluctuations in populations.

This research examined the abundance and species richness of hoverflies, day-flying Lepidoptera and bees, using adapted timed transect walks of 200m x 3m (see Chapter 2). This approach for recording multiple taxa is common (e.g. Baldock *et al.*, 2015; Riedinger *et al.*, 2014; Jauker *et al.*, 2009). This study aimed to explore the requirements of flower visiting insects using grasslands, and hand netting enabled the identification of individuals using forage resources. The restriction of the transect width from the recommended 5m transect width for butterflies (Pollard and Yates, 1993), to 3m, meant that minimal numbers of butterflies were recorded and therefore foraging, basking and commuting were also recorded for this group. This may indicate greater sensitivity to disturbance in butterflies than hoverflies and bees, which should be considered in future research. Improved video capture technology may enable the recording of pollinators without the elements of recorder bias and disturbance effects (August *et al.*, 2015), although this is likely to be at the cost of identification to species for smaller or more cryptic species. Furthermore, it should be noted that smaller, less visually apparent species are often under-recorded and future research methods should try and address these biases (Dennis *et al.*, 2006).

6.4 Future research possibilities

Understanding pollinators movements in terms of distance travelled and pattern of movement is of utmost importance for understanding the appropriate scales to use in habitat suitability modelling. For example, butterflies have been shown to be affected by environmental variables at a broad range of spatial scales, which is a reflection on species dispersal abilities (Krauss *et al.*, 2003). Whilst harmonic radar techniques are becoming more viable for research, in terms of size

of transponders, they remain an expensive choice and impractical for many smaller taxa. Emergence mark and recapture can be insightful for species which have very specific oviposition habitat (Rotheray *et al.*, 2014). Similarly, tracking of pollen from uncommon garden plants such as *Phacelia tanacetifolia* may allow tracking of hoverfly and solitary bee movements across a landscape (Wratten *et al.*, 2003).

Landscape permeability is of particular interest to landscape ecologists, understanding how organisms move and disperse through differing habitat types. At present little is known about how travelling through habitats affects energy expenditure and behaviours in invertebrates. The ability to score habitats on the basis of their permeability enables cost-distance analysis, a more useful metric of connectivity. Cost-distance analysis is a connectivity measure that not only takes into account the distances of habitat patches but the ease of travel between them; for example, neighbouring grassland patches separated by only 100m may be less connected if that 100m consisted of urban industrial habitat rather than a woodland. This is of particular note where habitat potential is disregarded, such as urban areas whose values are only coming to light in recent years.

The literature shows conflicting opinions on the role of hedgerows in landscapes, with some finding hedgerows to act as an important forage source, provision of nesting/oviposition habitat and use for navigation, whilst others are seen as a barrier to dispersal, or presenting a greater risk of predation (Dennis *et al.*, 2013). Better understanding of how hedgerows affect overall pollinator fitness and movements would improve interpretation of model outputs. It is a complex matter, hedgerows in otherwise resource poor habitats, such as in large areas of monoculture, may act as a barrier to dispersal, slowing movement to more preferable habitat, whilst in richer landscape matrices they may act as additional habitat resource and aid navigation. Additionally, dispersive flight behaviour can differ between and within butterfly species and between different landscapes creating noise in assumptions made on the effects of hedgerows on pollinator behaviour (Shreeve and Dennis, 2011).

Greater understanding of the ecology of species, particularly common species will enable greater prediction of ecosystem services and insight into how best to manage landscapes to support them. To date, models have largely been restricted to a limited number of species (e.g. Gill and

Sangermano, 2016; Lonsdorf *et al.*, 2009), purely theoretical and untested in the field (e.g. Schulp *et al.*, 2014, see also section 6.5), or at a national or continental scale (e.g. Polce *et al.*, 2013). This study highlighted the difficulty of inferring general patterns from limited datasets, recognizing a need for greater engagement and consistency in recording schemes to enable predictive habitat suitability modelling at the landscape-scale. Whilst a behavioural ecology approach may be more appropriate (Shreeve and Dennis, 2011), information is lacking for many species. Understanding of seasonal fluctuations in both pollinators and floral resources, flower visitor flight and dispersal ability, and quantification of individual habitat types ability to provide both forage and oviposition habitat, are important for a more rigid modelling framework (Lonsdorf *et al.*, 2009). Habitat suitability modelling for butterflies has been mostly restricted to large scale, low resolution studies, often based on climatic envelope models for the purpose of exploring the potential impacts of climate change (Porfirio *et al.* 2014; Eskildsen *et al.*, 2013; Syfert *et al.*, 2013). Modelling attempts for hoverflies are even more infrequent, highlighting a gap in current knowledge, despite the importance of hoverflies as both pollinators and biological pest control agents (Aguirre-Gutiérrez *et al.*, 2013).

The community recorded in this study was shown to be nested (Chapter 3). As nestedness was not the primary aim of this research it was not possible to identify the causative factors from the data collected. However, this presents an opportunity to develop the research presented in this thesis, gathering more extensive data on local habitat quality and using the enhanced landcover and cropping data to gain a better understanding of community structure and drivers.

Understanding consumer choices in regards to ethical or environmental food production could reveal an approach to payments for ecosystem services as consumer demand drives markets. Whilst the recession hit the organics market in 2008, a steady increase has been seen in recent years, with an increase of 4.8% opposed to -0.9% in conventional groceries (Soil Association, 2016; Financial Times, 2016) indicating that that consumers wish to make more informed decisions on their food choices. Customers show willingness-to-pay for goods on the basis of informed choices, for example in the instance of movement away from caged egg production (Defra, 2017); however, ambiguity behind the benefits of extensive farming may be a barrier for consumer decision. Research into a proposed "Bee Friendly Farm" certification scheme could enable a new incentive to farmers, particularly those not currently subsidized by the Countryside

Stewardship schemes, to enlist a more ecologically sensitive approach. Considerations may be: habitat creation, hedgerow management, wildflower strips and suitable pesticide use. The plight of pollinators in the UK has garnered much attention in the media over recent years and opportunity should be taken to utilize the public's sympathies to the environments gain.

6.5 Future of pollinator conservation within the Nene Valley NIA

The Nene Valley Nature Improvement Area was originally funded for three years (2012-2015) with the intention of the project becoming self-sufficient through cooperation of NGOS, local businesses and local authorities. To date the project has been highly successful with partnership agreements for development, habitat restoration projects and mapping of ecosystem services. Restoration and management of semi-natural habitats should remain a priority, particularly along the river valley itself where restoration and creation of grassland habitats may attract funding through flood prevention and payment for ecosystem service schemes. Continuation of the NIA is essential to ensure a collaborative approach to sustainable development in the Nene Valley and secure funding for further research and conservation.

Habitat restoration and conservation projects are often long-term endeavours, and steps should be taken to ensure long-term future resilience of pollinator populations. Projects and schemes should be organized through a central scheme of self-sustainability and/or longevity of funding. Frequently, projects last either as long as the funding remains, usually 3-4 years, or with changes of government (Adams *et al.*, 2016).

In 2017 a new wildlife recording project, WILDside, will be launched funded by the Heritage Lottery Fund. The project is a collaborative project primarily between the Northamptonshire Biodiversity Records Centre (NBRC) and The Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire, which will involve other environmental professionals and amateurs. The project seeks to improve natural history skills within the county by training recorders and amateurs and to fill the knowledge gaps both in terms of unrecorded taxa and geographical area. This project could encourage standardized sampling of pollinators within Northamptonshire as well as improving the geographical spread of records. This would enable other methods of

ecological modelling to be carried out such as ensemble modelling. In addition, focus should be applied to adopting and expanding current uptake of national recording schemes such as the Butterfly Monitoring Scheme, which as can be seen in Figure 6.2 is low in comparison with neighbouring areas.

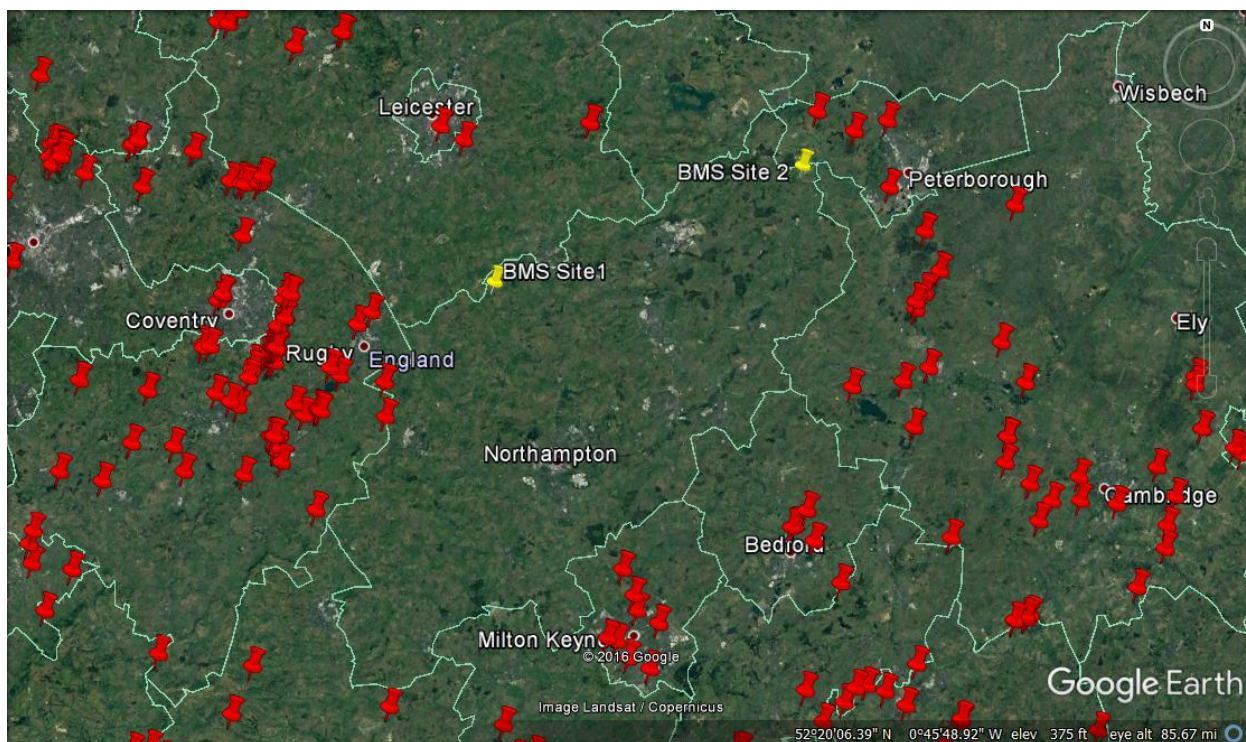


Figure 6.2 Location of BMS survey sites within Northamptonshire (in yellow) and surrounding areas (in red) (Google Earth; Locations from Botham *et al.*, 2016)

Issues of recording and monitoring feed into the National Pollinator Strategy, launched in 2014 to initiate a collaborative approach to pollinator conservation between governmental and non-governmental organisations (Defra, 2014). Research and publication of the strategy can also feed into projects such as the voluntary conservation measures for landowners promoted by the Campaign for the Farmed Environment and B-Lines, Buglifes project to create a network of connected wildflower strips covering England to promote pollinators movements across the landscape (Defra, 2014). Social research should be undertaken to understand how best to encourage the public and landowners to engage with such strategies.

Restoration and creation of habitats creates opportunity for implementation of long term research projects, forming greater understanding of optimal methods for both creation and management of habitat. Development of the University of Northampton's Waterside campus provides an opportunity for on-site monitoring and recording, giving insight into how developments may become more ecologically sustainable. Furthermore, it presents opportunity to gain a greater understanding of phenologies, important in the context of climatic change and urbanization in surrounding areas. Temporal effects should be better understood on a species level for the region to enable improved survey design.

Further to the statement on weather in Section 6.2, the effects of diurnality on species behaviour should also be explored, particularly in the context of environmental factors such as sunlight and temperature and nectar production in flowers. Research is currently limited to a small number of species such as: the differing foraging behaviours of *Eristalis tenax* (Gilbert, 1985), the circadian rhythms of honey bee's dependent on function within the hive (Elekovich and Roberts, 2005) linking environmental conditions with diurnality in desert solitary bees (Stone *et al.*, 1999) and distinct differences in diurnality between butterfly species (Wikström *et al.*, 2009).

In parallel with this study, researchers at the University of Northampton mapped ecosystem service provision, including pollination, using a GIS toolkit known as EcoServ (Rouquette, 2015a). EcoServ predicts crop pollination supply based on likelihood of visitation calculated from distance to habitat. EcoServ's predictions of pollination supply are based on the methodology used by Schulp *et al.* (2014) who mapped pollination in Europe at a 1km² resolution. Predicted data (visitation probability) were compared with species occurrence data from Global Biodiversity Information Facility (GBIF) (Schulp *et al.*, 2014) and showed a weak but significant correlation; however, it is noted that the test data is subject to the same biases found in many biological records datasets. The EcoServ model, which predicts at a 10m resolution (Winn *et al.*, 2015), has not yet been tested in the field, which provides opportunity to test it through survey of both pollinator abundances and richness and their efficacy at delivering pollination services through seed set studies. Findings from this future research could highlight landscapes areas that would benefit from semi-natural habitat restoration to improve pollination service. Similarly, improvement of crop mapping enables the quantification, in terms of economic value, of this service (CEH, 2017).

6.6 Other considerations

Departure from the European Union is likely to have three main modes of effect in terms of agricultural landscapes: changes to trade agreements, changes to farming subsidies and changes to payments for agri-environment schemes (IEEP, 2016). Exit from the European Single Market could increase the cost of imports, driving domestic production, which unchecked, could lead to intensification of farming practices (Van Berkum *et al.*, 2016). At present the majority of farming income comes from subsidies (68% of income 2010-2014) via the EU Common Agricultural Policy (CAP), therefore how the domestic policies change is likely to have a profound impact on UK agriculture (IEEP, 2016). Within this area, funding for agri-environment schemes, which also come via the EU CAP, may change depending on governments willingness to assign budgets. However, it should be noted that whilst there is much uncertainty in regards to funding and trade, departure also presents opportunity to reform policy for enhanced environmental protection.

Engaging the public with conservation is essential for continued funding and support. Within urban areas more naturalistic green spaces, as opposed to highly managed spaces, are associated with socializing and as spaces for freedom of expression (Özgüner and Kendle, 2006). Positive links between access to green space and health are becoming increasingly common in the literature (Wolch *et al.*, 2014; Irvine *et al.*, 2013; Maas *et al.*, 2006). Bringing semi-natural habitats into the urban environment increases their accessibility and stokes the imagination of the public, whilst reducing wealth generated inequalities in health due to lack of access (Van den Berg *et al.*, 2016; Wolch *et al.*, 2014). Management of these areas may not need to be financially draining, with wildflower areas requiring less intensive management than traditional amenity grassland, through the promotion of 'green gyms', and encouraging volunteering through health (Christie *et al.*, 2015).

6.7 Closing statement

Grasslands are of great importance supplying both oviposition, nesting and foraging resources, as well as hosting great plant diversity and supporting a number of other organisms. Within agricultural landscapes grasslands support flower visitors, providing pollination services, reduce agricultural run-off and through proper management restore soils to fertility. Maintaining habitat of high quality and heterogeneity both at the local and landscape-scale is key to ensure pollinator stability for the future. As the study of ecosystem services develops it is hoped that a more economically sustainable approach to conservation can be delivered. It has been reported that landowners may be influenced to engage with conservation through a better understanding of the benefits of schemes rather than merely just the process (Batáry *et al.*, 2015). Spatially explicit models provide an accessible platform to educate landowners and influence policy. This study has demonstrated a method of producing visual habitat models to aid planning and conservation processes and highlighted a need for a long-term pollinator recording network and accurate landscape data.

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Appendices

Appendix 1.1 Pollinator life histories

This thesis examines three groups of flower visiting insects: bees, hoverflies and butterflies, based on their potential, through high flower visitation rates, to act as pollinators (Winfree *et al.*, 2011). Below the taxa are introduced and broad taxonomy and life history is discussed.

Bees (Order Hymenoptera Superfamily Apoidea)

The most recognised of the insect pollinators, *Apis mellifera*, the honey bee, represents only the smallest fraction of the UK's pollinator diversity. The Superfamily to which it belongs, the Apoidea, possesses a high diversity both in morphology and life cycle. At present there are over 270 described species of bee in Britain and Ireland (Falk and Lewington, 2015).

Belonging to the clade Anthophila, in Britain bees are represented by six families as follows (family accounts adapted from Falk and Lewington, 2015).

Andrenidae: are known colloquially as mining bees and are solitary, soil nesting bees represented by two genera in Britain: *Andrena* (67 species) and *Panurgus* (2 species). Individuals in this group are characterised by facial sutures below the antennal sockets. Common species found in Britain include: *A. haemorrhoa* (orange-tailed mining bee), *A. fulva* (tawny mining bee) and *A. cineraria* (ashy mining bee) (see Figure A.1).



Figure A.1 *Andrena haemorrhoa*, *Andrena fulva* and *Andrena cineraria* (Left to right) (Source: Walters, 2011; Falk, 2011; Owens, 2011)

Apidae: Represented by nine genera in Britain, displaying great morphological and ecological diversity, the family contains both eusocial and solitary bees and kleptoparasites (see Figure A.2 and Appendix 1.2). This group includes the familiar *Bombus* spp. (Bumblebees), a group consisting of 25 species) (see Figure A.2 and the honey bee (*A. mellifera*)).



Figure A.2 *Nomada fabriciana* and *Bombus pascuorum*, an example of the large morphological differences within Apidae (Source: Early, 2011; Owens, 2010)

Colletidae: Represented by two genera in Britain: *Colletes* and *Hylaeus*. *Colletes* (plasterer bees) are largely ground nesting, and of medium size. Most of the nine species in Britain possess distinctive bands of hair on the abdomen. *Hylaeus*, (yellow faced bees) are small with short bi-lobed tongues with the ability to carry pollen in their crop, to be later regurgitated in the nest; 12 species are described in Britain.

Halictidae: Represented by five genera in Britain are short-tongued species exhibiting a wide range of morphological and life history traits (see Appendix 1.3).

Megachilidae: Represented in Britain by eight genera; *Megachile* (leafcutter bees) are long-tongued species many of which having large jaws adapted to cutting plant materials (see Appendix 1.4).

Melittidae: Represented in the UK by *Dasygaster*, *Macropis* and *Melitta*, short-tongued solitary bees. *Macropis* bees collect floral oils to waterproof nests, allowing ground nesting

in wetland soils. Species within this family are often oligolectic, collecting pollen and nectar from one or only on a few species of plant.

Day-flying Lepidoptera (Order Lepidoptera)

Butterflies are not central place foragers, and as such do not exhibit provisioning behaviour, allowing unidirectional movements across landscapes. Adult butterflies do not feed on pollen, collecting only nectar as a source of both energy and water (Thomas and Lewington, 2011). Oviposition often occurs on specific host plants, which will then become the larval food source. The group is represented by six families within the British Isles and 57 species as follows (Butterfly Conservation, 2014; family accounts adapted from Thomas and Lewington, 2011).

Hesperiidae, known colloquially as skippers are represented by 13 species within the UK and are identified by their unbranching wing veins. Larvae of this group feed within shelters produced from their larval plant hosts. Common species of this family include *Thymelicus sylvestris* (small skipper), whose food plant and larval host plant is most commonly the grass *Holcus lanatus* (Yorkshire fog) but is also known to utilise other grass species (see Figure A.3).



Figure A.3 *Thymelicus sylvestris* (left) and *Aglais io* (right) (Source: Butterfly Conservation, 2016a; Butterfly Conservation, 2016b)

Nymphalidae, represented in the British Isles by three clades: Danaoid, Nymphaloid and Satyroid (Freitas and Brown, 2004). In the British Isles, the Danaidae is represented by *Danaus plexippus* (monarch butterfly) an occasional migrant from North America. The

Nymphaloid clade, otherwise known as the aristocrats, is represented by 18 species in the British Isles, including the fritillaries and the admirals. Common Nymphaloid species include *Aglais io* (peacock) (see Figure A.3), and *Aglais urticae* (small tortoiseshell) which, as its Latin name suggests, has strong larval associations with nettles. The Satyroid clade is represented by 11 species in Britain, most species are brown in colouration with eye-spots on the outer edge of the wings. One of the most common species in the British Isles, *Maniola jurtina* (meadow brown), is strongly associated with grasslands, its larvae feeding on many species of grass.

There are 11 species of Pieridae, the white and yellow butterflies, in Great Britain. Within the family, are included species commonly regarded as 'pests' *Pieris brassicae* (large white) and *P. rapae* (small white), females of which oviposit and feed on species of the Brassicaceae family.

The families Riodinidae and Papilionidae are only represented by one species each in the British Isles, *Hamearis lucina* (duke of burgundy) and *Papilio machaon* (swallowtail) respectively. *H. lucina*, a species associated with woodland, holds a high conservation priority due to its large population decline in recent years and through contraction of its range (Goodenough and Sharp, 2016).

Lycaenidae, a group of 20 species, including the blues, coppers and hairstreaks are of particular conservation interest in the UK. Blue butterflies have strong associations with ant species, for instance, *Maculinea arion* (large blue), which became extinct in the UK in 1979 (Thomas *et al.*, 2009). Discovery of its larval parasitic relationship with species of *Myrmica* ant enabled correct habitat management and led to its successful reintroduction in 1983 (Thomas *et al.*, 2009).

The burnet moths (Zygaenidae) a group of day-flying moths, belonging to the genus *Zygaena* were treated as butterflies for the purposes of this study due to their similarity in ecology, function and ease of identification in the field (Franzén and Ranius, 2004).

Hoverflies (Order Diptera, Family Syrphidae)

Syrphidae do not exhibit central place foraging; although some species may remain close to the oviposition site, many will disperse. In the British Isles the Syrphidae is represented by three subfamilies: Syrphinae, Eristalinae and Microdontinae (the following accounts are adapted from Ball and Morris, 2015).

Syrphinae: A large subfamily represented by 118 species in the British Isles, distributed between 3 tribes. The larvae of this sub-family are largely associated with aphids and thus may have strong associations with agricultural landscapes (see Appendix 1.5). This group contains many mimics; including the bumblebee mimic *Volucella bombylans* (see Figure A.4)



Figure A.4 *Volucella bombylans* (left) and *Chrysotoxum veralli* (right) (Source: Hoverfly Recording Scheme, 2016; Howard, 2016)

Eristalinae is represented by 10 tribes in the British Isles and demonstrates a broad variation in both morphology and ecology. Species such as *Chrysotoxum veralli* exhibit mimicry (see Figure A.4). Larvae may be associated with living or decaying plant matter, aquatic environments or parasitic on other organisms such as bumblebees or aphids (see Appendix 1.6).

Microdontinae are represented by only one genus, *Microdon*, in the British Isles. The larvae of *Microdon* are nationally scarce and are associated with ant nests.

Appendix 1.2 UK Apidae Summary

Genus (No. species in Britain)	Sociality	Nesting habitat
<i>Anthophora</i> (5 species)	Solitary but may nest in aggregations	Ground or cliff/wall nesting
<i>Apis</i> (1 species)	Social (colonies consisting of tens of thousands of individuals)	Most frequently in artificially managed colonies
<i>Bombus</i> (25 species)	Mostly social bees with some species exhibiting cleptoparasitism	Largely ground nesting, within abandoned rodent nests or tussocks. Some species, namely <i>Bombus hypnorum</i> , will nest within buildings and trees.
<i>Ceratina</i> (1 species)	Solitary	Hollow plant stems.
<i>Epeolus</i> (2 species)	Cleptoparasites on <i>Colletes</i> spp.	Oviposits in <i>Colletes</i> burrows.
<i>Eucera</i> (2 species)	Solitary but may nest in aggregations	Ground nesting in sandy soils.
<i>Melecta</i> (2 species)	Cleptoparasites on <i>Anthophora</i>	Bite through the waterproof seal of <i>Anthophora</i> nests then oviposit and reseal the nest.
<i>Nomada</i> (34 species)	Cleptoparasites largely on <i>Andrena</i> spp.	Oviposit in unsealed nest cells.
<i>Xylocopa</i> (2 vagrant species)	Solitary	Dead wood, structural timbers and other cavities.

Appendix 1.3 UK Halictidae

Genus (No. species in Britain)	Sociality	Nesting habitat
<i>Halictus</i> (8 species)	Both solitary and eusocial species	Ground nesting or in vertical surfaces
<i>Lasioglossum</i> (34 species)	Both solitary and eusocial species	Ground nesting
<i>Sphecodes</i> (17 species)	Cleptoparasites	Ovipositing in a number of species burrows
<i>Dufourea</i> (2 species)	Solitary nesting in aggregations	Sandy soils
<i>Rophites</i> (1 species)	Solitary nesting in aggregations	Sandy soils

Appendix 1.4 UK Megachilidae

Genus (No. species in Britain)	Sociality	Nesting habitat
<i>Anthidium</i> (1 species)	Solitary	Nest in cavities in wood, plant stems and walls
<i>Stelis</i> (4 species)	Cleptoparasites on other megachilids	May lay eggs in multiple cells of host nests.
<i>Heriades</i> (1 species)	Solitary	Nesting in dead wood and plant stems
<i>Chelostoma</i> (2 species)	Solitary	Nesting in cavities in wood, walls and plant stems.
<i>Osmia</i> (12 species)	Solitary	Largely nesting in pre-existing cavities lined with collected mud or plant material
<i>Hoplitis</i> (2 species)	Solitary	Nesting in hollow plant stems
<i>Megachile</i> (7 species)	Solitary	Line cavities with leaf sections.
<i>Coelioxys</i> (7 species)	Cleptoparasitic on <i>Megachile</i> and <i>Anthophora</i>	Pointed abdomen used to break host nest cells for oviposition.

Appendix 1.5 UK Syrphinae

Tribe	Species	Notes
Bacchini	30	Larvae are largely aphidphagous, with one species, <i>Xanthandrus comtus</i> feeding on micro-moth caterpillars.
Paragini	4	Small hoverflies feeding largely on yellow flowers. Larvae feed on aphids.
Syrphini	84	Larvae feeding largely on aphids, some with very strong associations with agricultural landscapes. Some species larvae are believed to be associated with ants nests.

Appendix 1.6 UK Eristalinae

Tribe	Species	Notes
Eristalini	28	Includes bee mimics. Most species larvae are aquatic, associated with rotting vegetation, manure and rot holes and some groups such as the Anasmiya are strongly associated with aquatic habitats even in adulthood.
Volucellini	5	Larvae are associated with bumblebee nests.
Merodontini	7	Groups larvae largely associated with plant bulbs. This group includes the bumblebee mimic <i>Merodon equestris</i> .
Xylotini	20	Consisting of a number of bee and sawfly mimics. Larvae are associated with rotting vegetation, in particular tree stumps.
Callicerini	3	Represented by 3 species of very restricted geographical distribution. Larvae are found in water filled rot holes in trees.
Sericomyiini	3	Bumblebee and wasp mimics with aquatic larvae.
Pelecocerini	3	Restricted geographical distribution, associated with heathland and coniferous plantation.
Pipizini	20	Larvae largely aphidophagous.
Cheilosini	43	Larvae are mainly associated with plant root, stems and bulbs, although the genus <i>Rhingia</i> are associated with dung.
Chrysogastrini	29	Larvae are largely associated with ponds and ditches.

Appendix 1.7 Summary of field results

	Total number of transects	Species richness insects	Species richness bee	Species richness hoverfly	Species richness butterfly	Total insect abundance	Total bee abundance	Total hoverfly abundance	Total butterfly abundance
Badby south meadow	3	19	13	3	3	109	80	3	26
Barford	3	8	5	0	3	19	9	0	10
Barlow	3	12	7	1	3	38	32	2	4
Barnes	3	11	3	5	3	27	12	8	7
Bugbrooke	3	13	1	9	3	38	1	29	8
Bulwick	3	16	8	5	3	26	15	5	6
Burton latimer	3	17	8	3	6	23	10	2	10
Daventry	3	8	3	0	5	15	3	0	12
Delapre	3	13	3	2	8	30	13	2	15
Ditchford	3	22	9	9	4	27	11	12	4
Dovecote	4	17	6	9	2	23	11	9	3
Duston	4	12	3	2	7	41	4	4	33
Glamis	3.7	24	7	9	8	79	48	14	17
Hollowell	3	5	2	1	2	11	3	1	7
Irchester	3	10	3	3	4	16	6	6	4
Kingscliffe	3	8	2	2	4	15	8	2	5
Kingsthorpe meadow	4	24	15	8	2	63	37	18	8
Kingsthorpe north	4	7	2	1	4	13	2	1	10
Lyvedon	3	22	8	9	5	105	83	13	9
Naseby	3	7	2	5	0	42	17	25	0
Newton	4	26	11	9	5	99	38	24	37
Oundle	3	11	2	6	3	64	37	22	5
Pitsford	4	16	4	2	10	140	4	2	134
Rothwell	3	18	8	1	9	78	43	1	34
Rushton	3	13	4	5	4	18	7	5	6
Ryeholmes	4	4	1	0	3	9	3	0	6
Stanwick	4	13	4	4	5	30	7	5	18
Summerleys	5	28	8	9	11	130	40	12	78
Sywell	2.5	14	7	4	3	33	20	8	5
Tailby	4	16	5	7	4	32	8	18	6
Titchmarsh	3	16	5	8	3	36	8	11	17
Twywell hills and dales	3	13	7	2	4	41	28	2	11
Weedon	2.7	9	4	3	2	18	6	4	8
West lodge farm	3	14	5	4	5	189	170	9	10

Appendix 1.8 Species recorded in 2013 and 2015

	2013	2015
<i>Aglais urticae</i>	0	1
<i>Aglais io</i>	1	1
<i>Anasiyma lineata</i>	0	1
<i>Anasiyma transfuga</i>	0	1
<i>Andrena bicolor</i>	1	0
<i>Andrena chrysoseles</i>	1	1
<i>Andrena cineraria</i>	1	1
<i>Andrena haemorrhoa</i>	1	1
<i>Andrena nigroaenea</i>	1	1
<i>Andrena nitida</i>	1	1
<i>Andrena similis</i>	1	1
<i>Andrena wilkella</i>	0	1
<i>Anthocharis cardamines</i>	0	1
<i>Anthophora plumipes</i>	1	1
<i>Apis mellifera</i>	1	1
<i>Bombus bohemicus</i>	0	1
<i>Bombus campestris</i>	1	1
<i>Bombus hortorum</i>	1	1
<i>Bombus hypnorum</i>	1	1
<i>Bombus lapidarius</i>	1	1
<i>Bombus lucorum/terrestris</i>	1	1
<i>Bombus rupestris</i>	1	0
<i>Bombus vestalis</i>	1	0
<i>Bombus pascourum</i>	1	1
<i>Cheilosia bergenstammi</i>	1	0
<i>Cheilosia</i>	1	1
<i>albitarsis/ranunculi</i>		
<i>Cheilosia lasiopa</i>	1	0
<i>Cheilosia pagana</i>	1	1
<i>Cheilosia vernalis</i>	1	0
<i>Chrysotoxum veralli</i>	1	0
<i>Episyrrhus balteatus</i>	1	1
<i>Eristalis hybridus</i>	1	0
<i>Eristalis abusivus</i>	1	0
<i>Eristalis horticola</i>	1	0
<i>Eristalis interruptus</i>	1	0
<i>Eristalis</i>	1	1
<i>interruptus/arbustorum</i>		
<i>Eristalis pertinax</i>	0	1
<i>Eristalis tenax</i>	1	1
<i>Eristilini sp.</i>	1	1
<i>Eumerus strigatis</i>	0	1
<i>Eupeodes corallae</i>	0	1
<i>Eupeodes latifasciatus</i>	1	1
<i>Eupeodes luniger</i>	1	1
<i>Gonepteryx rhamni</i>	1	1
<i>Halictus rubicundus</i>	0	1

<i>Helophilus hybridus</i>	1	0
<i>Helophilus pendulus</i>	1	1
<i>Lasioglossum albipes</i>	1	0
<i>Lasioglossum calceatum</i>	1	1
<i>Lasioglossum leucozonium</i>	1	0
<i>Lasioglossum malachurum</i>	0	1
<i>Lasioglossum morio</i>	0	1
<i>Lejogaster metallina</i>	1	1
<i>Leptidea sinapsis</i>	1	0
<i>Leucozona lucorum</i>	0	1
<i>Lycaena phlaeas</i>	1	1
<i>Maniola jurtina</i>	1	1
<i>Melanargia galathea</i>	1	0
<i>Melanogaster hirtella</i>	1	1
<i>Melanostoma mellinum</i>	1	1
<i>Melanostoma scalare</i>	1	0
<i>Meliscaeva auricollis</i>	1	0
<i>Merodon equestris</i>	1	1
<i>Neoascia geniculata</i>	1	0
<i>Nomada fabriciana</i>	0	1
<i>Nomada panzeri</i>	0	1
<i>Nomada ruficornis</i>	1	0
<i>Ochlodes sylvanus</i>	1	0
<i>Osmia bicornis</i>	1	1
<i>Osmia spinulosa</i>	1	0
<i>Parahelophilus consimilis</i>	0	1
<i>Parahelophilus versicolour</i>	0	1
<i>Pararge aegeria</i>	1	0
<i>Pieris brassicae</i>	1	1
<i>Pieris napi</i>	1	1
<i>Pieris rapae</i>	1	1
<i>Pipizella viduata</i>	1	0
<i>Platycheirus albimanus</i>	1	1
<i>Platycheirus ambiguus</i>	0	1
<i>Platycheirus manicatus</i>	1	0
<i>Platycheirus peltatus</i>	1	0
<i>Platycheirus scambus</i>	1	0
<i>Platycheirus scutatus</i>	1	1
<i>Platycheirus sp.</i>	1	0
<i>Polyommatus icarus</i>	1	1
<i>Pyrgus malvae</i>	0	1
<i>Pyronia tithonus</i>	1	1
<i>Rhingia campestris</i>	1	1
<i>Scaeva pyrastris</i>	0	1
<i>Sphaerophoria interrupta</i>	1	0
<i>Sphaerophoria scripta</i>	1	1
<i>Sphaerophoria sp.</i>	1	1
<i>Sphecodes monilicornis</i>	0	1
<i>Sphecodes reticulatus</i>	1	0
<i>Syritta pipiens</i>	1	0
<i>Syrphus ribesii</i>	1	1

<i>Syrphus vitripennis</i>	1	0
<i>Thymelicus sylvestris</i>	1	1
<i>Tyria jacobaeae</i>	0	1
<i>Vanessa cardui</i>	1	0
<i>Volucella bombylans</i>	1	0
<i>Zygaena filipendulae</i>	1	0
<i>Zygaena lonicerae</i>	0	1
	80	68

Appendix 1.9 Spearman's rank correlation results between principal components and dependent variables at three different study scales (250m, 1000m and 3000m)

250m

		AVBEE	AVHOV	AVBUT	RBEE	RHOV	RBUT
PC1	R	-.364*	.020	.235	-.151	-.099	.103
	P	.034	.913	.181	.395	.579	.562
PC2	R	-.098	.041	-.240	-.140	-.038	-.296
	P	.582	.820	.171	.431	.831	.089
PC3	R	-.308	-.060	-.363*	-.458**	-.098	-.316
	P	.076	.738	.035	.007	.582	.069
PC4	R	-.024	.067	-.072	.029	.141	-.108
	P	.893	.707	.687	.873	.426	.545
PC5	R	-.401*	-.235	.124	-.286	-.180	.061
	P	.019	.182	.484	.101	.309	.734
PC6	R	.076	-.307	.081	.151	-.297	.132
	P	.669	.078	.651	.394	.088	.457
PC7	R	-.014	.037	-.024	-.085	.066	-.004
	P	.936	.837	.894	.631	.709	.984
PC8	R	-.193	-.235	.086	-.267	-.255	.001
	P	.274	.182	.629	.127	.145	.994
PC9	R	-.075	-.020	.217	.084	-.027	.396*
	P	.671	.909	.217	.635	.882	.020
PC10	R	.074	-.117	-.060	-.030	-.101	-.062
	P	.676	.510	.734	.867	.570	.726
PC11	R	.109	-.015	.104	.086	.046	.058
	P	.540	.933	.560	.630	.795	.743
PC12	R	-.234	.051	-.320	-.130	.057	-.317
	P	.182	.774	.065	.463	.751	.068

1000m

		AVBEE	AVHOV	AVBUT	RBEE	RHOV	RBUT
PC1	R	-.437**	-.231	.293	-.215	-.248	.133
	P	.010	.188	.092	.222	.157	.454
PC2	R	-.107	-.110	.209	.041	-.062	.036
	P	.546	.535	.236	.819	.726	.838
PC3	R	-.131	.062	-.010	-.168	.041	-.008
	P	.460	.730	.955	.343	.819	.966
PC4	R	.252	-.113	.156	.316	-.169	.156

	P	.151	.526	.378	.069	.339	.378
PC5	R	-.035	.029	.276	-.087	-.092	.273
	P	.845	.872	.114	.624	.603	.118
PC6	R	-.270	-.497**	-.284	-.257	-.555**	-.383*
	P	.123	.003	.103	.143	.001	.025
PC7	R	-.142	.023	.116	-.087	-.039	.122
	P	.422	.897	.512	.624	.826	.491
PC8	R	.250	.321	-.171	.054	.203	-.037
	P	.154	.065	.333	.764	.250	.836
PC9	R	-.120	.022	-.189	-.213	-.049	-.042
	P	.497	.900	.284	.227	.784	.812
PC10	R	.144	.161	-.265	.153	.178	-.219
	P	.417	.364	.129	.387	.313	.213
PC11	R	-.317	-.150	-.047	-.222	-.138	-.085
	P	.068	.398	.790	.208	.436	.631
PC12	R	.047	.419*	-.008	.051	.430*	-.224
	P	.792	.014	.964	.774	.011	.202

3000m

		AVBEE	AVHOV	AVBUT	RBEE	RHOV	RBUT
PC1	R	-.321	.101	.196	-.216	.176	.139
	p	.064	.570	.267	.220	.318	.432
PC2	R	-.307	-.286	.031	-.294	-.369*	-.044
	P	.077	.101	.861	.092	.032	.806
PC3	R	.385*	.045	.058	.312	.071	.189
	P	.025	.802	.744	.073	.688	.285
PC4	R	-.243	-.189	.161	-.070	-.203	-.079
	P	.167	.284	.363	.693	.250	.658

PC5	R	0.000	-.136	.095	.030	-.195	.078
	P	1.000	.444	.594	.865	.269	.662
PC6	R	.014	-.015	.079	.182	.014	-.020
	P	.935	.932	.657	.302	.935	.910
PC7	R	.280	.088	.236	.299	.009	.403*
	P	.108	.620	.179	.086	.960	.018
PC8	R	.072	.190	.150	.019	.307	.101
	P	.685	.283	.396	.915	.078	.570
PC9	R	-.046	-.003	.226	-.043	-.023	.221
	P	.794	.988	.199	.808	.897	.208
PC10	R	.129	.275	.083	.010	.293	-.075
	P	.468	.115	.642	.954	.092	.672
PC11	R	-.179	-.290	.120	-.214	-.352*	.260
	P	.311	.096	.499	.225	.041	.138
PC12	R	-.253	-.123	-.185	-.432*	-.130	-.181
	P	.149	.489	.294	.011	.462	.305

Appendix 1.10 Spearman's Rank Correlations and Mann Whitney U test results

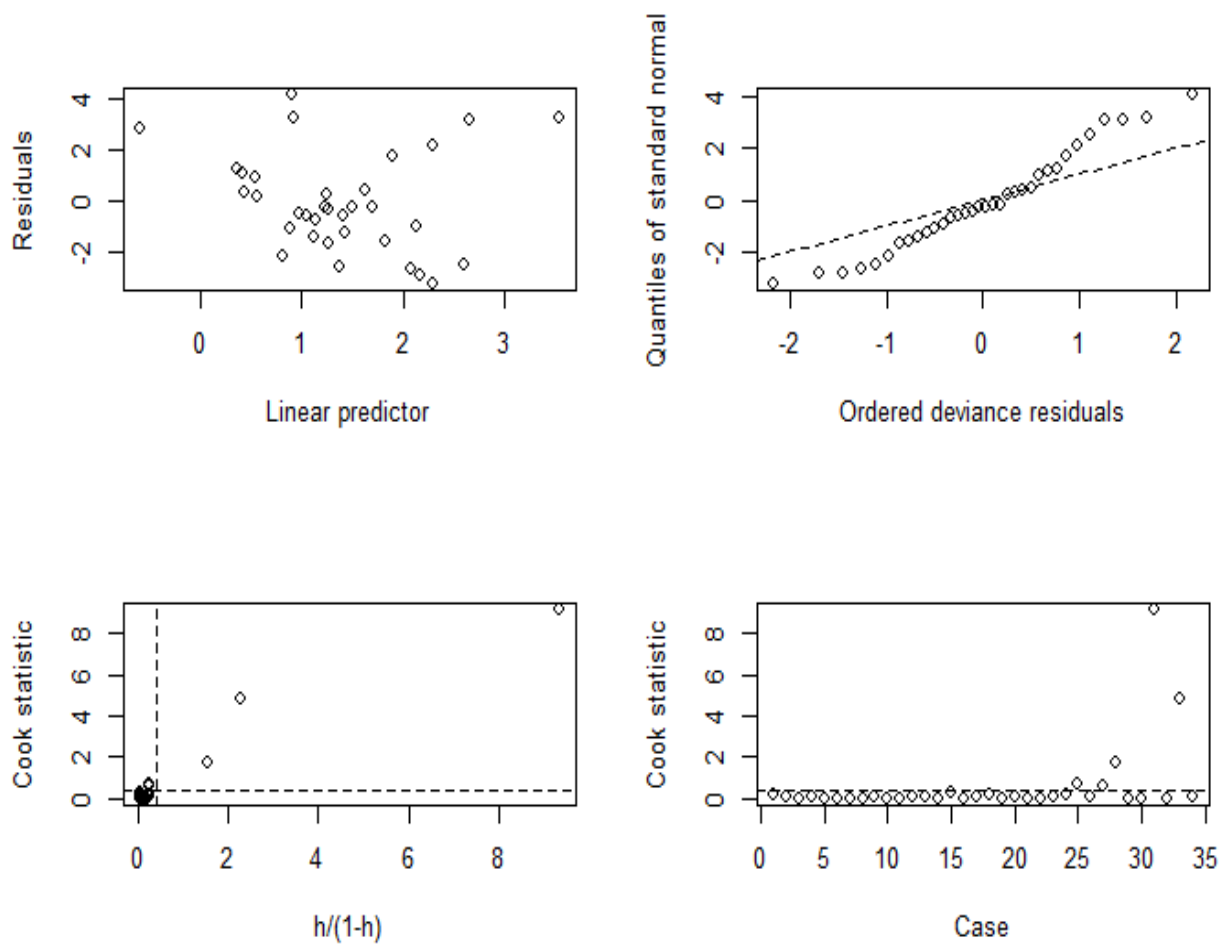
Available as an Excel Spreadsheet from the author.

Appendix 1.11 Univariate results output

Variable	Species richness			Abundance		
	DFL	Hoverflies	Bees	DFL	Hoverflies	Bees
W250	140.64	166.05	167.55	231.75	169.52	427.34
W1000	141.04	166.00	165.56	233.62	168.43	402.86
W3000	142.50	165.93	165.52	254.17	168.75	394.66
SW250	145.05	166.04	168.48	322.11	168.95	381.19
SW1000	145.21	165.33	167.55	322.01	169.02	401.31
SW3000	145.20	164.47	168.40	324.82	169.23	437.76
BU250	145.18	162.52	166.14	343.53	168.12	448.25
BU1000	144.52	164.67	167.61	340.84	168.71	452.30
BU3000	144.50	165.79	168.39	341.65	169.97	444.47
SNH250	145.24	160.62	167.66	345.98	167.11	452.53
SNH1000	145.25	158.54	167.32	346.12	163.68	447.17
SNH3000	144.80	166.04	165.80	327.67	169.89	380.59
PEL250	145.02	166.07	168.02	339.15	169.25	424.88
PEL1000	145.14	165.71	167.55	337.97	169.60	437.11
PEL3000	144.68	166.05	168.51	346.35	169.91	443.42
PELHL250	142.73	165.31	167.21	333.84	168.66	453.15
PELHL1000	144.25	165.50	167.67	344.00	169.85	453.48
PELHL3000	144.26	165.17	167.92	345.58	170.01	451.66

HE250	143.21	165.75	162.87	346.25	169.74	442.73
HE1000	143.60	165.98	167.07	337.00	169.87	434.71
HE3000	144.66	165.74	162.54	339.69	169.93	426.53
SR250	141.31	165.51	164.61	325.92	170.03	452.19
SR1000	145.09	159.96	168.49	339.30	168.18	452.12
SR3000	144.54	162.30	165.72	346.20	169.58	416.77
C250	144.31	163.65	163.97	343.92	169.92	367.58
C1000	145.21	160.92	164.69	338.53	168.54	407.67
C3000	145.24	164.87	168.51	341.81	169.25	446.42
SNG250	145.05	165.85	168.23	345.12	169.94	415.03
SNG1000	145.22	162.88	166.58	346.21	165.87	450.10
SNG3000	145.23	160.58	168.51	346.35	168.14	442.69
WA250	144.93	163.55	167.83	346.35	163.16	446.18
WA1000	145.25	163.33	166.27	343.65	166.22	451.61
WA3000	145.25	149.69	166.06	346.04	159.34	438.05

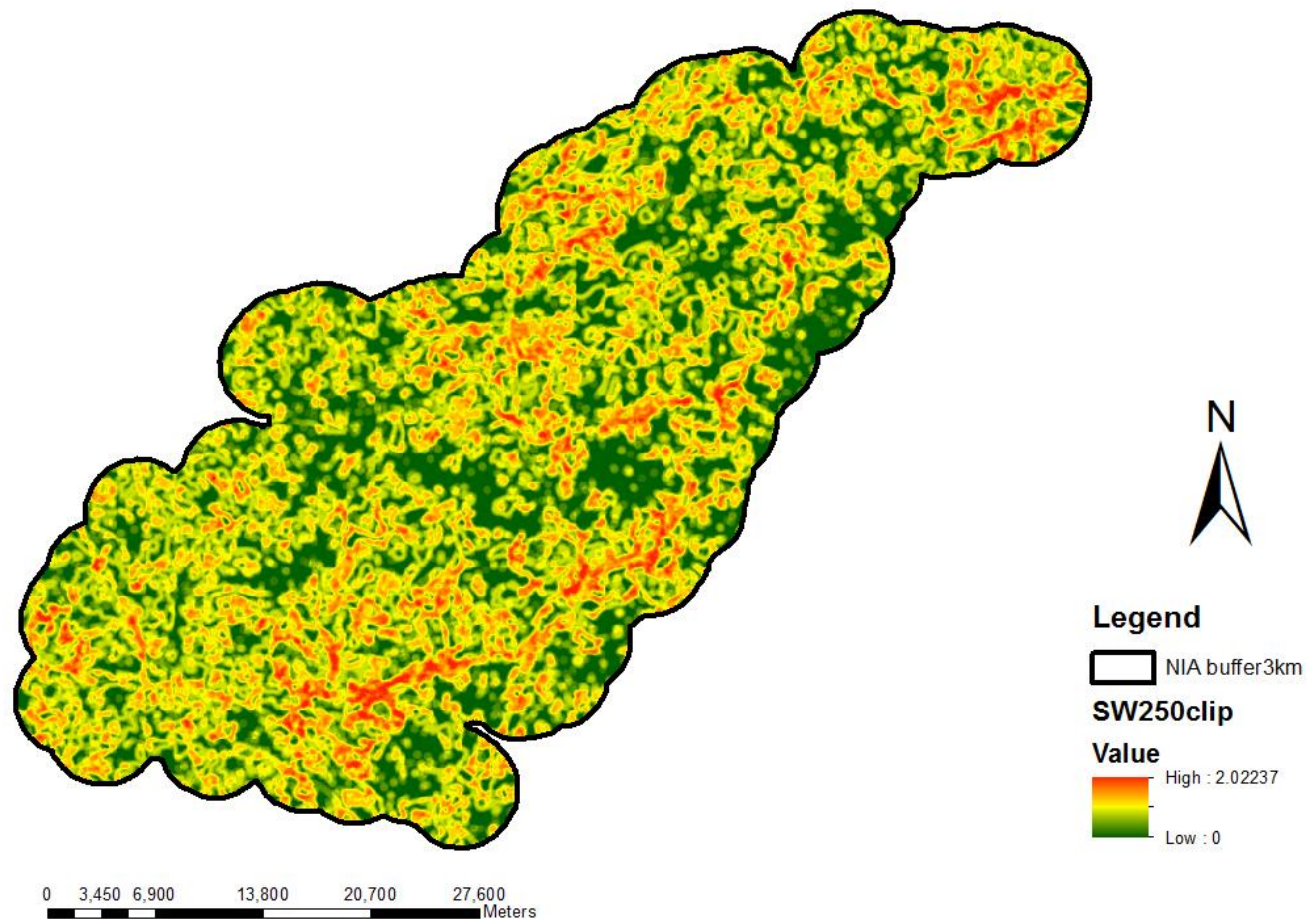
Appendix 1.12 Diagnostic plot of top day-flying Lepidoptera abundance model residuals demonstrating overdispersion within the data (chapter 5)



Appendix 1.13 Moran's I values for top models in Chapter 4 and Chapter 5

	Chapter 4 top models			Chapter 5 top models		
	RHOV	RBEE	RDFL	RHOV	RBEE	RDFL
Observed	-0.08	-0.16	-0.09	-0.09	-0.11	-0.11
Expected	-0.03	-0.03	-0.03	-0.03	-0.03	-0.03
P value	0.44	0.03	0.28	0.31	0.20	0.16

Appendix 1.14 Example of Shannon-Wiener habitat diversity map (sampled at the 250m scale) for the Nene Valley NIA and 3km buffer



Appendix 1.15 Example of adapted R code used to produce partial effects plots for hoverfly species richness in Chapter 5

```

data1 <- read.csv(file.choose())
library(MuMIn)
library(ggplot2)
library(gridExtra)
data5 <- data1[1:36]
data5 <- as.data.frame(scale(data5[,]))
data5$RBUT <- data1$RBUT
mod1 <- glm(RBUT ~ GRAZED + SR250, data = data5, family = poisson)
mod2 <- glm(RBUT ~ GRAZED, data = data5, family = poisson)
mod3 <- glm(RBUT ~ RESTORED + GRAZED, data = data5, family = poisson)
mod4 <- glm(RBUT ~ HAYCUT + GRAZED + SR250, data = data5, family = poisson)
mod5 <- glm(RBUT ~ GRAZED + HE250 + SR250, data = data5, family = poisson)
mod6 <- glm(RBUT ~ GRAZED + HE250, data = data5, family = poisson)
mod7 <- glm(RBUT ~ HAYCUT + GRAZED, data = data5, family = poisson)
mod8 <- glm(RBUT ~ RESTORED + HAYCUT + GRAZED, data = data5, family = poisson)
mod9 <- glm(RBUT ~ RESTORED + GRAZED + HE250, data = data5, family = poisson)
mod10 <- glm(RBUT ~ RESTORED + GRAZED + SR250, data = data5, family = poisson)
mod11 <- glm(RBUT ~ NEW + GRAZED + SR250, data = data5, family = poisson)
mod12 <- glm(RBUT ~ NEW + GRAZED, data = data5, family = poisson)
mod13 <- glm(RBUT ~ GRAZED + SITEAREA, data = data5, family = poisson)
mod14 <- glm(RBUT ~ DESIGNATION + GRAZED, data = data5, family = poisson)
mod15 <- glm(RBUT ~ RESTORED + HAYCUT + GRAZED + SR250, data = data5, family = poisson)

average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)

data5$X <- NULL
par(mfrow=c(4,4))
newdata <- as.data.frame(lapply(lapply(data5[,-1], mean), rep, 100))
nseq <- function(x, len= length(x)) seq(min(-2, na.rm = TRUE), max(2, na.rm=TRUE), length = len)
newdata$HE250 <- nseq(data5$HE250, nrow(newdata))
pred <- predict(average, newdata, full = TRUE, type = "link", backtransform= TRUE, se.fit = TRUE)
data2 <- data.frame(HE250pred = pred$fit, newHE250=newdata$HE250, HE250SE = pred$se.fit)
data3 <- with(data2, data.frame(HE250pred, HE250SE, HE250lwr = HE250pred-1.96*HE250SE, HE250upr =
HE250pred +1.96*HE250SE))
data3$HE250pred <- pred$fit
data3$newHE250 <- newdata$HE250
data3$HE250SE <- pred$se.fit
data3$HE250lwr <- data3$HE250pred-1.96*data3$HE250SE
data3$HE250upr <- data3$HE250pred+1.96*data3$HE250SE
p <- ggplot(data3, aes(x= newHE250, y= HE250pred))
p <- ggplot(data3, aes(x=newHE250, y= HE250pred)) + coord_cartesian(ylim=c(0,7))
graph <- p + theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())
+geom_line(colour="yellow", size = 1)
HE250RBUT <- graph + geom_ribbon(data = data3, aes(ymin=HE250lwr, ymax=HE250upr), alpha = 0.4,
fill = "yellow") + xlab("Scaled HE250") + ylab("D.F.L. richness")
HE250RBUT

newdata <- as.data.frame(lapply(lapply(data5[,-1], mean), rep, 100))
nseq <- function(x, len= length(x)) seq(min(-2, na.rm = TRUE), max(2, na.rm=TRUE), length = len)
newdata$SITEAREA <- nseq(data5$SITEAREA, nrow(newdata))
pred <- predict(average, newdata, full = TRUE, type = "link", backtransform= TRUE, se.fit = TRUE)
data3$SITEAREApred <- pred$fit
data3$newSITEAREA <- newdata$SITEAREA
data3$SITEAREASE <- pred$se.fit
data3$SITEAREAlwr <- data3$SITEAREApred-1.96*data3$SITEAREASE
data3$SITEAREaupr <- data3$SITEAREApred+1.96*data3$SITEAREASE
p <- ggplot(data3, aes(x= newSITEAREA, y= SITEAREApred))
p <- ggplot(data3, aes(x=newSITEAREA, y= SITEAREApred)) + coord_cartesian(ylim=c(0,7))
graph <- p + theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())
+geom_line(colour="red", size = 1)
SITEAREARBUT <- graph + geom_ribbon(data = data3, aes(ymin=SITEAREAlwr, ymax=SITEAREaupr), alpha
= 0.4, fill = "red") + xlab("Scaled SITEAREA") + ylab("D.F.L. richness")
SITEAREARBUT

```

```

newdata <- as.data.frame(lapply(lapply(data5[,-1], mean), rep, 100))
nseq <- function(x, len= length(x)) seq(min(-2, na.rm = TRUE), max(2, na.rm=TRUE), length = len)
newdata$SR250 <- nseq(data5$SR250, nrow(newdata))
pred <- predict(average, newdata, full = TRUE, type = "link", backtransform= TRUE, se.fit = TRUE)
data3$SR250pred <- pred$fit
data3$newSR250 <- newdata$SR250
data3$SR250SE <- pred$se.fit
data3$SR250lwr <- data3$SR250pred-1.96*data3$SR250SE
data3$SR250upr <- data3$SR250pred+1.96*data3$SR250SE
p <- ggplot(data3, aes(x= newSR250, y= SR250pred))
p <- ggplot(data3, aes(x=newSR250, y= SR250pred)) + coord_cartesian(ylim=c(0,7))
graph <- p + theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())
+geom_line(colour="blue", size = 1)
SR250RBUT <- graph + geom_ribbon(data = data3, aes(ymin=SR250lwr, ymax=SR250upr), alpha = 0.4,
fill = "blue") + xlab("Scaled SR250") + ylab("D.F.L. richness")
SR250RBUT

```

```

grid.arrange(SR250RBUT, HE250RBUT, SITEAREARBUT, ncol=2)
g <- arrangeGrob(SR250RBUT, HE250RBUT, SITEAREARBUT, ncol=2)
ggsave("DFLaveraged.png", path= "C:/Users/Kathryn/Dropbox/PhD/Corrections/second run/3rd March
2018", g)

```

```

data1 <- read.csv(file.choose())
data1$HAYCUT[data1$HAYCUT == "0"] <- "No haycut"
data1$HAYCUT[data1$HAYCUT == "1"] <- "Haycut"
mod1 <- glm(RBUT ~ factor(GRAZED) + SR250, data = data1, family = poisson)
mod2 <- glm(RBUT ~ factor(GRAZED), data = data1, family = poisson)
mod3 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED), data = data1, family = poisson)
mod4 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED) + SR250, data = data1, family = poisson)
mod5 <- glm(RBUT ~ factor(GRAZED) + HE250 + SR250, data = data1, family = poisson)
mod6 <- glm(RBUT ~ factor(GRAZED) + HE250, data = data1, family = poisson)
mod7 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED), data = data1, family = poisson)
mod8 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED), data = data1, family =
poisson)
mod9 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + HE250, data = data1, family = poisson)
mod10 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + SR250, data = data1, family = poisson)
mod11 <- glm(RBUT ~ factor(NEW) + factor(GRAZED) + SR250, data = data1, family = poisson)
mod12 <- glm(RBUT ~ factor(NEW) + factor(GRAZED), data = data1, family = poisson)
mod13 <- glm(RBUT ~ factor(GRAZED) + SITEAREA, data = data1, family = poisson)
mod14 <- glm(RBUT ~ factor(DSIGNATION) + factor(GRAZED), data = data1, family = poisson)
mod15 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED) + SR250, data = data1,
family = poisson)
average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)
HAYCUT_scenarios <- data.frame(SR250 = mean(data1$SR250), HE250 = mean(data1$HE250), SITEAREA =
mean(data1$SITEAREA), GRAZED = 0, RESTORED = 0, HAYCUT = c("No haycut", "Haycut"), NEW = 0,
DESIGNATION = 0 )
HAYCUT_pred <- as.data.frame(predict(average, newdata = HAYCUT_scenarios, full = TRUE, se.fit =
TRUE, type = "response"))
HAYCUT_pred$lwr <- HAYCUT_pred$fit - (HAYCUT_pred$se.fit*1.96)
HAYCUT_pred$upr <- HAYCUT_pred$fit + (HAYCUT_pred$se.fit*1.96)
HAYCUT_pred$HAYCUT <- HAYCUT_scenarios$HAYCUT
HAYCUTplot <- ggplot(HAYCUT_pred, aes(x = HAYCUT, y = fit, ymin = lwr, ymax = upr)) +
coord_cartesian(ylim=c(0,10)) + geom_pointrange() + ylab("D.F.L. richness") + xlab("Haycut
taken")

```

```

data1 <- read.csv(file.choose())
data1$GRAZED[data1$GRAZED == "0"] <- "Not grazed"
data1$GRAZED[data1$GRAZED == "1"] <- "Grazed"
mod1 <- glm(RBUT ~ factor(GRAZED) + SR250, data = data1, family = poisson)
mod2 <- glm(RBUT ~ factor(GRAZED), data = data1, family = poisson)
mod3 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED), data = data1, family = poisson)
mod4 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED) + SR250, data = data1, family = poisson)
mod5 <- glm(RBUT ~ factor(GRAZED) + HE250 + SR250, data = data1, family = poisson)
mod6 <- glm(RBUT ~ factor(GRAZED) + HE250, data = data1, family = poisson)
mod7 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED), data = data1, family = poisson)
mod8 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED), data = data1, family =
poisson)

```

```

mod9 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + HE250,data = data1, family = poisson)
mod10 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod11 <- glm(RBUT ~ factor(NEW) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod12 <- glm(RBUT ~ factor(NEW) + factor(GRAZED),data = data1, family = poisson)
mod13 <- glm(RBUT ~ factor(GRAZED) + SITEAREA,data = data1, family = poisson)
mod14 <- glm(RBUT ~ factor(DSIGNATION) + factor(GRAZED),data = data1, family = poisson)
mod15 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED) + SR250,data = data1,
family = poisson)
average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)
GRAZED_scenarios <- data.frame(SR250 = mean(data1$SR250), HE250 = mean(data1$HE250), SITEAREA =
mean(data1$SITEAREA), GRAZED = c("Not grazed", "Grazed"), RESTORED = 0, HAYCUT = 0, NEW = 0,
DESIGNATION = 0 )
GRAZED_pred <- as.data.frame(predict(average, newdata = GRAZED_scenarios, full = TRUE, se.fit =
TRUE, type = "response"))
GRAZED_pred$lwr <- GRAZED_pred$fit - (GRAZED_pred$se.fit*1.96)
GRAZED_pred$upr <- GRAZED_pred$fit + (GRAZED_pred$se.fit*1.96)
GRAZED_pred$GRAZED <- GRAZED_scenarios$GRAZED
GRAZEDplot <- ggplot(GRAZED_pred, aes(x = GRAZED, y = fit, ymin = lwr, ymax = upr)) +
coord_cartesian(ylim=c(0,10)) + geom_pointrange() + ylab("D.F.L. richness") + xlab("Grazed")

data1 <- read.csv(file.choose())
data1$RESTORED[data1$RESTORED == "0"] <- "Not restored"
data1$RESTORED[data1$RESTORED == "1"] <- "Restored"
mod1 <-glm(RBUT ~ factor(GRAZED) + SR250, data = data1, family = poisson)
mod2 <- glm(RBUT ~ factor(GRAZED),data = data1, family = poisson)
mod3 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED),data = data1, family = poisson)
mod4 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod5 <- glm(RBUT ~ factor(GRAZED) + HE250 + SR250,data = data1, family = poisson)
mod6 <- glm(RBUT ~ factor(GRAZED) + HE250,data = data1, family = poisson)
mod7 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED),data = data1, family = poisson)
mod8 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED),data = data1, family =
poisson)
mod9 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + HE250,data = data1, family = poisson)
mod10 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod11 <- glm(RBUT ~ factor(NEW) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod12 <- glm(RBUT ~ factor(NEW) + factor(GRAZED),data = data1, family = poisson)
mod13 <- glm(RBUT ~ factor(GRAZED) + SITEAREA,data = data1, family = poisson)
mod14 <- glm(RBUT ~ factor(DSIGNATION) + factor(GRAZED),data = data1, family = poisson)
mod15 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED) + SR250,data = data1,
family = poisson)
average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)
RESTORED_scenarios <-data.frame(SR250 = mean(data1$SR250), HE250 = mean(data1$HE250), SITEAREA =
mean(data1$SITEAREA), GRAZED = 0, RESTORED = c("Not restored", "Restored"), HAYCUT = 0, NEW = 0,
DESIGNATION = 0 )
RESTORED_pred <- as.data.frame(predict(average, newdata = RESTORED_scenarios, full = TRUE, se.fit
= TRUE, type = "response"))
RESTORED_pred$lwr <- RESTORED_pred$fit - (RESTORED_pred$se.fit*1.96)
RESTORED_pred$upr <- RESTORED_pred$fit + (RESTORED_pred$se.fit*1.96)
RESTORED_pred$RESTORED <- RESTORED_scenarios$RESTORED
RESTOREDplot <- ggplot(RESTORED_pred, aes(x = RESTORED, y = fit, ymin = lwr, ymax = upr)) +
coord_cartesian(ylim=c(0,10)) + geom_pointrange() + ylab("D.F.L. richness") + xlab("Site
restored")

data1 <- read.csv(file.choose())
data1$DESIGNATION[data1$DESIGNATION == "0"] <- "Not designated"
data1$DESIGNATION[data1$DESIGNATION == "1"] <- "Designated"
mod1 <-glm(RBUT ~ factor(GRAZED) + SR250, data = data1, family = poisson)
mod2 <- glm(RBUT ~ factor(GRAZED),data = data1, family = poisson)
mod3 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED),data = data1, family = poisson)
mod4 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod5 <- glm(RBUT ~ factor(GRAZED) + HE250 + SR250,data = data1, family = poisson)
mod6 <- glm(RBUT ~ factor(GRAZED) + HE250,data = data1, family = poisson)
mod7 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED),data = data1, family = poisson)
mod8 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED),data = data1, family =
poisson)
mod9 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + HE250,data = data1, family = poisson)
mod10 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod11 <- glm(RBUT ~ factor(NEW) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod12 <- glm(RBUT ~ factor(NEW) + factor(GRAZED),data = data1, family = poisson)

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mod13 <- glm(RBUT ~ factor(GRAZED) + SITEAREA,data = data1, family = poisson)
mod14 <- glm(RBUT ~ factor(DSIGNATION) + factor(GRAZED),data = data1, family = poisson)
mod15 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED) + SR250,data = data1,
family = poisson)
average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)
DESIGNATION_scenarios <-data.frame(SR250 = mean(data1$SR250), HE250 = mean(data1$HE250), SITEAREA
= mean(data1$SITEAREA), GRAZED = 0, DESIGNATION = c("Not designated", "Designated"), HAYCUT = 0,
NEW = 0, RESTORED = 0 )
DESIGNATION_pred <-as.data.frame(predict(average, newdata = DESIGNATION_scenarios, full = TRUE,
se.fit = TRUE, type = "response"))
DESIGNATION_pred$lwr <- DESIGNATION_pred$fit - (DESIGNATION_pred$se.fit*1.96)
DESIGNATION_pred$upr <- DESIGNATION_pred$fit + (DESIGNATION_pred$se.fit*1.96)
DESIGNATION_pred$DESIGNATION <- DESIGNATION_scenarios$DESIGNATION
DESIGNATIONplot <- ggplot(DESIGNATION_pred, aes(x = DESIGNATION, y = fit, ymin = lwr, ymax =
upr)) + coord_cartesian(ylim=c(0,10)) + geom_pointrange() + ylab("D.F.L. richness") + xlab("Site
designated")

data1 <- read.csv(file.choose())
data1$NEW[data1$NEW == "0"] <- "No"
data1$NEW[data1$NEW == "1"] <- "Yes"
mod1 <-glm(RBUT ~ factor(GRAZED) + SR250, data = data1, family = poisson)
mod2 <- glm(RBUT ~ factor(GRAZED),data = data1, family = poisson)
mod3 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED),data = data1, family = poisson)
mod4 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod5 <- glm(RBUT ~ factor(GRAZED) + HE250 + SR250,data = data1, family = poisson)
mod6 <- glm(RBUT ~ factor(GRAZED) + HE250,data = data1, family = poisson)
mod7 <- glm(RBUT ~ factor(HAYCUT) + factor(GRAZED),data = data1, family = poisson)
mod8 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED),data = data1, family =
poisson)
mod9 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + HE250,data = data1, family = poisson)
mod10 <- glm(RBUT ~ factor(RESTORED) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod11 <- glm(RBUT ~ factor(NEW) + factor(GRAZED) + SR250,data = data1, family = poisson)
mod12 <- glm(RBUT ~ factor(NEW) + factor(GRAZED),data = data1, family = poisson)
mod13 <- glm(RBUT ~ factor(GRAZED) + SITEAREA,data = data1, family = poisson)
mod14 <- glm(RBUT ~ factor(DSIGNATION) + factor(GRAZED),data = data1, family = poisson)
mod15 <- glm(RBUT ~ factor(RESTORED) + factor(HAYCUT) + factor(GRAZED) + SR250,data = data1,
family = poisson)
average <- model.avg(mod1, mod2, mod3, mod4, mod5, mod6, mod7, mod8, mod9, mod10, mod11, mod12,
mod13, mod14, mod15)
NEW_scenarios <-data.frame(SR250 = mean(data1$SR250), HE250 = mean(data1$HE250), SITEAREA =
mean(data1$SITEAREA), GRAZED = 0, NEW = c("No", "Yes"), HAYCUT = 0, DESIGNATION = 0, RESTORED = 0
)
NEW_pred <-as.data.frame(predict(average, newdata = NEW_scenarios, full = TRUE, se.fit = TRUE,
type = "response"))
NEW_pred$lwr <- NEW_pred$fit - (NEW_pred$se.fit*1.96)
NEW_pred$upr <- NEW_pred$fit + (NEW_pred$se.fit*1.96)
NEW_pred$NEW <- NEW_scenarios$NEW
NEWplot <- ggplot(NEW_pred, aes(x = NEW, y = fit, ymin = lwr, ymax = upr)) +
coord_cartesian(ylim=c(0,10)) + geom_pointrange() + ylab("D.F.L. richness") + xlab("Site restored
<5 years")

grid.arrange(HAYCUTplot, GRAZEDplot, RESTOREDplot, NEWplot, DESIGNATIONplot, ncol=2)
g <- arrangeGrob(HAYCUTplot, GRAZEDplot, RESTOREDplot, NEWplot, DESIGNATIONplot, ncol=2)
ggsave("DFL categorical.png", path= "C:/Users/Kathryn/Dropbox/PhD/Corrections/second run/3rd
March 2018", g)

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