

Effects of land use on bee diversity

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Declaration of Originality

This thesis is the product of my own work, unless mentioned here or in the text. I collected none of my own ecological data; a number of researchers (listed in Chapter 2) have generously shared their data. Lawrence Hudson and Igor Lysenko have designed and maintained the PREDICTS database, which I have used throughout my PhD. All data collation and curation procedures were designed and refined in collaboration with the PREDICTS team. All chapters have been commented on by my supervisor, Andy Purvis. Chapter 3 has been published in the *Journal of Applied Ecology* and has benefitted from comments by co-authors and anonymous reviewers. Chapter 6 is currently in preparation for submission and has been commented on by co-authors (including a number of data providers).

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Abstract

Bees are a diverse group of insects specialised to use floral resources throughout their lifecycle, making them one of the most important groups of pollinators. Land-use change and agricultural intensification can reduce the diversity of these species, with potential consequences for plant communities and a number of globally-important crops. Some key knowledge gaps limit our ability to inform conservation activities, however. Which species or groups of species are most vulnerable to human land use and agricultural intensification? Do different aspects of bee community diversity respond similarly to land-use pressures? Are the same patterns repeated around the world? Where has bee diversity been most heavily impacted? I have collated a global dataset of bee diversity from the published literature and integrated it with information on land use, species' traits and phylogeny in order to answer these questions. I have shown that functional traits interact in complex ways with land-use pressures in order to influence the occurrence and abundance of European bees; in spite of these complexities, general lessons can still be learnt about management priorities. I have found that species sensitivities to some—but not all—land-use transitions are phylogenetically non-random, highlighting particularly vulnerable clades. These functional and phylogenetic differences scale up to influence community-level diversity, but there are spatial mismatches: taxonomic diversity responds differently to land-use pressures than do functional and phylogenetic diversity. While the dataset I have collated is the most extensive of its kind, the majority of available, accessible data are from European and North American bumblebees - a bias that has also affected previous similar analyses. I show that these biases can affect predictions of land-use impacts on bee diversity if regional differences in diversity, biotic sensitivity and threat intensity are not considered, highlighting the importance of primary data collection in undersampled regions, which are highly economically vulnerable to pollination deficits.

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CHAPTER 1

Introduction

Land-use change is considered one of the major pressures on terrestrial biodiversity (Foley *et al.* 2005; Sala *et al.* 2000). Over recent decades, habitat loss, degradation and fragmentation have continued apace, while - at a global scale - species abundance and diversity have declined and extinction rates have risen (Millenium Ecosystem Assessment 2005; Newbold *et al.* 2015; Pimm *et al.* 2014; Tittensor *et al.* 2014). These declines in biodiversity show no indication of stopping but are set to continue (Butchart *et al.* 2010; Newbold *et al.* 2015; Tittensor *et al.* 2014): although the causes of land-use change are complex (Balmford *et al.* 2009; Lambin *et al.* 2001; Meyer & Turner II 1992), many putative drivers such as population size and gross domestic product (Forester & Machlist 1996) are projected to increase (Harfoot *et al.* 2014; van Vuuren *et al.* 2011).

Agricultural expansion and intensification—perhaps the major causes of biodiversity loss to date—are of particular concern (Green 2005; Norris 2008). Over the past 300 years, the area of cropland and pasture has already increased by over six fold (Goldewijk 2001); agriculture is now one of the most dominant land uses on the planet, covering over 30% of the Earth's surface (Ellis *et al.* 2010; Hurtt *et al.* 2011). As global populations and affluence continue to rise, food production must be enhanced to meet the increasing and changing demand (Foley *et al.* 2011; Godfray *et al.* 2010).

These land-use pressures can influence biodiversity both by directly inducing additional mortality, and indirectly through the losses of resources such as suitable habitat for foraging and nesting (Owens & Bennett 2000). Resulting population declines and extinctions can lead to the collapse of interactions with associated biota (Wardle *et al.* 2011). For instance, as mutualistic networks are often phylogenetically patterned, an extinction event can cause extinction cascades of closely-related species (Rezende *et al.* 2007). Anthropogenic changes

can also open up opportunities for other species to increase in abundance and dominate newly-created habitats (McKinney & Lockwood 1999; Wardle *et al.* 2011). Community composition is significantly altered by these species losses and gains (McKinney & Lockwood 1999; Thomas 2013; Wardle *et al.* 2011), with human-dominated land uses maintaining markedly different biodiversity than natural and semi-natural land uses (Newbold *et al.* 2015). Such large-scale changes in community composition could have severe consequences for ecosystem function and stability (Cardinale *et al.* 2006; Hooper *et al.* 2005; Naeem & Li 1997; Naeem *et al.* 1994; Zavaleta *et al.* 2009), especially if functionally-important species are also the most sensitive to land-use pressures (Kaiser-Bunbury *et al.* 2010; Larsen *et al.* 2005; Smith & Knapp 2003; Zavaleta *et al.* 2009) or if resource availability is particularly heterogeneous (Tylianakis *et al.* 2008). Indeed, a global meta-analysis revealed that biodiversity loss has effects on ecosystem functioning that are similar in magnitude to the direct impacts of elevated CO₂ and nitrogen addition (Hooper *et al.* 2012).

Ecosystem functioning may not decline linearly with losses in biodiversity, however (Brook *et al.* 2013; Cardinale *et al.* 2012; Mace *et al.* 2014). Instead, there is evidence to suggest that there are tipping points – critical levels of biodiversity loss, beyond which the entire system may shift state (Andersen *et al.* 2009; Scheffer *et al.* 2001). While most evidence for such tipping points exist at the local level (Brook *et al.* 2013; Loreau *et al.* 2001), there is concern that there may also be regional, biome and global tipping points (Barnosky *et al.* 2012; Hughes *et al.* 2013; Mace *et al.* 2014; Rockström *et al.* 2009; Steffen *et al.* 2015), although this has been debated (Brook *et al.* 2013). Traversing any such boundaries would, according to the Planetary Boundaries theory (Mace *et al.* 2014; Rockström *et al.* 2009; Steffen *et al.* 2015), compromise the integrity of the biosphere, reducing ecosystem service provision to levels that jeopardise human well-being (Rockström *et al.* 2009). Worryingly, changes in the provision of ecosystem goods and services can also influence human activities (such as land-use conversion), potentially causing a negative feedback and further declines in biodiversity and ecosystem functioning (Hooper *et al.* 2005).

While biodiversity as a whole is important for maintaining biosphere integrity in the long term (Steffen *et al.* 2015), losses in functionally-important species may have more severe consequences in the short term (Díaz *et al.* 2007; Myers *et al.* 2007). For instance,

Larsen *et al.* (2005) showed using simulations (based on real communities) that losses in the most functionally-important dung beetle and bee species resulted in the most severe losses in ecosystem function, particularly at intermediate levels of species richness. There has therefore been widespread concern about the state of pollinators across the globe (an extremely functionally important group) and how they are responding to increasing pressure from land-use change and intensification.

Changes in the diversity of animal pollinator communities can have cascading effects on the rest of the ecological system through their impacts on plants. Pollinators are essential for the maintenance of plant diversity, as over 85% of flowering plant species rely on animal pollinators to at least some extent (Ollerton *et al.* 2011), including a number of crop species (Klein *et al.* 2007). Modelling approaches suggest that progressive loss of pollinator species from a system can cause a collapse in the entire plant-pollinator network (Lever *et al.* 2014). For instance, a number of theoretical studies have shown that there is a critical level of habitat loss beyond which point mutualistic networks disassemble and local extinction ensues (Fortuna & Bascompte 2006; Keitt 2009). Empirical studies also suggest that habitat loss has significant impacts on the structure of plant-pollinator interaction networks, reducing stability (Spiesman & Inouye 2013), with smaller areas unable to maintain a high richness and evenness of links in their interaction networks (Sabatino *et al.* 2010). It is not surprising therefore that parallel declines have been reported between animal pollinators and plant populations (Biesmeijer *et al.* 2006), although more recent evidence points to a delay in losses of plant diversity (Carvalho *et al.* 2013), perhaps indicating plants are more resistant to habitat loss than pollinator species (Burkle *et al.* 2013; Taki & Kevan 2007).

As well as their importance for wild plant populations, pollinators are also vital for food security. Although only a minority (35%) of global crop production requires animal pollination (Ghazoul 2005; Klein *et al.* 2007)—because a few wind-pollinated cereals make up such a high proportion of the total—this is still a large enough figure to make pollinators both extremely economically valuable as well as functionally important within ecosystems (Costanza *et al.* 1997; UK National Ecosystem Assessment 2011). Crops with a higher dependence on animal pollinators already tend to have lower rates of yield increase and among-year stability than wind-pollinated crops (Garibaldi *et al.* 2011a). Thus, a decline in the diversity

and abundance of pollinators is likely to exacerbate these crops' yield instability leading to crop losses. Such yield losses could result in increased food prices and malnutrition (Eilers *et al.* 2011), and in turn influence international trade policies that may worsen the problem for some areas of the world (Aizen *et al.* 2009; Garibaldi *et al.* 2011a; Potts *et al.* 2010; Swinnen & Squicciarini 2012). An increase in the use of commercial pollinators, such as honeybees, is unlikely to be able to counter these yield losses: production of honeybee hives has so far been unable to keep pace with the demand for pollination (Aizen & Harder 2009) and, even if the recent declines in bee-keeping are reversed, some crops rely heavily on other wild species for pollination (Javorek *et al.* 2002; Kevan *et al.* 1990). In addition, commercial species can be vulnerable to disease (Ghazoul 2005; van Engelsdorp *et al.* 2008) and may transmit pathogens to wild species (Graystock *et al.* 2013).

Given their societal and ecological importance, the conservation of wild pollinators is seen as a priority for biodiversity conservation. Global Biodiversity Outlook 4 (Secretariat of the Convention on Biological Diversity & CBD 2014; Tittensor *et al.* 2014) uses trends in pollinator extinction risks as one of only three available indicators of the societal benefits provided by biodiversity that was available for assessing progress towards meeting the Convention on Biological Diversity's Aichi Target 14:

“By 2020, ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods and well-being, are restored and safeguarded, taking into account the needs of women, indigenous and local communities, and the poor and vulnerable.”

The taxonomic biases in the available data on the state of biodiversity are so strong, however, that this attempt to report on the benefits accrued from wild pollinators is based exclusively on data for mammalian and avian pollinators. At present, the intention is to include insect pollinators into the calculation of the Pollinator Red List Index by 2020 (UNEP-WCMC 2011), using a Sampled Red List approach (Lewis & Senior 2011). Thus, research is urgently needed that may lead to useful indicators of the state of pollinating insect communities globally and regionally.

The majority of pollinator research focusses on bees (Hymenoptera: Apidae: Apoidea),

as they are the most important single pollinating group (Danforth *et al.* 2006; Kevan & Baker 1983) in both temperate and tropical regions (Food and Agriculture Organization of the United Nations 1995; Garibaldi *et al.* 2011b). Unlike other key pollinating insects, such as flies (Orford *et al.* 2015; Ssymank *et al.* 2008), bees use floral resources throughout their entire life-cycle: bees put floral nectar, pollen, oils, waxes, perfumes and resins to a variety of uses, including nutrition, nest construction and sexual attractants (Buchmann 1987; Danforth *et al.* 2006). Bees are therefore highly specialised flower-visiting insects (anthophiles). They are also an extremely diverse group—morphologically, behaviourally and taxonomically—with over 20,000 species across the globe (Ascher & Pickering 2013; Kevan & Baker 1983; Michener 2000), making them an important focus for conservation efforts in their own right as well as for the services they provide (Kleijn *et al.* 2015).

Recent research suggests that some of the biggest threats facing bees are from habitat loss through agricultural expansion and urbanisation, as well as habitat degradation, which includes the intensification of agricultural practices (Brown & Paxton 2009; Kuldna *et al.* 2009; Potts *et al.* 2010). Habitat conversion may directly affect mortality rates if existing nesting sites are destroyed, and may have indirect impacts by reducing the availability of floral and nesting resources (Forrest *et al.* 2015; Hernandez *et al.* 2009). In contrast, both urban and agricultural areas can also provide nesting sites as well as additional nectar and pollen supplies (Anderson *et al.* 2013; Keitt 2009; Kells *et al.* 2001; Sattler *et al.* 2011; Westphal *et al.* 2003, 2009) and a nectar season lengthened by exotic plants (Salisbury *et al.* 2015).

Land-use intensification can likewise influence bees both directly and indirectly. Intensive farming is characterised by a high-input, high-output system where the use of pesticides and fertilizers is commonplace (Reidsma *et al.* 2007; Seufert *et al.* 2012). Although the sale and use of pesticides is regulated, many of the chemicals still have impacts on non-target organisms. For example, neonicotinoid pesticides have been shown to restrict the growth of colonies and queen production in bumblebees and limit the foraging success and survival of honeybees (Henry *et al.* 2012; Whitehorn *et al.* 2012). In addition, farm management practices such as tillage can greatly influence the survival of some ground-nesting bee species (Shuler *et al.* 2005). In terms of indirect effects, herbicides and fertilizers can reduce plant diversity, as can removal of hedgerows to increase field size, potentially limiting

the floral resources available to bee species (Kleijn *et al.* 2009; Potts *et al.* 2003; Roulston & Goodell 2011).

Given the range and magnitude of pressures facing bees, it seems paradoxical that recent meta-analyses have shown only weak responses of bees to land-use pressures (Montero-Castaño & Vilà 2012; Winfree *et al.* 2009). The resolution probably lies in the fact that responses of bees to human impacts are extremely variable (Cariveau & Winfree 2015; Winfree *et al.* 2011). For example, a recent review by Winfree *et al.* (2011) found that, in studies investigating how bee abundance or species richness varied with increasing human use, 40% showed a negative effect, 13% showed a positive effect, and 46% showed no significant effect. Such a high proportion of contrary significant results can most easily be explained by invoking real heterogeneity in responses. A number of hypotheses have been proposed to explain the variation.

The first hypothesis is that responses may depend on the landscape context—which can vary among studies—as well as on site-level pressures (Winfree *et al.* 2011). Landscape-scale characteristics can be important determinants of bee diversity (Carvalho *et al.* 2010; Garibaldi *et al.* 2011c; Schweiger *et al.* 2005). Bees are relatively mobile organisms, which often have spatially separated nesting and foraging sites (Gathmann & Tscharrntke 2002; Rands & Whitney 2011). Thus, pressures in the surrounding landscape are likely to influence the diversity of bees sampled at a focal site; increases in agricultural and urban extent reduce availability of foraging and nesting habitats, whilst the fragmentation that accompanies such land-use changes can make it increasingly difficult for bees to move between habitats (Dormann *et al.* 2008; E. *et al.* 2009; Kremen *et al.* 2007). The effectiveness of biodiversity-friendly farming techniques has been shown to depend on the surrounding landscape (Brittain *et al.* 2010; Concepción *et al.* 2012). However, a recent global synthesis found little evidence for an interactive effect between local land-use and landscape characteristics, although both were important in driving bee species abundance and richness (Kennedy *et al.* 2013); and other analyses explicitly designed to test the importance of local vs landscape factors have found mixed effects (reviewed by Winfree *et al.* 2011).

A second hypothesis is that species may vary in their sensitivity to a given pressure, presumably as a result of having different functional response traits (Bartomeus *et al.* 2013a;

De Palma *et al.* 2015; Rader *et al.* 2014; Williams *et al.* 2010, 2009), and the distribution of these traits within a community can affect resilience to pressures (Moretti *et al.* 2009). In support of this hypothesis, species' sensitivities to land-use pressures do vary among taxa (as would be expected if the traits mediating responses are phylogenetically conserved: McKinney 1997; Purvis 2008). For instance, bumblebees—the most extensively-studied bee genus—have shown clearer population declines over time than other bees in North America (Bartomeus *et al.* 2013a) and some European countries (Carvalho *et al.* 2013).

Species' traits may interact with landscape-scale effects to mediate sensitivity to human pressures. Because larger bee species tend to forage over greater distances than do smaller species, they may perceive the landscape at different spatial scales. Thus, ecological traits may influence the relative importance of site-level and landscape-scale effects on species' presence and abundance at a site (Gabriel *et al.* 2010; Steffan-Dewenter *et al.* 2002).

A number of studies have explored how ecological traits of species—such as body size, reproductive capacity and niche breadth—can influence the way in which bees respond to land-use pressures (Murray *et al.* 2009; Roulston & Goodell 2011; Steffan-Dewenter *et al.* 2002), although these analyses have often been based on few species and sites, or on museum specimens rather than ecological data (e.g. Bartomeus *et al.* 2013a; Vázquez & Simberloff 2002). In addition, it is still unclear to what extent vulnerability traits are specific to a particular threat (Owens & Bennett 2000; Purvis *et al.* 2005). Chapter 3 of this thesis attempts to answer this question, by providing the most extensive analysis to date of how ecological traits influence the response of bee populations to different land-use pressures in Europe.

Trait-based analyses necessarily use the information on ecological characteristics that is readily available: basic morphological measurements, simplified categorizations of behaviours, and sometimes extreme estimates of phenology (e.g., using the first and last day in the year a species has ever been recorded to estimate flight-season duration). These trait data also often have many gaps in knowledge even in well-studied regions such as Europe. If species' responses to land-use pressures are mediated by traits that we do not commonly measure, then—even if all species have the same trait-response relationships—trait-based approaches will not be able to explain much of the response variation. Low explanatory power could

also arise if species' responses are largely idiosyncratic, i.e., if all species have different trait-response relationships. One way to assess which of these two possibilities is more likely to be the reason for low explanatory power is to explore whether more closely-related species respond in similar ways (phylogenetic signal) (Díaz *et al.* 2013), and assessing whether phylogenetic or functional distances are better able to explain variation in sensitivity. A lack of phylogenetic signal would suggest responses are truly idiosyncratic. If there is strong phylogenetic signal, and phylogenetic distances have better explanatory power, then there is probably an aspect of species characteristics that we have not yet captured. This possibility has not yet been assessed for bees but could have important implications for ecosystem function: if sensitivities are phylogenetically clustered, entire clades may decline together which—if different clades occupy different regions of overall functional diversity—could imperil pollination services (Díaz *et al.* 2013). Therefore, Chapter 4 takes a phylogenetic approach to determine whether species' sensitivities to land-use pressures are phylogenetically patterned, and whether phylogenetic differences explain more of the variation than functional differences.

A third important source of variation in bee responses to human impacts among studies is the measure of diversity that is used (Winfree *et al.* 2011). Many studies focus on bee abundance or species richness; although both of these can be important for pollination services (Albrecht *et al.* 2012; Rogers *et al.* 2014), they do not—cannot—fully capture diversity (Magurran & McGill 2011; Purvis & Hector 2000). Although some work has looked how functional diversity changes in response to human impacts, effects on phylogenetic diversity has thus far not been assessed. Chapter 5 assesses how taxonomic, functional and phylogenetic diversity of European bee communities respond to land use and related pressures, showing that there are significant spatial mismatches between the diversity measures. The fine-scale maps of the state of each of these aspects of biodiversity, relative to a pre-impact baseline, are an important step towards producing a broadly-based and appropriate indicator of the regional and global status of and trends in insect pollinators. Two main obstacles remain: a need for regular—ideally annual—data on pressures (to allow maps to be produced for multiple time periods), and an assessment of whether the pressure-diversity relationships seen in Europe—the region with the richest data sets—hold worldwide (to clarify whether

spatial extrapolation is defensible).

Chapter 6 explores this last point, assessing the final potential source of the observed heterogeneity in responses seen among relevant studies: large-scale geographic variation in the intensity or nature of extrinsic pressures (Cariveau & Winfree 2015) and/or the pressure-diversity relationships. Such variation may be particularly important when global syntheses are based on geographically and taxonomically biased data (which is often the case, Archer *et al.* 2014), as they may limit our ability to generalise results to other regions. I therefore explore (in Chapter 6) whether bee community responses to land-use pressures vary significantly among regions and between bumblebees and other bees: if not, the pressure-diversity relationships seen in the best-studied regions can perhaps be extrapolated worldwide; but if they do vary, each region may need sufficient data to fit within-region models.

Until now, answering the questions posed above has been difficult because the relevant data have been fragmented; though there have been many large syntheses of ecological data, none are well-suited to the purposes of this thesis. The Living Planet Index, though it contains a large amount of temporal data on population trends, only contains vertebrate biodiversity data that are not linked to pressures (Collen *et al.* 2009); without linked biodiversity and pressure data, we cannot formulate dose-response models of local biodiversity change with land-use pressures, which are more relevant for policy makers and land managers. Where invertebrates are included in the available datasets, they are often vastly underrepresented although they constitute the majority of biodiversity (McGill *et al.* 2014; Scheffers *et al.* 2012; Wilson 1987). The conservation status is known for less than 1% of invertebrate species (Collen *et al.* 2012); although the Red List of European Bees has recently been published, the majority of species are still classed as Data Deficient (Nieto *et al.* 2015). Many databases have very restrictive requirements for inclusion, which further limits their comprehensiveness. For instance, the statistical analysis underpinning the GLOBIO3 model requires that each data set included in the database makes comparisons between pristine and disturbed sites (Alkemade *et al.* 2009), but few studies fulfil this criterion: most biodiversity data are collected in western Europe and North America (Meyer *et al.* 2015), where pristine sites are extremely rare. Similarly, meta-analyses require a comparison between a ‘control’ group and a ‘treatment’ group (e.g. organic vs conventional or semi-natural vegetation vs cropland), again greatly

restricting the amount of data that can be used in a single analysis.

I have therefore collated a global dataset of bee diversity across 3785 sites that differ in their land-use class and/or use intensity. Chapter 2 describes the collated dataset in full. Briefly, I searched the published literature for biodiversity data where samples were taken at two or more sites, using the same sampling method, across different land-use classes or intensities (but not necessarily including a ‘pristine’ site). The raw data, rather than effect sizes or summaries, were used in further analyses. Usually, these raw data had not been published in full – as well as being fragmented, the relevant data were largely not directly discoverable through searches (‘dark data’: Hampton *et al.* 2013) and were at risk of being lost to science. This database has allowed me to estimate how bee species diversity varies with land use and related pressures, across space. There are of course caveats to this approach. Space-for-time substitution, though widely used, may not be a true reflection of land-use change and intensification impacts on biodiversity (Dullinger *et al.* 2013). Extinction debt may occur in bee species (Cusser *et al.* 2015), although it is less common in short-lived invertebrates than longer-lived vertebrate communities (Kuussaari *et al.* 2009). In addition, the categorisation of land-use class and intensity is extremely coarse, making it difficult to link results back to specific pressures, such as increases in pesticide use versus loss of floral diversity, for instance. Nevertheless, this dataset has allowed me to investigate bee responses to land-use and related pressures at multiple levels of biological organisation: population-level (Chapter 3), species-level (Chapter 4) and community-level (Chapters 5 and 6).

CHAPTER 2

Database Construction

2.1 ABSTRACT

Bees are important pollinators of a multitude of plant species, both commercial and wild. In order to understand and predict how anthropogenic change impacts bee diversity and thus the provision of pollination services, spatio-temporally accurate data on biodiversity are needed, along with matching information on human impacts. I compiled a database of bee diversity from known locations, from 117 peer-reviewed comparative studies, each of which surveyed multiple sites in a comparable way. Data from non-bee species that were sampled using the same methodology were also included in the database to permit comparisons between bees and other taxa. Each unique location is accompanied by further detail such as the land-use class and land-use intensity, classified from the original journal article or information provided by the authors. Geographic coordinates are also recorded for each location, to enable augmentation of the database with remotely-sensed information. The database contains 200,783 diversity measurements (an abundance or occurrence measurement for a species at a site), from 3785 unique locations and 2356 species. Bees comprise 55% of the dataset records. This database should assist in the formulation of spatio-temporally accurate models assessing or predicting the impact of anthropogenic change on bee communities.

2.2 INTRODUCTION

Bees are efficient pollinators of a multitude of plant species, including many global crops (Jauker *et al.* 2012; Klein *et al.* 2003; Ollerton *et al.* 2011). Although most staple crops are wind pollinated, over a third of globally produced crops (in volume) are dependent upon

animal pollinators to some extent (Ghazoul 2005; Klein *et al.* 2007; Kremen *et al.* 2007). This makes bees a group that is both functionally important and economically valuable (Costanza *et al.* 1997; UK National Ecosystem Assessment 2011).

Bee populations are facing a number of threats from human impacts, however, including land-use change and intensification, which could have serious consequences for future food security (Aizen *et al.* 2009; Klein *et al.* 2007; Potts *et al.* 2010; Tittensor *et al.* 2014). Conserving pollinators in agricultural systems is not a simple task, however, as measures to improve food security are often to the detriment of pollinators (Foley *et al.* 2011).

Assessing how bee species are responding to land-use change and agricultural intensification requires spatio-temporally accurate data on bee diversity in sites facing different land-use pressures. Ideally, before-after-control-impact studies would be used for this purpose. However, such data are still rare. I have therefore focussed on spatial comparisons, which are much more prevalent and geographically widespread in the literature. I have compiled a database of pre-existing data on the biodiversity of bees from published scientific studies, where a study comprises data collected from at least two locations using the same methodology. This database will enable researchers to explore environmental correlates of bee diversity, in order to inform management practices in agricultural landscapes. In addition, the geographic extent of the database, consisting of almost 3800 sites, will permit analyses across spatial scales which echo that of policy, in order to make generalisations that are relevant to policy makers.

This database has some key differences from the data set of Kennedy *et al.* (2013). My dataset represents a variety of land-use classes (including Urban areas and Primary and Secondary vegetation, as well as various agricultural land uses), rather than just agricultural fields, enabling comparison of responses to different land-use cover types. In addition, I included data from any other taxa that were sampled alongside bee species, although this has not been the focus of this thesis. This dataset permits analyses testing whether bees respond to anthropogenic change differently from other taxa. A third difference increases the breadth and longevity of the data. Whereas Kennedy *et al.* (2013) required GIS maps for each location, I require only for studies to include geographic coordinates of sites. This criterion is more often met, particularly in more recent studies, and enables augmentation of the database with remotely-sensed information in order to further characterise the study sites and surrounding

areas quantitatively and consistently (See Chapter 3). Kennedy *et al.* (2013)'s database is designed to assess the impact of bee populations on agricultural yields, for which it is uniquely useful. My focus is broader, encompassing a range of policy-relevant ecological questions.

2.3 MATERIALS AND METHODS

The database collated here uses the same structure and data-handling procedures as the PREDICTS project's (www.predicts.org.uk) database, which I helped to design and refine. These are described fully in Hudson *et al.* (2014), though I give a summary below.

Whereas the PREDICTS database does not focus on either a particular taxon or a particular kind of landscape, I have focussed on bees in agricultural landscapes (where at least one site was in or adjacent to agriculture). I identified papers potentially containing data using systematic searches of the Web of Science database between 2011-2013 (Table 2.1). Journal alerts were also searched regularly for these keywords. When reviews were found through these searches, references therein were scanned for relevance.

Table 2.1: Terms used to search the Web of Science database for papers potentially containing useful data.

	Web of Knowledge search terms
1	"(arthropod* OR bee* OR pollinat*) AND (abundance OR diversity) AND (agricultur* OR anthropogenic OR land use OR threat)"
2	"pollinat* AND land-use AND diversity"
3	"pollinat* habitat abundance*"
4	"pollinat* threat"
5	"pollinat* agricultur*"

Papers had to meet the following criteria for relevance:

1. Data were collected at two or more sites or years, provided that the same sampling method was used for both samples.
2. At least one of the sample sites was defined as in or adjacent to agricultural land.
3. Geographic coordinates of each site were known.
4. Samples included bee species (that is, within the group Apidae *sensu lato*). If other taxa were also sampled, these data were also included in the database.
5. One of the following aspects of diversity was measured: abundance, alpha diversity, functional diversity or occupancy. This could be at any taxonomic resolution. Where visitation rate was studied, this was only considered a comparable index of abundance if visitation rate was assessed on the same flower or flower mix across sites.
6. Data were available for each site and each taxon.

If all these criteria were met, I attempted to obtain data on the location, biodiversity and anthropogenic pressures at each site (see Table 2.2). Where raw data were not published within the paper or supplementary files (the usual case), I requested them from the paper's corresponding author. Within each published data source (typically a paper), there can be a number of studies: a study can only include abundance measurements which were sampled

using the same methodology at each site. Differences in sampling effort within a study were corrected for when necessary, by assuming that abundance increases linearly with sampling effort. I also classified samples taken from multiple countries as different studies, in order to account for broad-scale biogeographic differences in diversity. Within each study, there are then multiple sampled sites. Any blocked or split-plot design was recorded so that the spatial structure of the sites could be accounted for in the analyses.

I also collated and curated diversity data for other taxonomic groups reported by the same sources. Where other groups were sampled alongside bees using the same methodology, they were entered into the same study. Where other taxa were collated using different methods to bees, these were considered separate studies. As the analyses presented in this thesis only focus on bee taxa, I only present a subset of the database: studies that included bee diversity data, ignoring studies from within the same source that held no data on bees.

Table 2.2: Description of variables contained within the dataset

Variable	Description
Sample dates (start, end)	Day, month and year of the first and last biodiversity sample. If the temporal resolution available is coarse, the earliest possible start date and latest possible end date are given
Sample location (Decimal Degrees)	Latitude and longitude
Coordinates source/tool	Note on whether coordinates were provided or extracted from an image
Estimated precision for coordinates, unit and value	Where coordinates were extracted from an image, the estimated precision of these coordinates
Site area unit and value	If known, the size of the sample site
Sample effort unit and value	For example, the number of sweep net samples taken

Maximum linear extent	The maximum linear extent (in metres) encompassed by samples at a site. This is an estimate of the maximum distance between sampling points within a site (e.g. the length of a transect or the distance between pan traps) and so can be considered a measure of sampling grain or extent.
Predominant land use	The land-use class where biodiversity sampling took place, according to Appendix Table A.1: Primary vegetation, Secondary vegetation (young, intermediate age, mature, indeterminate age), Pasture, Cropland, Plantation forest or Urban. Where sampling points straddled more than one land-use class, the larger class was chosen
Use Intensity	Classified according to table Appendix Table A.1 as light, medium or intense use
Fragmentation layout	Classified according to Appendix A.1.1
Habitat, as described in the source	Free text field for a description of habitat as given by original authors
Taxon Name	Name of taxon, at any taxonomic resolution
Note for non-standard names	Indication of taxonomic resolution of name
Abundance metric	Abundance or diversity measure
Abundance metric unit	Unit of abundance or diversity measurement; e.g., abundance can be measured as the number of individuals or groups etc
Datum	Diversity measurement per site per species
Study target	This defines whether the original authors only recorded diversity measurements for specific targeted taxa, or whether they recorded biodiversity measurements for all species that were sampled.

As my data collection was mainly focussed in agricultural areas, I developed additional fields for data entry. I classified agricultural sites by Farm Type (FF1, FF2 and FF3), according to a hierarchy (Appendix A.1.2), based on the Farm Types of the European Commission Farm Accounting Data Network and the International Standard Industrial Classification of All Economic Activities (Department of Economic and Social Affairs of the United Nations Secretariat 2008). In addition, I recorded whether or not an agricultural field was part of an agri-environment scheme or other ‘friendly farming’ scheme (AES: yes/no/unknown) and whether the field was under organic management (Organic: yes/no/unknown). I also included a free text field for the crop name, if known, for an agricultural field. Where additional threat information was provided (e.g., pesticide load), these were also recorded.

Other members of the PREDICTS team also collated data sets relevant to my work (from 2011 to present). I therefore included these in my analyses and in the subsequent descriptions of the database.

2.4 RESULTS

Of approximately 1600 sources I found through Web of Science searches, the majority (about 70%) were excluded based on the abstract. Few papers made their data available, and fewer than half the corresponding authors agreed to share their data. I collated data from 56 sources (93 studies) containing data on bee diversity. Other team members collated a total of 24 further studies (from 17 sources). In total, the dataset includes 200,783 diversity measurements (over 55.3% of which are for bees) from 3785 sites.

Table 2.3: Data sources and sample sizes. mMLE = maximum Maximum Linear Extent (in meters) of any site in the source. MLE is the maximum distance between sampling points within a site (See Table 2.2). nr = not reported. Numbers of taxa are the numbers of unique taxa for which diversity measurements are given (so, if diversity measurements are available only for all bees combined, this would count as one taxon). The percentage of bee species with a known binomial name is also given (% binomial).

Reference	Country	Sampling years	Studies	Sites	Bee taxa (% binomial)	Other taxa	mMLE	Collator ¹
Afrotropic			4	43	78	2342		
Basset <i>et al.</i> (2008)	Gabon	2001	1	12	51 (19.61%)	1806	70	AR1
Chima <i>et al.</i> (2013)	Nigeria	2012	1	4	1 (100%)	38	nr	AD1
Gaigher & Samways (2010)	South Africa	2006	1	10	6 (0%)	383	nr	SE2
Grass <i>et al.</i> (2013)	South Africa	2011	1	17	21 (9.52%)	115	100	AD1
Australasia			11	412	150	560		
Blanche <i>et al.</i> (2006)	Australia	2005	2	11	8 (89.36%)	17	nr	AD1
Cunningham <i>et al.</i> (2013)	Australia	2007	1	24	69 (100%)	0	nr	AD1
Lentini <i>et al.</i> (2012)	Australia	2009 - 2010	1	104	36 (100%)	0	nr	AD1
Kessler <i>et al.</i> (2009)	Indonesia	2004	1	15	9 (0%)	24	nr	HP1
Ewers <i>et al.</i> (2013)	New Zealand	2000	2	194	1 (100%)	0	nr	CC1
Malone <i>et al.</i> (2010)	New Zealand	2006 - 2007	1	2	9 (100%)	0	nr	AD1
Todd <i>et al.</i> (2011)	New Zealand	2007	1	20	9 (100%)	442	27.3	SH1
Rader <i>et al.</i> (2014)	New Zealand	2008	1	24	5 (100%)	20	nr	CC1
Litchwark (2013)	New Zealand	2011	1	18	14 (100%)	63	nr	CC1
Indo-Malay			4	16	1	0		

¹Collators are the PREDICTS team members who initially collected and curated the data. AD1 = Adriana De Palma, AR1 = Alex Robinson, CC1 = Charlotte Chng, SC1 = Sara Contu, SE1 = Susy Echeverría-Londoño, SE2 = Susan Emerson, SH1 = Sam Hill, DI1 = Dan Ingram, HP1 = Helen Phillips, VB1 = Victoria Burton

Liow <i>et al.</i> (2001)	Singapore, Malaysia	1999	4	16	1 (0%)	0	3000	AD1
Nearctic			18	781	245	118		
Boutin <i>et al.</i> (2009)	Canada	2000	3	60	3 (0%)	116	nr	VB1
Richards <i>et al.</i> (2011)	Canada	2003	3	18	127 (95.04%)	0	nr	AD1
Hatfield & Lebuhn (2007)	United States	2002 - 2003	1	120	13 (100%)	0	nr	AD1
Shuler <i>et al.</i> (2005)	United States	2003	1	25	5 (60%)	0	nr	AD1
McFrederick & LeBuhn (2006)	United States	2003 - 2004	2	40	5 (100%)	0	nr	AD1
Winfree <i>et al.</i> (2007a)	United States	2003	2	80	1 (0%)	0	nr	AD1
Kwaiser & Hendrix (2008)	United States	2004	2	18	53 (97.22%)	1	nr	AD1
Julier & Roulston (2009)	United States	2006	1	20	3 (100%)	0	250	AD1
Tonietto <i>et al.</i> (2011)	United States	2006	1	18	67 (89.55%)	0	nr	AD1
Cameron <i>et al.</i> (2011)	United States	2007 - 2009	2	382	8 (100%)	1	nr	AD1
Neotropic			16	286	436	775		
Vázquez & Simberloff (2002)	Argentina	1999	1	8	25 (52%)	104	nr	AD1
Quintero <i>et al.</i> (2010)	Argentina	2000	1	4	14 (35.71%)	38	1280	AD1
Schüepf <i>et al.</i> (2012)	Belize	2009	1	15	43 (100%)	65	nr	SC1
Tonhasca <i>et al.</i> (2002)	Brazil	1997	1	9	21 (100%)	0	10	AD1
Barlow <i>et al.</i> (2007)	Brazil	2005	1	3	22 (75%)	0	3500	HP1
Smith-Pardo & Gonzalez (2007)	Colombia	1997	4	48	300 (46.2%)	0	nr	SE1

Parra-H & Nates-Parra (2007)	Colombia	2003	1	26	21 (100%)	0	nr	SE1
Poveda <i>et al.</i> (2012)	Colombia	2006 - 2007	2	34	4 (0%)	468	23	SE1
Tylianakis <i>et al.</i> (2005)	Ecuador	2003	1	48	16 (0%)	16	71	DI1
Vergara & Badano (2009)	Mexico	2004	1	16	7 (71.43%)	8	nr	AD1
Fierro <i>et al.</i> (2012)	Mexico	2009	1	3	4 (100%)	0	346.41	AD1
Rousseau <i>et al.</i> (2013)	Nicaragua	2011	1	72	2 (100%)	81	30	DI1
Paleartic			64	2247	644	788		
Verboven <i>et al.</i> (2012)	Belgium	2009	1	9	6 (66.67%)	0	11.34	AD1
Billeter <i>et al.</i> (2007) ¹ , Diekötter <i>et al.</i> (2008) ¹ and Le Féon <i>et al.</i> (2010) ¹	Belgium, Czech Republic, Estonia, France, Germany, Netherlands, Switzerland	2001 - 2002	14	873	276 (98.46%)	7	nr	AD1
Kruess & Tschardt (2002)	Germany	1996	2	34	17 (100%)	18	nr	AD1
Meyer <i>et al.</i> (2007)	Germany	2000, 2005	2	30	14 (75%)	8	34.51	AD1
Diekötter <i>et al.</i> (2006)	Germany	2001	1	124	2 (100%)	0	353.55	AD1
Meyer <i>et al.</i> (2009)	Germany	2004	1	32	109 (100%)	75	nr	SC1
Herrmann <i>et al.</i> (2007)	Germany	2005	2	26	1 (100%)	0	800	AD1
Holzschuh <i>et al.</i> (2011)	Germany	2007	2	134	3 (33.33%)	1	100	AD1
Weiner <i>et al.</i> (2011)	Germany	2007	1	29	59 (100%)	460	333	AD1
Nielsen <i>et al.</i> (2011)	Greece	2004	4	32	1 (0%)	0	nr	AD1

Power & Stout (2011)	Ireland	2009	1	20	9 (88.89%)	24	1200.24	AD1
Davis <i>et al.</i> (2010)	Ireland, United Kingdom	2005, 2007, 2008, 2009	1	12	1 (100%)	0	nr	AD1
Quaranta <i>et al.</i> (2004)	Italy	2000	1	2	31 (100%)	0	200	AD1
Yamaura <i>et al.</i> (2012)	Japan	2009	1	6	47 (100%)	0	nr	AD1
Yoon <i>et al.</i> (2012)	Korea, Republic of	2000 - 2012	1	215	6 (100%)	1	nr	AD1
Kohler <i>et al.</i> (2007)	Netherlands	2004 - 2005	4	19	26 (95.48%)	56	1500	AD1
Goulson <i>et al.</i> (2008)	Poland	2006	1	32	22 (100%)	0	200	AD1
Mudri-Stojnic <i>et al.</i> (2012)	Serbia	2011	1	16	55 (100%)	8	nr	AD1
Öckinger & Smith (2006)	Sweden	2004	1	36	11 (100%)	64	800	AD1
Franzén & Nilsson (2008)	Sweden	2005	1	16	83 (100%)	43	nr	AD1
Samnegård <i>et al.</i> (2011)	Sweden	2009	1	9	31 (100%)	0	90	AD1
Oertli <i>et al.</i> (2005)	Switzerland	2001	1	7	237 (100%)	0	395.98	AD1
Albrecht <i>et al.</i> (2010)	Switzerland	2003 - 2004	2	202	75 (100%)	0	nr	AD1
Schüepp <i>et al.</i> (2011)	Switzerland	2008	1	30	11 (72.73%)	69	0.2	AD1
Darvill <i>et al.</i> (2004)	United Kingdom	2001	1	17	3 (66.67%)	0	100	AD1
Marshall <i>et al.</i> (2006)	United Kingdom	2003	2	84	25 (100%)	0	nr	AD1
Hanley (2005)	United Kingdom	2004 - 2005	1	6	11 (100%)	0	1000	AD1
Knight <i>et al.</i> (2005)	United Kingdom	2004	1	12	1 (100%)	0	3.16	AD1
Connop <i>et al.</i> (2011)	United Kingdom	2005	1	5	2 (100%)	0	nr	AD1
Goulson <i>et al.</i> (2010)	United Kingdom	2007	1	14	2 (100%)	0	200.25	AD1
Hanley <i>et al.</i> (2011)	United Kingdom	2007 - 2010	1	34	6 (100%)	0	200.04	AD1

Redpath <i>et al.</i> (2010)	United Kingdom	2008	1	11	7 (85.71%)	0	nr	AD1
Blake <i>et al.</i> (2011)	United Kingdom	2008 - 2010	2	6	8 (75%)	2	90	AD1
Bates <i>et al.</i> (2011)	United Kingdom	2009	1	24	58 (100%)	50	56.6	AD1
Osgathorpe <i>et al.</i> (2012)	United Kingdom	2009 - 2010	2	45	11 (90.91%)	1	nr	AD1
Hanley (2011)	United Kingdom	2011	1	8	23 (82.61%)	110	nr	AD1
Fowler (2014)	United Kingdom	2011	1	36	75 (100%)	0	nr	SC1

2.4.1 GEOGRAPHIC REPRESENTATION

Data are available for 3785 sites, from 33 countries and 5 continents. The data are still biased towards temperate areas, however, in spite of targeted data collation in the southern hemisphere (see Table 2.3 and Fig. 2.1). However, in areas where there are fewer studies in the dataset, often these have a large taxonomic breadth (indicated by the large, opaque points).

2.4.2 TAXONOMIC REPRESENTATION

The dataset has a broad taxonomic coverage, with diversity measurements for 2356 taxa. Data are available for 41 arthropod orders as well as 1 vertebrate order. Of this dataset, the 906 bee species (See A.2.1 for species list) constitute 55% of the dataset records and 38% of the species, although this still covers only 4.4% of global bee species richness (Ascher & Pickering 2013). Hoverflies (Diptera: Syrphidae), represent another important pollinator group, for which I have abundance records from 149 species.

The studies included in the dataset appear to be quite distinct in terms of species composition: 48% of the species in the dataset occur in only one study, with 87% of database species present in 1–5 studies. Some species, however, particularly honeybees (*Apis mellifera*) and many bumblebees (genus *Bombus*), are present in as many as 56 studies.

In general, studies focus on multiple species within the order Hymenoptera (Fig. 2.2). Ten

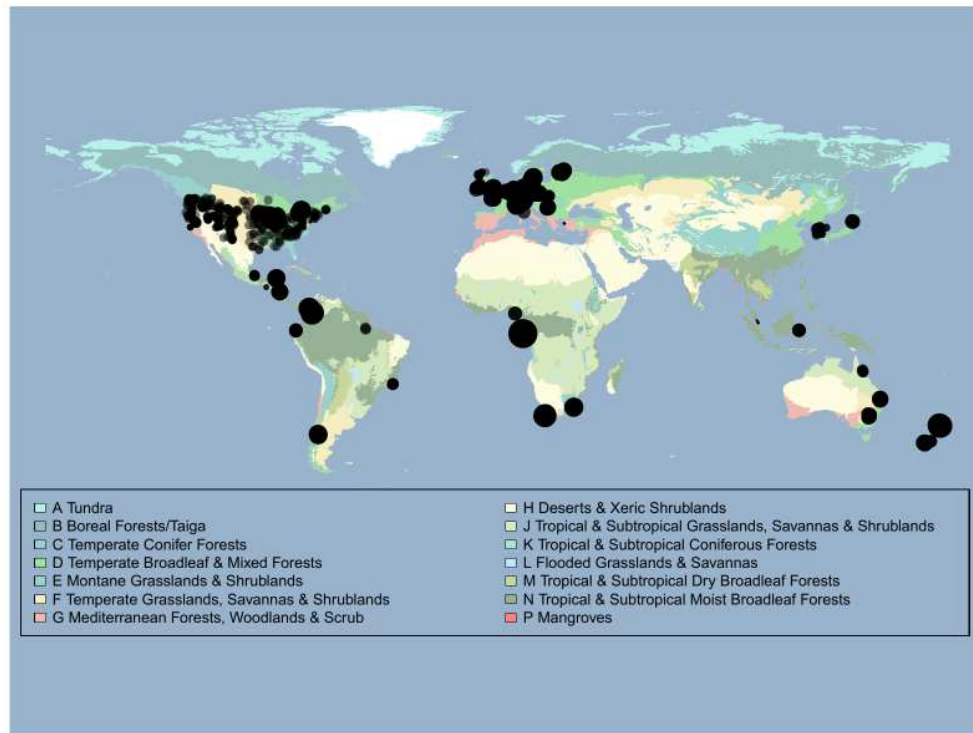


Figure 2.1: Location of sites across the globe (coloured by terrestrial biome) for which I have collated bee species diversity measurements. Points are scaled relative to the number biodiversity samples at that site (larger points have more samples). All points have the same level of transparency; where points appear fully opaque, this indicates that this is a relatively narrow but densely sampled area, with a number of overlapping sites.

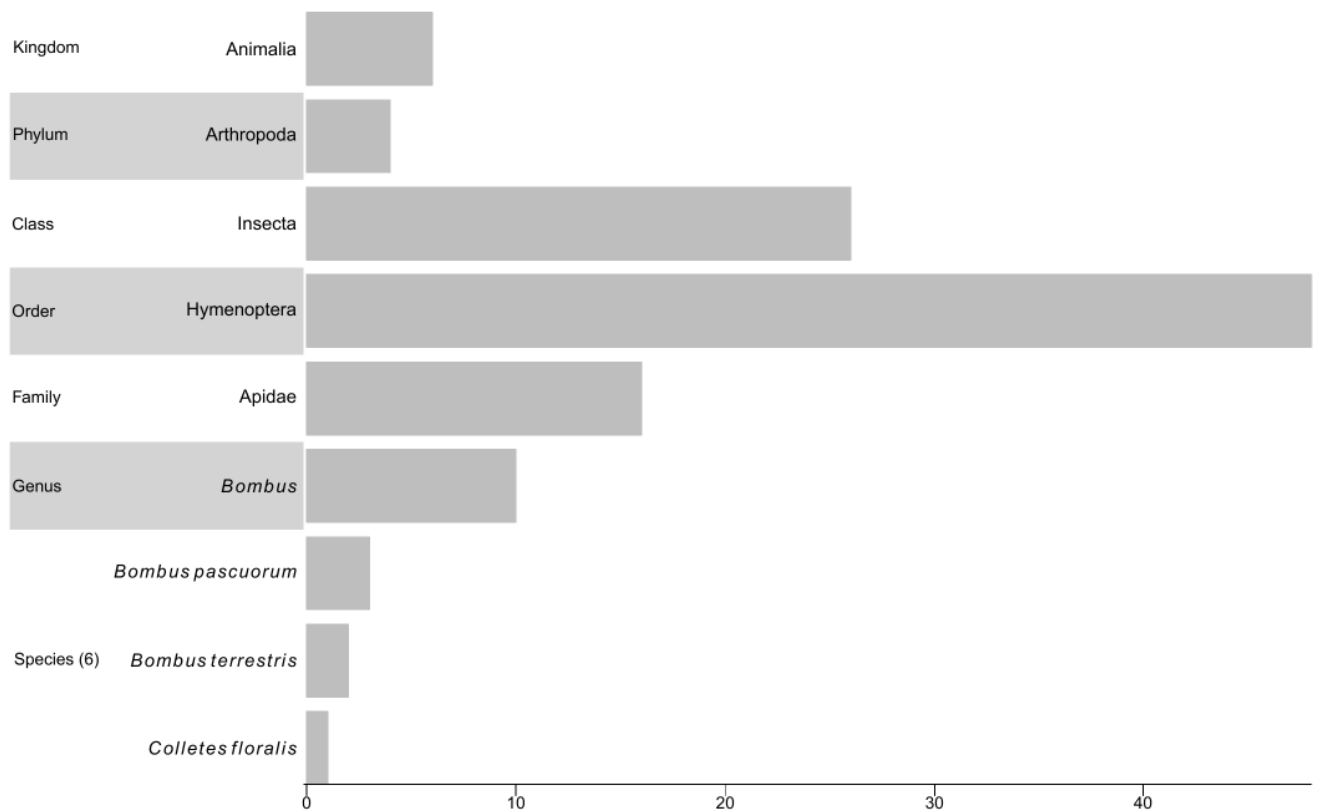


Figure 2.2: Number of studies by the lowest taxonomic group. For instance, one study only recorded *Colletes floralis* individuals, while over 20 studies recorded taxa from multiple orders within the Class Insecta.

studies, however, focus only on the genus *Bombus*, while six studies focus only on a single particular species (Fig. 2.2).

GEOGRAPHIC RANGE SIZE

The geographic range size for bee species were calculated using the Global Biodiversity Information Facility (GBIF, www.gbif.org). GBIF data were downloaded on 28th April 2015 using the `rgbif` package Version 0.8.0 (Chamberlain *et al.* 2015) in R Version 3.1.2 (R Core Team 2014). The area occupied was estimated by a species by summing the area of the grid cells (0.5°) containing a record in the GBIF database.

Using ordinary linear regression, I assessed whether there was a significant relationship between bee species' geographic range size and the number of records in my database (i.e.,

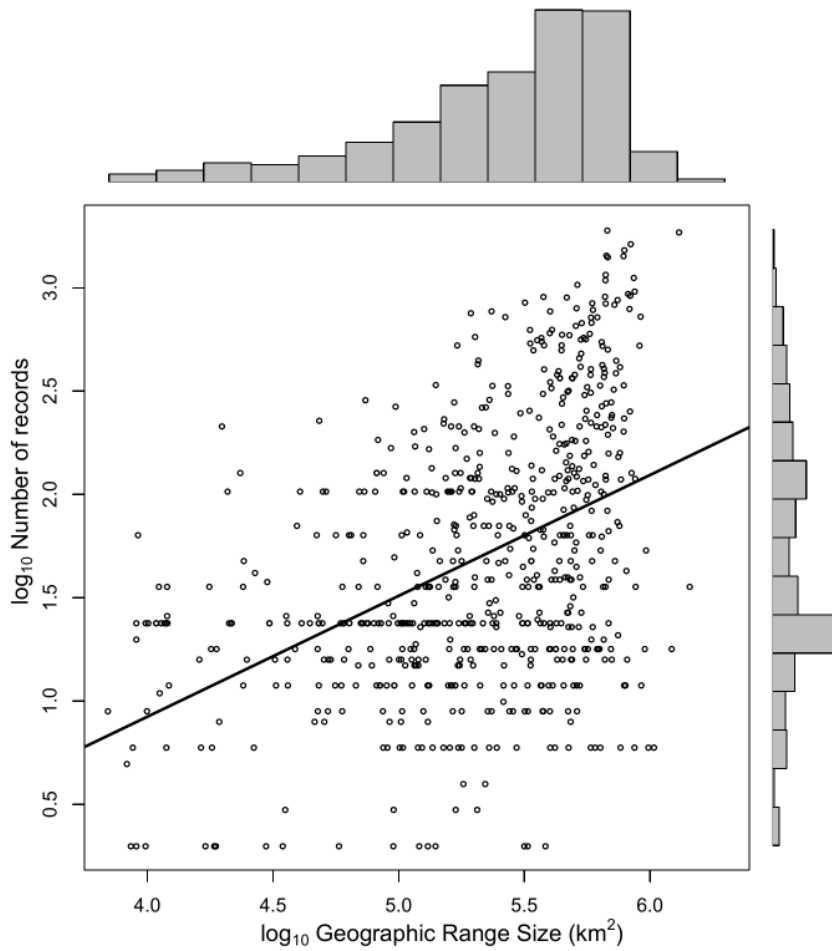


Figure 2.3: The geographic range size for each bee species is plotted against the number of records in the database for that species. Geographic range size was estimated from GBIF records. 231 species with known binomial names have been excluded as they have no records in GBIF.

the number of sites in studies where it was reported – the species was not necessarily present at each site). Both variables were $\log_{10}$ -transformed to meet the assumptions of normality. Unsurprisingly, species with larger range sizes had significantly more records in the dataset ($t_{1,1786} = 12.5, p < 0.001$, Fig. 2.3). However, the adjusted R^2 value of this model was fairly low (0.19), as even some widespread species seldom occurred in the database.

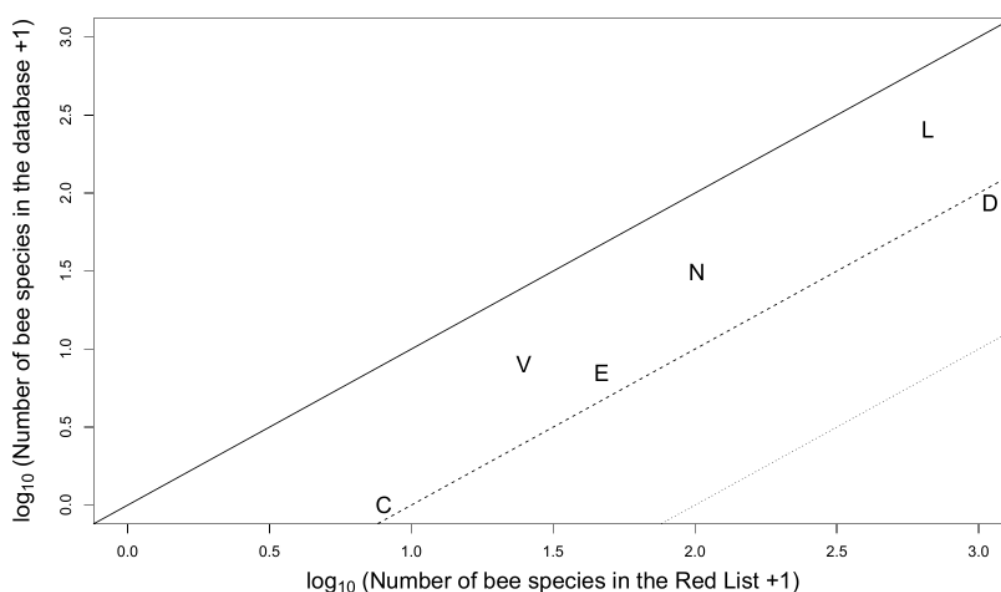


Figure 2.4: Number of species in different European Red List Categories in the Red List and in the database. V = Vulnerable, N = Near Threatened, E = Endangered, D = Data Deficient, C = Critically Endangered. The solid, dashed and dotted lines indicate the 100, 10 and 1% representation, respectively.

INTERSECTION WITH THE EUROPEAN RED LIST OF BEES

There are 383 species in my dataset that are easily matched to the European Red List of bees. The majority of species in the dataset are classed as Least Concern, but there are 85 species that are classed as Data Deficient (Fig. 2.4). This provides an opportunity as the dataset can be used to estimate the sensitivity of species to land-use pressures, filling in some of the knowledge gaps in the Red List (See Chapter 4). Critically endangered and data-deficient species are, unsurprisingly, underrepresented in the database.

2.5 INFORMATION ON LAND-USE PRESSURES

2.5.1 ADDITIONAL AGRICULTURAL FIELDS

Predominant habitat, use intensity and fragmentation layout are known for the majority of sites. Only rarely, however, did authors provide information in their papers or when asked

regarding the additional agricultural fields: Agri-environment schemes were reported for 6 sources, Organic or Conventional farming for 9 sources, Crop for 20 sources and Farm Type at its coarsest scale was reported for 23 sources. This limited dataset prohibited my use of these fields in subsequent analyses, although they are likely to be important factors (Brittain *et al.* 2010; Tuck *et al.* 2014b). For instance, in a broader analysis of datasets in the tropics (without a specific taxonomic focus), oil palm was found to contain significantly lower species richness than fields of plantation forest (Phillips *et al.*, submitted).

2.6 LIMITATIONS

Although the dataset is large, there are still taxonomic and geographic gaps. In addition, there are missing data for some land-use pressures, meaning that there are limits to analyses, particularly when one wishes to explore the effect of interacting pressures on bee diversity and abundance; for instance, Use Intensity $\times$ Farm Type.

The data are based on spatial comparisons, rather than time-series or before-after comparisons. While this increases the amount of available data (increasing the taxonomic and geographic breadth of the dataset as a result), it also means that I cannot fully explore the impact of land-use *change* on biodiversity (Magurran *et al.* 2010) as the possibility of biotic lag is ignored; it can take many years for the impact of a land-use transition to be seen. However, space-for-time substitution has been shown to be informative about the impact of other environmental changes on biodiversity, such as climate change (Blois *et al.* 2013).

Not all the data I have collated will be openly available, which reduces the transparency of my analyses and results (Mouquet *et al.* 2015). For those sources whose authors permitted open release, the data will be made freely available via data.nhm.ac.uk, by early 2016.

2.6.1 PUBLICATION BIAS

It is possible that more studies showing a negative impact of human-dominated land uses on species diversity will be published and therefore incorporated into the database. If so, this could bias results. I have carried out a crude test of publication bias using meta-analytical techniques. I used only data from bee species where abundance was measured in at least

three natural sites (Primary or Secondary vegetation) and in at least three human-dominated sites (Agricultural or Urban). This resulted in data from 38 studies. The log-response ratio was then calculated between abundances in natural vs human-dominated sites. This division, while simplistic, captures the major land-use effects on community composition (Newbold *et al.* 2015). A simple, fixed-effects meta-analysis was then performed, and the log-response ratio plotted against the standard error of the study; a traditional funnel plot. The effect sizes are approximately symmetrically distributed around the mean response (Fig. 2.5). It is important to note that, in all the analyses that follow, larger data sets naturally receive more weight, so that high-variance estimates are de-emphasised.

2.7 CONCLUSIONS

Global analyses need global data on biodiversity observations (Scholes *et al.* 2012). No individual researcher can produce this. Although efforts have been made to collate large amounts of biodiversity data, these are often far from representative of biodiversity. In particular, these datasets hold little or no data on arthropods although they constitute the majority of biodiversity (Scheffers *et al.* 2012; Wilson 1987). Other datasets that are more taxonomically broad, such as GBIF, are unstructured (or the design is not evident) and often hold only presence-only data. As a result, it is extremely difficult to test hypotheses about how human impacts affect biodiversity. They also show strong biases (Meyer *et al.* 2015). I have therefore focussed on structured data — matched surveys in different land uses— on (where possible) species diversity, in a single clade (Apidae *sensu lato*). This database is, to my knowledge, the most extensive of its type. The vast majority of these data will shortly be made publicly available, to facilitate other analyses.

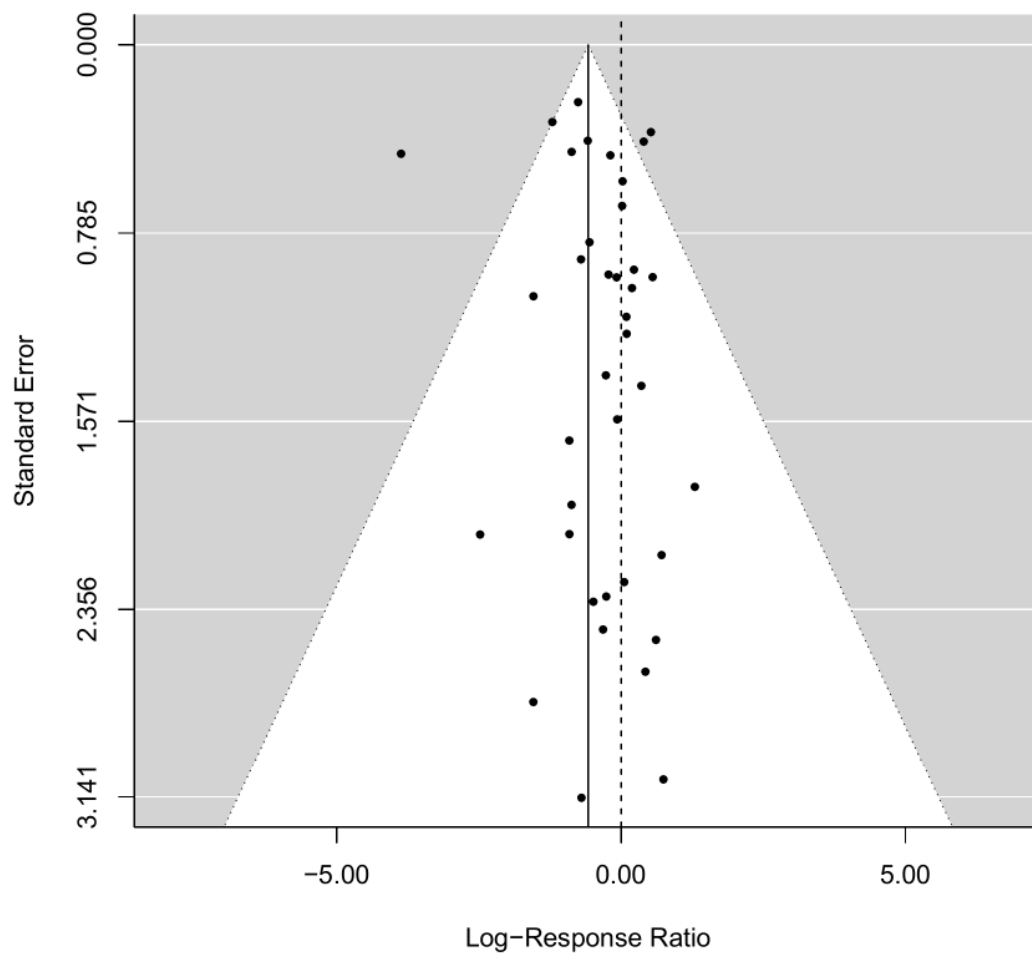


Figure 2.5: Funnel plot showing the spread of effect sizes around the mean effect of human-dominated land uses on bee abundance (solid line). The dashed line indicates no effect of human-dominated land use.

Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes

3.1 ABSTRACT

Bees are a functionally important and economically valuable group, but are threatened by land-use conversion and intensification. Such pressures are not expected to affect all species identically; rather, they are likely to be mediated by the species' ecological traits. Understanding which types of species are most vulnerable under which land uses is an important step towards effective conservation planning. We collated occurrence and abundance data for 257 bee species at 1,584 European sites from surveys reported in 30 published papers (70,056 records), and combined them with species-level ecological trait data. We used mixed-effects models to assess the importance of land use (land-use class, agricultural use-intensity and a remotely-sensed measure of vegetation), traits, and trait $\times$ land use interactions, in explaining species occurrence and abundance. Species' sensitivity to land use was most strongly influenced by flight season duration and foraging range, but also by niche breadth, reproductive strategy and phenology, with effects that differed among cropland, pastoral and urban habitats. Rather than targeting particular species or settings, conservation actions may be more effective if focused on mitigating situations where species' traits strongly and negatively interact with land-use pressures. We find evidence that low-intensity agriculture can maintain relatively diverse bee communities; in more intensive settings, added floral

resources may be beneficial, but will require careful placement with respect to foraging ranges of smaller bee species. Protection of semi-natural habitats is essential, however; in particular, conversion to urban environments could have severe effects on bee diversity and pollination services. Our results highlight the importance of exploring how ecological traits mediate species responses to human impacts, but further research is needed to enhance the predictive ability of such analyses.

3.2 INTRODUCTION

Bees are key providers of pollination services, which are vital for food security and the persistence of many wild plants (Klein *et al.* 2007; Ollerton *et al.* 2011). However, many bee species are threatened by changing and intensifying land use (Ollerton *et al.* 2014; Potts *et al.* 2010).

Land-use change, such as conversion from semi-natural habitats to human-dominated land-uses, can greatly impact bee communities. Urbanization, agricultural expansion and abandonment are ongoing drivers of land-use change in Europe (Verburg *et al.* 2006), which can affect bee diversity through reduced floral and nesting resources (Forrest *et al.* 2015; Hernandez *et al.* 2009). Semi-natural habitats are prime targets for land conversion (Verburg *et al.* 2006). Such habitat loss can affect pollination of crops as well as of wild flowers: as central place foragers, bees often forage up to a few kilometres away from their nests (Greenleaf *et al.* 2007) so semi-natural habitat can provide spill-over of pollination services to nearby cropland and vice-versa (Blitzer *et al.* 2012).

Agricultural intensification—through decreased crop diversity and increased external inputs—is another major pressure, which can impact bees directly by increasing mortality and indirectly by decreasing resource availability (Potts *et al.* 2010; Roulston & Goodell 2011). For instance, neonicotinoid pesticides restrict colony growth and queen production in bumblebees, and limit foraging success and survival of honeybees (Henry *et al.* 2012; Whitehorn *et al.* 2012). Nitrogen fertilizer and herbicides can affect bees indirectly by reducing the diversity of plants (Kleijn *et al.* 2009) and thus foraging resources (Roulston & Goodell 2011). Reductions in non-crop habitat as management intensifies can reduce the availability of

nesting sites, while increased tillage in cropland disturbs the nesting sites of some species (Shuler *et al.* 2005).

These pressures are unlikely to affect all species identically, but are expected to be mediated by species' traits (Murray *et al.* 2009; Roulston & Goodell 2011). In general, species with narrower niches—in terms of space, time, phenotype, or interspecific interactions—are predicted to be more sensitive than generalists (Den Boer 1968; Kassen 2002). Bee species' traits may specifically influence vulnerability to land use; for instance, larger foraging ranges facilitate foraging in fragmented landscapes, but may increase the likelihood of contact with pesticides and indicate greater resource needs. Other traits can influence susceptibility to demographic stresses and stochastic events; for example, a higher reproductive capacity may buffer species against disturbances, but may indicate greater resource requirements.

Identifying traits that render species vulnerable to human impacts can help inform and guide effective conservation priorities. Most previous attempts to identify ecological correlates of bee vulnerability to human impacts have focused on a relatively small number of sites and threats, or on museum collections rather than ecological survey data (e.g. Bartomeus *et al.* 2013a; Vázquez & Simberloff 2002). One exception is Williams *et al.*'s (2010) global multi-species analysis, which found that some traits correlated with vulnerability to multiple threats: for instance, above-ground versus below-ground nesting influenced species' susceptibility to fire, isolation and agricultural management practices. Vulnerability traits can also be threat-specific (Owens & Bennett 2000; Purvis *et al.* 2005), in which case conservation actions would need to focus on populations experiencing 'dangerous' combinations of local pressures and ecological traits. For instance, social species may be more sensitive in intensively-used cropland—where enhanced foraging capacity can increase exposure to pesticides and thus affect mortality and colony success—but relatively less sensitive in urban areas, where greater foraging capacities may enable persistence (Banaszak-Cibicka & Zmihorski 2012).

In the broadest analysis of European bees to date, we explore whether ecological traits influence the responses of 257 bee species to local land-use pressures at 1,584 European sites. Unlike the study by Williams *et al.* (2010), we analyse multiple traits within the same models. We aim to identify the traits and land-use pressures associated with a species having low probability of occurrence and low abundance; we also aim to estimate the relative importance

of land use, traits and the interaction between them in shaping species' occurrence and abundance. We hypothesize that resource and phenological niche breadth, foraging range and reproductive strategy will all influence species' sensitivity to land use.

3.3 MATERIALS AND METHODS

3.3.1 DATA COLLATION

Data were sought from published comparisons where bee abundance and occurrence were sampled in multiple sites within agricultural landscapes. Papers based on potentially suitable data were identified by systematically searching Web of Science during 2011-2012 (See Chapter 2), searching journal alerts and assessing references cited in reviews. Criteria for selection were (i) multiple European sites were sampled for bee abundance or occurrence using the same sampling method within the same season; (ii) at least one site was <1km from agricultural land; (iii) geographic coordinates were available for each site; and, (iv) sites were sampled since February 2000, so that diversity data could be matched with remote-sensed data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). MODIS data were chosen over other remote-sensed imagery as they are available at high spatial (250m) and temporal (16 day) resolutions and are easily integrated into R analyses (Tuck *et al.* 2014a).

We extracted site-level occurrence and abundance data from suitable papers where possible. Raw data were usually not included within the paper or supplementary files so we asked corresponding authors for these data. Relevant data were available from 30 papers, hereafter referred to as sources. Some sources separately report data collected in different ways or seasons. We term each separate data set a 'study': within, but not between, studies, diversity data can be compared straightforwardly among sites because sampling protocols were the same. We also split data sets that spanned multiple countries into separate studies for each country to account for biogeographic variation in diversity. Differences in sampling effort within a study were corrected for, assuming that recorded abundance increases linearly with sampling effort. Within each study, we recorded any blocked or split-plot design. In all but one case, this was the sampling design of an observational study. Only one study included was an experimental project, where only the control data were extracted; this study had

extremely low influence on the final models (based on Cook's distance, influence.ME package, Nieuwenhuis *et al.* 2012) and did not qualitatively change the results.

The major land use and use intensity at each site was assessed based on information in the associated paper, using the scheme described in Hudson *et al.* (2014, see Chapter 2 Appendix for more details). Land use was classified as secondary vegetation, cropland, pasture or urban. The use-intensity scale—a qualitative measure of the extent of human disturbance—is coarse (three levels: minimal, light and intense), but can be applied in a wide range of settings (Hudson *et al.* 2014). Many combinations of land use and use intensity had too few sites to permit robust modelling; the data were therefore coarsened into a single factor (hereafter, Land Use and Intensity, LUI), collapsing levels to ensure adequate sample sizes. The final dataset had the following LUI classes: secondary vegetation (165 sites), minimally-used cropland (168), lightly-used cropland (415), intensively-used cropland (653), pasture (138), and urban (45).

As well as using a coarse, discrete representation of land use, we also used remotely-sensed mean Normalized Difference Vegetation Index (NDVI), to capture additional variation in vegetation between sites. NDVI is highly correlated with above-ground biomass and net primary productivity (Pettorelli *et al.* 2005), and often correlates positively with plant and invertebrate species richness even at relatively small spatial scales (e.g. Gould 2000; Lassau & Hochuli 2008). For each site, we downloaded MODIS MOD13Q1 (collection 5) NDVI data (composited for 16 days) at 250m spatial resolution for up to three years, with the final year being the year of sampling. Poor-quality observations were removed and linear interpolation applied to remaining data. The time series was averaged to give mean NDVI (henceforth, mNDVI). NDVI data were downloaded and processed using the MODISTools package (Tuck *et al.* 2014a). In our dataset, high mNDVI is unlikely to be driven by densely forested areas (which may not benefit bees in temperate systems, Winfree *et al.* 2007b): wooded sites were only present in two of 24 sources (three sites in woodland and two in mixed woodland and agriculture) and these sources were not particularly influential in the final models (as judged by Cook's distance values; all ≤ 0.097).

Data on species traits were compiled by Stuart P.M. Roberts and Michael Kuhlmann; morphometric data came from museum specimens and other traits from many published and unpublished sources (Appendix Table B.1). We used traits reflecting resource specialization,

phenology, reproductive strategy and foraging range. Flight season duration and intertegular distance were treated as continuous variables, and all other traits as factors. Sample sizes were increased by collapsing factor levels where necessary to permit robust modelling (Table 3.1 and Appendix Table B.1).

Table 3.1: Ecological trait data (after coarsening) available for European bee species. Numbers in parentheses indicate the number of species with these traits

Trait of interest	Proxy for trait of interest	Explanation
Niche Breadth	Lecty Status: Obligately oligolectic (63), Polylectic/Flexible (147), Species with no lecty status (47)	Obligately oligolectic species can be monolectic (foraging on one plant species) or oligolectic (forage on plants from <4 genera). Polylectic species are generalist foragers (collecting pollen from five or more plant genera) (Murray <i>et al.</i> 2009). Species that can be polylectic are placed within the latter group. Species with no lecty status are parasitic (they lay eggs in other species' nests) so do not collect pollen, but may respond more quickly to disturbance than other species, thus indicating the status of the total bee community (Sheffield <i>et al.</i> 2013).
	Tongue Length: Short (157), Long (100)	This is a family-specific trait, not the physical tongue length of each individual or species. It has been suggested that long-tongued bumblebees tend to forage on Fabaceae, and so are more specialized than short-tongued species (Goulson <i>et al.</i> 2005).

Nesting Strategy: Excavators (141), Pre-existing cavity dwellers (116)	Excavators are species that excavate their own nests, often requiring bare hard ground or pithy stems; in this analysis, all species in this category nest below ground but one. Pre-existing cavity dwellers (e.g. bumblebees) nest above ground in pre-existing cavities such as empty snail shells, regardless of nest location, or are parasitic (Potts <i>et al.</i> 2005).
Phenology Duration of the flight season: From two to twelve months (257)	Longer flight seasons increase the number of flowering species with which a bee overlaps. Flight season duration is calculated using the earliest and latest date in the year a specimen has ever been recorded; in reality, this is an overestimate as phenology depends on weather conditions that vary between years.
Voltinism: Obligately univoltine (224),e Multivoltine/Flexible (33)	Multivoltine species lay eggs multiple times throughout the year (most are bivoltine, laying twice), and so have a higher reproductive capacity than univoltine species which lay only one brood per year. Univoltine species may be particularly vulnerable to disturbances that coincide with the time of reproduction (Brittain & Potts 2011). Voltinism can vary with geography and the climate; species that can vary brood production depending on environmental conditions are classed as multivoltine/flexible.

Reproductive strategy	Sociality: Obligately solitary (203), Not obligately solitary (54)	Social bees have a higher foraging and reproductive capacity, and have a faster response to resource provision, than solitary bees, which may buffer them against human impacts. However, sociality requires continuous brood production, which may increase time stress and resource requirements. Enhanced foraging capacity may also increase pesticide exposure (as foragers using various resources in different areas may bring pesticide-containing pollen and nectar back to the nest, Brittain & Potts 2011). Social species also tend to have low effective population sizes, which may make populations more susceptible to human impacts (Chapman & Bourke 2001).
Foraging distance	Inter-tegular distance (ITD): From one to six mm (257)	ITD is a proxy for dry weight (Cane 1987; Hagen & Dupont 2013) and foraging distance in bees (Greenleaf <i>et al.</i> 2007). Although alternative measures of body size do exist (e.g. wingspan), their relationship with foraging distance is either understudied or inconsistent among genera (Cane 1987; Westphal <i>et al.</i> 2006). Only data for females were used.

3.3.2 ANALYSIS

We excluded 14 sites for which LUI or mNDVI were not available, and 12 species for which not all trait values were known.

The diversity data were zero-inflated with a positive mean–variance relationship, but were not exclusively counts (because abundance measurements included densities) so a discrete error distribution (e.g. Poisson) could not be used. Instead, the analysis was carried out in two stages, equivalent to a hurdle model, using mixed-effects models (lme4 package version 1.1-6, Bates *et al.* 2013). Species presence (and detection) was modelled using a binomial error structure; then the (log-transformed) abundance of present species was modelled using normal errors (Newbold *et al.* 2014). Model assumptions were checked and found to be reasonable (e.g. Appendix Fig. B.1).

We used mixed effects models to account for non-independence of data due to differences in collectors (source), sampling methodologies and biogeography (study), the spatial structure of sites (block), and taxonomy (family and species). The initial, maximal random-effects structure was block (nested within study within source), crossed with species (nested within family). We also tested an alternative structure of block (nested within study within sampling method), but this performed less well (results not shown), so was not pursued. More complicated random effect structures (e.g. random slopes) could not be fitted due to computational limitations. Both the presence and abundance models had the same initial maximal fixed-effects model structure, containing all land use (LUI and mNDVI) and trait variables, as well as all two-way interactions between land use and traits. We determined the best random-effects structures using likelihood ratio tests (Zuur *et al.* 2009), comparing all formulations.

Full models were assessed for multicollinearity using generalized variance inflation factors (GVIFs, Zuur *et al.* 2009), which never breached the threshold of 10 (Appendix Tables B.1 and B.2). We used backwards stepwise model simplification based on likelihood ratio tests to reduce model complexity as far as possible and to determine whether interactive effects between traits and land use were retained in the final model (Zuur *et al.* 2009). Model simplification reduced the GVIFs (Appendix Table B.3). We assessed robustness of parameter estimates by bootstrapping data points, using 1,000 iterations for the abundance model and

(because of computational limitations) 100 iterations of the occurrence model. We inferred significance of parameter estimates from the 95% bootstrapped confidence intervals (bCIs, Cauty & Ripley 2014) and computed ANOVA tables using type III Wald tests (car package, Fox & Weisberg 2011).

Where the minimum adequate model included significant trait $\times$ land-use interactions, we evaluated the relative importance of land use, traits and their interactions. The following models were constructed for both species occurrence and abundance (if present):

1. Interactive model: the minimum adequate model
2. Additive model: as 1, but with all interactions removed
3. Traits model: as 2, but with all land-use variables removed
4. Land-use model: as 2, but with all trait variables removed
5. Null model: only random effects included.

The importance of interactive terms was assessed by comparing the additive model with the interactive model; the importance of traits versus land use was assessed by comparison with the additive model. We chose not to use information criteria for these comparisons. Akaike's Information Criterion, with its low penalty per extra parameter (2 units), can overestimate the importance of predictors with more parameters when, as here, the dataset is large (Arnold 2010; Link & Barker 2006), whilst the penalty for the Bayesian Information Criterion (the log of the sample size) can be too stringent when, as here, the data are not independent (Jones 2011). Calculating appropriate penalty terms for complex mixed-effects models is far from straightforward (Delattre *et al.* 2014). We therefore assessed the relative importance of interactive effects in the minimum adequate models using marginal R^2_{glmm} values (R^2 for mixed models), i.e., the variance explained by fixed effects alone (Barton 2013; Nakagawa & Schielzeth 2013). Specifically, we calculated the decrease in explanatory power when the predictor set of interest was excluded from the model (similar to the process for linear models in Ray-Mukherjee *et al.* 2014), as a percentage of the marginal R^2_{glmm} when the predictor set was included. We used the same approach to estimate the importance of each trait and each land-use variable separately. These 'unique' contributions of focal predictors when isolated

from other variables may underestimate or overestimate the full contribution of the focal predictors, depending on the covariation among explanatory variables.

We performed a randomization test to ensure that differences in R^2_{glmm} values were not merely caused by differences in model complexity (Nakagawa & Schielzeth 2013). In each trial (1,000 for abundance models and 100 for occurrence models), we randomized the species names in the trait dataset, conserving the between-trait correlations and dataset structure, but breaking any link between traits and occurrence or abundance. We calculated marginal R^2_{glmm} values from interactive, additive and traits-only models fitted to the randomized data (the land-use-only and null models were unaffected by the randomization). We counted how often marginal R^2_{glmm} from the randomized data exceeded that of the original models, and expressed the difference as a z-score. If interactive models are favoured simply because they have more parameters (i.e. a bias caused by an incorrect penalty for complexity), the observed marginal R^2_{glmm} will be approximately the average of the values across randomizations.

All analyses were carried out using R: A Language and Environment for Statistical Computing version 2.15.3 (R Core Team 2013).

3.4 RESULTS

3.4.1 MODEL RESULTS

Many trait $\times$ land use interactions were retained after model simplification, explaining a significant amount of variation in both species occurrence and abundance if present (Tables 3.2 and 3.3; see Appendix Table B.1 and Table B.2 for full coefficients). Effects of trait $\times$ land use interactions were often different for species occurrence and abundance. A decrease in the number of species might enable remaining species to persist at higher abundances (Newbold *et al.* 2014).

Table 3.2: Anova table for minimum adequate model of probability of presence. Stars indicate the level of significance: <0.05*, <0.01**, <0.001***. The minimum adequate model had a marginal R^2_{glmm} of 0.07 and a conditional R^2_{glmm} of 0.58. Acronyms: LUI = Land-use and intensity, ITD = inter-tegular distance (body size), mNDVI = mean NDVI

Term	χ^2	Df	Sig
(Intercept)	52.19	1	***
LUI	64.71	5	***
mNDVI	28.39	1	***
Sociality	4.18	1	*
Lecty status	32.11	2	***
Tongue length guild	2.53	1	
Voltinism	0.32	1	
Duration of flight season	18.32	1	***
ITD	5.75	1	*
Nest construction	0.00	1	
LUI $\times$ Sociality	36.20	5	***
mNDVI $\times$ Sociality	16.90	1	***
LUI $\times$ Lecty status	66.39	10	***
mNDVI $\times$ Lecty status	31.20	2	***
LUI $\times$ Tongue length guild	11.33	5	*
mNDVI $\times$ Tongue length guild	7.75	1	**
LUI $\times$ Voltinism	48.66	5	***
LUI $\times$ Duration of flight season	43.81	5	***
mNDVI $\times$ Duration of flight season	5.30	1	*
LUI $\times$ ITD	45.15	5	***
mNDVI $\times$ ITD	12.18	1	***
LUI $\times$ Nest construction	25.23	5	***

Table 3.3: Anova table for minimum adequate model of abundance. Stars indicate the level of significance: <0.05*, <0.01**, <0.001***. The minimum adequate model had a marginal R^2_{glmm} of 0.02 and a conditional R^2_{glmm} of 0.71. Acronyms: LUI = Land-use and intensity, ITD = inter-tegular distance (body size), mNDVI = mean NDVI

Term	χ^2	Df	Sig
(Intercept)	0.37	1	
LUI	12.39	5	*
mNDVI	7.56	1	**
Sociality	4.36	1	*
Lecty status	7.92	2	*
Tongue length guild	11.45	1	***
Voltinism	1.37	1	
Duration of flight season	5.05	1	*
ITD	7.34	1	**
LUI $\times$ Sociality	23.76	5	***
mNDVI $\times$ Lecty status	9.13	2	*
LUI $\times$ Tongue length guild	12.16	5	*
mNDVI $\times$ Tongue length guild	21.55	1	***
LUI $\times$ Voltinism	40.02	5	***
LUI $\times$ Duration of flight season	17.14	5	**
mNDVI $\times$ ITD	12.35	1	***

Table 3.4: The fit to data of a null model, models with traits only and land-use only, and additive and interactive models with both land use and traits. The interactive model is the minimum adequate model. AIC may favor more complex models (Arnold 2010; Link & Barker 2006), but AIC weights are presented for comparison. Variance of taxonomic random effects are also given (species within family and family).

Response	Model name	Marginal R^2_{glmm}	Conditional R^2_{glmm}	AIC weights	Species within family variance	Family variance
Probability of presence	Null model	0.000	0.552	0.000	1.097	0.131
	Land use only	0.008	0.571	0.000	1.100	0.132
	Trait only	0.053	0.560	0.000	0.803	0.164
	Additive	0.058	0.577	0.000	0.805	0.166
	Interactive	0.067	0.579	1.000	0.830	0.162
Abundance of present species	Null model	0.000	0.692	0.000	0.116	0.018
	Land use only	0.004	0.694	0.000	0.116	0.019
	Trait only	0.010	0.696	0.000	0.102	0.033
	Additive	0.012	0.697	0.000	0.102	0.034
	Interactive	0.020	0.708	1.000	0.104	0.043

3.4.2 IMPORTANCE OF TRAIT $\times$ PRESSURE INTERACTIONS

Models where interactions were excluded (additive models) explained 13% and 37% less variation in occurrence and abundance respectively, than the interactive models did (marginal R^2_{glmm} , Table 3.4). Traits were relatively more important than land use: the traits-only model explained 85% and 70% as much variation in occurrence and abundance, respectively, as the additive model, while land-use-only models only explained 9% and 17% as much variation in occurrence and abundance as the additive model (marginal R^2_{glmm} , Table 3.4). These results are not an artefact of model complexity. The observed occurrence models had higher

marginal R^2_{glmm} than every randomization (z scores: trait-only model = 19.87; additive—traits and land use—model = 19.77; interactive model = 15.53). The observed abundance models outperformed every randomization for the interactive model (z = 4.69), and 97% of the additive (z = 4.49) and trait-only models (z = 5.09).

Including traits increased models' marginal R^2_{glmm} (variance explained by fixed effects), but the conditional R^2_{glmm} values (variance explained by fixed and random effects) change less, because the effect of traits can also be explained as taxonomic differences in the random-effects structure (Table 3.4, Appendix Table B.3).

3.4.3 IMPORTANCE OF VARIABLES

Interactions between LUI and traits were more important than interactions between mNDVI and traits (Fig. 3.1); we therefore focus on the former in the main text (see Appendix B.4 for full mNDVI results).

In human dominated land uses, species with shorter flight seasons were associated with lower probabilities of occurrence than species with longer flight seasons, although the magnitude of the relationship varied among land uses (Fig. 3.2). Among species that were present, shorter flight seasons were associated with lower abundances in all land uses, except for minimally-used cropland (Fig. 3.2).

Other traits were less important in determining species' occurrence and abundance (Fig. 3.1), but still had significant effects on species sensitivity (Tables 3.2 and 3.3). Species with smaller ITD were particularly sensitive to intensively-used cropland (estimate = 0.11, bCIs: 0.02,0.18). Oligolectic, solitary, univoltine, long-tongued and nest-excavating species were less likely to be present in human-dominated land uses relative to secondary vegetation, particularly in intensively-used cropland and urban areas (Fig. 3.3). If present, however, the abundances of these species did not differ strongly from secondary vegetation (Fig. 3.4a).

Species with narrower dietary breadths (obligately oligolectic) were generally more sensitive to land use than dietary generalists (Fig. 3.3a, c, d). Short-tongued species were sensitive to some land uses in terms of probability of presence (Fig. 3.3e) but, if present, increased in abundance in some cases (Fig. 3.4c).

The effects of ecological traits on species' sensitivity were not always consistent across

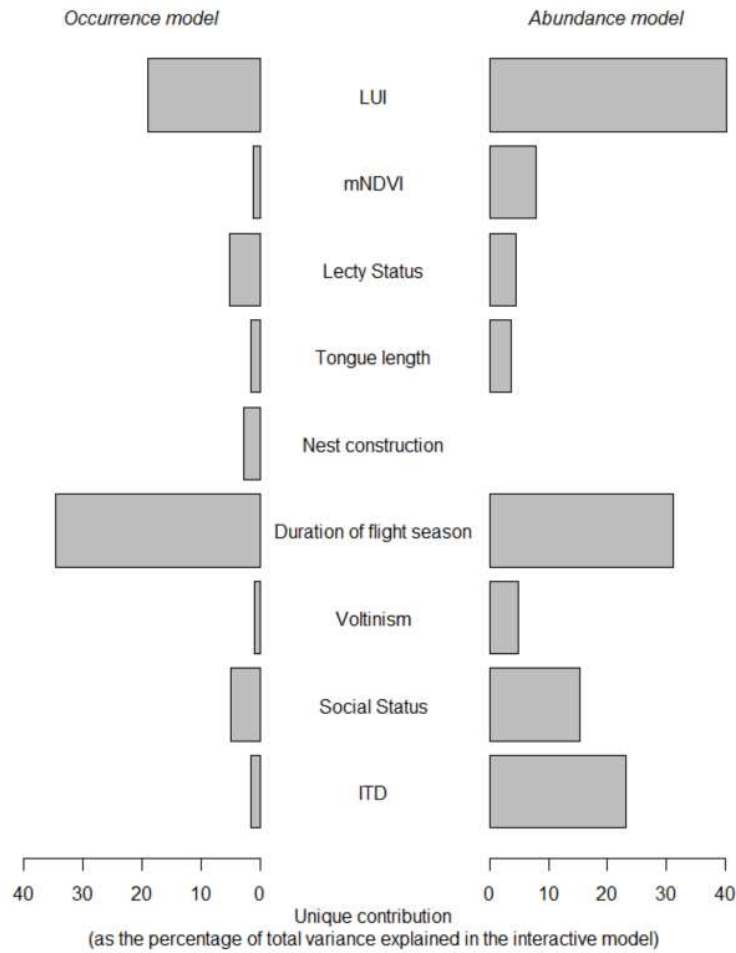


Figure 3.1: Unique contribution of variables to the explanatory power of minimum adequate models of occurrence and abundance. Contribution is reported as the reduction in variance explained by fixed effects (marginal R^2_{glmm}) when the variable and all its interactions are removed from the model, as a percentage of the total variation explained by fixed effects in the minimum adequate models

land uses. For example, species that were not obligately solitary were more sensitive than solitary species to lightly-used cropland (Fig. 3.3b), but less sensitive to pasture.

Figure 3.2: Relationship between flight season duration and a) probability of species presence and b) abundance of present species, in different habitat types, as estimated from the minimum adequate models. Error bars represent half the standard error, to ease comparison. The legend indicates the coefficient estimate extracted from the model with 95% bootstrapped confidence intervals (bCIs) in parentheses. The coefficients for human-dominated land-uses are the difference in slope between the given land use and that of secondary vegetation. If bCIs do not cross zero, the estimate is taken to be significant.

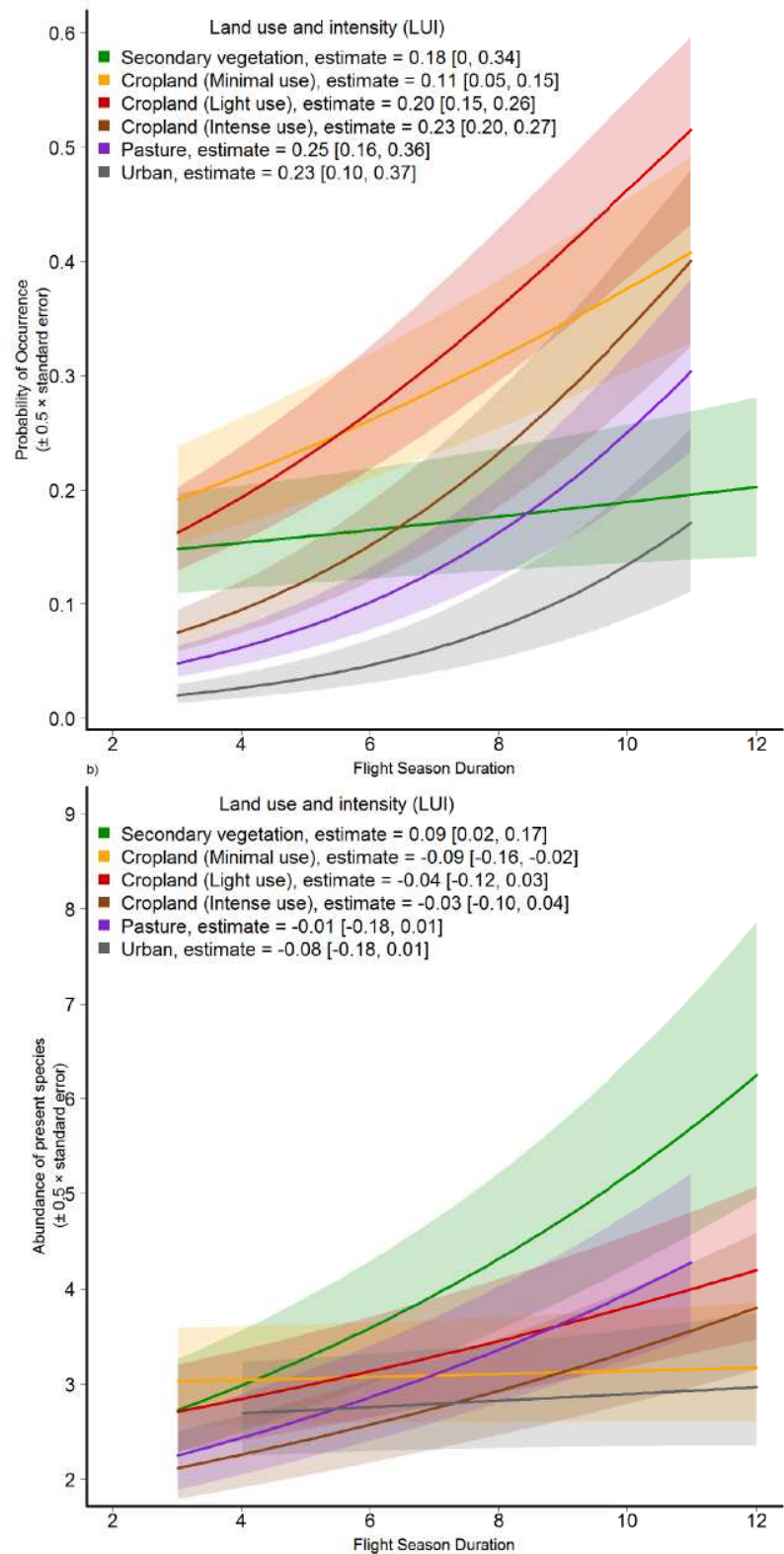
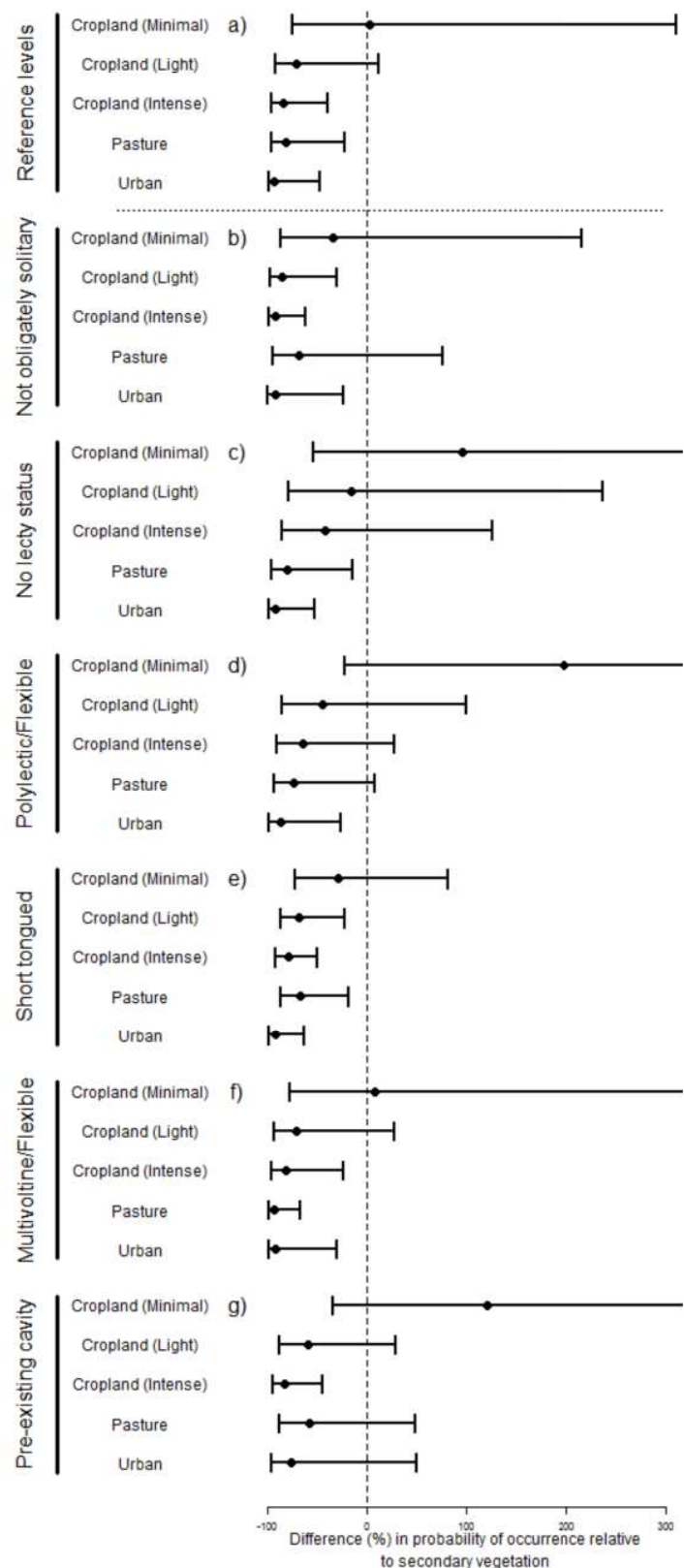


Figure 3.3: Land use and intensity (LUI) impact on species with differing (categorical) ecological traits. For each trait level, this is shown as the % difference in probability of occurrence relative to secondary vegetation, with 95% confidence intervals (CIs) calculated from the model. The trait reference levels in the models were oligolectic, solitary, univoltine, long-tongued, and nest excavating species. The effect of LUI on species with these trait values is presented in panel a, and the effects on species with other trait values in panels b-g. Therefore, to compare the sensitivity of long-tongued species and short-tongued species to LUI, one would compare panels a and e. CIs in some panels extend beyond the plot region



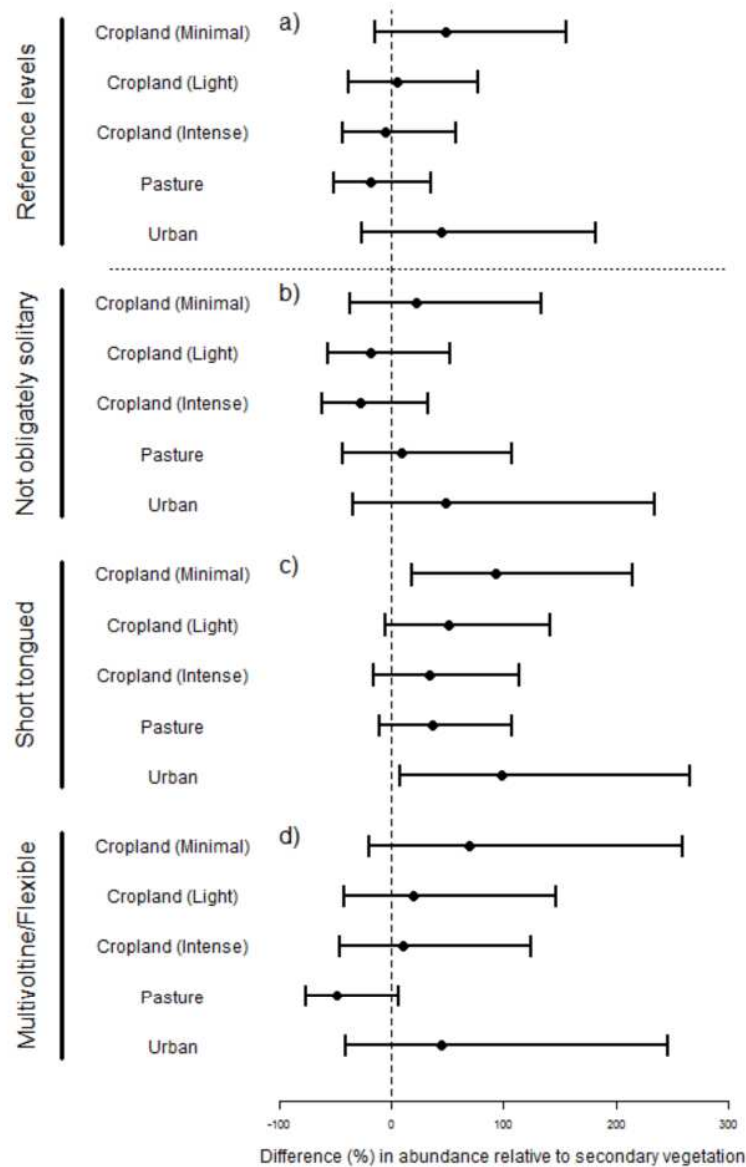


Figure 3.4: Land use and intensity (LUI) impact on species with differing (categorical) ecological traits. For each trait level, this is shown as the % difference in abundance relative to secondary vegetation, with 95% confidence intervals calculated from the model. The trait reference levels in the model included oligolectic, solitary, univoltine, long-tongued species. The effect of LUI on species with these trait values is presented in panel a, and the effects of species with other trait values in panels b-d. Therefore, to compare the sensitivity of long-tongued species and short-tongued species to LUI, one would compare panels a and c.

3.5 DISCUSSION

Land-use change and intensification are considered to be major pressures on European bees (Ollerton *et al.* 2014; Potts *et al.* 2010). However, our analyses of 257 species at 1,584 sites suggest that these pressures alone explain little of the variation in the presence and abundance of bee species, as effects are often indirect (through reduced floral and nesting resources) and are masked by heterogeneity in species' responses (Roulston & Goodell 2011). We show that species' functional traits—phenology, foraging range, niche breadth and reproductive strategy (sociality)—influence their sensitivity to human-dominated land use, but do so in ways that differ among cropland, pastoral and urban habitats.

3.5.1 LAND-USE EFFECTS ON SPECIES PERSISTENCE AND ABUNDANCE

The probability of presence for most species was strongly reduced in intensively-used cropland relative to secondary vegetation, except for pollen generalists (polylectic, flexible or parasitic species); maintaining stable nesting habitats as well as floral resources may therefore help conserve diversity in such systems (Forrest *et al.* 2015). Species with shorter flight seasons—the most important trait in explaining occurrence and abundance patterns (Fig. 3.1)—were less likely to be present and were less abundant in intensively-used cropland, perhaps as this trait confers a higher risk of asynchrony with key floral resources. These results are consistent with previous findings in butterflies, that floral specialists with shorter flight seasons are more likely to be rare and threatened (Barbaro & van Halder 2009; Dennis *et al.* 2004). Previous studies of bees show less consistent patterns, although they assessed relatively few sites and species (e.g. Connop *et al.* 2010; Vázquez & Simberloff 2002). Although our analyses are based on different datasets, these results are similar to those in Williams *et al.* (2010), who found that social species and pollen specialists were particularly sensitive to agricultural intensification.

Small species were also particularly sensitive to intensive agriculture, perhaps because larger species are able to forage further from their nest (Greenleaf *et al.* 2007; Wright *et al.* 2015). These results suggest that the placement of floral margins will need careful planning with respect to species' nesting habitats (Wright *et al.* 2015). Long-distance

foraging may increase susceptibility to some landscape-scale threats (e.g. pesticide exposure), but local conditions are likely to be more important for bee diversity and pollination services in temperate systems (Benjamin *et al.* 2014; Kennedy *et al.* 2013).

Even in lightly-used cropland, short-tongued species that are not obligately solitary had significantly lower probability of occurrence relative to secondary vegetation, perhaps because their greater foraging breadth and capacity exposes them more to pesticides (Williams *et al.* 2010). In contrast, minimally-used cropland maintained diverse bee communities—although species with shorter flight seasons were still vulnerable—suggesting an advantage of organic and other low-intensity farming practices.

Many species were sensitive to pasture, though sociality, polylecty, cavity nesting and long flight seasons were associated with lower sensitivity. Social and polylectic species have enhanced foraging capacity, enabling effective exploitation of available resources and persistence in a patchy mosaic. Small species were also less sensitive to pasture than to other land-uses, perhaps because forage is available within smaller distances of nesting sites.

Most species, including those with shorter flight seasons, were less likely to be present in urban areas than in secondary vegetation; only cavity-nesting species were unaffected. If present, however, most species tended to be fairly abundant, especially short-tongued species. Our results are congruent with previous studies that have found a negative impact of urbanisation on bees (Hernandez *et al.* 2009) accompanied by an increase in the numbers of cavity-nesting species (Fortel *et al.* 2014a; Hernandez *et al.* 2009). Although other studies have found little difference in diversity between urban areas and semi-natural habitats (Baldock *et al.* 2015), our results suggest that further loss of secondary vegetation as a result of urbanization may be particularly detrimental to bee communities and to pollination services, as the loss of dietary generalists can greatly affect plant-pollinator networks (Memmott *et al.* 2004).

3.5.2 LIMITATIONS OF THE STUDY

Our dataset is large, but only contains 12.5% of European bee species, with biases towards Western Europe and bumblebees. In addition, little of the variation in species' diversity was explained by fixed effects in our models: most was attributed to heterogeneity between

sources (Appendix Table B.3), reflecting differences in sampling methodology, intensity and timing, as well as land-use practices or pressures that we did not consider. In addition, we used a small number of species' functional traits that were coarsely categorized and omitted intraspecific variation. Further collation of relevant trait information could greatly enhance the predictive ability of models such as these.

Some effects may be influenced by differential detectability; for instance, larger species that are active for longer are more likely to be sampled. This is in part why we have focussed on differences in sensitivity—changes between secondary vegetation and human-dominated land uses—rather than absolute differences in occurrence and abundance between species. However, detectability may vary among land uses. For instance, with visual sampling methods such as aerial transects, small species may be less frequently sampled in denser vegetation where they are more difficult to see. This may be in part accounted for by the inclusion of mNDVI in our models (as NDVI correlates with net primary productivity), but it is still important to consider possible effects of sampling bias on analyses such as these.

3.5.3 CONCLUSION

We have presented the most comprehensive analysis to date of how ecological traits affect bee species' responses to human impacts in Europe. Our results suggest that conservation and management activities should not simply focus on particular land uses or particular traits, but how they interact. Our findings have implications for ecosystem services and food security for two reasons. First, many of the traits affecting species' sensitivities to land use also influence pollination efficiency (de Bello *et al.* 2010). Second, trait-based vulnerability of species also reduces functional diversity (Forrest *et al.* 2015), which is important for insurance against disturbances, pollination efficiency (Albrecht *et al.* 2012) and stability under climate change (Bartomeus *et al.* 2013b). However, to fully understand the implications for pollination provision, further data are required on how traits influence pollination efficacy.

3.6 ACKNOWLEDGEMENTS

We are grateful to all those who contributed data to this project, in particular to members of the Greenveins project. A paper describing the collated dataset in full is forthcoming. We are also thankful to the PREDICTS team, especially Tamera I. Hussein, for assistance with data collation and curation, to Shiniki Nakagawa and Kim Nimon for statistical advice, and to three anonymous reviewers. The compilation of the traits dataset was funded by the EU FP7 project 'Status and Trends of European Pollinators' (244 090, www.STEP-project.net). ADP is funded by the BBSRC (grant BB/F017324/1); LNH, IL, TN and AP were supported by the NERC (grant NE/J011193/1 to AP). This paper is a contribution from the Imperial College Grand Challenges in Ecosystems and the Environment Initiative.

CHAPTER 4

Varying phylogenetic signal in bee species' sensitivity to different land uses

4.1 ABSTRACT

Bee species worldwide are facing a future of increased land-use change and intensification. Species are unlikely to respond identically to these pressures; rather, closely-related species with similar ecological characteristics are likely to respond similarly (i.e., show phylogenetic signal). This could have severe consequences for ecosystem functioning if whole clades are at risk. We use the PREDICTS database to assess the sensitivity of 495 bee species to agricultural expansion, intensification and urbanization. We relate these estimates to the recently-published Bee Tree of Life to assess phylogenetic signal. In addition, we assess whether variation in sensitivity is better explained by phylogenetic differences or functional trait differences. We found strong phylogenetic signal in species' sensitivity to agricultural land but only a weak signal in sensitivity to more intensive agriculture or urban areas. Where phylogenetic signal was strong, phylogenetic distances between species far exceeded the ability of functional traits to explain species sensitivities, suggesting that more subtle ecological differences may be driving variation in sensitivity to these land-use pressures. Agricultural expansion has the potential to significantly undermine ecosystem service provision. The expansion of urban areas, however, may maintain more robust communities, but further work is needed to understand the heterogeneity in species responses to urbanization.

4.2 INTRODUCTION

Land-use change and intensification are already important drivers of terrestrial biodiversity loss (Newbold *et al.* 2015; Ollerton *et al.* 2014) and are predicted to worsen in the future (Hurt *et al.* 2011), with most scenarios seeing further loss of natural and semi-natural land, driven by agricultural expansion and urbanisation, as well as increased degradation as a result of agricultural intensification (Hurt *et al.* 2011). The effect such global change will have on bee populations could have serious consequences for food-security worldwide (Klein *et al.* 2007), and may have knock on effects on wild plant populations (Ollerton *et al.* 2011) as bee species are the most specialised and important pollinators of flowering plants globally (Danforth *et al.* 2006).

Species are unlikely to respond to these land-use changes identically; rather, more closely related species may respond more similarly than distantly related species (Díaz *et al.* 2013). That is, species sensitivity to change may show strong phylogenetic signal. Phylogenetic signal has been reported in other taxa for response to chemical exposure (Chiari *et al.* 2015; Larras *et al.* 2014), climate change (Comte *et al.* 2014; Thuiller *et al.* 2011) and fragmentation (Vranckx *et al.* 2012). In bees, phylogenetic signal was found in relative population declines over long temporal scales in North American (Bartomeus *et al.* 2013a). However, little research has so far explored phylogenetic signal in bee sensitivities to particular threats, such as land-use conversion.

Phylogenetic signal in species sensitivities could prove useful for guiding conservation efforts (Mace *et al.* 2003). Direct data on the vulnerability of bee species to anthropogenic pressures is woefully incomplete: even in Europe, an intensively studied region, over 50% of bee species are graded as Data Deficient in the European Red List (Nieto *et al.* 2015). Ecological traits can mediate species responses to human impacts (Bartomeus *et al.* 2013a; Burkle *et al.* 2013; De Palma *et al.* 2015; Rader *et al.* 2014; Scheper *et al.* 2014; Williams *et al.* 2010), but scarcity of data limits the conservation application of this knowledge. If these traits are phylogenetically conserved (Burkle *et al.* 2013), as many aspects of ecology are (Freckleton *et al.* 2002), phylogeny alone may be sufficient to make useful predictions of species' sensitivities to human impacts (Helmus *et al.* 2010). Phylogeny may even surpass

functional traits in terms of explaining species sensitivities if variation in responses is driven by a broader set of ecological differences than are captured by available trait data. In addition, the presence of phylogenetic signal may open opportunities to efficiently monitor bee communities at higher taxonomic levels (Bevilacqua *et al.* 2012; Guénard *et al.* 2011; Kallimanis *et al.* 2012), potentially saving time, money, and bees (Lebuhn *et al.* 2013; Tepedino *et al.* 2015), and facilitating citizen science.

Phylogenetic signal in sensitivity may make monitoring easier, but it increases the risk that disturbance will have severe impacts on ecosystem functioning (Díaz *et al.* 2013), as the order of species losses has greater impacts on ecosystem functioning than the extent (Wolf & Zavaleta 2014). If whole clades of the tree of life are at risk (Díaz *et al.* 2013), phylogenetic diversity and redundancy of bee communities may also decline; although there is some debate (Cardinale *et al.* 2015), phylogenetic diversity can be important for ecosystem functioning and stability (Cadotte *et al.* 2012). The protection of phylogenetic diversity (by conserving those clades that are most vulnerable) may also be important for maintaining robust pollination networks: high phylogenetic diversity can correlate with interaction diversity (Miranda & Parrini 2015), as closely-related species also tend to share resources (Naisbit *et al.* 2012; Rezende *et al.* 2007).

Understanding which disturbances prompt the most phylogenetically patterned response may therefore indicate where ecosystem services might be at greatest risk and so where conservation action be most important. However, it is unclear whether responses to different pressures will all show phylogenetic signal (Díaz *et al.* 2013). The link between ecological traits and the response to human impacts are not always straightforward (De Palma *et al.* 2015; Díaz *et al.* 2013). In addition, if species' sensitivities are related more to behavioural traits than morphological ones, phylogenetic signal may be less evident as behavioural traits are more labile (Blomberg *et al.* 2003). In urban areas, where nesting behaviour is particularly important in determining species responses, we may therefore find lower phylogenetic signal than in other land-use transitions (Hernandez *et al.* 2009).

We use data from 86 studies and 2599 sites to assess the sensitivity of almost 500 bee species (from 91 genera) to human-dominated land uses, including agriculture and urban areas, and to increasing agricultural intensity. We test for phylogenetic signal in the sensitivity

of species to these land use pressures, accounting for uncertainty in sensitivities. Using trait data for European bee species, we assess whether phylogenetic differences are better able than functional traits to explain variation in species' sensitivities.

4.3 MATERIALS AND METHODS

See Chapter 2 for details of the data collation and curation procedures. In this analyses, we use only data where bee species abundance was measured at multiple sites. Species were only included in the dataset if they were sampled in both primary or secondary vegetation as well as an agricultural or urban site, or if they were sampled in agricultural sites of differing use intensity (See Table 4.1). In addition, we only included a species in the dataset if the scientific name was known, so that it could be matched to a phylogeny. This resulted in a dataset of 86 studies spanning 495 bee species.

4.3.1 SPECIES SENSITIVITY

We calculate the Species Sensitivity Index (SSI) as the log-response ratio of species abundance in intact vs converted land uses:

$$SSI = \ln\left(\frac{\text{mean abundance in converted land use}}{\text{mean in intact land use}}\right) \quad (4.1)$$

We focus on four particular land transitions (Table 4.1). The largest dataset is a comparison between species abundances in natural/semi-natural land with all human-dominated land uses combined, as a recent synthesis showed that human-dominated land uses are more similar to each other than to natural or semi-natural land (Newbold *et al.* 2015). However, within this broad categorisation, specific transitions may influence species in different ways, so we also explore separately the impact of agricultural land, urban land, and increasing agricultural intensity. The land-use classes within the dataset (Chapter 2) were therefore coarsened depending upon the land-use comparison of interest, allowing species abundances to be compared between intact (natural and semi-natural) land uses and converted (human-dominated) land uses, or between lower and higher intensity agriculture (Table 4.1).

Table 4.1: Land-use transitions of interest and the component land-use classes. Dataset sample sizes are also given: number of studies, species and species that match with the recently-published Bee Tree of Life (Hedtkke *et al.* 2013)

Land-use comparison	Intact	Converted	Studies	Species	Species in the phylogeny
Loss of natural and semi-natural habitat	Primary & Secondary vegetation	Cropland, Pasture, Plantation forest & Urban	86	494	137
Agricultural expansion	Primary & Secondary vegetation	Cropland, Pasture & Plantation forest	84	442	116
Urbanisation	Primary & Secondary vegetation	Urban	54	146	56
Agricultural intensification	Agricultural sites (as defined above) with a continuous use-intensity scale from 1 (minimal use) to 3 (intense use)		60	287	87

For each species, abundance was modelled as a function of the land-use category (intact vs converted) or agricultural intensity. Study identity was included as a covariate to account for differences in sampling effort, methodology and biogeography. Generalized linear models were used with a Poisson error structure unless overdispersion required use of a quasipoisson structure (Crawley 2007). Study identity would ideally be treated as a random variable, but for many species the number of studies were too small to accurately estimate random effect variances (Fox *et al.* 2015), so it was treated as a fixed effect (approximately 80% of species in our dataset had data from six or fewer studies). The land-use estimate (the log-response ratio) and standard error were extracted from the model as a measure of the Species Sensitivity Index (SSI) and its associated uncertainty.

In many cases, complete separation of the data (for example, when a species is always absent from converted sites but always present in intact sites) meant that estimates and standard errors of the slope were extreme and unreliable using R's glm function. Therefore, we instead used Bayesian generalized linear models with weakly informative priors (bayesglm function, arm package, Gelman *et al.* 2008). An alternative would be add a small non-zero value to zero abundances. When separation is not an issue, these two methods provided similar model estimates; when separation is an issue, the latter method was more conservative in terms of the estimated sensitivity, but tended to be less conservative in terms of the standard errors (Appendix Fig. C.1). In addition, altering the data requires an arbitrary decision about the value used to replace the zeros, and results were sensitive to this decision (Appendix Fig. C.2).

4.3.2 PHYLOGENETIC TREE

We use a recently-published phylogeny of over 1300 bee species from around the world (Hedtke *et al.* 2013). Of the species present in our dataset, 137 could be matched to the phylogenetic tree. However, species presence or absence in the phylogeny was not random: species absent from the tree tended to have higher uncertainty in SSI, although there was no difference in SSI (see Appendix C.2). Therefore, we used a birth-death polytomy resolver (pastis package in R, Thomas *et al.* 2013) to estimate the placement of missing species given their taxonomic affinities: congeners were constrained to be a sister in a monophyletic clade,

unless the phylogenetic tree provided evidence against genus monophyly. Where species did not have congeners in the phylogenetic tree, we used higher-level taxonomic constraints for species placement; we only used such constraints where nodes had greater than 95% bootstrap support. *Caenaugochlora*, *Chlerogella*, *Pereirapis*, *Pseudaugochlora*, *Chalepogenus* and *Agapostemonoides* were restricted to their respective tribes, where monophyly was strongly supported (Hedtke *et al.* 2013). Note that *Agapostemonoides* was constrained within the tribe Caenohalictini, which is sometimes considered only a subtribe within the Halictini tribe (Danforth *et al.* 2008). *Pachyprosopis* (Euryglossinae: Colletidae) was constrained to be sister to the tribes Euryglossinae, Scapterinae, and Xeromelissinae, but species were not permitted to enter the clades formed by the Xeromelissinae or Hylaeinae (Almeida & Danforth 2009; Hedtke *et al.* 2013). The genus *Ceylalicthus* was constrained to be placed within its subfamily, Nomiodinae. Where synonyms were identified using the ITIS database (taxize package, R package version 0.3.0, Chamberlain & Szocs 2013; Chamberlain *et al.* 2014a), these were merged (e.g., *Homalictus punctatus* was synonymised with *Lasioglossum punctatus*). Where the published phylogeny had species placements that appear very discrepant (i.e., the placement of *Ceratina japonica* and *Anthophora pillipes* outside of their otherwise monophyletic groups and placed with fairly distantly related species) and were noted as such by the authors of the tree (Hedtke *et al.* 2013), these were considered missing species and their placement was estimated using the pastis package (Thomas *et al.* 2013) and MrBayes (Ronquist *et al.* 2012).

For twenty-eight bee clades with missing species (these were usually subfamilies or tribes which had greater than 70% bootstrap support; See Appendix Table C.1 for details), a phylogenetic tree was developed using a birth-death model with zero extinction rate and exponential speciation rate using MrBayes version 3.2 (Ronquist *et al.* 2012), for at least 100,000,000 generations and four runs, with samples taken every 10000 generations. Tracer v1.4.1 was used to track effective sample sizes to assess convergence of parameter estimates. The standard deviation of split frequencies of the four independent runs were also assessed (with a value of less than 0.01 suggesting that models had converged: Ronquist *et al.* 2012). From each of the converged runs, we then sub-sampled from the post-burn-in (10% burn-in) posterior distribution of each bee clade to produce 1000 within-clade trees. A large clade of apid bees

did not reach parameter convergence in any of the four independent runs, but measures of phylogenetic signal within the clade were not significantly different between runs (analysis of variance, $F_{3,996} = 1.27$, n.s.), so a random sample from all runs were taken. Random samples (without replacement) were then taken from the set of within-clade trees for each bee clade. The original tree was rate smoothed using PATHd8 (a computationally efficient method for large phylogenetic trees, Britton *et al.* 2007), with the root age constrained to one; incomplete clades were then pruned. To graft the completed within-clade trees back onto this pruned, rate-smoothed tree, the clade was first scaled to have a depth of 1; the edge lengths were then scaled by the age of the crown node of the clade. The resulting 1000 composite trees were used in further analyses to ensure that results are robust to species placement; not accounting for phylogenetic uncertainty can lead to incorrect estimates of precision (de Villemereuil *et al.* 2012).

As birth-death polytomy resolvers can bias trait-based analyses (Rabosky 2015), we perform all analyses on both the original tree and the set of complete trees for comparison. As the rate-smoothing procedure might also influence phylogenetic signal, we also perform the analyses on the rate-smoothed incomplete tree.

4.3.3 PHYLOGENETIC ANALYSES

Phylogenetic signal was tested using Pagel's λ (Pagel 1999), which has been shown to produce reliable estimates when sample sizes are large, as here (Münkemüller *et al.* 2012). The method used accounted for within-species variation in the sensitivity index (i.e., the standard errors of estimates) following Ives *et al.* (2007), as incorporated into the R package phytools (Revell 2012). We also tested for phylogenetic signal without accounting for uncertainty in species sensitivity. As bumblebees have previously been found to respond differently to human impacts from other species (Chapter 6, Bartomeus *et al.* 2013a; Carvalheiro *et al.* 2013), we carried out the same analysis for bumblebees alone and for all species except bumblebees to assess whether any phylogenetic signal in the overall dataset is driven by differences in sensitivity deeper within the tree.

We further assessed whether variation in SSI was best explained by phylogenetic distance (pairwise distances, picante package, Kembel *et al.* 2010), functional distance (gowdis dissimi-

larity, FD package, Laliberté & Legendre 2010), or phylogenetic functional distance (Cadotte *et al.* 2013). The latter is defined as:

$$FPDist = (aPDist^p + (1 - a)FDist^p)^{1/p} \quad (4.2)$$

where PDist is the phylogenetic pairwise distance, FDist is the trait pairwise distance, p is the p -norm distance and a is the weighting of FDist and PDist to FPDist. We use the values $a = 0.5$ and $p = 2$ (following the methods in the pez package, Pearse *et al.* 2015). Analyses were run using distance-based generalised linear models (dbstats package, Boj *et al.* 2015, 2014) weighted by the inverse squared standard errors (the sample variance) of the SSI. We also modelled species sensitivity as a function of a randomly-generated distance matrix (with original values drawn from a normal distribution). Models were compared using an adapted version of Akaike's Information Criterion (AIC) (dbstats package Boj *et al.* 2015, 2014). We also calculated the pseudo R^2 as:

$$1 - \frac{\text{Residual Deviance}}{\text{Null Deviance}} \quad (4.3)$$

Ecological traits were available for European bee species, and were collated from both the peer-reviewed and grey literature. Morphometric measurements were taken from museum specimens. Traits included information on species body size (strongly correlated with foraging range), flight season duration, dietary breadth, nesting strategy, and reproductive phenology and strategy (See Chapter 3 for details). This analysis will provide an indication of whether phylogeny is better than functional traits at capturing the ecological variation in species characteristics that may be driving differences in SSIs. However, only 177 species matched both our dataset (and only five of these also matched the original phylogeny).

4.4 RESULTS

4.4.1 PHYLOGENETIC SIGNAL

The strength of phylogenetic signal in species sensitivity varied across land-use comparisons (Fig. 4.1). The strongest signal was found in comparisons between semi-natural and natural

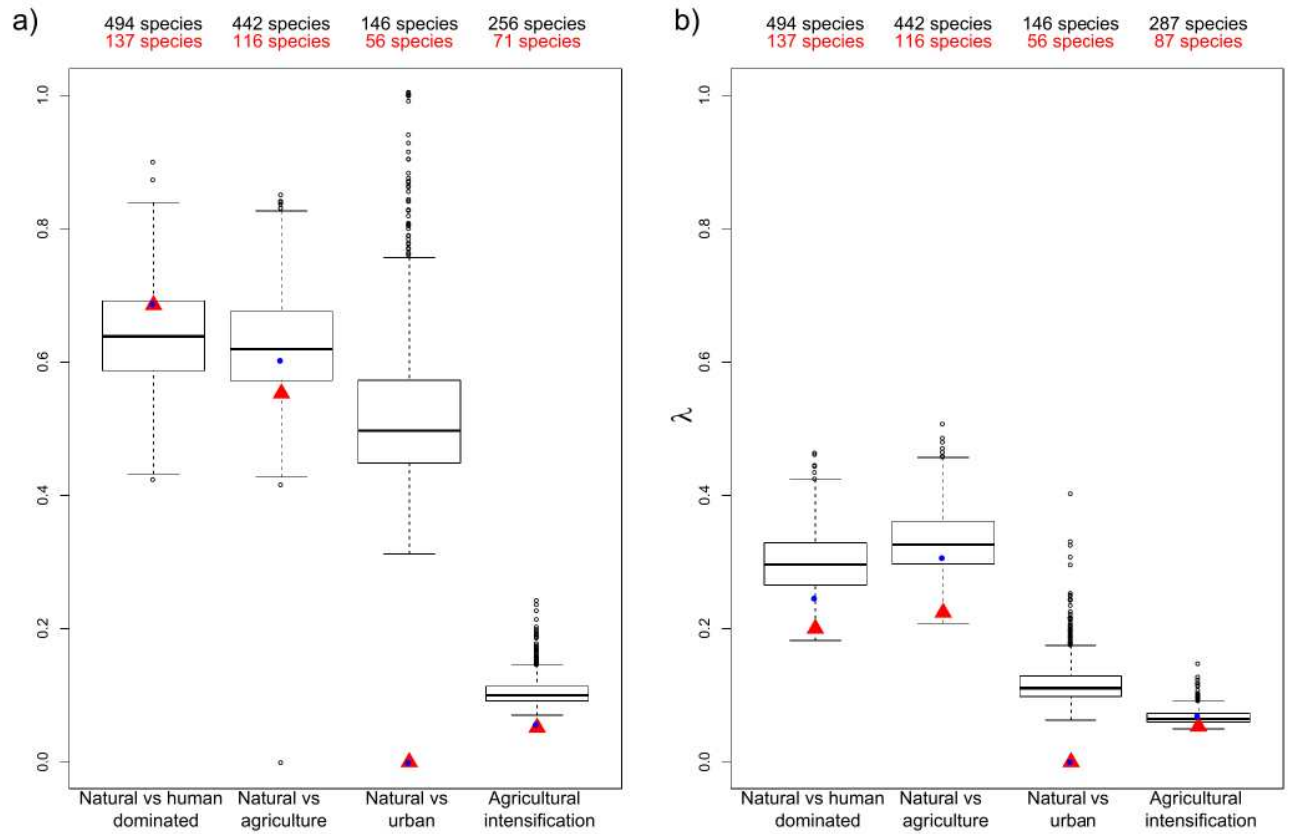


Figure 4.1: Phylogenetic signal in species' sensitivity to various land use pressures, when a) standard errors are accounted for, and b) when they are ignored. Blue circles and red triangles indicate the values for the original tree and rate-smoothed tree respectively, without additional species added in. Numbers in red show the number of species included in these tests. Boxplots show the distribution of λ values across the 1000 completed trees, with numbers in black showing the number of species included in these tests.

land vs. human-dominated land uses, with significant λ values for all phylogenetic trees ($p < 0.01$ for the original tree and all complete trees, and $p < 0.05$ for the rate smoothed tree). Species sensitivities to agriculture showed similarly high λ values: λ values were significant for both the original and rate-smoothed tree ($p < 0.05$), and for the majority of completed trees. The signal in sensitivity to urban land and to more intensive agricultural practices depended on which phylogeny was used, being very low except for the completed trees (Fig. 4.1).

Weighting the analyses by the standard error of species sensitivity was extremely important. λ values were markedly lower when standard errors were not accounted for (Fig. 4.1), although

sensitivity to agricultural intensification showed similar levels of phylogenetic signal regardless of the method used.

There was no phylogenetic signal within the bumblebees. When bumblebees were excluded from analyses, the phylogenetic signal was eroded in the rest of the dataset, particularly when assessing species sensitivity to all human-dominated land-uses, perhaps because sample sizes were greatly reduced (Table 4.2). When using the completed trees, phylogenetic signal was still often evident, albeit reduced, outside of bumblebees for both agricultural expansion and loss of natural vegetation (Table 4.2).

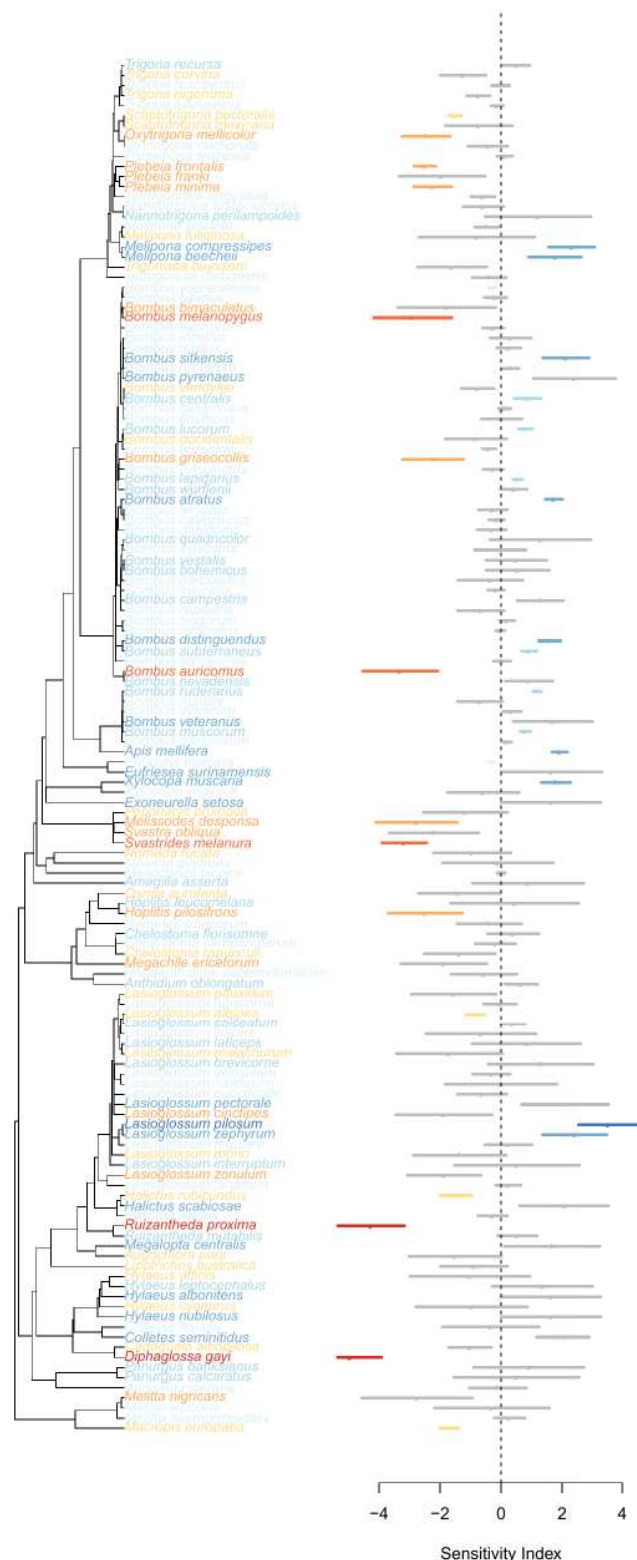
Sensitivity to:	Tree	Within bumblebees	Outside of bumblebees
Human- dominated land	Original	0.000	0.000
	Rate- smoothed	0.000	0.000
	Completed	0.000	0.616
Agricultural land	Original	0.000	0.999
	Rate- smoothed	0.000	0.999
	Completed	-0.000	0.604
Urban land	Original	0.000	0.239
	Rate- smoothed	0.000	0.252
	Completed	0.127	0.217
Higher- intensity agriculture	Original	0.000	0.053
	Rate- smoothed	0.000	0.051
	Completed	-0.000	0.123

Table 4.2: λ values of the sensitivity of bumblebees (within bumblebees) and other species (outside of bumblebees) to land-use change. For the completed trees, this is the mean λ value across 1000 completed trees

4.4.2 RELATIVE IMPORTANCE OF TRAITS AND PHYLOGENY

Using the rate-smoothed tree, species' sensitivities to human-dominated land uses, and to agriculture in particular, were better explained by phylogeny than by functional or functional-phylogenetic distance, while functional distance was the best explanator of sensitivity to agricultural intensification (Table 4.3). For species sensitivity to urban areas (testable only with 27 species), phylogenetic distance as an explanatory variable resulted in the lowest AIC

Figure 4.2: Phylogenetic signal in species' sensitivity to all human-dominated land uses. Tips of the phylogeny are coloured according to the species' sensitivity: from blue to red indicate less to more sensitive. The right panel shows species sensitivity $\pm$ the standard error. Points are coloured when the species' abundance was significantly different between (semi-) natural vegetation and human-dominated land uses.



Phylogenetic tree and Sensitivity Index plot for 100 bee species. The tree on the left shows relationships, with species names color-coded by tribe. The plot on the right shows the Sensitivity Index for each species, with a vertical dashed line at 0. The x-axis ranges from -6 to 6.

Species listed (from top to bottom):

- Trigona recurva*
- Trigona fulvipes*
- Trigona fuscipennis*
- Trigona fulviventris*
- Oxytrigona pectoralis*
- Oxytrigona mellicolor*
- Oxytrigona medicorum*
- Pyramica testacea*
- Plebeia frontalis*
- Plebeia varians*
- Plebeia minima*
- Nannotrigona perilampoides*
- Melipona compressipes*
- Melipona beecheii*
- Bombus vosnesenskii*
- Bombus bifarius*
- Bombus jonellus*
- Bombus mixtus*
- Bombus pratorum*
- Bombus pyrenaeus*
- Bombus centralis*
- Bombus flavus*
- Bombus lucorum*
- Bombus terrestris*
- Bombus rufocinctus*
- Bombus lapidarius*
- Bombus wurflenii*
- Bombus atratus*
- Bombus terreus*
- Bombus californicus*
- Bombus dalmanus*
- Bombus quadricolor*
- Bombus sylvestris*
- Bombus vestalis*
- Bombus bohemicus*
- Bombus insularis*
- Bombus campestris*
- Bombus rupestris*
- Bombus hortorum*
- Bombus vulgaris*
- Bombus distinguendus*
- Bombus subterraneus*
- Bombus terrestris*
- Bombus nevadensis*
- Bombus ruderarius*
- Bombus sylvarum*
- Bombus veteranus*
- Bombus muscorum*
- Apis mellifera*
- Apis mellifera*
- Eufriesea surinamensis*
- Xylocopa muscaria*
- Exoneurella setosa*
- Svastrides melanura*
- Nomada lucata*
- Melicta albifrons*
- Melictinus bicolor*
- Amegilla aenea*
- Amegilla aenea*
- Hoplitia leucomelana*
- Chelostoma florissomne*
- Chelostoma campanularum*
- Megachile arctostaphylos*
- Lasioglossum arctostaphylos*
- Lasioglossum calceatum*
- Lasioglossum calceatum*
- Lasioglossum laticeps*
- Lasioglossum laticeps*
- Lasioglossum brevicorne*
- Lasioglossum villosum*
- Lasioglossum laticorne*
- Lasioglossum minor*
- Lasioglossum interruptum*
- Lasioglossum ruficornis*
- Lasioglossum tanarium*
- Halictus rubicundus*
- Halictus scabrosus*
- Ruizantheda proxima*
- Ruizantheda mutabilis*
- Megalopta centralis*
- Hylaeus albonitens*
- Hylaeus nubilosus*
- Colletes seminudus*
- Diphaglossa gayi*
- Parurgus banksianus*
- Parurgus calceatus*
- Angitia cinerea*
- Melitta nigricans*
- Melitta leucomelana*
- Melitta haemorrhoidalis*
- Macropis europaea*

Sensitivity Index plot (x-axis: -6 to 6, y-axis: Species names). The plot shows the Sensitivity Index for each species, with a vertical dashed line at 0. The x-axis ranges from -6 to 6.

value, but was within less than 3 AIC units of the next best model (the randomly-generated distance matrix). Using the completed trees, sample sizes were greatly increased but results did not change qualitatively. Across the 1000 completed trees, phylogenetic distances had the lowest AIC score on average for SSIs to human-dominated land uses in general, as well as to agricultural and urban land. For SSIs to more intensive agriculture, functional distances still performed better than other distance measures.

Sensitivity to:	Distance Measure	AIC	AIC weights	R^2	Species
Human-dominated land	FDis	171.123	0.005	0.502	55
	PDis	160.438	0.993	0.508	
	FPDis	173.108	0.002	0.444	
	Random	189.187	0.000	0.040	
Agricultural land	FDis	172.317	0.186	0.503	53
	PDis	169.366	0.813	0.453	
	FPDis	182.745	0.001	0.348	
	Random	189.349	0.000	0.073	
Urban land	FDis	78.839	0.003	0.337	27
	PDis	67.896	0.704	0.488	
	FPDis	71.459	0.119	0.457	
	Random	70.692	0.174	0.114	
Higher-intensity agriculture	FDis	91.553	0.993	0.526	45
	PDis	110.004	0.000	0.068	
	FPDis	109.213	0.000	0.162	
	Random	101.567	0.007	0.117	

Table 4.3: Akaike's Information Criterion (AIC) values of models assessing species sensitivities as a function of functional, phylogenetic and functional-phylogenetic distances (FDis, PDis and FPDis). PDis and FPDis were calculated using the rate-smoothed tree. Note that the number of species are small as these are the species which matched both the rate-smoothed phylogenetic tree and the trait dataset.

4.5 DISCUSSION

Bee species show significant heterogeneity in their responses to land use and land-use practices, which in the past has been attributed to differences in ecological traits (De Palma *et al.* 2015; Rader *et al.* 2014; Williams *et al.* 2010; Winfree *et al.* 2009). Our results reveal that phylogeny often predicts the pattern of responses better than do functional traits. These findings can help to direct conservation priorities by identifying vulnerable or resistant species and opening up opportunities to predict the sensitivity of species that may not yet have been

thoroughly studied (Purvis *et al.* 2000). On the other hand, they highlight how ecosystem services may be undermined under future agricultural expansion, as whole clades may be vulnerable (Díaz *et al.* 2013). However, our results suggest that the impact of urbanisation and agricultural intensification may be more difficult to predict based on phylogeny alone, and that ecosystem service provision may therefore be correspondingly resistant to these land-use changes.

4.5.1 VARYING PHYLOGENETIC SIGNAL AMONG LAND-USE PRESSURES

Species' sensitivity to human-dominated land uses showed strong phylogenetic signal, with a λ value of 0.68 (using incomplete phylogenetic trees). Human-dominated land uses have previously been found to hold very different species communities than natural land uses, suggesting that there is a strong ecological filter permitting some species to persist but not others (Newbold *et al.* 2015). This is likely to be because of differences in species ecological traits, which allow some species to take advantage of the altered conditions (De Palma *et al.* 2015). Sensitivity to agricultural land showed similarly strong phylogenetic signal, suggesting that this was the main driver of the phylogenetic patterning.

In contrast, phylogenetic signal in species' responses to agricultural intensification and urban areas was extremely weak. For urban areas at least, this was expected. Previous research has found that species sensitivity to urban areas is related to behavioural traits in particular, such as nesting strategy (Hernandez *et al.* 2009), which tend to be more labile than morphological ones (Blomberg *et al.* 2003); this means that it is less likely that phylogenetic signal will be evident either in species sensitivities or in the traits underpinning them. In addition, recent research shows contradictory effects of urban areas on bee species, with positive (Fortel *et al.* 2014b; Hernandez *et al.* 2009), neutral (e.g., Baldock *et al.* 2015) and negative effects (e.g. Bates *et al.* 2011; Fortel *et al.* 2014a; Hernandez *et al.* 2009), suggesting that responses to urban areas are highly idiosyncratic. In part, this may be because studies of urban bees often have a shifting baseline; the semi-natural habitats used for comparison are often in a highly altered landscape, so differences seen in diversity may not be as extreme as they would be if the baseline was a truly pristine condition.

The lack of signal to agricultural intensification was, by contrast, a surprise. Our sample

was a relatively even spread of sensitivities (the mean sensitivity, weighted by the inverse of their variance, was not significantly different from 0; results not shown), but there was very little phylogenetic pattern (with λ values close to 0.1). Agricultural intensification may be a non-selective pressure, influencing a number of species irrespective of ecological traits (Fritz & Purvis 2010). Certainly, a previous analysis exploring trait-vulnerability correlations in bees found complex effects with little overall explanatory power (Chapter 3, De Palma *et al.* 2015). A second possibility is that our criteria for assessing intensity of use mix multiple separate pressures; each component might on its own produce phylogenetically patterned responses, but the signal may be lost when they are mixed.

Alternatively, species responses to agricultural intensity may genuinely be more idiosyncratic than to other land-use pressures, diluting the clade-wide phylogenetic patterns. For instance, the effects of agricultural intensity on biodiversity can depend on a number of factors including the field diversity, landscape composition and climatic region (Kennedy *et al.* 2013).

Another possibility is that particularly vulnerable species have already been excluded from the community, as sensitivity to agricultural expansion was strongly phylogenetic patterned. If this is the case, then ecosystem service provision may already be undermined as soon as conversion to agricultural land takes place, regardless of the management practices that are used. This possibility—that the first extinction filter leaves a strong phylogenetic signal whereas the responses of the survivors to subsequent pressures are less patterned—was suggested as an explanation for the lack of phylogenetic signal in mammalian extinction risks in regions with a long history of intense human activity (Fritz *et al.* 2009). It is a worrying possibility in the context of resilience of pollination services, as it suggests that the damage has already been done to agricultural systems; although community-level measures of biodiversity may be enhanced by low-intensity agricultural practices in comparison to more intensively-used systems (Kennedy *et al.* 2013), the composition of communities may have already been irreversibly altered.

4.5.2 ECOLOGICAL CHARACTERISTICS

In a small subset of European bees, species' sensitivities to human-dominated land use in general and to agricultural land were more strongly related to phylogenetic differences than to functional or functional-phylogenetic distances (a combination of functional and phylogenetic differences between species, Cadotte *et al.* 2013). This was somewhat unexpected as previous analyses have revealed that functional traits can significantly influence species sensitivities to a number of land uses and land-use practices in a variety of systems (De Palma *et al.* 2015; Rader *et al.* 2014; Williams *et al.* 2010). Taken with our results, this suggests that species sensitivities are influenced by ecological differences that are not adequately encapsulated by the fairly limited range of traits often used in these analyses, while phylogeny may provides a closer approximation to these unmeasured characteristics (Faith 2013). For instance, the phylogenetic relatedness of bee species can inform the structure of plant-pollinator networks (Chamberlain *et al.* 2014b; Rezende *et al.* 2007); as ecological interactions are lost more quickly than species in a system (Valiente-Banuet *et al.* 2015), the network of a given species could have a strong influence on its resilience to disturbances.

In contrast, functional distances were better at explaining differences in species' sensitivities to agricultural intensification than phylogenetic distances. Although this analysis was based on a fairly small sample size of only 45 species (and 135 with the gap-filled phylogeny), the importance of traits in mediating species' sensitivities to intensive agricultural practices is congruent with some previous work (Rader *et al.* 2014; Williams *et al.* 2010). It is still unclear what drives species' sensitivities to urban areas, however: although phylogenetic distances were the best at explaining species' sensitivities to urban land, they were not far better than random distances. Further research into urban bees is needed to better understand the implications of urbanisation for diversity and ecosystem services (Hernandez *et al.* 2009).

4.5.3 ACCOUNTING FOR UNCERTAINTY

Our results showed marked contrasts depending on whether or not uncertainty in species sensitivity index was accounted for. In some cases, the strength of λ was three fold greater when measurement error was accounted for, as expected by Ives *et al.* (2007). Our results

strengthen the increasing literature which calls for measurement error to be accounted for in phylogenetic analyses (Hardy & Pavoine 2012; Silvestro *et al.* 2015). For instance, Silvestro *et al.* (2015) showed that even small measurement error (10%) can bias results, while Garamszegi & M (2010) showed that accounting for measurement error can drastically change the effect size in comparative analyses.

In addition, manipulating the tree either through rate smoothing or by estimating the placement of missing species could also influence the results, which is why we present results from the original tree as well as adapted trees. Rate-smoothing only slightly changed the size of λ , but for the most part had very little effect. Repeating the analyses on the gap-filled tree (using a birth-death framework to estimate the placement of missing species) can be important in assessing the robustness of conclusions. Species missing from the phylogeny may not be missing at random, potentially biasing the results. In this case, species that were missing tended to have larger intra-specific variation in sensitivity (Appendix C.2). The missing species therefore would have been generally down-weighted in the analyses, which may be why our conclusions did not change depending on the tree used. The only instance where λ was markedly different was for species' sensitivities to urban areas. However, this is not surprising given the very low sample size of species: only 56 species in our dataset matched to the phylogenetic tree.

Uncertainty in our analysis may also arise from the original phylogenetic tree. Scheper *et al.* (2014) argue against using phylogeny in their analysis on the basis that phylogenetic trees are continuously challenged. However, the tree used here is the most comprehensive phylogeny of bees that has been compiled to date and is often consistent with previous work at higher taxonomic levels (Hedtke *et al.* 2013).

4.5.4 IMPLICATIONS

Our results could have important consequences for ecosystem service provision under continuing land-use change. The strong phylogenetic signal in species sensitivities to human-dominated land uses like agriculture means that losses of diversity are likely to be concentrated within only a subset of clades, where they will be correspondingly more severe. Such clustering of losses can greatly reduce the phylogenetic diversity of a system (Díaz *et al.* 2013)

and hence its ability to function under environmental change (e.g. Cadotte *et al.* 2012). If there is similar phylogenetic patterning in species effects on ecosystem function, this could imperil ecosystem service provision even in the absence of other environmental change (Díaz *et al.* 2013). Indeed, non-random losses of species can impact ecosystem functioning in a range of systems (Kremen 2005; Zavaleta *et al.* 2009). On the other hand, there was no significant evidence of phylogenetic signal in species sensitivities to urban land or to more intensive agriculture, suggesting that ecosystem functioning is relatively robust to these changes (Díaz *et al.* 2013). However, conversion to agricultural land may have already taken its toll on the species in the system. In addition, directing conservation efforts in these systems may be difficult; it is likely that a number of species, with varying ecological traits, will be vulnerable.

Our results highlight opportunities to fill gaps in knowledge. For the majority of bee species, even in well-studied regions such as Europe, little is known about their current status or vulnerability to human impacts (Nieto *et al.* 2015) and there are extensive gaps in trait data (Chapter 5). The strong phylogenetic patterning in species' sensitivities to agricultural expansion could help to predict the sensitivity of understudied species, identifying those that are most vulnerable or resistant so that conservation actions can be effectively prioritised. For instance, many species of bumblebees showed positive, if any, response to agricultural land, but were often negatively influenced by increasing agricultural intensity (Appendix Fig. C.4). This combination of results suggests that these species are well maintained in these systems, but only under certain management practices. However, our analyses are not based on a random sample of species (Meyer *et al.* 2015), which could limit transferability to other taxa. Non-random sampling of species is an inherent difficulty in analyses such as these (e.g. Boakes *et al.* 2010, showed that publications on Galliformes have increasingly focussed on threatened species over the last few decades). This problem may be exacerbated when incorporated with functional trait and phylogenetic information: species with both trait and genetic data may be more common, and so easily studied, species (Mace *et al.* 2003). Ideally, the results would be validated using an independent sample of species sensitivities; however, this is beyond the scope of this study.

Nevertheless, our results provide a basis for which to make, test, and inform predictions about species sensitivities, which could eventually have important benefits for conservation

prioritisation, as well as identifying land-use pressures that may most impact pollination services. However, impacts on real systems will not simply depend on which species are most sensitive, but also their abundances. Analyses of how these results scale up to changes in abundance-weighted phylogenetic diversity of communities will be essential to identify spatial patterns in diversity and potential areas of pollination deficit (Thuiller *et al.* 2011).

CHAPTER 5

Land-use impacts on taxonomic, functional and phylogenetic diversity of bee communities in Europe

5.1 ABSTRACT

Agricultural intensification and urbanisation are important drivers of biodiversity change in Europe. The impact of these changes on bee communities has been of particular concern for researchers and policy makers alike; bees can be adversely impacted by human-dominated land uses and can potentially indicate wider ecosystem health. Different aspects of community diversity may be more or less sensitive to these pressures, however, as well as independently influencing ecosystem service provision (pollination). To obtain a comprehensive understanding of human impacts on European bee diversity, it is important therefore to assess multiple, complementary indices of diversity. We collated data on bee community diversity from the published literature and supplemented them from the PREDICTS database (www.predicts.org.uk). We used Rao's Quadratic Entropy to calculate comparable measures of taxonomic, functional and phylogenetic diversity from site-level data on species abundances, using seven ecological trait variables and a comprehensive phylogenetic framework (using a birth-death polytomy resolver). We use data from 1446 sites and 337 species in Europe to investigate how taxonomic, functional and phylogenetic diversity of bee communities vary with a variety of human pressures including land-use class, land-use intensity, human population density and proximity to roads. We combine these models with statistically downscaled

estimates of land use in 2005 to estimate and—at a scale of 1km²—map the losses in diversity, relative to a natural or semi-natural baseline, and compare losses to date of taxonomic, functional and phylogenetic diversity. We found that all facets of diversity were generally lower in more intensive cropland and pasture than in secondary vegetation. However, while increasing human population density correlated with lower functional and phylogenetic diversity in some land uses, there was no relationship with taxonomic diversity. These differences led to marked spatial mismatches in losses; for instance, while taxonomic diversity increased slightly in urban areas, high population densities led to losses in functional and phylogenetic diversity. These results highlight the importance of exploring multiple measures of diversity.

5.2 INTRODUCTION

Bees are widely considered to be the most important group of pollinators, especially in temperate systems (Danforth *et al.* 2006; Kevan & Baker 1983), although the importance of other insects to pollination services has probably been underestimated (Orford *et al.* 2015). Declines in bee community diversity as a result of human-dominated land use could therefore have serious consequences for pollination services. Agricultural intensification and abandonment as well as urbanisation are important drivers of biodiversity change in Europe (Stoate *et al.* 2009; Verburg *et al.* 2006). Bees can be adversely impacted by human-dominated land uses, such as intensively-managed cropland (De Palma *et al.* 2015; Forrest *et al.* 2015). No single measure of assemblage diversity can capture the full breadth of either ecosystem service provision or sensitivity to land-use change, however.

Taxonomic diversity of pollinators can enhance crop yield and stability and enhance plant reproductive success (Albrecht *et al.* 2012; Rogers *et al.* 2014), but other aspects of assemblage diversity can also influence ecosystem service provision. Functionally diverse bee communities help to maintain plant diversity (Fontaine *et al.* 2006), enhance plant reproduction (Albrecht *et al.* 2012) and increase the volume and stability of crop yields (Hoehn *et al.* 2008). Higher phylogenetic diversity can also enhance ecosystem service provision (e.g. ecosystem stability in plants: Cadotte *et al.* 2012), although little evidence is available for its impact on pollination services. As functional traits are often phylogenetically con-

served (Freckleton *et al.* 2002), phylogenetic diversity can relate to the functional diversity of communities (Srivastava *et al.* 2012). However, phylogenetic diversity may represent ecological differences between species more accurately than functional diversity does (Srivastava *et al.* 2012, Chapter 4) and can also reflect interspecific interactions (e.g. between plants and pollinators, Rezende *et al.* 2007), so may not be interchangeable with functional diversity (Flynn *et al.* 2011, Chapter 4).

Although these facets of diversity are positively correlated to each other, they may respond differently to pressures. For example, Forrest *et al.* (2015) showed that while relatively high species diversity could be maintained in low-intensity cropland, functional diversity was reduced relative to natural habitat. To obtain a comprehensive understanding of human impacts on biodiversity, it is important therefore to assess multiple, complementary indices of diversity (Vandewalle *et al.* 2010). So far, however, little research has explored whether different facets of bee diversity show similar responses to land use and related pressures, or whether the losses in diversity are congruent across space.

We use data from 1446 sites and 337 species to assess differences in taxonomic, functional and phylogenetic diversity across land uses in Europe. While previous analyses have found that species' sensitivities to land use can be influenced by functional traits and phylogeny (Chapter 3 and 4), it is still unclear how these effects scale up to influence the diversity of whole communities. We cross resulting models with fine-scale estimates of land use across Europe to estimate the losses of bee diversity, relative to an undisturbed baseline, in order to explore whether the losses in different facets of diversity are congruent across space.

5.3 METHODS

5.3.1 BIODIVERSITY DATA

Data were extracted from the PREDICTS database, the details of which have been published previously (See Hudson *et al.* 2014). Briefly, data were sought from ecological surveys where bee species abundance and occurrence were sampled comparably in multiple sites facing different land-use pressures (See Chapter 2 for details). For this analysis, data were only included if the entire bee community was sampled; i.e., studies where they did not only target

a single species or a small subset of species.

5.3.2 LAND-USE DATA

For each site in the dataset, we classified the land use and use intensity based on information in the associated paper and using the scheme described in Hudson *et al.* (2014) (See Chapter 2). Land use was classified as primary vegetation, secondary vegetation (young, intermediate, mature and indeterminate age), cropland, pasture or urban. The use-intensity scale is a qualitative, coarse measure of human disturbance (three levels: low, medium and high) (Hudson *et al.* 2014). As not all combinations of land use and intensity had enough datapoints for robust modelling, we collapsed levels as appropriate. This resulted in the following levels of combined land use and intensity (hereafter LUI): (semi-) natural vegetation (including both primary and secondary vegetation, 121 sites); pasture (76 sites); low-intensity cropland (208 sites), medium-intensity cropland (417 sites) and high-intensity cropland (577 sites); and urban (47 sites). In addition, we use global layers to estimate, for each site, the human population density (Balk *et al.* 2006; CIESIN *et al.* 2011), for the pixel (30 arc seconds) containing the site. The same was done for proximity to nearest road (Center for International Earth Science Information Network *et al.* 2013) after a gridded map was created by Tim Newbold (Python code written for the *arcpy* module of ArcMap Version 10.0: ESRI 2011), based on the original vector maps.

5.3.3 LAND-USE MAPS

The maps of land use were generated by Andrew Hoskins and Simon Ferrier (CSIRO), by downscaling the harmonized land-use dataset for 2005 (Hurt *et al.* 2011). Briefly, the harmonized land-use data describe the proportion of each 0.5° grid cell in each of five land uses (primary vegetation, secondary vegetation, cropland, pasture and urban). First, a generalised additive model (quasibinomial errors and logistic link) was used to analyse the land-use estimates (0.5°) as a function of nine explanatory variables (30 arc-seconds resolution). These explanatory variables were evapotranspiration, temperature, precipitation, topographic wetness, slope, soil carbon, accessibility to humans, human population density and land cover. The fine-grained fitted values were then taken from the generalised additive

models and were rescaled multiplicatively until the aggregated mean for each 0.5° grid cell matched the estimates from the harmonized land-use data. The rescaled fitted values were then subjected to a constrained optimization algorithm to generate estimates for all five land uses that summed to 1 within each grid cell. The final estimates were entered back into the generalised additive models as response variables, and the whole procedure was iterated until a convergence criterion was met. Grid cells under ice or water were excluded from the analysis, and were masked from the final land-use maps (Ferrier *et al.*, in prep.).

Maps of land use and intensity were derived by combining the above land-use class maps (CSIRO) and agricultural use-intensity maps (1km² resolution for the year 2000: Temme & Verburg 2011), after reprojecting the land-use and human-population density maps to an Albers equal area projection (resolution of 1km²). The land use maps had multiple values per grid square for the percentage covered by each land-use class. The maps of agricultural use-intensity only had one value for each grid square, pertaining to whether the cell corresponded to extensive pasture, intensive pasture, light, moderate or intensive cropland, or other land uses. These were easily matched to our use-intensity definitions, becoming: low-, medium- and high-intensity cropland. As the agricultural use-intensity data were available only for the EU27 Countries, we restricted all datasets to this political boundary. To combine the maps, we used the use intensity maps to classify the intensity of cropland where grid cells overlapped with the land-use class maps. There were many grid squares containing a very small amount of cropland that were not classified as such in the use intensity maps. We classified these as low-intensity; such grid squares generally contained too little agricultural land for PREDICTS to have classified it as high intensity.

5.3.4 TRAIT DATA

Trait data were collected by Stuart P.M. Roberts and Michael Kuhlmann from a variety of sources, including published and unpublished literature. Morphometric measurements were taken from museum specimens. Trait data pertained to flight season and foraging range (body size), reproductive strategy and phenology, dietary breadth and nesting strategy (See Chapter 3 for details). Thirty seven species had missing data; 34 species had no trait data at all. We used missForest (Stekhoven & Buhlmann 2012) to impute missing trait information,

including phylogenetic eigenvectors (Diniz-Filho *et al.* 2012) as predictor variables (using the phylogenetic tree published by Hedtke *et al.* 2013). The normalised root mean squared error for predictions of continuous variables was 0.164, and the proportion of falsely classified entries for categorical variables was 0.046 (numbers close to zero indicate a good predictive ability, while numbers closer to one indicate poor predictive ability). This method was used as it has recently been shown to be an accurate method of imputing trait data when phylogenetic information is available and when categorical as well as continuous traits are used (Penone *et al.* 2014). Because phylogeny is used in the imputation, functional diversity is likely to be biased towards phylogenetic diversity, relative to what a complete data set might show.

5.3.5 PHYLOGENETIC TREE

A recently published phylogeny of bee species includes some, but not all, of the species in our dataset (Hedtke *et al.* 2013). Incompletely resolved trees may bias estimates of phylogenetic diversity. In addition, species that are missing from the phylogenetic tree can have greater intra-specific variation in their response to land-use pressures (See Chapter 4). We therefore used a birth-death polytomy resolver (pastis package, Thomas *et al.* 2013) and MrBayes (version 3.2, Ronquist *et al.* 2012) to estimate the placement of these species given their taxonomic affinities, producing 1000 complete trees (See Chapter 4 for details). We randomly sampled 100 trees for use in further analyses to ensure that results were robust to species placement; not accounting for phylogenetic uncertainty can lead to incorrect estimates of precision (de Villemereuil *et al.* 2012).

5.3.6 RESPONSE VARIABLES

We used Rao's quadratic entropy, Q (Rao 1982)—an abundance-weighted measure of diversity—to calculate the taxonomic, functional and phylogenetic diversity of communities:

$$Q = \sum_{i,j} d_{ij} p_i p_j \quad (5.1)$$

where d_{ij} is the distance—whether taxonomic, functional or phylogenetic—between species i and j , and p_i and p_j are their relative abundances.

Rao's Q provides a useful framework for assessing and comparing trends in taxonomic, functional and phylogenetic diversity: each facet is calculated by applying Equation 5.1 to the relevant distance matrix. For taxonomic diversity, the dissimilarity between each species is equal to one (i.e., each species is considered fully distinct from all others). Gower's dissimilarity matrix (as suggested by Ricotta & Moretti 2011) was calculated for functional diversity as this method allows quantitative as well as categorical traits (Gower 1971). The similarity index was transformed following Debastiani & Pillar (2012, SYNCSEA package). For phylogenetic diversity, the dissimilarity between species is the mean distance to the nearest common ancestor (picante package, Kembel *et al.* 2010). We calculated the mean phylogenetic diversity across the sample of 100 trees. All diversity measures were then transformed into effective numbers, using the linear transformation suggested by Jost (2006); for taxonomic diversity, this equates to the inverse Simpson's Index, which can be thought of as the number of common species (Hill 1973).

Previous work has looked in detail into how Rao's Q behaves as a measure of functional diversity. This metric has been shown to respond to environmental change in a number of animal groups, and can complement taxonomic diversity measures (Vandewalle *et al.* 2010). In addition, the metric is closely related to other functional diversity measures, such as Functional Dispersion (Laliberté & Legendre 2010), Functional Diversity (Scherer-Lorenzen *et al.* 2007) and, to a lesser extent, Functional Richness (Laliberté & Legendre 2010; Mouchet *et al.* 2010).

5.3.7 ANALYSIS

Using R statistical software (version 3.1.2 R Core Team 2014), we first tested the correlation between taxonomic diversity and the other measures of diversity among sites within studies. Mixed-effects models were used including functional or phylogenetic diversity as response variables, log-transformed taxonomic diversity and UN subregion as the explanatory variables (including interaction), and random effects to account for the non-independence of data due to differences in sampling methodology and biogeography ('study') and the spatial structure of sites ('block'). The best random-effect structure was first assessed by comparing Akaike's Information Criterion for all possible random effect structures, which included random slopes

(within ‘study’) (Zuur *et al.* 2009). Then, the best fixed-effects structure was assessed using backwards stepwise model simplification based on likelihood ratio tests, with models fitted using Maximum Likelihood (Crawley 2007; Zuur *et al.* 2009). We used marginal R^2_{glmm} values (MuMIn package, Barton 2013) to determine how much variance in diversity was explained by taxonomic diversity.

We then analysed taxonomic, functional and phylogenetic alpha diversity as a function of land use and intensity (LUI), distance to nearest road and human population density using Bayesian linear mixed effects models (blme package, Chung *et al.* 2013). UN subregion was considered as a fixed effect to control for differences in baseline diversity across geographic regions, as the inclusion of this geographic variable can improve the predictive and explanatory power of models (See Chapter 6). We considered all two-way interactions between land use and the other variables. Site-level taxonomic diversity was log-transformed prior to analysis in order to normalise residuals. Human population density was $\log(+1)$ -transformed to improve normality and continuous variables were scaled to reduce collinearity. Full models were assessed for multicollinearity using generalised variance inflation factors (GVIFs, Zuur *et al.* 2009), which were all below 4.

The initial random effects structure was as described above. The best random and fixed effect structures were determined as before. Type II anova tables were computed for the final model (car package, Fox & Weisberg 2011), and significance of coefficient estimates were assessed by calculating the bootstrapped confidence intervals for 1000 bootstrap samples; if bootstrapped confidence intervals do not cross zero, the coefficient is taken to be significant.

We used the coefficient estimates from these models (fitted using Restricted Maximum Likelihood) to determine the loss in biodiversity relative to the undisturbed baseline. The baseline is taken to be (semi-)natural vegetation with a human population density of zero. This approach is similar to that used by Reidsma *et al.* (2006) to derive a measure of ‘ecosystem quality’, although their measure relied on dose-response relationships between biodiversity and agricultural intensity synthesised through a literature review, while our approach uses direct analysis of preliminary data from Europe. We also show the spatial mismatch between diversity measures. We modelled functional and phylogenetic diversity as a function of taxonomic diversity using ordinary least squares regression, and mapped the residuals of

these models. We then modelled these residuals against one another, to explore the spatial mismatch between losses in functional and phylogenetic diversity, after correlations with taxonomic diversity had been accounted for.

5.4 RESULTS

Taxonomic diversity explained over 75% of the variation in both functional ($\chi^2 = 569.25$, $df = 1$, $p < 0.0001$) and phylogenetic diversity ($\chi^2 = 741.94$, $df = 1$, $p < 0.0001$). There were positive relationships between all diversity measures, although the slope varied among studies. Fixed effects and random effects together accounted for over 85% of the variation in both functional and phylogenetic diversity.

Taxonomic, functional and phylogenetic diversity were all significantly related to land use and intensity. Taxonomic diversity was significantly reduced in pasture and both medium- and high-intensity cropland relative to (semi-)natural vegetation (Fig. 5.1 and Appendix Table D.1). The response of functional and phylogenetic diversity to land-use class and intensity was more complex; the response depended on the level of human population density (Fig. 5.2). Functional diversity declined significantly more strongly with human population density in medium-intensity cropland than in more natural land uses (estimate = -4.04, bootstrapped confidence intervals, bCI = -7.16, -0.84). At mean levels of human population density, functional and phylogenetic diversity were significantly lower in pasture and both medium- and high-intensity cropland relative to (semi-)natural vegetation (Appendix Tables D.2 and D.3). Distance to roads was not retained in any of the models.

There was particularly poor spatial congruence between taxonomic diversity and functional diversity (Fig. 5.3b); in some cases, the losses of taxonomic diversity were 50 percentage points (pp.) more severe, or 9 pp. less severe, than the losses in functional diversity. Similarly, the loss of taxonomic diversity was up to 40 pp. more severe and 18 pp. less severe than losses in phylogenetic diversity (Fig. 5.3d). In particular, urban areas that showed high taxonomic diversity tended to have losses in other aspects of diversity. The differences between the losses of functional and phylogenetic diversity were less marked. However, even after accounting for the correlation with taxonomic diversity, there were still spatial mismatches in

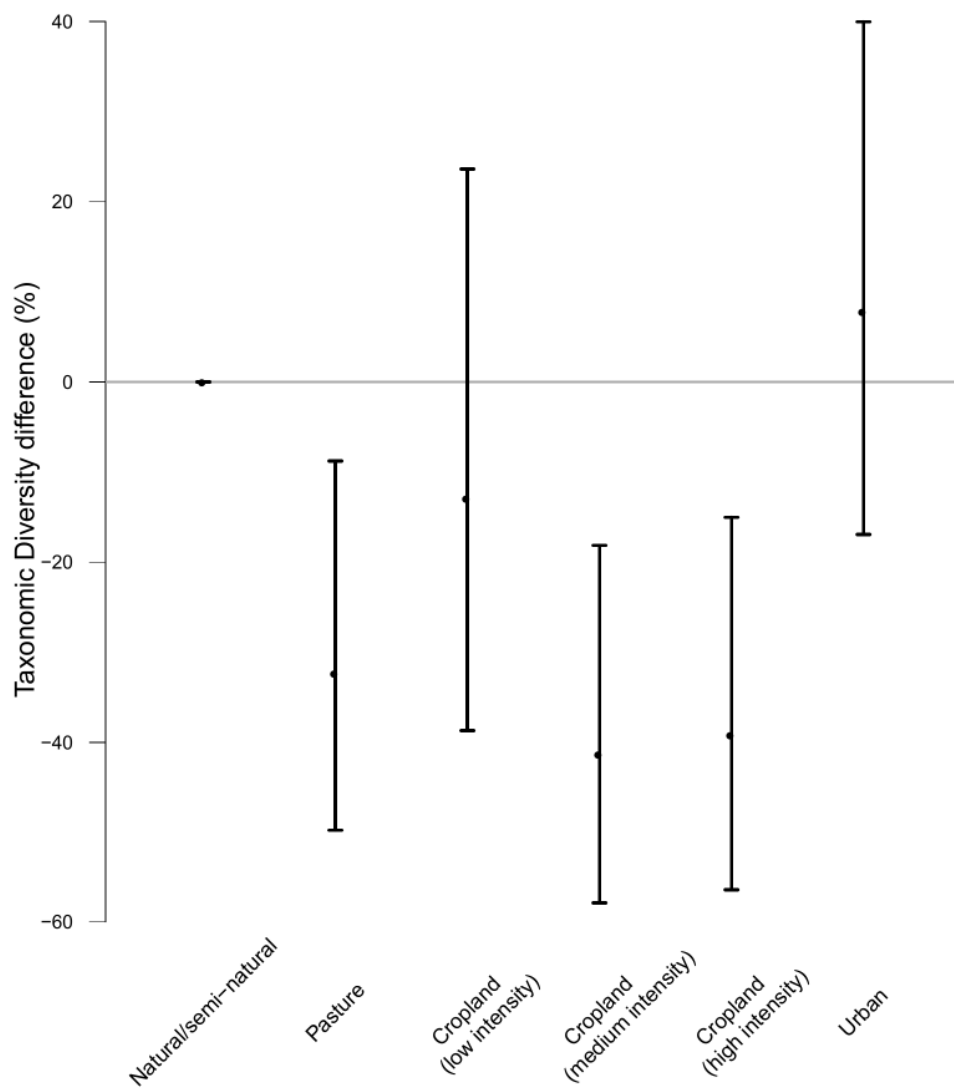


Figure 5.1: Percentage difference in taxonomic diversity in different land uses, relative to the natural/semi-natural baseline

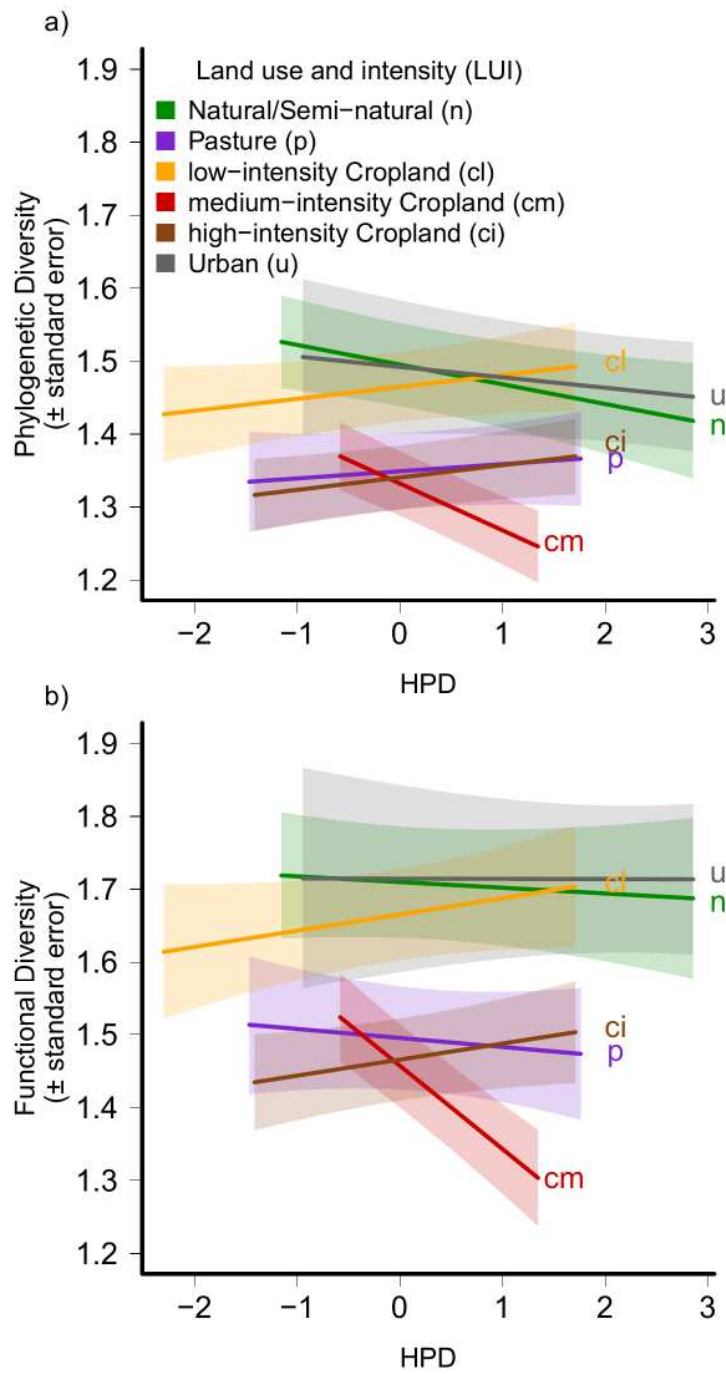


Figure 5.2: Relationship of a) Phylogenetic diversity and b) Functional diversity with human population density (log-transformed and scaled) in different land uses

losses of phylogenetic and functional diversity (Fig. 5.3e).

The average losses of local diversity varied considerably across countries (Table 5.1). Average losses of local functional and phylogenetic diversity were much lower than for other diversity measures, as only two countries have lost more than 10% of diversity on average. In contrast, 19 countries have lost more than 10% of their average local taxonomic diversity.

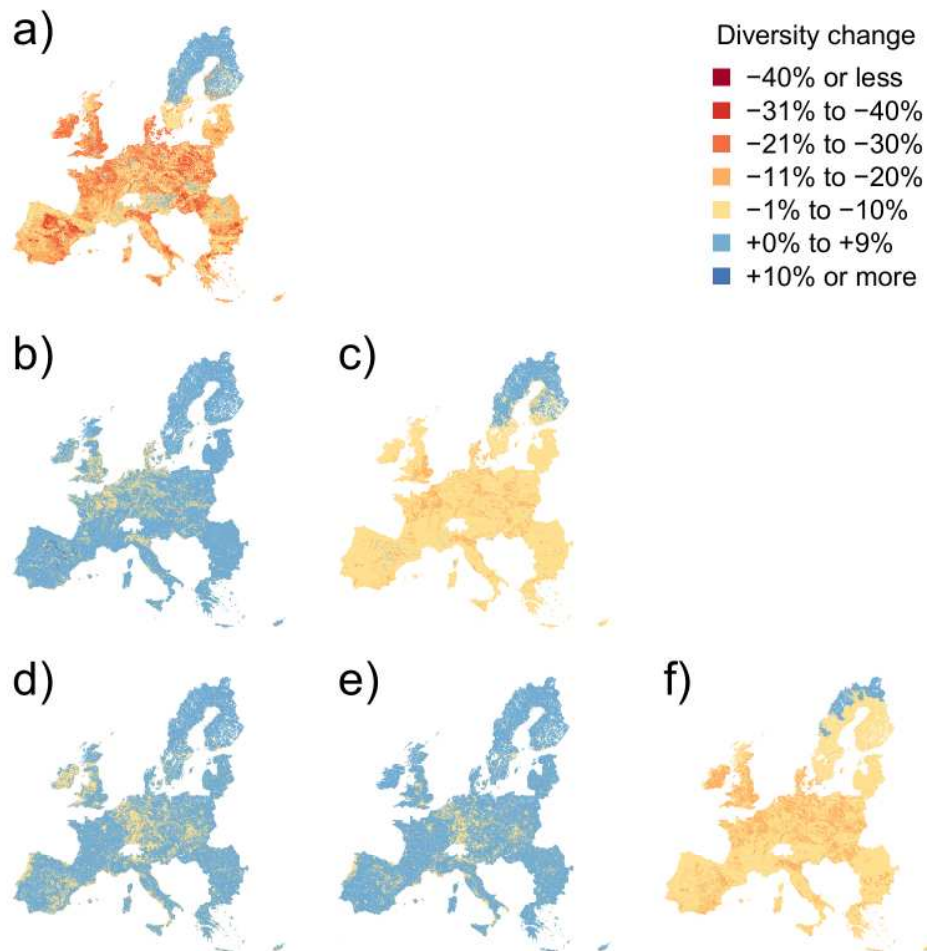


Figure 5.3: Change in a) taxonomic, c) functional and f) phylogenetic diversity across Europe. A value of 0 would indicate an intact community (similar diversity to natural/semi-natural vegetation); negative numbers indicate a loss in diversity, positive numbers a gain. Panel b) shows the residuals of a model between a) and c), panel d) shows the residuals of a model between a) and f), and panel e) shows the residuals of a model between b) and d). These maps were produced using Alber's equal area conical projection.

Table 5.1: Mean losses in diversity ($\pm$ standard error) in each EU27 country. TD = Taxonomic Diversity, FD = Functional Diversity, PD = Phylogenetic Diversity.

Country	Mean loss in TD ($\pm$ standard error)	Mean loss in FD ($\pm$ standard error)	Mean loss in PD ($\pm$ standard error)
Austria	-8.3 ($\pm$ 9.02)	-4.1 ($\pm$ 3.06)	-7.5 ($\pm$ 2.67)
Belgium	-13.2 ($\pm$ 8.58)	-6.2 ($\pm$ 3.25)	-9.8 ($\pm$ 2.25)
Bulgaria	-12.5 ($\pm$ 8.85)	-5.2 ($\pm$ 2.7)	-8.5 ($\pm$ 2.33)
Cyprus	-13.1 ($\pm$ 6.39)	-5.9 ($\pm$ 2.5)	-9.2 ($\pm$ 2.64)
Czech Republic	-14.3 ($\pm$ 10.11)	-6.2 ($\pm$ 3.76)	-9.3 ($\pm$ 3.04)
Hungary	-18.9 ($\pm$ 10.04)	-7.4 ($\pm$ 3.49)	-10.4 ($\pm$ 2.56)
Lithuania	-12.3 ($\pm$ 6.72)	-5.2 ($\pm$ 1.77)	-8.5 ($\pm$ 1.74)
Latvia	-9.8 ($\pm$ 6.39)	-4.2 ($\pm$ 1.85)	-7.1 ($\pm$ 2.25)
Luxembourg	-10.7 ($\pm$ 6.25)	-5.1 ($\pm$ 2.24)	-8.7 ($\pm$ 1.68)
Netherlands	-15.5 ($\pm$ 8.97)	-7.2 ($\pm$ 3.27)	-10.6 ($\pm$ 2.03)
Poland	-16.6 ($\pm$ 10.56)	-6.8 ($\pm$ 3.55)	-9.8 ($\pm$ 2.71)
Malta	-9.1 ($\pm$ 3.98)	-4.4 ($\pm$ 1.88)	-8.8 ($\pm$ 1.34)
Romania	-11 ($\pm$ 7.01)	-4.9 ($\pm$ 2.26)	-8.3 ($\pm$ 2.15)
Slovakia	-11.8 ($\pm$ 10.83)	-5.4 ($\pm$ 3.97)	-8.5 ($\pm$ 3.32)
Slovenia	-7.2 ($\pm$ 7.57)	-3.8 ($\pm$ 3.07)	-6.9 ($\pm$ 3.07)
Germany	-14.3 ($\pm$ 9.89)	-6.6 ($\pm$ 3.62)	-9.9 ($\pm$ 2.51)
Denmark	-21 ($\pm$ 8.8)	-8.6 ($\pm$ 3.69)	-11.2 ($\pm$ 2.69)
Estonia	-9 ($\pm$ 5.47)	-4.2 ($\pm$ 1.9)	-7 ($\pm$ 2.34)
Spain	-14.7 ($\pm$ 9.29)	-5.7 ($\pm$ 3.09)	-8.9 ($\pm$ 2.95)
Finland	-1.5 ($\pm$ 4.09)	-1 ($\pm$ 1.26)	-2.7 ($\pm$ 2.23)
France	-14 ($\pm$ 8.77)	-6.1 ($\pm$ 3.31)	-9.1 ($\pm$ 2.76)
United Kingdom	-17.3 ($\pm$ 8.46)	-7.6 ($\pm$ 3.19)	-10.6 ($\pm$ 2.7)
Greece	-13.7 ($\pm$ 8.03)	-5.8 ($\pm$ 2.92)	-8.8 ($\pm$ 2.74)
Ireland	-19.9 ($\pm$ 5.74)	-8.5 ($\pm$ 2.22)	-11.6 ($\pm$ 2.18)
Italy	-13.1 ($\pm$ 8.83)	-5.9 ($\pm$ 3.54)	-9.1 ($\pm$ 2.79)

Sweden	-2 ($\pm$ 5.07)	-1.3 ($\pm$ 1.97)	-2.9 ($\pm$ 2.8)
Portugal	-9.9 ($\pm$ 6.52)	-4.7 ($\pm$ 2.23)	-8.1 ($\pm$ 2.04)

5.5 DISCUSSION

Species' responses to human impacts are extremely varied (Cariveau & Winfree 2015); while some species benefit from human-dominated land uses, others are very intolerant of land-use change (Banaszak-Cibicka & Zmihorski 2012; Bates *et al.* 2011; Cariveau *et al.* 2013; De Palma *et al.* 2015). However, our work has shown that, despite this heterogeneity, bee community diversity is significantly reduced in human-dominated land uses relative to natural and semi-natural vegetation. This may in part explain why some studies have found that diversity in species responses does not stabilize pollination service provision (Cariveau *et al.* 2013). As the abundance-weighted diversity measures used are designed to be most influenced by dominant species in the community (Bello *et al.* 2007; Leinster & Cobbold 2012), our results suggest that even abundant, common species—likely to be the most economically important for pollination service provision (Kleijn *et al.* 2015; Winfree *et al.* 2015)—are also responding negatively to human impacts.

5.5.1 RESPONSES OF BEE DIVERSITY TO LAND USE AND RELATED PRESSURES

Our analyses revealed that bee taxonomic diversity was significantly reduced in pasture and higher intensity cropland, but was generally maintained in low-intensity agricultural land. These results suggest on average a conservation benefit of organic cropland, with relatively high levels of functional and phylogenetic diversity even in densely populated areas. Indeed, previous research has found that less intensive agricultural practices result in higher species (Tuck *et al.* 2014b) and functional richness (Rader *et al.* 2014) of bees, particularly where the surrounding landscape is inhospitable (Kennedy *et al.* 2013).

Urban areas also maintained relatively high diversity. Although our number of urban areas was relatively small, this result is consistent with previous findings that bee abundance and species richness are similar in urban areas and nature reserves (Baldock *et al.* 2015). However,

human population density significantly influenced functional and phylogenetic diversity in different land uses (Fig. 5.2). In particular, higher human population density reduced the functional and phylogenetic diversity found in lightly-used cropland. This suggests that although urban areas may help maintain taxonomic diversity, functional and phylogenetic diversity in the surrounding landscape may be at risk, even where agricultural practices are less intensive. These findings are of particular importance as, in the coming years, urbanisation is likely to be an important driver of changes to biodiversity and ecosystem service provision in Europe (Eigenbrod *et al.* 2011). A sprawling pattern of urbanisation could reduce agricultural productivity (Eigenbrod *et al.* 2011); our results suggest that human population growth in agricultural areas could also be more detrimental to bee diversity than increasing the density of existing urban areas (Sushinsky *et al.* 2013), potentially causing further declines in agricultural productivity.

5.5.2 LOSSES OF LOCAL BEE DIVERSITY ACROSS EUROPE

The significant effects of land use, intensity and human population density on bee diversity suggest strong spatial patterns of loss across Europe. Relative to the undisturbed baseline, we infer marked average losses in local taxonomic diversity throughout the EU27, particularly in high-intensity agricultural landscapes. Over half of the countries across the region have lost more than 10% of their average local taxonomic diversity. Countries in Western Europe have seen particularly high impacts, where much of the land has is covered by intensive cropland and pastures, whereas Sweden and Finland were generally only minimally impacted (note that we do not attempt to estimate changes in overall gamma diversity in countries or across Europe). However, it is unclear whether there is a threshold of bee diversity beyond which pollination services are greatly imperilled, or at what spatial scale such thresholds are most relevant (Brook *et al.* 2013; Mace *et al.* 2014).

The losses in taxonomic diversity tended to be more extreme than losses in functional or phylogenetic diversity. However, because the measure of taxonomic diversity assumes that all species are maximally (and equally) dissimilar to one another, this is expected; if all species in the community were equally distinct in terms of their ecological traits or phylogenetic distance, the diversity would be equal to taxonomic diversity. Therefore, the fact that losses

in taxonomic diversity tend to be more extreme than losses in functional and phylogenetic diversity suggests that communities may be losing ecologically similar and closely related species. This is expected, as previous research has shown that ecological traits mediate species responses to human impacts (Chapter 3), and that there is strong phylogenetic signal in bee species' sensitivity to some land-use classes (Chapter 4). In addition Nee & May (1997) showed that phylogenetic diversity can be relatively well maintained even if most species are lost.

5.5.3 CONGRUENCE BETWEEN DIFFERENT FACETS OF DIVERSITY

Importantly, although taxonomic diversity explained over 75% of the variation in functional and phylogenetic diversity, the three measures did not always respond in the same way to land use and related pressures. Therefore, while different facets of diversity are strongly related (as has been shown previously by Stevens & Tello 2014), taxonomic diversity is not an effective surrogate for functional or phylogenetic diversity when considering responses to human impacts (Cisneros *et al.* 2015). This has implications for how conservation actions are prioritised and evaluated, as taxonomically diverse assemblages may be phylogenetically and functionally impoverished; in some areas, losses in phylogenetic diversity at times almost 20 percentage points greater than losses in taxonomic diversity.

There was fairly good congruence between losses functional and phylogenetic diversity, although changes in phylogenetic diversity were slightly less extreme. This suggests that phylogenetic trees can be informative even with incomplete genetic information. As trait data are time-consuming to obtain and still have many gaps, these results imply that phylogenetic diversity may be an efficient and effective alternative to functional diversity. However, it is unclear whether functional and phylogenetic diversity have similar effects on ecosystem service provision. Also, an important caveat here is that the functional and phylogenetic diversity of communities were not fully independent; phylogeny was used to impute missing trait information for 71 of the 337 species.

5.5.4 LIMITATIONS OF THE STUDY AND OPPORTUNITIES FOR FURTHER RESEARCH

Our estimates of diversity loss may be underestimates as we do not account for biotic lag, although evidence for extinction lags exist for a number of taxonomic groups in Europe, including dragonflies, grasshoppers and plants (Dullinger *et al.* 2013). Incorporating land-use history may therefore help to identify where extinction lags are likely to be present and so where our estimates may be incorrect (Cusser *et al.* 2015).

Landscape context can be an important driver of bee diversity (Carré *et al.* 2009; Montero-Castaño & Vilà 2012; Tschardt *et al.* 2012). We did not explore the effect of landscape context on bee community diversity, as it may be less important in temperate regions than in other areas (Kennedy *et al.* 2013). However, this offers a promising avenue of further research.

It is likely that we have overestimated the benefit of primary vegetation for bee diversity. In temperate regions, wooded areas are often not particularly beneficial for bees (Winfree *et al.* 2007b) and so diversity often increases with the presence of low amounts of disturbance that open up habitats. However, our sample size for primary vegetation was too small to estimate diversity in these areas.

Our study is limited to Europe; a highly altered, intensively-managed landscape. Our conclusions are therefore unlikely to be generalizable to other less altered systems (Winfree 2013, Chapter 6). Further collation of trait and genetic data on bee species across the globe will be necessary to explore the losses of local diversity in other regions.

5.5.5 CONCLUSION

We have provided the first assessment of how taxonomic, functional and phylogenetic diversity of bee communities is impacted by land-use class, land-use intensity and human population density in Europe. We show that responses to human impacts—and estimated losses across Europe—are not equivalent across these facets of diversity. This research highlights the need to explore multiple measures of diversity, to gain a comprehensive understanding of biodiversity loss and the potential implications for ecosystem functioning.

CHAPTER 6

Predicting bee community responses to land-use changes: effects of geographic and taxonomic biases

6.1 ABSTRACT

Land-use change and intensification threaten bee populations worldwide, potentially imperilling pollination services. Global models are needed to better characterise, project, and perhaps mitigate the responses of bees to these human impacts. The available data are, however, geographically and taxonomically unrepresentative—most data are from bumblebees in North America and Western Europe—raising concerns that model results may not be generalizable to other regions and taxa. To assess whether the geographic and taxonomic biases of data could undermine use of models for conservation policy, we have collated from the published literature a global dataset of bee diversity at sites facing land use change and intensification, and assess whether bee responses to land-use class and intensity vary across 11 regions (Western, Northern, Eastern and Southern Europe; North, Central and South America; Australia and New Zealand; South East Asia; Middle and Southern Africa) and between bumblebees and other bees. Our analyses highlights strong regionally-based responses of total abundance, species richness and Simpson's diversity to land-use classes and intensities, caused by regional variation in the sensitivity of species and potentially in the nature of threats. These results suggest that global extrapolation of models based on geographically and taxonomically restricted data may underestimate the true uncertainty,

increasing the risk of ecological surprises.

6.2 INTRODUCTION

Bees are the most important group of pollinators of economic crops (Food and Agriculture Organization of the United Nations 1995; Garibaldi *et al.* 2011b; Kevan & Baker 1983). They are highly specialized, with both larvae and adults relying on floral products such as pollen and nectar (Kevan & Baker 1983). Human impacts can reduce the diversity of pollinator assemblages (Potts *et al.* 2010; Winfree *et al.* 2009) and therefore can impact pollination efficiency and provision: a particular concern in agricultural settings, as over 35% of the volume of crops produced globally depend upon animal pollination to some extent (Klein *et al.* 2007). Pollinator shortages can lead to reduced crop quality and yield (Garratt *et al.* 2014; Richards 2001), with potentially large economic impacts (Kevan & Phillips 2001). There has therefore been much research into responses of bee communities to human impacts, such as land-use change and intensification.

A number of syntheses have attempted to identify general trends in the response of bees to human impacts (Kennedy *et al.* 2013; Winfree *et al.* 2009). However, their datasets have often been geographically limited, with the majority of data arising from North America and Western Europe (Archer *et al.* 2014). The geographic patterns of bee decline and diversity are not understood sufficiently well to ensure that such generalisations are valid (Archer *et al.* 2014; Mayer *et al.* 2011). If species' responses to disturbance vary among regions, geographically-restricted models will be inadequate to support broad conclusions. The consequences of basing management strategies on extrapolations from such models could be severe, as many under-studied regions have a high economic dependency upon animal-pollinated crops (Archer *et al.* 2014; Gallai *et al.* 2009) and may generally have limited governmental capacity to adapt to environmental changes (Mora *et al.* 2013).

Geographic variation in bee community responses could arise because differences in land-use history, context and practices mean that the threats facing assemblages differ across regions. Species subject to very recent disturbance may be more vulnerable, whereas extinction filters (Balmford 1996; Fritz *et al.* 2009) may have already removed many susceptible

species from landscapes with a long history of current pressures, such as in North-western Europe where the landscape has been used intensively for centuries. Extinction debt may make matters worse still, if the full impact of land-use changes is not yet evident (Dullinger *et al.* 2013; Kuussaari *et al.* 2009). In addition, differences in landscape composition across regions can influence species' responses. For instance, Winfree *et al.* (2009) found that habitat loss and fragmentation significantly affected bee communities, but only in areas where little natural habitat still remained.

Bee community responses may also vary regionally because community composition varies geographically. Taxa can differ in their intrinsic susceptibility to land-use change and intensification, through having different functional response traits (De Palma *et al.* 2015; Rader *et al.* 2014; Williams *et al.* 2010), the distribution of which within a community can affect resilience to pressures (Moretti *et al.* 2009). A geographic bias towards North America and Western Europe has also resulted in a taxonomic bias; for instance, bumblebees (Apidae: *Bombus*) are particularly diverse in these areas, whereas large areas of the world have no native bumblebee species (e.g., most of Africa and Australasia). In addition, bumblebees are large, often abundant species with long flight seasons, making them relatively easy to sample and, in many cases, to identify. Bumblebees may be more sensitive than other species due to their ecological traits and habitat requirements (Colla & Packer 2008), which have been shown to influence responses to human impacts and vulnerability to decline (Bartomeus *et al.* 2013a; Williams *et al.* 2009). In addition, bumblebees have shown clearer declines than other bees in North America (Bartomeus *et al.* 2013a) and some European countries (Carvalho *et al.* 2013), so they may be atypical of broader bee diversity.

We compiled a global dataset of bee diversity from published sources of bee assemblages in sites differing in pressures such as land use, and used this to explore whether models of responses to human impacts are robust against geographic and taxonomic biases. Specifically, we hypothesized that bee responses to land-use pressures should vary significantly with region and with taxonomic group (i.e., bumblebees or other bees) and so will not be transferable across regions and taxa. Improved understanding in this area will help to clarify whether knowledge based on a few regions and taxa are sufficient to underpin policy decisions as well as highlight systems for future study.

6.3 METHODS

6.3.1 DATA COLLATION

The data collation procedures are described in Chapter 2 and Hudson *et al.* (2014). For this analysis, we used only data where bee abundance or diversity was sampled. We did not include studies that recorded only particular target species (for instance, studies that were only interested in the abundance of a single species across sites), so that site-level diversity measures would be meaningful. The final dataset for the analysis included 89,473 diversity measurements from 647 bee species at 2241 sites from across the globe (Table 6.1). Many combinations of land use and use intensity had too few sites to permit robust modelling. The data were therefore coarsened to give a variable of combined Land Use and Intensity (LUI) with the following levels, each with at least 160 sites: primary vegetation, secondary vegetation, low-intensity cropland, medium-intensity cropland, high-intensity cropland, pasture; plantation forest and urban areas were under-represented in the dataset, with only 82 and 74 sites respectively. Sites were also classified by region and subregion (according to UN definitions), with Middle and Southern Africa combined into a single category to increase the sample size (Table 6.1).

Table 6.1: Number of sites by UN region and subregion.

UN region	UN subregion	Number of sites
Europe	Western Europe	1204
	Northern Europe	289
	Eastern Europe	64
	Southern Europe	50
Americas	North America	179
	Central America	103
	South America	119
Oceania	Australia and New Zealand	163
Asia	South Eastern Asia	31

6.3.2 ANALYSIS

For each site, we calculated three measures of bee community diversity as our response variables: total abundance, within-sample species richness and Simpson's diversity. Simpson's diversity was calculated as:

$$D = \sum P_i^2 \quad (6.1)$$

where P_i is the proportion of individuals belonging to species i . Although the inverse Simpson's index ($1/D$) is more commonly used, we use the dominance form (D) as the residuals of models are normally distributed. However, a lower D value corresponds to higher diversity.

As total abundance measurements are not necessarily integers (e.g. densities and effort-corrected measures), use of the Poisson error structure was not possible, so total abundance was $\log+1$ transformed before modelling to normalise residuals and equalise variance. Species richness was modelled with Poisson error distribution and log-link function; Simpson's diversity was modelled using Gaussian errors (model checking showed that these treatments were appropriate).

We constructed models for each response variable, using mixed-effects models (Bates *et al.* 2014, lme4 package) to account for non-independence of data due to differences in collectors ('source'), sampling methodologies and biogeographic source pools ('study') and the spatial structure of sites ('block'); the initial random effect structure was therefore block nested within study within source. If overdispersion was detected in models of species richness, an observation-level random effect was included to account for this (a Poisson-lognormal model, Harrison 2014). The initial fixed-effects structure of models included LUI, subregion and their interaction. Subregion was treated as a fixed rather than random effect as we are interested in testing the effect, rather than simply estimating the variance associated with geographic subregion (Fox *et al.* 2015).

The best random-effects structure was assessed using likelihood ratio tests (Zuur *et al.* 2009),

with models fit using Restricted Maximum Likelihood for total abundance and Simpson's diversity, and Maximum Likelihood for species richness. We then attempted to simplify the fixed-effects structure using backwards stepwise model simplification and likelihood ratio tests, with models fit using Maximum Likelihood (Crawley 2007; Murtaugh 2009; Zuur *et al.* 2009). However, to better appreciate the uncertainty in the models (Whittingham *et al.* 2006), if the interaction between LUI and subregion remained in the minimum adequate model, we also constructed the following models: additive model (with LUI and subregion included as additive effects); LUI only (univariate model); and subregion only (univariate). We then compared the explanatory power and predictive error of the interactive model with these simpler alternatives.

Explanatory power was calculated using the MuMIn package in R (Barton 2013), as the marginal and conditional R^2_{glmm} values: i.e., the variance explained by fixed effects alone and by fixed and random effects combined, respectively (Nakagawa & Schielzeth 2013). Predictive error was calculated as the Mean Squared Error (MSE) from ten-fold cross validation, where the model was iteratively fit to nine-tenths of the data (training set), and validated on the final tenth (validation set); we did this by randomly assigning sites into ten approximately equal-sized groups (Rodríguez *et al.* 2010). As the data are structured, the training data may not be fully independent of the validation data (Wang & Gelman 2015), but any bias in prediction error that this causes will apply equally to all models being compared as the random effect structures are identical. In addition, some combinations of explanatory variables only occur in few studies or sources; splitting the dataset by these higher-level strata would mean that some combinations would rarely appear in the training data, leading to overestimates of predictive error.

The dataset was then subsetting to include only studies where both bumblebees (*Bombus*) and other bees were sampled (bumblebees contributed to over 21% of the bee diversity measurements). We calculated the site-level diversity measures separately for each group and fitted the initial model with a three-way interaction between LUI, subregion and taxonomic group (*Bombus* or otherwise). The initial random structure was as above, but included a site-level random effect to account for multiple samples (bumblebees and other bees) being taken from the same site. As above, we first attempted to simplify the initial model (both

in terms of random effects and then fixed effects) and, if the initial three-way interaction remained in the model, compared the explanatory power and predictive error with simpler models, where responses to LUI were permitted to vary with subregion (LUI, subregion and their interaction) or with taxonomic group (LUI, taxonomic group and their interaction).

To further understand heterogeneity in community response to LUI, planned comparisons were performed (multcomp package, Hothorn *et al.* 2008). Within each subregion (and each taxonomic group, if assessed), we tested for differences between natural vegetation (primary vegetation) and other land uses; between semi-natural vegetation (secondary vegetation) and other land uses; whether minimally-used cropland differed from lightly-used cropland; and whether lightly-used cropland differed from intensively-used cropland. To avoid rank-deficiency, LUI and subregion were collapsed into a single factor in these models. Not all comparisons were possible in all subregions.

All analyses were carried out using R 3.1.0.

6.4 RESULTS

For total abundance, Simpson's diversity and species richness, the minimum adequate models were those in which responses to LUI were free to vary among geographic subregions. These models also always had the greatest explanatory power and were always among the models having the lowest predictive error (Fig. 6.1).

For total abundance, the interaction between LUI and subregion explained a highly significant amount of variation ($\chi^2 = 125.01$, $df = 26$, $p < 0.0001$) (Fig. 6.2), which resulted in this model having the lowest predictive error compared to simpler models. The interaction between LUI and subregion was also significant for Simpson's diversity ($\chi^2 = 62.49$, $df = 26$, $p < 0.0001$) and species richness ($\chi^2 = 45.08$, $df = 26$, $p < 0.05$) although these models had slightly higher predictive error than models based on subregion alone.

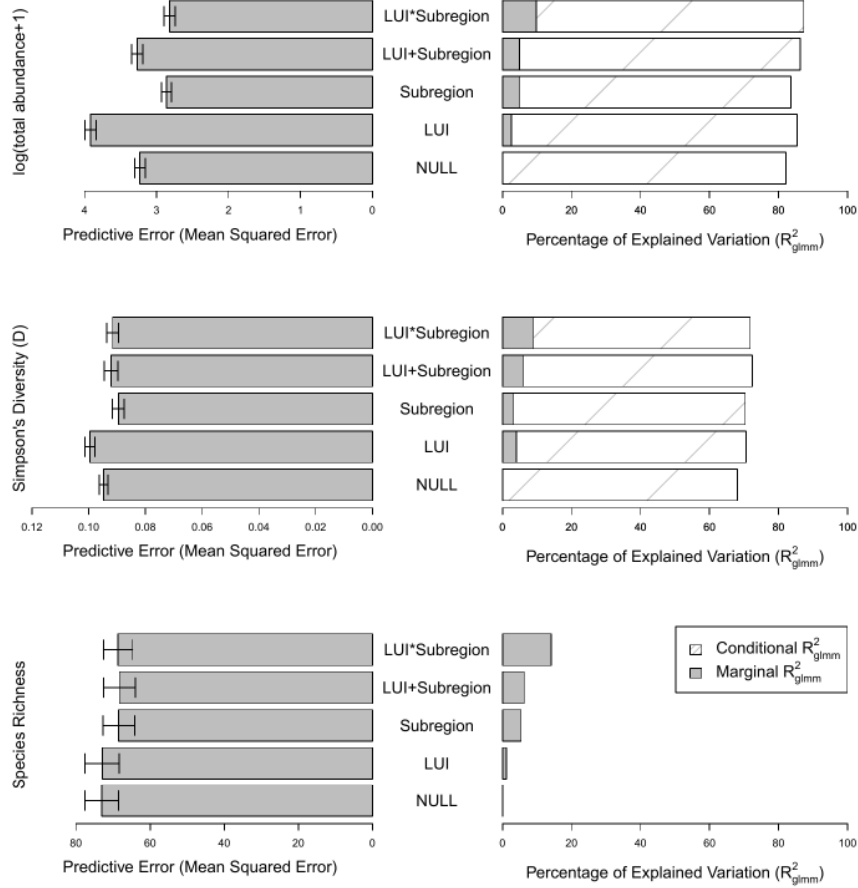


Figure 6.1: The predictive error and explanatory power of models that include only the intercept (NULL), Land Use and Intensity (LUI) alone, Subregion alone, additive effects (LUI+Subregion), or interactive effects (LUI*Subregion). The marginal R^2_{glmm} is the variance explained by fixed effects; the conditional R^2_{glmm} is the variance explained by both random and fixed effects. Note that for generalised linear mixed models such as our species richness models, Conditional R^2_{glmm} cannot yet be calculated.

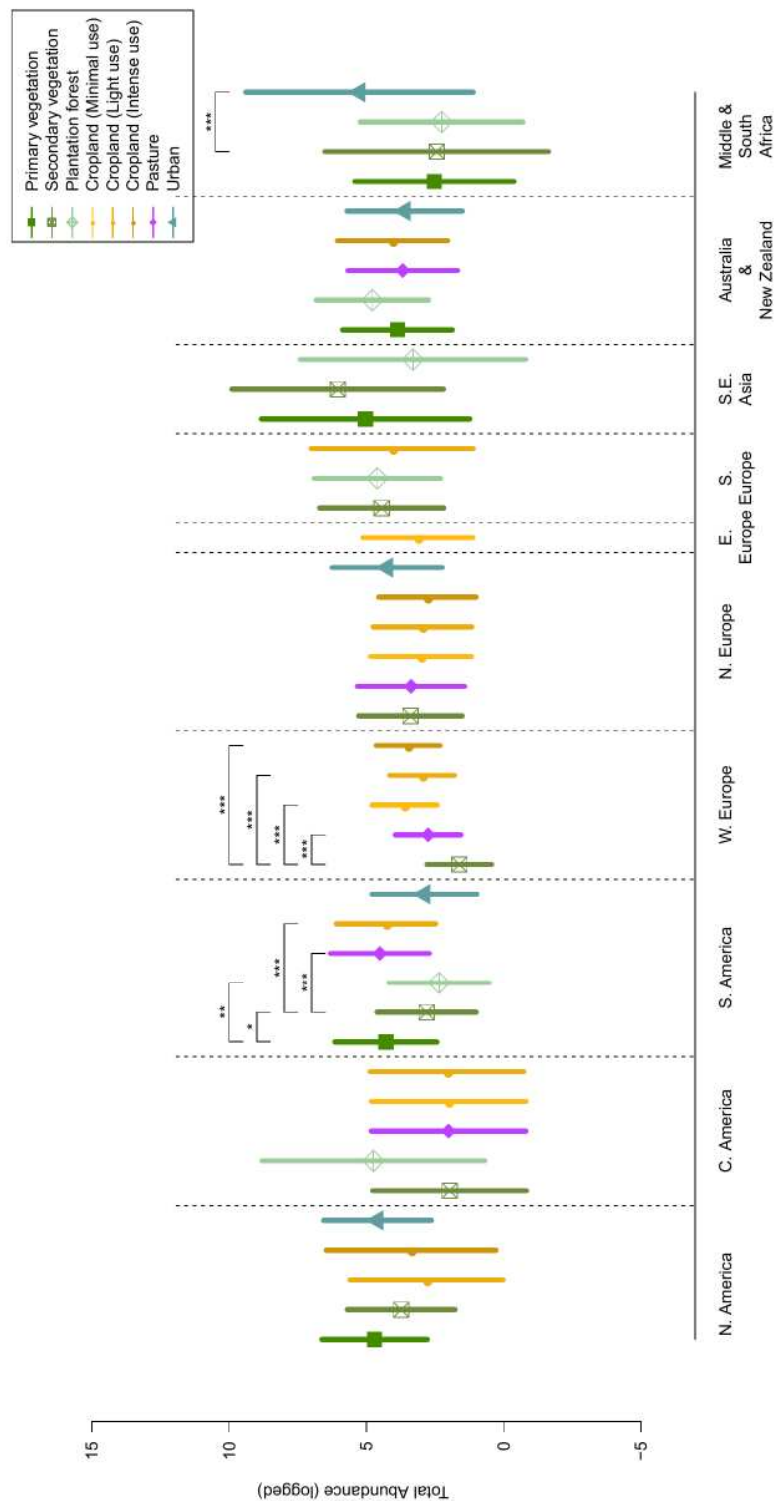


Figure 6.2: Predicted means of total (logged) abundance of bees for different land-use classes in each subregion. Significant results of multiple comparisons are also shown ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$).

As Fig. 6.2 shows, the response of total bee abundance to land use differed significantly among regions. In Western Europe, agricultural land maintained higher bee abundances than secondary vegetation (minimally-used cropland: $z = 8.25$; lightly-used cropland: $z = 5.33$; intensively-used cropland: $z = 9.16$; all $p < 0.001$; pasture: $z = 4.09$, $p < 0.01$). Low-intensity cropland also maintained higher diversity than secondary vegetation (Simpson's diversity: $z = -4.18$, $p < 0.01$, Species richness: $z = 3.3$, $p < 0.05$) or medium-intensity cropland (Simpson's diversity: $z = 5.67$; Species richness: -4.88 , $p < 0.001$ for both).

In South America, there was a similar trend: cropland and pasture maintained higher bee abundances than secondary vegetation ($z = 4.58$ and $z = 5.63$ respectively; $p < 0.001$ for both). However, this was accompanied by a decrease in diversity (i.e., an increase in Simpson's index: $z = 4.53$, $p < 0.001$). Relative to primary vegetation, bee abundance was significantly lower in both secondary vegetation ($z = -3.45$, $p < 0.05$) and plantation forest. ($z = -4.16$, $p < 0.01$).

Urbanization also had differing effects between subregions, with reduced species richness in South America relative to primary vegetation ($z = -3.42$, $p < 0.05$), but increased total abundance in Middle and Southern Africa ($z = 5.17$, $p < 0.001$).

When the dataset was split by genus (*Bombus* vs. others), the best models for each response variable (according to likelihood ratio tests) included significant three way interactions between LUI, subregion and genus (total abundance: $\chi^2 = 198.80$, $df = 11$, $p < 0.001$; Simpson's diversity: $\chi^2 = 25.87$, $df = 11$, $p < 0.05$; species richness: $\chi^2 = 67.88$, $df = 11$, $p < 0.001$). These models also had the greatest explanatory power and lowest predictive error, compared with simpler models (Fig. 6.3).

Planned comparisons provided more detail into these context- and taxon-specific differences in response to human impacts. In Western Europe, both bumblebees and other species responded similarly in terms of total abundance, which was lower in secondary vegetation than in cropland (e.g. in minimally-used cropland, *Bombus*: $z = 7.43$, $p < 0.001$; other species: $z = 9.81$, $p < 0.001$). However, bumblebee species richness tended to be higher in minimally-used cropland than secondary vegetation ($z = 5.27$, $p < 0.001$), which was not true for other bees ($z = 3.07$, n.s.). Simpson's diversity of non-*Bombus* was lower in pasture than secondary vegetation ($z = 3.28$, $p < 0.05$), but this was not true for bumblebees ($z = -2.46$, n.s.).

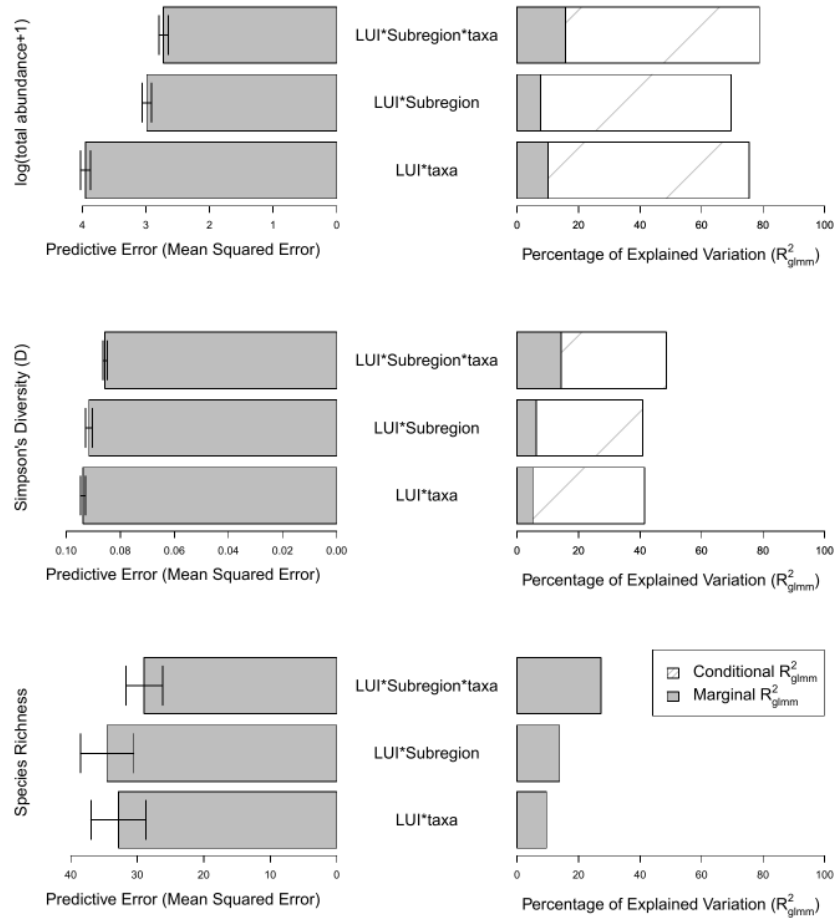


Figure 6.3: The predictive error and explanatory power of models that include three-way interactions between Land Use and Intensity (LUI), Subregion and taxonomic group (*Bombus* or not), and models with two-way interactions between LUI and taxa, or LUI and Subregion. Note that for generalised linear mixed models such as our species richness models, Conditional R^2_{glmm} cannot yet be calculated.

Bumblebees also responded differently from other bee species in North America. Diversity was lower in secondary vegetation relative to primary vegetation in terms of both total abundance ($z = -3.61$, $p < 0.05$) and species richness ($z = -3.82$, $p < 0.01$), but this was not true for other bees. However, other genera in North America appeared to be relatively more sensitive to transitions from primary vegetation to cropland, with relative declines in Simpson's diversity and species richness (e.g. compared to lightly-used cropland, $z = 3.47$, $p < 0.05$ and $z = -4.21$, $p < 0.001$ respectively), and to urban areas (species richness: $z = -3.98$, $p < 0.01$).

6.5 DISCUSSION

Bees are facing declines across the globe as a result of changing and intensifying land use (Ollerton *et al.* 2014; Potts *et al.* 2010). Detailed statistical models that relate bee diversity to drivers of change have the potential to inform mitigation and conservation efforts and to help safeguard food security. However, the transferability of models based on restricted data to other regions and taxa is not guaranteed (Archer *et al.* 2014; Petchey *et al.* 2015). If responses to threats are context-dependent, extrapolation from well-known study systems could carry significant risks for food security. The areas where food production is most highly dependent upon animal pollination are also those for which the fewest data are available (Archer *et al.* 2014; Gallai *et al.* 2009; Lautenbach *et al.* 2012), due to a lack of infrastructure and funding in many areas of the world (Archer *et al.* 2014); these same areas are often poorly buffered against the disruption of ecosystem service provision from whatever cause (Challinor *et al.* 2007), meaning that effects of any ecological surprises on human wellbeing could be more severe here than elsewhere. We have shown that bee community responses to land-use change and agricultural intensification can be highly context-dependent, but whether this impacts the transferability of models depends on the facet of diversity that is of interest.

The response of total abundance, Simpson's diversity and species richness of bee communities to Land Use and Intensity (LUI) varied significantly with geographic subregion, in line with our hypotheses and with previous work in tropical regions (Gibson *et al.* 2011; Phillips *et al.*, submitted). For total abundance, the greatest predictive ability could only be achieved

by allowing regional variation in responses to LUI, while for other aspects of diversity, it was necessary to allow at least regional variation in baseline diversity. This suggests that conclusions based on geographically restricted data cannot reliably be generalized to other regions. Indeed, bee community responses to agricultural intensification varied between regions; only in Western Europe was there an evident decline in diversity with increasing use-intensity of cropland, in line with previous suggestions that agricultural land-use intensity is more important in temperate than in tropical or subtropical systems (Kennedy *et al.* 2013). The most significant impact of plantation forest, however, was seen in South America, where abundance was significantly lower than in primary vegetation; this is congruent with a previous meta-analysis by Gibson *et al.* (2011) that focussed on tropical areas. The effects of urbanisation likewise depended on the subregion—with increased abundance in Africa but decreased species richness in South America—but these inferences were based on relatively few data. More data from more regions are needed to better understand the impact of urbanisation on bee communities (Hernandez *et al.* 2009).

It is likely that the geographic variation in responses is in part due to differences in community composition (Archer *et al.* 2014). We found that taxonomic biases towards bumblebees, which frequently dominate datasets geographically limited to North America and Western Europe, can mask the responses of other species. In Western Europe, for instance, non-bumblebees had lower species diversity in pasture than in secondary vegetation, while bumblebees did not show the same effect. Bumblebees have longer flight distances than many smaller bees, so may be better able to persist in more human-dominated land-uses, where foraging resources tend to be further from nesting sites and may even benefit from mass-flowering crops such as oilseed rape (Westphal *et al.* 2003).

The effect of taxonomic group on responses to LUI also differed between subregions, however, suggesting that other factors—such as geographic variation in the nature of threats or additional variation in community composition—may also affect generalities (Cariveau & Winfree 2015). For instance, solitary reproduction of bees is more common in temperate areas than the tropics (Roubik 1992). Previous work has shown that trait-based models of species distributions are only transferable—even within a subregion—when landcover is similar (Powney *et al.* 2014). Transferability *across* subregions is likely to be even more

difficult: variability in the sensitivity of bee communities will be influenced by a complex interaction between the phylogeny of communities and variation in the threatening processes, but such effects are difficult to disentangle. Further work into phylogenetic patterns of sensitivity may shed light on this aspect. Another important extension to our work would be to explore the interaction of multiple threatening processes (Vanbergen & Initiative 2013), as the pressures faced by bee communities can vary regionally (Brown & Paxton 2009). For instance, competition with introduced species and fragmentation are likely to be more important drivers of native bee diversity in the Neotropics than in temperate regions (Freitas *et al.* 2009).

Although our dataset includes over 2000 sites from five continents, it is still both geographically and taxonomically biased. Africa and Asia in particular are poorly represented meaning that we may still be underestimating the uncertainty in bee responses to land use in these regions. Nonetheless, our analysis has important implications for pollinator research and conservation action. We show that results based on geographically- and taxonomically-restricted datasets may not be transferable to other regions. Responses vary across regions due to a combination of differences in the inherent vulnerability of species and variation in the nature of threats. The provision of pollination services can be influenced by the abundance (Garibaldi *et al.* 2013; Winfree *et al.* 2015), species diversity (Vergara & Badano 2009) and species richness (Hoehn *et al.* 2008; Rogers *et al.* 2014; Vergara & Badano 2009) of bee communities, although the relative importance of each facet of diversity appears to vary with study system (Garibaldi *et al.* 2013; Vergara & Badano 2009). Therefore, if we are to safeguard pollinators and the services they provide, enhanced research effort to enhance the representativeness (if not the amount) of available data will be needed to make context-dependent recommendations and to better understand the state of pollination services worldwide.

CHAPTER 7

Discussion

Bee species do not all respond in the same way to land-use pressures (Cariveau & Winfree 2015). I have used the most extensive compilation to date of relevant bee diversity data (Chapter 2) to show that ecological traits and phylogenetic relationships can help to explain the heterogeneity among species' responses (Chapter 3 and 4), and that these effects scale up to influence taxonomic, functional and phylogenetic diversity at the community level (Chapter 5). The results make a significant contribution to the field, helping to (i) identify which species are most sensitive to land-use pressures, (ii) show where pollination services may be most at risk from continued land-use change and (iii) emphasise the need for not just more data, but more representative data (Chapter 6, Meyer *et al.* 2015).

7.1 DRIVERS OF VARIATION IN BEE SPECIES SENSITIVITY TO LAND-USE PRESSURES

Although there have been many attempts to assess how ecological traits mediate bee species' responses to human impacts (e.g. Bartomeus *et al.* 2013a; Vázquez & Simberloff 2002; Williams *et al.* 2010), the analysis presented in Chapter 3 is the most comprehensive to date for European bees (De Palma *et al.* 2015). I found that several ecological traits can influence bee species' sensitivity to land-use pressures, with flight season duration being the most important of those analysed. Species with shorter flight seasons are more sensitive to human-dominated land uses than species with longer flight seasons, potentially because there is an enhanced chance of a mismatch with floral resources. A high proportion of the variation in sensitivity was left unexplained in this analysis, but Chapter 4 showed that this is not mainly because of idiosyncrasies in species' sensitivities; instead, species' sensitivities to human-

dominated land uses—in particular, to agricultural land—showed very strong phylogenetic signal. To put this into context, other traits that show similar phylogenetic signal (mean λ value of around 0.7) include host specificity among genera of parasites, geographic range size in British butterflies and North American sucker fishes and body weight in Australian marsupials (Freckleton *et al.* 2002).

In other groups, sensitivity traits often show phylogenetic signal (Collen *et al.* 2011; Freckleton *et al.* 2002) as can measures of decline such as extinction risk (Fritz & Purvis 2010) and sensitivity to pressures including climate change (Thuiller *et al.* 2011), over-harvesting (Fritz & Purvis 2010) and pollution (Chiari *et al.* 2015). Chapter 4 pools species' local responses globally to estimate phylogenetic signal in species' sensitivity to particular land-use transitions, while attempting to compensate for the incompleteness of available phylogenies. This represents the first assessment of phylogenetic signal in species' responses to land use, and the first analysis of its type for bees. Díaz *et al.* (2013) proposed that, if specific response functions (SRFs: species' change in abundance or biomass induced by an environmental driver) show strong phylogenetic signal, this could—depending on whether species' ecological role is also phylogenetically patterned—seriously endanger ecosystem service provision, as whole clades (and the functions they perform) may be at risk. However, they were unable to fully implement their analytical framework because of a lack of data on SRFs (for which they instead used rough proxies). Species' sensitivities to particular land-use transitions are SRFs. Chapter 4 gives the first analysis of SRFs for land-use pressures in bees, and it shows that sensitivities to human-dominated land uses (in particular, to agricultural land) are strongly phylogenetically patterned.

One of the most intriguing findings of Chapter 4 was that phylogenetic differences were better at explaining variation in sensitivity than were ecological traits, even though these same traits were shown to influence the response of European bees to land-use pressures (De Palma *et al.* 2015, Chapter 3;[]). This result suggests that the important ecological characteristics that drive species sensitivity or resistance to human impacts may not be the ones that are commonly captured. Increased research effort to create more complete phylogenetic trees—based on comprehensive genetic data rather than constraining positions of unsequenced species based on taxonomy, as done here—may therefore be more beneficial than collecting ecological trait

data if the aim is to identify intrinsically vulnerable species as the focus of conservation efforts. If the aim is to gain a mechanistic understanding of what drives vulnerability in order to inform conservation practices, then this phylogenetic approach yields few answers (Cardillo & Meijaard 2012; Fisher & Owens 2004; Murray *et al.* 2011). For this latter goal, we first need to understand which ecological differences are driving the phylogenetic signal in species sensitivities.

Though more trait data are often called for by researchers, Chapter 4 highlights that we may have missed a step: *which* traits should we be measuring? Perhaps the interactions between species—which ecological characteristics such as diet breadth and phenology play a role in defining—are most important. Alternatively, it may be that phylogeny better captures the variation in ecological traits within species and this plasticity may confer a wider ecological tolerance (Chevin *et al.* 2010). In addition, some traits may facilitate plasticity in others, enhancing resistance to environmental change (Den Boer 1968). If so, it is possible that this effect will be better captured by phylogenetic relationships, rather than the traits that indirectly influence sensitivity. For example, having a longer flight season means that a species overlaps with the flowering times of many more plant species, so it may be better able to shift its diet. It is so far unclear what may drive intraspecific phenotypic variation, although such plasticity has been shown in some species. For instance, *Bombus terrestris* shows enhanced diet generalization if foraging with high densities of conspecifics (Fontaine *et al.* 2008).

7.2 A MORE COMPREHENSIVE VIEW OF DIVERSITY

Chapter 5 showed that taxonomic diversity should not be used alone to assess the state of bee diversity at a regional scale. Although taxonomic diversity is related to both functional and phylogenetic diversity, there were significant spatial mismatches between diversity measures. These mismatches were most acute in urban areas, which may maintain taxonomic diversity of bees, but not functional or phylogenetic diversity where human population density is high. Previous research into protected areas has similarly found that focus on only a single aspect of diversity can undermine others, through spatial mismatches (Stuart-Smith *et al.* 2013; Zupan *et al.* 2014). Functional and phylogenetic diversity can be important correlates of

ecosystem functioning (Albrecht *et al.* 2012; Cadotte *et al.* 2012; Flynn *et al.* 2011; Hoehn *et al.* 2008) and can stabilise ecosystem service provision through functional redundancy (Faith *et al.* 2010; Naeem 1998), so exploring how they respond to land-use pressures may be important for managing pollination services.

By analysing multiple measures of diversity, Chapter 5 also raises a concern that biotic homogenisation may be more widespread and serious across Europe than has been previously recognised (McKinney & Lockwood 1999). Carvalheiro *et al.* (2013) showed that biotic homogenization in Europe has slowed over time, but the analysis only looked at taxonomic diversity, which Chapter 5 shows is not a safe proxy for other aspects of diversity (although losses were generally less severe for other diversity measures). An important step forward would be to investigate the phylogenetic and functional compositional similarity of communities (Chapter 5 could be extended to include this; Ricotta & Szeidl 2009).

7.2.1 IMPLICATIONS FOR CURRENT INDICATORS OF POLLINATION SERVICES

The trend in pollinator population sizes over time is an important indicator for biodiversity policy, and is used to assess the state of ecosystem service provision (Tittensor *et al.* 2014), even though the indicator currently uses only data on vertebrate pollinators. My results show that monitoring taxonomic diversity alone (i.e., counting all species equally) gives an incomplete picture of the state of bee diversity. As functional and phylogenetic diversity are both likely to be important in maintaining ecosystem functioning (an important policy goal), these aspects of diversity should be monitored as well, or even instead, even though the lack of data on ecological traits and genetic make-up for many species makes this difficult. The maps I present in Chapter 5 provide one-time ‘snapshots’ of the state of pollinator communities, and have the potential to be developed into an indicator with a much larger empirical basis than that used currently. The expectation is that fine-scale global land use maps will be produced for at least each year between 2010 and 2020, alongside projections to 2050 (Simon Ferrier, personal communication). Combining models such as mine with these maps will enable Europe-wide trends over time in a range of diversity measures to be estimated. Caveats for such projections include the assumption that there are no extinction debts and that the responses to land-use pressures are linear, even as the amount of natural and semi-natural

habitats in the landscape continues to decline. The first assumption is unlikely to be true: extinction debt has been indicated for bees (Cusser *et al.* 2015), although it is likely to be quickly repaid in short-lived taxa (Kuussaari *et al.* 2009). It is more difficult to assess whether the second assumption is likely to be valid, because most analyses of bee responses to local land use do not account for the landscape context (Winfrey *et al.* 2011). It is possible that there will be fewer refugia and source populations of bees as more semi-natural vegetation is lost from the landscape, so communities may be more susceptible to local land-use changes (Lindenmayer *et al.* 2008). Low-intensity farming practices may also be less effective as landscapes continue to be transformed (Brittain *et al.* 2010), although differing results have been found (Batáry *et al.* 2011). Nonetheless, such an extension of my work would provide the first regional assessment of the state of bee diversity using meaningful and complementary diversity measures.

7.3 THE IMPORTANCE OF REPRESENTATIVE DATASETS

Fine-scale land use data will be available for the whole world, but the results from Chapter 6 show that it is not safe to extrapolate the pressure-response models from Europe to the whole world. Responses of bee communities to land use and intensity vary significantly among both regions and taxa (bumblebees, *Bombus*, or other species). This result exemplifies an obvious point: if models are based on biased data, they are unlikely to be transferrable to other taxa and regions. Meta-analyses are increasingly common (Sigman 2011), but my results show that not only the amount of data underpinning the models is important, but also the spread. Even in my dataset, Africa and Asia are still under-represented (Chapter 2). This is in part why many of the analyses in this thesis are restricted to Europe, which has exceptionally good coverage. Further data collation in other areas will be necessary to properly explore the global consequences of land-use change on bee diversity. If more data can be collated, it will also be possible to produce global maps of bee diversity losses, similar to those in Chapter 5, for taxonomic and phylogenetic diversity at least (the paucity of trait data are likely to preclude functional diversity for the time being). These results also highlight the important contribution that the PREDICTS database—which has incorporated

most of the data that I have collated—has made to biodiversity research. The PREDICTS database is the most representative collation of data on terrestrial biodiversity data responding to land use and related pressures, with good representation across taxa and biomes. The PREDICTS project can therefore produce the most representative estimates of how local land-use impacts terrestrial biodiversity, compared with other projects with similar aims (e.g. Alkemade *et al.* 2009).

7.4 LIMITATIONS

Throughout the thesis, I have presented the limitations to each analysis, but there are a few broader issues that warrant further exploration.

7.4.1 FOCUS ON BEES

This thesis focussed on bees as they are widely considered to be the most important pollinating taxa (Danforth *et al.* 2006; Kevan & Baker 1983). A diversity of pollinating taxa may be important for ecosystem service provision. For instance, many fly species are pollinators (Larson *et al.* 2001; Ssymank *et al.* 2008); as flies can transport pollen further than bees in some systems (Rader *et al.* 2011), they may be vital for maintaining genetic diversity in plant populations. In addition, flower-visitation by birds is more common in temperate systems than previously thought (da Silva *et al.* 2014). Therefore, while the analyses presented in this thesis could inform management of pollination services, they are incomplete. It is so far unclear whether the responses of bees to land-use pressures are typical of other pollinating taxa. Given the extremely heterogeneous responses within bees that have been explored in this thesis, it seems unlikely that the results could be transferrable to other taxonomic groups. Certainly, species richness and composition are rarely congruent across taxa, generally depending on the scale of measurement (Westgate *et al.* 2014). I also did not attempt to link biodiversity of bees with that of plants, which could have been especially informative about losses of interactions and the stability of the system (Burkle *et al.* 2013; Sabatino *et al.* 2010; Spiesman & Inouye 2013).

There are also many basic knowledge gaps in the study of bees that have limited the

analyses in this thesis. For instance, the geographic range sizes of bees are generally only available at extremely coarse scales even in well-studied regions (Nieto *et al.* 2015); the only alternative is to estimate range sizes for a limited set of species using records from the Global Biodiversity Information Facility (GBIF, www.gbif.org). The latter has its own issues with biases and errors in data entry (Meyer *et al.* 2015; Yesson *et al.* 2007). If more refined data were available, the analyses in my chapters could be extended to be more informative. For instance, Chapter 4 showed that there is strong phylogenetic signal in bee species' sensitivities to certain land-use transitions, which means that the sensitivity of unsampled species could be predicted from phylogenetic information alone. If range size data were also available, we would not only know which species are most sensitive, but also which are most exposed to land-use changes currently or in the future.

7.4.2 FOCUS ON SPATIAL COMPARISONS

The approach taken in this thesis, and by the PREDICTS project, is to compare species diversity across sites that differ in their land-use class or intensity in order to provide an estimate of how land-use change impacts local diversity. As mentioned above, this approach ignores the possibility of biotic lag: that the full impacts of land-use changes may not be realised for decades. Studies that use space-for-time substitution are generally more readily available than time-series data or before-after-control-impact (BACI) studies, which enabled me to gather as much data as possible. However, while spatial comparisons often suggest declines in biodiversity (Gibson *et al.* 2011; Newbold *et al.* 2015), time-series data on assemblage diversity often show stable trends (Dornelas *et al.* 2014; Vellend *et al.* 2013). It is unclear whether the difference between these two approaches reflects undersampling of land-use transitions in the time-series data, spatial comparisons focusing on single rather than multiple pressures, or a difficulty with space-for-time substitution (Cardinale 2011; McGill *et al.* 2014).

7.5 SCALE EFFECTS

The analyses in this thesis have focussed on different levels of biological organisation: population, species and community level. I have only looked at responses of local (site-level) biodiversity to local land-use pressures, rather than looking at multiple spatial scales. I do not consider this to be a problem, per se, as local-scale changes are more relevant for ecosystem service provision and so for land managers and policy-makers, but is undoubtedly a narrow view of biodiversity, which can show markedly different trends depending on the spatial scale studied (Carvalho *et al.* 2013; McGill *et al.* 2014). The data collected in this project are not well suited to exploring biodiversity at larger spatial scales, although it is possible to explore how local biodiversity responses are influenced by land-use pressures at multiple spatial scales.

An important advantage of the dataset that I have collated is that all the sites have geographic coordinates and known sampling dates. This means that the dataset can be augmented with remotely-sensed information. This should enable landscape- and site-scale information on land-use composition and complexity to be extracted for each site. A comprehensive analysis of how landscape and local land-use variables may interact to influence bee populations in agricultural land has already been conducted by Kennedy *et al.* (2013). As my dataset also contains information on non-agricultural sites, broader analyses are possible. For instance, at present, the scale at which landscape context influences local bee abundance and diversity is not well defined, especially as it can differ between species (Goulson *et al.* 2010; Kremen *et al.* 2004; Steffan-Dewenter *et al.* 2002). Solitary bees tend to respond more to local landscape structure, within a radius of about 750m, while social bees are influenced by much larger scales, up to 3000m radius in the case of honey bees (Steffan-Dewenter *et al.* 2002). In addition, most of the landscape analyses that have been performed previously have used somewhat arbitrary spatial scales, which are in some cases also extremely large (e.g. 16km² in Schweiger *et al.* (2005)). Such scales may not be appropriate for management, which must work with a limited amount of time and money (van Delden *et al.* 2011; Zhang *et al.* 2007). The dataset that I have compiled could be used to determine empirically the spatial scale that is most relevant for maintaining different aspects of bee diversity and so which should be

used when attempting management at a landscape scale.

7.6 CONCLUDING REMARKS

Bees are a diverse and ecologically important group of species that are increasingly threatened by land-use change and intensification. However, our understanding of how bee diversity is changing and will change in future is complicated by the vast heterogeneity in species responses (Cariveau & Winfree 2015). I have used multiple approaches to show how ecological characteristics and phylogenetic relationships can shape species' sensitivities to land-use pressures, providing opportunities to predict—and hopefully mitigate—biodiversity declines. My results also emphasise the potential issues with extrapolating results between different measures of diversity and between taxa and regions. There are a number of questions still to be answered. Where are species with high sensitivity to land-use change also likely to be most exposed to these changes? What spatial scale should land-managers focus on to conserve local biodiversity? As the majority of data that I have collated will soon be made open-access—thanks to the willingness of many researchers who shared their data with me to also share them more widely—I hope that these questions will soon be answered.

CHAPTER 8

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APPENDIX A

Chapter 2 Appendix

A.1 DATABASE CONSTRUCTION AND DEFINITIONS

Table A.1: Land-use class and intensity definitions as used in Hudson *et al.* (2014)

Level 1 Land Use	Predominant Land Use	Minimal use	Light use	Intense use
No evidence of prior destruction of the vegetation	Primary forest	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that is severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
	Primary Non-Forest	As above	As above	As above
Recovering after destruction of the vegetation	Mature Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Intermediate Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Young Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Vegetation (indeterminate age)	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use

Human use (agricultural)	Plantation forest		
	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.
	Cropland		
	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
	Pasture		
	Pasture with minimal input of fertiliser and pesticide, and with low stock density (<i>not</i> high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, <i>and</i> with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).

Human use (urban)	Urban	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.
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A.1.1 HABITAT FRAGMENTATION DEFINITIONS

Constructed in collaboration with Helen Phillips (part of the PREDICTS team).

Category	Site Level Definition
Well within unfragmented habitat.	Sample site is well within the unfragmented landscape - this is scale dependent, with information being obtained from the study/author.
Within unfragmented habitat but at or near its edge.	Sample site is at the edge of the unfragmented landscape - this is scale dependent, with information being obtained from the study/author.
Within a remnant patch (perhaps at its edge) that is surrounded by other habitats.	Sample site is located in a patch of older, well-established habitat type (e.g., Primary forest, mature secondary forest). This site can be at the edge of the patch, and therefore surrounded by other habitat types.
Representative part of a fragmented landscape.	Either; relatively unknown what the site level habitat is like, either due to lack of information or due to the site being large enough to encompass multiple habitat types, or; the sample site is of a particular habitat type that is inherently fragmented and dominates the landscape, e.g., the site is in an agricultural field and the landscape is comprised of many fields.
Part of the matrix surrounding remnant patches.	Site is located outside of the remnant, older habitat type in a more recently established habitat type. Ideally, the exact distance will be known and can be entered in the excel spreadsheet.
Cannot decide.	Unknown (information not provided).

A.1.2 HIERARCHY OF FARM TYPES

1. Plant Crops

1.1. Field crops

1.1.1. Cereals, oilseed and protein crops

1.1.2. Rice

1.1.3. COP and rice combined

1.1.4. Root crops

1.1.5. Cereals and root crops combined

1.1.6. Field vegetables

1.1.7. Tobacco

- 1.1.8. Cotton
 - 1.1.9. Feed crops
 - 1.1.10. Various crops combined
 - 1.1.11. Unknown field crop
- 1.2. Horticulture
 - 1.2.1. Market garden vegetables
 - 1.2.2. Flowers and ornamentals
 - 1.2.3. General market gardening cropping
 - 1.2.4. Unknown horticultural crops
- 1.3. Permanent crops
 - 1.3.1. Vineyards
 - 1.3.2. Fruit, nuts and seeds
 - 1.3.3. Olives
 - 1.3.4. Various crops combined
 - 1.3.5. Unknown permanent crop
- 1.4. Unknown arable farming
- 2. Livestock
 - 2.1. Grazing livestock
 - 2.1.1. Dairy
 - 2.1.2. Cattle
 - 2.1.3. Sheep
 - 2.1.4. Sheep and cattle
 - 2.1.5. Goats
 - 2.1.6. Various grazing livestock
 - 2.1.7. Unknown grazing livestock
 - 2.2. Granivore
 - 2.2.1. Pigs
 - 2.2.2. Poultry
 - 2.2.3. Various granivores
 - 2.2.4. Unknown granivorous livestock
 - 2.3. Unknown livestock
- 3. Mixed farming
 - 3.1. Mixed cropping
 - 3.1.1. Market gardening and permanent crops
 - 3.1.2. Field crops and market gardening

- 3.1.3. Field crops and vineyards
- 3.1.4. Field crops and permanent crops
- 3.1.5. Mixed cropping - mainly field crops
- 3.1.6. Mixed cropping - mainly market gardening
- 3.1.7. Mixed cropping - mainly permanent crops
- 3.1.8. Unknown mixed cropping
- 3.2. Mixed livestock
 - 3.2.1. Mixed livestock - mainly grazing
 - 3.2.2. Mixed livestock - mainly granivores
 - 3.2.3. Unknown mixed livestock
- 3.3. Mixed crops-livestock
 - 3.3.1. Field crops and grazing livestock
 - 3.3.2. Various crops and livestock combined
 - 3.3.3. Unknown mixed crops-livestock
- 3.4. Unknown mixed farming
- 4. Unknown farm type

A.2 DATABASE CONTENT

A.2.1 LIST OF BEE TAXA FOUND IN THE DATASET

<i>Agapostemon melliventris</i>	<i>Amegilla chlorocyanea</i>
<i>Agapostemon semimelleus</i>	<i>Amegilla pulchra</i>
<i>Agapostemon texanus</i>	<i>Amegilla quadrifasciata</i>
<i>Agapostemon virescens</i>	<i>Amphylaeus nubilosellus</i>
<i>Agapostemonoides hurdi</i>	<i>Ancyloscelis apiformis</i>
<i>Aglaoapis tridentata</i>	<i>Andrena afrensis</i>
<i>Allodape interrupta</i>	<i>Andrena agilissima</i>
<i>Allodape mea</i>	<i>Andrena alfkenella</i>
<i>Allodapula variegata</i>	<i>Andrena angustior</i>
<i>Amegilla albigena</i>	<i>Andrena anthrisci</i>
<i>Amegilla asserta</i>	<i>Andrena arabis</i>
	<i>Andrena barbareae</i>

Andrena barbilabris

Andrena bicolor

Andrena brevipalpis

Andrena bucephala

Andrena carantonica

Andrena carlini

Andrena chrysopus

Andrena chrysosceles

Andrena cineraria

Andrena cinerea

Andrena clarkella

Andrena coitana

Andrena combinata

Andrena commoda

Andrena congruens

Andrena cressonii

Andrena curvungula

Andrena decipiens

Andrena dentata

Andrena denticulata

Andrena distinguenda

Andrena dorsata

Andrena dunningi

Andrena enslinella

Andrena erigeniae

Andrena erythronii

Andrena ezoensis

Andrena falsifica

Andrena flavipes

Andrena florea

Andrena floricola

Andrena florivaga

Andrena forbesii

Andrena fucata

Andrena fulva

Andrena fulvago

Andrena fulvata

Andrena fulvida

Andrena fuscipes

Andrena gravida

Andrena haemorrhoea

Andrena hattorfiana

Andrena hebes

Andrena helianthiformis

Andrena helvola

Andrena hippotes

Andrena humilis

Andrena illinoiensis

Andrena intermedia

Andrena kerriae

Andrena knuthi

Andrena labialis

Andrena labiata

Andrena lagopus

Andrena lapponica

Andrena lathyri

Andrena longitibialis
Andrena mandibularis
Andrena minutula
Andrena minutuloides
Andrena miserabilis
Andrena mitis
Andrena munakatai
Andrena nasonii
Andrena nasuta
Andrena nigrihirta
Andrena nigroaenea
Andrena nigroolivacea
Andrena nitida
Andrena nitidiuscula
Andrena niveata
Andrena opacifovea
Andrena ovatula
Andrena pandellei
Andrena pilipes
Andrena polita
Andrena praecox
Andrena probata
Andrena proxima
Andrena quintilis
Andrena ranunculorum
Andrena rosae
Andrena rudbeckiae

Andrena ruficrus
Andrena rufizona
Andrena sakagamii
Andrena semilaevis
Andrena semirugosa
Andrena similis
Andrena strohmei
Andrena subopaca
Andrena synadelpha
Andrena tarsata
Andrena thaspiae
Andrena thoracica
Andrena tibialis
Andrena ungeri
Andrena vaga
Andrena varians
Andrena ventralis
Andrena viridescens
Andrena vulpecula
Andrena watasei
Andrena wheeleri
Andrena wilkella
Andrena yamato
Anthidiellum notatum
Anthidiellum strigatum
Anthidium gayi
Anthidium manicatum
Anthidium montanum
Anthidium oblongatum

Anthidium punctatum

Anthophora aestivalis

Anthophora atroalba

Anthophora balneorum

Anthophora crassipes

Anthophora dispar

Anthophora furcata

Anthophora plumipes

Anthophora quadrimaculata

Anthophora retusa

Anthophora terminalis

Anthophora walshii

Apis cerana

Apis mellifera

Augochlora nigrocyanea

Augochlora nominata

Augochlora pura

Augochlora repandirostris

Augochlorella aurata

Augochloropsis auriventris

Augochloropsis callichroa

Augochloropsis metallica

Augochloropsis vesta

Bombus affinis

Bombus ardens

Bombus argillaceus

Bombus atratus

Bombus auricomus

Bombus barbutellus

Bombus bifarius

Bombus bimaculatus

Bombus bohemicus

Bombus californicus

Bombus caliginosus

Bombus campestris

Bombus centralis

Bombus citrinus

Bombus consobrinus

Bombus dahlbomii

Bombus distinguendus

Bombus diversus

Bombus fervidus

Bombus flavifrons

Bombus gerstaeckeri

Bombus griseocollis

Bombus hortorum

Bombus humilis

Bombus hypnorum

Bombus hypocrita

Bombus ignitus

Bombus impatiens

Bombus insularis

Bombus jonellus

Bombus lapidarius

Bombus lucorum

Bombus melanopygus

Bombus mesomelas
Bombus mixtus
Bombus monticola
Bombus muscorum
Bombus nevadensis
Bombus norvegicus
Bombus occidentalis
Bombus pascuorum
Bombus pensylvanicus
Bombus pomorum
Bombus pratorum
Bombus pyrenaeus
Bombus quadricolor
Bombus ruderarius
Bombus ruderatus
Bombus rufocinctus
Bombus rupestris
Bombus schrencki
Bombus semenoviellus
Bombus sichelii
Bombus sitkensis
Bombus soroensis
Bombus subterraneus
Bombus sylvarum
Bombus sylvestris
Bombus ternarius
Bombus terrestris

Bombus terricola
Bombus ussurensis
Bombus vagans
Bombus vandykei
Bombus vestalis
Bombus veteranus
Bombus vosnesenskii
Bombus wurflenii
Braunsapis calidula
Braunsapis diminuta
Braunsapis facialis
Braunsapis luapulana
Braunsapis simillima
Cadeguala albopilosa
Caenagochlora perpectinata
Calliopsis andreniformis
Callohesma calliopsisiformis
Callohesma ornatula
Callohesma pedalis
Camptopoeum frontale
Centris ferruginea
Centris flavifrons
Centris obscurior
Centris varia
Cephalotrigona zexmeniae
Ceratina australensis
Ceratina calcarata
Ceratina chalybea
Ceratina chloris

<i>Ceratina cucurbitina</i>	<i>Coelioxys octodentata</i>
<i>Ceratina cyanea</i>	<i>Coelioxys rufescens</i>
<i>Ceratina dupla</i>	<i>Coelioxys rufitarsis</i>
<i>Ceratina eximia</i>	<i>Coelioxys simillima</i>
<i>Ceratina flavipes</i>	<i>Colletes americanus</i>
<i>Ceratina japonica</i>	<i>Colletes compactus</i>
<i>Ceratina megastigmata</i>	<i>Colletes cunicularius</i>
<i>Ceratina nigrolabiata</i>	<i>Colletes daviesanus</i>
<i>Ceratina placida</i>	<i>Colletes floralis</i>
<i>Ceratina regalis</i>	<i>Colletes fodiens</i>
<i>Ceratina satoi</i>	<i>Colletes howardi</i>
<i>Ceratina strenua</i>	<i>Colletes hyalinus</i>
<i>Ceratina viridicincta</i>	<i>Colletes latitarsis</i>
<i>Ceratina viridis</i>	<i>Colletes marginatus</i>
<i>Ceratina zeteki</i>	<i>Colletes nigricans</i>
<i>Ceylalicthus perditellus</i>	<i>Colletes robertsonii</i>
<i>Chalepogenus caeruleus</i>	<i>Colletes seminitidus</i>
<i>Chelostoma campanularum</i>	<i>Colletes sierrensis</i>
<i>Chelostoma distinctum</i>	<i>Colletes simulans</i>
<i>Chelostoma florisomne</i>	<i>Colletes succinctus</i>
<i>Chelostoma grande</i>	<i>Colletes susannae</i>
<i>Chelostoma rapunculi</i>	<i>Corynura prothysteres</i>
<i>Chlerogella elongaticeps</i>	<i>Dasypoda altercator</i>
<i>Coelioxys afra</i>	<i>Dasypoda argentata</i>
<i>Coelioxys banksi</i>	<i>Diphaglossa gayi</i>
<i>Coelioxys conoidea</i>	<i>Dufourea dentiventris</i>
<i>Coelioxys inermis</i>	<i>Dufourea inermis</i>
	<i>Dufourea minuta</i>
	<i>Dufourea monardae</i>

Epicharis albofasciata

Epicharis maculata

Epicharis monozona

Epicharis rustica

Eucera clypeata

Eucera eucnemidea

Eucera hamata

Eucera interrupta

Eucera longicornis

Eucera nigrescens

Eufriesea brasilianorum

Eufriesea concava

Eufriesea lucifera

Eufriesea macroglossa

Eufriesea mussitans

Eufriesea ornata

Eufriesea pulchra

Eufriesea purpurata

Eufriesea surinamensis

Euglossa analis

Euglossa bursigera

Euglossa chalybeata

Euglossa championi

Euglossa cognata

Euglossa cordata

Euglossa crassipunctata

Euglossa cyanura

Euglossa cybelia

Euglossa deceptrix

Euglossa dressleri

Euglossa fimbriata

Euglossa flammea

Euglossa hansonii

Euglossa hemichlora

Euglossa heterosticta

Euglossa ignita

Euglossa imperialis

Euglossa intersecta

Euglossa magnipes

Euglossa mixta

Euglossa modestior

Euglossa nigropilosa

Euglossa orellana

Euglossa parvula

Euglossa pleosticta

Euglossa sapphirina

Euglossa securigera

Euglossa singularis

Euglossa townsendi

Euglossa tridentata

Euglossa truncata

Euglossa variabilis

Euglossa viridis

Euglossa viridissima

Euhesma neglectula

Eulaema bombiformis

Eulaema cingulata
Eulaema meriana
Eulaema nigrifacies
Eulaema nigrita
Eulaema polychroma
Eulaema seabrai
Eulaema speciosa
Euryglossa adelaidae
Euryglossa depressa
Euryglossa edwardsii
Exaerete frontalis
Exaerete smaragdina
Exoneurella setosa
Frieseomelitta nigra
Habralictus xanthinus
Halictus compressus
Halictus confusus
Halictus gemmeus
Halictus kessleri
Halictus langobardicus
Halictus leucaheneus
Halictus ligatus
Halictus maculatus
Halictus parallelus
Halictus patellatus
Halictus pollinosus
Halictus quadricinctus

Halictus rubicundus
Halictus scabiosae
Halictus seladonius
Halictus semitectus
Halictus sexcinctus
Halictus simplex
Halictus smaragdulus
Halictus subauratus
Halictus tumulorum
Heriades carinatus
Heriades crenulatus
Heriades leavitti
Heriades truncorum
Heriades variolosus
Hoplitis claviventris
Hoplitis lepeletieri
Hoplitis leucomelana
Hoplitis pilosifrons
Hoplitis producta
Hoplitis spoliata
Hylaeus affinis
Hylaeus albocuneatus
Hylaeus albonitens
Hylaeus amiculinus
Hylaeus angustatus
Hylaeus annularis
Hylaeus annulatus
Hylaeus asperithorax
Hylaeus brevicornis

Hylaeus capitosus

Hylaeus chlorosomus

Hylaeus clypearis

Hylaeus communis

Hylaeus confusus

Hylaeus cyanurus

Hylaeus difformis

Hylaeus floralis

Hylaeus gibbus

Hylaeus gredleri

Hylaeus hyalinatus

Hylaeus illinoisensis

Hylaeus kahri

Hylaeus lateralis

Hylaeus leptocephalus

Hylaeus mesillae

Hylaeus modestus

Hylaeus nigrinus

Hylaeus nubilosus

Hylaeus paulus

Hylaeus punctatus

Hylaeus punctulatus

Hylaeus relegatus

Hylaeus rinki

Hylaeus signatus

Hylaeus sinuatus

Hylaeus styriacus

Hylaeus variegatus

Isepeolus septemnotatus

Isepeolus viperinus

Lasioglossum admirandum

Lasioglossum aeratum

Lasioglossum affine

Lasioglossum albipenne

Lasioglossum albipes

Lasioglossum albocinctum

Lasioglossum apristum

Lasioglossum aspratulum

Lasioglossum asteris

Lasioglossum atlanticum

Lasioglossum bicingulatum

Lasioglossum bidentatum

Lasioglossum brazieri

Lasioglossum brevicorne

Lasioglossum breviventre

Lasioglossum brisbanense

Lasioglossum calceatum

Lasioglossum callidum

Lasioglossum cambagei

Lasioglossum cinctipes

Lasioglossum clelandi

Lasioglossum clypeare

Lasioglossum coeruleum

Lasioglossum cognatum

Lasioglossum convexiusculum

Lasioglossum coriaceum

Lasioglossum corvinum

Lasioglossum costulatum

Lasioglossum cressonii

Lasioglossum cupromicans

Lasioglossum dampieri

Lasioglossum disabanci

Lasioglossum discum

Lasioglossum divergens

Lasioglossum dreisbachi

Lasioglossum ebeneum

Lasioglossum euboense

Lasioglossum exiliceps

Lasioglossum expansifrons

Lasioglossum fattigi

Lasioglossum foxii

Lasioglossum fratellum

Lasioglossum fulvicorne

Lasioglossum glabriusculum

Lasioglossum griseolum

Lasioglossum gynochilum

Lasioglossum helichrysi

Lasioglossum hemichalceum

Lasioglossum hiltacum

Lasioglossum illinoense

Lasioglossum imitator

Lasioglossum interruptum

Lasioglossum laeve

Lasioglossum laevigatum

Lasioglossum laevissimum

Lasioglossum lanarium

Lasioglossum laticeps

Lasioglossum lativentre

Lasioglossum leucopus

Lasioglossum leucozonium

Lasioglossum lineare

Lasioglossum lineatulum

Lasioglossum lissonotum

Lasioglossum lucidulum

Lasioglossum majus

Lasioglossum malachurum

Lasioglossum marginatum

Lasioglossum mataroa

Lasioglossum michiganense

Lasioglossum minutissimum

Lasioglossum minutulum

Lasioglossum morio

Lasioglossum mundulum

Lasioglossum nigripes

Lasioglossum nigroviride

Lasioglossum nipponicola

Lasioglossum nitidiusculum

Lasioglossum nitidulum

Lasioglossum occidens

Lasioglossum pallens

Lasioglossum paradmirandum

Lasioglossum paraforbesii

Lasioglossum parvulum
Lasioglossum pauperatum
Lasioglossum pauxillum
Lasioglossum pectorale
Lasioglossum peraustrale
Lasioglossum perpunctatum
Lasioglossum pilosum
Lasioglossum politum
Lasioglossum problematicum
Lasioglossum pruinatum
Lasioglossum punctatissimum
Lasioglossum punctatum
Lasioglossum puncticolle
Lasioglossum pygmaeum
Lasioglossum quadrinotatum
Lasioglossum quadrisignatum
Lasioglossum rohweri
Lasioglossum rufitarse
Lasioglossum sabulosum
Lasioglossum sagax
Lasioglossum scitulum
Lasioglossum sculpturatum
Lasioglossum semilucens
Lasioglossum sexnotatum
Lasioglossum sexsetum
Lasioglossum sexstrigatum
Lasioglossum smeathmanellum

Lasioglossum sordidum
Lasioglossum speculatum
Lasioglossum sphecodoides
Lasioglossum sphecodopsis
Lasioglossum subfasciatum
Lasioglossum sulthicum
Lasioglossum tegulare
Lasioglossum tricinctum
Lasioglossum uncinatum
Lasioglossum urbanum
Lasioglossum versatum
Lasioglossum villosulum
Lasioglossum viridatum
Lasioglossum willsi
Lasioglossum xanthopus
Lasioglossum zephyrum
Lasioglossum zonulum
Lasioglossum zophops
Leioproctus amabilis
Leioproctus boltoni
Leioproctus carinatus
Leioproctus fulvescens
Leioproctus hudsoni
Leioproctus imitatus
Leioproctus maritimus
Leioproctus metallicus
Leioproctus paahaumaa
Leioproctus pango
Lestrimelitta niitkib

Liotrigona bottegoi
Lipotriches australica
Lipotriches excellens
Lipotriches flavoviridis
Lipotriches halictella
Lipotriches moerens
Lipotriches muscosa
Lipotriches semipallida
Lithurgus cornutus
Macropis europaea
Macropis fulvipes
Manuelia gayi
Manuelia postica
Megachile albisecta
Megachile alpicola
Megachile analis
Megachile apicalis
Megachile apicata
Megachile atrella
Megachile brevis
Megachile callura
Megachile campanulae
Megachile canifrons
Megachile captionis
Megachile centuncularis
Megachile circumcincta
Megachile clara

Megachile crassipes
Megachile discolor
Megachile ericetorum
Megachile ferox
Megachile heriadiformis
Megachile inermis
Megachile latimanus
Megachile leachella
Megachile ligniseca
Megachile lucidiventris
Megachile macularis
Megachile mendica
Megachile montivaga
Megachile nigriventris
Megachile oblonga
Megachile parietina
Megachile pilidens
Megachile pugnata
Megachile pyrenaea
Megachile pyrenaica
Megachile relativa
Megachile rotundata
Megachile semiluctuosa
Megachile sequior
Megachile serricauda
Megachile texana
Megachile versicolor
Megachile willughbiella
Megachile zaptlana

Megalopta centralis

Melecta albifrons

Melecta luctuosa

Melipona beecheii

Melipona compressipes

Melipona fasciata

Melipona fuliginosa

Melissodes agilis

Melissodes apicata

Melissodes bimaculata

Melissodes comptoides

Melissodes denticulata

Melissodes desponsa

Melissodes druriella

Melissodes subillata

Melissodes trinodis

Melitta dimidiata

Melitta haemorrhoidalis

Melitta leporina

Melitta nigricans

Melitta tricineta

Melitturga clavicornis

Meroglossa torrida

Mesocheira bicolor

Nannotrigona mellaria

Nannotrigona perilampoides

Nannotrigona testaceicornis

Nomada alboguttata

Nomada armata

Nomada articulata

Nomada bethunei

Nomada bifasciata

Nomada castellana

Nomada comparata

Nomada conjungens

Nomada denticulata

Nomada emarginata

Nomada erigeronis

Nomada fabriciana

Nomada facilis

Nomada femoralis

Nomada ferruginata

Nomada flava

Nomada flavoguttata

Nomada flavopicta

Nomada fucata

Nomada fulvicornis

Nomada goodeniana

Nomada guttulata

Nomada hirtipes

Nomada integra

Nomada lathburiana

Nomada leucophthalma

Nomada marshamella

Nomada melathoracica

Nomada obtusifrons

Nomada okubira

Nomada panzeri

Nomada pygmaea

Nomada ruficornis

Nomada rufipes

Nomada sexfasciata

Nomada sheppardana

Nomada shirakii

Nomada signata

Nomada stoeckherti

Nomada striata

Nomada succincta

Nomada zonata

Nomia maneei

Osiris barrocoloradensis

Osiris mourei

Osiris panamensis

Osmia albiventris

Osmia atriventris

Osmia aurulenta

Osmia bicolor

Osmia brevicornis

Osmia caerulea

Osmia conjuncta

Osmia cornifrons

Osmia gallarum

Osmia labialis

Osmia leaiana

Osmia lignaria

Osmia mustelina

Osmia parietina

Osmia pumila

Osmia rufa

Osmia simillima

Osmia submicans

Osmia tergestensis

Osmia uncinata

Osmia xanthomelana

Oxytrigona daemniaca

Oxytrigona mediorufa

Oxytrigona mellicolor

Pachyprosopis eucalypti

Pachyprosopis flavicauda

Pachyprosopis haematostoma

Pachyprosopis trichopoda

Panurgus banksianus

Panurgus calcaratus

Panurgus dentipes

Paratetrapedia calcarata

Paratrigona isopterophila

Partamona bilineata

Partamona cupira

Partamona testacea

Pasites maculatus

Patellapis stirlingi

Peponapis limitaris

Peponapis pruinosa

Pereirapis semiaurata

Plebeia franki

Plebeia frontalis

Plebeia minima

Protandrena bancrofti

Pseudapis diversipes

Pseudaugochlora graminea

Pseudopanurgus albitarsis

Rhodanthidium septemdentatum

Rophites algirus

Rophites canus

Rophites quinquespinosus

Ruizantheda mutabilis

Ruizantheda proxima

Scaptotrigona mexicana

Scaptotrigona pectoralis

Scaptotrigona xanthotricha

Sphecodes albilabris

Sphecodes alternatus

Sphecodes banksii

Sphecodes coptis

Sphecodes crassus

Sphecodes dichrous

Sphecodes ephippius

Sphecodes ferruginatus

Sphecodes geoffrellus

Sphecodes gibbus

Sphecodes heraclei

Sphecodes hyalinatus

Sphecodes japonicus

Sphecodes miniatus

Sphecodes monilicornis

Sphecodes niger

Sphecodes nipponicus

Sphecodes okuyetsu

Sphecodes pellucidus

Sphecodes profugus

Sphecodes puncticeps

Sphecodes ranunculi

Sphecodes reticulatus

Sphecodes rufiventris

Sphecodes scabricollis

Sphecodes simillimus

Sphecodes spinulosus

Stelis lateralis

Stelis punctulatissima

Stelis signata

Svastra obliqua

Svastrides melanura

Tetragonisca angustula

Tetragonula carbonaria

Tetraloniella alticincta

Tetraloniella lyncea

Tetraloniella nana

Tetraloniella scabiosae

Thygater crawfordi
Thyreus waroonensis
Trachusa byssina
Triepeolus helianthi
Trigona corvina
Trigona fulviventris
Trigona fuscipennis
Trigona muzoensis
Trigona nigerrima
Trigona recursa
Trigonisca buyssoni
Trigonisca schulthessi
Xylocopa imitator
Xylocopa lachnea
Xylocopa muscaria
Xylocopa transitoria
Xylocopa valga
Xylocopa violacea
Xylocopa virginica

APPENDIX B

Chapter 3 Appendix

B.1 SPECIES TRAITS DATASET

Table B.1: Original and coarsened factor levels of species traits

Trait	Coarsened factor levels	Original levels	Rationale
Nesting trait	Excavators	Excavators in the soil or vegetation	This trait was coarsened to represent two distinct nesting strategies: those that build their own holes versus those that don't. Excavators are particular about nesting sites, often requiring hard, bare ground or pithy stems, whilst those that don't excavate use existing cavities or old nesting sites, regardless of nest location.
	Non-excavators	Carder bees, renters, masons, cleptoparasites and social parasites	
Sociality	Obligately solitary	Solitary, solitary or communal,	The sociality of the species was defined according to how their offspring are raised, because this relates to reproductive capacity. Social species, or those that raise their young in social nests (such as social parasites), are able to produce greater numbers of offspring because there are more workers to provision those offspring. Primitively eusocial species are able to adjust their reproductive capacity, often according to resource requirements: for example, <i>Halictus rubicundus</i> is social in warmer, more resource rich areas but solitary in other areas.
	Not obligately solitary	communal, cleptoparasitic Highly eusocial, primitively eusocial, solitary/primitively eusocial, polymorphic, social parasites	
Lecty	No Lecty status	No Lecty status	Species with no lecty status are those which do not collect their own pollen, for example cleptoparasites. Phenotypic flexibility can be considered as a form of generalism so species that can be either oligolectic or polylectic are considered in the same category as the pollen generalists.
	Obligately oligolectic Polylectic/Flexible	Oligolectic Polylectic, oligolectic or polylectic	
Voltinism	Univoltine	Univoltine	Species were split into two categories: those with only one generation per year, and those that do have or can have more than one generation per year, as the latter are predicted to be less impacted by local threats.
	Multivoltine/Flexible	Bivoltine, multivoltine, univoltine or bivoltine, univoltine or multivoltine	

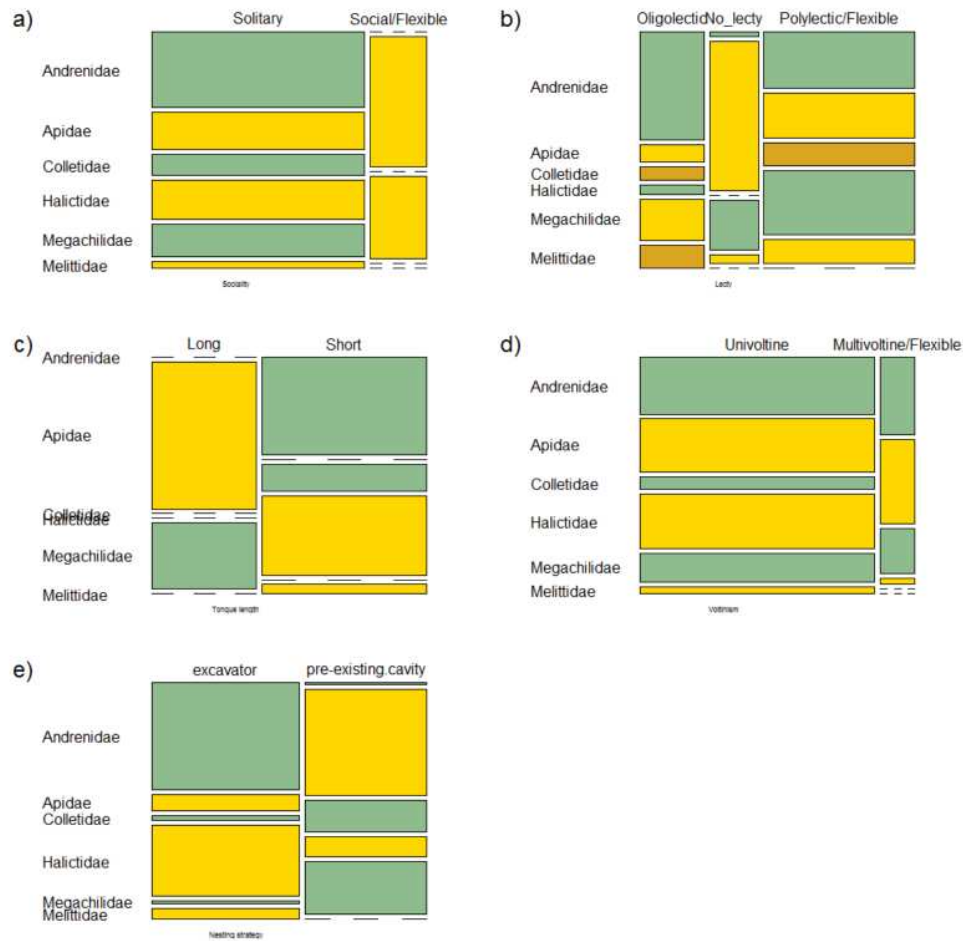


Figure B.1: Mosaic plots showing the distribution across families of the following categorical traits: a) Sociality, b) Lecty status, c) Tongue length, d) Voltinism, and e) Nesting strategy.

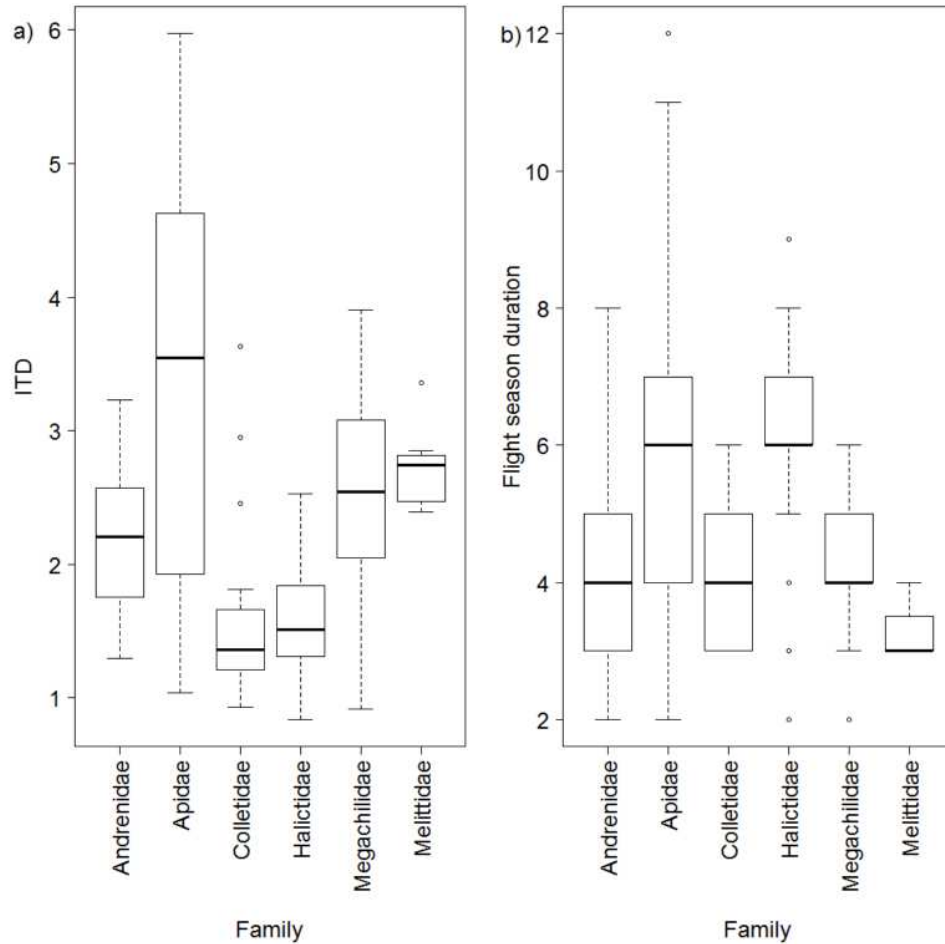


Figure B.2: Box plots showing the distribution across bee families of a) Inter-tergular distance (ITD) and b) Flight season duration.

B.2 DATA ON VEGETATION INDICES

Vegetation indices are based upon the light spectrum that is reflected by vegetation: leaf pigments, such as chlorophyll, strongly absorb radiation in the red spectral region, but absorb very little from the near infrared region (Huete 2006; Huete *et al.* 2002). Vegetation indices calculate the ratio of the infrared to red reflectance, where low values indicate low greenness and vice-versa. The normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) are based on very similar calculations, but their behaviour differs between regions. Whilst NDVI can become quickly saturated in high biomass regions, EVI is still

sensitive to variation in canopy cover, but EVI is more sensitive to topographic conditions than the NDVI (Matsushita *et al.* 2007). Therefore, Chapter 3 which is focussed in European areas, uses NDVI rather than EVI.

B.3 MODEL CHECKING

Table B.1: Variance inflation factors (corvif function, Zuur *et al.* 2009) for the dataset used to model probability of species occurrence. GVIF is the generalized variance inflation factor. Df is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables. None of the variables were removed during backwards stepwise model simplification so the GVIFs here are applicable both to the maximal and minimum adequate model for probability of species occurrence.

Explanatory Variable	GVIF	Df	GVIF ^{0.5Df}
LUI	1.22	5	1.02
mNDVI	1.19	1	1.09
ITD	2.66	1	1.63
Nest construction	4.38	1	2.09
Sociality	1.96	1	1.40
Lecty status	1.85	2	1.17
Voltinism	1.27	1	1.13
Tongue length guild	5.52	1	2.35
Duration of flight season	1.88	1	1.37

Table B.2: Variance inflation factors (corvif function, Zuur *et al.* 2009) for the dataset used to model abundance of present species, before model simplification. GVIF is the generalized variance inflation factor. Df is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables.

Explanatory Variable	GVIF	Df	GVIF ^{0.5Df}
LUI	1.33	5	1.03
mNDVI	1.28	1	1.13
ITD	2.98	1	1.73
Nest construction	8.65	1	2.94
Sociality	2.58	1	1.61
Lecty status	1.90	2	1.17
Voltinism	1.60	1	1.26
Tongue length guild	9.60	1	3.10
Duration of flight season	2.83	1	1.68

Table B.3: Variance inflation factors (corvif function, Zuur *et al.* 2009) for the dataset used to model abundance of present species, after backwards stepwise model simplification based on likelihood ratio tests. GVIF is the generalized variance inflation factor. Df is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables.

Explanatory Variable	GVIF	Df	GVIF ^{0.5Df}
LUI	1.31	5	1.03
mNDVI	1.28	1	1.13
ITD	2.96	1	1.72
Sociality	2.58	1	1.61
Lecty status	1.68	2	1.14
Voltinism	1.59	1	1.26
Tongue length guild	3.64	1	1.91
Duration of flight season	2.82	1	1.68

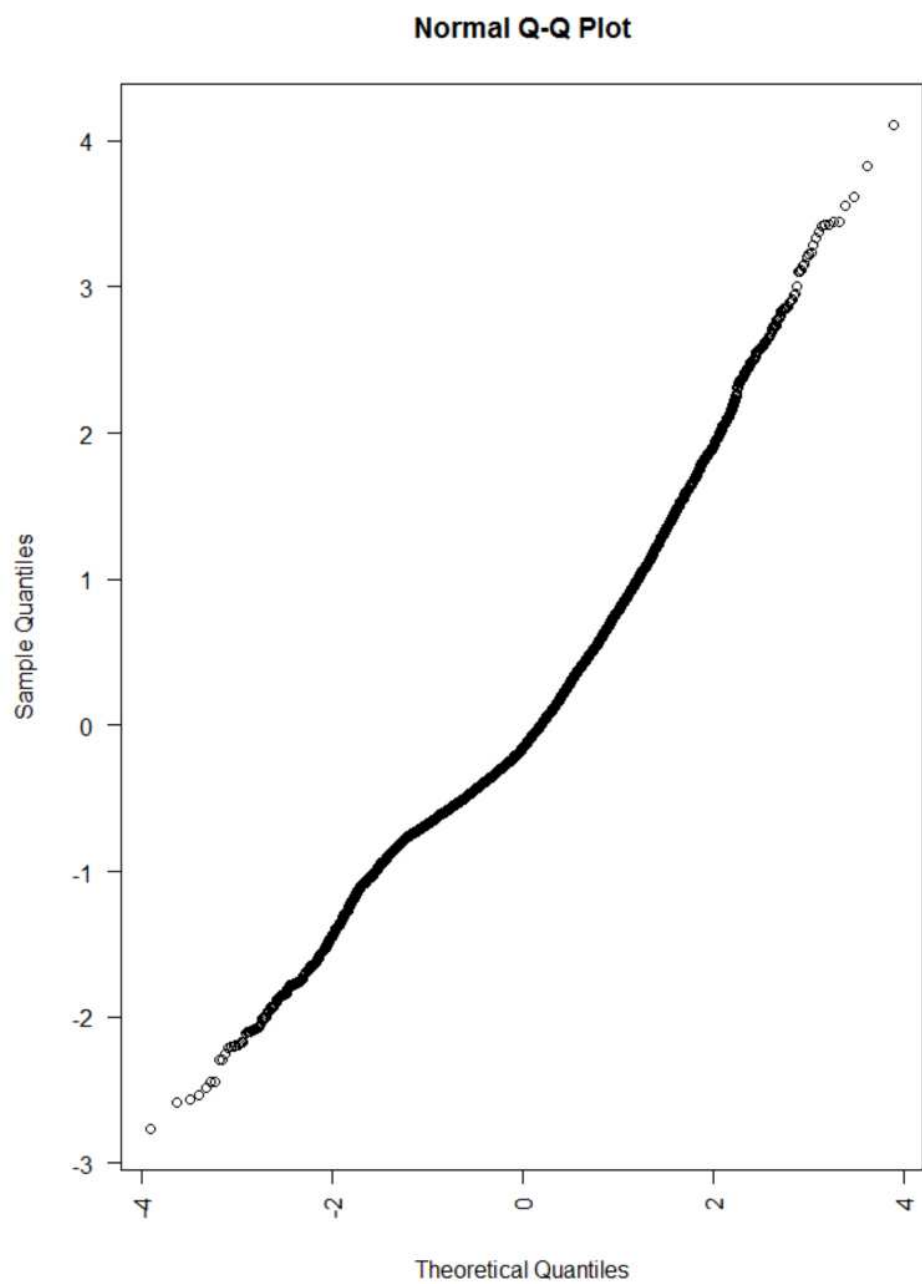


Figure B.1: Q-Q plot to assess residuals in the log-transformed abundance model for normality.

B.4 MODEL RESULTS

The following coefficient tables are the model outputs (estimate and standard errors) from mixed effects models in R: A Language and Environment for Statistical Computing version 2.15.3 (R Core Team 2013). These are treatment contrasts, i.e, differences are given between each level and the reference level (oligolectic, solitary, univoltine, short-tongued species in secondary vegetation). The predicted mean of the response variable can be calculated from these tables. For interactions between categorical traits, we can calculate the probability of occurrence of a given trait level in a given land-use class, as a percentage of the probability of occurrence for that same trait level in secondary vegetation. Similarly, this can be done for the abundance of present species. These percentages are provided in the final column of the following coefficients table. Such calculations are not as meaningful for continuous variables, so are not given (denoted by a dash).

Table B.1: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (bias, standard error, confidence intervals) for the model of species occurrence. Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero. The first level of each factor forms part of the intercept terms and so do not explicitly appear in the coefficients table (oligolectic, solitary, univoltine, long-tongued, nest excavating species in secondary vegetation). For each trait level and land-use combination, we also show the probability of species presence as a percentage of the probability of presence for that same trait level in secondary vegetation.

Variable	Coefficient	Original estimate	Standard error	Bias	bootstrapped Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Difference (%) in Probability of occurrence for trait level in given land use, relative to secondary vegetation
Intercept	(Intercept)	-6.42	1.14	-0.00	0.73	-7.98	-4.51	*
LUI	Cropland (Minimal use)	0.02	0.71	-0.01	0.25	-0.49	0.51	2
LUI	Cropland (Light use)	-1.22	0.68	0.01	0.27	-1.79	-0.59	*
LUI	Cropland (Intense use)	-1.81	0.67	0.01	0.20	-2.18	-1.36	*
LUI	Pasture	-1.69	0.73	-0.10	0.54	-2.89	-0.67	*
LUI	Urban	-2.61	1.00	0.02	0.84	-4.23	-0.88	*
mNDVI	mNDVI	7.61	1.21	0.01	0.78	5.96	9.08	*
Social Status	Not obligately solitary	-0.61	0.43	-0.05	0.38	-1.57	0.12	*
Lecty Status	No lecty status	2.41	0.77	-0.02	0.50	1.29	3.46	*
Lecty Status	Not obligately oligolectic	2.52	0.60	-0.02	0.34	1.93	3.26	*
Tongue length	Short tongue	0.82	0.72	-0.04	0.53	-0.45	1.90	-
Voltinism	Not obligately univoltine	0.00	0.28	-0.06	0.25	-0.53	0.58	-
Flight season duration	Flight season duration	0.18	0.09	-0.00	0.08	-0.00	0.34	-
ITD	ITD	0.39	0.16	0.02	0.11	0.18	0.64	*
Nest construction	Pre-existing cavity dweller	-0.55	0.49	0.01	0.31	-1.16	0.10	-
LUI × Social Status	Cropland (Minimal use) × Not obligately solitary	-0.44	0.26	0.00	0.15	-0.71	-0.13	*
LUI × Social Status	Cropland (Light use) × Not obligately solitary	-0.65	0.25	0.00	0.13	-0.90	-0.34	*
LUI × Social Status	Cropland (Intense use) × Not obligately solitary	-0.62	0.25	-0.00	0.12	-0.86	-0.36	*
LUI × Social Status	Pasture × Not obligately solitary	0.54	0.33	-0.03	0.35	-0.06	1.25	-68
LUI × Social Status	Urban × Not obligately solitary	0.11	0.34	0.08	0.34	-0.64	0.83	-92

mNDVI × Social Status	mNDVI × Not obligately solitary	1.94	0.47	0.04	0.44	0.80	2.87 *	-
LUI × Lecty Status	Cropland (Minimal use) × No lecty status	0.65	0.47	0.03	0.21	0.19	1.12 *	92
LUI × Lecty Status	Cropland (Light use) × No lecty status	1.05	0.45	0.05	0.20	0.59	1.49 *	-16
LUI × Lecty Status	Cropland (Intense use) × No lecty status	1.26	0.44	0.02	0.17	0.92	1.64 *	-42
LUI × Lecty Status	Pasture × No lecty status	0.06	0.48	0.08	0.34	-0.61	0.83	-80
LUI × Lecty Status	Urban × No lecty status	0.09	0.66	0.09	0.58	-0.99	1.41	-92
LUI × Lecty Status	Cropland (Minimal use) × Not obligately oligolectic	1.07	0.35	0.00	0.14	0.82	1.39 *	187
LUI × Lecty Status	Cropland (Light use) × Not obligately oligolectic	0.62	0.33	0.02	0.13	0.36	0.95 *	-45
LUI × Lecty Status	Cropland (Intense use) × Not obligately oligolectic	0.78	0.32	-0.02	0.11	0.58	1.02 *	-64
LUI × Lecty Status	Pasture × Not obligately oligolectic	0.35	0.35	0.05	0.30	-0.23	1.01	-73
LUI × Lecty Status	Urban × Not obligately oligolectic	0.56	0.57	0.11	0.62	-0.56	2.23	-87
mNDVI × Lecty Status	mNDVI × No lecty status	-4.86	0.92	-0.07	0.56	-6.01	-3.74 *	-
mNDVI × Lecty Status	mNDVI × Not obligately oligolectic	-3.97	0.77	-0.02	0.46	-5.14	-3.06 *	-
LUI × Tongue length	Cropland (Minimal use) × Short tongue	-0.36	0.49	0.03	0.18	-0.68	0.08	-28
LUI × Tongue length	Cropland (Light use) × Short tongue	0.09	0.47	0.02	0.18	-0.30	0.57	-68
LUI × Tongue length	Cropland (Intense use) × Short tongue	0.24	0.46	0.01	0.14	-0.10	0.59	-79
LUI × Tongue length	Pasture × Short tongue	0.58	0.50	0.01	0.30	-0.04	1.19	-67
LUI × Tongue length	Urban × Short tongue	0.09	0.57	-0.01	0.48	-0.82	1.48	-92
mNDVI × Tongue length	mNDVI × Short tongue	-1.72	0.61	0.02	0.41	-2.41	-0.79 *	-
LUI × Voltinism	Cropland (Minimal use) × Not obligately univoltine	0.05	0.21	0.03	0.15	-0.25	0.41	7
LUI × Voltinism	Cropland (Light use) × Not obligately univoltine	-0.01	0.20	0.04	0.12	-0.23	0.33	-71
LUI × Voltinism	Cropland (Intense use) × Not obligately univoltine	0.10	0.20	0.03	0.11	-0.07	0.37	-82

LUI × Voltinism	Pasture × Not obligately univoltine	-1.02	0.24	-0.02	0.19	-1.44	-0.70	*	-93
LUI × Voltinism	Urban × Not obligately univoltine	0.14	0.26	0.04	0.22	-0.19	0.66		-91
LUI × Flight season duration	Cropland (Minimal use) × Flight season duration	0.11	0.05	0.00	0.02	0.05	0.15	*	-
LUI × Flight season duration	Cropland (Light use) × Flight season duration	0.20	0.05	0.00	0.02	0.15	0.26	*	-
LUI × Flight season duration	Cropland (Intense use) × Flight season duration	0.23	0.05	0.01	0.02	0.20	0.27	*	-
LUI × Flight season duration	Pasture × Flight season duration	0.25	0.06	0.00	0.05	0.16	0.36	*	-
LUI × Flight season duration	Urban × Flight season duration	0.23	0.08	-0.01	0.07	0.10	0.37	*	-
mNDVI × Flight season duration	mNDVI × Flight season duration	-0.23	0.10	0.00	0.08	-0.40	-0.07	*	-
LUI × ITD	Cropland (Minimal use) × ITD	-0.15	0.09	0.01	0.04	-0.24	-0.06	*	-
LUI × ITD	Cropland (Light use) × ITD	0.05	0.09	0.01	0.04	-0.03	0.12		-
LUI × ITD	Cropland (Intense use) × ITD	0.11	0.08	0.00	0.04	0.02	0.18	*	-
LUI × ITD	Pasture × ITD	-0.24	0.11	0.02	0.09	-0.41	-0.01	*	-
LUI × ITD	Urban × ITD	0.06	0.12	-0.02	0.09	-0.18	0.20	*	-
mNDVI × ITD	mNDVI × ITD	-0.67	0.19	-0.00	0.13	-0.96	-0.41	*	-
LUI × Nest construction	Cropland (Minimal use) × Pre-existing cavity dweller	0.77	0.46	0.01	0.17	0.41	1.15	*	121
LUI × Nest construction	Cropland (Light use) × Pre-existing cavity dweller	0.32	0.45	0.01	0.16	-0.05	0.71		-60
LUI × Nest construction	Cropland (Intense use) × Pre-existing cavity dweller	0.07	0.44	0.01	0.14	-0.15	0.46		-82
LUI × Nest construction	Pasture × Pre-existing cavity dweller	0.84	0.48	-0.01	0.34	0.21	1.66	*	-57
LUI × Nest construction	Urban × Pre-existing cavity dweller	1.20	0.54	0.04	0.48	0.35	2.29	*	-76

Table B.2: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (bias, standard error, confidence intervals) for the model of species abundance (when present). Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero. The first level of each factor forms part of the intercept terms and so do not explicitly appear in the coefficients table (Oligolectic, Solitary, Univoltine, long-tongued species in secondary vegetation). For each trait level and land-use combination, we also show the species abundance as a percentage of the abundance for that same trait level in secondary vegetation.

Variable	Coefficient	Original estimate	Standard error	Bias	bootstrapped Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Difference (%) in abundance for trait level in given land use, relative to secondary vegetation
Intercept	(Intercept)	-1.17	0.63	-0.00	0.62	-2.32	0.04	-
LUI	Cropland (Minimal use)	0.39	0.28	-0.01	0.27	-0.12	0.92	48
LUI	Cropland (Light use)	0.05	0.27	-0.01	0.27	-0.47	0.57	5
LUI	Cropland (Intense use)	-0.06	0.26	-0.01	0.27	-0.59	0.46	-6
LUI	Pasture	-0.21	0.26	-0.01	0.26	-0.75	0.28	-19
LUI	Urban	0.37	0.34	-0.02	0.35	-0.35	1.04	45
mNDVI	mNDVI	3.04	0.72	0.02	0.69	1.64	4.49	*
Social Status	Not obligately solitary	0.28	0.18	0.00	0.19	-0.10	0.65	*
Lecty Status	No lecty status	1.15	0.43	0.02	0.45	0.31	2.06	*
Lecty Status	Not obligately oligolectic	0.96	0.36	0.00	0.37	0.25	1.69	*
Tongue length	Short tongue	0.86	0.37	0.02	0.36	0.17	1.63	*
Voltinism	Not obligately univoltine	-0.10	0.18	0.00	0.18	-0.43	0.24	*
Flight season duration	Flight season duration	0.09	0.04	-0.00	0.04	0.02	0.17	*
ITD	ITD	0.23	0.08	0.00	0.08	0.06	0.39	*
LUI × Social Status	Cropland (Minimal use) × Not obligately solitary	-0.20	0.18	-0.00	0.18	-0.54	0.18	21
LUI × Social Status	Cropland (Light use) × Not obligately solitary	-0.26	0.17	-0.00	0.18	-0.60	0.11	-19
LUI × Social Status	Cropland (Intense use) × Not obligately solitary	-0.27	0.17	-0.00	0.17	-0.61	0.08	-28
LUI × Social Status	Pasture × Not obligately solitary	0.29	0.19	-0.00	0.20	-0.07	0.68	9
LUI × Social Status	Urban × Not obligately solitary	0.02	0.21	-0.01	0.22	-0.42	0.43	48
mNDVI × Lecty Status	mNDVI × No lecty status	-1.92	0.64	-0.02	0.65	-3.22	-0.71	*
mNDVI × Lecty Status	mNDVI × Not obligately oligolectic	-1.34	0.53	-0.01	0.54	-2.45	-0.28	*

LUI × Tongue length	Cropland (Minimal use) × Short tongue	0.26	0.16	-0.00	0.16	-0.05	0.59	93
LUI × Tongue length	Cropland (Light use) × Short tongue	0.36	0.15	-0.00	0.15	0.06	0.68 *	51
LUI × Tongue length	Cropland (Intense use) × Short tongue	0.35	0.15	-0.00	0.15	0.06	0.67 *	34
LUI × Tongue length	Pasture × Short tongue	0.52	0.16	0.00	0.16	0.22	0.86 *	36
LUI × Tongue length	Urban × Short tongue	0.32	0.18	-0.00	0.18	-0.03	0.67	99
mNDVI × Tongue length	mNDVI × Short tongue	-1.70	0.37	-0.01	0.35	-2.40	-1.03 *	-
LUI × Voltinism	Cropland (Minimal use) × Not obligately univoltine	0.13	0.18	-0.00	0.18	-0.21	0.47	69
LUI × Voltinism	Cropland (Light use) × Not obligately univoltine	0.13	0.17	-0.00	0.17	-0.21	0.45	19
LUI × Voltinism	Cropland (Intense use) × Not obligately univoltine	0.15	0.17	-0.00	0.16	-0.16	0.47	10
LUI × Voltinism	Pasture × Not obligately univoltine	-0.46	0.19	0.00	0.18	-0.81	-0.09 *	-49
LUI × Voltinism	Urban × Not obligately univoltine	-0.00	0.19	0.00	0.19	-0.37	0.37	44
LUI × Flight season duration	Cropland (Minimal use) × Flight season duration	-0.09	0.04	0.00	0.04	-0.16	-0.02 *	-
LUI × Flight season duration	Cropland (Light use) × Flight season duration	-0.04	0.04	0.00	0.04	-0.12	0.03	-
LUI × Flight season duration	Cropland (Intense use) × Flight season duration	-0.03	0.04	0.00	0.04	-0.10	0.04	-
LUI × Flight season duration	Pasture × Flight season duration	-0.01	0.04	0.00	0.04	-0.09	0.07	-
LUI × Flight season duration	Urban × Flight season duration	-0.08	0.05	0.00	0.05	-0.18	0.01	-
mNDVI × ITD	mNDVI × ITD	-0.41	0.12	-0.00	0.11	-0.64	-0.19 *	-

Table B.3: Random effect variances $\pm$ one standard deviation.

Random effect	Occurrence	Abundance
Source ID	2.17 ± 1.47	1.38 ± 1.17
Study within source	0.57 ± 0.75	0.08 ± 0.28
Block in study in source	0.27 ± 0.52	0.01 ± 0.12
Family	0.16 ± 0.40	0.07 ± 0.27
Species within family	0.83 ± 0.91	0.12 ± 0.33

B.4.1 INTERACTIONS BETWEEN TRAITS AND MNDVI

Species with smaller ITD were significantly more sensitive to areas of low habitat quality (mNDVI) than those with larger ITD (Fig. B.1). Species with narrow dietary breadths were more sensitive to habitat quality, responding significantly more positively to mNDVI than species that are polylectic (occurrence model estimate = -3.97, bCIs:-6.01,-3.74; abundance model estimate = -1.34, bCIs:-2.45, -0.28) or parasitic (occurrence model estimate = -4.86, bCIs:-5.14, -3.06; abundance model estimate, -1.92, bCIs:-3.22, -0.71). Similarly, long-tongued species were more sensitive to mNDVI than short-tongued species (occurrence model estimate = -1.71, bCIs:-1.44, -0.70; abundance model estimate = -1.70, bCIs:-2.40,-1.03). Social species were also more sensitive to decreasing mNDVI than solitary species (occurrence model estimate = 1.94, bCIs:0.80,2.87)

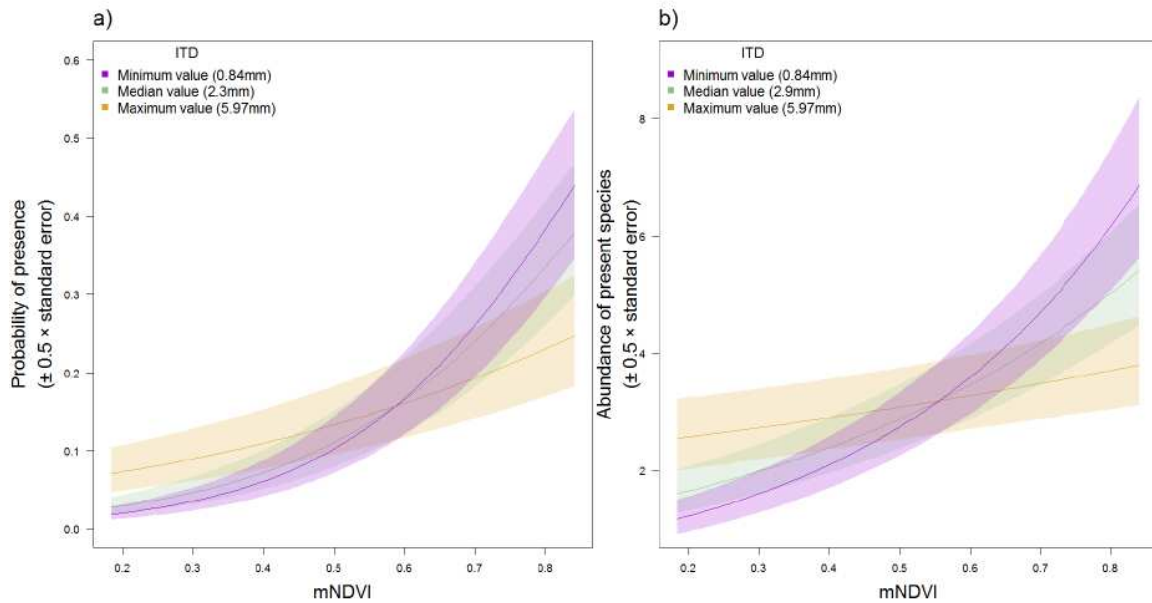


Figure B.1: Relationship between mNDVI and a) probability of species presence and b) the abundance of present species, predicted for three different body sizes (minimum, median, and maximum ITD values observed in the original dataset). Error bars represent half the standard error (estimated from model coefficients), to ease comparison. The coefficient estimate of $ITD \times mNDVI$ was -0.67 (bootstrapped Confidence Intervals, bCIs: -0.96, -0.41) for the occurrence model; and -0.41 (bCIs: -0.64, -0.19) for the abundance model. Where bCIs do not cross zero, the coefficient estimate is taken to be significant.

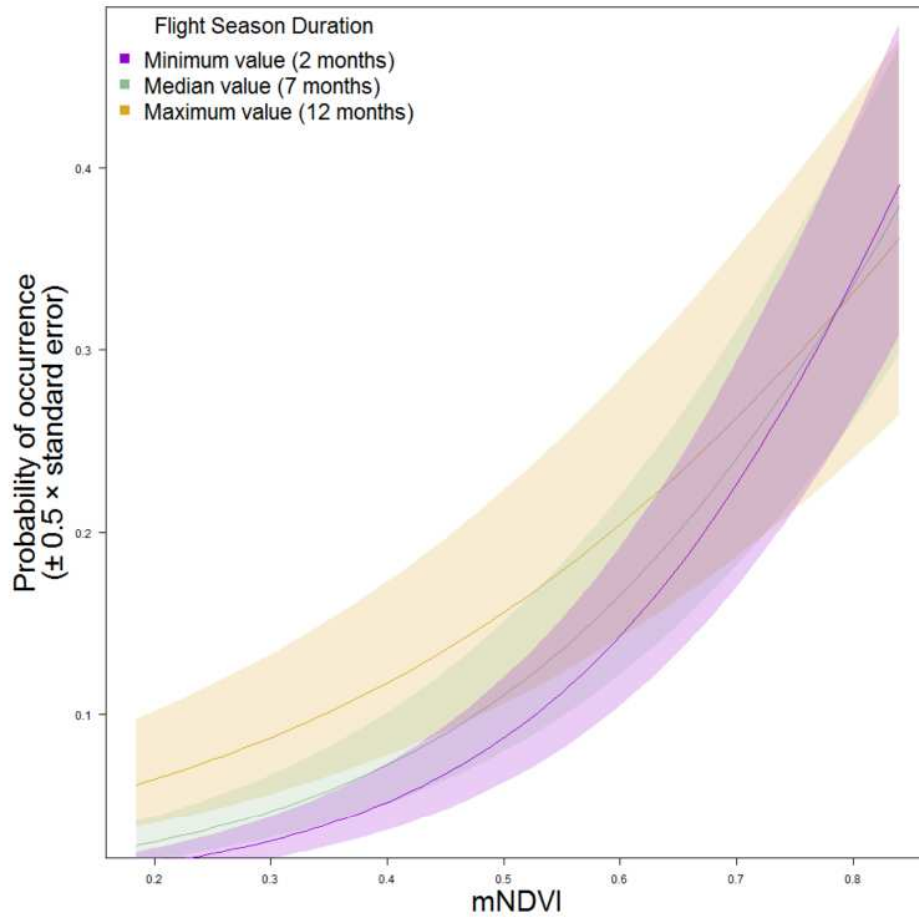


Figure B.2: Relationship between the probability of species presence and mNDVI, at three different flight season durations (minimum, median, and maximum). Error bars represent half the standard error, to ease comparison between slopes. Coefficient estimate of flight season duration $\times$ mNDVI = -0.23 (95% bootstrapped confidence intervals, bCIs = -0.40 and -0.07). Note that where bCIs do not cross zero, the coefficient estimate is taken to be significant.

APPENDIX C

Chapter 4 Appendix

C.1 COMPARING METHODS OF DEALING WITH COMPLETE SEPARATION OF DATA

Results shown are for species sensitivities to all human-dominated land-uses.

Figure C.1: The Species Sensitivity Index a) estimate and b) associated standard error as calculated using two methods: bayesian generalized linear models (bayesglm function, arm package, Gelman *et al.* 2008) or non-bayesian generalized linear models (glm function in R). The 1:1 line is shown. Points in grey are where species were present in some intact and some converted sites. Points in red and blue show cases where there was complete separation of the data (i.e., species were absent either from all intact sites or all converted sites). Panel a) shows that where there is no complete separation, estimates of SSI are similar between the two methods, but bayesian generalized linear models tend to provide more extreme estimates in cases of complete separation. Panel b) shows that the standard error of SSIs tended to be more conservative using the non-bayesian generalized linear models, particularly in cases of complete separation.

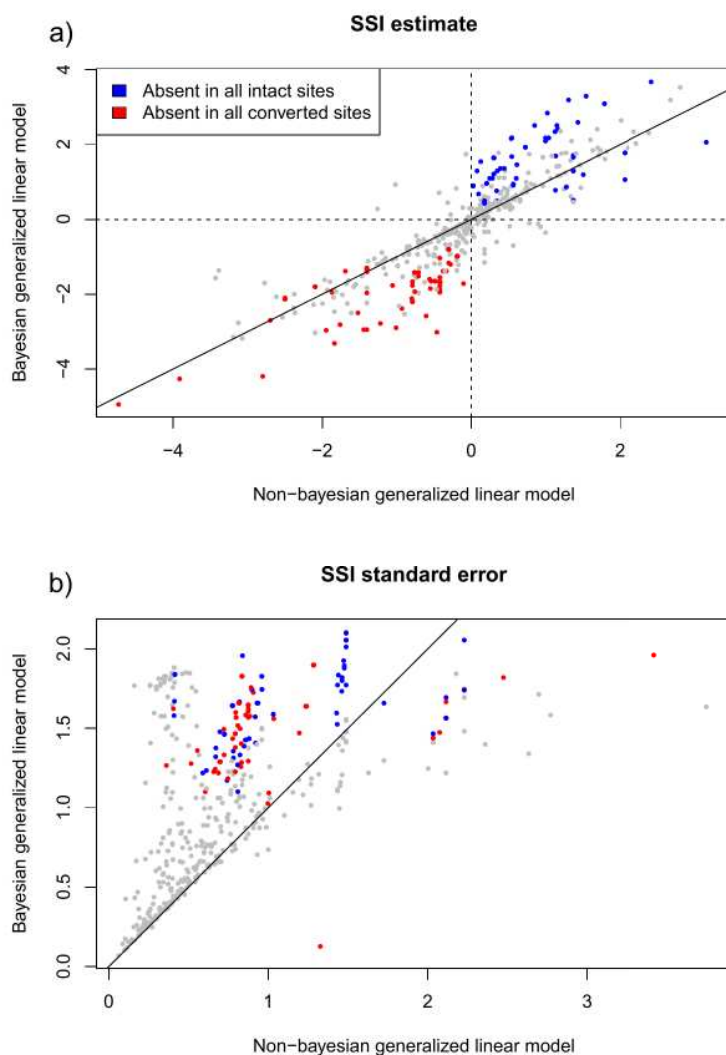
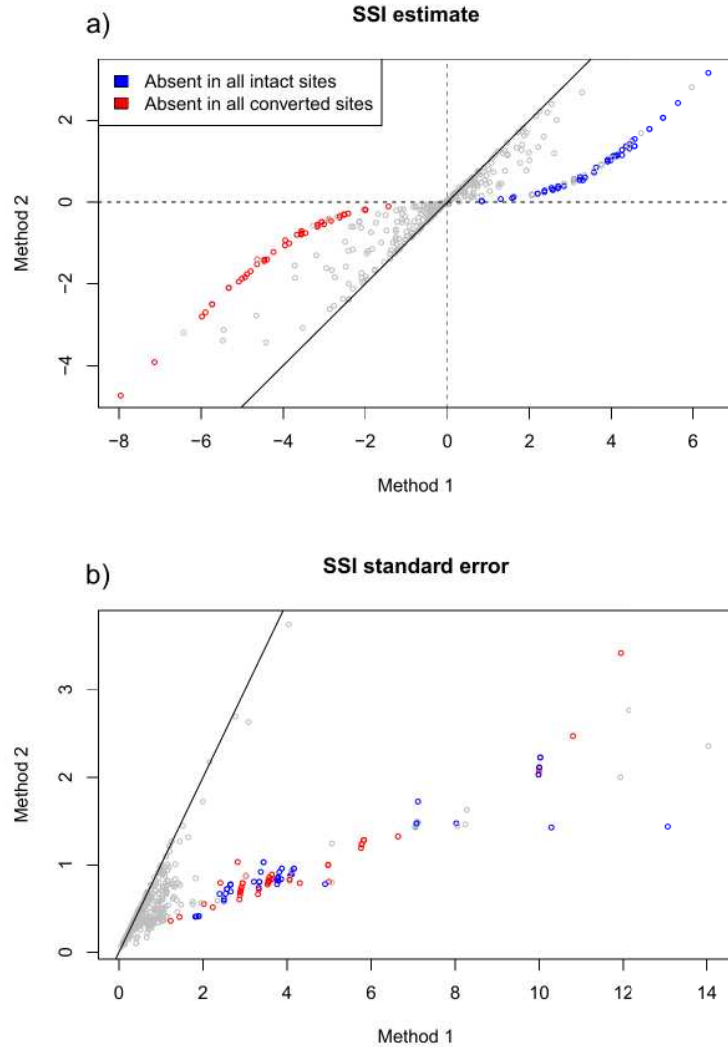


Figure C.2: The Species Sensitivity Index a) estimate and b) associated standard error as calculated using two methods. Method 1 replaces all zero values with the smallest non-zero abundance value across all studies in the dataset (0.1). In Method 2, if the abundance measurements in a study are count data, zero abundances get a value of 0.25; if the abundance measurements are not counts (e.g., densities or effort-corrected abundance), zero values are replaced with $0.25 \times$ the smallest non-zero value in that study. The 1:1 line is shown. Points in grey are where species were present in some intact and some converted sites. Points in red and blue show cases where there was complete separation of the data (i.e., species were absent either from all intact sites or all converted sites). Both the Species Sensitivity Index (SSI) estimates (panel a) and their associated standard errors (b) vary greatly with the method used.



C.2 VARIATION IN SSI DEPENDING ON PRESENCE IN THE ORIGINAL PHYLOGENETIC TREE

Using ordinary linear models, I assessed whether the estimate or standard error of Species Sensitivity Indices (SSIs) varied depending on whether or not species were already in the phylogenetic tree constructed by Hedtke *et al.* (2013). Standard errors were log-transformed to improve normality of residuals. Model assumptions were checked and were found to be reasonable.

SSI estimates did not vary significantly between species already in the tree and those that were missing ($F_{1,493} = 0.158, p = 0.69$). In contrast, standard errors were significantly lower for species already present in the tree relative to those that were missing from the tree ($F_{1,493} = 27.45, p < 0.001$).

Table C.1: Details of bee clades (subsections of the tree, within each of which the placement of missing species was estimated using *pastis* (Thomas *et al.* 2013) and MrBayes (Ronquist *et al.* 2012)). Percentage bootstrap support for the node is shown for the genus tree from Hedtke *et al.* (2013) unless indicated otherwise. The number of generations run in MrBayes is also provided (some larger clades were run for longer in order to reach convergence).

Family	Clade	Bootstrap support	Generations (millions)
Apidae	Meloponini, Bombini, Apini	74	200
Apidae	Euglossini	100	100
Apidae	Centridini (Centris)	100	100
Apidae	Centridini (Epicharis)	100	100
Apidae	Allodapini and Ceratinini	100	100
Apidae	Manuelini	NA ¹	100
Apidae	Xylocopini	85 ²	100
Apidae	Epeolini, Brachynomadini, ammobatoidini, Biastini, Townsendiellini, Neolarrini, Nomadini, Hexepeoplinae, Ammobatini, Melectini, Caenoprospidini, Ericrocidini, Rhathymini, Esepeolini, Osirini (Epeoloides), Protepeolini, Osirini (Osiris), Tetrapedini (Coelioxoides), Osirini (Parepeolus)	99	100
Apidae	Eucerini, Ancylini, Emphorini, Tapinotaspidini, Exomalopsini, Emphorini	100	100
Apidae	Anthophorini	100	100
Andrenidae	Andreninae	100	100
Andrenidae	Panurginae	99	100
Halictidae	Halictini	97	100
Halictidae	Sphecodini	100	100
Halictidae	Caenohalictini	99	100
Halictidae	Augochlorini	100	100
Halictidae	Nomiinae	100	100
Halictidae	Rophitinae	100	100
Halictidae	Nomiodinae	100	100
Melittidae	Melittidae	98	100
Coletidae	Hylaeinae, Scapterinae, Euryglossinae, Xeromelissinae	97	200
Coletidae	Colletini	100	100
Coletidae	Neophashaeinae	100	100
Megachilidae	Megachilini	100	100

¹No value available as only one species from this tribe is in the original tree

²Taken from species-level tree as only one genus is in this clade

Megachilidae	Lithurgini	100	100
Megachilidae	Heriades	100	100
Megachilidae	Anthidini (anthidiellum & anthidini)	100	100
Megachilidae	Osmini	100	100

C.3 SPECIES SENSITIVITIES

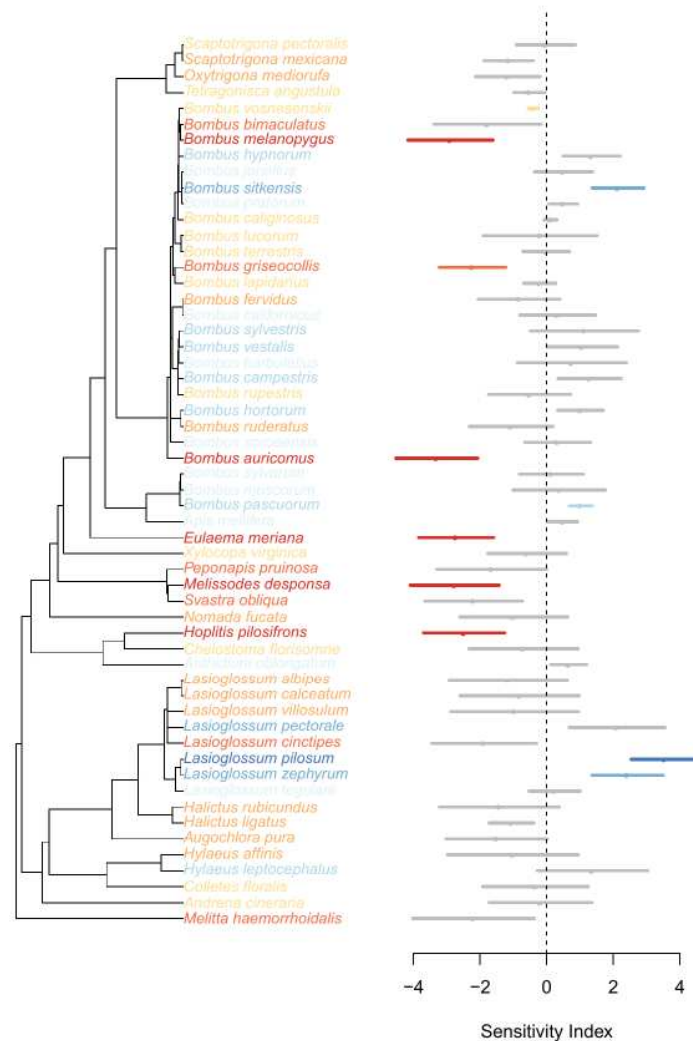


Figure C.3: Phylogenetic signal in species' sensitivity to urban areas. Tips of the phylogeny are coloured according to the species' sensitivity: from blue to red indicate less to more sensitive. The right panel shows species sensitivity $\pm$ the standard error. Points are coloured when the species' abundance was significantly different between (semi-) natural vegetation and urban areas.

APPENDIX D

Chapter 5 Appendix

Table D.1: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (standard error, bias, confidence intervals) for the model of log-transformed taxonomic diversity. Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero (indicated by significance stars). The first level of the land-use and intensity factor (Natural/semi-natural vegetation) forms part of the intercept term and so does not explicitly appear in the coefficients table.

Coefficient	Original estimate	Standard error	bootstrapped Standard error	Bias	Lower 95% Confidence Interval	Upper 95% Confidence Interval	
Intercept	1.46	0.15	0.16	-0.00	1.16	1.77	
Pasture	-0.39	0.15	0.16	0.01	-0.71	-0.08	*
Low-intensity cropland	-0.14	0.18	0.19	0.01	-0.50	0.23	
Medium-intensity cropland	-0.53	0.17	0.18	0.01	-0.89	-0.20	*
High-intensity cropland	-0.50	0.17	0.17	0.01	-0.84	-0.15	*
Urban	0.08	0.13	0.13	0.01	-0.18	0.35	

Table D.2: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (standard error, bias, confidence intervals) for the model of functional diversity. Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero (indicated by significance stars). The first level of the land-use and intensity factor (Natural/semi-natural vegetation) forms part of the intercept term and so does not explicitly appear in the coefficients table. As log-transformed human population density (HPD) was scaled, the intercept is the mean logged HPD.

Coefficient	Original estimate	Standard error	bootstrapped Standard error	Bias	Lower 95% Confidence Interval	Upper 95% Confidence Interval	
Intercept	1.71	0.08	0.08	0.00	1.56	1.87	
Pasture	-0.21	0.08	0.08	-0.00	-0.38	-0.06	*
Low-intensity cropland	-0.04	0.09	0.10	-0.00	-0.23	0.14	
Medium-intensity cropland	-0.25	0.09	0.09	-0.00	-0.44	-0.08	*
High-intensity cropland	-0.24	0.09	0.09	-0.00	-0.43	-0.07	*
Urban	0.00	0.11	0.11	0.00	-0.20	0.21	
Semi-natural vegetation: HPD	-0.30	1.15	1.18	-0.02	-2.61	1.88	
Pasture: HPD	-0.17	1.75	1.81	-0.04	-3.74	3.46	
Low-intensity cropland: HPD	1.15	1.64	1.68	-0.02	-2.18	4.40	
Medium-intensity cropland: HPD	-4.04	1.59	1.61	-0.00	-7.16	-0.84	*
High-intensity cropland: HPD	1.13	1.48	1.53	0.01	-1.84	4.17	
Urban: HPD	0.29	1.71	1.65	0.07	-2.85	3.80	

Table D.3: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (standard error, bias, confidence intervals) for the model of phylogenetic diversity. Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero (indicated by significance stars). The first level of the land-use and intensity factor (Natural/semi-natural vegetation) forms part of the intercept term and so does not explicitly appear in the coefficients table. As log-transformed human population density (HPD) was scaled, the intercept is the mean logged HPD.

Coefficient	Original estimate	Standard error	bootstrapped Standard error	Bias	Lower 95% Confidence Interval	Upper 95% Confidence Interval	
Intercept	1.50	0.06	0.06	-0.00	1.38	1.61	
Pasture	-0.15	0.06	0.06	0.00	-0.26	-0.03	*
Low-intensity cropland	-0.03	0.07	0.07	0.00	-0.16	0.10	
Medium-intensity cropland	-0.16	0.06	0.06	-0.00	-0.29	-0.03	*
High-intensity cropland	-0.15	0.06	0.07	0.00	-0.29	-0.02	*
Urban	-0.00	0.08	0.08	-0.00	-0.17	0.16	
Semi-natural vegetation: HPD	-1.03	0.79	0.79	-0.00	-2.62	0.50	
Pasture: HPD	1.40	1.20	1.25	-0.01	-0.96	3.79	
Low-intensity cropland: HPD	1.65	1.10	1.13	0.03	-0.52	3.89	
Medium-intensity cropland: HPD	-1.41	1.07	1.09	0.01	-3.50	0.83	
High-intensity cropland: HPD	1.67	1.00	1.02	0.04	-0.33	3.87	
Urban: HPD	0.48	1.17	1.19	0.05	-1.82	2.92	

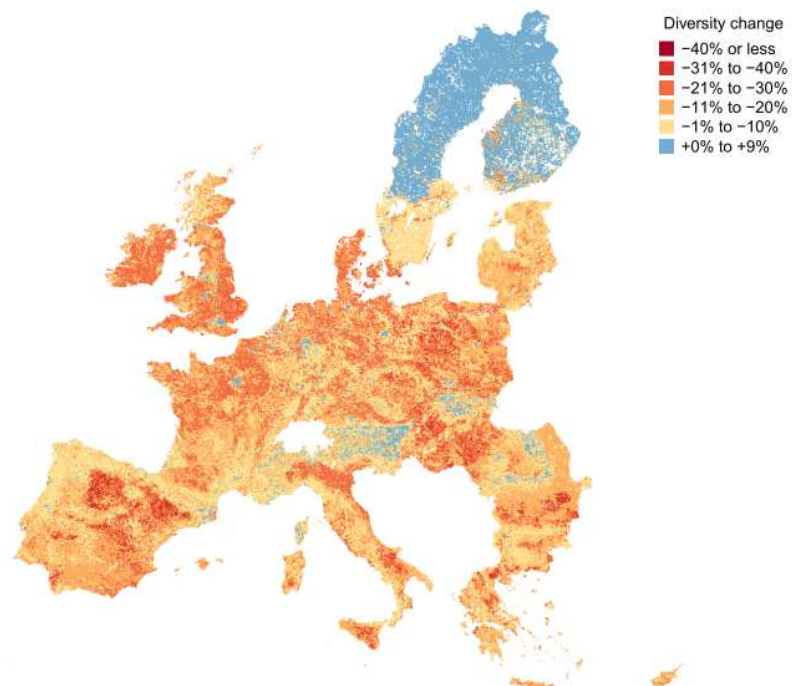


Figure D.1: Percentage difference in taxonomic diversity in different land uses, relative to the natural/semi-natural baseline, for EU27 Countries at a 1km² resolution.

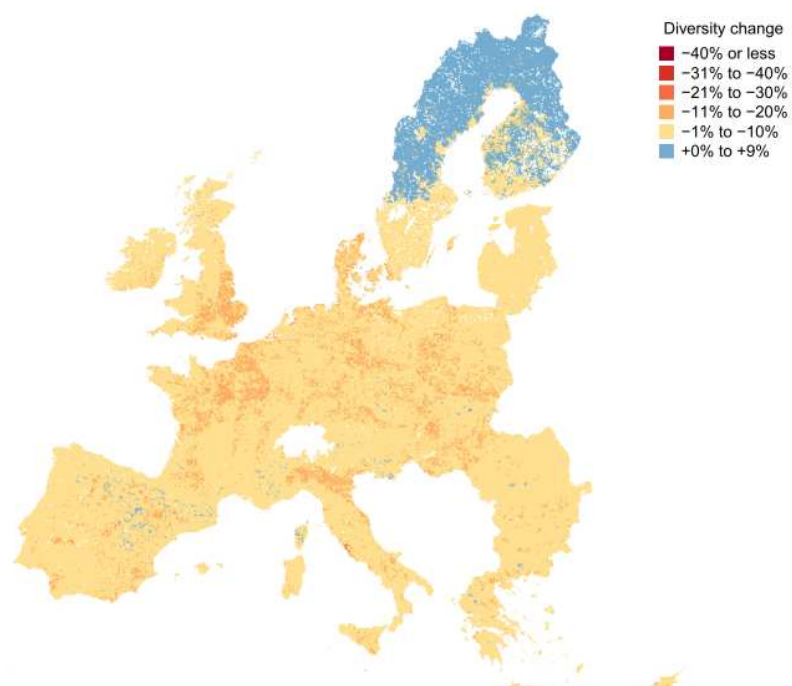


Figure D.2: Percentage difference in functional diversity in different land uses, relative to the natural/semi-natural baseline, for EU27 Countries at a 1km² resolution.

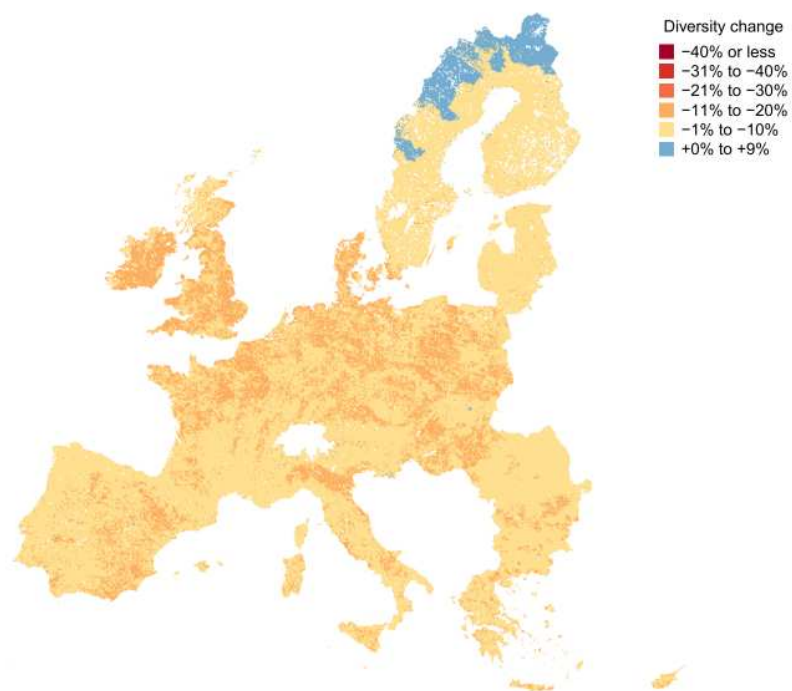


Figure D.3: Percentage difference in phylogenetic diversity in different land uses, relative to the natural/semi-natural baseline, for EU27 Countries at a 1km² resolution.

APPENDIX E

Additional activities

Thank you to the BBSRC and Imperial College London for funding my fellowship at the Parliamentary Office of Science and Technology. I produced the following report for Parliamentarians during my placement and organised a Parliamentary event on the National Pollinator Strategy.



Ancient Woodland



Ancient woodlands are irreplaceable features of our landscapes that can be high in biodiversity or cultural value. This POSTnote summarises the challenges of conserving the biodiversity and cultural heritage of these sites to provide social and economic benefits, while still meeting the development needs of society.

Ancient Woodland in the United Kingdom

Ancient woods are defined in the UK as areas that have been continuously wooded since 1600 (or 1750 in Scotland).⁵⁻⁷ Ancient woods have been used by humans for centuries, providing timber and grazing for livestock,⁸ and can be subdivided into two types:

- Ancient Semi-Natural Woodland (ASNW), which is composed of native trees and shrubs, though it may have been previously managed.^{8,9}
- Plantations on Ancient Woodland Sites (PAWS), which were planted with (often non-native) broadleaved trees and conifers after the First and Second World Wars.^{5,10} PAWS are often less biodiverse than ASNW, but can retain some features of ancient woods.¹¹⁻¹⁴

The UK's varied climate and geology has led to a diversity of ancient woodland forms, classified according to the variety and frequency of native tree species present.¹⁵ They cannot be recreated, as their composition is a product of environmental conditions and historic management that will not occur again. In addition, many environmental and cultural benefits provided by ancient woods cannot be replicated by recently developed or planted woods, although some benefits are provided by all woodland types (Box 1). The Woodland Trust argues that the irreplaceable status of ancient woodland is not adequately recognised at present and that all sites should be fully protected from

Overview

- Ancient woods cover 2%¹ of UK land and are viewed by NGOs and statutory agencies as important natural and historic resources.
- Ancient woods are recognised in UK planning policy, but do not have statutory protection.²⁻⁴
- Areas of ancient woodland were originally mapped to act as a proxy for areas of high biodiversity, but it is difficult to conclusively identify and value ancient woodland.
- Ancient woods cannot be recreated so conservation efforts focus on improving the condition and resilience of existing sites.
- Opinion varies on which measures could effectively contribute to environmental compensation if ancient woods are unavoidably lost to development.

development. However, the need for development is growing; the Government is committed to increasing housing availability¹⁶⁻¹⁹ and to improving infrastructure through projects like the High Speed Rail Link (HS2).²⁰⁻²²

Box 1. Benefits of Ancient Woodland

- The longevity and historical management of ancient woods have given rise to rich, distinctive communities of plants and animals,^{23,24} some of which are of international importance (e.g. lichen in Scottish ancient pinewoods).²⁵
- Ancient woodland soils are relatively undisturbed, and may preserve distinct species communities and natural ecological processes, such as decomposition and nutrient cycling.^{26,27}
- Ancient woods are often high in biodiversity,²³ which can enhance the value of environmental and social wellbeing benefits of woods.^{28,29}
- The soils and veteran (ancient) trees in ancient woods are important carbon stores³⁰ and may help to reduce net carbon emissions.³¹
- Ancient woods are a rich historical, cultural and symbolic resource. They often contain archaeological relicts of previous ways of life, such as hearths or kilns.³² Veteran trees are also archaeological relicts, as their age and structure are often a result of past human use.
- Like all green spaces, woods provide a range of social benefits for humans, including improving physical and mental wellbeing.³³
- All woods, including ancient and recently planted woods, can contribute to flood mitigation, fuel production, carbon sequestration and reduction of air and noise pollution.³⁴

The Status of Ancient Woodland

The extent and distribution of UK ancient woodland is suggested on the Ancient Woodland Inventory (AWI).⁵ According to the AWI, ancient woodland is widely dispersed, covering approximately 2% of the UK's land mass.^{1,5}

Identifying Ancient Woodland

The AWI was first developed in the 1980s to map ancient woodland as a proxy for likely areas of high biodiversity. The AWI provisionally identifies ancient woods by comparing current and historical maps, but identification can be supported with other lines of evidence.⁵ In England, Wales and Northern Ireland, the initial maps used to develop the AWI date back only to the 1800s.^{5,35} With some map interpretation, the presumption is that any woods existing in the 1800s were likely to be present since 1600 unless evidence is provided to the contrary.³⁶ In Scotland, the definition of ancient woodland was shifted to coincide with the earliest sufficient map evidence (1750).³⁶ Identification is still not conclusive in any country, as map evidence is not infallible, but classifications can be supported using multiple lines of evidence, including:

- Historical evidence, such as earlier historical maps and documents detailing woodland management.³⁷
- Archaeological relics of traditional woodland management, such as hearths and kilns. Woodland boundary features are also considered archaeological structures that are distinctive in ancient woods.³⁷
- Biological features such as coppice stools and veteran (ancient) trees that can indicate how long the wood has been in existence. In addition, the presence of ancient woodland 'indicator species' can help to identify ancient woods.³⁸ These are species of plants, animals and lichens that have a strong association with ancient woodland, such as Herb-Paris, the Black Hairstreak butterfly and Tree Lungwort.^{8,39}
- The landscape context, such as whether the land is particularly steep or infertile, as ancient woods are likely to be located in areas unsuitable for agriculture. Ancient woods are also often close to old parish boundaries or common land.³⁷

Interpretation of this evidence involves expert judgement as combinations of these features can also be found in recent woods.^{38,40-42} The identification of ancient woods on the AWI is ongoing, but the evidence for these classifications is not peer-reviewed.

Revision of the Ancient Woodland Inventory

The AWI is not a complete overview of ancient woodland status; not only can some sites be incorrectly included because of difficulties in interpreting evidence, but some sites are also incorrectly excluded. Depending on the purpose of the historical map source, woods may have been recorded inaccurately, if at all, as is often the case with wood-pasture.^{36,37} Wood-pasture is a form of ancient woodland that has been managed for timber and grazed by domestic livestock and deer.⁴³ Veteran trees, which can be centuries old, are often present; they have high cultural value and are host to many rare species of plants and

invertebrates.⁴⁴ However, wood-pasture is often not included on the AWI as it was rarely marked on historical maps due to its low tree density, and ancient woodland indicator plants may not be present.^{5,36,41}

The original AWI also deliberately excluded sites that were smaller than two hectares;⁵ there were simply too many small sites to identify, as it was traced by hand. Using current mapping software, the AWI has been revised to include these small sites for many areas of the UK. However, validating the identification of small sites is difficult and costly as the historical and biological evidence are often uncertain.^{23,45} Continued revisions may provide a more complete overview of ancient woodland occurrence, but with uncertain accuracy. Revisions may also be quickly outdated as Local Authorities, land-owners and developers are not required to report ancient woodland loss. Data on woodland loss could be gained from the National Forest Inventory (NFI), which regularly uses aerial photographs to assess the area, amount and location of woods in Great Britain.⁴⁶

Assessing the Value of Sites

The value of ancient woods will depend on the condition of the site. For instance, some small, poorly managed ancient woods have been found to be lower in plant diversity than larger, sustainably managed woods.²³ Readily available data on woodland condition could inform planning decisions by Local Authorities: loss of a high-condition site that provides greater environmental and cultural benefits or linkages to other sites may be less desirable than loss of a low-condition site providing fewer benefits. However, the AWI does not contain information on site condition beyond its status as PAWS or ASNW.³⁶ Local Authorities may lack the expertise or time to make these assessments: many no longer have in-house ecologists or archaeologists, or the funds to train or contract in these specialists.⁴⁷

Even where expertise is available, environmental, cultural and wellbeing benefits are difficult to evaluate (POSTnote 378 and 421). Visual assessments of species occurrence can give an indication of a site's ecological condition,⁴¹ but may be too superficial as they exclude other important features such as soil structure and fauna.⁴⁷ In addition, there is little information on the historical value of sites,⁴⁷ despite advances in remote sensing technology that aid identification of archaeological relics.⁴⁸ It is even more difficult to assess site value in terms of its wider importance in the landscape and human wellbeing benefits. However, the 2011 UK National Ecosystem Assessment and its follow on projects are advocating new ways of valuing environmental and social benefits.

Planning Policy

As a habitat type, ancient woodland has no statutory protection *per se*, but it is explicitly mentioned in planning policy in Great Britain:

- English policy prohibits developments that damage ancient woods "unless the benefits of the development... outweigh the loss".² This is echoed in the Draft National Networks policy statement for developing nationally

important infrastructure⁴⁸ and Natural England's Standing Advice for Ancient Woodland and Veteran Trees.⁵⁰

- Scottish policy recognises that the value of ancient woods should be considered in planning decisions.³
- Welsh policy states that ancient woods should be protected from development that would result in significant damage.⁴

Implementing these policies is challenging as it is difficult to conclusively identify and value ancient woods. This is not an issue in Northern Ireland, where planning policy does not specifically mention ancient woods, instead aiming to protect all existing woods "wherever possible".⁵¹

Additional Protection

Some features in ancient woods are protected (Box 2) and sites can also be designated for their wildlife value. Many ancient woods are Local Wildlife Sites⁵² and are encompassed by the Biodiversity Action Plan list of priority habitats (NERC Act 2006). Some sites also have statutory designation as National Nature Reserves, Special Areas of Conservation, or Sites or Areas of Special Scientific Interest (SSSI/ASSI).⁵³ Statutory designation offers the strongest legal protection from loss and deterioration in condition, but only 20% of ancient woods are SSSIs.^{53,54} In addition, there is no SSSI equivalent for culturally important woods, potentially leaving sites with high historic but low ecological value with less protection.

No Net Loss of Biodiversity & Ancient Woodland

Planning policy attempts to balance the value of ancient woodland with the need for development. If damage to ancient woodland cannot be avoided or mitigated, Defra suggests that developers in England should compensate for such damage by providing the highest biodiversity benefits possible in return. However, the Woodland Trust argues that there will be a net loss of biodiversity if ancient woodland is damaged, as compensation cannot re-create ancient woodland.

Offsetting and Compensation

Biodiversity offsetting provides a biodiversity gain through conservation activities (POSTnote 369). Guidance from the Business and Biodiversity Offsets Programme states that offsetting requires like for like replacement of biodiversity.⁵⁵ Replacement of ancient woodland, and hence offsetting, is

Box 2. Legislation Protecting Features of Ancient Woodland

- Trees can be protected from felling through The Forestry (Felling of Trees) Regulations (1979 for Great Britain and 2013 for Northern Ireland) and Tree Preservation Orders.
- Many species that commonly inhabit ancient woods are protected by The EU Habitats Directive, the EU Wild Birds Directive, The Wildlife and Countryside Act 1981 (Great Britain) and The Wildlife (Northern Ireland) Order 1985, The Conservation of Habitats and Species Regulations 2010 (England & Wales), The Habitat Regulations 1994 (Scotland) and The Conservation (Natural Habitats, etc.) Regulations (Northern Ireland) 1995.
- Archaeological relics in ancient woods may be scheduled and protected by The Ancient Monuments and Archaeological Areas Act 1979 and the Historic Monuments and Archaeological Objects (Northern Ireland) Order.

not possible.^{50,56,57} However, offsetting metrics for ancient woods have been produced for the HS2 development. The Environmental Audit Committee has considered whether offsetting metrics should be used to determine what compensation (as opposed to offsets) is adequate for damage to ancient woods.⁵⁸ Compensation through the creation of other habitats, such as new woods can provide habitats for many species of interest but does not replace lost ancient woodland features.^{23,59} Studies suggest that compensatory habitat may be of higher value if well managed and located close to existing ancient woods while avoiding damage to other important habitats.^{23,59,60}

Habitat Translocation

The Joint Nature Conservation Committee suggests that partial compensation for ancient woodland loss may be provided by habitat translocation (Box 3).⁶¹ This process attempts to salvage some ancient woodland features by moving soil, ground flora, and coppice stools – along with the accompanying invertebrates – to a new area.^{62,63} This will not replace the full value of the original habitat; the soil composition, structure, biodiversity and ecological processes cannot be replicated.⁵⁰ Practitioner guidelines have been compiled from case studies, but few long-term or experimental studies exist, so outcomes are uncertain.^{64,65} Given the expense of translocation and the risk of failure, Natural England suggests that in addition to translocation, undertaking conservation activities to enhance the value of remaining ancient woodland sites would be a more appropriate form of compensation.

Monitoring and Management of Compensation Habitat

Long-term management and monitoring of compensation activities can help ensure that a high biodiversity gain is achieved⁶² but there is no legal obligation for management or monitoring. Commentators suggest that if minimum requirements were in place, they must be sufficiently high to guarantee environmental benefits. There is also no automatic requirement for developers to assure funding for long-term activities (50-100 years).

Conservation Policy

UK forestry policy emphasises the importance of conserving ancient woods by improving and maintaining site condition.⁶⁷⁻⁷⁰ Compensation for loss to development could include such conservation activities (Box 4).

Box 3. Ancient Woodland Translocation for the Channel Tunnel

The development of the Channel Tunnel Terminal resulted in the loss of Biggins Wood, a five hectare ancient wood.⁶³ In 1986, the developers (Eurotunnel) attempted to preserve some of the site value by habitat translocation. Soil and ground flora were transferred to a receptor site using a dump truck and the site planted with native trees and shrubs. Six years after translocation, a woodland had developed on the receptor site that contained most of the plant species originally recorded in Biggins Wood (83 of 99 species), but also 93 additional species.⁶³ Some consider this to be a failure because of low similarity between the ancient wood and receptor site, but it is difficult to judge the outcome of this scheme given the lack of long-term monitoring.⁶⁶

Improving Woodland Condition

Most UK ancient woods have been unmanaged for decades.⁹ In some larger sites, natural ecological processes may maintain biodiversity but in others, lack of management has led to over-shading, reducing biodiversity.⁹ Standing deadwood and overgrown vegetation because of lack of management can also lower accessibility, affecting social benefits.⁷¹ Re-instating stages of felling and regrowth to woods that have been traditionally managed in this way may enhance the value of sites, and felled timber can be sold as wood fuel.

Managing Animal Species

Management of animal species may also help to improve site condition, but there are often different priorities to address from conservationists, hunters, land-owners and the public. For instance, pheasant rearing provides an economic gain to many woodland owners and can promote site management.⁷² Although pheasant rearing may reduce biodiversity by overstocking, good management can seek to balance both ecological and economic benefits.⁷³⁻⁷⁵ Overgrazing by deer can also reduce the number of plant and animal species present in ancient woods.^{74,76,77} In Scotland, overgrazing is the biggest cause of damage to ancient woodland condition and loss, with development causing far fewer losses of ancient woods.⁷⁸

Habitat Restoration

PAWS tend to have lower biodiversity than ASNW¹³ but they can have high cultural importance and may still retain many valuable semi-natural features, such as pockets of ancient woodland indicator species.¹⁴ The aim of restoration is to maintain and enhance these features by removing planted conifers or other non-native species.⁸¹ However, conifers can provide economic benefits to the land-owners. It is uncertain which method of restoration – gradual conifer removal or clear-felling – is best for simultaneously conserving biodiversity and cultural heritage, whilst ensuring economic viability, as research on long-term effects is lacking.^{74,82-85} However, the Woodland Trust favours gradual conifer removal in most cases.⁸⁶

Mitigating Impacts from Surrounding Land-Uses

Small ancient woods are particularly vulnerable to impacts from surrounding land-uses, such as chemical pollutants from development and agriculture.^{87,88} For instance, fertiliser from cropland can alter the soil chemistry, plant species presence and plant growth 100m into an adjacent ancient

Box 4. A21 Scheme Compensation

The approved development to widen the A21 will damage or destroy 9 ha of ancient woodland. This includes 5.1 ha of ASNW and 3.9 ha PAWS, planted with sweet chestnut trees. As compensation for loss, ancient woodland soil, ground flora and coppice stools will be translocated to sites with similar soil characteristics to original sites, which can increase the chances of success.⁹² This will create 18.1 ha of new woodland (double the area lost); the Highways Agency, who are the developers, have made a commitment to manage the area for at least 25 years. 26.4 ha of remaining ancient woods will be managed for ten years to improve condition.^{79,90}

wood. Planting buffers around the site can help mitigate this damage, but the necessary width is not well defined.⁸⁹ In addition, buffers can alter the woodland boundary features, which archaeologists often see as historically significant and which can shelter many important species.⁹⁰⁻⁹²

Promoting resilience to environmental change

Ancient woods are likely to change character in response to future environmental change.⁹³ For example, lowland beech trees, which are vulnerable to drought, may be replaced by oak as summers become drier.^{93,94} It may not be possible to mitigate the impacts of some pressures, such as nitrogen pollution (Box 5). In addition, it is unknown how different forms of environmental change will interact to affect woods.⁹³ For instance, tree diseases are a major threat to ancient woods,⁹ but it is difficult to predict outbreaks under changing climatic conditions.^{95,96} Increasing the species diversity of woods may maximise the chances that some species will survive unpredictable changes, particularly in Scotland where native tree diversity is lower.⁹⁷ This could be done by creating new woods to expand ancient woods, as larger sites tend to have higher biodiversity.²³ Woodland creation through planting offers the opportunity to use non-native or non-local trees that may be more resilient to environmental change.⁹⁸ Woods created through natural regeneration can be high in biodiversity if located close to ancient woods that act as seed sources.²³

Increasing Landscape Connectivity

Ancient woods are often isolated and surrounded by human-dominated land-uses, such as agriculture. This can make it difficult for species to move between woods. Increasing landscape connectivity aims to enhance species movement through the landscape by increasing the amount of semi-natural habitat, such as woodland. With careful planning, increased connectivity may allow species to move to cooler areas as the climate warms, increasing their resilience to climate change without disrupting the historic landscape.⁹² It is unknown whether this will aid ancient woodland plants,⁹⁹ as they tend to have very low mobility,^{100,101} or whether it will instead help spread pests, pathogens and grazing deer (POSTnote 300). In addition, species may not survive if there are no areas to move to, but increasing the amount of high-quality woodland could be achieved by restoring PAWS and creating new woods.^{99,102,103}

Box 5. Nitrogen Pollution

Over 90% of UK woods have exceeded the critical load of nitrogen: that is, the amount of nitrogen deposited to the ground from air pollution is high enough to affect sensitive aspects of the environment.^{104,105} Nitrogen deposition can alter the composition of lichen and plant species in woodland,^{25,106} and increase plant susceptibility to drought and disease.¹⁰⁸ The environmental impacts of nitrogen deposition are already visible in some sites¹⁰⁷ but little is known about how to mitigate these impacts.⁸³

Endnotes

For references, please see:

http://www.parliament.uk/documents/POST/postpn465_Ancient-WoodlandReferences.pdf