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Wild bee diversity across space and time
the role of land use/land cover and climate

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Wild bee diversity across space and time:
the role of land use/land cover and climate

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"*the more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction*"

– Rachel Carson

Summary

Wild bee diversity across space and time: the role of land use/land cover and climate

by Leon MARSHALL

Rapid anthropogenic environmental changes have a widespread detrimental effect on global patterns of biodiversity. Climate change and land use/land cover (LULC) change have long been recognized as two of the drivers of biodiversity loss and shifts in species' distributions. Climate and LULC changes can alter species' habitats through changes in temperature, rainfall and extreme weather patterns, and land conversions from areas rich in resources to areas with insufficient resources. Species are then forced to move into areas with tolerable conditions and adequate resources or face local extinction. To be able to interpret historical dynamics, recognize present day patterns, and project changes under potential futures, it is essential to understand in detail climate and LULC requirements of different species at a variety of different extents and locations.

Wild bees represent an ideal study organism to explore these themes. Wild bee species are needed to pollinate the majority of wild flowers and can greatly influence crop pollination, supporting food provisioning for humans. Wild bees have also experienced significant changes in many areas over the last 100 years, showing large shifts in their distribution patterns, declines in diversity and abundance, and many local extinctions. In order to protect wild bees and mitigate the influence of rapid global changes, it is necessary to quantify the influence of LULC and climate effects on wild bees. Consequently, the general objective of this thesis is to examine how LULC and climate conditions impact the diversity and distribution patterns of wild bee species at different spatial and temporal scales.

To achieve the general objective we focused on three aims: to (1) test the efficacy of using statistical modelling tools to understand wild bee distributions

in the present and future, and suggest how to improve these methods; (2) provide novel understanding of how wild bee community assemblages are structured at large geographical scales and what drives this structure; and (3) quantify and compare how past, present, and future changes to wild bee and specifically, bumblebee distributions are expected to be influenced by LULC and climate changes.

In order to accomplish these aims a variety of statistical techniques were utilized throughout the thesis. In particular, a common theme of the thesis is the use of species distribution models (SDM) to model the relationship between wild bee occurrence records and the environment, and to use this relationship to project distribution patterns. Furthermore, species interactions, phylogenetic relationships and functional species traits were included in the analyses to provide more ecological detail in explaining the observed patterns of diversity and distribution. Firstly, we introduce the background and knowledge gaps in chapter 1, general introduction and then present the material and methods used in the thesis in chapter 2. The three aims are explored across four chapters (3-6) with narrower objectives each representing a separate scientific study. Finally, we explore the relevance and implications of the thesis in chapter 7, general discussion.

The objective of Chapter 3 was to quantify the performance of species distribution models when modelling wild bee distributions. Specifically, we examined how habitat suitability predictions for Dutch wild bees are contingent on the LULC context where a species is predicted to occur and the functional trait groupings of all species. Independent collections made after the construction of SDMs were used to test the models. In total 52 wild bees species, of the total 193 modelled species, were collected in independent collections from agricultural habitats, specifically, arable fields and orchards. The 52 wild bee species were grouped into 4 separate functional trait groups representing small intermediate specialist, small generalist, highly specialised, and large generalist species. Habitat suitability projections were significantly better for highly specialised species and species collected in orchard habitats. The results suggest that SDMs for wild bees can be more or less useful depending on the species modelled. Specifically, projections made for specialist species and within stable habitats are likely to be the most accurate.

The objective of chapter 4 was to build on the results and implications of chapter 3 and to quantify and visualize the influence of habitat filtering and co-occurrence when modelling the assembly patterns of wild bee species. Again, this study was focused on the Netherlands. Firstly, the spatial co-occurrence of all 297 wild bee species was analysed. Wild bee species generally showed a strong positive correlation in co-occurrence. Suggesting, that many wild bee species are found together significantly more than expected by chance alone. Following this, a joint SDM (JSDM) approach was used to classify the significance of habitat filtering, biotic interactions, functional traits and phylogenetic relatedness on the geographic patterns of wild bee assemblages. The results showed that habitat filtering explained the majority of the geographic distribution of wild bee assemblages. The relationship between wild bee species and the environmental conditions was only weakly explained by traits but showed a strong phylogenetic signal, suggesting closely related species have similar habitat filtering requirements. Including species co-occurrence matrices into the JSDM approach improved model performance signifying that there are unexplained factors that certain species pairs require not captured in the modelling process. Overall, the study provides a clear representation of the geographic distribution of wild bee assemblages, the factors influencing this distribution and provides clear implications for wild bee conservation. The results indicate potential conservation units in the form of spatially explicit community and habitat profiles as well as outlining potential indicator species, which are representative of diverse and distinct assemblages.

The objective of chapter 5 was to look at aspects of habitat filtering at broader temporal and spatial scales and precisely to quantify the influence of dynamic land use/land cover projections on the projected distributional change of bumblebees under climate change. Using three model types, (1) only climate change covariates, (2) climate change and static LULC covariates and (3) climate change and dynamic LULC covariates the distribution of 48 bumblebees were modelled at the European and BENELUX scale. There were clear differences in the projections of range changes produced by the different model types. The implication of these results for modelling wild bee species under changing climate are that when available LULC change projections should be utilized in prospective biodiversity scenarios. Furthermore, the results indicate the need for improved and detailed LULC change projections that take into account smaller scale natural habitat types and land management.

Chapter 6 presents a historical look at the impacts of environmental changes in the Pyrenees with the objective to measure a specific case of how the composition and distribution of a wild pollinator group has changed over time due to the influence of LULC and climate changes. Using two collections datasets, one from 1889 and a follow-up conducted in 2005-06, the composition and distribution of the bumblebee, day-flying Lepidoptera and their visited plants were compared. Overall, all groups show an upward shift in mean elevation, but this shift is not evenly spread across all species. For the bumblebees, specialist species are found higher up the mountain and also experience greater shifts in their elevation. Furthermore, community composition does not change drastically. There is also an indication that pollinators and their visited plants are shifting in unison. The results lend support to predicted climate change effects on biodiversity, and indicate certain specialized species that could be in danger of significant declines if conservation efforts are not implemented.

In conclusion, this thesis highlights the significance of historical wild bee occurrence data and the utility of SDMs for investigating key environmental requirements of wild bee species and assessing long-term trends in distribution. We show that wild bees distribution patterns are highly dependent on LULC conditions in the present and future. The work also emphasizes the strong interaction between climate and LULC and how necessary it is to incorporate both in future biodiversity scenarios. It also shows for the first time influence of co-occurrence patterns on the formation of national wild bee assemblages. Which in turn increased our knowledge the processes behind patterns of distribution and multiple measures of diversity, including community, functional and phylogenetic. Finally, this thesis provides significant advice to conserve wild bee species individually and collectively.

The results clearly indicate areas of interest for future studies, which should focus on the complexities and the interactions of the relationships shown here.

The drivers of wild bee decline strongly interact and therefore should be examined simultaneously. In particular, greater focus is needed on the ecological drivers of wild bee distribution patterns, including dispersal capabilities, biotic interactions with flowering plants, other bees and pathogens, as well as how physiological tolerance will influence the impacts of global change. Additionally, future LULC maps and projections which incorporate high-resolution depictions of natural areas and differences in land management will improve our ability to analyse and understand the environmental requirements of wild bees. As wild bee species are expected to continue to decline globally this thesis increases the knowledge and tools available to ensure that high diversity wild bee communities continue to persist.

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List of Abbreviations

AES	**A**gri **E**nvironment **S**chemes
AIC	**A**kaike **I**nformation **C**riterion
ALARM	**A**ssessing **LA**rge-scale environmental **R**isks with tested **M**ethods
ANOVA	**AN**alysis **O**f **VA**riance
ASL	**A**bove **S**ea **L**evel
AUC	**A**rea **U**nder the **C**urve
BAMBU	**B**usiness **A**s **M**ight **B**e **U**sual
BENELUX	**BE**lgium **NE**therlands **LUX**embourg
BIC	**B**ayesian **I**nformation **C**riterion
BBG	**B**estand **B**odem**G**ebruik Productbeschrijving
BRP	**B**asis**R**egistratie Gewas**P**ercelen
COM	**C**limate **O**nly **M**odel
DLM	**D**ynamic LULC **M**odel
EIS	**E**uropean **I**nvertebrate **S**urvey
GIS	**G**eographic **I**nformation **S**ystems
GBM	**G**eneralised **B**oosted **M**odels
GHG	**G**reen**H**ouse **G**as
GLM	**G**eneralised **L**inear **M**odels
GPS	**G**lobal **P**ositioning **S**ystem
GRAS	**GR**owth **A**pplied **S**trategy
HMSC	**H**ierarchical **M**odelling of **S**pecies **C**ommunities
HSD	**H**onestly **S**ignificant **D**ifference
INL	**I**ndex **N**atuur en **L**andschap
IPBES	**I**ntergovernmental science-policy **P**latform on **B**iodiversity and **E**cosystem **S**ervices
IPCC	**I**ntergovernmental **P**anel on **C**limate and **C**hange
JSDM	**J**oint **S**pecies **D**istribution **M**odels
KNMI	**K**oninklijk **N**ederlands **M**eteorologisch **I**nstituut
LMM	**L**inear **M**ixed effects **M**odels
LULC	**L**and **U**se / **L**and **C**over
MAXENT	**MAX**imum **ENT**ropy
MCA	**M**ultiple **C**orrespondence **A**nalysis
MCMC	**M**arkov **C**hain **M**onte **C**arlo
ML	**M**aximum **L**iklihood
MYA	**M**illions of **Y**ears **A**go
PCA	**P**rinciple **C**omponents**A**nalysis
PNC	**P**hylogenetic **N**iche **C**onservatism
SDM	**S**pecies **D**istribution **M**odels
SEDG	**S**ustainable **E**uropean **D**evelopment **G**oal
SLM	**S**tatic LULC **M**odel
RCP	**R**epresentative **C**oncentration **P**athways
ROC	**R**eceiver **O**perating **C**haracteristic

1 General Introduction

L. Marshall

1.1 Overview

Biodiversity is declining globally and some scientists suggest that we are in the midst of a sixth mass extinction event (Barnosky et al. 2011; Ceballos et al. 2015). The central drivers of this extinction are anthropogenic in nature, including climate change, due to increases in atmospheric CO2 and other gases, and land use/land cover (LULC) change, due to urbanization and agricultural intensification among other pressures, (Millennium Ecosystem Assessment 2005; Bellard et al. 2012; Pimm et al. 2014; Ostberg et al. 2015). Bees represent an important group of global pollinators, the majority of which are free living and not managed by humans, i.e. wild. In well studied regions with long-term species records wild bees show a declining trend, particularly the more conspicuous bumblebees (Williams 1982; Biesmeijer et al. 2006; Goulson et al. 2008; Potts et al. 2010; Cameron et al. 2011; Bommarco et al. 2012; Bartomeus et al. 2013; Carvalheiro et al. 2013). Land use/land cover and climate change have been outlined as two of the main drivers of these observed declines, by limiting access to and removing important habitat and feeding resources required by wild bees (Potts et al. 2010; Vanbergen & The Insect Pollinators Initiative 2013). Therefore, to protect wild bees and the pollination services they provide it is of vital importance to understand how LULC and climate interact to drive diversity and distribution of wild bee species. Furthermore, the effects of LULC and climate on wild bee diversity and distribution will vary dependent on the spatial and temporal scale at which it is analysed (Carsten 2005).

Therefore, **the general objective of this thesis is to examine how LULC and climate conditions impact the diversity and distribution patterns of wild bee species at different spatial and temporal scales.** For the majority of wild bee species there is an absence of information regarding the processes which influence their relationship with the environment. Therefore, due to the complexity of these patterns we rely on statistical techniques to explore relationships and hypothesize processes. Using long-term occurrence records and high resolution environmental information we create species distribution models (SDMs), which allow us to predict how environmental factors influence the diversity and distribution of wild bees and how these may change in the future. Consequently, the general objective of the thesis can be split into two separate focus areas; (1) methodological, how SDMs can be used and improved to model the relationship between land use, climate, wild bee species occurrence and community assemblage patterns and (2) applied, how does the relationship between land use and climate influence the distribution patterns of wild bee species and assemblages and what are the implications regarding their decline and conservation.

1.2 Biodiversity and Biodiversity Loss

1.2.1 Measuring Biodiversity

Biological diversity (biodiversity) is a broad concept which includes the entire variability of life on earth and its interactions (Wilson 1988). The concept of biodiversity is often strongly related to ecosystems and ecosystem functioning, specifically that higher biodiversity maintains more complex, higher-quality ecosystems, which consequently provides more services and can better withstand disturbances (MacArthur 1955; Peterson et al. 1998). Biodiversity measurements act as a vital criterion in ecology and conservation and can be measured in a variety of ways (Williams et al. 1993). Biodiversity is often portrayed simply as species richness, the total number of separate species found in a chosen location, however this does not represent all diversity and therefore importance or value of a particular location. Other measurements of biodiversity can be classified at different levels of organization: (i) ecological diversity e.g. landscapes, ecosystems; (ii) genetic diversity e.g. populations, genes; and (iii) organismal diversity e.g. number of species or families (Heywood & Watson 1995; Purvis & Hector 2000). In this thesis we do not limit our definition of biodiversity to species richness. Specifically, in the different chapter's we measure biodiversity using a variety metrics, including beta-diversity [1], functional and phylogenetic diversity, and diversity of interactions. These metrics are used at different scales, examining diversity at local fine-grained scales but also at for whole assemblages and communities and at national scales.

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[1] Beta-diversity is the ratio between regional and local species diversity (Whittaker 1960).

Not only is it important what measure of biodiversity we use but the scale at which it is measured is also essential. For a long time the distribution patterns of biodiversity were thought to be consistent across spatial scale gradients, however changes in both spatial extent (how large a geographic area is) and grain size (unit at which biodiversity is measured) can result in varying conclusions of biodiversity trends (Carsten 2005). Conclusions as to whether biodiversity trends are positive or negative can change depending on the spatial scale at which the analysis occurs (Purvis & Hector 2000). The ability to detect biodiversity patterns depends on the scale at which measurements are made and to define this scale it is necessary to recognize or hypothesize the processes driving these patterns and the scale at which these processes operate (Levin 1992). When examining biodiversity patterns two characteristics of scale are of significant importance, focus and extent. Focus refers to the spatial resolution at which measurements are made, for example measuring species occurrence could be within 10×10 m areas; extent refers to the total geographical space in which measurements are made, for example Europe or the Netherlands (Willig et al. 2003). At different scales different processes are driving the observed patterns, for example at the local scale observed species richness in a community may be driven by resource availability, habitat requirements and biotic interactions. At the regional scale the total diversity, from which the local community is derived, may be driven by geology, the size of the area or climatic conditions. Finally at the broad-scale the regional species diversity is likely affected by evolutionary processes including speciation and extinction (Huston 1999; Gaston 2000). It is therefore fundamental that multiple scales are compared and contrasted when measuring biodiversity patterns using statistical techniques (Gaston 2000).

The same holds true for the importance of the temporal scale at which biodiversity is measured. Changes in global biodiversity can be measured on many time-scales from geological time periods where evolutionary patterns of biodiversity and extinctions can be measured (Purvis & Hector 2000), to more recent term time periods that show the influence of human society on biodiversity through climate (Parmesan & Yohe 2003; Root et al. 2003) and LULC change (Foley et al. 2005), or short-term temporal scales where biodiversity is measured before and after specific disturbances (Hooper et al. 2005). Given the significance of scale, **we specifically target a variety of spatial and temporal scales, and resolutions to measure diversity and distribution patterns throughout this thesis.**

1.2.2 Biodiversity Loss

Globally, biodiversity is being lost at an alarming rate and has been described as a sixth mass extinction event, with the main cause being anthropogenic, due in a large part to the pressure humans impart on the landscape and climate (Barnosky et al. 2011; Ceballos et al. 2015). Pimm and Raven (2000) conclude that even a best case scenario of protecting global biodiversity hotspots from these anthropogenic pressures would still result in the loss of 18% of species. The potential impacts of these biodiversity losses could be far reaching and necessitate actions and initiatives to protect, restore and manage biodiversity. The importance of biodiversity can be considered distinct and separate from humans, often referred to as intrinsic value; from a conservation perspective this implies that biodiversity should be protected because it has a right to exist (Pearson 2016). A more practical view of nature and biodiversity expresses its instrumental value and what use biodiversity has to humans. Consequently, a common inquiry is how much species loss can we afford before the ecosystem functioning is negatively affected and in turn human well-being (Cardinale et al. 2012; Hooper et al. 2012). Specifically, biodiversity loss may impact the stability of food provisioning, regulation and ability to recover from disturbances and natural disasters, and directly impact human health (Díaz et al. 2006; Worm et al. 2006; Cardinale et al. 2012). For example, the loss of crop pollination by wild bees directly impacts food provisioning services (Klein et al. 2007).

1.2.3 Drivers of Biodiversity Loss

Climate Change

Biodiversity loss is occurring due to a number of factors, many of a directly anthropogenic nature. Two of the main drivers, and focus of this thesis, are climate and LULC changes (Millennium Ecosystem Assessment 2005; Bellard et al. 2012; Pimm et al. 2014; Ostberg et al. 2015). Observed changes to the climate over the last century are unmistakable, and have manifested as warmer atmosphere and ocean temperatures, a loss of snow and ice, and an increase in sea level (IPCC 2014). These changes have been driven by anthropogenic greenhouse gas(GHG) emissions which have led to levels of these gases in the atmosphere far higher than ever experienced in modern history and far beyond fluctuations expected by natural variability (IPCC 2014). The implications of warming temperatures on biodiversity include changes in species geographic ranges, alterations to migration patterns and timing, and shifts in community structure and interactions. Increase in temperatures, particular at higher latitudes and elevations are expected to push species polewards and to higher elevations as well as causing shifts to their phenology[2] (Parmesan & Yohe 2003; Menzel et al. 2006). Extreme weather events such as heat waves and heavy rainfall may lead to higher rates of mortality and eventually, population extinctions, alterations to morphological and behavioural characteristics, and mismatches between interacting species (Parmesan et al. 2000).

The likelihood of continued GHG emissions means that existing climate change effects are predicted to worsen in the future. Simulated global surface temperatures suggest increases between 0.3-1.7°C under low emission scenarios (Representative Concentration Pathways (RCP) 2.6) 1.1-3.1°C under medium scenarios (RCP 4.5, RCP 6.0), and 2.6-4.8°C under extreme remission scenarios (RCP 8.5) by 2100 (Fig 1.1; IPCC, 2014). These scenarios of climate change have been used to predict future changes to global biodiversity (Bellard et al. 2012). Pereira et al. (2010) estimate overall losses between 11% and 58% for vertebrates by 2100 under different scenarios of climate change. Thomas et al. (2004) estimate that between 18-35% of species could be committed to extinction under future climate change ranging from low to high emission scenarios. Examining biodiversity loss due to climate change depends on a number of factors including scale effects, scenarios used, species interactions and interactions with other drivers (see Fig 1.2; Bellard et al. 2012). It is therefore vital to try and understand the biology of the species and their interactions with other species and the environment when trying to predict diversity and distribution patterns under a changing climate.

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[2] Phenology is the study of how the environment influences the life-cycle timing of species and populations.

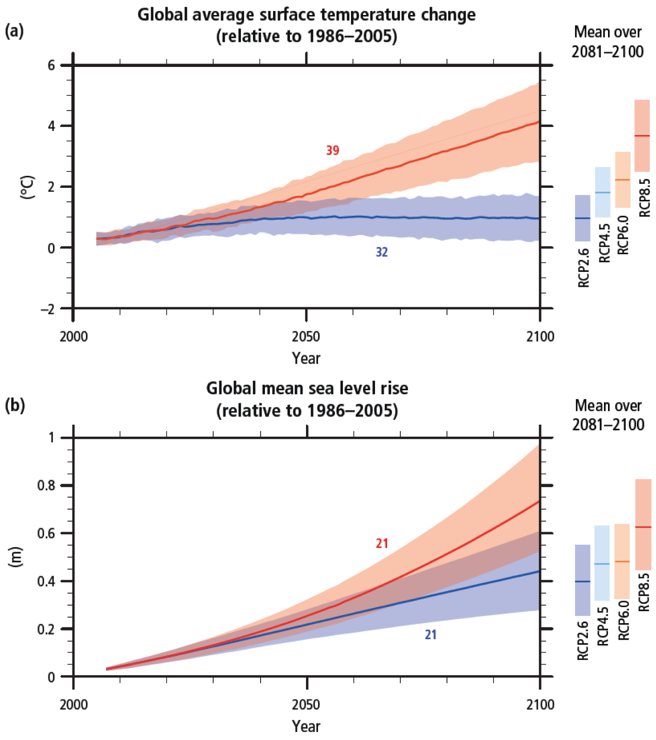

FIG. 1.1: **Modelled changes in global average surface temperature (a) and global mean sea level rise (b) from 2006 to 2100.** The lowest and highest emission scenarios are shown. Coloured bars at the right hand size show the mean and uncertainty for all scenarios. The number above the lines refers to the number of models used to calculate the multi-model mean. Source: figure taken from IPCC (2014).

Land Use/Land Cover Change

Land use/land cover (LULC) change due to intensification of the landscape results in the loss of habitat resources needed by many species and has been proposed as the leading cause of biodiversity loss in the last century (Millennium Ecosystem Assessment 2005; Pimm et al. 2014). One of the leading causes of habitat loss is the conversion of natural areas such as semi-natural grasslands, forest and wetlands into agricultural systems and urban areas (Foley et al. 2005). The loss of natural habitats and the degradation of remaining habitat has already led to biodiversity losses. Terrestrial vertebrate species have declined by 58% between 1970 and 2012, with habitat loss cited as the main cause (WWF

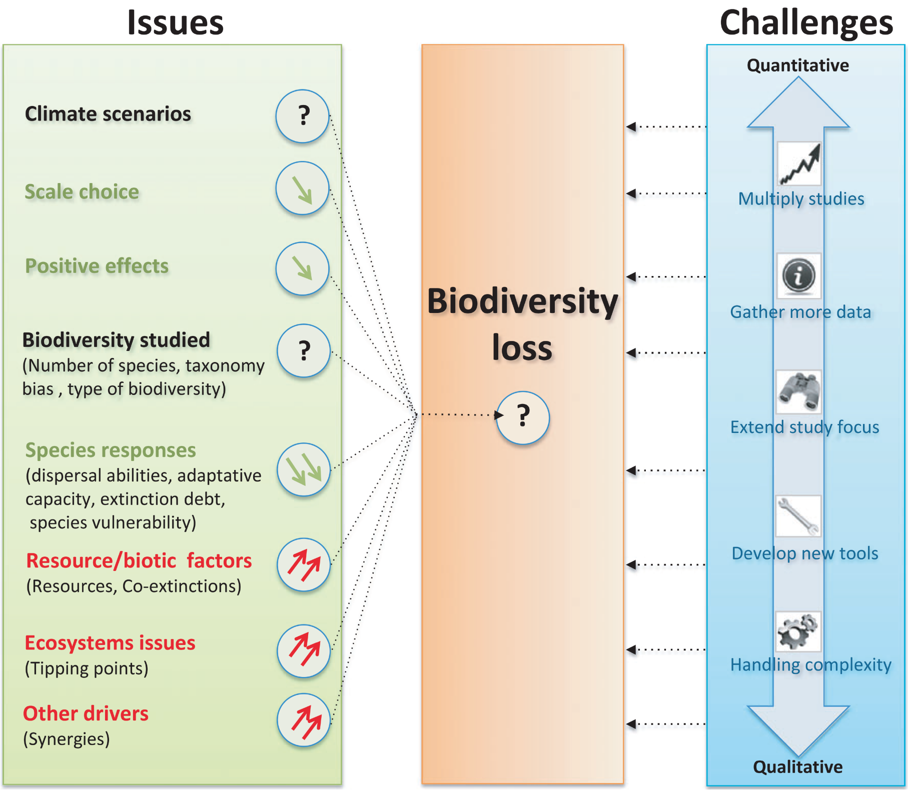

FIG. 1.2: **Issues and challenges for measuring biodiversity losses due to climate change.** Multiple interacting issues are responsible for biodiversity loss. The effect of these issues is often over or underestimated. Therefore there is a number of challenges to better estimate the influence of the different issues. Green factors are likely overestimated, while red factors are likely underestimated; black factors and question marks are used when the direction or extent of error in estimation is unknown; double arrow means a very large expected effect. Source: figure taken from Bellard et al. (2012).

2016). Newbold et al. (2015) estimate that terrestrial biodiversity losses due to land-use and associated changes has already decreased average per sample richness by 13.6% and in the worst affected areas this sample may have decreased by 76%. Newbold et al. (2016) suggest from measurements of remaining biodiversity in local ecosystems that up to 58% of total global surface has been pushed past the safe limit of biodiversity loss, particularly grassland habitats. As with climate change, LULC changes are expected to continue occurring into the future, especially as human populations increase. Global scenarios and expert opinions suggest that significant LULC changes in the future will have the most influence on biodiversity loss for all biomes (Sala et al. 2000).

Compared to modelled climate change projections there are fewer projections of how LULC will likely change in the future (Rounsevell et al. 2006; Titeux et al. 2016). This does not reflect accurately the extent to which LULC is expected to impact biodiversity. The few studies that do utilize LULC change models reach varying conclusion about the importance of LULC change for modelling future biodiversity patterns. Sohl (2014) shows that model performance is lower and range size is greater when LULC projections are excluded from future scenarios of bird distributions in the US. However, Martin et al. (2013) conclude that LULC change projections *in their current form* do not improve future distribution predictions of a European butterfly species. Using only LULC covariates Ficetola et al. (2010) modelled the distribution of bullfrogs, suggesting that habitat suitability would remain relatively stable. However, overall, **LULC and climate change are often examined in isolation** and the interactions between the two, particularly when used to project biodiversity changes, represents a significant gap in our knowledge of how biodiversity losses are likely to progress in the future (de Chazal & Rounsevell 2009; Titeux et al. 2016). **Throughout this thesis we aim to examine the effects of LULC and climate on biodiversity simultaneously, in the past, present and in the future.**

1.2.4 Measuring Biodiversity Loss

As stated earlier, the importance of LULC and climate as drivers of biodiversity loss is indisputable but measuring and predicting their effects at the global scale remains an immense task. Accordingly there are a number of tools available to measure these different types of biodiversity at different scales. The proliferation of online databases for occurrence records, phylogenetic data, conservation status, geographic maps, among others, allows for the collation and dissemination of biodiversity data on a global scale (Purvis & Hector 2000). However, these data generally only come from a few areas in the world and have multiplied in recent years leading to both a spatial and temporal bias in our view of global biodiversity (Boakes et al. 2010). To remedy this situation researchers need detailed occurrence records at the species level that come from long-term monitoring. To ensure accurate estimates of total diversity different collection techniques are required, for example distance sampling[3] or mark recapture[4] allow for the calculation of accurate species abundance values. However, generally these methods are time consuming and expensive and therefore, count statistics (occurrences) are often used (Yoccoz et al. 2001). Furthermore, to understand long-term biodiversity trends it is often necessary to use older collection records, often collated and stored in natural history museums (Ponder et al. 2001). To estimate and predict biodiversity patterns and trends researchers rely on statistical tools to draw conclusions on the distribution of species in areas and time periods that would be infeasible or impossible to sample in their totality. In particular species distribution models (SDMs), which are used throughout this thesis, combine known occurrence records and environmental variables to predict for unsampled areas where species are likely to be distributed (Elith & Leathwick, 2009). Improving our ability to predict and understand biodiversity patterns in the past, present, and future is essential if we are to manage and avoid the problems associated with global changes.

1.3 Wild Bees

Wild bees comprise approximately 20 000 species found worldwide on all continents except for Antarctica (Michener 2000). There are 7 extant families of bees (Fig 1.3). A broad functional distinction between wild bees can be made based on their sociality. The majority of bees are solitary bees which means that the females build their own nests with food resources to deposit their offspring (Linsley 1958). The offspring emerge after the female has died. The non-solitary bees are organized into colonies, with division of labour, and are referred to as social species. These range from highly eusocial bees, where the queen is dependent on the colony and develops differently to other females which are incapable of forming their own colonies; primitively eusocial colonies have queens and workers

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[3] Distance sampling is a method to estimate the total species richness of a chosen area. The methodology is based on line or point transects, the species are surveyed along these lines or from these points and are measured as a perpendicular or radial distance (Buckland et al. 2015).

[4] Mark recapture involves sampling species richness by capturing a subset of a population of species, marking these species and then resurveying the population, the resulting proportion of marked individuals should represent their proportion in relation to the total population size (Southwood & Henderson 2009).

that share morphological and behavioural similarities (Libbrecht & Keller 2015). In Europe the only highly eusocial bees are the western honeybees (*Apis mellifera*). Primitively social species in Europe include species in the genera *Bombus* (bumblebees) and *Lasioglossum*. The bumblebees comprise over 250 species globally in the genus *Bombus* which is the only extant genus in the tribe Bombini which is found in family Apidae (Fig 1.3; Michener 2000). Some bees display a vastly different life history whereby they parasitise the nests of other bees. In the bumblebees there is a sub genus, *Psithyrus* spp.; species of this subgenera subdue or kill the queen of existing colonies and lay eggs reared by the workers of the original colony (Goulson 2010). In the solitary bees this cleptoparasitic behaviour also exists, where females lay eggs in the nest of another bee species and either the larva or the female kills the existing host egg and the new larva utilize the available food provisions (Rozen 2001). The two most diverse genera of cleptoparasitic bees in Europe are *Nomada* spp. and *Sphecodes* spp. The high diversity of wild bees in species number and behaviours means that for many species there is minimal data on distribution patterns and many studies on wild bees focus on the larger, more conspicuous and longer flying bumblebees (Potts et al. 2016b). **Studies looking at the entire community of wild bees in a large geographic area are uncommon, therefore we aim to analyse the patterns of distribution and community structure of all wild bees** at a national scale in chapters 3 and 4. In chapters 5 and 6 the larger spatial and temporal scales involved limit the analysis of long-term changes to the bumblebees for which far more species occurrence data is available.

The important ecological role that the majority of bees provide is the pollination of different plant species. Animals are estimated to be responsible for the pollination of approximately 87% of all flowering plants (Ollerton et al. 2011). Bees are considered as the most important of all animal pollinators because of their diversity, hairiness and reliance on floral resources (Potts et al. 2016a; Ollerton 2017). Bees and angiosperms can form highly specialized mutualisms and the diversity in both groups is strongly linked (Johnson & Steiner 2000; Ollerton 2017). These specialized relationships can be vulnerable to changes in the environment (Schleuning et al. 2016), as both the plant and bee species are dependent on the abundance and survival of the other. However, often the variety of

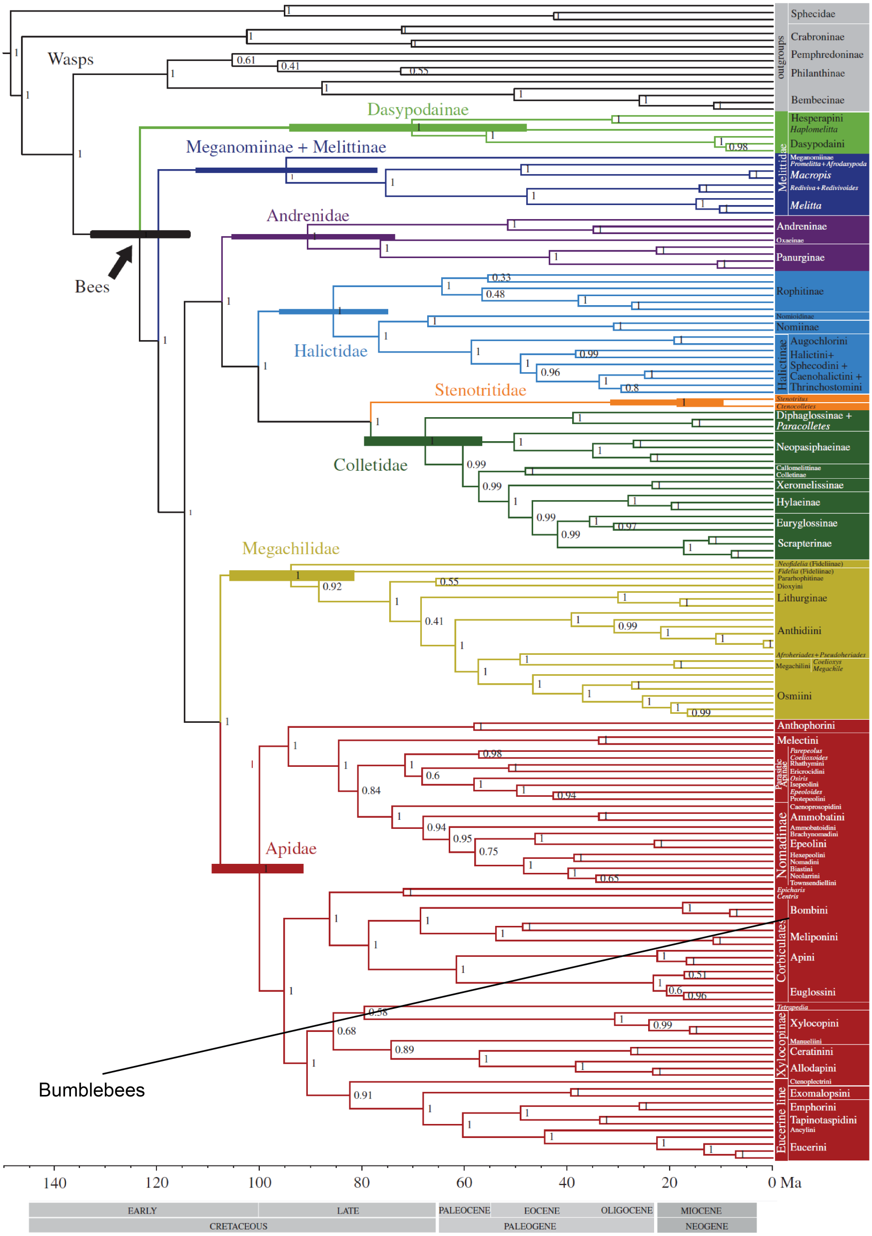

FIG. 1.3: **Time calibrated phylogenetic tree of all bees.** Location of Bumblebees in the bombini tribe shown. Species from six of the seven families are found in the Netherlands, all but Stenotritidae. Source: figure taken and adapted from Cardinal and Danforth (2013).

interactions and generalization of certain species maintains wild plant-pollinator networks (Memmott et al. 2004). Furthermore, as crop pollinators, bees are vitally important for humans. Approximately 75% of crops require some form of animal pollination to improve productivity, of which bees are the most common pollinators (Klein et al. 2007). The importance of pollination services by wild bees can also be measured economically. Total global pollination value has been estimated at over 300 billion us dollars (Lautenbach et al. 2012). Honeybees constitute the most widespread single pollinator species across all crops, but wild pollinator communities contribute as much to world crop pollination (Garibaldi et al. 2013). In addition, pollinator diversity leads to higher and more stable yields (Garibaldi et al. 2011) as different species play important roles at different scales (Winfree et al. 2018). Honey bees, which only comprise seven of the total bee species globally are intensively managed by humans and therefore face their own unique threats which do not necessarily overlap with those faced by wild bees. The landscape ecology and distribution patterns of honey bees are not dealt with in this thesis.

In different crop systems honey bees are usually the most abundant pollinator but are far from being the most efficient[5] and effective[6] crop pollinators, generally visiting fewer flowers per individual and producing lower quality yields when the only pollinator (Garibaldi et al. 2013). A number of wild bee species have an influential role in crop production, this is only a subset of the total wild bee diversity, but is crucial nonetheless (Kleijn et al. 2015). Even in the absence of honey bees wild bees are effective crop pollinators and can improve a number of aspects of crop production, most importantly increasing yield and quality (Garibaldi et al. 2013). Wild pollinators may contribute to crop pollination by replacing managed pollinators (Winfree et al. 2007; Garibaldi et al. 2011), by altering managed pollinator's foraging behaviour (Greenleaf & Kremen 2006; Carvalheiro et al. 2011; Brittain et al. 2013) and improving seed and fruit set through combined pollination (Chagnon et al. 1993). The diversity of wild bees required for pollination of a single crop is limited to a small subset of total diversity (Kleijn

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[5] Pollinator efficiency is the total contribution of a pollinator species to the fruit or seed set of a crop including visitation frequency (Willcox et al. 2017).

[6] Pollinator effectiveness refers to the total seed set of fruit per single pollinator visit (Willcox et al. 2017).

et al. 2015). However, pollinator species turnover across a landscape implies that a far higher total diversity is required to pollinate crops in large-scale agricultural areas (Winfree et al. 2018). Therefore, it is necessary to study wild bee diversity and distributions patterns together at the community scale as the services they provide are likely tied closely to interactions between and within species assemblages. Therefore, **in chapter 4 we take a comprehensive view of wild bee species assemblage patterns to understand how the entire wild bee community interacts and how this is linked to the surrounding landscape**, in particular how the climate and LULC conditions influence the geographic distribution of wild bee assemblages. The pollination service provided by wild bees is under pressure. The global decline of wild bees will significantly impact the pollination services they provide and consequently have a pronounced impact on human society. **This indicates a need to understand where wild bees are distributed and how different factors affect their distribution and diversity patterns** in order to ensure continued provision of their pollination services.

1.3.1 Wild Bee Decline

The important role wild bees play in different ecosystems is under threat. There is considerable evidence of decreases in species richness and diversity of wild bees. However, detailed evidence of decline is only available for a few well studied areas. In the Netherlands and Britain a comparison between species records before and after 1980 showed a considerable decline in species richness of wild bees in many areas, which correlated with a decline in pollinated plants (Biesmeijer et al. 2006). This is supported by a more recent study in Belgium, the Netherlands and the UK that shows significant declines in richness and a shift towards a more homogeneous community before 1990, but suggests that these declines have decreased since 1990 (Carvalheiro et al. 2013). In the United States (US) a study looking at 438 bee species over 140 years found that whilst only bumblebee species showed a significant decline, communities became more homogenized and in particular the diversity of alien species increased (Bartomeus et al. 2013). In Belgium, a comparison of the relative number of species before and after 1950 showed that 25.2% were decreasing nationally, with bumblebees shown to be particularly vulnerable (Rasmont et al. 2005; Vray 2018). Select bumblebees in the

UK and Ireland, generally those emerging late, have also shown significant decreases in range since the 1960s (Williams 1982; Goulson et al. 2006; Fitzpatrick et al. 2007).

At the local scale there are studies that have re-sampled areas where surveys had been conducted in the past. These studies also, generally, show a decreasing trend in wild bee species richness. Bumblebees in Illinois showed dramatic losses over 60 years with half of the species previously found absent from the latest surveys (Grixti et al. 2009). Grasslands in Brazil surveyed 20 years apart over a 60 year period showed a 22% decrease in wild bee species richness (Martins et al. 2013). A study in Colorado grasslands showed more positive results, they observed a generally stable wild bee community when comparing occurrences from 1907 against 2001-05 (Kearns & Oliveras 2009). This suggests that declines are unlikely to be occurring everywhere and that certain spatial locations and habitats are more vulnerable. For example when comparing 14 sites over an 80 year period in the UK, Senapathi et al. (2015) found that species richness declines of bees and wasps were correlated to changes in land cover and particularly in habitats at the borders between land covers. Long-term studies of changing populations are a vital resource to help improve our understanding of how and why wild bees are declining (Bartomeus et al. 2018). Therefore, efforts should be made to repeat surveys when historical data is available, in chapter 6 we have the unique opportunity to compare a mountain pollinator population in 1889 against 2005-06.

The majority of studies have looked at declines in species richness but long-term trends of decline in population size/abundance of wild bee species are almost unknown (Potts et al. 2016b). This is reflected clearly in the IUCN red list of European bees, whereby 57% of species are classified as data deficient, indicating that there is not enough data on species occurrences along a temporal gradient to draw conclusions on population trends (Fig 1.4a; Nieto et al. 2014). The exception to this are the bumblebees, which at the European level have almost all been assessed for the IUCN red list (91.2%). Twenty eight percent of the 68 European bumblebees are included as either near threatened (4.4%), vulnerable (11.8%), endangered (10.3%) or critically endangered (1.5%); and overall 45.6% of all European bumblebees show a decreasing population trend (Fig 1.4b; Nieto et

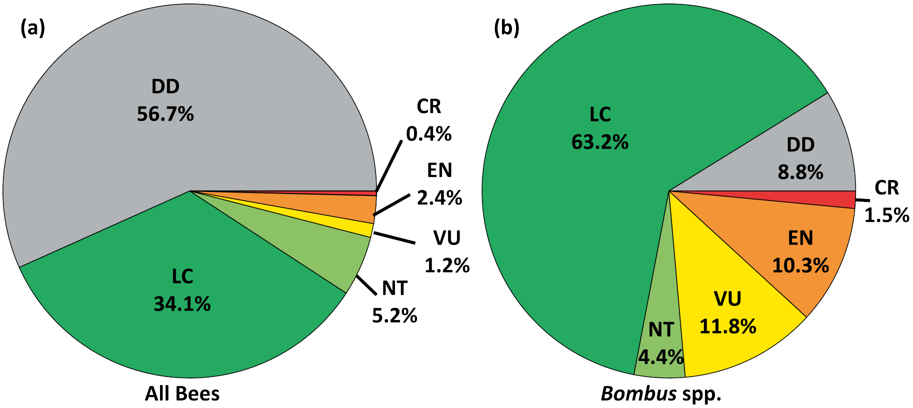

FIG. 1.4: **Summary of the number of bee species within each Red List threat category in Europe.** a) All European bee species. (b) Only European bumblebees. DD: data deficient; LC: least concern; NT: near threatened; VU: vulnerable; EN; endangered; CR: critically endangered. Source: data taken from the European Red List of Bees (Nieto et al. 2014).

al. 2014). Certain species of US bumblebees were found to be declining in relative abundance at the national scale, with up to 96% decline recorded, higher pathogen levels were found in those species with greater declines (Cameron et al. 2011). In Scandinavia the relative abundance of bumblebee species has changed significantly in clover fields. In Sweden two species became far more abundant and the others declined over 70 years (Bommarco et al. 2012). In Denmark over a 60 year period in red clover fields the abundance of long-tongued bumblebees severely declined and 5 species were lost completely (Dupont et al. 2011).

A further measure of decline involves measuring the decline in the services wild bees provide, namely pollination services. Any decline in wild bee diversity or population sizes will result in a decrease in pollination services be that crop pollination or wild flower pollination. In a long-term comparison across 120 years Burkle et al. (2013) found that in a complex plant-pollinator network in Illinois the overall network structure deteriorated and 50% of bee species were lost. Furthermore, a review of studies on the effects of habitat fragmentation on plant reproduction implied that pollination limitation is the most likely cause of decreased reproductive success of plants (Aguilar et al. 2006). Therefore, any decline in pollinators should directly result in a decline in wildflower pollination services. Declines in crop pollination services have also been observed, the decline in clover fields of bumblebees in Sweden also resulted in declines to the clover yield (Bommarco et al. 2012). The outcomes of these declines in services could lead to the over-reliance on generalist pollinators for wild flowers and the overreliance on managed bees in agricultural systems (Potts et al. 2010).

The available evidence suggests widespread wild bee declines, however the causes of these declines may be various and interactive. The trends observed in many countries also imply that wild bee declines will be an ongoing concern in the future and suggest that habitat loss due to LULC and climate changes may be a significant driver. We therefore examine different temporal scales during the thesis to provide an overall picture of the influence of these drivers.

1.3.2 Drivers of Wild Bee Diversity and Declines

The factors which drive wild bee distribution patterns and inevitably influence their decline are numerous and are unlikely to act in isolation. In the review by Potts et al. (2010) the main drivers of decline are listed as LULC changes, increasing pollution and pesticide use, lower diversity in feeding resources, invasive species, pests and pathogens and climate change. Brown et al. (2016) use a horizon scan method to split these drivers into key issues that pollinators are likely to face in the future. The common theme of the different drivers of wild bee decline is that they either directly result in the mortality or decreased reproductive success of individuals or indirectly reach the same outcome by preventing access to or remove feeding and habitat resources. At the broad scale two drivers have significant effects on the availability of necessary resources, namely LULC change and climate change. It is therefore important to understand how these two drivers interact to drive the wild bee distribution patterns, diversity and decline. Hence, we intend to study these drivers at a variety of spatial and temporal scales, to observe in part how they influence observed distribution patterns of wild bees in the past, present and future. A current knowledge gap in studies of wild bee decline concerns how these different drivers interact and influence each other as well as wild bees (Potts et al. 2016b). We explain in detail the existing research into these drivers below. We also outline the influence of other drivers as well as LULC and climate change because these drivers do not act in isolation and LULC and climate changes can directly affect the other drivers and vice versa (see Fig 1.5).

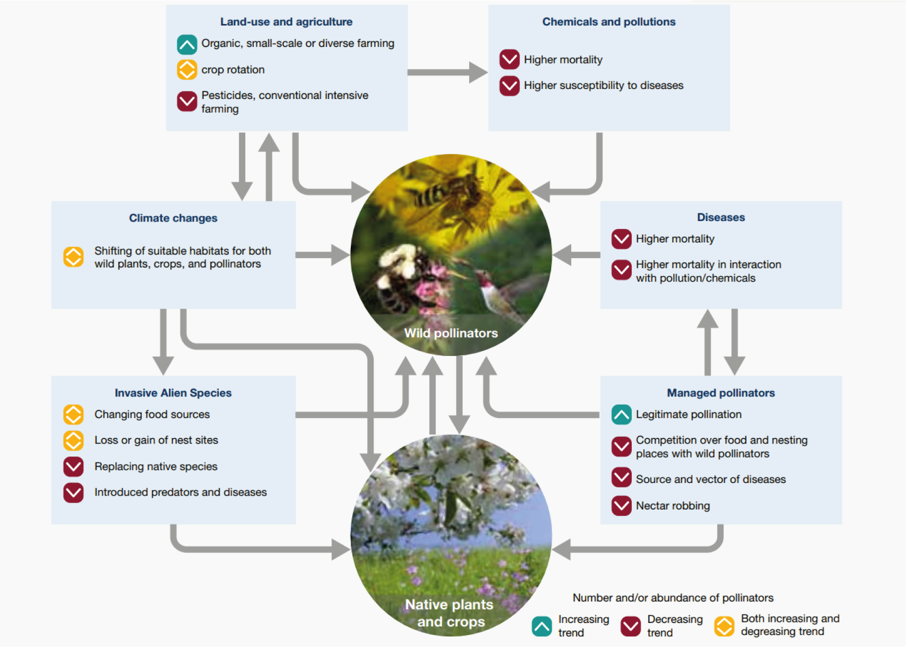

FIG. 1.5: **Overview of the interactive and combined impacts of different pressures on pollinators and pollination.** Source: figure taken from Potts et al. (2016b).

Land Use/Land Cover Impacts on Wild Bees

Landscape ecology explores how the biodiversity within a landscape is affected by the structure and arrangement of surrounding land uses and land covers. The wide diversity in physiology and behaviour of wild bees means that the landscapes they occupy can vary greatly in size. Two key values regulate the landscape size of a wild bee; the distance from their nesting area to suitable food resources and their maximum flight distance (Roulston & Goodell 2011). Land use/land cover effects on wild bees can be summarized from the perspective of bees nest and forage choices in a landscape, i.e. does a particular LULC allow for the presence of sufficient nesting and foraging resources for a diverse community of wild bees? Therefore, a suitable landscape for a wild bee has the required flowering plants and the necessary nesting substrates within its maximum flying distance all in an area with suitable climate conditions. Wild bees do not respond uniformly to environmental conditions and species-specific response exist (Cariveau & Winfree 2015). However, overall, it is widely accepted that the degradation and loss of habitat negatively influences pollinator communities by decreasing population size, altering composition and causing local extinctions (see review Potts et al. 2016b). The impact of anthropogenic transformation of LULC types is one of the main issues faced by wild bee species, specifically the conversion of unmanaged natural areas such as certain forests and wetlands into intensively managed agricultural and urban areas. In the last century these conversions have removed swathes of suitable nesting and feeding habitat of wild bees.

A large body of research exists regarding the interaction between agricultural land use and different measurements of wild bee biodiversity (Potts et al. 2016b). Generally the consensus is that modern day intensive agriculture has a negative impact on wild bee diversity (Potts et al. 2010). However, just as agriculture practices exist in a gradient of low intensity to high intensity, so too do their effects on biodiversity. The problems caused by agricultural landscapes for wild bees are enhanced as the intensity of agricultural practices increases. In general, agricultural intensification results in complex natural ecosystems being converted into simple heavily managed systems. For example Ollerton et al. (2014) found that the extinctions observed of pollinating bees and wasps in the UK were strongly tied to the increase in agricultural intensification beginning in the 1920s. Such loss of heterogeneity and complexity of the landscape produces declines in the richness, diversity and abundance of wild bees (Winfree et al. 2011). On the other hand less intensive farming methods, with lower levels of pesticide use, fertilizer, more heterogeneous crop cover in smaller areas can provide suitable habitats for many species of wild bees (Holzschuh et al. 2008; Kennedy et al. 2013). These methods combined with more sensible and restrained use of pesticides, herbicides and fertilizer alongside biological methods of pest control can create an agricultural landscape in which a far higher diversity of wild bees can survive (Potts et al. 2016b). Specifically, agricultural areas with a modified landscape that allows for a greater heterogeneity in LULC, increases diversity and the ability of wild bees to colonize agricultural landscapes (Winfree et al. 2011; Senapathi et al. 2015).

The absence of flower rich habitat in managed systems negatively influences wild bee biodiversity (Potts et al. 2016b). In a review of floral resource restoration Vaudo et al. (2015) conclude that high diversity floral resources should be added to areas with high agricultural intensification. Due to the high diversity of bees species, managers should take into account the nutritional needs of the species they wish to benefit. Kennedy et al. (2013) also conclude that the most important LULC factor for bees in agricultural areas is the presence of nearby high-quality habitat with feeding and nesting resources. The presence of suitable nesting habitat is also an important determinant of wild bee diversity. Carrié et al. (2018) found that the presence of slopes (important for nesting) was positively correlated to wild bee diversity in French agricultural landscapes. Another negative impact associated with intensive agriculture is the loss of connectivity between areas with suitable resources. Increased fragmentation means smaller patch sizes of suitable habitats and this supports lower wild bee diversity (Steffan-Dewenter et al. 2002; Bommarco et al. 2010). Whereas a more connected habitat should allow for more species in a smaller habitat patch area (Steffan-Dewenter 2003; Kennedy et al. 2013).

Intensive landscape modification resulting in both lower connectivity and higher fragmentation does not only impact diversity measurements of wild bees but also affects the pollination services they provide. Fragmentation has been linked to a decrease in reproductive success of plants which require pollination (Aguilar et al. 2006). In crop pollination, as the distance from suitable habitat increases the richness of pollinators in crop systems decreases (Ricketts et al. 2008). These suitable habitats need to occur within a specific distance to the agricultural system and this estimate varies, and is likely dependent on the specific species of crop pollinator (Garibaldi et al. 2014; Potts et al. 2016a). For example, bumblebees, which travel further than the majority of wild bees are positively affected by the presence of mass flowering crops at the landscape level, such as oil seed rape (Westphal et al. 2003).

Alongside agricultural land use changes, urbanization of the landscape over the last centuries has had significant impacts on biodiversity (Seto et al.

2012). The impacts of urbanization on wild bees vary and not all urbanization is detrimental to all wild bees; the degree of homogeneity, fragmentation and connectivity are also important when discussing wild bee diversity in an urban context (Potts et al. 2016b). Large-generalist bees appear to do well in an urban context. Carré et al. (2009) found that bumblebee density increased with urban habitat cover and in the UK the urban bee community was found to be more generalist (Baldock et al. 2015). The benefits that urban areas may provide stem from the increased heterogeneity of LULC patches (McKinney 2008). For example urban gardens provide necessary nesting and floral resources for many species (Goddard et al. 2010). Urban areas may also provide resources for above ground cavity nesting bees but have decreased availability of exposed soils for ground-nesting bees (Cane et al. 2006). Additionally, urban parks in San Francisco have been shown to support larger bumblebee populations compared to parks in a less urbanized setting (McFrederick & LeBuhn 2006). Alternatively, Martins et al. (2013) propose that the abundance and species richness losses of wild bees in Brazil are due to increased habitat loss and feeding resource homogenization caused by urbanization. Fortel et al. (2014) found, along an urbanization gradient near Lyon, France, that wild bee abundance was lower with increased urbanization and that diversity was highest in intermediate Urban areas. Finally, the structure of urban areas may interact with another driver of wild bee distribution, climate change, by creating warmer micro-climates which allow for the presence of species that would not have suitable conditions nearby outside the urban area (Seto & Shepherd 2009).

In both urban and agricultural areas diversity of wild bees increases with the quantity of patches of suitable high-quality habitat. This habitat is often classified as natural or semi-natural and often supports large source communities of wild bees (Öckinger & Smith 2006). Less abundant, more natural habitats which can maintain a broad diversity of nesting substrates and wild flower resources allow for a variety of niches and therefore specialization and greater diversity. Flower-rich grasslands are an example of habitats which contain these necessary resources in abundance. For example low grazing pressure and less mowing often results in higher pollinator diversity (Potts et al. 2016b). More specifically these grasslands often contain many leguminous species which are important food source for bees. In the UK the loss of flower-rich grasslands and in particular leguminous species was correlated with fewer long-tongued bumblebee colonies (Goulson et al. 2005). In Europe heathland is strongly associated with a particular wild bee community. In the UK the loss of heathland is tied to the loss of flower-rich habitat as a driver of bumblebee declines, specifically those species specializing on Ericaceae species found in heathlands (Goulson et al. 2005). The same importance of heathland was found for specialist bumblebees in Belgium (Moquet et al. 2016). Furthermore, Forup et al. (2008) discovered that restored heathlands in the UK supported less complex plant-pollinator networks compared to historic undisturbed heathland sites. Due to the variety of LULC and their effects on wild bee species we intend to build upon the knowledge of how diverse groups of bee species in different areas are affected by these different LULC, and at the same time **increase the scientific knowledge on the role LULC plays in defining wild bee distribution and diversity patterns.** Particularly by looking at habitat filtering[7] to explain distribution patterns and examining how changes to LULC in the future may affect these patterns. Specifically, in this thesis we aim to utilize high resolution LULC data available in the past, present and future to examine its influence at different spatial and temporal scales. **We intend to show for the first time how a national community of wild bees is spatially structured in relation to its habitat** among other factors (chapter 4). Furthermore, we illustrate, for **bumblebees, the influence that LULC data could have in conjunction with climate change at a broad national and continental scale in the future** (chapter 5) and has had in a mountain habitat in the past (chapter 6).

Climate Impacts on Wild Bees

Climate change is expected to influence biodiversity patterns in three main ways, affecting the phenology of species as well as causing them to shift polewards and higher in elevation (Parmesan & Yohe 2003). The influence of climate change on wild bees has been well studied and its significance as a driver of wild bee decline

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[7] Habitat filtering is defined as the establishment and survival of species in response to the environmental characteristics of a habitat, species unsuited to a particular habitat are ‘filtered’ out (Keddy 1992).

is expected to become more apparent in the near future (Potts et al. 2016a). Phenological shifts in the breeding, flying time, emergence, and flowering of bees and their host plants to earlier in the year could lead to a mismatch in pollination systems, affecting pollination services and henceforth the survival of wild bees and wild plants (Fig 1.6; Hegland et al. 2009; Potts et al. 2016b). Menzel et al. (2006) estimates this phenological shift in Europe as approximately 30% of plants showing a trend of flowering significantly earlier in the year. In a review of climate change impacts on plant pollinator networks Hegland et al. (2009) observe that in many cases the phenological shifts in plants and pollinators may occur simultaneously and at the same rate, but that mismatches have been observed. For example, in Japan, early flowering plants were observed flowering even earlier when spring temperatures were higher, this did not coincide with bumblebee emergence and resulted in a lower seed production (Kudo & Ida Takashi 2013). Long-term studies into changing phenology of wild bees support these patterns of earlier emergence. Bartomeus et al. (2011) calculated that 10 generalist bees species in the US have shifted 10 days earlier on average across the last 130 years but with the majority of change in the last 40 years. Moreover, phenological shifts were highlighted as one of the potential causes of loss of connectivity and general degradation of a plant pollinator network over 120 years (Burkle et al. 2013). These results suggest that phenological shifts have been ongoing and are likely to increase with greater climate change effects predicted in the near future.

Shifts in the ranges of suitable wild bee habitat are also anticipated as a consequence of climate change. The long-term historical patterns of climate change on wild bee species require a large time-series of wild bee diversity in the same areas. This information is difficult to obtain and therefore, studies of climate effects on wild bees are generally restricted to countries with a culture of taking and maintaining entomological records which extends far into the past; namely western European countries and the US. The most comprehensive examination of the effects of long-term climate change on wild bee ranges was conducted by Kerr et al. (2015) who looked at bumblebee species range shifts in the past 110 years in Europe and the US. They found comparable broad scale responses by species across the two continents with species showing an overall decrease in range due

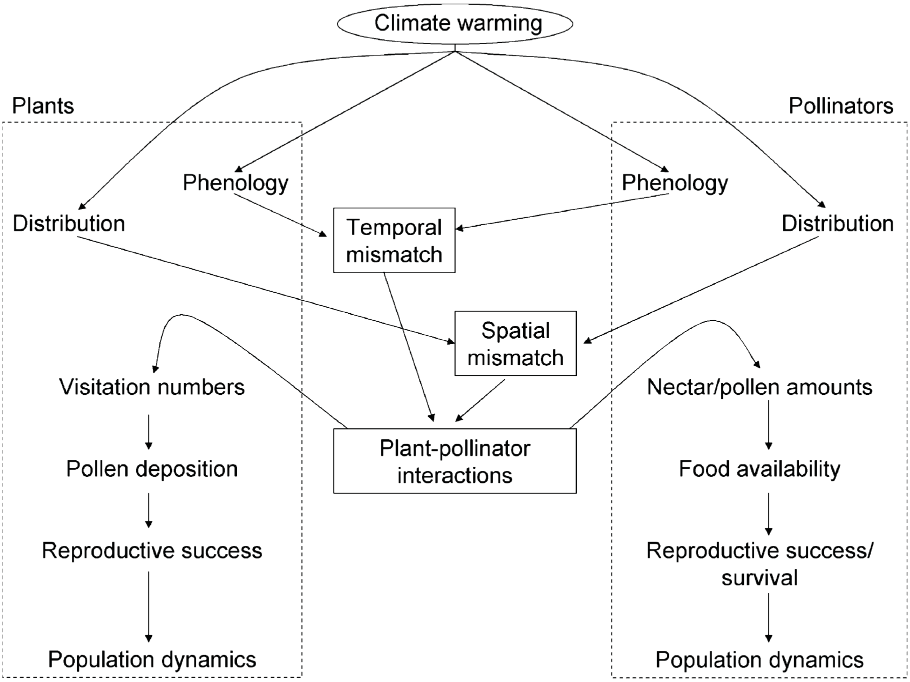


FIG. 1.6: **Overview of how climate warming may affect the phenology and, distribution of plants and pollinators.** Source: figure from Hegland et al. (2009).

to losses at their Southern limits and the absence of equivalent changes at their Northern limits, suggesting that bumblebee species cannot track climate change. In addition certain southern species increased in elevation in both study areas (Kerr et al. 2015). However, there is a larger body of research showing historical change in range and increase in elevation for butterflies due to climate change than for wild bees (Wilson et al. 2005; Wilson et al. 2007; Chen et al. 2009; Chen et al. 2011; Bedford et al. 2012; Devictor et al. 2012); **more research is required to see if these patterns persist for wild bees. In chapter 6 we intend to see how bumblebee elevation patterns have increased during 115 years of LULC and climate change in a mountain habitat.**

The effects of LULC and climate do not occur in isolation but most definitely interact (Dale 1997) and *"there remain relatively few published assessments of the combined effect of LULC and climate change on pollinators and pollination"*

(Potts et al. 2016b). Additionally, the studies that do exist generally concern butterflies (Warren et al. 2001; Forister et al. 2010) or pollination services (Giannini et al. 2015). **Therefore the interactive effects of climate and LULC change on wild bee distribution remain a hole in our knowledge of drivers of decline.** Kerr et al. (2015) examine this interaction and concluded that climate is the main driver behind observed pattern changes in bumblebee distribution over the last century. This may be the case statistically at very large continental scales with only increases in agricultural LULC, as used in the study. However in reality this appears unlikely, as LULC changes have been shown to impact wild bees at finer scales. For example, increases in temperature, which are likely to cause local wild bee extinctions can be mitigated by increasing the amount of semi-natural habitat and green areas (Papanikolaou et al. 2016). In this thesis **we intend to directly examine the effects of climate and LULC in conjunction, using modelled future conditions with changes of both drivers (chapter 5) and looking at how fine scale historic changes in both LULC and climate have affected a single community over a large time period (chapter 6).**

Other Causes of Wild Bee Decline

A large body of research exists around the effects of pesticides on wild bees, which differ depending on the species, the type of pesticide, the toxicity of the pesticide and the means of exposure, among many others (Potts et al. 2016b). The danger posed to wild bees by pesticides also differs when measured in the laboratory as opposed to in the field and so far the majority of pesticides effects have only been tested on a few of the most common bees, therefore the overall patterns on wild bees in general require further research (Arena & Sgolastra 2014). Pesticides such as Neonicotinoids have been shown to have lethal and sub-lethal effects on honey bees, bumblebees and mason bees (Tsvetkov et al. 2017; Woodcock et al. 2017). Land use and pesticide pressure strongly interact, specifically high intensity managed landscapes have higher rates of pesticide use (Foley et al. 2005).

Invasive species pressures on wild bees include those from invasive bees, invasive plants and other invasive animals. For example the widespread introduction of *B. terrestris* as a managed pollinator around the world has led to novel pathogens being introduced and to competitive displacement of native bumblebees and a loss in productivity of native plants (Morales et al. 2017; Aizen et al. 2018). Introduced honey bees are also linked to an increase in pathogens to which social wild bees are particularly vulnerable, for example deformed wing virus which is spread through Varroa destructor, is also present in bumblebees (Genersch et al. 2006). Honey bees can also displace local species through competition (Goulson 2003b; Howlett & Donovan 2010). In areas with few floral resources the negative effects of competition with introduced bees are likely to be more extreme and result in changes to the previously present bee fauna (Roubik & Wolda 2001; Hudewenz & Klein 2013). Invasive plants can lead to bee declines by dominating within a system and changing the structure of plant-pollinator networks (Hudewenz & Klein 2013; Albrecht et al. 2014), and potentially the availability of forage resources or by offering lower quality resources and directly impacting bee health (Potts et al. 2016b). Invasive species pressure as a driver of decline for wild bees is also expected to strongly interact with LULC and climate (Vanbergen et al. 2018). Managed systems, such as urban and agricultural areas, can facilitate invasive species establishment and climate is expected to increase the spread of invasive species globally (Foley et al. 2005; Hellmann et al. 2008).

Pathogens and pests can result in mortality and decreased reproductive success causing declines in bee populations (Vanbergen & The Insect Pollinators Initiative 2013). A number of parasites and pathogens affect solitary wild bees ranging from viruses to bacteria and animal pests, including a number of pathogens found in honey bees (Ravoet et al. 2014; Potts et al. 2016b). Pest and pathogen pressure can be increased with LULC and climate changes. The chance of disease spread from managed bees to wild bees is expected to increase in agricultural areas and the distribution and spread of diseases is expected to increase with climate changes; furthermore species weakened by pesticide use are likely to be more vulnerable to pests and pathogens (Schweiger et al. 2010; Vanbergen & The Insect Pollinators Initiative 2013).

It is clear that the impact of potential drivers of declines do not act in isolation. While it is still difficult to look at all factors together, due to issues of data availability and scale, efforts should be made to explore these interactions in greater detail. We do not explicitly examine the roles of these other drivers as this is out of the scope of the thesis. However, the work presented is part of a larger project which looks to examine the many drivers of wild bee decline in isolation and in conjunction (BELBEES; see Materials and Methodology 2.1). The results from this thesis, concerning LULC and climate impacts, will be combined with studies of the other drivers into a meta-analysis to determine the overall influence of all hypothesized drivers of decline.

We focus in this thesis on climate and LULC as drivers for a number of reasons. Both drivers are expected to significantly impact wild pollinators; on the European red list the major threats to wild bees are almost exclusively related to LULC and climate (Fig 1.7; Nieto et al. 2014; Potts et al. 2016b). Climate change has been shown repeatedly to have a strong influence on the distribution patterns on a number of other pollinator groups, specifically the butterflies and has been shown to be influential to bee distribution at continental scales (Kerr et al. 2015; Rasmont et al. 2015a; Settele et al. 2008). Climate change is also expected to strongly correlate with other potential drivers of wild bee decline (Potts et al. 2010). Climate change also represents an issue which has global significance at the scientific level but is also a key issue politically and for society in general (IPCC 2014). In a meta-analysis across 54 separate studies the most influential factor on negative trends in bee communities was found to be from habitat loss and fragmentation (Winfree et al. 2009). Additionally, two of the key conservation initiatives regarding wild bees is the restoration of natural habitat and the introduction of diverse agricultural landscapes (Winfree 2010). Understanding the relationship between species diversity distribution and LULC will provide direct benefits for achieving this conservation goal. Additionally, in terms of data availability, climate and LULC information is far more abundantly available than other drivers. This allows us to explore their impacts across large spatial and temporal scales. They are also the only drivers for which we have future change projections available (Bellard et al. 2012; De Rosa et al. 2016). The focus on climate and LULC is not to suggest that these are the only two factors which will have a meaningful impact on wild bees. The true extent of the effect of pests, pathogens, pesticides and invasive species is still being determined (Potts et al. 2016b), and the ideal situation would be to have data available for all drivers at multiple spatial and temporal scales.

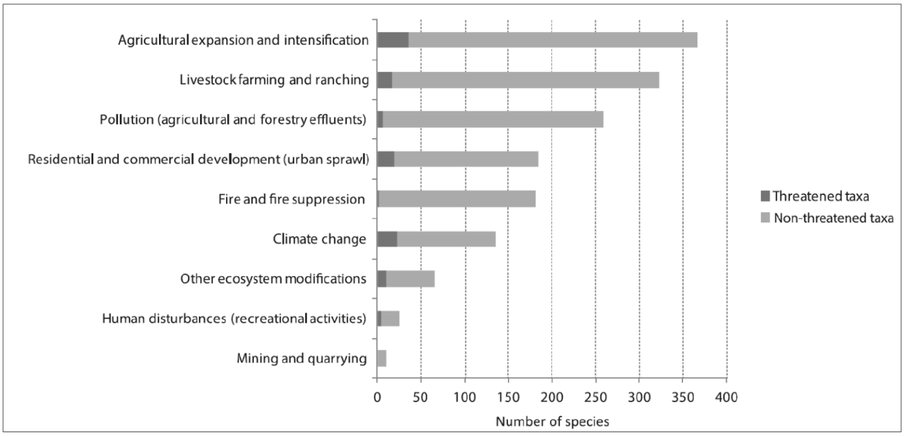


FIG. 1.7: **Major threats to wild bees in Europe.** Based on data from the European Red List for Bees. Source: figure from Nieto et al. (2014).

1.3.3 Modelling Wild Bee Distribution Patterns

As mentioned before, climate and LULC impacts on wild bee species are complex and vary due to many processes. Therefore, to understand patterns and interactions between wild bee diversity and distribution, and LULC and climate effects researchers use modelling techniques. Modelling techniques include mechanistic/process based modelling and phenomenological/statistical modelling. Process based modelling is specified by the biological processes (mechanisms) behind the observed data, based on a theoretical understanding of the ecological mechanisms driving a species response to, for example, changing environmental conditions (Cuddington et al. 2013). Statistical modelling on the other hand seeks to find a relationship between different variables which best describes the observed data. In other words, a mechanistic model explains why and how the parameters interact as observed whereas the statistical modelling approach only describes the relationship, with the assumption that the observed relationship continues beyond the observed data (Hilborn & Mangel 1997). Long-term goals for modelling wild bees would be to move toward more process based models for wild bees but currently only managed bees such as honey bees, *B. terrestris* and some managed mason bees (*Osmia* spp.) can adequately be modelled this way (Becher et al. 2018). During this thesis we use statistical models, with a focus on species distribution modelling, because when examining the total diversity or wild bees, including bumblebees, it becomes apparent that the biological and ecological processes which drive the distribution patterns for the majority of species are not well understood and still require analysis. We therefore aim to find patterns and relationships which can be used to infer the processes that may be behind the observed data.

Species Distribution Modelling

Species distribution models (SDM) are popular tools to understand and predict biodiversity patterns. They are statistical tools used to combine species occurrence records as presence/absence or abundance with measurements of spatial environmental conditions (Elith & Leathwick 2009). The desire to understand the influence of environmental factors such as climate and LULC has on species and communities is a persistent aspect of ecology, and with the increase in computer performance and statistical techniques the methods and applications of SDMs have increased greatly (Guisan & Zimmermann 2000). Species distribution models may also be known as bioclimatic models, climate envelopes, ecological niche models (ENMs) and habitat models among others; these terms are often interchangeable but can also be used to indicate differences in modelling approach (Elith & Leathwick 2009). There are a number of uses of SDMs in the fields of ecology, biogeography and evolution. These include but are not limited to locating un-sampled areas of high species diversity, quantifying a species environmental niche, calculating a species invasive potential, measuring the impact of future changes in climate and LULC on species distributions, providing support for management and conservation planning and modelling species assemblages and communities (Guisan & Thuiller 2005). Throughout this thesis we specifically use SDMs to quantify niche space (Chapters 3, 4 and 5), find unsampled high-diversity areas (Chapter 3), measure the impact of future LULC and climate change (Chapter 5), provide support for conservation planning (Chapter 4) and estimate species assemblages (Chapter 4). Constructing a SDM requires, in its simplest form, three elements: (1) species occurrences collected in the field, (2) a representation of the environment in the form of predictor variables and (3) a technique by which to interpret the relationship between (1) and (2) (Guisan & Zimmermann 2000). These three inputs are combined to create projections of species distributions in time and space (Fig 1.8).

Species occurrence data can be obtained in a number of ways. Franklin (2010) describes these sources in two distinct groups based on the scale of collection data, ecological scale and biogeographical scale. Ecological scale refers to targeted species collections, at consistent fine resolutions, which do not need to be aggregated for SDMs; biogeographical data refers to pre-existing data sets at different resolutions and with different sampling intensities and purposes and therefore require aggregation (Franklin 2010). At the ecological scale SDMs use data obtained from a sampling approach designed specifically for the purpose of the SDM. This method is likely to result in higher resolution occurrence data, improved model accuracy, and often includes co-occurrence and absence data (Franklin 2010). Another source of similar, high-quality data are biological surveys and species inventories. These surveys often provide long-term high-resolution data repeated yearly for the same geographic area; an example from the Netherlands is the national monitoring of butterfly species conducted yearly along the same routes across the whole flying season (van Swaay et al. 2011). However, these methods involve significant time and energy costs and sampling the full range of even a single species can require extremely intensive work.

At the biogeographical scale the occurrence data consists of collated data from many existing surveys (Austin 2007), and large datasets of historical museum collections (Newbold 2010). The occurrence records used in this thesis are most representative of this type of biogeographical data. These data are often from a variety of sources and need to be aggregated to the same spatial and temporal scales and resolutions. This allows the construction and interpretation of broad-scale SDMs using many occurrence records. However, this introduces a number of caveats to the modelling process, the coarser resolution introduces greater environmental heterogeneity and may blur the true relationship between the recorded environmental conditions and the conditions in which the species occurs, furthermore the temporal variation within and between years for occurrence records cannot adequately be captured with a single snapshot of the environmental conditions in a particular moment (Franklin 2010; Newbold 2010).

Additionally, aggregating species occurrence records in this manner can introduce species absences where they do not exist, because they were not the target species in the sampling (Franklin 2010). Given these caveats, these detailed big datasets still represent a great resource for constructing large-scale predictions of species distributions. A number of methods exist to limit biases associated with sampling bias and data aggregation, see materials and methods 2.3.1 for more details.

Occurrence data is also needed to test the performance of SDMs which is usually done using cross-validation methods with a partitioned subset of the training data are used to validate model performance (Elith & Leathwick 2009). However, the ideal situation is to use data independently collected from the training data, the reality is that due to the difficulty in obtaining high quality occurrence data the majority of studies do not have a second independent testing dataset. **In chapter 3 we collect an independent dataset and use it to test the performance of SDMs in agricultural habitats.**

Forecasting and hindcasting in time are common uses of SDMs, to fill gaps in historical distribution records and to estimate the potential shifts and changes in distribution of species under future global conditions (Elith & Leathwick 2009). Studies too often focus on bioclimatic envelope models alone, which become increasingly less useful at finer scales (Pearson & Dawson 2003). Whilst climate may be the most important predictor at broad scales, at finer scales more specific environmental predictors related to disturbance and resource use are necessary (Araújo & Rozenfeld 2014). The introduction of LULC data has been shown to improve model predictive performance for certain species (Pearson et al. 2004; Thuiller et al. 2004). Soil conditions have also been shown to improve SDM performance for insect species (Titeux et al. 2009). Land use/land cover change variables are likely to strongly improve model performance and ecological significance of forecasting models but are almost never used and represent a large gap in the knowledge of modelling future biodiversity scenarios (Titeux et al. 2016). As a tool, forecasting SDMs can be vitally important in informing future management and conservation efforts to prevent biodiversity loss. However their efficacy can be improved upon through more informed covariate selection (Austin & Van Niel 2011). Therefore, throughout this thesis **we examine climate**

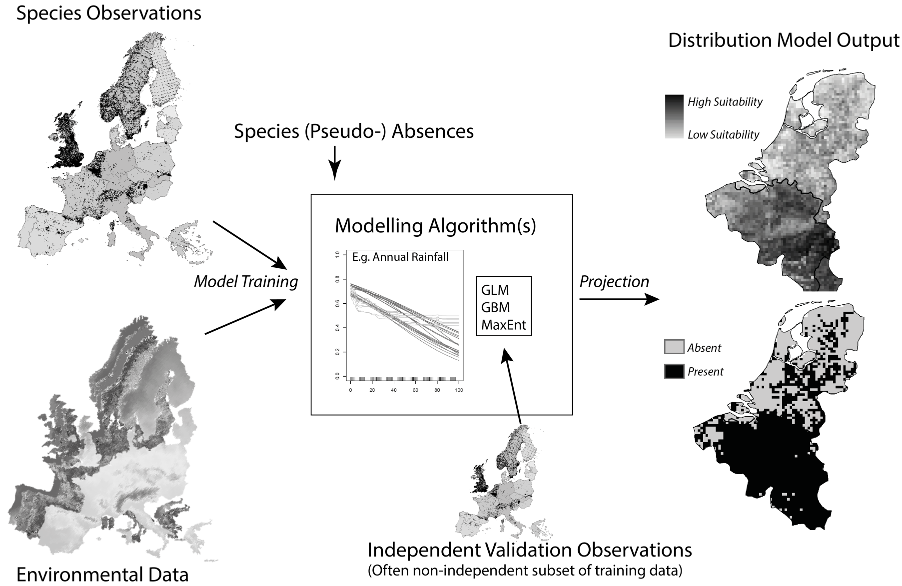


FIG. 1.8: **Simplified workflow of the data sources necessary and process to construct a species distribution model (SDM).** Species distribution models require spatial observation of species occurrence, true absence or pseudo-absences and spatial data of environmental conditions. Different algorithms can then be used to create mathematical representation of a species known distribution in environmental space. These models should evaluated with independent collected data to determine the predictive performance, these data are rarely available and often a subset of the training is retained from training to be used as a validation dataset. These models are then projected onto geographic areas that can be inside or outside the geographic space of the training area and at different time periods. These projections can be visualized as habitat suitability maps of high and low suitability or these maps can be simplified into maps of presence or absence which can be combined with other species' distribution maps to form estimates of species richness and community assembly.

and LULC as predictors of species distributions, comparing and contrasting their importance at different spatial and temporal scales.

One of the other ways to improve SDMs is related to one the most common criticisms of SDMs: that by focusing on the environmental conditions only, a number of important aspects of the ecology of a species is ignored. One of these aspects is the biotic interactions between species which can play an important role in the realized niche that a species occupies and may also result in niche limitation in areas otherwise environmentally suitable (Götzenberger et al. 2012). The solution to this problem is to include these interspecific biotic interactions in the SDM process. The most straightforward method to account for species interactions is to include, as covariates, the distribution patterns of known, a priori, interacting species (Wisz et al. 2012). For example, Gutiérrez et al. (2005) demonstrated that the geographical distribution of an ant species was the most important predictor of the distribution of its mutualist butterfly. The same results were observed for woodpeckers and owls; facilitative and competitive species interactions improved model performance (Heikkinen et al. 2007). This has been touched upon in wild bees as well, with model performance increasing when bee host and parasites are modelled together (Giannini et al. 2013). The key aspect of this methodology is that the interactions must be known or at least have some evidence a priori. This is rarely the case and other methods of including biotic interactions need to infer these relationship from the data available (Wisz et al. 2012). One such method, which is used in chapter 4 of this thesis, is multiple independent equations, which is a form of joint species distribution modelling (JSDM); each species is modelled with its habitat requirements and the resulting residuals are compared to a correlation matrix of all species co-occurrence, to determine if patterns in the residuals are shared by species which co-occur more or less than expected by chance (Ovaskainen et al. 2010; Pollock et al. 2014; Ovaskainen et al. 2015; Ovaskainen et al. 2017). **These methods however are rarely used in the majority of SDM studies and represent a significant absence in the literature and should be continued to be explored with various species groups (Wisz et al. 2012), which is what we intend to do with wild bee communities in chapter 4.**

Species distribution models have been applied to wild bees in different contexts, measuring historical drivers of change (Aguirre-Gutiérrez et al. 2016; Aguirre-Gutiérrez et al. 2017a), determining potential crop pollination service losses (Polce et al. 2013; Polce et al. 2014; Giannini et al. 2017), finding undersampled areas (Penado et al. 2016), calculating invasive risk (Lecocq et al. 2016) and quantifying potential climate change effects (Rasmont et al. 2015a). With this thesis we aim to add three additional topics to this list. Specifically, testing model performance and the role of traits for wild bee SDMs with independent datasets, inferring wild bee interactions and community assembly, and testing potential impacts of LULC and climate change on bumblebees in conjunction. Wild bees represent a difficult group to model as they are small, diverse and highly mobile and include species with a large variety of traits. However, due to their importance as pollinators and the cost and difficulty associated with widespread sampling it is important to utilize statistical techniques to understand their patterns of diversity and distribution. This is especially important as many wild bee species are threatened by global changes to LULC and climate and in turn so are the benefits they provide through pollination (Potts et al. 2016a; Potts et al. 2016b).

Modelling Land Use/Land Cover Effects on Wild Bees

Land use/land cover is a key driver in the diversity and distribution of wild bees. For certain species of bees or by generalizing bee behaviour it is possible to look at more process based models. For example, investigators can directly model the relationship between land use and pollination services. Kremen et al. (2007) show how an agent-based model of pollination services can be used to predict influence of LULC change on pollination services in the form of yield and monetary value by taking into account markets, pollinator biology and government policies. Over time similar models have been built and take into account more factors that may influence crop pollination services, such as preferential foraging by pollinators, dispersal capacity and population growth (Häussler et al. 2017). The impact of LULC changes on plant-pollinator networks have also been modelled and can be used to predict how plants will benefit or be disadvantaged by landscape disturbance and the loss of biotic interactions (Weiner et al. 2014). These models often suggest that negative LULC changes will lead to a more generalist and homogeneous community of wild bees.

However, due to the scarcity of and difficulty in obtaining long-term occurrence records and the huge variation in ecology and behaviour of wild bees, researchers often use statistical techniques to interpolate and extrapolate the relationships between wild bee diversity and distribution, and LULC to different spatial and temporal scales. For example the historical distribution patterns of wild bees in the Netherlands were modelled for three time periods to determine which environmental variables explained the majority of the variation in the distribution of species across time (Aguirre-Gutiérrez et al. 2017a). The authors concluded that overall, landscape composition was a key factor in explaining distribution patterns and that habitat fragmentation was more important in the earlier time period than the latter. Additionally, in the Netherlands, SDMs of LULC and climate were used to model spatial shifts in the distribution of wild bees grouped by their functional traits; Aguirre-Gutiérrez et al. (2016) clearly show that generalist species have shown a greater range expansion than specialists and that small bees have shifted further North than larger bees. Crop pollination service models have been combined with SDMs of climate and LULC conditions to predict pollination services and the role of managed wild pollinators in different locations across the UK (Polce et al. 2013). Overall, SDMs with LULC covariates can be used in different situations to derive importance, predict distributions, influence conservation and predict service provision of wild bees. These studies are often limited by the quality and detail of the available LULC variables. As greater more detailed and up-to-date LULC maps become available then habitat filtering patterns should be continued to be explored. **In chapter 4 we use the latest LULC maps available to determine the classes which are most important for diverse and distinct wild bee assemblages at the national scale.**

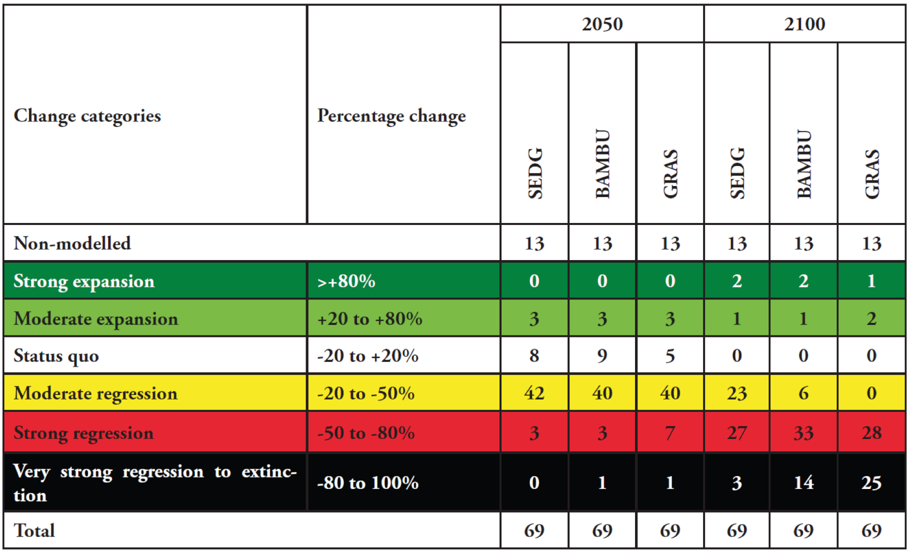
While LULC changes in the past and present have been clearly shown to influence wild bee diversity and distribution, projected future LULC changes are rarely used in studies of biodiversity despite their importance as a driver of decline for many species (Titeux et al. 2016). For wild bees in particular the knowledge of the influence of future LULC changes is almost non-existent. Using global data on wild bee occurrences De Palma et al. (2016) examined the difficulties inherent in extrapolating models of future LULC changes on wild bee communities due to the geographical and taxonomic restrictions of many data. Geographical regions showed considerable differences in the relationship between different diversity indices and LULC (De Palma et al. 2016). Land use/land cover change effects remain a significant absence in the prediction and estimation of future conservation priorities and measures for wild bees. **We aim to build upon studies that have looked at future climate change effects and examine the combined role with LULC change, using available LULC change projections (chapter**

5).

Modelling of Climate Change Impacts on Wild Bees

Climate change is often claimed to be greatest threat to biodiversity in mainstream media, a statement which is often challenged by historical evidence that overexploitation of species and the loss of habitat have most impacted threatened and extinct species (Millennium Ecosystem Assessment 2005; Maxwell et al. 2016). However, there are still many examples of studies which examine the impact of climate change on wild bee diversity and distribution in isolation. Overall, the modelling of wild bee diversity and distribution under climate change paints a bleak picture with many areas likely to suffer significant losses of species richness and abundance, and many species likely to experience substantial range declines. However, modelling of climate effects is not limited to looking at future changes and SDMs have also been used to find under sampled areas with suitable climate for bumblebees (Penado et al. 2016) and to predict the invasive potential of different populations of *B. terrestris* in Europe based on each population's climate preferences (Lecocq et al. 2016). In regards to modelling climate change effects on wild bees **the biggest gap in the knowledge persists around how climate change has - and is likely to - interact with other drivers to influence distribution patterns.**

The studies which examine how communities of wild bees have altered in the past usually focus on shifts in phenology, range or elevation. These same measurements are used to see how potential changes may occur in the future. Memmott et al. (2007) used different scenarios of climate change to predict phenological shifts in interaction networks. Depending on the model conditions the pollinators were predicted to lose up to 50% of their floral resources. A simplified summary of modelled climate change on range changes suggests that species would need to move up to 100km within the next century to maintain within the bounds of their current climate suitability (Leadley et al. 2010). Rasmont et al. (2015) modelled the future distributions of 56 bumblebee at the European scale under three climate change scenarios until 2050 and 2100; the majority of species are expected to decrease in total suitable range size across the whole continent particularly under the more extreme climate change scenarios (see Fig 1.9). Furthermore, the modelled distributions suggest a latitudinal and elevation increase for the majority of species (Rasmont et al. 2015a). **We intend to build upon the results of climate only modelling for bumblebees at the European level by incorporating LULC change variables into the model and quantifying the interaction and influence of LULC and climate change in combination.**



Change categories	Percentage change	2050			2100		
		SEDG	BAMBU	GRAS	SEDG	BAMBU	GRAS
Non-modelled		13	13	13	13	13	13
Strong expansion	>+80%	0	0	0	2	2	1
Moderate expansion	+20 to +80%	3	3	3	1	1	2
Status quo	-20 to +20%	8	9	5	0	0	0
Moderate regression	-20 to -50%	42	40	40	23	6	0
Strong regression	-50 to -80%	3	3	7	27	33	28
Very strong regression to extinction	-80 to 100%	0	1	1	3	14	25
Total		69	69	69	69	69	69

FIG. 1.9: **Projected changes in climatically suitable areas for European bumblebee species in 2050 and 2100.** The values represent the number of species in each change category. SEDG: 'Sustainable European Development Goal', a moderate change scenario driven by economic, social and environmental policies, related to stabilizing atmospheric greenhouse gases emissions and stopping the loss of biodiversity BAMBU: 'Business as Might Be Usual', based on extrapolated current socio-economic and policy decisions. GRAS: 'Growth Applied Strategy', a maximum change scenario driven by policies of deregulation and economic growth. Source: figure taken from Rasmont et al. (2015).

Statistical models are an important tool and can be used to discover and represent relationships between the environment and diversity/distribution. - However, it is important to recognize model complexity and ensure that ecologically relevant information is available from the chosen models. One such way to provide additional ecological relevance is to try and estimate the influence of more processes and species-specific information, for example looking at shared similarities in traits and phylogenetic relatedness between species.

1.3.4 Wild Bee Traits and Phylogenetic Relatedness

Wild bees represent a globally diverse group, with species which respond differently to changing environmental conditions. To simplify these patterns bees are often grouped together based on their functional traits (Biesmeijer et al. 2006; Williams et al. 2010; Bartomeus et al. 2013; De Palma et al. 2015). Traits are defined as phenotypic characteristics that are measured on individual organisms and are referred to as functional when they interact with the environment and other species to affect performance and subsequently an individual's fitness[8] (McGill et al. 2006; Wong et al. 2018). These traits can be morphological (e.g. tongue length), behavioural (e.g. sociality), physiological (e.g. heat tolerance) or ecological (e.g. diet breadth). The degree of sociality or parasitism can have a strong influence on how abiotic and biotic conditions affect bee survival and how bee species use resources in the landscape. For example, in central Europe cuckoo bee richness has been shown to be positively affected by habitat complexity, and social bumblebee richness by the percentage of semi-natural habitats (Hopfenmuller et al. 2014). The richness of cuckoos bees is also strongly determined by the distribution and abundance of the hosts species; bumblebee hosts with a large range and that are classified as non-threatened are likely to support more cuckoo bees (Suhonen et al. 2015, 2016). Parasites also have the potential to act as indicator species representing higher quality wild bee habitat and responding earlier to disturbances (Sheffield et al. 2013).

Wild bee species can also display differences in their nesting habits, feeding specialization, phenology among many others (for greater detail see Materials and Methods section 2.2.4). In particular the response of species to drivers of decline such as LULC change can be attributed to their traits. In a global review above-ground nesting bees were shown to be more sensitive to the loss of suitable habitat and agricultural intensification than below-ground nesters (Williams et al. 2010). Bommarco et al. (2010) observed that the response of species to habitat loss in Northern European countries could be measured by their traits, with small generalist bees experiencing greater impacts than small specialist bees. This may be explained by De Palma et al. (2015), they found that

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[8] Fitness refers to the measure of the reproductive success (number of offspring) provided by a particular genotype of phenotype.

overall specialist feeding, long-tongued species that nest below-ground did not occur readily in habitats strongly influenced by humans. They also observed that the length of flight period significantly affected the abundance and occurrence of wild bees; species with a longer flight season duration were shown to be more likely to occur and be abundant with increased land use intensity (De Palma et al. 2015). Small solitary bees also showed greater vulnerability to habitat loss in calcareous grasslands (Jauker et al. 2012).

Declines in diversity and changes in distribution for wild bees also show trends, which can be attributed to trait specifications. In the US Bartomeus et al. (2013) detected that the greatest loss in relative abundance was experienced by feeding specialists and species with large body sizes. In the UK and Netherlands, Biesmeijer et al. (2006) also observed that feeding and habitat specialists had shown greater decline than other groups. This is supported by Aguirre-Gutiérrez et al. (2016) where habitat generalists in the Netherlands have shown more range expansion than specialists in the last 60 years. Crop pollination effectiveness is strongly linked to the traits of crop pollinating species, in general a higher functional diversity results in a higher quality pollination and yield (Hoehn et al. 2008; Winfree & Kremen 2009). Overall, traits represent an important tool to classify and explain the response of highly diverse wild bee communities globally into patterns which can be linked to conservation and management strategies. **However, the variability of responses to LULC impacts of different traits groups across varying geographic locations requires more studies looking at how wild bee traits influences observed patterns of distribution and diversity. Therefore, we use wild bee traits to look at SDM model performance, community assembly patterns and long-term changes in distribution.**

Along the same line as functional traits, phylogenetic relationships between species can be used to group and simplify species and their responses to different drivers. A phylogenetic relationship indicates the relative period in the past were two species had the same common ancestor, species which share a more recent common ancestor are more closely related than species that share a common ancestor further in the past (Baum & Smith 2013). For example the wild bee family Colletidae are more closely related to the Halictidae, common ancestor approximately 95mya than the Andrenidae, common ancestor approximately 105mya (see Fig 1.3). Overall, however, very few studies have looked at how phylogenetic patterns of wild bees influences the impacts of LULC and climate drivers. Looking at phylogenetic patterns may influence how we view the threatened status of bumblebee species (Vereecken 2017), which is appropriate as the decline in bumblebees globally is not evenly spread across different subgenera (Arbetman et al. 2017). De Palma et al. (2017) additionally show that wild bee decline is more extreme when outlined in terms of phylogenetic diversity than simply species diversity. These studies show that phylogenetic diversity and relatedness could be key measurements to help frame and understand the diversity and distribution patterns of wild bees. Therefore, as the use of traits and trait based metrics have become more apparent in the literature so too has the need for more studies that link diversity and distribution of wild bees to phylogenetic measurements. **Along with multiple other factors, in chapter 4 we use a phylogenetic distance matrix for 204 wild bees to provide preliminary evidence for how habitat filtering in a diverse community of wild bees is affect by the phylogenetic relationship between species.** Wild bee diversity is vast and there is almost certainly not a one size fits all explanation of their relationship with LULC and climate effects. However, being able to simplify and represent these relationships based on traits or phylogenetics provides important knowledge which can be used to better conserve wild bees.

1.3.5 Conservation of Wild Bees

The conservation and management of wild bees is a necessity given the observed declines and the strongly anthropogenic nature of the drivers of this decline. However, due to the large diversity in wild bee species globally, there is unlikely to be a one size fits all approach to their conservation. Conservation initiatives need to incorporate knowledge as to how the variety of wild bee species respond to the different drivers of decline and diversity. Therefore, there is a huge variety in the potential methods for conserving wild bee diversity (Brown & Paxton 2009; Winfree 2010). One of the most direct approaches to wild bee conservation is formally protecting species classified as threatened (Winfree 2010). An example of this is seven species of *Hylaeus* bees and the rusty patched bumblebee (*B. affinus*) in the US which were added to the list of endangered US species in 2016 and 2017, ensuring their protection (Guertin 2016). However, insect protection is incredibly low, globally compared to other animal groups and the expected number of vulnerable insects does not coincide with global conservation of insect species (Black et al. 2001). Furthermore, this method suffers from the fact that for over 50% of wild bee species in Europe and for far more globally there is not enough evidence available to make informed decisions on their threatened status (Nieto et al. 2014).

A more complete and achievable strategy for wild bee conservation is at the community level, specifically attempting to restore wild bee habitat to maximize diversity and abundance. In general this method has most often been applied in an agricultural context, where bees provide important services (Winfree 2010; Garibaldi et al. 2017). Habitat restoration specifically involves restoring floral and nesting resources required by wild bee species. This involves detailed knowledge on the necessary resources for the wild bee community that needs to be restored in the landscape. Due to the fact that many floral restoration projects are focused on agricultural areas (Winfree 2010), this is likely to emphasize the conservation of generalist species, which can be sustained with a relatively low species richness of plants (Carvell et al. 2006; Winfree 2010).

In many countries worldwide, agriculture is the dominant form of land use. Therefore improving agricultural practices and the surrounding landscape can have a positive influence on wild bees. A shift to less intensive farming practices should improve wild bee abundance and richness even without improvements made to the surrounding landscape (Carrié et al. 2017). Organic farming alone showed benefits to overall species richness of solitary wild bees whereas small scale farming practices were necessary to improve bumblebee richness in wheat fields in Central Germany (Happe et al. 2018). However, these impacts will be improved upon with landscape level changes to increase wild bee habitat. The restoration of hedgerows was shown to have higher rates of persistence and species colonization in intensive agricultural areas and increased native bee diversity in adjacent fields in California (Morandin & Kremen 2013; Meyer et al. 2017).

A specific method of wild bee conservation in agricultural landscapes is the use of agri-environmental schemes (AES) in which land owners are rewarded for providing biodiversity conservation measures on their land. One of the most common forms of AES is the restoration of floral resources in the form of floral strips alongside agricultural habitats. The benefits of floral strips for restoring wild bee diversity and abundance vary depending on the local landscape context, in particular how much floral richness was increased in the local landscape with the introduction of the floral strips (Scheper et al. 2015). In general the effectiveness of AES seems to occur in heterogeneous landscapes with moderate land use intensity and the presence of some semi-natural habitat elements compared to already diverse habitats with large amount of semi-natural and natural habitat or highly intensive landscapes with no nearby source populations (Kleijn et al. 2011). Additionally, AES do not seem to provide the necessary resources or be applied in the landscape with the greatest need, to benefit the most threatened wild bee species (Kleijn & Sutherland 2003; Kleijn et al. 2006).

The importance of forested areas for conserving wild bees is not as well studied, as the needs of forest bees are not as well-known as the needs of other wild bee species (Winfree 2010). However, certain wild bee species rely on forest resources in at least part of their life-cycle, for example Euglossine bees in Brazil (Roubik 2001). Ensuring the maintenance of diverse floral resources that require forested areas will in turn protect and manage the wild bee species that require these resources.

Alongside floral resources, restoration of nesting sites is a an equally important conservation measure. However, the knowledge of the nesting resources required by most species is unknown or at least only partially understood. Wild bee hotels for above ground bees are often used in agricultural and urban areas to provide nesting resources, but they only benefit a small subset of total wild bee diversity and may expose wild bees to an increased pathogen and pest risk (MacIvor & Packer 2015). The restoration and maintenance of soils and unmanaged land is required for the many belowground nesting bees but overall the soil requirements for wild bees vary markedly (Cane 1991). Additionally, forest fragmentation can have varying impacts on different wild bee assemblages, for example, stingless bees[9] which require tree cavities to nest are unlikely to be found far from substantial forest areas (Brosi et al. 2007). Restoration of habitats is possible, but it is not a simple fix and improvements to the landscape can be followed by a lag of 4-8 years before bee populations respond (Iles et al. 2018). Therefore, preserving already diverse wild bee habitat is a must.

Natural habitats with high importance and special wild bee communities with high conservation value are rarely managed or protected with the explicit goal of protecting wild bees. **Throughout this thesis we specifically set out to discuss the results obtained in the context of wild bee conservation and management.** In the context of bee decline this thesis will have greater impact if the results obtained can be distilled into conclusions than can be disseminated and understood by interested parties in the effort to ensure the protection and conservation of wild bee species.

1.4 Thesis outline

Pollinator decline is a high profile issue globally, and threats faced by wild bees are likely to persist in the future and declines are expected to continue (Brown et al. 2016). As discussed above, in this thesis we aim to fill a number of gaps related to understanding wild bee diversity, distribution and declines. **The general objective of this thesis is to examine how land use/land cover (LULC) and climate conditions impact the diversity and distribution patterns of wild bee species at different spatial and temporal scales.** Specifically we aim to **(1) test the efficacy of using statistical modelling tools to understand wild bee distributions in the present and future** and suggest how to improve these methods; **(2) provide novel understanding of how wild bee community assemblages are structured at large geographical scales and what drives this structure**; and **(3) quantify and compare how past, present, and future changes to wild bee and specifically, bumblebee distributions**

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[9] Stingless bees refer to species in the tribe Meliponini, they are highly social species usually found in tropical and subtropical areas globally and produce honey (Michener 2000).

are expected to be influenced by LULC and climate changes (Fig 1.10). These aims are tackled throughout the different chapters of the thesis at different spatial and temporal scales (Fig 1.11). Firstly, in **chapter 2, material and methods**, we describe in detail the different data sources and methodologies used in the scientific chapters. The document is then split into four chapters representing separate scientific studies, each with a clear objective directly related to the general objective (Table 1.1), followed by a general discussion.

- **Chapter 3. Quantify the performance of SDMs when modelling wild bee distributions.**

In this chapter we use SDMs to model the distribution of wild bee species in the Netherlands based on their climate and LULC preferences with the specific aim to see how model performance depends on landscape context and the functional traits of the species modelled. We use independent collections from stable agricultural habitats (orchards) and unstable agricultural habitats (arable fields) to test the performance of the SDMs, which is rarely done for biodiversity studies (Elith & Leathwick 2009; Newbold et al. 2010). We examine how habitat suitability values from the model projections depend on the LULC context where a species was collected and the functional group to which that species belongs. This study answers the question of whether LULC and climate species distribution models accurately model the Dutch wild bee fauna and if that accuracy is higher for particular trait groups and in stable or less stable agricultural habitats.

Chapter 3 looks at individual species distributions, however, wild bee species are not distributed independently of each other and form assemblages where certain species are more likely to be found together than others. The role of co-occurrence in structuring assemblage distribution is rarely explored for other taxa and has never been explored for wild bees (Wisz et al. 2012). Therefore, in chapter 4 we look at the community structure of the entire wild bee population of the Netherlands.

- **Chapter 4. Quantify and visualize the influence of habitat filtering and co-occurrence when modelling the assembly patterns of wild**

bee species.

In this chapter we use joint species distribution models to examine how habitat filtering based on high resolution LULC and climate conditions interacts with the co-occurrence of wild bee species. Biotic interactions are rarely accounted for in SDMs. For bees only Giannini et al. (2013) has modelled bee parasites and bee hosts together, which showed improved model performance. Therefore, chapter 4 represents a novel look at how co-occurrence among wild bees influences their distribution patterns. Furthermore, we examine whether these patterns are phylogenetically related and produce spatially explicit wild bee assemblage maps which can be used in wild bee conservation.

Chapter 3 and 4 show a clear importance of habitat filtering in individual species distribution and assemblage patterns. Therefore, in chapter 5 we expand our focus to show how LULC change will influence projected bumblebee declines under a changing climate.

- **Chapter 5. Quantify the influence of dynamic land use/land cover projections on the projected distributional change of bumblebees under climate change**

Chapter 5 represents an increase in spatial and temporal scale and examines the interaction between projected LULC and climate change on the modelled distribution patterns of bumblebee at the European and Belgium, Netherlands and Luxembourg (BENELUX) scale. We examine and quantify the range change and range shifts of 48 European bumblebees when modelled with (1) only climate change covariates, (2) climate change and static LULC covariates and (3) climate change and dynamic LULC covariates. Chapter 5 represents a novel approach to examining the effects of global change on wild bees, as LULC change projections are rarely used in biodiversity studies and never with bees. Additionally, chapter 5 examines the interaction between two of the main drivers of wild bee decline, climate and LULC change, which are often examined in isolation (Potts et al. 2010).

modelled future changes to bumblebees represent an important tool for conservation and management. However, observed changes in the future, at the large scale are less effective without a comparison to actual observed changes in bumblebee distribution and diversity patterns at the finer scale. Therefore, in chapter 6 we present a case study showing how measured climate and LULC changes over 115 years have affected a mountain plant and pollinator community in a high diversity area of the Pyrenees.

- **Chapter 6. Measure a specific case of how the composition and distribution of a wild pollinator group has changed over time due to the influence of LULC and climate changes.**

We quantify the range and diversity changes in bumblebees, butterflies and their host plants surveyed in 1889 and 2005-06 (115 year period), with particularly focus on elevation shifts that have occurred in the alpine habitat. Similar studies often focus on butterflies alone and do not encompass such a large time difference between surveys (Wilson et al. 2007; Chen et al. 2009). Chapter 6 provides context into the impacts that climate and LULC change have already had on biodiversity patterns. Altogether these four chapters represent important insights into understanding how wild bee distributions patterns are influenced by LULC and climate at varying scales, and how this interacts with ecological differences between species. Moreover, we explore how we can best measure this influence and how this information can inform wild bee conservation measures.

In chapter 7, the general discussion, we present a synthesis of the results from the different chapters. We discuss the results in terms of their relevance to species distribution modelling and the distribution and diversity of wild bees, with a focus on the knowledge gaps that we have outlined here. Furthermore, we discuss the implications of the results with a focus on their significance to wild bee research and conservation. We finally broaden the focus of the discussion to future research prospects within the context of modelling wild bee distribution and diversity patterns, before summarizing the conclusions of the thesis as a whole.

TABLE 1.1: **Thesis overview and principle results**: How do land use/land (LULC) cover and climate conditions affect the diversity and distribution patterns of wild bee species at different spatial and temporal scales?

Chapter Aim	Specific Questions	Methods	Main Results
Chapter 3: quantify the performance of SDMs when modeling wild bee distributions	(1) How does the accuracy of SDMs vary depending on agricultural context? (M) (2) How does the accuracy of SDMs vary depending on species traits? (M)	Compare SDM performance of different species in different locations using an independent dataset	The performance of species distribution models of wild bees in the Netherlands depends on species' traits, habitat and collection technique. **Published:** Marshall et al. (2015) Ecology and Evolution
Chapter 4: quantify and visualize the influence of habitat filtering and co-occurrence when modeling the assembly patterns of wild bee species	(1) Do certain wild bee species indicate the presence of others? (M) (2) What is the influence of habitat filtering on the patterns of wild bee occurrence? (A) (3) Do species traits and phylogenetic relationships influence wild bee distributions and spatial co-occurrence? (A) (4) How are wild bee assemblages geographically distributed in the Netherlands? (A) (5)What are the conservation implications of the resulting wild bee assemblage patterns? (A)	Use joint SDMs with co-occurrence data in a Bayesian framework to estimate wild bee assemblages	Community assembly patterns of wild bees in the Netherlands are driven by habitat filtering and show a strong phylogenetic niche conservatism. However, including biotic interactions improves model Performance. **Submitted:** Marshall et al. (2018) Ecography
Chapter 5: quantify the influence of dynamic land use land cover projections on the projected distributional change of bumblebees under climate change	(1) Does the inclusion of dynamic LULC variables alter the SDM projections of bumblebee range changes under climate changes and with static LULC? (M) (2) Does the relationship between LULC or climate models depend on the spatial scale, resolution or change scenario? (M) (3) What does the interaction between land use and climate change for future SDM models mean for the conservation of bumblebees? (A)	Compare the modeled distribution of 48 European bumblebees in 2050 and 2100 under three scenarios, using climate models, static land use models and dynamic land use models	Including dynamic LULC change models alongside climate models significantly changes projected distributions of European and BENELUX bumblebees. **Published:** Marshall et al. (2018) Global Change Biology
Chapter 6: measure a specific case of how the composition and distribution of a wild pollinator group has changed over time due to the influence of land use and climate changes	(1) Have significant climate and LULC changes occurred in the Pyrenees National Park in the last 115 years? (A) (2) Has the composition of the bumblebee, butterfly and plant community altered and/or shifted in elevation over 115 years? (A) (3) Do bumblebee traits explain the observed elevation patterns and shifts? (A)	Compare collections of wild pollinators and their host plants from 1889 and 2005-06 to see how diversity and distributions have shifted and whether climate and land use changes have occurred simultaneously	Pyrenees bumblebees, butterflies and their host plants have shown a considerable increase in elevation over the last 115 years alongside changing LULC and climate. **In preparation:** Marshall et al. (2018)

Following each question the (M) refers to questions more methodological in nature and the (A) questions that are more applied. SDM = species distribution model, BENELUX = Belgium, Netherland and Luxembourg.

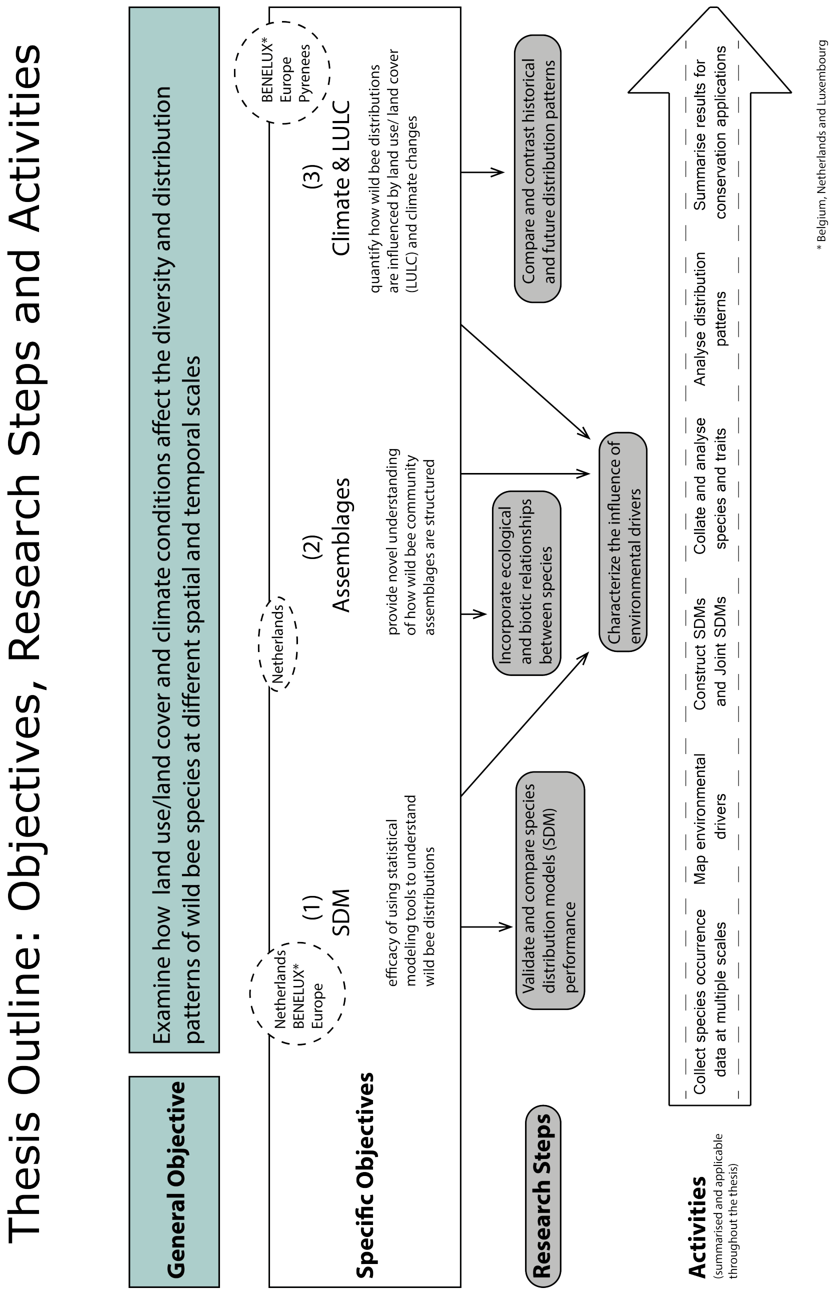


FIG. 1.10: **Thesis outline**

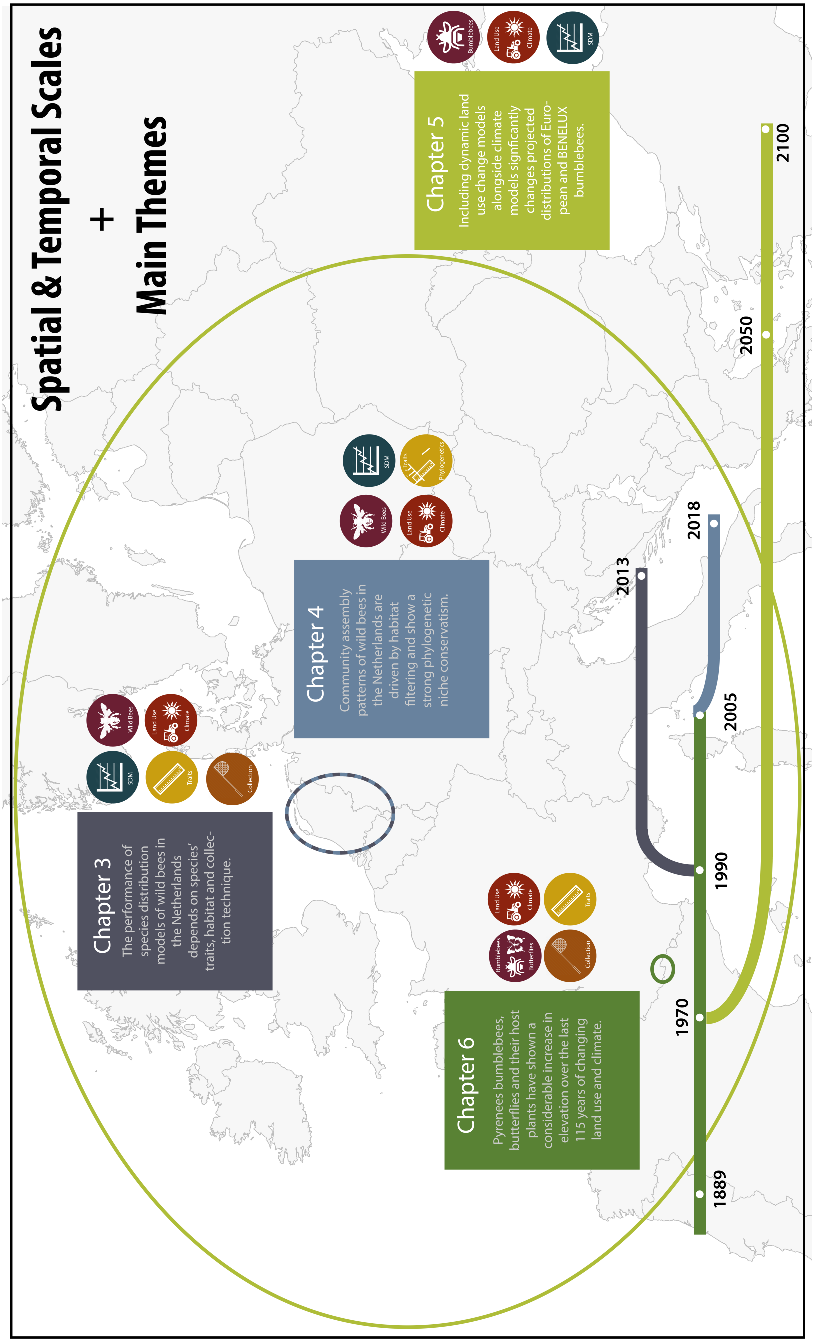
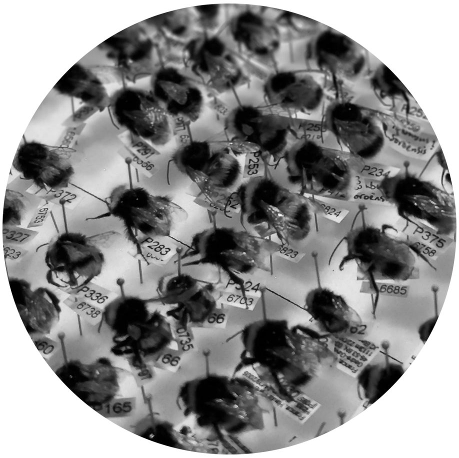


FIG. 1.11: **Summary of spatial and temporal scales, main themes and main results of thesis.**

2 Materials and Methodology

L. Marshall



2.1 BELBEES

As mentioned earlier, this thesis is part of the federal project BELBEES ("Multidsiciplinary assessment of BELgian wild bee decline to adapt mitigation management policy", www.belbees.be; Fig 2.1). The BELBEES project is a conservation research project funded by the Federal Science Policy (BELSPO; BR / 132 / A1 / BELBEES) with the objective to estimate the decline of wild bees in Belgium using a multidisciplinary approach in order to adapt conservation policy. This project brings together several partners: the University of Mons (Pierre Rasmont, project coordinator), Royal Institute of Natural Sciences of Belgium (Jean-Luc Boevé), Ghent University 1 (Dirk de Graaf), University of Namur (Nicolas Dendoncker), University of Liège Gembloux Agro Bio-Tech (Marc Dufrêne), Ghent University 2 (Guy Smagghe), and naturalist associations Natagora (Wallonia) and Natuurpunt (Flanders). The goals of the BELBEES project are to (1) collect all old data available in databases and collections to identify the area that have been well sampled in the past. In the same places, new wild bee specimens will be collected in the wild to be compared to old specimens; (2) identify the role of the five potential drivers by analysing specimens (diseases, genetics, pesticides), pollen load (food resource, pesticides) and biophysical environment (food resource, habitat structure, climate change); and (3) analyse the respective roles and interactions between the five drivers through meta-analyses, and to model wild bee distribution dynamics with a part of the drivers (land use and climate change). The work presented in this thesis focuses on the third goal, in particular "*to model wild bee distribution dynamics with a part of the drivers (land use and climate change*)".

2.2 Data Overview

Throughout this thesis we rely on data in a variety of formats and from a variety of sources to test our objectives. Broadly these data can be defined as spatially explicit species occurrence data and representations of environmental conditions. Specifically, the work presented here requires occurrence data with known locality information. Ideally, these data should have the locality recorded in the form of GPS coordinates, so that records can be mapped at a high resolution. The land

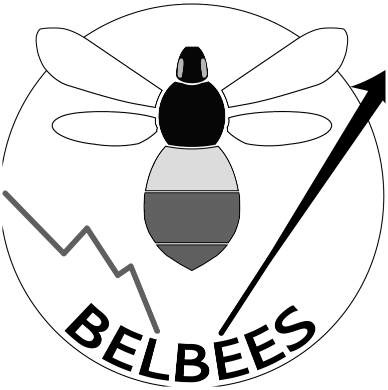


Fig. 2.1: BELBEES Logo

use and climate data is also available in the form of spatially explicit maps. Depending on the source these maps can either be in raster format or vector format. Raster data consists of a matrix of grid cells each with a particular value. These values can either be thematic, i.e. representing a particular LULC, or continuous, i.e. representing changing temperatures across a landscape. The advantages of using raster-based maps is that they represent a simple and easily interpretable structure using spatial and statistical analyses, they are the best format to represent continuous data such as temperature and rainfall and they can easily be combined with other data sources when aggregating (ESRI 2013). The disadvantages of using rasters to store data are that restrictions on cell dimensions can lead to spatial inaccuracies and a loss of precision when aggregating data, they can also become very large datasets and take a lot of time and computer power to analyse (ESRI 2013). The other format of LULC and climate data that we use in this thesis is vector data. Vector data is also a coordinate based mapping format and it represents geographical information as either points, lines or polygons. The advantages of using vector maps are that the data can be presented at its original resolution and with accurate representations of geographic locations (ESRI 2013). The disadvantages of using vector maps are that they cannot accurately present continuous data, high resolution vectors can be processing intensive and within polygons data cannot be filtered (ESRI 2013). We use a combination of both formats to maximize the quality of the environmental data. The other data we use in the thesis is ecological and genetic and comes from expert opinion and literature resources as well as separate analysis (see sections 2.2.4 and 2.2.5).

2.2.1 Wild Bee Occurrence Data

The distribution patterns of wild bees analysed in this thesis are estimated from wild bee occurrence data collected from a variety of sources. These sources include museum collection data, validated and verified citizen science data, and data systematically sampled as part of scientific research projects. Museum collection data represents a high-quality source of specimens often going far back in time and with high taxonomic reliability (Newbold 2010). Museum collection data is often the only source of historical wild pollinator occurrences on which trends of diversity and distribution can be measured over long time periods (Bartomeus et al. 2018). However, there are a number of biases associated with museum occurrences, these include spatial and temporal biases, biases towards certain very rare or very common specimens over others, and biases due to unknown sampling effort (Ponder et al. 2001; Graham et al. 2004; Boakes et al. 2010). Citizen science data can also be a great source of widespread and numerous species occurrence data. The involvement of a large number of individuals means that far more records can be collected in a shorter period of time, than it would take a skilled amateur or expert researcher (van der Wal et al. 2015). The greatest difficulty with citizen science records is ensuring their accuracy taxonomically and spatially. This requires expert knowledge to be used to verify and validate records of citizen scientists. The increase in high-quality portable photographic equipment makes this job easier and enhances the value of citizen science records (Suzuki-Ohno et al. 2017). Data collected as part of systematic scientific studies is the highest quality data available often involving repeated visits to the same areas to sample the same community using the same methods. Unfortunately these data are also the most costly requiring considerable time, energy and greater monetary costs.

The wild bee and bumblebee collection data used throughout the thesis have been collated from a range of sources and have been made available to use through intensive long term database management. The wild bee data of the Netherlands used in chapters 3 and 4 was obtained from a database containing historical museum occurrences, citizen science data, and scientific collections

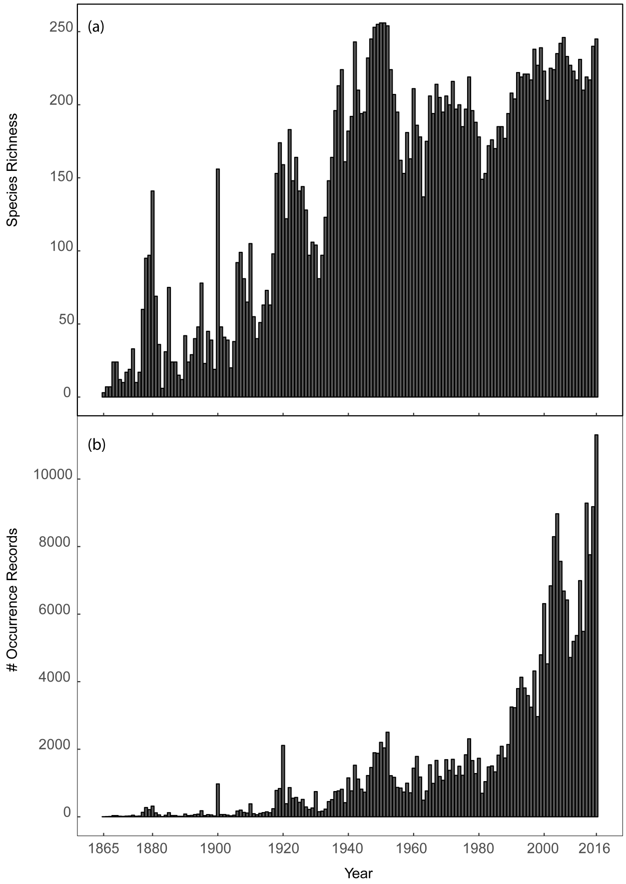


FIG. 2.2: **European Invertebrate Survey (EIS) Wild Bee Database for the Netherlands**. (a) Total number of species collected per year between 1865 and 2016. (b) Total number of occurrence records collected per year between 1865 and 2016.

(Fig 2.2). This database is managed by The European Invertebrate Survey Kenniscentrum Insecten (EIS; `https://www.eis-nederland.nl/`). The database contains a total of 245 755 collection records made between 1800 and 2016 for a total of 362 species. During this time period eleven species have been found only once, and the species with most recorded occurrences, 10 946, is *Bombus pascuorum*. The highest yearly species richness was recorded in the 1950s (Fig 2.2a), but the greatest number of occurrence records have been in recent years, 2016 contained the most records for a single year (Fig 2.2b). A large part of the data has been published in 'de Nederlandse bijen' by Peeters et al. (2012).

In chapter 3 we build species distributions models using a subset of the data from 1990 until 2013. To limit the chance of over-fitting the data and because we were interested in species likely to be found when doing independent surveys, we limited the number the species modelled to those with at least 30 records (Fig 2.3). Therefore, a total 194 species of 25 genera remained. We also collated collection records of wild bees from 73 agricultural locations which we used as an independent dataset to test model performance, in total 52 unique wild bee species were collected from these 73 locations (Fig 2.3a).

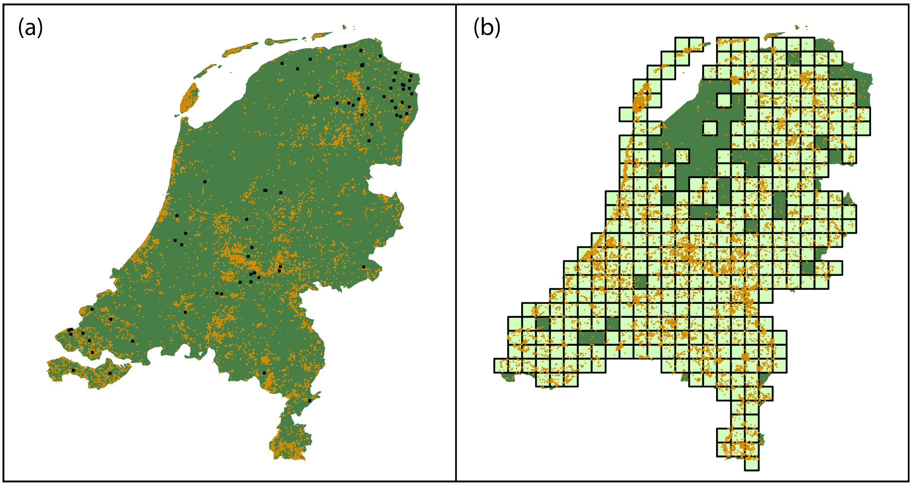


FIG. 2.3: **Geographic distribution of wild bee occurrence data in the Netherlands.** (a) Wild bee occurrence records used in Chapter 3, collected between 1990 and 2013 for species with a minimum of 30 records (193 species). Orange points represent the occurrence records. Black squares refer to 73 locations where independent collections were made by which to test SDM performance. (b) Wild bee occurrence records used in Chapter 4, collected between 2005-2016 (304 species). Orange points represent the occurrence records. Light green squares represent 10 x 10 km areas where high-quality consistent sampling has occurred within this time frame. Orange points represent the occurrence records.

In chapter 4 we used the same data source to model wild bee distributions in the Netherlands (Fig 2.3b). However, in this case we were interested in co-occurrence patterns between species, therefore we decreased the time period of occurrence records (2005-2016) and limited our analysis to species with at least 5 records. A total of 204 species were modelled. In both chapters there is sufficient wild bee occurrence data so that the majority of the Netherlands is included. Certain biases exist in the South and towards coastal areas, but overall the collection records are relatively evenly spread (Fig 2.3).

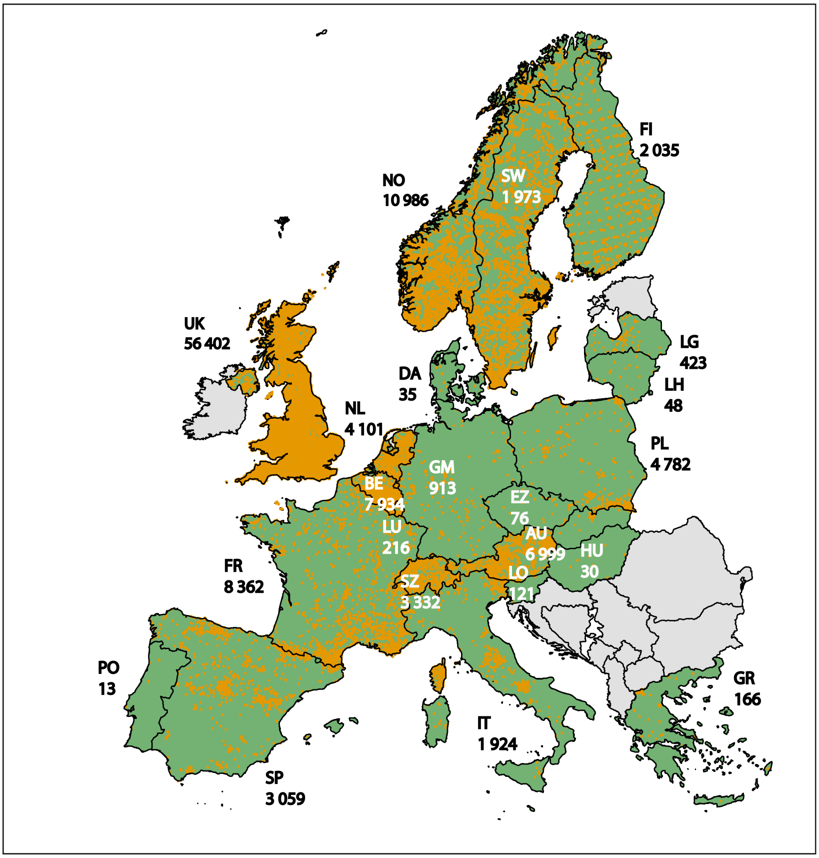


Fig. 2.4: **Geographic distribution of bumblebee species in European areas between 1970 and 2000 as defined by future ALARM scenarios of Land Use Change (Green areas).** Number of records per country after removing duplicate species records at the same location. AU: Austria; BE: Belgium; DA: Denmark; EZ: Czech Republic; FI: Finland; FR: France; GM: Germany; GR: Greece; HU: Hungary; IT: Italy; LG: Latvia; LH: Lithuania; LO: Slovakia; LU: Luxembourg; NL: Netherlands; NO: Norway; PL: Poland; PO: Portugal; SP: Spain; SW: Sweden; SZ: Switzerland; UK: United Kingdom.

In chapters 5 and 6 we focused our analysis on a subset of wild bees, the bumblebees (*Bombus* spp.). Firstly, in chapter 5 we used bumblebee collection records collated as part of the EU FP7 project STEP (Potts et al. 2011) which is aggregated and available to view on the Atlas Hymenoptera webpage (Fig 2.4; Rasmont & Iserbyt 2013). The STEP project was created with the general aim *"to assess the current status and trends of pollinators in Europe, quantify the relative* *importance of various drivers and impacts of change, identify relevant mitigation strategies and policy instruments, and disseminate this to a wide range of stakeholders"* (Potts et al. 2011). A result of this project was the collation and organization of historical wild bee collections from many European countries into a single database. We extracted the bumblebee data used in chapter 5 from this database. Due to the availability of future LULC change projections our total study area included 22 European countries. These 22 countries were chosen as they were included in the geographical range of the Assessing LArge-scale environmental Risks with tested Methods (ALARM) Scenarios (Spangenberg et al. 2012; Fig 2.4). We tried to ensure that we could get as close to the total climatic range for all bumblebee species to ensure that the responses to changing conditions were accurate and within the tolerances of each species. The occurrence records used were collected between 1970 and 2000 to ensure that there were enough records per species and to match the time frame for which the climate data was recorded. Overall, within these spatial and temporal restrictions, 63 wild bee species were found. For the final analysis we limited the database to the 48 species with a minimum of 50 unique occurrences (see Table S5.1 in supporting information chapter 5). For each of the 48 species we aggregated their collection records to 4 different spatial grid resolutions used in the modelling process; 5 × 5 km, 10 × 10 km, 20 × 20 km and 50 × 50 km. As with the Dutch wild bee occurrence data, *B. pascuorum* (16 899 observations) was the most abundant across Europe.

The bumblebee data show a clear bias towards certain areas, in particular the United Kingdom has far more records than any other country, Northern Europe is over represented and the Alps and Pyrenees mountain ranges are heavily sampled compared to other locations (Fig 2.4). In the case of the bumblebee data, because there is unevenness in the sampling, it is more likely that the species will have a number of records in close proximity and this will introduce a spatial auto correlation effect that does not represent the true distribution of the species. Positive spatial autocorrelation occurs when a value is more likely to occur close in space to other similar values. To deal with the potential for spatial-auto correlation bias in the occurrence records we used a method of re-sampling to minimize the effect of aggregations of records in particular areas. This method was adapted from Broennimann et al. (2012). For each species at the different spatial grid resolutions we (1) took a random grid cell occurrence as the starting location; (2) removed all occurrences of the same species in adjacent grids cells; (3) reselected a random grid cell occurrence; (4) repeated the process of removing adjacent grid cells. This process was continued until grid cell occurrences did not have adjacent occurrence of the same species. The re-sampling process resulted in a more even range of occurrences and limited the impact of potential spatial auto-correlation effects.

2.2.2 Land Use Data

Netherlands Scale

The Dutch rural land-use file version six (LGN 6) file is a raster file with a resolution of 25 × 25 m. The file represents land use in the Netherlands for the years 2007/2008. The theme and geometry of TOP10NL vector forms the basis for LGN6 for the majority of classes. Moreover, satellite images, aerial photographs and spoil and nature maps were also used (Hazeu et al. 2010). In total 39 different types of land use are distinguished in the raster file. The LGN6 raster was used in chapter 3 where the land use classes were reclassified and aggregated together to form 9 land use types used to model wild bee distribution patterns (Table 2.1). These 9 land use classes were then converted into percentage cover per 1 × 1 km grid cells. Model selection resulted in a final selection of 5 land use classes used in the final SDM: Percentage Cover Agriculture, Coniferous Forest, Moors/Peats, Sandy Soils, and Urban.

TABLE 2.1: **Reclassification table of the original LGN6 land use map to the 9 most general land use classes in the Netherlands.** Land use type translated from Dutch.

Number	Original land use type	Reclassified land use type
1	Managed grassland	Grassland
2	Maize	Agriculture
3	Potatoes	Agriculture
4	Beets	Agriculture
5	Cereals	Agriculture
6	Other crops	Agriculture

Table 2.1 continued from previous page

7	Greenhouses	Urban
8	Orchards	Agriculture
9	Flower bulbs	Agriculture
10	Deciduous forest	Deciduous forest
11	Coniferous forest	Coniferous forest
12	Fresh water	Not available
13	Salt water	Not available
14	Construction in primary urban area	Urban
15	Construction in secondary urban area	Urban
16	Primary forest in built-up areas	Mixed forest
17	Secondary forest in built-up areas	Mixed forest
18	Grass in primary urban area	Grassland
19	Bare soil in primary urban area	Urban
20	Roads and railways	Urban
21	Buildings in the outlying	Urban
22	Grass in secondary urban area	Grassland
23	Salt marshes	Swamps
24	Open sandy coastal area	Sandy soil vegetation
25	Dunes with low vegetation (<1m)	Sandy soil vegetation
26	Dunes with high vegetation (>1m)	Sandy soil vegetation
27	Dune heath	Sandy soil vegetation
28	Open drifting sand and / or river sand	Sandy soil vegetation
29	Heather	Moors/Peat
30	Moderately grazed heath	Moors/Peat
31	Strongly grazed heath	Moors/Peat
32	Moors/Peat	Moors/Peat
33	Forest bog area	Mixed forest
34	Other swamp vegetation	Swamps
35	Reed vegetation	Swamps
36	Forest in wetland	Mixed forest
37	Natural grassland	Grassland
38	Nurseries	Agriculture

Table 2.1 continued from previous page

39	Fruit farms	Agriculture

The TOP10NL is a nationwide vector of the topography of the Netherlands. TOP10NL originated from aerial photographs, panoramic photographs, field recordings and information from external sources (Kadaster 2012). We used the TOP10NL vector in chapter 3 to obtain measurements of different linear features in the Dutch landscape (Fig 2.5).

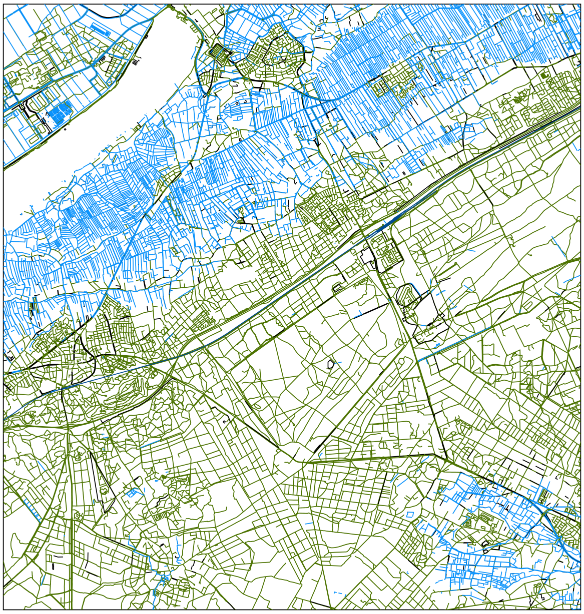


Fig. 2.5: **An example of linear features available from the TOP10NL Vector**. Blue: water features, green: roads and black: train tracks.

In chapter 4 we used land use classes for the Netherlands with far higher thematic resolution. We utilized three separate sources to obtain a detailed overview of LULC in the Netherlands. The three sources can broadly be described as nature, agriculture and urban. The nature map was a vector of nature types across the Netherlands called the Index Natuur en Landschap (INL; Inter Provinciaal

Overleg 2016). The INL was produced with landscape management in mind and the map is split into types of nature (17) with each nature type having a number of possible management types, 49 in total. Each of these 49 land use management types was then aggregated into 7 broader categories of nature land cover types to model wild bee habitat filtering (Table 2.2). These 7 land use classes were:

1. Water
2. Heathland
3. Semi-natural woodland
4. Production woodland
5. Marsh and swampland
6. Semi-natural grassland
7. Dune areas

TABLE 2.2: **Reclassification table of the Index Natuur en Landschap (INL) to 7 natural land cover classes in the Netherlands.** Land cover type translated into English from the original Dutch (Inter Provinciaal Overleg 2016).

Code	Original Management Type	English Management Type	Aggregation
N01.01	Zee en wad	Sea and mudflats	Water
N01.02	Duin- en kwelderlandschap	Dune and salt marsh landscape	Peat/Marshland
N01.03	Rivier- en moeraslandschap	River and marsh landscape	Peat/Marshland
N01.04	Zand- en kalklandschap	Sand and lime landscape	NaturalGrassland
N02.01	Rivieren	Rivers	Water
N03.01	Beek en bron	Brook and water source	Water
N04.01	Kranswierwater	Algae fields	Water
N04.02	Zoete plas	Sweet puddle	Water
N04.03	Brak water	Brackish water	Water
N04.04	Afgesloten zeearm	Closed sea arm	Water
N05.01	Moeras	Swamp	Peat/Marshland
N05.02	Gemaaid rietland	Mowed reed	Peat/Marshland
N06.01	Veenmosrietland en moerasheide	Sphagnum meadows and marshland	Peat/Marshland
N06.02	Trilveen	Floating mat peat	Peat/Marshland
N06.03	Hoogveen	Moors	Peat/Marshland
N06.04	Vochtige heide	Moist heather	Heathland
N06.05	Zwakgebufferd ven	Weak buffered bog	Peat/Marshland
N06.06	Zuur ven of hoogveenven	Acid bog or high peat	Peat/Marshland
N07.01	Droge heide	Dry heather	Heathland
N07.02	Zandverstuiving	Sand drift	Heathland
N08.01	Strand en embryonaal duin	Beach and embryonic dune	Dune

Table 2.2 continued from previous page

N08.02	Open duin	Open dune	Dune
N08.03	Vochtige duinvallei	Moist dune valley	Dune
N08.04	Duinheide	Heathland dune	Heathland
N09.01	Schor of kwelder	Salt marsh	Peat/Marshland
N10.01	Nat schraalland	Wet nutrient poor grassland	NaturalGrassland
N10.02	Vochtig hooiland	Moist meadowland	NaturalGrassland
N11.01	Droog schraalland	Dry nutrient poor grassland	NaturalGrassland
N12.01	Bloemdijk	Flower embankment	NaturalGrassland
N12.02	Kruiden- en faunarijk grasland	Herbs and fauna rich grassland	NaturalGrassland
N12.03	Glanshaverhooiland	Ryegrass meadow	NaturalGrassland
N12.04	Zilt- en overstromingsgrasland	Silt and flood grassland	NaturalGrassland
N12.05	Kruiden- en faunarijke akker	Herbs and fauna rich fields	NaturalGrassland
N12.06	Ruigteveld	Rough field	NaturalGrassland
N13.01	Vochtig weidevogelgrasland	Wet meadow bird grassland	NaturalGrassland
N13.02	Wintergastenweide	Winter migrant bird grassland	NaturalGrassland
N14.01	Rivier- en beekbegeleidend bos	River and stream accompanying forest	NaturalForest
N14.02	Hoog- en laagveenbos	High and low peat forest	NaturalForest
N14.03	Haagbeuken- en essenbos	Hornbeam and ash forest	NaturalForest
N15.01	Duinbos	Dune forest	NaturalForest
N15.02	Dennen-, eiken-, en beukenbos	Pine, oak, and beech forest	NaturalForest
N16.03	Droog bos met productie	Dry forest with production	ProductionForest
N16.04	Vochtig bos met productie	Moist forest with production	ProductionForest
N17.01	Vochtig hakhout en middenbos	Moist chopping wood and middle forest	ProductionForest
N17.02	Drooghakhout	Dry chestnut	NaturalForest
N17.03	Park- en stinzenbos	Park and estate forests	NaturalForest
N17.04	Eendenkooi	Duck decoy	Water
N17.05	Wilgengriend	Willow forest	NaturalForest
N17.06	Vochtig en hellinghakhout	Moist and slope chopping wood	NaturalForest

The agricultural land use information in chapter 4 comes from the Basisregistratie Gewaspercelen (BRP, EZK 2015). All users of agricultural parcels in the Netherlands must record, annually, the type of crop which has been grown on a particular parcel of land. The BRP is the spatially-explicit vector representation of this information and contains the locations of all agricultural parcels in the Netherlands including the crops grown each year. We used the BRP to create three classes used to model wild bee habitat filtering.We reclassified them using expert opinion and literature reviews. A decision was made as to whether they flower and if they do flower, do they reward visiting pollinators. Of the 56 crop types 26 were classified as potential food sources for bees which corresponds to 14% of the total number of crop parcels in the Netherlands. Furthermore, we classified all areas which are defined as agricultural grasslands.

Finally, urban and other land use information not obtained from the previous two files was extracted from the Bestand Bodemgebruik Productbeschrijving (BBG; CBS 2012). The BBG is a vector file which represents functional land use in the Netherlands with 37 land use types and is recorded from aerial photographs, map material and other digital sources. In particular the BBG separates land use types found in urban areas. The BBG covers the entirety of the Netherlands. We aggregated the Urban land use classes of the BBG into two classes, urban gray and urban green. Urban green refers to recreational areas and gardens within an urban setting. However, we observed that, when aggregated to 10 × 10 km grid cells, both urban grey and green were strongly positively correlated and therefore could not be adequately separated in their ecological significance. We therefore made the decision to aggregate them together in a single urban class.

To calculate the covariates needed to model wild bee habitat filtering we first needed to join all three sources (nature, agriculture and urban) together and deal with any spatial mismatches and/or overlaps. To do this we ranked each of the three sources to produce a hierarchy whereby the highest ranked map would take precedence in case of overlap and disagreement in classes. The ranking included the nature map first, as we believed that the nature map would most accurately represent the distinctions between important LULC classes for bees and it was the most recent of the three files. Secondly, we chose the agricultural parcel map because it has a higher accuracy and greater focus than the urban map. The urban map is also the oldest of the three sources. Using ArcGIS software we merged the three maps together removing overlapping areas based on the aforementioned hierarchy (ESRI 2013). The merged map was then converted into a 10 × 10 m raster. Each of the LULC classes in the raster were then aggregated as percentage cover measurements at a 10 × 10 km grid resolution. Twelve classes remained of which 10 (freshwater and saltwater were removed) were used to model wild bee habitat filtering and community assembly patterns in chapter 4 (Fig 2.6).

European Scale

Corine land cover (CLC) is an inventory of LULC at the European scale produced first in 1990 and then again 2000, 2006 and 2012 (EEA 2000). The CLC is a

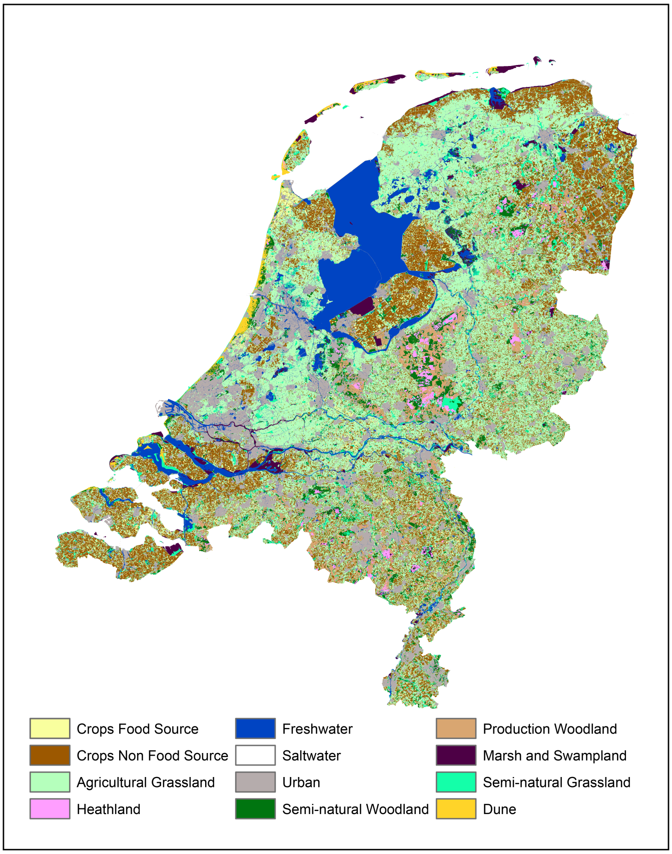


FIG. 2.6: **Final map used in chapter 4 to measure habitat filtering in wild bee species.** Aggregation of three sources, (1) Index Natuur en Landschap (INL; Inter Provinciaal Overleg 2016); (2) Basisregistratie Gewaspercelen (BRP, EZK 2015); and (3) Bestand Bodemgebruik Productbeschrijving (BBG; CBS 2012).

raster with a resolution of 100 × 100 m. The CLC is bases on satellite images and integration with existing geographic information systems (GIS). In chapter 5 the baseline LULC used for training the species distribution models is aggregated and reclassified from the CLC 2000. The baseline map (2000) was reclassified to 6 classes and a 250 × 250 m resolution to match the future projections of LULC change:

1. Settlement

2. Arable
3. Permanent crops
4. Grassland
5. Forest
6. Other

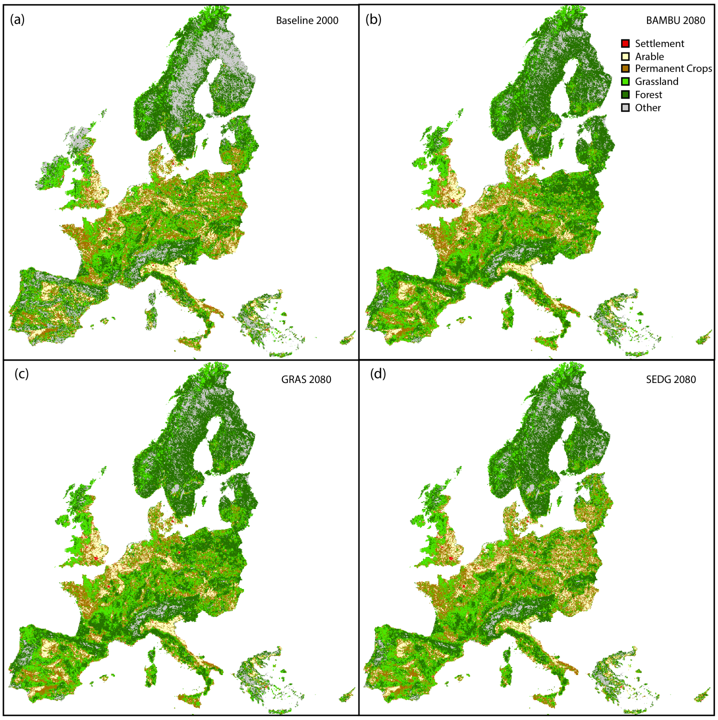


FIG. 2.7: **ALARM scenarios of Land Use Change for 2080.** (a) Baseline map from aggregated 2000 Corine Land Cover map. (b) Business as might be usual (BAMBU) land use projection for 2080. (b) Business As Might Be Usual (BAMBU) land use projection for 2080. (c) GRowth Applied Strategy (GRAS) land use projection for 2080. (d) Sustainable European Development Goal (SEDG) land use projection for 2080.

From this baseline a set of future LULC change scenarios was created (Rounsevell et al. 2006; Spangenberg et al. 2012). Three storyline, socio-economic, scenarios were produced and included a business as might be usual scenario, a liberal growth scenario and a more sustainable scenario (for more detail see methods in chapter 5 and Spangenberg et al. 2012). Simulated LULC change was undertaken by combining a variety of different models, specifically econometric, ecosystem, land use and climate models (Spangenberg et al. 2012). The timeframes of the different models ranged between 2000 and 2100. The resulting output consisted of land use maps for 2020, 2050 and 2080 for each of the three scenarios. Each of these map outputs was downscaled to 250 × 250 m to match the data from the present (Dendoncker et al. 2006). We utilized the maps for 2050 and 2080 for 5 of the LULC classes, emitting 'other' because it is difficult to ascribe ecological meaning to the variety of classes of which it is comprised (Fig 2.7). To use in the SDMs each LULC class was aggregated to a percentage cover raster at 5 × 5 km, 10 × 10 km, 20 × 20 km and 50 × 50 km grid resolutions.

The scenarios used in these analyses represent three different narratives or storylines of LULC at the European scale. The storylines describe the policies, philosophies and instruments behind the scenarios. This information is then used with quantitative data related to the economy, climate and land use to simulate potential futures. The three scenarios can be broadly described as exploratory (GRAS and BAMBU) and normative (SEDG). Exploratory scenarios take trends from the present and extrapolate into the future analysing the response of LULC to specific questions. Normative scenarios by contrast involve backcasting from a desired future condition, and describing the decision making that would lead to said scenario. Each storyline (scenario) results in projections of climate and socio-economic trends. These two projections, alongside the storyline then influence the spatially explicit land use model, which we use in our analyses in chapter 5. The list below shows a elaborated overview of each of the three scenarios, a simpler representation is available in the methods section of chapter 5. All this information is taken from Spangenberg et al. (2012).

- **'Business as Might Be Usual' (BAMBU)**—IPCC A2 scenario; mean projected temperature rise in Europe at 2100 is 4.7°C; an intermediate change scenario based on extrapolated current and proposed socio-economic and policy decisions. Policy decisions that already exist at the EU level are included. For example the energy policy is focused on reducing greenhouse gas emissions by 20% by 2020 and 80% by 2080, while increasing nuclear and renewable energy sources. Trade policy promotes free trade and EU funds are targeted at infrastructure and growth in developing areas.

- **‘Growth Applied Strategy’ (GRAS)**—IPCC A1FI; mean projected temperature rise in Europe at 2100 is 5.6°C; a maximum change scenario driven by policies of deregulation and economic growth with a focus on globalization. For example the energy policy is focused on increasing efficiency and only implementing renewable sources where cost effective. Trade policy promotes free trade at the global scale and EU funds will be eliminated.
- **‘Sustainable European Development Goal’ (SEDG)**—IPCC B1 scenario; mean projected temperature rise in Europe at 2100 is 3.0°C; a moderate change scenario driven by economic, social and environmental policies, related to stabilizing atmospheric greenhouse gases emissions and stopping the loss of biodiversity, leading to an environment in good condition, a healthy economy and international cooperation. For example the energy policy is focused on reducing greenhouse gas emissions by 75%, increasing renewable energy sources and shifting consumption. Trade policy includes reduce global sourcing and EU funds are targeted at local green developments, education and employment.

Pyrenees Scale

In chapter 6, historical land use maps of the Pyrenees National Park for the late 19th century were not available. Therefore we used land cover data from Historical HILDA the project ”Historic Land Dynamics Assessment” (HILDA) version 2.0 (Fuchs et al. 2013; Fuchs et al. 2015). This project aimed to reconstruct land use at the scale of Europe from 1900 to 2010, based on data available for each decade at a spatial resolution of 1 × 1 km. Land cover is classified into six categories.

1. Forests: including transition zones between bushes and forest, tree nurseries, and reforestation areas.
2. Grasslands: including natural grasslands, wetlands and pastures.
3. Cultivated land: including orchards and arable land.
4. Human settlements: buildings, roads, railways etc. and green urban areas.

5. Water
6. An ”other” category grouping the areas of ruderal vegetation, beaches, bare floors, rocks, etc.

We used these maps and categories to calculate modelled shifts in land use change for a 10 km buffer around the area were wild pollinators were collected in 1889 and 2005-06.

2.2.3 Climate Data

Netherlands Scale

In chapter 3 we used the 19 Bioclim variables available from `worldclim.org` (Table 2.3). The 19 Bioclim variables are available at the global scale and are described as biologically meaningful. These 19 variables are derived from monthly temperature and rainfall values and are available as 30 second resolution rasters (Hijmans et al. 2005). These variables are calculated with climate data from 1960 until 1990. For each bioclimatic variable we clipped the extent to the outline of the Netherlands and re-projected the raster to a 1×1 km resolution. During the SDM process we then selected the final variables based on correlations between covariates, ecological significance to bees and importance in the SDM. This resulted in 5 of the 19 Bioclim variables being used:

1. Mean diurnal range of monthly temperature (Bio2)
2. Mean temperature of warmest quarter (Bio10)
3. Precipitation of driest month (Bio14)
4. Precipitation of warmest quarter (Bio18)
5. Temperature seasonality (Bio4)

In chapter 4 we wanted to improve the spatial and temporal accuracy and use climate measurements specific to the Netherlands. Therefore, we calculated the same 19 Bioclim variables (Table 2.3) but this time using a Netherlands specific source for the temperature and rainfall values. Specifically, we downloaded daily temperature and rainfall statistics from Royal Netherlands Meteorological Institute (KNMI) online API (available at `https://data.knmi.nl/wms/cgi-bin/wms.cgi`). We downloaded daily temperature minimum, maximum and means, and rainfall for everyday between 2005 and 2014 as raster files, each containing 48,297 values. Again, 5 of the Bioclims were used in the final analysis:

1. Minimum temperature of coldest month (Bio6)
2. Mean temperature of driest quarter (Bio9)
3. Mean temperature of warmest quarter (Bio10)
4. Annual precipitation (Bio12)
5. Precipitation of driest month (Bio14)

TABLE 2.3: **Overview of bioclimatic variables used in species distribution modelling** (Hijmans et al. 2005) The 19 bioclimatic variables, available from worldclim.org and can be produced using the Dismo R package (Hijmans et al. 2017).

Temperature		**Moisture**	
Bio1	Annual Mean Temperature	Bio12	Annual Precipitation
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Bio13	Precipitation of Wettest Month
Bio3	Isothermality (BIO2/BIO7) (* 100)	Bio14	Precipitation of Driest Month
Bio4	Temperature Seasonality (standard deviation of annual temperature *100)	Bio15	Precipitation Seasonality (Coefficient of Variation)
Bio5	Max Temperature of Warmest Month	Bio16	Precipitation of Wettest Quarter
Bio6	Min Temperature of Coldest Month	Bio17	Precipitation of Driest Quarter
Bio7	Temperature Annual Range (BIO5-BIO6)	Bio18	Precipitation of Warmest Quarter
Bio8	Mean Temperature of Wettest Quarter	Bio19	Precipitation of Coldest Quarter
Bio9	Mean Temperature of Driest Quarter		
Bio10	Mean Temperature of Warmest Quarter		
Bio11	Mean Temperature of Coldest Quarter		

European Scale

The climate data used in chapter 5 represents temperature and rainfall variables for 1971-2000 as the baseline period and climate change projections for 2021-2050 and 2071-2100 (New et al. 1999; Mitchell et al. 2004). These variables were available globally at 10 minute resolution. We used these values to produce 14 climate variables with which analyse the climate requirements of European bumblebees of which, after accounting for correlation and ecological significance, 5 were selected (see supporting information chapter 5, Table S5.2).

The future climate change projections were created using the same scenarios used for the future land use change models and each scenario is associated with a scenario of climate change from the Intergovernmental Panel on Climate Change (IPCC 2001). Specifically, BAMBU is connected to the IPCC A2 scenario, GRAS is connected to A1F1 and SEDG the B1 scenario (Spangenberg et al. 2012). The IPCC scenarios use representative concentration pathways (RCPs) which are modelled trajectories (until 2100) of four greenhouse gases. These models were integrated into the ALARM scenario projections of climate change for 2050 and 2100. Precisely, the final climate scenarios were derived from a coupled Atmosphere-Ocean General Circulation Model (HadCM3; New et al. 1999). For each scenario and each of the five climate variables we aggregated them to rasters at 50 × 50 km and 20 × 20 km resolution grids, and downscaled them to 10 × 10 km and 5 × 5 km resolution grids.

Pyrenees Scale

For the Pyrenees study area in chapter 6 it was neccesarry to have long-term high resolution climate data to observe if climate change is ongoing in the region. We therefore utilized the ClimateEU software, version 4.63, (available at `http://tinyurl.com/ClimateEU`). Using coordinates and elevation values in the surrounding area we extracted monthly temperature conditions in the Pyrenees National Park from 1900 until 2009 (Hamann et al. 2013; Wang et al. 2016). For a detailed methodology see Hamann et al. (2013).

2.2.4 Trait Data

Trait data represent an important tool that can be used to group species according to shared characteristics. Species traits are often used as a proxy for the taxonomic separation between species and can be useful to attribute a measure of diversity in functions rather than a purely species diversity (Keddy 1992). One of the main goals of including traits in ecological studies is to simplify complex ecological systems (Dray & Legendre 2008). The trait data used within this thesis was extracted from the “European bee traits database” (established by ALARM, `www.alarm-project.ufz.de`, and developed by STEP, `www.STEP-project.net`). The extraction for the Netherlands used in chapters 3 and 4 consisted of traits data for 349 species. The traits used in the thesis were selected based on ecological relevance to habitat selection and data availability for the majority of wild bee species. The traits used include:

1. habitat specialization: a number from 1 - 8 representing the number of habitat types a species has been found in. These 8 habitat types broadly denote the number of biomes present in Europe.

2. feeding specialization (Lecty): a categorical variable with 5 levels. Polylectic defines a bee species which collects pollen from multiple unrelated flowers. Oligolectic refers to bees which only collect pollen from a single plant family or genus. Monolectic bees only collect from a single plant family and represent the most specialized feeding habit. Some species are classified as oligolectic or polylectic as certain populations of the species may exhibit both behaviours. Finally parasitic species which do not collect pollen are classified as having no lectic status. For the thesis we have simplified this characteristic to three classes, with monolectic species grouped with oligolectic species and those species representing both behaviours grouped based on the more commonly observed behaviour. We chose to simplify the classifications to these three classes because we believe these classifications capture the likely relationship that a bee species will have with its environment. Specifically, whether a bee species requires a flower rich habitat, or if the presence of a particular plant genus or family is more important (Michener 2000).

3. body size: a continuous variable measured as the distance in millimetres between wing tegulas. The tegula is defined as *‘the anterior most independent sclerite associated with the wing base’* (Headrick & Gordh 2009). In other words the plate on the thorax of the bee where the wing joins the body.

4. sociality: categorical variable of 9 classes ranging solitary bees to highly eusocial bees with cleptoparasites and social parasites. Sociality is described in detail in the introduction section (1.3). For the purpose of the thesis we simplified sociality to three classes. Solitary bees, bees which show any form of sociality and parasitic bees. In this thesis we do not consider honey bees, which is the only highly eusocial species in Europe, therefore sociality refers only to those species classified as primitively eusocial.

5. nesting habit: as with sociality nesting habit refers to a large number of potential behaviors which are simplified in the context of this thesis. In chapter 3 we either classified bee as below or above-ground nesters. Which was changed in chapter 4, with species classified as either excavators who create their own nest spaces or renters who use existing cavities. In practice the majority of excavator species are also classified as belowground nesters therefore there is little difference between the classifications made in chapter 3 or chapter 4. We simplified this trait to only two variables because, as with lecty we believe that at the landscape scale more detailed classifications would not be captured by the LULC and climate resolution used. Parasites were classified based on the nesting habit of their most common host.

6. length of flight period: continuous variable of the number of months a species is found flying throughout the year.

7. voltinism: a categorical variable which refers to the number of broods or generations that a species has within a single year. Categories were simplified to either univoltine, a single generation per year, or multivoltine, two or more generations per year. Species whose populations show different behaviors were again classified based on the most commonly observed behavior.

2.2.5 Phylogenetic Data

In chapter 4 we use a matrix of phylogenetic relatedness to measure phylogenetic niche conservatism among Dutch wild bees. The matrix and the database to produce it was gathered and processed by Grégoire Noël from the University of Liège, Gembloux Agro-Bio Tech. The following outlines the process he used.

Molecular data selection

Mitochondrial gene of cytochrome oxidase I (COI), or barcode sequences (Ratnasingham & Hebert 2007), is commonly sequenced for identifying bee species (e.g. Magnacca & Brown 2012; Schmidt et al. 2015). When COI sequences were available, one barcode, at least, was randomly extracted on 29th April 2016 from GenBank (Benson et al. 2014) for each Belgian bee species, of which Dutch wild bees species are a subset (N.J. Vereecken, personal communication). In total, 355 bees barcodes were retrieved. Four random barcodes of Crabronidae wasps family (*Pison chilense, Philantus triangulum, Bembix troglodytes, Sphecius speciosus*), recognized as sister group of Anthophila clade (Danforth et al. 2013; Hedtke et al. 2013) were also added to molecular dataset as an out-group to root phylogenetic tree. See Table S4.4 for accession details for all species.

All COI bees sequences were aligned using ClustalX v.2.1. (Larkin et al. 2007) with defaults parameters and pairwise deletion for gap treatments. After quality control of all barcodes, the obtained alignment included at most 1481 nucleotide characters. jModelTest 2.1.10. (Darriba et al. 2012) was used to explore best nucleotide substitution model on our aligned DNA barcode sequences. Generalized Time-Reversible model with invariables sites and gamma model of rate heterogeneity (GTR + I + Γ; Tavaré 1986) was selected as best nucleotide substitution model for our aligned COI sequences.

For phylogenetic reconstruction, maximum likelihood (ML) method was conducted in RAxML v.7.7.1. (Stamatakis et al. 2008; Stamatakis 2014) on the CIPRES Science Gateway (Miller et al. 2010; http://embnet.vital-it.ch/raxml-bb/). 100 rapid bootstrap inferences were executed and followed by a thorough ML search. All free model parameters will be estimated by RAxML sofware. ML estimate of alpha-parameter, I + Γ model parameters were estimated up to an accuracy of 0.001 Log Likelihood units. Bipartition information from best known ML tree (i.e. best ML tree compiled from ML boostrapping in Newick format)

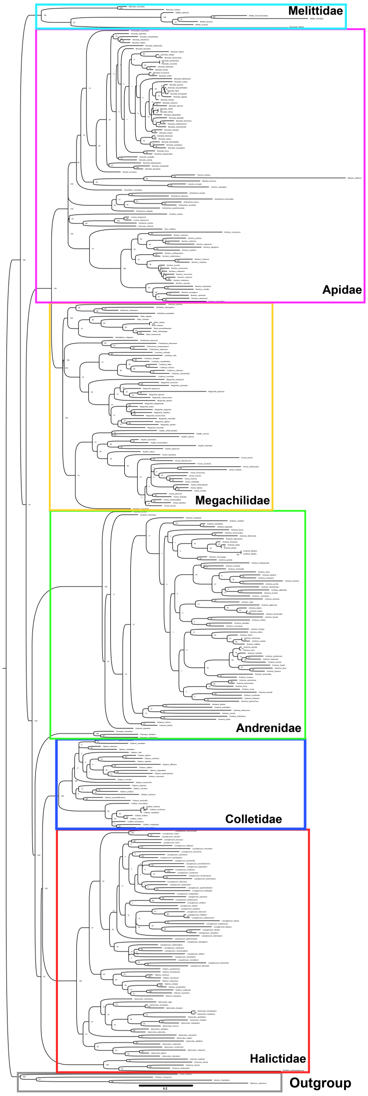


FIG. 2.8: **ML tree constructed using 355 COI sequences (1481 bp) of Belgian bees species from public repositories (GenBank).** This phylogenetic tree is rooted with an outgroup of 4 Crabronidae wasps COI sequences: *Pison chilense, Philantus triangulum, Bembix troglodytes, Sphecius speciosus*. All bees families are encompassed by colored rectangle. Values at node depict bootstrap support (%) in the ML method. This phylogenetic tree was drawn using FigTree v.1.4.3. (Rambaut 2017) and modified with Inkscape v.0.92.2. Phylogenetic tree created by Gregoire Noel.

was used to draw wild bees phylogenetic tree (Fig 2.8) by FigTree v.1.4.3. (Rambaut 2017). Then, branch lengths of bees phylogenetic tree were calculated by setting the p-parameter to 1 (Hoiss et al. 2012).

Phylogenetic reconstruction

All COI bees sequences were aligned using ClustalX v.2.1. (Larkin et al. 2007) with defaults parameters and pairwise deletion for gap treatments. After quality control of all barcodes, the obtained alignment included at most 1481 nucleotide characters. jModelTest 2.1.10. (Darriba et al. 2012) was used to explore best nucleotide substitution model on our aligned DNA barcode sequences. Generalized Time-Reversible model with invariables sites and gamma model of rate heterogeneity (GTR + I + Γ; Tavaré 1986) was selected as best nucleotide substitution model for our aligned COI sequences.

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2.3 Methods Overview

In this thesis we use statistical analyses to evaluate complex ecological questions related to how wild bee species interact with their environment. To do this we use a variety of different statistical techniques and approaches to deal with different problems. We utilize regression techniques to estimate the relationship between different variables, using both maximum likelihood and Bayesian approaches.

Regression techniques allow us to make causal inferences on which processes may be driving observed patterns. Furthermore, we use machine learning[1] methods within a species distribution modelling framework to classify habitat suitability at different spatial scales and resolutions. All the statistical methods used are capable of analysing the large datasets available regarding wild bees and their environments. In the following section these statistical methods are outlined and discussed.

2.3.1 Species Distribution modelling

Species distribution models (SDMs) are statistical tools which take known occurrences of species and use computer algorithms to create a mathematical representation of the environmental space occupied by a species. This representation can then be used to project the distribution of the species into different environmental spaces. We use SDMs in chapters 3, 4 and 5 in this thesis.

SDM Occurrence Data

In the wild bee data section (2.2.1) we outlined the eclectic nature of the wild bee occurrence records used in this thesis and the potential biases associated with them. There are a number of techniques available to improve the quality of these data for their use in SDM. The first step of analyses with these datasets is detailed mining of the records to determine the spatial and temporal quality and reliability of each occurrence record. For example, in chapter 5 species occurrence records are either recorded with GPS point coordinates or on a grid. When aggregating the species records to different grid resolutions we removed all records that were recorded at a lower resolution than our grid, and therefore unreliable. We also did this by limiting our analyses to species with a certain number of species records to avoid modelling under-sampled species. Furthermore, as mentioned in the wild bee data section (2.2.1) we employed re-sampling methods to avoid spatial auto-correlation due to spatially biased sampling (Broennimann et al. 2012). In chapter 5 we specifically incorporate spatial auto-correlation into the models to

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[1] Machine learning refers to automated methods of data analysis which can detect patterns in big data sources. Machine learning can be used for regression and classification problems and progressively improves model performance building upon each model (Murphy 2012).

quantify the effect that it has on the relationship between species and their niches (Ovaskainen et al. 2017). We also use species records across a temporal range to ensure a more detailed sample. This is a direct trade-off with knowing the exact conditions of where and when a species was found, but we decided that having sufficient records with which to model the species was more important.

The available data is described as presence-only data as true absence values are unavailable (Barbet-Massin et al. 2012a). This stems from the fact that a small and highly mobile wild bee individual cannot be classified as absent in a survey, regardless of the collection effort. Therefore, we need to provide the models with areas where we estimate the species is absent. This is often done by taking a background sample of locations used in the SDM and randomly defining areas where a species has not been found as an absence, these absences are referred to as pseudo-absences (Phillips et al. 2009). To deal with the bias of areas that have not been sampled within our study boundary we utilize target background sampling, whereby the background sample from which pseudo-absence values are obtained is only taken from areas where wild bees have been surveyed previously and limiting the introduction of incorrect absences (Phillips et al. 2009; Mateo et al. 2010).

Furthermore, when projecting into a unknown time period it is important to train models with as much data as possible to fully capture the entire range of the species being modelled, limiting the species to part of geographical range is likely to result in inaccurate predictions (Titeux et al. 2017). We have attempted to do this in chapter 5 by using species occurrence records from the entire extent of the LULC covariates, even when projecting onto the smaller BENELUX region.

Variable Selection

Selecting the appropriate environmental covariates with which to model a species distribution is a fundamental step in the SDM process. When selecting covariates focus should be applied to ecological theory and the known causal relationship between a specific covariate and species occurrence (Guisan & Zimmermann 2000). Understanding causality is additionally important when deciding between correlated variables (Dormann et al. 2013). For example, when projecting into the future under climate change scenarios the selection of climate variables can result in different projections and may signify the difference between a projected species extinction and no visible change (Harris et al. 2013). Guisan & Thuiller (2005) separate environmental factors into three categories, described here with examples appropriate for wild bee species; (1) limiting factors associated with the eco-physiology of a species, e.g. the majority of bumblebees occur in areas where summer temperatures are between 5-25°C (Goulson 2010); (2) disturbances which modify environmental systems, e.g. intensive agriculture limiting resources for wild bees (Kremen et al. 2002); and (3) resources which can be used by the target species e.g. availability of heathland as a feeding resource for specialized wild bees (Moquet et al. 2016) or sandy soils as a nesting resource (Cane 1991). The most available and commonly used predictor variables are climate variables, as they are the most readily available variables at the global scale (Elith & Leathwick 2009). Nineteen bioclimatic variables are commonly used in studies of climate effect on species distributions and represent an attempt to increase the causal relationship between species distribution and climate by calculating climate variables more illustrative of species ecology and directly applicable to SDMs (Table 2.3; Busby 1991; Hijmans et al. 2005; Hijmans & Elith 2014).

Algorithms

Once a prospective modeller has chosen the species collection data and covariates then the next step involves selecting the appropriate algorithm to train the model and statistically represent the relationship between occurrence and the environment. There are many algorithms available to use in SDM studies. The choice of algorithm can make a significant difference to model outputs, and can vary in fit, variable selection and predictive accuracy (Aguirre-Gutierrez et al. 2013). In chapter 3 we used maximum entropy (MaxEnt) to construct the SDMs, in chapter 4 we used GLMs as part of a hierarchical Bayesian framework and in chapter 5 we used an ensemble modelling approach of three different algorithms, generalized linear models (GLMs), generalized boosted regressions model (GBMs) and MaxEnt.

MaxEnt

Maximum entropy[2] (MaxEnt) is an algorithm for modelling the distribution of species. MaxEnt is used when only presence occurrence records are available and there are no recorded absences for a species (Phillips & Dudík 2008). Therefore MaxEnt is an ideal method to use with museum collections (Elith et al. 2011). MaxEnt is perhaps the most widely used methodology for SDM studies because of its robust ability to deal with a variety of presence-only data and explanatory covariates (Phillips et al. 2006; Phillips & Dudík 2008; Elith et al. 2011; Merow et al. 2013).

MaxEnt estimates a species distribution within a given geographic space, specifically it compares the variation in probability density within the covariate space in presence locations against the probability density of a background sample of the same covariate space (Elith et al. 2011). In other words MaxEnt defines the suitability of certain habitats for the modelled species. MaxEnt requires covariates which explain the habitat available within a defined landscape boundary (background) and spatially explicit occurrence records of species found within this landscape (presence-only records). MaxEnt will then use this information to provide a conditional (conditional to the species being present) probability of presence at the chosen resolution for each species. MaxEnt does this by first calculating the conditional density of the covariates in areas where the species is present $f_1(z)$ and the unconditional density of covariates across the total study area $f(z)$. The estimate of $f_1(z)$ is made based on the presence values, many distributions are possible so MaxEnt tries to choose the distribution closest to that of the background total study area $f(z)$. The probability distribution across locations is then estimated based on the ratio between $f_1(z)$ and $f(z)$ (Elith et al. 2011). This is fit as a log linear model similar in form to a generalized linear model (GLM). The resulting estimates can be seen as a measure of habitat suitability per location. The relationship between species presence and the model covariates is often more complicated than a simple linear relationship and therefore MaxEnt provides different feature options which can be used to fit more complex relationships. MaxEnt has 5 feature types for the covariates; (1) linear (the covariate itself); (2) quadratic (the square of the covariate); (3) product (the

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[2] Maximum entropy modelling refers to the idea in information theory that when defining an unknown response with a statistical model, the best solution will always be the one with maximum entropy (Jaynes 1957). Entropy being a measure of the information produced by a random data source.

product of two covariates); (4) threshold (a step function where a different response to the covariate is possible above and below a threshold) and (5) hinge (similar to the threshold but the different response above and below the threshold is a linear relationship). For a more detailed explanation of the theory and statistical basis of MaxEnt's use in ecology see Elith et al. (2011). In chapter 3 we use MaxEnt species distribution models to model the distribution of 193 wild bees in the Netherlands, using 13 covariates of land use and climate conditions. We chose to use only MaxEnt models because MaxEnt had previously been the best performing method for a similar group of species, hoverflies, in the same geographic extent (Aguirre-Gutierrez et al. 2013). In chapter 5 we also use MaxEnt but this time as part of an ensemble mode to increase our ability to account for uncertainty and variation observed when modelling different species.

Generalised linear models (GLMs)

Generalised linear models (GLMs) are a technique for weighted linear regression with model observations distributed to different exponential families fit with maximum likelihood (Nelder & Baker 1972). A simple linear model is described as:

$$Y = x + X\beta + \epsilon$$

Where Y is the response variable, x refers to the intercept, X is a vector of the known values of the independent explanatory variables, β is a vector of the regression parameters for each explanatory variable; and ϵ is the error and any unexplained model variation (Guisan et al. 2002). Alongside the linear predictor outlined above the generalized linear model introduces a probability function distribution for the necessary exponential family and a link function (Nelder & Baker 1972). The role of the link is to define the relationship between the mean of the response variable (distribution function)[3] and the chosen linear predictors, (Guisan et al. 2002). The link function transforms the expected value of response variable and allows it to depend on the explanatory variables. The majority of

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[3] The mean of the distribution function refers to average value of the cumulative distribution function that describes the distribution of the residuals of a binomial response variable (0 or 1).

SDMs use presence/absence data and therefore are best modelled with a binomial distribution with a logit or probit link function (Guisan et al. 2002; Hijmans & Elith 2014). A GLM is described as:

$$g(E(Y)) = LP = x + X\beta$$

Where the expected value of the response variable $E(Y)$ with a link function $g()$ is associated with a linear predictor, X (Guisan et al. 2002). Whilst not the most consistent or accurate algorithms GLMs provide a simpler interpretation than many of the other algorithms used in SDM analysis (Elith & Graham 2009; Aguirre-Gutierrez et al. 2013). Generalized linear models also allow stepwise variable selection using Akaike Information Criterion (Akaike 1998; Guisan et al. 2002). GLMs are used in chapter 4 with a probit function as part of Bayesian framework and in chapter 5 with a link function as part of an ensemble SDM.

Generalised boosted regressions model (GBMs)

Generalised boosted regressions model (GBMs) utilize gradient boosting, a method of regression which uses a large ensemble of multiple models in the form of decision trees (Friedman et al. 2000). The algorithm used as part of an ensemble model in chapter 5 is a boosted regression tree. Each of the models that form the large ensemble of models is a single regression tree (Friedman 2001). Each regression tree is sequential to the previous and therefore learns from the errors of each previous tree. For SDMs, GBMs use a Bernoulli distribution (0 or 1, present or absent) as the response variable. GBM permeates through each relationship between covariate and response in the form of regression trees (Friedman 2001). Each tree is fitted incrementally with each tree predicting the residuals of the tree before it (Friedman et al. 2000; Elith et al. 2008). This iterative process results in a final model that predicts presences based on continuously adding trees and re-weighting the relationships within the data to reflect previous poor models (Friedman et al. 2000). Cross-validation, when the data is split into testing and training subsets to test the accuracy of the trained model, is used to validate iterative trees in the building process. Furthermore, to avoid over-fitting the model, it is important to specify the maximum number of trees which can be fitted (Elith et al. 2008).

Ensemble modelling

Ensemble modelling as used in chapter 5 involves utilizing a variety of approaches, fitting multiple model algorithms and then analysing the resulting projections (Araujo & New 2007). Ensemble models can be utilized in two ways; either by selecting the best model based on your chosen validation criteria (Elith et al. 2006) or by creating a consensus of all model predictions, as we do in chapter 5 (Barbet-Massin et al. 2012b). Consensus ensemble modelling provides significant benefits over modelling with a single algorithm, Instead of providing a single value of habitat suitability per grid cell it allows for the calculation of averages and variances measures overall and per choice of input, algorithms, model features, scale and resolution (Marmion et al. 2009; Thuiller 2014b). Ensemble modelling techniques are often applied to forecasting species distributions under shifting global climate and LULC states because they offer the possibility of calculating and presenting the inherent variability associated with projections into variable future conditions (Araujo & New 2007). In Chapter 5 we utilize median ensemble predictions of three algorithms. The three models chose were GLMs, GBMs and MaxEnt. The decision to include these three algorithms was based on their performance in modelling hoverflies, a species group with similar mobility and behaviour to bees (Aguirre-Gutierrez et al. 2013). Authors found that GLMs performed well for widespread common species and also represent a more easily interpreted model, GBMs had higher consistency in variable selection and also obtained good models for more widespread species, whereas MaxEnt does well with more narrow distribution and species with fewer records (Aguirre-Gutierrez et al. 2013). Therefore, we believed that a combination of these three model types would adequately deal with the variation in spatial distribution and number of records in the European bumblebee collection records.

Validation

Following the training of models a vitally important step is to test the model performance to justify the use of the model for its particular purpose. Model verification measures how well a model fits the data used to train it, whereas the more important step is validation which compares the SDM to independently collected species occurrence data (Araújo & Guisan 2006). The most common way models are validated is with a split-sample approach as part of a cross-validation procedure, where a subset of the data is not used to train the model and is instead used to test the accuracy of the model predictions; this process is repeated with several split samples to measure model performance across the whole range data (Elith & Leathwick 2009). In all three chapters where we use SDMs we use cross-validation technique to validate the models. Cross-validation involves a priori splitting the occurrence records into training and testing subsets. In all three chapters with SDMs we apply the same 80% training and 20% testing split. When using cross validation a number of different statistics can be calculated to measure model performance. These statistics are calculated using a confusion matrix[4] were observed testing records are compared to predicted occurrences (Fielding & Bell 1997). It provides four values: sensitivity (true positive fraction), specificity (true negative fraction), the false positive fraction (1-sensitivity) and false negative fraction (1-specificity; Table 2.4). Sensitivity is measured as a ratio between sites where the model has correctly predicted a true presence and the total number of presences sites. Specificity is the ratio between absence sites correctly predicted as such and total number of absences or pseudo-absences. To obtain these measures habitat suitability values from the SDM must be converted into binary presence or absence predictions (Fielding & Bell 1997). This is done using a threshold, see Threshold section.

TABLE 2.4: **Confusion matrix showing the discriminatory ability of a Species Distribution Model (SDM).**

		Actual Occurrences	
		Present	**Absent**
Model Prediction	**Present**	a	b
	Absent (Pseudo-absences)	c	d
		Sensitivity	**Specificity**
		a/(a+c)	d/(b+d)

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[4] A confusion matrix is a table that describes the efficacy of a classification model (SDM) to predict known values.

A commonly used statistic to validate the model based on the ability of the model to discriminate between presence and absence is the area under the curve (AUC) of the receiver operating characteristic (ROC). The ROC is measured as the relationship between the rate of false positives (1-specificity) and the sensitivity. The AUC is independent of the threshold as it checks discrimination across a range of thresholds. A model is deemed to be accurate when it shows a curve that has high sensitivity (y-axis) with low values for the fraction of false positives (x-axis, Fig 2.9; Jiménez-Valverde 2012). In other words, the AUC value represents relationship between the proportion of true positives and the proportion of false positives when the threshold varies from 0 to 1. A model which shows no discrimination, a random predictor, is represented by an AUC of 0.5. In the case where there are no absences available the specificity is plotted against the background or pseudo-absence points predicted as present. This changes the interpretation slightly, as in this case the AUC measures whether the model discriminates a true presence site from a random background site (Phillips et al. 2006). Therefore, in all the cases where we use cross-validation in the thesis we use the AUC value. In chapter 3 we additionally outline in detail how we use independently collected data to test model performance.

Threshold

Threshold values are required for many SDM applications to convert projected habitat suitability values into presence or absence predictions (Jiménez-Valverde & Lobo 2007). We utilize threshold values to convert the predictions of bumblebee distributions under future conditions into binary presence absence maps. This allows us to look at specific locations and determine if a species has lost or gained suitable habitat from the present to the future. A number of methods are available to select thresholds, for more information see Liu et al. (2005) and Jiménez-Valverde and Lobo (2007). We used the threshold point at which the model maximizes the sum of sensitivity and specificity (mas SSS) values (Thuiller et al. 2015). Max SSS has been criticized as a threshold criterion for presence only models, specifically because without true absence data specificity is unreliably calculated (Braunisch & Suchant 2010; Merow et al. 2013). However, Liu et al. (2013) show that max SSS consists in calculating a threshold value regardless of

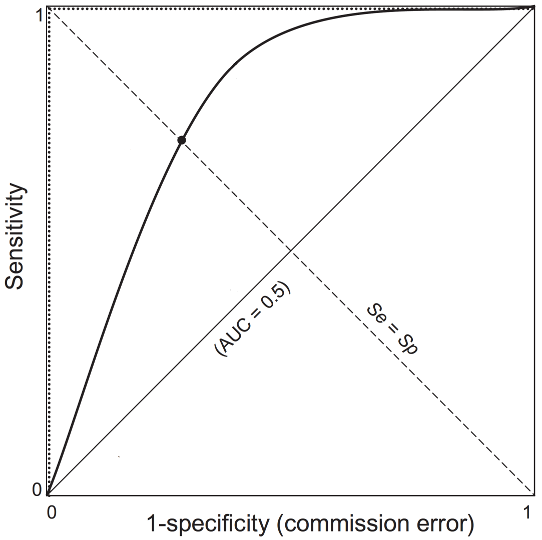

Fig. 2.9: **Receiver operating characteristic (ROC) curve.** Dotted line shows a model with perfect discrimination area under the ROC curve (AUC) of 1. Black thick line, curve of a model showing imperfect discrimination. Diagonal black line shows a model with no discrimination, AUC = 0.5. The dashed line shows points at which sensitivity (Se) equals specificity (Sp). Source: figure modified from Jiménez-Valverde (2012).

whether presence/absence or presence only data is used, it is also objectively selected and uses both sensitivity and specificity predictions. Therefore, we believe it is the most appropriate threshold selection to use to convert habitat suitability values into presence absence maps.

2.3.2 Linear Mixed Effects Models (LMM)

Linear mixed effects models (LMM) and generalized linear mixed effects models (GLMM) are an extension of linear regression and generalized linear modelling (see Species Distribution Models). The key component of a LMM is that it contains both fixed and random effects (Zuur et al. 2009). In general LMMs are used when the data have a hierarchical nested structure, where measurements are repeated across the same units or groups of units (Bolker et al. 2009; Zuur et al. 2009). In other words the model assumes that measurements coming from the same 'unit' are non-independent. For example, multiple measurements of species richness from the same agricultural field are non-independent as they are likely to be affected by the conditions specific to that field. The random structure is useful when dealing with a random subset of a larger population. The agricultural fields in the example are a subset of a many agricultural fields which could be sampled. For example, if a researcher is interested in what environmental factors influence species richness measurements they are most likely not interested in the inherent variability between different agricultural fields, in this case the fields should be treated as a random effect. The fixed effects of the LMM work exactly as described in a GLM. The random effect component of the model allows for each statistical unit to have a different baseline value of the response variable in the form of a random intercept which the model estimates (Winter 2013). The linear mixed effect model takes the form of:

$$Y = x + X\beta + Zu + \epsilon$$

Where Y is the response variable; x refers to the intercept; X is a vector of the known values of the independent explanatory variables (fixed effects); β is a vector the regression parameters for each explanatory variable; Z is the random component of the fixed X (random effects); and u the random components to the fixed β and ϵ is the residual error and any unexplained model variation. We use LMMs in chapters 3 and 5 to examine how model performance and distribution metrics are affected by different explanatory covariates, given that we have multiple measurements from sites and for species.

3 Testing projected wild bee distributions in agricultural habitats: predictive power depends on species traits and habitat type

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3.1 Abstract

Species distribution models (SDM) are increasingly used to understand the factors that regulate variation in biodiversity patterns and to help plan conservation strategies. However, these models are rarely validated with independently collected data and it is unclear whether SDM performance is maintained across distinct habitats and for species with different functional traits. Highly mobile species, such as bees, can be particularly challenging to model. Here, we use independent sets of occurrence data collected systematically in several agricultural habitats to test how the predictive performance of SDMs for wild bee species depends on species traits, habitat type, and sampling technique. We used a species distribution modelling approach parametrized for the Netherlands, with presence records from 1990 to 2010 for 193 Dutch wild bees. For each species, we built a Maxent model based on 13 climate and landscape variables. We tested the predictive performance of the SDMs with independent datasets collected from orchards and arable fields across the Netherlands from 2010 to 2013, using transect surveys or pan traps. Model predictive performance depended on species traits and habitat type. Occurrence of bee species specialized in habitat and diet was better predicted than generalist bees. Predictions of habitat suitability were also more precise for habitats that are temporally more stable (orchards) than for habitats that suffer regular alterations (arable), particularly for small, solitary bees. As a conservation tool, SDMs are best suited to modelling rarer, specialist species than more generalist and will work best in long-term stable habitats. The variability of complex, short-term habitats is difficult to capture in such models and historical land use generally has low thematic resolution. To improve SDMs' usefulness, models require explanatory variables and collection data that include detailed landscape characteristics, for example, variability of crops and flower availability. Additionally, testing SDMs with field surveys should involve multiple collection techniques.

3.2 Introduction

Pollinators are responsible for the pollination of over 80% of flowering plants (Ollerton et al. 2011), and the vast majority of global food crops benefit from animal pollination, with approximately half of these crops being highly dependent (Klein et al. 2007). While the honeybee (*Apis mellifera* L.) is considered the most economically valuable pollinator species for agriculture, wild pollinators can be more efficient per individual in enhancing the yield and quality of many crops (Klein et al. 2007; Garibaldi et al. 2013). Yet, their diversity has declined in Europe (Biesmeijer et al. 2006; Dupont et al. 2011; Bommarco et al. 2011; Carvalheiro et al. 2013) and elsewhere (Bartomeus et al. 2013; Martins et al. 2013). These declines have been attributed to a multitude of factors, such as land-use intensification, climate change, alien species, and pests and pathogens (Potts et al. 2010; Vanbergen & The Insect Pollinators Initiative 2013). Several pollinator-friendly practices have been, and continue to be, applied to provide semi-natural and natural resources within agricultural landscapes (Kleijn et al. 2011; Garibaldi et al. 2014). However, as wild pollinators often require specific environmental conditions (Cane et al. 2006), the efficiency of such practices can depend on the characteristics of the surrounding landscape and other environmental variables (Scheper et al. 2013). Understanding which environmental factors determine where wild bees occur in the landscape is essential for the success of such targeted interventions.

Species distribution models (SDMs) can help in understanding how the distribution of and decline in wild bee species is regulated by land-use and climate variables (Elith & Leathwick 2009). Due to the increase in computer power and data availability, species distribution modelling is becoming a widely used ecological tool in studies of biodiversity, predicting occurrence of species in unknown areas, and predicting future occurrences (Franklin 2013). These predictions can help prioritize areas in need of conservation interventions and estimate the impact of environmental change, such as human land-use changes (Guisan & Thuiller 2005; Polce et al. 2013). However, while SDMs are generally based on haphazardly collected data of varying spatial and temporal scale (e.g., museum collection data) and aggregated over a number of years, they are often used to test hypotheses at finer scales and at particular moments in time (Guisan & Thuiller 2005). The efficacy of SDMs for these purposes is therefore a reason of concern.

The importance of testing the accuracy of SDMs is widely recognized (Elith & Leathwick 2009). However, such accuracy tests often use subsets of the same collection data used to build the model. These tests violate the independence expected between training and testing data (Bahn & McGill 2013). Additionally, these tests require a large number of collection points for the data partitioning to be valid (Allouche et al. 2006; Fawcett 2006). Testing the models by collecting independent presence data is the ideal approach, but is rarely applied due to logistic constraints, particularly when dealing with highly mobile organisms (Evangelista et al. 2008; Peltzer et al. 2007). Therefore, for many animal species, it is uncertain whether SDMs can accurately predict species presence in specific locations, and hence, how useful and reliable the results can be in guiding policy for the protection of biodiversity, or estimating the presence of economically valuable species.

In this study, we test the performance of SDMs in correctly predicting wild bee occurrences from recent field surveys and how this varies between species and landscape. As the effects of disturbance and fragmentation depend on sociality, body size, and nesting behavior of bees (Bommarco et al. 2010; Williams et al. 2010; Brittain & Potts 2011), we expect the performance of the SDMs to depend on these traits. Previous studies show that specialized, plant and amphibian species, with specific habitat requirements, are more accurately modelled (Evangelista et al. 2008; Peltzer et al. 2007; Newbold et al. 2010), and we hypothesize that the bees specialized in habitat and feeding will have higher habitat suitability predictions for their occurrences than generalist, widespread species. Additionally, we expect that rarer species will have higher predicted habitat suitability due to the reduced geographical range they usually occupy (Franklin et al. 2009; Rebelo & Jones 2010). Finally, as the SDMs will be based on species records with variable spatial and temporal precision, we hypothesize model predictions in agricultural habitats which have a greater temporal stability (e.g., orchards) will have higher suitability values than for agricultural areas subjected to accentuated temporal changes (such as crop rotation) or subjected to ephemeral establishment of areas rich in flower resources (e.g., wildflower strips).

3.3 Methods

3.3.1 Species distribution model development

This study focuses on the Netherlands, a region for which we have access to relatively extensive and detailed data on species distributions, land use, and climate. The bee collection data were provided by European Invertebrate Survey (Peeters et al. 2012). We used records collected since 1990, and due to the number of available explanatory variables, we included species for which we had more than 30 recorded observations. This led to a total of 193 species across 25 genera (from a total availability of 304 species in 30 genera). A total of 43 989 observations were used to model the species' distributions. The number of collection points per species modelled ranged from 31 (*Bombus cryptarum* Fabricius, *Lasioglossum pallens* Brullé, and *L. rufitarse* Zetterstedt) to 1862 (*B. pascuorum* Scopoli).

We modelled the distribution of these 193 species across the Netherlands using R (R Core Team, 2012) with package biomod2 (Thuiller et al. 2009) and the species distribution modelling algorithm Maxent (Phillips & Dudík 2008). We chose Maxent because it has previously performed well on similar data for a variety of evaluation measures and is robust against overfitting (Phillips et al. 2006; Aguirre-Gutiérrez et al. 2013). The models were constructed with the BIOCLIM climate variables obtained from WORLDCLIM database (Hijmans et al. 2005), and land-use variables obtained from the Dutch rural land-use file version six (Hazeu et al. 2012) and the TOP10NL (Kadaster, 2012). The original resolution of the land-use variables was 25 $\times$ 25 m; to match the coarser resolution of the bee collections and climate data, we rescaled the land-use data to 1 km^2 by calculating the percentage cover (i.e., percentage of 25 $\times$ 25 m cells) of each land-use class within each 1 km2.

Some precipitation and temperature variables for different parts of the year (i.e., warmest, coldest, and wettest quarters of the year) were strongly correlated (Pearson's pair-wise correlation coefficient >0.7). In these situations, we selected the variable thought to have a greater impact on the distribution of bees, such as the variables related to the periods when bees are most active, for example, the warmest quarter. To minimize the overall number of explanatory variables in the model and avoid problems of overfitting, we ran initial MAXENT models for each species with all environmental variables available (27 variables) and then looked at the variable importance value of each variable across all species. We then selected the variables that were consistently among the three most important variables for each species and removed those that were not. The final SDM incorporated thirteen variables: seven land-use variables, five climate variables, and elevation (see Table S3.1).

Maxent requires a background sample to be selected from the covariates included in the model (Elith et al., 2011; Phillips et al. 2009). We used target-group sampling to select our background points (Phillips et al. 2009; Mateo et al. 2010). We specified that this background sample could only be selected from areas where wild bee species have been found since 1990. This approach is more objective and realistic than taking the background sample from sites that have not been sampled, accounting for potential sampling bias (Phillips et al. 2009; Elith et al. 2011), and provides more accurate results (Mateo et al. 2010). We ran the model 11 times for each species: 10 times with random subsets of 80% of the data and once with 100% of the data. Using a common procedure of validation of SDMs, we then used the remaining 20% of the data to produce area under the curve (AUC) values, which is a measure of the proportion of instances correctly predicted against the proportion of absences incorrectly predicted as presences (Jiménez-Valverde 2012). All species models had an AUC of at least 0.6.

We validated the full models (run with 100% of the data) with independent datasets collected during field surveys (see methods below). Model output consisted of a habitat suitability score between 0 and 1 for each species per 1 km2, with 0 indicating not suitable and 1 most suitable.

3.3.2 Field surveys

The data used to test the predictive performance of the SDMs were collected from four independent studies, details of which are described below (for site locations see Fig S3.1). Bee species collected and identified to species level were used to test the models. The different studies were independent of each other, data being gathered in different time periods, by different collectors, and using a systematic survey across several sites and over short time periods. They were experimentally set-up to test particular research questions associated with specific farm types and habitats: arable oilseed rape fields and associated field margins; arable fields with wildflower strips, and apple and pear orchards. While these agricultural landscapes do not represent Dutch farmland as a whole, they cover important types of agricultural landscape with different levels of temporal stability. Orchards are perennial crops maintained for several years; arable fields have annual crops, with crop species rotating every 1 or 2 years. Measures to enhance biodiversity in arable fields (permanent field margins vs. annual wildflower strips) will also interfere with the temporal stability of the landscape. The studies also differed with respect to the sampling methods used.

Furthermore, the SDMs presented here are independently validated based on data from agricultural sites only. In order to fully understand the efficacy of SDMs for modelling wild bee species distributions, natural habitats can also be included, in which bee diversity is much larger than in agricultural habitats (Ricketts et al. 2008).

Arable oilseed rape fields and field margins (sampling method: Transect)

Data were collected in 2011 and 2012 in 16 arable oil seed rape fields and surrounding boundaries located in the eastern part of the Netherlands. Bee surveys were conducted along 150 m^2 transects (15 min pure collecting time per transect). When sampling within fields, two transects of 1×150 m were used, one located at the edge of the field and one located in the center of the field. Field boundary transects varied in size depending on the length and width of the field boundaries (but were in most cases 2×75 m). Oil seed rape fields were surveyed twice a year during oil seed rape flowering, and the field boundaries were surveyed four times a year: twice during and twice after the flowering period of the oil seed rape. Bees were collected using net and hand trapping and identified to species level in the laboratory.

Arable fields with wildflower strips (sampling method: Pan Trap)

In 2011 (first season of wildflower strips) and 2012 (second season), data were collected on 68 arable fields throughout the Netherlands using pan traps. Wildflower strips had been established along the edge of each arable field. Each wildflower strip was 3–9 m in length. The arable fields consisted of potato, sugar beet, or cereal crops. Pan trapping was conducted once at each site. All pan traps were yellow and four were placed at each site, in a square formation two traps in the wildflower strip and two traps in the field each 20 m apart. Each set of pan traps was left for a 24-h period. All species of insects collected in the pan traps were identified, the majority to species level.

Apple and pear orchards (sampling method: Transect)

Six apple and six pear orchard locations were sampled in 2010 and 2011, and 15 apple orchards were sampled in 2013. All sites were located more than 3 km apart within the province of Gelderland in the Netherlands. Flower visiting bees were surveyed using transect walks. Each orchard was surveyed twice per year during blooming, once in the morning and once in the afternoon with at least three and at most 7 days separating surveys. In each orchard, bees were surveyed using a single transect between two rows of trees along the length of each orchard with the transect subdivided into 25-m-long plots (mean number of plots per orchard ±SE: 8.5 ±1.0 for apple in 2011 and 2012; 9.7 ±0.5 for pear in 2011 and 2012; exactly 12 for apple in 2013). Each transect plot was surveyed during a 10-minute period. All flower visitors were collected by net and hand trapping. Easily recognizable species were generally identified in the field; all other species were collected and identified in the laboratory.

Apple Orchards (sampling method: Pan Trap)

In 2013, field surveys were performed at nine apple orchards throughout the Netherlands. Field surveys of bee diversity were conducted using pan traps (Westphal et al. 2008). Each farm was located within a 1 km^2 square landscape sector that corresponded to the scale and positioning of our SDM. Pan trapping was conducted on three separate occasions: before, during, and after apple flowering. For each 1 km^2 site, eight pan traps were positioned, four within the Elstar cultivar (one at each corner) and four located outside the orchard but within the $1km^2$ zone. Each pan trap set consisted of three pan traps (yellow, blue, and white) and was left for a period of 24-h. Bees present in the pan traps were separated from other insect groups and identified to species level.

3.3.3 Testing the model with independent datasets

In this project, the performance of the SDM is assessed as the habitat suitability (0–1) provided by the SDM for the areas where individual wild bees were collected during independent surveys. Suitability values can be considered as a percentage of chance that a species will be present in the area (see the interpretation of Elith et al. (2011) of the MAXENT logistic output). Therefore, we consider the SDMs with higher habitat suitability values for collected occurrences to have superior predictive performance. Furthermore, the habitat suitability value contains more information than the usual binary (presence or absence) classifications based on specificity and sensitivity calculated statistics (Bahn & McGill 2013). We analysed the predictive performance of the SDMs only for species that were collected during the independent field surveys. We did not analyse predictive performance for species not found during the field surveys as we cannot assume that that absence during the survey is indicative of true absence from the site.

To test whether the predictive performance of SDMs depended on species traits, we divided the 56 noncleptoparasite species collected in our field studies into trait groups (52 species were included in the final analysis; we removed four species, which were found only in forest edges near oil seed rape fields and not in either orchards or arable fields [See Table S3.2]). We considered six ecological traits from the "European bee traits database" (established by ALARM, `www.alarm-project.ufz.de`, and developed by STEP, `www.STEP-project.net`): habitat specialization, (continuous scale from 1 to 8 related to the number of habitat types a species occurs in, specialist to generalist), feeding specialization (oligolectic, feeding on one plant species or polylectic, feeding on multiple plant species), body size (intertegular distance of females, where the wings join the thorax), sociality (solitary or social; social species included eusocial as well as primitively eusocial species, all others were classified as solitary), nesting habit (above or

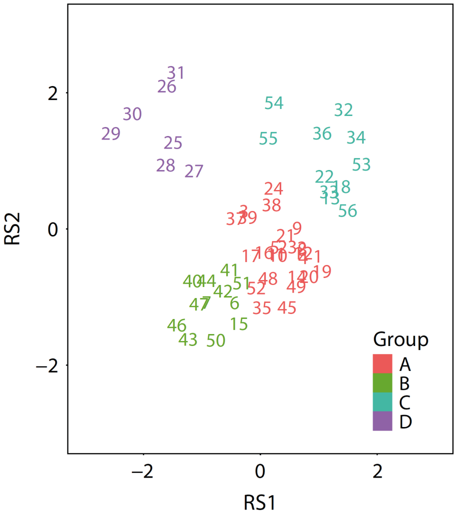

Fig. 3.1: **Results of Hill & Smith multivariate approach based on six biological traits across 2 axes, (RS1 and RS2).** Four groups selected. Groups A-D (See Table 3.1). RS1 is positively directed by oligolectic, solitary, below ground bees. RS1 is negatively directed by social, habitat generalist aboveground bees with long flight periods. RS2 is positively directed by large, oligolectic, social bees which nest aboveground. RS2 is negatively directed by polylectic below ground nesting bees (see Table S3.4). Each number refers to a bee species listed in alphabetical order (see Table S3.2).

belowground, belowground species included any renters or excavators which used nests in the ground all others were considered aboveground), and length of flight period (period active during the year; from 8 to 36 weeks). We identified trait groups using the Redundant Hill & Smith dimensional scaling technique. This method was chosen as it allows for concurrent analysis of both categorical and continuous ecological trait data by defining the categorical variables by the means of the continuous variables (Hill & Smith 1976; Barnagaud et al. 2014). The analysis was conducted using R package ade-4, which first uses principal component analysis to process the continuous variables and correspondence analysis for the categorical variables and then the Hill and Smith analysis to compare the relationship between the two (Dray & Dufour 2007). Four distinct species groups were selected (groups A–D; see Table 3.1; Fig 3.1). The three most important variables involved in the analysis were nesting habit, feeding specialization, and sociality. Each group contained at least 5 species (See Table S3.2). We can typify group A as polylectic, habitat specialists; group B as small, polylectic, habitat generalists; group C as oligolectic, habitat specialists; and group D as large, polylectic, habitat generalists (consisting of *Bombus* species only). Two species were not clearly allocated to one of the above four groups *Megachile ligniseca* (Kirby) and *M. versicolor* (Smith, F.). However, they were classified as part of group C, with whom they share the most traits (Fig 3.1).

TABLE 3.1: **Trait summary of the four bee species groups selected using the Hill and Smith method of multiple correspondence analysis (MCA), based on six biological traits across 2 axis.**

Group	Habitat specialization	Diet specialization	Body size	Sociality	Nesting habit	Flight period	Dominant genera
A (26) Small intermediate specialists	Specialists	Polylectic	Small	Solitary	Below	Short	Andrena
B (12) Small generalists	Generalists	Polylectic	Small	Mixed	Below	Long	Lasioglossum
C (11) Highly specialized bees	Specialists	Oligolectic	Intermediate	Solitary	Mixed	Short	N/A
D (7) Large generalists	Generalists	Polylectic	Large	Social	Mixed	Long	Bombus

Numbers in brackets refer to the number of species selected in each group. Habitat specialization, continuous variable, representing the number of habitat types, from 1 (specialist) to 8 (generalist). Diet specialization, factor oligolectic or polylectic (oligolectic, feeding on one plant species or polylectic, feeding on multiple plant species). Body size, continuous, intertegular distance of females (mm), sociality, factor, solitary or social. Nesting habit, factor, below, or aboveground. Flight period continuous, 4–36 weeks. Dominant genera, the genera that makes ≥70% of the species diversity in that group.

We tested whether the habitat suitability predicted by our SDMs for these 52 species varied between trait group (A–D) and habitat (orchard or arable field), using linear mixed effect models (LMM), with R package lme4 (Bates et al. 2013). The sampling method (transect vs. pan traps) used in the field surveys was also included as an explanatory variable in the LMM, to account for any possible methodological bias. Due to the nested structure of the data, multiple collection sites within separate studies, we included site within study as a random effect variable. Additionally, as the species collected were only a subset of all the species modelled for the Netherlands, we included species as a random effect variable.

Detailed collections of multiple individuals in the same area are required to predict the distribution of species abundance alongside habitat suitability predictions (Van Couwenberghe et al. 2013). Because of its scope and resolution, this was not feasible for our SDM. Nevertheless, we included the number of records used to build SDMs in the analysis as a proxy for species rarity and probability of detection.

We compared all possible combinations of the variables described above, and their two- way interactions, and selected the most parsimonious model based on the lowest Akaike information criterion, corrected for finite sample size (AICc). We also compared the mixed effect models with the Bayesian information criterion (BIC), which punishes extra terms more harshly than the AIC and AICc (Burnham & Anderson 2002).

3.4 Results

3.4.1 Testing the model with independent datasets

A total of 446 individuals of 52 species (excluding cleptoparasites) were collected at 133 sampling locations and were used to analyze the predictive performance of our SDMs. The abundance and richness of wild bees varied between habitat types, species trait groups, and sampling technique (see Figs. S3.2 and S3.3).

The habitat suitability values obtained from the SDMs, for each of the occurrences collected, varied between the different types of habitat where the collection took place, and also among the different species trait groups (Table 3.2, Fig 3.2). Although the number of records differed significantly between groups (see Fig S3.4), the habitat suitability of the model was not significantly affected by this variable (ANOVA, chi-square test, $P = 0.13$). The sampling method used to collect the independent wild bee occurrences significantly affected the measure of SDM habitat suitability overall. Moreover, significant interactions were found between sampling and group and sampling and habitat type; the effect of habitat type decreased for transect collections and the effect of species trait groups was also lower for transect collections than pan trap collections (see Table 3.2).

Data were available for all groups in each of the habitat types and collection techniques except group C. Species of this group were not collected in pan traps

TABLE 3.2: **Effect of species trait group (G), sampling technique (S), and landscape type (L) on species distribution model predictive performance (habitat suitability of species occurrences).** Number of observations was 436 of 52 unique species. P-values were obtained from likelihood ratio tests where deviance between models with the term and without the term where compared. n.s = P > 0.05. The symbol "–" represents a variable not included in the model. All interactions where tested and those which contributed significantly to any of the models remained. Random terms (all models): "1 | Study/Site," "1 | Species"

Response Variable	**G**	**S**	**L**	**G:S**	**G:L**	**S:L**	**DF**	**AICc**	**ΔAICc**
Accuracy									
Model 1 (Best Model)	0.042	<0.001	0.1	<0.001	–	0.025	422	5636.1	0
Model 2	0.042	<0.001	0.1	<0.001	0.3	0.035	419	5638.9	2.79
Model 3	0.044	<0.001	0.1	<0.001	–	–	423	5639	2.9
Model 4	0.05	0.001	–	<0.001	–	–	424	5639.5	3.39
Null Model	–	–	–	–	–	–	431	5685.8	49.64
								BIC	**ΔBIC**
Model 1 (Best Model)	0.05	0.001	–	<0.001	–	–	424	5687.7	0
Model 2	0.044	<0.001	0.1	<0.001	–	–	423	5691.2	3.47
Model 3	0.042	<0.001	0.1	<0.001	–	0.025	422	5692.2	4.51
Model 4	–	0.001	–	–	–	–	430	5701.4	13.71
Null Model	–	–	–	–	–	–	431	5706	18.31

within orchards (Fig 3.2B). Overall, the occurrences of highly specialized bees (group C) had higher average suitability values than the other three groups (Fig 3.2); significantly more than group A and group B species ($P < 0.036$ and 0.037, Fig 3.2, See Table S3.3). Furthermore, the modelled habitat suitability values for species occurrences from group D were significantly lower when comparing transects with pan traps ($P < 0.001$, See Table S3.3).

Overall the bee species collected in orchard habitats had higher predicted habitat suitability than those collected in arable field habitats (Table S3.3). This result was particularly accentuated for bees collected with pan traps (Fig. 3.2A and B). Furthermore, within orchard sites, the pan trap collected bees were more accurately predicted than the transect-collected bees (Fig. 3.2B and D).

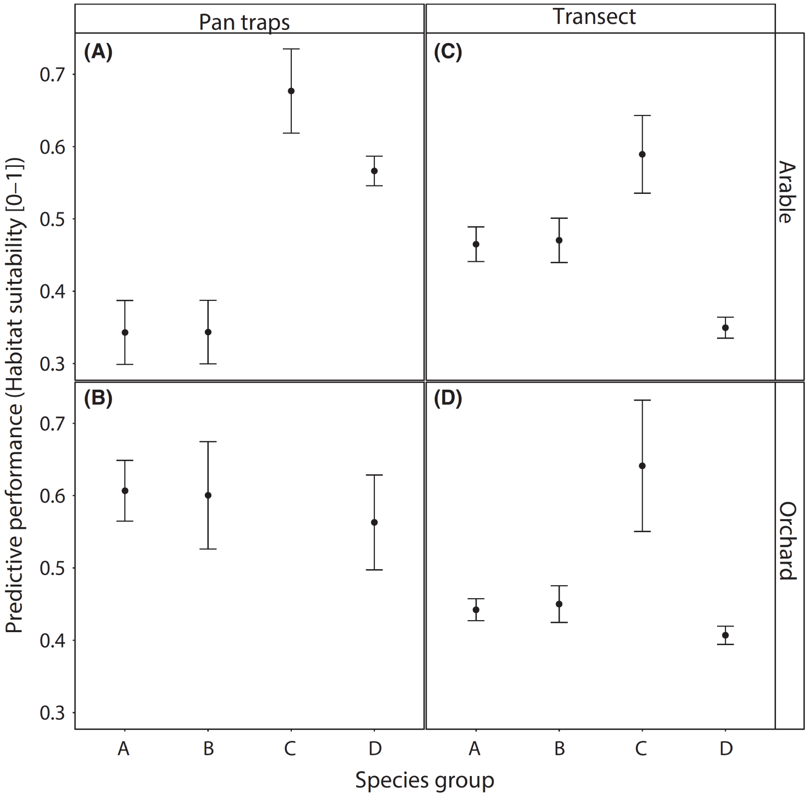

FIG. 3.2: **Mean and standard error of habitat suitability for collection points of the four species groups, in both landscape types (Orchard and Arable) and for both sampling techniques (Pan Trap and Transect).** Group A = small, intermediate specialists, group B = small generalists, group C = highly specialized bees, group D = large generalist bees. See Table S3 for pairwise comparisons between effects.

3.5 Discussion

Field surveys are rarely used to test species distribution models (SDM), particular those investigating spatial patterns of highly mobile animals such as bees (Fielding & Bell 1997; Jiménez-Valverde et al. 2008). We analysed the SDM habitat suitability scores of independent wild bee occurrences, and we show that the performance of SDMs to predict wild bee occurrences in field surveys depends on species traits and on the characteristics of the target habitat and sampling technique. Below we discuss the implications of these findings and the limitations of our study.

3.5.1 Variation of model predictive performance among different species trait groups

Wild bee species with different traits can have contrasting responses to environmental conditions. Specialist bees have been shown to be more strongly affected by agricultural intensification, habitat loss, and fragmentation than generalists (Bommarco et al. 2010; Williams et al. 2010). Habitat and feeding specialists are generally more restricted in their range of suitable habitats, while large, generalist bees such as bumblebees have greater mobility and can meet their resource requirements in a wider range of habitats (Hanley et al. 2011). This probably explains the better model performance for highly specialized species, indicating that SDMs are better able to discriminate their more restricted habitats. Similar patterns have been demonstrated for other taxa (Evangelista et al. 2008; Peltzer et al. 2007; Newbold et al. 2010; Trumbo et al. 2011). This finding suggests that while the 1 km^2 resolution used in this study is appropriate for predicting the distribution of specialized bee species, a more detailed sampling data or different set of predictor variables would likely be needed to obtain better predictions for more generalist species. Furthermore, the differences between model predictive performance for specialized and generalist bees suggest that the SDM may be more useful for conservation purposes focused on more specialized species which are more likely to suffer declines (Biesmeijer et al. 2006), than for predicting crop pollinators which are commonly more generalist species (but see Polce et al. 2013).

Model performance varied between studies using different sampling techniques which suggests that pan trap and transect collections sample different parts of a bee community and that the SDMs do not predict these subsets equally. Indeed, Cane et al. (2000) found that transect walks sampled the bee community better than pan trapping, where many abundant and specialized bee species were absent. In contrast, Westphal et al. (2008) showed that pan trapping and transects sampled similar species composition, but that pan traps generally sampled more of the wild bee community than transect surveys. However, these results are strongly limited by the intensity of each method, the experience of the transect surveyors, whether the pan traps are painted UV bright and whether they were placed at vegetation height. Bumblebees (trait group D: large generalists) showed distinct trends related to sampling technique. The occurrences of bumblebees collected during transects had lower predicted habitat suitability in the models than those from pan traps. This difference was particularly marked in arable fields which were generally predicted in our SDM to be unsuitable habitats, but where bumblebees were frequently detected. Bumblebees can travel long distances and respond very rapidly to the presence of unexpected mass-flowering events of attractive crops, such as when annual crops like oil seed rape start blooming (Hanley et al. 2011). However, bumblebees and other highly social species have been shown to have higher flower and site constancy than smaller, solitary bees (Osborne & Williams 2001; Gegear & Laverty 2004) and therefore may be less likely to be caught in pan traps. The use of multiple collection techniques for independently testing the performance SDMs is therefore essential (see also Westphal et al. 2008).

3.5.2 Variation of model predictive performance among different landscapes

Overall, the wild bees collected in orchards were predicted with significantly higher suitability values than the species collected in arable fields, particularly when using pan traps and for small, mainly solitary bees (groups A and B). In this study, the category “arable fields” includes a variety of crops, some having periods of intense flowering very attractive to bees (e.g., oil seed rape, Delaplane & Mayer 2000), while others are less attractive to bees (e.g., sugar beet and wheat, Delaplane & Mayer 2000). Additionally, in annual crop fields, the type of crop is frequently rotated, and so continuously changes between years (Stoate et al. 2001), and several were subjected to recent changes as a result of agri-environment schemes (AES) that involved the establishment of field margins or annual wildflower strips (Kleijn et al. 2006). These characteristics make arable fields far more temporally unstable than orchards. The species data used to build the

SDMs spans 20 years and during that time it is likely that the arable fields have comprised a variety of crops and for the majority of this time AES had not been implemented. AES that increase flowering species within farmland (e.g., implementation of wildflower strips, establishing field margins) also increase the time window in which flower resources are available (e.g., Haaland et al. 2011) and provide temporary connectivity between less desirable habitat types, for a number of insects including bees (Carvalheiro et al. 2012; Holzschuh et al. 2013). The results suggest that the variables used to construct the SDMs do not represent the AES or the seasonal changes in crop flowering, which is reflected by the wild bee occurrences in otherwise predicted unsuitable habitats.

The high heterogeneity of this landscape type combined with a lack of spatial and temporal cover in the data used to build the SDMs is hence a likely explanation for the poorer performance of SDMs in arable fields in comparison with orchards. Again this reinforces the idea that SDMs of this type are less suitable for predicting pollination service delivery to arable crops than for predicting the occurrence of threatened species and their habitats.

3.5.3 Implications for future studies using species distribution models

The analysis implies that the models with higher predictive performance have correctly represented the ecological niche of a species. SDMs are often used to make decisions regarding areas of conservation importance or also in the case of pollinators, where crops and pollinators overlap (Franklin 2013; Polce et al. 2013). Therefore, models with habitat suitability scores strongly correlated to temporally independent presences will have a higher efficacy in decision making. The results of our study suggest that studies using SDMs to predict bee species occurrences would benefit from more specific information about landscape type, crop type, including fine-scale vegetation and AES data and information on flower availability within the landscape during different seasons of the year (sampling season) (Pearce et al. 2001). Unfortunately, such detailed information is rarely available, and the efficacy of long-term collection data are limited by the historically available land-use and climate information with which to model it. However, increased thematic resolution in the future, specifically for agricultural land use should assist in increasing the performance for certain species trait groups whose distributions are not accurately predicted by the lower thematic resolution of the current models. Temporally unstable habitats represent another difficulty for the development of valuable SDMs. Our results imply that a particular habitat is only suitable under certain conditions, such as when wildflower strips are blooming or when certain crops are flowering. As climatic and land-use characteristics are subject to annual variation, and as pollinators can be susceptible to small scale habitat changes (e.g., presence of flower strips within farmland, Scheper et al. 2013), the model data are likely to be too coarse temporally to accurately predict the suitable habitat of a species at a specific moment in time. Species collection data, particularly those aggregated in museum collections generally cover long time periods, whereas crop rotation and AES occur in the short-term. This suggests that temporal variation between habitat and species will remain difficult to separate in distribution models, and habitat suitability conclusions for fine-scale landscape features will be difficult to produce. To overcome these caveats, SDMs need to be built with data specific to the year and season that a species was sampled. For example, in the Netherlands, AES are organized as regional collectives. Therefore, SDMs built and tested with detailed information from before and after the introduction of AES landscape features can be used to model the effectiveness and the changes resulting from AES and ensure ongoing monitoring and help determine future policy decisions.

Information on biotic interactions (e.g., bumblebee cleptoparasites and bumblebee hosts) can also increase the predictive performance of the wild bee SDMs (Giannini et al. 2013). This suggests that where clear ecological relationships are present including biotic information should improve the SDMs, particularly for the more generalist species which were not adequately modelled by climate and land use alone.

3.6 Conclusions

Species distribution models are an important tool in ecological studies that can provide guidance for conservation management action and potentially also for management of ecosystem services. By comparing the predictions of SDMs developed for multiple bee species with independently collected field data, we show the performance of such models is highly dependent on species traits and on the spatial and temporal heterogeneity of the targeted habitat. While our analysis has only considered wild bees the results are not restricted to wild bees and suggest that other mobile and functionally varied species groups related to agricultural crops (e.g., hoverflies) may show similar trends to what we have observed here.

3.7 Acknowledgments

We would like to thank Laura Roquer Beni and Ya Hsien Huang for their assistance in the field collections and for sorting the data; Boki Luske from the Louis Bolk Institute who found us orchard owners willing to participant in the project. Additionally, we would like to acknowledge all the farmers who allowed and helped us to work in their orchards. Thanks also to Thibaut DeMeulemeester from the Naturalis Biodiversity Centre for specimen identifications.

3.8 Supporting Information

Tables

TABLE S3.1: **List of environmental variables included in MAXENT species distribution modelling.**

Type	Variables
Climate	Mean Diurnal Range of Monthly Temperature Mean Temperature of Warmest Quarter Precipitation of Driest Month Precipitation of Warmest Quarter Temperature Seasonality
Land Use	Line Density of Simple Ditches Line Density of Tree Alleys Percentage Cover Agriculture Percentage Cover Coniferous Forest Percentage Cover Moors/Peats Percentage Cover Sandy Soils Percentage Cover Urban
Topography	Elevation

TABLE S3.2: **List of species per species trait group.**

Species	Group	ID Number	Final Analysis
Andrena angustior	A	1	YES
Andrena barbilabris	A	2	YES
Andrena chrysosceles	A	4	YES
Andrena cineraria	A	5	YES
Andrena fucata	A	8	YES
Andrena fulva	A	9	YES
Andrena gravida	A	10	YES
Andrena haemorrhoa	A	11	YES
Andrena helvola	A	12	YES
Andrena humilis	A	13	YES
Andrena labiata	A	14	YES

Table S3.2 continued from previous page

Andrena nigroaenea	A	16	YES
Andrena praecox	A	18	YES
Andrena semilaevis	A	19	NO
Andrena subopaca	A	20	YES
Andrena tibialis	A	21	YES
Andrena vaga	A	22	YES
Andrena varians	A	23	YES
Colletes daviesanus	A	33	YES
Dasypoda hirtipes	A	34	YES
Lasioglossum sexstrigatum	A	49	YES
Panurgus calcaratus	A	56	YES
Andrena carantonica	B	3	YES
Andrena dorsata	B	6	YES
Andrena flavipes	B	7	YES
Andrena minutula	B	15	YES
Andrena nitida	B	17	YES
Halictus tumulorum	B	35	YES
Hylaeus communis	B	37	YES
Hylaeus confusus	B	38	YES
Hylaeus gibbus	B	39	NO
Lasioglossum calceatum	B	40	YES
Lasioglossum fratellum	B	41	NO
Lasioglossum leucopus	B	42	YES
Lasioglossum leucozonium	B	43	YES
Lasioglossum malachurum	B	44	YES
Lasioglossum minutissimum	B	45	YES
Lasioglossum morio	B	46	YES
Lasioglossum pauxillum	B	47	YES
Lasioglossum sexnotatum	B	48	YES
Lasioglossum villosulum	B	50	YES
Lasioglossum xanthopus	B	51	YES
Lasioglossum zonulum	B	52	YES
Anthophora plumipes	C	24	YES
Chelostoma florisomne	C	32	YES
Heriades truncorum	C	36	YES
Macropis europaea	C	53	YES
Megachile ligniseca	C	54	NO
Megachile versicolor	C	55	YES
Bombus hortorum	D	25	YES
Bombus hypnorum	D	26	YES
Bombus jonellus	D	27	YES

Table S3.2 continued from previous page

Bombus lapidarius	D	28	YES
Bombus pascuorum	D	29	YES
Bombus pratorum	D	30	YES
Bombus ruderarius	D	31	YES

TABLE S3.3: **Post hoc multiple pair wise comparison of difference in least square means, table for all significant interactions as selected in best model (AICc).**

Species Trait Group	**Estimate**	**Error**	**p-value**	**Sig.**
A-B	0.0173	0.04777	0.98	
A-C	-0.1539	0.05553	0.035	*
A-D	0.0078	0.05257	0.99	
B-C	-0.1712	0.06217	0.037	*
B-D	-0.0095	0.05937	0.99	
C-D	0.1617	0.0646	0.068	.
Habitat Type				
Arable-Orchard	-0.0818	0.02432	0.003	**
Sampling Technique				
PanTraps-Transect	0.0932	0.02763	0.002	**
Group:Sampling				
PanTraps A - Transect A	0.0334	0.03602	0.98	
PanTraps A - PanTraps B	0.0412	0.05787	1	
PanTraps A - Transect B	0.0267	0.05534	1	
PanTraps A - PanTraps C	-0.1868	0.08105	0.27	
PanTraps A - Transect C	-0.0877	0.06143	0.81	
PanTraps A - PanTraps D	-0.103	0.06053	0.64	
PanTraps A - Transect D	0.1519	0.05957	0.16	
Transect A - PanTraps B	0.0079	0.05535	1	
Transect A - Transect B	-0.0066	0.04772	1	
Transect A - PanTraps C	-0.2201	0.07829	0.09	.
Transect A - Transect C	-0.121	0.05462	0.31	
Transect A - PanTraps D	-0.1363	0.05667	0.22	
Transect A - Transect D	0.1185	0.05274	0.3	
PanTraps B - Transect B	-0.0145	0.03643	0.99	
PanTraps B - PanTraps C	-0.228	0.08562	0.13	
PanTraps B - Transect C	-0.1289	0.06748	0.5	
PanTraps B - PanTraps D	-0.1442	0.06611	0.33	
PanTraps B - Transect D	0.1107	0.06582	0.66	
Transect B - PanTraps C	-0.2135	0.08352	0.16	

Table S3.3 continued from previous page

Transect B - Transect C	-0.1144	0.06125	0.53	
Transect B - PanTraps D	-0.1297	0.0635	0.42	
Transect B - Transect D	0.1251	0.05951	0.37	
PanTraps C - Transect C	0.0991	0.07632	0.87	
PanTraps C - PanTraps D	0.0838	0.08367	0.96	
PanTraps C - Transect D	0.3387	0.08603	0.003	**
Transect C - PanTraps D	-0.0153	0.06862	1	
Transect C - Transect D	0.2396	0.06527	0.007	**
PanTraps D - Transect D	0.2548	0.02918	<0.001	***
Sampling:Habitat				
Arable PanTraps - Orchard PanTraps	-0.1439	0.04137	0.006	**
Arable PanTraps - Arable Transect	0.0311	0.02964	0.71	
Arable PanTraps - Orchard Transect	0.0114	0.03033	0.98	
Orchard PanTraps - Arable Transect	0.175	0.04231	<0.001	***
Orchard PanTraps - Orchard Transect	0.1553	0.0423	0.003	**
Arable Transect - Orchard Transect	-0.0197	0.02474	0.85	

TABLE S3.4: **Column coordinates for species traits used in group selection ordination analysis.**

Species Trait	RS1	RS2
Habitat Specialisation	-0.7315954	-0.2495703
Body size	-0.3839457	0.7020075
Lecty (Oligolectic)	1.354881	0.9099223
Lecty (Polylectic)	-0.25945	-0.1742404
Sociality (Social)	-1.29095	0.3822533
Sociality (Solitary)	0.430316	-0.1274178
Nesting (Above)	-0.49199	1.3259499
Nesting(Below)	0.120265	-0.3241211
Length of flight period	-0.86646	-0.2017732

Figures

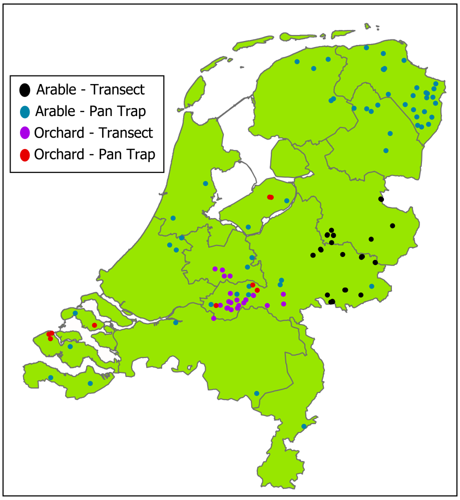

FIG. S3.1: **Field-survey locations by landscape type and collection technique.**

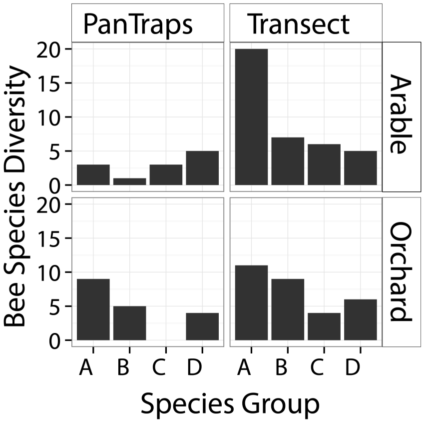

FIG. S3.2: **Species richness (number of species) collected at each site.**

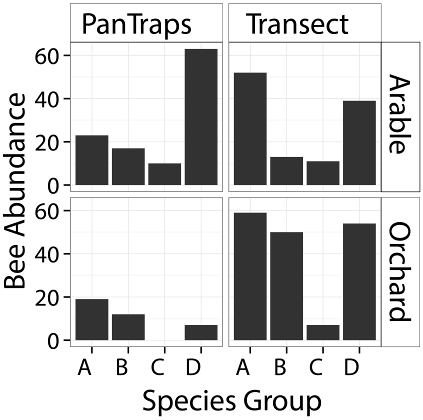

FIG. S3.3: **Abundance (number of individuals) collected at each site.**

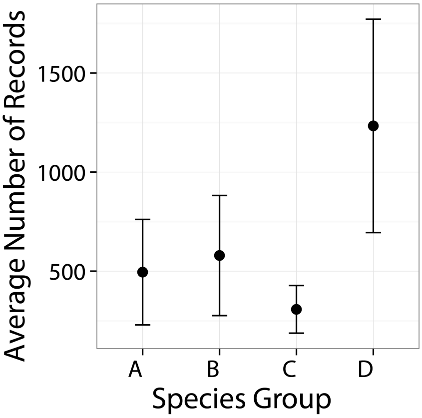

FIG. S3.4: **Average number of records per species group, with standard deviation error bars.**

4 Wild bee assembly patterns: the importance of co-occurrence, habitat filtering, traits, and phylogeny

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4.1 Abstract

Species assemblages form following interactions between various processes. One of the key and most difficult processes to quantify is the influence of biotic interactions and species co-occurrence. In this study, we explore how co-occurrence, habitat filtering, species traits and phylogenetic relatedness influence species distribution and affect assemblage formation, using wild bees in the Netherlands as a test case. Our results show that habitat filtering explains the majority of the geographic distinction between species, but positive co-occurrence patterns of wild bees improves our understanding of the relationship between habitat and spatial distribution. We also observe a pattern of phylogenetic niche conservatism among closely-related species not captured by traits. The results show that co-occurrence is a necessary input to improve predictions of community assembly patterns and that closely-related species share habitat requirements. These results imply that knowledge about species assemblages can be used as a basis for landscape conservation strategies.

4.2 Introduction

Wild bees perform an important role in managed and natural ecosystems providing pollination services for many crop species and wild plants (Kleijn et al. 2015, Potts et al. 2016a). Nevertheless, wild bees in Europe have declined in the last 100 years (Biesmeijer et al. 2006; Carvalheiro et al. 2013; Potts et al. 2016b). One of the main drivers behind these declines is the loss of nesting and feeding resources through land use/land cover changes such as agricultural intensification and urbanization (Nieto et al. 2014; Vanbergen et al. 2013). New national and international policies should therefore be developed to promote the conservation of wild bees and strengthen management efforts aiming to ensure the persistence of their sheer biodiversity (Potts et al. 2010). Despite global concern of wild bee diversity losses many aspects of wild bee landscape ecology are still not well understood, particularly how different drivers of decline interact, what ecological processes drive community assembly, and how different measurements of diversity respond to these environmental changes.

The correlation between species and their traits, phylogeny and habitat filtering have been used to understand, and predict species distribution patterns. For example, traits and trait diversity are increasingly used in studies of wild bee distribution because of their correlation to ecosystem functions, including pollination (Fründ et al. 2013; Martins et al. 2015), but also to drivers of decline (De Palma et al. 2017). Phylogenetic diversity, while at least partly correlated to functional trait diversity and species richness, may provide additional power in the estimation of community structure, functioning and conservation (Flynn et al. 2011, Vereecken 2017). Several recent studies have reported on habitat filtering, linked to changes in phylogenetic diversity of wild bees (Hoiss et al. 2012; Sydenham et al. 2015). Alternative biodiversity metrics, rather than solely species richness, are important for conservation, particularly in situations where communities with reported low species richness may actually represent a diverse functional and phylogenetic community assemblage (Aguirre-Gutiérrez et al. 2017b; Dorchin et al. 2018).

To reach a more precise understanding of wild bee community assembly and their trends, one needs to study both the environmental conditions under which each species thrives or declines and the influence of biotic factors, such as co-occurring species. The Dutch wild bee fauna distribution patterns have been modelled previously, but only for single species separately, ignoring the role of co-occurrence and community assembly (Aguirre-Gutiérrez et al. 2017a; Marshall et al. 2015). Species community assembly is based on the assumption that co-occurrence among species is non-random (Phillips 1931). Community assembly is driven ecologically by dispersal capabilities followed by habitat filtering and biotic interactions. In essences, species persist at a location only if they arrive there, find suitable habitat conditions and are not excluded by other species already present (Boulangeat et al. 2012; Götzenberger et al. 2012). Predicting the distribution of species and therefore estimating community structure often considers species individually and focuses on habitat filtering alone (Elith & Leathwick 2009). A simple method to estimate community structure is with Species Distribution Models (SDMs) and involves stacking all the individual species distribution projections (Calabrese et al. 2014). However this method ignores the interaction between species. Joint SDMs (JSDMs) represent a method to model the community as a whole by incorporating habitat filtering at the community level and utilizing statistical co-occurrence between all species in the community (Ovaskainen et al. 2015; Pollock et al. 2014). JSDMs additionally provide approaches to incorporate traits and phylogenetic relationships as explanatory factors in community composition (Pollock et al. 2012), allowing inference on the functional and phylogenetic diversity of the communities, and not only at the species level.

In this study, we use JSDMs, species traits, and phylogenetic relationships to investigate the role of environmental and biotic factors in community level structure of wild bees in the Netherlands. Firstly, explicitly ignoring the influence of habitat covariates, we describe patterns of co-occurrence, using a probabilistic model of co-occurrence (Veech 2013), and compare these patterns to phylogenetic and trait relationships. Secondly, we use a framework for modelling multiple JSDMs referred to as Hierarchical modelling of Species Communities (HMSC; Ovaskainen et al. 2017). This framework predicts community composition and incorporates habitat filtering, together with the ”biotic niche”, namely the co-occurrence matrix. More specifically, we address the following five questions. (1) Do certain wild bee species indicate the presence of others? (2) What is the influence of habitat filtering on the patterns of wild bee occurrence? (3) Do species traits and phylogenetic relationships influence wild bee spatial co-occurrence and assembly patterns? (4) How are wild bee assemblages geographically distributed? (5) What are the conservation implications of the resulting wild bee assemblage patterns?

4.3 Materials and Methods

4.3.1 Species Data

The collection records for wild bees in the Netherlands were obtained from the European Invertebrate Survey (EIS; Peeters et al. 2012) . We used species occurrence records collected since 2005 in order to analyse communities representative of the contemporary fauna while ensuring a large number of collection records. The occurrence records in the EIS database are collated from many sources and include museum collection data, verified and validated citizen science data, and data systematically sampled as part of scientific research projects. The objective of the study is to look at co-occurrence and assemblage patterns among wild bees. Hence, we need to ensure that we use spatially explicit occurrence records from areas that have been repeatedly well-sampled. Consequently, we conducted detailed data mining on the occurrence database.

At 10 × 10 km, we selected occurrence records that represent repeated sampling within each grid cell. We used select criteria which we applied to each grid cell: (1) at least two recorded occurrences, (2) records collected before and after July within the same year, (3) at least two unique years between 2005 and 2017, (4) at least five different species must have been collected. The selected sites and species were then coerced into a site ×species matrix to use directly in the analyses. Finally, for the HMSC analysis we limited the models to only species with a least five records. This resulted in 70 species being excluded from the HMSC part of the analysis (see Table S4.1 and S4.2 in Supporting Information).

4.3.2 Environmental Data

Climate data was calculated from daily values of minimum, maximum, and mean temperature and rainfall from the Koninklijk Nederlands Meteorologisch Instituut (KNMI) using the API available from (`https://data.knmi.nl/datasets`). These values were used to produce the 19 bioclimatic variables (Hijmans et al. 2005).

Two-dimensional land use data were collated from three separate sources; (1) nature, Index Natuur en Landschap (Inter Provinciaal Overleg 2016); (2) agriculture, Basisregistratie Gewaspercelen (EZK 2015); (3) urban, the Bestand Bodemgebruik Productbeschrijving (CBS 2012) . After removing all agricultural and landscape feature classes from the nature map, we created a hierarchy whereby the nature map would take precedence over the agricultural map which would in turn take precedence over the urban map. Therefore, areas which would be disputed would automatically default to the class as defined by the map highest in the hierarchy. We made this decision because we believed that the nature map would most accurately represent the distinctions between important land use classes for bees. Furthermore, this hierarchy also represented decreasing age, with the urban map being the oldest and consequently least up-to-date. The potential implications of this selection would be that areas of natural habitat may be overestimated and urban areas underestimated.

To avoid collinearities between covariates, we compared the Pearson correlation coefficients between all pairs of environmental variables and ensured no pairs had values higher than 0.7 (Dormann et al. 2013). In the cases where two climate variables were highly correlated, we selected the variable that we assessed as having the greatest ecological relevance to wild bee species. The final selection includes ten land use and five climate classes (Fig 4.2 and see Table S4.3): crops food source, crops non-food source, agri-grassland, urban, heathland, semi-natural woodland, production woodland, marsh and swampland, semi-natural grassland, dune, minimum temperature of coldest month, mean temperature of driest quarter, mean temperature of warmest quarter, annual precipitation, and precipitation of the driest month.

4.3.3 Traits Data

We considered seven ecological traits from the "European bee traits database" (established by ALARM, `www.alarm-project.ufz.de`, and developed by STEP, www.STEP-project.net); (1) habitat specialization, (1 to 8, number of habitat types where a species occurs); (2) feeding specialization (oligolectic, polylectic, no lectic status); (3) body size (inter-tegular distance of females); (4) sociality (solitary, social or parasite); (5) nesting habit (excavators or renters), and (6) length of flight period (2 to 10 months); (7) voltinism (univoltine or bivoltine/multivoltine). These same traits have been used in previous studies of wild pollinators in the Netherlands showing relationships with historical habitat changes and present day prevalence (Aguirre-Gutiérrez et al. 2016; Marshall et al. 2015). Trait data were incomplete for 29 species (see Table S4.2).

4.3.4 Phylogenetic Data

The bees molecular phylogeny was produced on the basis of different sequences of the mitochondrial gene cytochrome oxidase 1 (CO1) available on GenBank (Benson et al. 2014). This phylogenetic tree was reconstructed based on nucleotide character state (i.e. ATCG) with maximum likelihood (ML) optimality criterion method. This ML tree was then converted into a distance matrix based on the length of the branches separating species and a species by species correlation matrix. Please see material and methods, section 2.2.5 for greater detail on the methods, the underlying data and resulting phylogenetic tree and Table S4.4. Phylogenetic data was absent for 25 species (see Table S4.2).

4.3.5 Pairwise Spatial co-occurrence

Using a matrix of sites and species (presence/absence), the pairwise probabilistic model calculates the total probabilities for spatial co-occurrence for two species across the total number of sites and compares them against the observed spatial co-occurrence (Veech 2014). A species-pair can be classified as positive (significantly more sites), negative (significantly less sites) or random (non-significant difference). Unlike other methods the probabilistic model does not require randomization, avoiding issues of type I and II errors found in other spatial co-occurrence methods (Veech 2013). We used a linear model to compare the relationship between pairwise spatial co-occurrence probabilities against phylogenetic distance and traits based dissimilarity (1- Gower similarity coefficient; Gower, 1971).

4.3.6 Hierarchical modelling of Species Communities

We used a framework with the purpose of Hierarchical modelling of Species Communities (HMSC), utilizing Bayesian JSDMs to classify species' relationships with their environmental conditions, whilst accounting for the possible influence of co-occurrence, traits and phylogeny on these patterns (Ovaskainen et al., 2017). This method allows us to test specific hypotheses of community assembly based on widespread, but erratic, spatially explicit occurrences.

We conducted the analysis on a 10 km grid (363 sites) of species occurrence (204 species) across the Netherlands. Each species was modelled with a generalized probit linear model of presence/absence as a function of environmental conditions and random spatial effects. The pairwise association/co-occurrence matrix was included in the model as a latent factor of random variation per species per site; covariation between each species pair estimates if they occur together more often than expected. The effect to which variation in niche was additionally explained by traits was measured for each species response to each environmental covariate. Finally, the presence of phylogenetic niche conservatism (PNC) among closely-related species was tested by measuring whether the residual variance of the model is independent of phylogeny. Non-independence, and by proxy PNC, implies that closely-related species have more similar niches than distantly-related species.

Each model is run as a Markov Chain Monte Carlo (MCMC) with 24000 iterations where the first 4000 iterations are removed giving the Markov Chain time to reach its equilibrium distribution. All explanatory factors are scaled between 0 and 1. Random spatial autocorrelation is included as x and y coordinates.

The models are examined using MCMC trace plots to ensure that adequate mixing has occurred and that the latent variables are satisfactorily predicted. Predictive power of the model is measured in two ways using Tjur R^2 which is described as *"the mean model prediction for those sampling units where the species occurs, minus the mean model prediction for those sampling units where the species does not occur"* (Guillaume Blanchet et al. 2017). Furthermore, we use the area under the curve (AUC) of the receiver operating characteristic (ROC) value which measures the degree of false positives and false negatives between the true values and the predicted values (Bahn & McGill 2013).

4.3.7 Assemblages

Using the final model of the HMSC we made predictions using all sites, to produce a site-by-site similarity index and classify the Netherlands into regions of similar assemblages. We used K-means clustering, whereby the data are partitioned into the selected number of assemblages with the express goal of minimizing the sum of squares between the points and the centre of the chosen clusters. The Hartigan-Wong algorithm was used, set to 1000 iterations and 100 random samples (Hartigan & Wong 1979). The run which most successfully minimizes the sum of squares was chosen. We used the 'elbow method', selecting the number of clusters (communities) at the point after which the explained variation no longer increases. We present the geographic distribution of community assemblages for all clustering quantities up to and including the cut-off value.

For each assemblage we calculated: a PCA of difference in land use, total species richness, phylogenetic species variability (PSV), functional diversity and percentage cover of Natura2000 sites. Furthermore, using ANOVA and Tukey's HSD, we defined the most representative species for each community profile as those whose abundance records in a particular assemblage are significantly greater than their abundance in the other assemblages. Finally, for each site, we tested how community similarity changes geographically. We tested this by plotting per site community similarity against geographic distance. We do this for similarity values obtained from spatial predictions only (all environmental variables set to their mean values) and with both spatial and environmental factors included.

4.4 Results

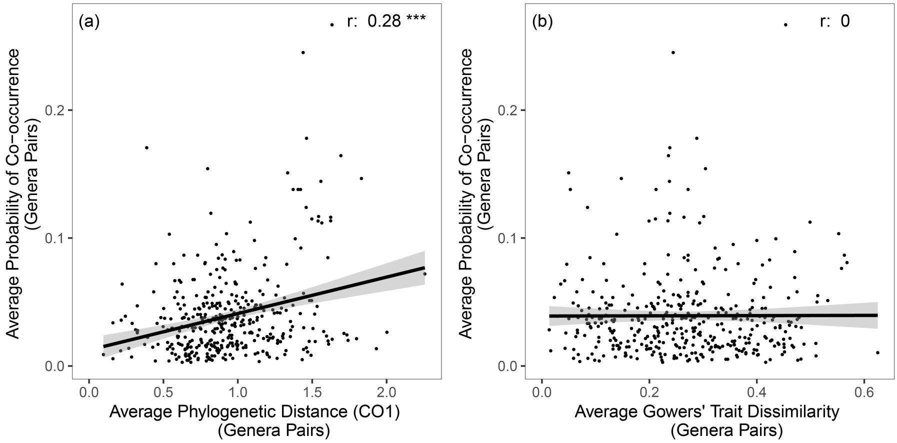

FIG. 4.1: **Scatterplot showing co-occurrence probability against phylogenetic distance and trait dissimilarity at** 10×10**.** (a) Average co-occurrence probability per genus pair vs. Average phylogenetic distance per genus pair(CO1 gene. (b) Average co-occurrence probability per genus pair vs. Average Gower's trait dissimilarity per genus pair.

4.4.1 Spatial co-occurrence patterns

We examined 297 potential species interactions, or 43956 pairs of species. The number of analyzable pairs, 24234, indicates that the database has a many species with few records and that many wild bee species are not expected to co-occur at all. The majority of spatial co-occurrence patterns between wild bee species were positive (64.5%) and very few interactions negative (0.6%). The species pair with the most observed co-occurrences was *Bombus lapidarius* and *B. pascuorum*, these two species are also the two most abundant species in the collections. The co-occurrence patterns per species pair were compared to the phylogenetic distance and trait dissimilarity between each species pair. Overall at 10×10km we see weak to no evidence for a relationship between phylogenetic distance and trait dissimilarity and the co-occurrence of species pairs. There is a significant positive relationship whereby genera which are more phylogenetically-distant are more likely to co-occur, however, the Pearson correlation coefficient (r) of 0.28

suggests this is weak (Fig 4.1a). When examined for all values this relationship is much weaker (r: 0.05) suggesting that there is no clear relationship at the species level (Fig S4.1a). Gower's trait dissimilarity index between genera shows a non-significant relationship with co-occurrence probability between genera (r: 0; Fig 4.1a). At the species level there is a significant positive relationship, however the r of 0.12 suggest this relationship is also weak (Fig S4.1b).

4.4.2 Habitat Filtering

Land use variables explain the majority of variation in habitat filtering for 151 of the 204 species (74%) and climate for the remaining 53 species (26%). Land use explains on average 57% of the variation, ranging from 26% to 90%, while climate explains 35% of the variation on average (from 6 to 70%). Spatial autocorrelation only accounted for a small percentage of the variation in species niche; 8% with a range of 0.3% to 37% (see Fig S4.2). A number of land use variables were included as important factors in the models, which varied by species (Fig 4.2a). Semi-natural grassland and urban areas were positive factor for a large majority of species (65% and 55% respectively). Heathland (positive, 15% and negative 6%) and dune (17% and 4%) areas were both beneficial and restrictive for some species. The balance of associations (negative vs. positive) was mostly negative for agricultural land use types, including cropland, as food-source (8%) and non-food-source (17%), and agricultural grassland (14%; Fig 4.2a).

The influence of the different land use variables is measured as the average effect size across the nine most species-rich genera (Fig 4.2b). The effect of semi-natural grassland is positive for all genera but higher for the species in the genera *Sphecodes*, *Nomada* and *Lasioglossum*. *Bombus* species are the only species for which crops positively influence their distribution (Fig 4.2b). The effect of heathland varies between genera and species within genera.

Only 11% of the variation in niches across all species could be appointed to differences in traits. Additionally, mean PNC across the 20,000 model iterations was 0.91 ± 0.02 provides strong evidence that closely-related species have more similar responses to the habitat covariates.

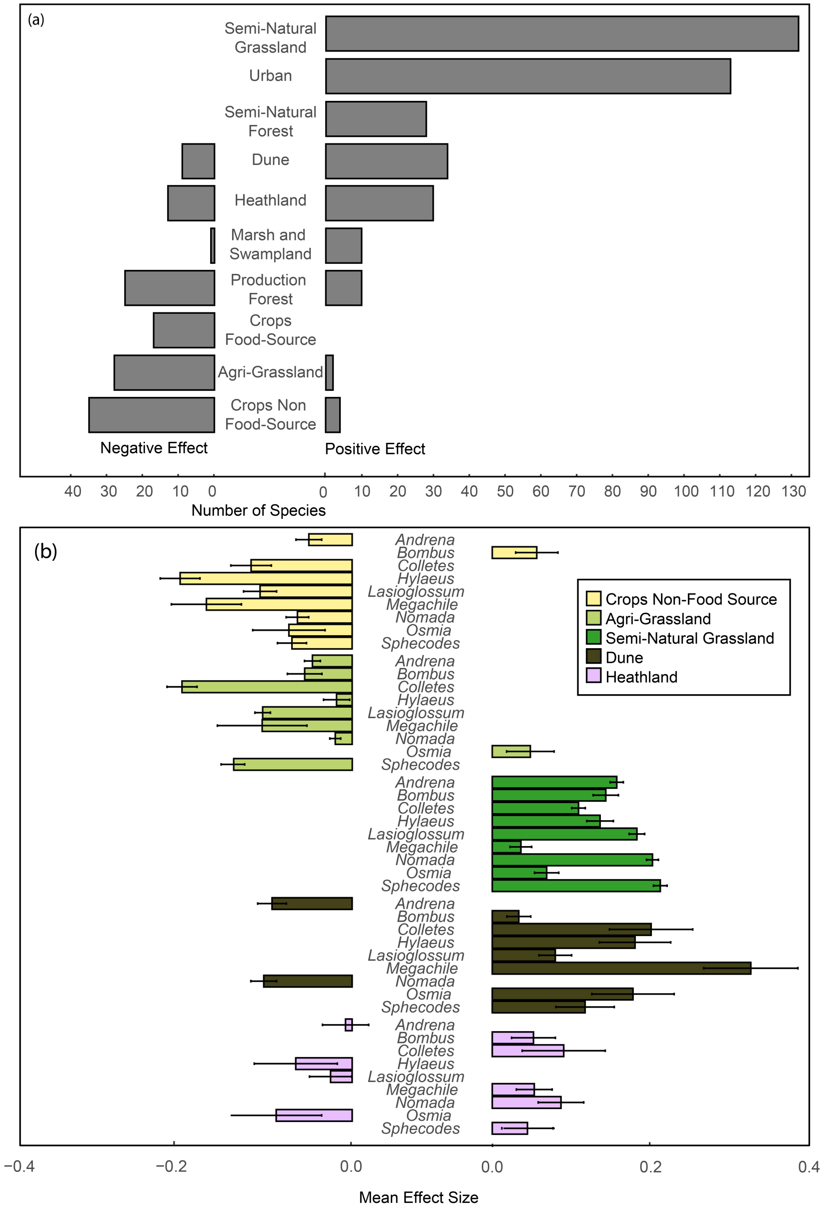

FIG. 4.2: **Land use filtering of wild bee species.** (a) Number of species (n=204) with significant influence (confidence interval outside zero) of land use covariates. (b) Mean and standard error of effect size for land use variables per genera. Genera shown comprise at least five species.

4.4.3 Biotic Interactions

Species with a higher positive correlation in their response to the models' latent variables are likely to increase in occurrence together. Indicating that the presence of wild bee species increases the likelihood of presence of other wild bee species. Particularly there is a strong spatial association between species found in the genera *Sphecodes, Andrena, Hylaeus, Nomada, Lasioglossum* and *Colletes* (see Fig S4.3). To test the overall influence of including the species pairwise association matrix in the model we examined the predictive power of the model with and without the latent factors included. Latent effects refer to variables, in this case three, which are calculated to account for the residual patterns across the species association matrix not explained by the explanatory variables. The models for all species improve with latent effects; overall the mean Tjur R^2 was 0.21 vs. 0.12 and the AUC 0.85 vs. 0.8 (Fig 4.3). Some models as measured by the Tjur R^2 are inaccurate particularly at the low and high prevalence. The difference in performance is less pronounced for those species with high or low prevalence.

4.4.4 Assemblages

The majority of explained variance is between two and seven clusters (Fig 4.4). Each increase in the number of clusters delimits a new assemblage with species and conditions different to those of other assemblages. Each assemblage is referred to by its number in Fig 4.4f. Assemblages 1 (A1), 2 (A2) and 6 (A6) are found in similar habitats with varying gradients of urban and agricultural land use (Fig 4.5a,b). Except for *Anthophora plumipes* a common urban species in A1, none of these three assemblages have any representative species. These sites have, on average, fewer species per site than other assemblages (A1:34, A2:35, and A6:37 species; Table 4.1). In terms of habitat, A3 is strongly represented by woodland and heathland areas and occurs in areas with the least agriculture (Fig 4.5a,b). Average species richness per site in A3 is high, 56 species, but it contains the lowest total species richness (121) of all assemblages. Even though A3 only includes seven 10×10km sites, there are a large number of representative species including four on the Dutch Red List. The majority of the area covered by A3 is designated as Natura2000 (76%, Table 4.1). Assemblage 4 occurs in the most heterogeneous and varied habitats in the South East (Fig 4.5a,b). It also has the

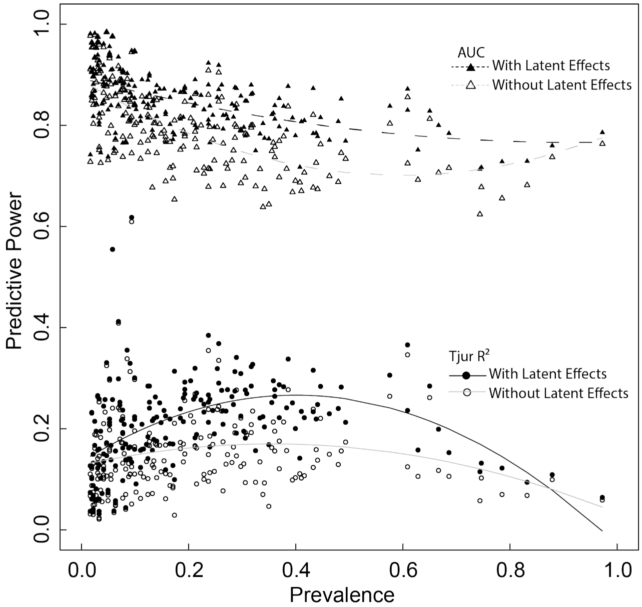

FIG. 4.3: **Model predictive performance.** Models with (black, closed) and without (grey, open) latent effects included. Two measures of predictive performance are used: Tjur R^2 (circles) and Area under the Curve (AUC; triangles). Latent effects refer to variables (3) which are calculated to account for the unexplained residual patterns across the species association matrix.

largest average richness per site (64). Accordingly, it has the most representative species including 9 species on the Dutch Red List.

Dune habitats (25%) and Natura2000 (41%) along the western coastline dominate the land use in the A5 range (Fig 4.5f and Fig 4.5a,b; Table 4.1). Similar to A3, A5 occupies only a small area of the Netherlands but has a high average species richness per site (51), a lower overall species richness (143) and many representative species, including seven red listed species, and a large percentage of the *Colletes* and *Megachile* species present in the Netherlands (Table 4.1). A greater quantity of heathland and woodland habitat is occupied by A7 than the other assemblages except for A3 (Fig 4.5a,b). This is reflected by the fewer representative species, including the red listed species *Nomada rufipes*, the specialist cleptoparasite of *Andrena fuscipes*, an oligolege on *Calluna* (Ericaceae), which is

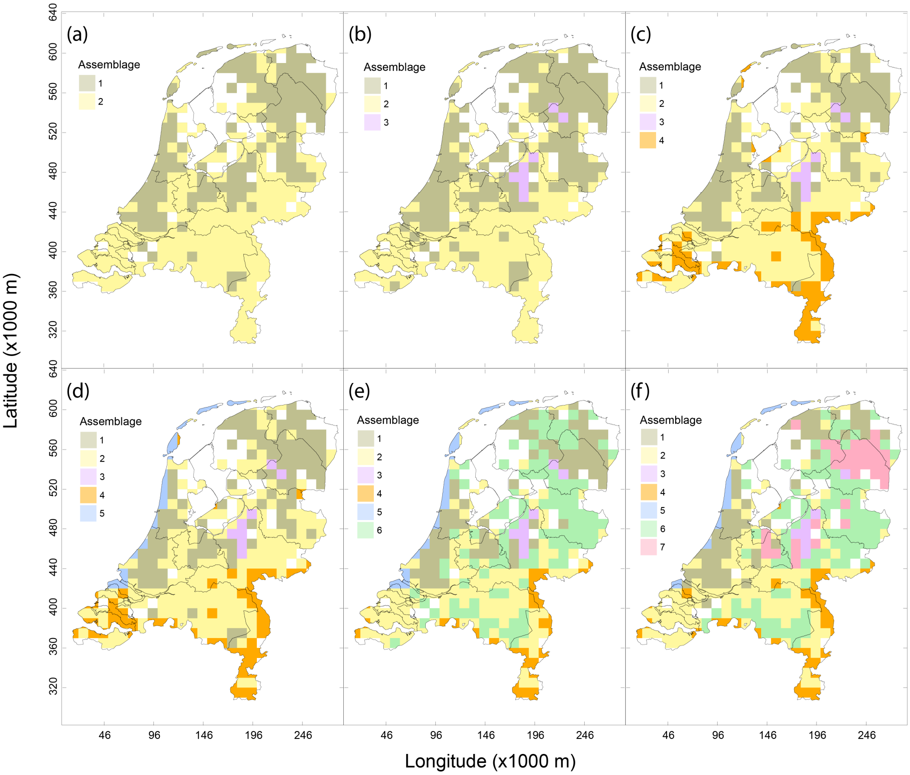

Fig. 4.4: **Geographic distribution of wild bee assemblages.** Showing number of selected clusters from (a)2 – (f) 7. Calculated using KMeans clustering 1000 iterations and 100 random samples.

also significantly more likely to be found as part of A3. There are no clear differences between the average phylogenetic and functional diversity per assemblage. Finally, the similarity between assemblages does not decrease based on spatial distance, indicating the observed patterns are not explained by latitude alone but were driven by changes in environmental conditions (Fig 4.5c).

4.5 Discussion

This research shows the importance of both environmental and biotic drivers on the structure of wild bee assemblages. Habitat filtering explains the majority of the distribution patterns. Including co-occurrence of bee species improves

TABLE 4.1: **Summary of the seven wild bee assemblages as chosen by K-means clustering.**

Assemblage	Phylogenetic species variability	Species Richness (n=204)	Functional Dispersion	Natura 2000 (%)	Representative Species
1	0.60 ±0.05	34 ±20 (164)	0.21 ±0.00	4%	*Anthophora plumipes*
2	0.60 ±0.05	35 ±25 (199)	0.21 ±0.00	7%	NA
3	0.61 ±0.01	56 ±28 (121)	0.22 ±0.01	76%	*Andrena fuscipes, Andrena lapponica, Andrena nigroaenea,* ***Bombus humilis****, Colletes succinctus, Epeolus cruciger, Lasioglossum lucidulum,* ***Nomada fuscicornis****,* ***Nomada rufipes****, Nomada succincta,* ***Panurgus banksianus****, Panurgus calcaratus*
4	0.62 ±0.03	64 ±41 (200)	0.22 ±0.01	11%	*Andrena dorsata, Andrena florea,* ***Andrena hattorfiana****, Andrena minutuloides, Andrena proxima,* ***Andrena semilaevis****,* ***Bombus rupestris****, Ceratina cyanea, Halictus scabiosae,* ***Hoplitis adunca****, Hylaeus cornutus, Hylaeus signatus, Lasioglossum laticeps,* ***Lasioglossum lativentre****, Lasioglossum malachurum,* ***Lasioglossum nitidulum****, Lasioglossum pauxillum, Melitta leporina, Melitta tricincta,* ***Nomada armata****, Nomada conjungens, Nomada fucata,* ***Nomada integra****, Nomada zonata, Sphecodes crassus, Sphecodes ferruginatus,* ***Sphecodes niger***
5	0.60 0.01	51 ±23 (143)	0.21 ±0.01	41%	***Andrena argentata****, Andrena barbilabris,* ***Andrena fulvago****, Anthidium punctatum,* ***Coelioxys conoidea****, Coelioxys mandibularis, Colletes cunicularius, Colletes halophilus, Colletes marginatus, Colletes succinctus, Dasypoda hirtipes,* ***Hoplitis claviventris****, Hylaeus confusus, Lasioglossum albipes, Lasioglossum leucozonium,* ***Lasioglossum nitidiusculum****, Lasioglossum punctatissimum,* ***Megachile circumcincta****, Megachile leachella, Megachile maritima, Megachile willughbiella,* ***Osmia aurulenta****, Sphecodes albilabris, Sphecodes puncticeps*
6	0.61 ±0.03	37 ±29 (188)	0.22 ±0.00	9%	NA
7	0.61 ±0.06	54 ±32 (172)	0.22 ±0.01	12%	*Andrena denticulata, Andrena fuscipes, Lasioglossum fratellum,* ***Nomada rufipes****, Nomada sheppardana*

The assemblage numbers refer to the assemblages shown in figures 4.4 and 4.5. Phylogenetic species variability measures the decrease in variance of hypothetical traits shared by all species in the assemblage, 0 implies very closely related species and 1 distantly related species. ± refers to the standard deviation of the mean value presented. Functional dispersion per site measure the differences between the occurrence of species and their pairwise Gower's trait dissimilarity. Representative species are species which are significantly more likely to be present in the assemblage than at least five of the other six assemblages (ANOVA, TukeysHSD). The representative species in Bold are those listed on the Dutch redlist of bees (Reemer, 2018).

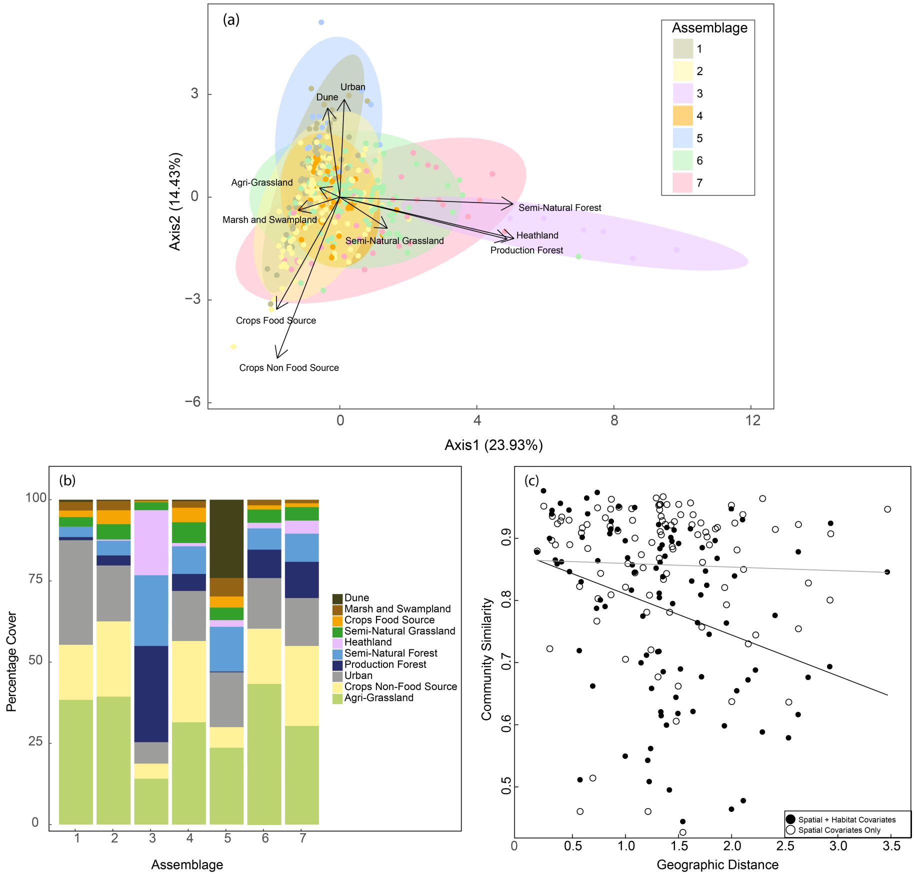

FIG. 4.5: **Community assemblage patterns of wild bees in the Netherlands.** (a) Ordination biplot of principal component analysis of percentage cover land use in each assemblage. (b) barplot showing percentage cover of land use classes in each assemblage. (c) Community similarity against geographical distance, black circles = full HMSC model, open circles = habitat variables standardized to their mean, therefore only spatial factors included in the model.

model quality and suggests that these patterns are at least partly non-random. Our results also illustrate that wild bee community assembly patterns can be explained in part due to pairwise phylogenetic relationships between species. The methods and results presented can be used to prioritize conservation planning for wild bees, and most likely other species groups, by indicating where and how community assembly patterns differ. In what follows, we explicitly answer our five research questions.

4.5.1 Do certain wild bee species indicate the presence of others?

The presence of wild bee species is positively associated with the occurrence patterns of other wild bee species, both when measured as spatial co-occurrence in a probabilistic model, and when measured as spatial autocorrelation in the Hierarchical modelling of Species Communities (HMSC) The positive associations between many species suggest the absence of direct competitive exclusion, due for example to floral resource limitation. At the landscape level, direct competition is unlikely as many species specialize in their nesting and feeding resources (Roulston & Goodell 2011). However, we do see evidence that phylogenetically similar genera on average are less likely to co-occur. This is in line with Gause's principle of exclusion, stating that complete competitors cannot co-exist (Hardin 1960). We expect that this effect of competitive exclusion is likely to be much clearer at the fine scale. It is difficult to ascertain from the results of the HMSC model whether the relationship between species pairs denotes (1) a true interaction or (2) if species share a response to missing explanatory covariates, or (3) if this is a bias in sampling method and intensity across sites (Ovaskainen et al. 2017). In particular, the addition of floral resources as an extra explanatory variable could explain part of the correlation between species and is necessary to understand the complexity of wild bee community assembly (Papanikolaou et al. 2017; Scheper et al. 2015). However, we can conclude that including the latent factors associated with the co-occurrence network, in a JSDM approach (Ovaskainen et al. 2017), increases model explanatory power, and that, alongside habitat filtering, the patterns of co-occurrence can be a useful input in understanding and predicting the distribution of wild bees species. This has previously only been shown for the distributions of single species with the interaction known a priori (Giannini et al. 2013).

4.5.2 What is the influence of habitat filtering on the patterns of wild bee occurrence?

Land use has a significant role in the distribution of wild bees in the Netherlands. Specifically, semi-natural grassland habitats, the most important areas for wildflowers, are positively influencing the distribution patterns of many species. The decline in these habitats is linked to the long-term decline of wild bees in European countries (Goulson et al. 2015; Potts et al. 2010). Cropland and agricultural habitats form a large portion of the Netherlands and are negatively associated with wild bee occurrence apart from a few widespread generalist bumblebees. Generally, due to the fact that they are intensively managed and provide few resources (Kremen et al. 2002). Heathlands represent a conflicting habitat for wild bees: it is a renowned suitable habitat for some specialized species (e.g. *Andrena fuscipes*, *Colletes succinctus* and their cleptoparasites), but also limits species not adapted to the specialized feeding resources (Moquet et al. 2016). Plant-pollinator networks in heathland habitats are also less complex than in more heterogeneous systems, but they tend to be more specialized (Forup et al. 2008). Therefore, as we detected, heathlands represent a unique habitat and assemblage vital for biodiversity. Dunes are also positively associated with a disproportionately large number of species. Dune areas represent a unique floral habitat with high bee diversity, despite their small area, and their maintenance and restoration is vital to wild bee diversity (Grootjans et al. 2002, Howe et al. 2010).

4.5.3 Do species traits and phylogenetic relationships influence wild bee spatial co-occurrence and assembly patterns?

Phylogenetic and functional trait differences correlate with extinction risk, and drivers of decline in wild bees (De Palma et al. 2017; Vereecken 2017). Competitive exclusion would suggest that similar species, in traits or phylogeny, are less likely to co-occur (Webb et al. 2002). We observe a degree of phylogenetic niche conservatism (PNC) in the HMSC, suggesting that, at the landscape scale, closely-related species share similar niches. However, when measured as co-occurrence no specific patterns emerge. From the data available we cannot conclude whether the evidence for PNC indicates an emergent property of the wild bee community in the Netherlands, or whether it is a process by which the community is structured (Losos 2008). This suggests a shared ecological trait between closely-related species (Crisp & Cook 2012). However, our results do not illustrate a clear relationship between traits and co-occurrence or niche requirements. This is unlike the patterns observed for plant species where trait-based environmental filtering is common (Messier et al. 2010). This indicates that a fundamental trait, or suite of traits, shared by closely-related species were unaccounted. The PNC presented is not a complete 'niche' and reflects conservatism to a select set of habitat variables, a more detailed niche definition, including feeding and nesting resources and the traits associated with them, is likely to lower the PNC dramatically as considerable specialization occurs in both feeding and nesting habits (Losos 2008). Unfortunately, these traits and niche requirements are poorly defined or missing entirely for many species and represent a significant gap in wild bee ecology. Increasing the available knowledge on these aspects of wild bee ecology could help us better understand the processes structuring wild bee assemblages. However, at least from a habitat perspective, phylogenetically-informed conservation practices could prove appropriate.

4.5.4 How are wild bee assemblages geographically distributed?

The observed variation in community assemblages is driven by changes in environmental conditions (i.e., land use and climatic context), rather than by purely geographic distance between sites and regions. Biotic homogenization is considered to be a response, alongside decline and loss, to anthropogenic disturbance, including urbanization and agricultural intensification (McKinney 2006). The wild bee fauna of the Netherlands appears to have experienced biotic homogenization during the last century (Carvalheiro et al. 2013), and the wild bee community assembly patterns reported in this study also reflect a broad similarity in wild bee assemblages across much of the country. However, at present, the Netherlands does not harbour a single uniform community. The seven assemblages identified include gradients from specialized habitats, to semi-natural habitats to more anthropogenic, managed systems. We observe three distinct assemblages that, while limited in range, comprise more specialized species groups that do not readily occur elsewhere; heather bees near wooded and protected areas, coastal dune bees and southern bees associated with a heterogeneous landscape and calcareous grasslands. These assemblages occur in areas likely to have high diversity of floral resources, which is strongly correlated with wild bee populations (Roulston & Goodell 2011).

The heathlands assemblage is comprised of known heathlands specialists, for example *B. humilis*, *Colletes succinctus*, *Andrena fuscipes*, *Epeolus cruciger* and *Nomada rufipes*, which are unlikely to be found in large populations elsewhere (Falk 1991, Peeters et al. 2012). Furthermore, the coastal dune assemblage includes species such as *C. halophilus*, which is associated with saltmarsh and coastal habitat where they require bare sandy soils for nesting and the saltmarsh specialist sea aster (*Aster tripolium*) as their main pollen host plant (Kuhlmann et al. 2007). The populations of these representative species are not only important at a national scale but also at the European scale, for example *C. halophilus*, *E. cruciger*, *C. succintus*, *Melitta tricincta* and *N. zonata* are considered as "least concern" in the Netherlands, however they are red listed at the European level (Nieto et al. 2014; Reemer 2018). This suggests that the assemblages in the Netherlands represent important populations for the continued survival of these species.

4.5.5 What are the conservation implications of the resulting wild bee assemblage patterns?

In a conservation context, the community profiles/assemblages can represent management units (Ovaskainen et al. 2017), i.e. not managing the wild bee community as a single homogenous unit, but still simplifying the complex interactions between species and resources. The results presented could be of primary interest to managers of nature reserves who are tasked with the conservation of wild bees. At the national scale the 'Netherlands National Pollinator Strategy' aims to increase the number of bees showing a stable or positive population trends and increase their distribution throughout the country by increasing feeding and nesting resources (Bijenstrategie 2018); this is in line with other countries that have recognized the decline of wild bees. The methodology used in this study identifies populations that would benefit from management at the habitat level. For example dune and heathland habitats exemplify areas that should be targeted to manage and protect important wild bee assemblages.

The results presented suggest that improving bee habitat in agricultural areas could have a significant impact, however, evidence from the Netherlands suggests that floral resources in agricultural habitats only benefits species already occurring nearby (Bukovinszky et al. 2017; Kleijn et al. 2006). This implies that natural heathland, dunes, and calcareous grasslands represent a last vestige for many bees. A logical next step would be to include representative and specialist bees as focal species in the descriptions and policy documents associated with these sites. The representative species for each assemblage could be used as indicator species and to measure if management is creating habitat for whole assemblages and not just common ubiquitous species. It is important to consider though that the a priori selection of species with at least 5 records limits the number of rare and highly specialized species. With more comprehensive sampling we could obtain a clearer picture of the processes behind assembly patterns and therefore best conservation practices.

This paper presents evidence that including pairwise species co-occurrence data into niche models improves the quality of prediction and therefore allows better estimation of species assemblages. Furthermore, we found preliminary evidence that closely-related wild bees share similar niche requirements. In some respects this paper represents statistical support for what many entomologists and amateur naturalists are already acutely aware of: that areas of high quality semi-natural habitat are of vital importance to the diversity of pollinators and that processes of wild bees assemblages and therefore their conservation cannot be examined in isolation.

4.6 Supporting Information

Tables

TABLE S4.1: **List of the 204 wild bee species included in the HMSC protocol.**

Andrena angustior	*Andrena apicata*	*Andrena argentata*	*Andrena barbilabris*
Andrena bicolor	*Andrena bimaculata*	*Andrena carantonica*	*Andrena chrysosceles*
Andrena cineraria	*Andrena clarkella*	*Andrena denticulata*	*Andrena dorsata*
Andrena flavipes	*Andrena florea*	*Andrena fucata*	*Andrena fulva*
Andrena fulvago	*Andrena fulvida*	*Andrena fuscipes*	*Andrena gravida*
Andrena haemorrhoa	*Andrena hattorfiana*	*Andrena helvola*	*Andrena humilis*
Andrena labialis	*Andrena labiata*	*Andrena lapponica*	*Andrena lathyri*
Andrena minutula	*Andrena minutuloides*	*Andrena nigroaenea*	*Andrena nitida*
Andrena ovatula	*Andrena pilipes*	*Andrena praecox*	*Andrena proxima*
Andrena rosae	*Andrena ruficrus*	*Andrena semilaevis*	*Andrena strohmella*
Andrena subopaca	*Andrena tibialis*	*Andrena vaga*	*Andrena ventralis*
Andrena wilkella	*Anthidiellum strigatum*	*Anthidium manicatum*	*Anthidium punctatum*
Anthophora furcata	*Anthophora plumipes*	*Anthophora quadrimaculata*	*Anthophora retusa*
Bombus bohemicus	*Bombus campestris*	*Bombus hortorum*	*Bombus humilis*
Bombus hypnorum	*Bombus jonellus*	*Bombus lapidarius*	*Bombus muscorum*
Bombus pascuorum	*Bombus pratorum*	*Bombus ruderarius*	*Bombus rupestris*
Bombus sylvestris	*Bombus terrestris*	*Bombus vestalis*	*Bombus veteranus*
Ceratina cyanea	*Chelostoma campanularum*	*Chelostoma florisomne*	*Chelostoma rapunculi*
Coelioxys conoidea	*Coelioxys elongata*	*Coelioxys inermis*	*Coelioxys mandibularis*
Colletes cunicularius	*Colletes daviesanus*	*Colletes fodiens*	*Colletes halophilus*
Colletes hederae	*Colletes marginatus*	*Colletes similis*	*Colletes succinctus*
Dasypoda hirtipes	*Epeoloides coecutiens*	*Epeolus cruciger*	*Epeolus variegatus*
Eucera nigrescens	*Halictus confusus*	*Halictus maculatus*	*Halictus rubicundus*
Halictus scabiosae	*Halictus tumulorum*	*Heriades truncorum*	*Hoplitis adunca*
Hoplitis claviventris	*Hoplitis leucomelana*	*Hylaeus brevicornis*	*Hylaeus communis*
Hylaeus confusus	*Hylaeus cornutus*	*Hylaeus hyalinatus*	*Hylaeus pectoralis*
Hylaeus pictipes	*Hylaeus punctulatissimus*	*Hylaeus signatus*	*Lasioglossum albipes*
Lasioglossum brevicorne	*Lasioglossum calceatum*	*Lasioglossum fratellum*	*Lasioglossum fulvicorne*
Lasioglossum laticeps	*Lasioglossum lativentre*	*Lasioglossum leucopus*	*Lasioglossum leucozonium*
Lasioglossum lucidulum	*Lasioglossum malachurum*	*Lasioglossum minutissimum*	*Lasioglossum morio*
Lasioglossum nitidiusculum	*Lasioglossum nitidulum*	*Lasioglossum parvulum*	*Lasioglossum pauxillum*
Lasioglossum punctatissimum	*Lasioglossum quadrinotatulum*	*Lasioglossum rufitarse*	*Lasioglossum semilucens*
Lasioglossum sexnotatum	*Lasioglossum sexstrigatum*	*Lasioglossum villosulum*	*Lasioglossum xanthopus*
Lasioglossum zonulum	*Macropis europaea*	*Macropis fulvipes*	*Megachile centuncularis*
Megachile circumcincta	*Megachile leachella*	*Megachile ligniseca*	*Megachile maritima*
Megachile versicolor	*Megachile willughbiella*	*Melecta albifrons*	*Melitta haemorrhoidalis*
Melitta leporina	*Melitta nigricans*	*Melitta tricincta*	*Nomada alboguttata*
Nomada armata	*Nomada bifasciata*	*Nomada conjungens*	*Nomada fabriciana*
Nomada femoralis	*Nomada flava*	*Nomada flavoguttata*	*Nomada flavopicta*
Nomada fucata	*Nomada fulvicornis*	*Nomada fuscicornis*	*Nomada goodeniana*
Nomada guttulata	*Nomada integra*	*Nomada lathburiana*	*Nomada marshamella*
Nomada obscura	*Nomada panzeri*	*Nomada ruficornis*	*Nomada rufipes*
Nomada sheppardana	*Nomada signata*	*Nomada stigma*	*Nomada striata*
Nomada succincta	*Nomada zonata*	*Osmia aurulenta*	*Osmia bicornis*
Osmia caerulescens	*Osmia cornuta*	*Osmia leaiana*	*Osmia spinulosa*
Osmia uncinata	*Panurgus banksianus*	*Panurgus calcaratus*	*Sphecodes albilabris*
Sphecodes crassus	*Sphecodes ephippius*	*Sphecodes ferruginatus*	*Sphecodes geoffrellus*
Sphecodes gibbus	*Sphecodes longulus*	*Sphecodes marginatus*	*Sphecodes miniatus*
Sphecodes monilicornis	*Sphecodes niger*	*Sphecodes pellucidus*	*Sphecodes puncticeps*
Sphecodes reticulatus	*Sphecodes rubicundus*	*Sphecodes scabricollis*	*Stelis breviuscula*
Stelis ornatula	*Stelis punctulatissima*	*Stelis signata*	*Xylocopa violacea*

TABLE S4.2: **Species collected in the Netherlands since 2005 with less than five record and/or missing phylogenetic or trait data.** Highlighted cells indicate species excluded for multiple reasons.

<5 Records	**Trait Data Missing**	**Phylogenetic Data Missing**
Andrena agilissima	*Andrena fulvata*	*Andrena fulvata*
Andrena coitana	*Andrena mitis*	*Andrena gelriae*
Andrena falsifica	*Andrena pusilla*	*Andrena nigriceps*
Andrena ferox	*Bombus norvegicus*	*Andrena synadelpha*
Andrena fulvata	*Chalicodoma ericetorum*	*Andrena varians*
Andrena gelriae	*Chelostoma distinctum*	*Bombus cryptarum*
Andrena intermedia	*Coelioxys conica*	*Bombus lucorum*
Andrena nitidiuscula	*Epeolus tarsalis*	*Bombus magnus*
Andrena niveata	*Halictus langobardicus*	*Chalicodoma ericetorum*
Andrena pandellei	*Hoplitis tridentata*	*Coelioxys conica*
Andrena polita	*Hylaeus incongruus*	*Epeolus tarsalis*
Andrena pusilla	*Hylaeus paulus*	*Halictus langobardicus*
Andrena tarsata	*Hylaeus rinki*	*Hylaeus annularis*
Andrena trimmerana	*Lasioglossum aeratum*	*Hylaeus dilatatus*
Andrena viridescens	*Lasioglossum intermedium*	*Hylaeus gredleri*
Anthophora aestivalis	*Lasioglossum sabulosum*	*Hylaeus incongruus*
Bombus barbutellus	*Lasioglossum tarsatum*	*Hylaeus paulus*
Bombus soroeensis	*Megachile dorsalis*	*Lasioglossum aeratum*
Bombus sylvarum	*Megachile genalis*	*Lasioglossum prasinum*
Chelostoma distinctum	*Megachile lagopoda*	*Lasioglossum quadrinotatum*
Coelioxys afra	*Megachile lapponica*	*Lasioglossum tarsatum*
Coelioxys alata	*Nomada ferruginata*	*Megachile dorsalis*
Coelioxys aurolimbata	*Nomada leucophthalma*	*Nomada baccata*
Coelioxys conica	*Nomada melathoracica*	*Stelis phaeoptera*
Coelioxys rufescens	*Nomada opaca*	
Colletes impunctatus	*Nomada pleurosticta*	
Eucera longicornis	*Nomada similis*	
Halictus langobardicus	*Nomada villosa*	
Halictus leucaheneus	*Osmia niveata*	
Halictus quadricinctus		
Hoplitis ravouxi		
Hoplitis tridentata		
Hylaeus annularis		
Hylaeus clypearis		
Hylaeus difformis		
Hylaeus gibbus		
Hylaeus leptocephalus		
Hylaeus paulus		
Hylaeus styriacus		
Lasioglossum aeratum		
Lasioglossum intermedium		
Lasioglossum lineare		
Lasioglossum minutulum		
Lasioglossum pallens		
Lasioglossum pygmaeum		
Megachile alpicola		
Megachile analis		
Megachile ericetorum		
Megachile genalis		
Megachile lagopoda		
Megachile pilidens		
Megachile rotundata		
Melecta luctuosa		
Nomada baccata		
Nomada distinguenda		
Nomada melathoracica		

Table S4.2 continued from previous page

Nomada mutica
Nomada opaca
Nomada pleurosticta
Nomada sexfasciata
Nomada villosa
Osmia parietina
Sphecodes hyalinatus
Sphecodes majalis
Sphecodes rufiventris
Stelis minima
Stelis minuta
Trachusa byssin

TABLE S4.3: **Environmental covariates used in the Hierarchical modelling of Species Communities (HMSC) protocol.** All covariates have pairwise correlation coefficients below 0.7.

Class	**Description**	**Source**	**Higher Classification**
crops food source	crops deemed a food source for insect pollinators, including fruit trees	BRP	Agricultural
crops non-food source	crops not deemed a food source for insect pollinators	BRP and BBG_CBS	Agricultural
agri-grassland	all grassland used for agricultural purposes	BRP and BBG_CBS	Agricultural
urban	all areas in urban conglomeration	BBG_CBS	Urban
heathland	all nature areas with a significant heather (Ericaceae) population	IMNAB	Nature
semi-natural woodland	woodland area without a production function	IMNAB	Nature
production woodland	woodland area with a production function	IMNAB	Nature
marsh and swampland	Marsh, peat, reed, salt-marsh and swamp area	IMNAB	Nature
semi-natural grassland	non-intensive agricultural grasslands and grasslands managed for nature	IMNAB	Nature
dune	open dune areas	IMNAB	Nature
salt water*	ocean related water bodies	BRP and BBG_CBS	Other
freshwater*	rivers, stream, lake, canals etc.	BRP and BBG_CBS	Other
Bio6	min temperature of coldest month	KNMI	Temperature
Bio9	mean temperature of driest quarter	KNMI	Temperature
Bio10	mean temperature of warmest quarter	KNMI	Temperature
Bio12	annual precipitation	KNMI	Rainfall
Bio14	precipitation of the driest month	KNMI	Rainfall

*Saltwater and freshwater were not included in the final analyses because they have little to no influence on the distribution patterns of wild bees.

TABLE S4.4: **Wild bees barcodes sequences retrieved from GenBank with their accession number, number of base pair (bp) and reference.**

Bee Species	**GenBank**	**bp**	**Reference**	**Bee Species**	**GenBank**	**bp**	**Reference**
Ammobates punctatus	KJ838996.1	630	Schmidt et al. 2015	*Hylaeus signatus*	KJ836815.1	658	Schmidt et al. 2015
Andrena agilissima	KJ838061.1	402	Schmidt et al. 2015	*Hylaeus sinuatus*	KJ839168.1	658	Schmidt et al. 2015
Andrena alfkenella	KJ839781.1	658	Schmidt et al. 2015	*Hylaeus styriacus*	KJ837075.1	658	Schmidt et al. 2015
Andrena angustior	JQ909640.1	654	Magnacca & Brown 2012	*Hylaeus variegatus*	KJ839619.1	658	Schmidt et al. 2015
Andrena apicata	JQ909642.1	654	Magnacca & Brown 2012	*Lasioglossum albipes*	GU706031.1	658	Schmidt et al. 2015
Andrena argentata	KJ838179.1	287	Schmidt et al. 2015	*Lasioglossum bluethgeni*	HM401099.1	658	Schmidt et al. 2015
Andrena barbilabris	KT604563.1	552	Schmidt et al. 2015	*Lasioglossum brevicorne*	HQ948053.1	625	Schmidt et al. 2015
Andrena bicolor	KJ839635.1	658	Schmidt et al. 2015	*Lasioglossum breviventre*	KJ836700.1	658	Schmidt et al. 2015
Andrena bimaculata	KJ839689.1	402	Schmidt et al. 2015	*Lasioglossum calceatum*	GU706037.1	658	Schmidt et al. 2015
Andrena carantonica	KJ839813.1	311	Schmidt et al. 2015	*Lasioglossum costulatum*	KJ839709.1	658	Schmidt et al. 2015
Andrena chrysopus	KJ837564.1	624	Schmidt et al. 2015	*Lasioglossum fratellum*	HQ954751.1	620	Schmidt et al. 2015
Andrena chrysopyga	HM376233.1	611	Schmidt et al. 2015	*Lasioglossum fulvicorne*	KJ839738.1	658	Schmidt et al. 2015
Andrena chrysosceles	JN262171.1	599	Schmidt et al. 2015	*Lasioglossum glabriusculum*	KJ839752.1	658	Schmidt et al. 2015
Andrena cineraria	KJ839533.1	407	Schmidt et al. 2015	*Lasioglossum intermedium*	KJ838212.1	658	Schmidt et al. 2015
Andrena clarkella	HQ954750.1	615	Schmidt et al. 2015	*Lasioglossum interruptum*	KJ839609.1	658	Schmidt et al. 2015
Andrena coitana	KJ836599.1	633	Schmidt et al. 2015	*Lasioglossum laevigatum*	HQ954752.1	602	Schmidt et al. 2015
Andrena combinata	KJ838976.1	658	Schmidt et al. 2015	*Lasioglossum laticeps*	KJ839464.1	658	Schmidt et al. 2015
Andrena curvungula	KJ839287.1	287	Schmidt et al. 2015	*Lasioglossum lativentre*	HM401249.1	658	Schmidt et al. 2015
Andrena decipiens	KJ839034.1	286	Schmidt et al. 2015	*Lasioglossum leucopus*	KJ839703.1	658	Schmidt et al. 2015
Andrena denticulata	KJ839112.1	658	Schmidt et al. 2015	*Lasioglossum leucozonium*	KJ839730.1	658	Schmidt et al. 2015
Andrena distinguenda	KJ839472.1	658	Schmidt et al. 2015	*Lasioglossum lineare*	KJ837544.1	421	Schmidt et al. 2015
Andrena dorsata	KJ839807.1	658	Schmidt et al. 2015	*Lasioglossum lucidulum*	KJ838100.1	658	Schmidt et al. 2015
Andrena falsifica	KJ839739.1	658	Schmidt et al. 2015	*Lasioglossum majus*	KJ839801.1	658	Schmidt et al. 2015
Andrena ferox	KJ839323.1	287	Schmidt et al. 2015	*Lasioglossum malachurum*	GU706055.1	658	Schmidt et al. 2015
Andrena flavipes	KJ839275.1	298	Schmidt et al. 2015	*Lasioglossum marginellum*	KJ838806.1	658	Schmidt et al. 2015
Andrena florea	KJ839804.1	658	Schmidt et al. 2015	*Lasioglossum minutissimum*	KJ837045.1	658	Schmidt et al. 2015
Andrena fucata	KJ839172.1	407	Schmidt et al. 2015	*Lasioglossum minutulum*	KJ838016.1	607	Schmidt et al. 2015
Andrena fulva	KJ839625.1	407	Schmidt et al. 2015	*Lasioglossum morio*	GU706057.1	658	Schmidt et al. 2015
Andrena fulvago	KJ839726.1	286	Schmidt et al. 2015	*Lasioglossum nitidiusculum*	KJ838160.1	630	Schmidt et al. 2015
Andrena fulvida	KJ839509.1	516	Schmidt et al. 2015	*Lasioglossum nitidulum*	KJ839608.1	658	Schmidt et al. 2015
Andrena fuscipes	KJ839791.1	658	Schmidt et al. 2015	*Lasioglossum pallens*	KJ839719.1	421	Schmidt et al. 2015
Andrena gravida	KJ839831.1	658	Schmidt et al. 2015	*Lasioglossum parvulum*	HM376230.1	658	Schmidt et al. 2015
Andrena haemorrhoa	KJ839829.1	658	Schmidt et al. 2015	*Lasioglossum pauperatum*	HM401252.1	615	Schmidt et al. 2015
Andrena hattorfiana	KJ839806.1	658	Schmidt et al. 2015	*Lasioglossum pauxillum*	KJ839504.1	658	Schmidt et al. 2015
Andrena helvola	KJ837363.1	658	Schmidt et al. 2015	*Lasioglossum politum*	KJ839729.1	658	Schmidt et al. 2015
Andrena humilis	KJ838908.1	657	Schmidt et al. 2015	*Lasioglossum punctatissimum*	HM376229.1	658	Schmidt et al. 2015
Andrena intermedia	KJ839529.1	293	Schmidt et al. 2015	*Lasioglossum puncticolle*	KJ838477.1	658	Schmidt et al. 2015
Andrena labialis	KJ839700.1	285	Schmidt et al. 2015	*Lasioglossum pygmaeum*	KJ839643.1	658	Schmidt et al. 2015
Andrena labiata	KJ839363.1	658	Schmidt et al. 2015	*Lasioglossum quadrinotatulum*	KJ839622.1	658	Schmidt et al. 2015
Andrena lapponica	KJ838738.1	658	Schmidt et al. 2015	*Lasioglossum rufitarse*	JN272460.1	612	Schmidt et al. 2015
Andrena lathyri	KJ839310.1	658	Schmidt et al. 2015	*Lasioglossum sabulosum*	KJ838136.1	408	Schmidt et al. 2015
Andrena limata	KJ839525.1	658	Schmidt et al. 2015	*Lasioglossum semilucens*	KJ837947.1	658	Schmidt et al. 2015
Andrena marginata	KJ837896.1	658	Schmidt et al. 2015	*Lasioglossum sexmaculatum*	KJ839463.1	286	Schmidt et al. 2015
Andrena minutula	KJ839124.1	277	Schmidt et al. 2015	*Lasioglossum sexnotatum*	KJ839283.1	658	Schmidt et al. 2015
Andrena minutuloides	KJ839473.1	658	Schmidt et al. 2015	*Lasioglossum sexstrigatum*	KJ836807.1	643	Schmidt et al. 2015
Andrena mitis	KJ839301.1	658	Schmidt et al. 2015	*Lasioglossum subfasciatum*	KJ839824.1	658	Schmidt et al. 2015
Andrena nana	KJ839631.1	658	Schmidt et al. 2015	*Lasioglossum subfulvicorne*	HQ948016.1	623	Schmidt et al. 2015
Andrena nigroaenea	KJ839613.1	658	Schmidt et al. 2015	*Lasioglossum villosulum*	KJ839019.1	658	Schmidt et al. 2015
Andrena nitida	KJ839744.1	658	Schmidt et al. 2015	*Lasioglossum xanthopus*	KJ837984.1	658	Schmidt et al. 2015
Andrena nitidiuscula	KJ839658.1	658	Schmidt et al. 2015	*Lasioglossum zonulum*	KJ838645.1	658	Schmidt et al. 2015
Andrena niveata	KJ836650.1	336	Schmidt et al. 2015	*Macropis europaea*	KJ839299.1	658	Schmidt et al. 2015
Andrena nycthemera	KJ839071.1	407	Schmidt et al. 2015	*Macropis fulvipes*	KJ838021.1	658	Schmidt et al. 2015
Andrena ovatula	KJ839684.1	407	Schmidt et al. 2015	*Megachile alpicola*	KJ838895.1	574	Schmidt et al. 2015
Andrena pandellei	KJ839827.1	402	Schmidt et al. 2015	*Megachile analis*	KJ837255.1	658	Schmidt et al. 2015
Andrena pilipes	KJ839665.1	407	Schmidt et al. 2015	*Megachile apicalis*	KJ839086.1	658	Schmidt et al. 2015
Andrena polita	KJ839692.1	658	Schmidt et al. 2015	*Megachile centuncularis*	KJ839746.1	658	Schmidt et al. 2015
Andrena potentillae	KJ839740.1	658	Schmidt et al. 2015	*Megachile circumcincta*	KJ839014.1	658	Schmidt et al. 2015
Andrena praecox	KJ839332.1	407	Schmidt et al. 2015	*Megachile ericetorum*	KJ839569.1	658	Schmidt et al. 2015

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Andrena proxima	HM401053.1	658	Schmidt et al. 2015	*Megachile genalis*	KJ839253.1	658	Schmidt et al. 2015
Andrena pusilla	KJ839537.1	283	Schmidt et al. 2015	*Megachile lagopoda*	HM401110.1	658	Schmidt et al. 2015
Andrena rosae	KJ839679.1	658	Schmidt et al. 2015	*Megachile lapponica*	HM401111.1	658	Schmidt et al. 2015
Andrena ruficrus	KJ837768.1	365	Schmidt et al. 2015	*Megachile leachella*	HM401115.1	658	Schmidt et al. 2015
Andrena semilaevis	KJ839666.1	658	Schmidt et al. 2015	*Megachile ligniseca*	KJ838291.1	658	Schmidt et al. 2015
Andrena similis	KJ839751.1	658	Schmidt et al. 2015	*Megachile maritima*	KJ839766.1	658	Schmidt et al. 2015
Andrena strohmella	KJ839400.1	270	Schmidt et al. 2015	*Megachile pilidens*	KJ839629.1	658	Schmidt et al. 2015
Andrena subopaca	KJ839374.1	658	Schmidt et al. 2015	*Megachile pyrenaea*	KJ839081.1	658	Schmidt et al. 2015
Andrena tarsata	JQ909697.1	654	Magnacca & Brown 2012	*Megachile rotundata*	GU706002.1	658	Schmidt et al. 2015
Andrena thoracica	KJ839789.1	658	Schmidt et al. 2015	*Megachile versicolor*	KJ839653.1	658	Schmidt et al. 2015
Andrena tibialis	KJ839449.1	658	Schmidt et al. 2015	*Megachile willughbiella*	KJ838579.1	658	Schmidt et al. 2015
Andrena trimmerana	KJ837431.1	658	Schmidt et al. 2015	*Melecta albifrons*	KJ839671.1	618	Schmidt et al. 2015
Andrena vaga	HM401049.1	658	Schmidt et al. 2015	*Melecta luctuosa*	KJ839507.1	634	Schmidt et al. 2015
Andrena ventralis	KJ839682.1	407	Schmidt et al. 2015	*Melitta dimidiata*	KJ837102.1	658	Schmidt et al. 2015
Andrena viridescens	KJ838743.1	657	Schmidt et al. 2015	*Melitta haemorrhoidalis*	KJ839641.1	658	Schmidt et al. 2015
Andrena wilkella	KJ838400.1	636	Schmidt et al. 2015	*Melitta leporina*	KJ839815.1	658	Schmidt et al. 2015
Anthidiellum strigatum	KJ839140.1	407	Schmidt et al. 2015	*Melitta nigricans*	KJ839607.1	658	Schmidt et al. 2015
Anthidium manicatum	KJ839261.1	658	Schmidt et al. 2015	*Melitta tricincta*	KJ838749.1	658	Schmidt et al. 2015
Anthidium oblongatum	KJ839708.1	658	Schmidt et al. 2015	*Nomada alboguttata*	KJ839408.1	658	Schmidt et al. 2015
Anthidium punctatum	KJ839528.1	658	Schmidt et al. 2015	*Nomada argentata*	KJ837071.1	658	Schmidt et al. 2015
Anthophora aestivalis	KJ839335.1	658	Schmidt et al. 2015	*Nomada armata*	KJ836882.1	658	Schmidt et al. 2015
Anthophora bimaculata	KJ839592.1	658	Schmidt et al. 2015	*Nomada bifasciata*	KJ839249.1	658	Schmidt et al. 2015
Anthophora furcata	KJ836670.1	658	Schmidt et al. 2015	*Nomada castellana*	KJ837163.1	658	Schmidt et al. 2015
Anthophora plagiata	KJ839757.1	658	Schmidt et al. 2015	*Nomada conjungens*	KJ837916.1	658	Schmidt et al. 2015
Anthophora plumipes	KJ839251.1	658	Schmidt et al. 2015	*Nomada distinguenda*	KJ839387.1	658	Schmidt et al. 2015
Anthophora quadrimaculata	KJ839773.1	610	Schmidt et al. 2015	*Nomada emarginata*	KJ836575.1	658	Schmidt et al. 2015
Anthophora retusa	KJ839223.1	402	Schmidt et al. 2015	*Nomada fabriciana*	KJ838946.1	658	Schmidt et al. 2015
Apis mellifera	KJ084478.1	658	Unpublished	*Nomada femoralis*	KJ837198.1	658	Schmidt et al. 2015
Biastes truncatus	KJ837962.1	434	Schmidt et al. 2015	*Nomada ferruginata*	KJ839795.1	658	Schmidt et al. 2015
Bombus barbutellus	KJ839426.1	571	Schmidt et al. 2015	*Nomada flava*	GU706040.1	658	Schmidt et al. 2015
Bombus bohemicus	KJ839694.1	658	Schmidt et al. 2015	*Nomada flavoguttata*	KJ839657.1	658	Schmidt et al. 2015
Bombus campestris	GU705899.1	658	Schmidt et al. 2015	*Nomada flavopicta*	KJ839305.1	658	Schmidt et al. 2015
Bombus distinguendus	KJ838613.1	426	Schmidt et al. 2015	*Nomada fucata*	KJ838364.1	658	Schmidt et al. 2015
Bombus hortorum	HM401455.1	623	Schmidt et al. 2015	*Nomada fulvicornis*	KJ839458.1	658	Schmidt et al. 2015
Bombus humilis	KJ839334.1	658	Schmidt et al. 2015	*Nomada furva*	KJ837852.1	603	Schmidt et al. 2015
Bombus hypnorum	KJ839370.1	658	Schmidt et al. 2015	*Nomada fuscicornis*	KJ838239.1	658	Schmidt et al. 2015
Bombus jonellus	KJ839707.1	658	Schmidt et al. 2015	*Nomada goodeniana*	KJ839226.1	658	Schmidt et al. 2015
Bombus lapidarius	GU705908.1	658	Schmidt et al. 2015	*Nomada guttulata*	KJ838987.1	658	Schmidt et al. 2015
Bombus muscorum	KJ838500.1	426	Schmidt et al. 2015	*Nomada hirtipes*	GU706039.1	658	Schmidt et al. 2015
Bombus norvegicus	KJ838809.1	631	Schmidt et al. 2015	*Nomada integra*	KJ839818.1	658	Schmidt et al. 2015
Bombus pascuorum	GU705929.1	658	Schmidt et al. 2015	*Nomada lathburiana*	KJ839024.1	658	Schmidt et al. 2015
Bombus pratorum	GU705924.1	658	Schmidt et al. 2015	*Nomada leucophthalma*	GU706028.1	658	Schmidt et al. 2015
Bombus ruderarius	KJ838712.1	658	Schmidt et al. 2015	*Nomada marshamella*	KJ838076.1	658	Schmidt et al. 2015
Bombus ruderatus	KJ746616.1	658	Schmidt et al. 2015	*Nomada melathoracica*	KJ839006.1	413	Schmidt et al. 2015
Bombus rupestris	KJ839543.1	658	Schmidt et al. 2015	*Nomada mutabilis*	KJ837610.1	523	Schmidt et al. 2015
Bombus soroeensis	KJ839741.1	658	Schmidt et al. 2015	*Nomada mutica*	KJ838713.1	658	Schmidt et al. 2015
Bombus subterraneus	KJ839421.1	658	Schmidt et al. 2015	*Nomada obscura*	KJ839517.1	658	Schmidt et al. 2015
Bombus sylvarum	KJ839388.1	658	Schmidt et al. 2015	*Nomada obtusifrons*	KJ838689.1	658	Schmidt et al. 2015
Bombus sylvestris	KJ839213.1	658	Schmidt et al. 2015	*Nomada opaca*	KJ837130.1	658	Schmidt et al. 2015
Bombus terrestris	JQ843670.1	658	Williams et al. 2012	*Nomada panzeri*	KJ838935.1	658	Schmidt et al. 2015
Bombus vestalis	KJ839596.1	658	Schmidt et al. 2015	*Nomada pleurosticta*	KJ836589.1	658	Schmidt et al. 2015
Bombus veteranus	HQ563800.1	658	Schmidt et al. 2015	*Nomada rhenana*	KJ838920.1	426	Schmidt et al. 2015
Bombus wurflenii	KJ839491.1	658	Schmidt et al. 2015	*Nomada roberjeotiana*	KJ839281.1	658	Schmidt et al. 2015
Ceratina cyanea	KJ839487.1	658	Schmidt et al. 2015	*Nomada ruficornis*	HM401081.1	658	Schmidt et al. 2015
Chelostoma campanularum	KJ837936.1	658	Schmidt et al. 2015	*Nomada rufipes*	KJ839802.1	658	Schmidt et al. 2015
Chelostoma distinctum	KJ839761.1	658	Schmidt et al. 2015	*Nomada sexfasciata*	KJ838028.1	658	Schmidt et al. 2015
Chelostoma florisomne	KJ838755.1	425	Schmidt et al. 2015	*Nomada sheppardana*	KJ839733.1	658	Schmidt et al. 2015
Chelostoma rapunculi	KJ839583.1	658	Schmidt et al. 2015	*Nomada signata*	HM401085.1	658	Schmidt et al. 2015
Coelioxys afra	KJ839415.1	658	Schmidt et al. 2015	*Nomada similis*	KJ838899.1	658	Schmidt et al. 2015
Coelioxys alata	KJ839560.1	658	Schmidt et al. 2015	*Nomada stigma*	KJ839803.1	658	Schmidt et al. 2015
Coelioxys aurolimbata	KJ839452.1	658	Schmidt et al. 2015	*Nomada striata*	KJ837440.1	658	Schmidt et al. 2015
Coelioxys conoidea	KJ839642.1	658	Schmidt et al. 2015	*Nomada succincta*	KJ838940.1	658	Schmidt et al. 2015

Table S4.4 continued from previous page

Coelioxys echinata	HM401148.1	658	Schmidt et al. 2015	*Nomada villosa*	KJ836696.1	658	Schmidt et al. 2015
Coelioxys elongata	KJ837365.1	658	Schmidt et al. 2015	*Nomada zonata*	KJ838959.1	658	Schmidt et al. 2015
Coelioxys inermis	KJ839147.1	658	Schmidt et al. 2015	*Osmia andrenoides*	KJ839211.1	658	Schmidt et al. 2015
Coelioxys mandibularis	KJ839664.1	453	Schmidt et al. 2015	*Osmia aurulenta*	KJ839495.1	658	Schmidt et al. 2015
Coelioxys rufescens	KJ837496.1	658	Schmidt et al. 2015	*Osmia bicolor*	KJ839576.1	658	Schmidt et al. 2015
Colletes cunicularius	KJ838571.1	658	Schmidt et al. 2015	*Osmia bicornis*	GU705983.1	658	Schmidt et al. 2015
Colletes daviesanus	KJ839724.1	658	Schmidt et al. 2015	*Osmia brevicornis*	KJ838945.1	658	Schmidt et al. 2015
Colletes fodiens	KJ839765.1	658	Schmidt et al. 2015	*Osmia caerulescens*	KJ836678.1	658	Schmidt et al. 2015
Colletes halophilus	DQ085543.1	650	Kuhlmann et al. 2007	*Osmia cerinthidis*	KC709832.1	1231	Haider et al. 2014
Colletes hederae	KJ839205.1	630	Schmidt et al. 2015	*Osmia cornuta*	KJ839784.1	658	Schmidt et al. 2015
Colletes impunctatus	KJ838765.1	573	Schmidt et al. 2015	*Osmia inermis*	HM401203.1	658	Schmidt et al. 2015
Colletes marginatus	KJ839430.1	590	Schmidt et al. 2015	*Osmia leaiana*	KJ838962.1	658	Schmidt et al. 2015
Colletes similis	KJ839777.1	658	Schmidt et al. 2015	*Osmia melanogaster*	HM401211.1	658	Schmidt et al. 2015
Colletes succinctus	KJ838166.1	562	Schmidt et al. 2015	*Osmia niveata*	KJ839221.1	657	Schmidt et al. 2015
Dasypoda hirtipes	HM401144.1	572	Schmidt et al. 2015	*Osmia parietina*	HM401222.1	658	Schmidt et al. 2015
Dufourea dentiventris	KJ839506.1	658	Schmidt et al. 2015	*Osmia pilicornis*	KJ839236.1	658	Schmidt et al. 2015
Dufourea halictula	HM401152.1	658	Schmidt et al. 2015	*Osmia rufohirta*	KJ839465.1	658	Schmidt et al. 2015
Dufourea inermis	KJ837444.1	597	Schmidt et al. 2015	*Osmia spinulosa*	KJ839239.1	658	Schmidt et al. 2015
Dufourea minuta	KJ837955.1	658	Schmidt et al. 2015	*Osmia uncinata*	HM401230.1	658	Schmidt et al. 2015
Epeoloides coecutiens	KJ838491.1	606	Schmidt et al. 2015	*Osmia xanthomelana*	KJ837282.1	658	Schmidt et al. 2015
Epeolus cruciger	KJ839532.1	658	Schmidt et al. 2015	*Panurgus banksianus*	KJ838905.1	658	Schmidt et al. 2015
Epeolus variegatus	KJ839152.1	658	Schmidt et al. 2015	*Panurgus calcaratus*	KJ839230.1	658	Schmidt et al. 2015
Eucera longicornis	KJ838283.1	658	Schmidt et al. 2015	*Panurgus dentipes*	KJ839720.1	658	Schmidt et al. 2015
Eucera nigrescens	KJ839524.1	658	Schmidt et al. 2015	*Rophites quinquespinosus*	KJ837651.1	408	Schmidt et al. 2015
Halictus confusus	KJ839330.1	658	Schmidt et al. 2015	*Sphecodes albilabris*	KJ839755.1	658	Schmidt et al. 2015
Halictus eurygnathus	KJ838838.1	658	Schmidt et al. 2015	*Sphecodes crassus*	KJ839769.1	658	Schmidt et al. 2015
Halictus leucaheneus	KJ839776.1	658	Schmidt et al. 2015	*Sphecodes ephippius*	KJ839466.1	658	Schmidt et al. 2015
Halictus maculatus	KJ839394.1	632	Schmidt et al. 2015	*Sphecodes ferruginatus*	KJ839819.1	658	Schmidt et al. 2015
Halictus quadricinctus	KJ839343.1	658	Schmidt et al. 2015	*Sphecodes geoffrellus*	KJ839602.1	658	Schmidt et al. 2015
Halictus rubicundus	JQ909730.1	654	Magnacca & Brown 2012	*Sphecodes gibbus*	KJ839094.1	658	Schmidt et al. 2015
Halictus scabiosae	KJ839219.1	658	Schmidt et al. 2015	*Sphecodes hyalinatus*	KJ839760.1	658	Schmidt et al. 2015
Halictus sexcinctus	HM401094.1	658	Schmidt et al. 2015	*Sphecodes longulus*	KJ839122.1	658	Schmidt et al. 2015
Halictus simplex	KJ838633.1	658	Schmidt et al. 2015	*Sphecodes majalis*	KJ837051.1	658	Schmidt et al. 2015
Halictus tumulorum	JQ909735.1	654	Magnacca & Brown 2012	*Sphecodes marginatus*	KJ839540.1	658	Schmidt et al. 2015
Heriades truncorum	KJ839762.1	658	Schmidt et al. 2015	*Sphecodes miniatus*	KJ839656.1	658	Schmidt et al. 2015
Hoplitis adunca	HM401196.1	658	Schmidt et al. 2015	*Sphecodes monilicornis*	KJ839567.1	658	Schmidt et al. 2015
Hoplitis anthocopoides	KJ839674.1	658	Schmidt et al. 2015	*Sphecodes niger*	KJ839630.1	658	Schmidt et al. 2015
Hoplitis claviventris	KJ838228.1	658	Schmidt et al. 2015	*Sphecodes pellucidus*	KJ839328.1	658	Schmidt et al. 2015
Hoplitis leucomelana	KJ839627.1	658	Schmidt et al. 2015	*Sphecodes puncticeps*	KJ839170.1	658	Schmidt et al. 2015
Hoplitis papaveris	KJ839424.1	658	Schmidt et al. 2015	*Sphecodes reticulatus*	KJ838156.1	658	Schmidt et al. 2015
Hoplitis ravouxi	KJ839378.1	658	Schmidt et al. 2015	*Sphecodes rubicundus*	HQ563096.1	604	Schmidt et al. 2015
Hoplitis tridentata	GU705987.1	658	Schmidt et al. 2015	*Sphecodes rufiventris*	KJ839699.1	658	Schmidt et al. 2015
Hoplitis villosa	KJ837562.1	658	Schmidt et al. 2015	*Sphecodes scabricollis*	KJ838552.1	421	Schmidt et al. 2015
Hylaeus angustatus	KJ839785.1	658	Schmidt et al. 2015	*Sphecodes spinulosus*	KJ839610.1	283	Schmidt et al. 2015
Hylaeus brevicornis	KJ839278.1	658	Schmidt et al. 2015	*Stelis breviuscula*	KJ839384.1	658	Schmidt et al. 2015
Hylaeus clypearis	KJ839428.1	658	Schmidt et al. 2015	*Stelis minima*	KJ837069.1	421	Schmidt et al. 2015
Hylaeus communis	KJ839696.1	658	Schmidt et al. 2015	*Stelis minuta*	KJ836896.1	647	Schmidt et al. 2015
Hylaeus confusus	HM401063.1	658	Schmidt et al. 2015	*Stelis odontopyga*	HM401240.1	658	Schmidt et al. 2015
Hylaeus cornutus	KJ839471.1	658	Schmidt et al. 2015	*Stelis ornatula*	KJ839723.1	658	Schmidt et al. 2015
Hylaeus difformis	KJ839041.1	658	Schmidt et al. 2015	*Stelis punctulatissima*	KJ839732.1	603	Schmidt et al. 2015
Hylaeus gibbus	KJ838734.1	658	Schmidt et al. 2015	*Stelis signata*	KJ839263.1	507	Schmidt et al. 2015
Hylaeus hyalinatus	KJ839386.1	658	Schmidt et al. 2015	*Tetralonia malvae*	KJ839598.1	658	Schmidt et al. 2015
Hylaeus leptocephalus	KJ838113.1	631	Schmidt et al. 2015	*Thyreus orbatus*	HQ948098.1	620	Schmidt et al. 2015
Hylaeus nigritus	KJ838326.1	658	Schmidt et al. 2015	*Trachusa byssina*	KJ839233.1	611	Schmidt et al. 2015
Hylaeus pectoralis	KJ839242.1	629	Schmidt et al. 2015	*Xylocopa violacea*	KJ836969.1	658	Schmidt et al. 2015
Hylaeus pictipes	KJ838603.1	658	Schmidt et al. 2015	*OUTGROUP species*			
Hylaeus pilosulus	HQ948063.1	580	Unpublished	*Philantus triangulum*	JQ040288.1	839	Unpublished
Hylaeus punctatus	KJ839293.1	658	Schmidt et al. 2015	*Sphecius speciosus*	EF203750.1	648	Hastings et al. 2008
Hylaeus punctulatissimus	KJ839035.1	658	Schmidt et al. 2015	*Bembix troglodytes*	EF203767.1	648	Hastings et al. 2008
Hylaeus rinki	KJ837486.1	658	Schmidt et al. 2015	*Pison chilense*	GQ374629.1	786	Heraty et al. 2011

Figures

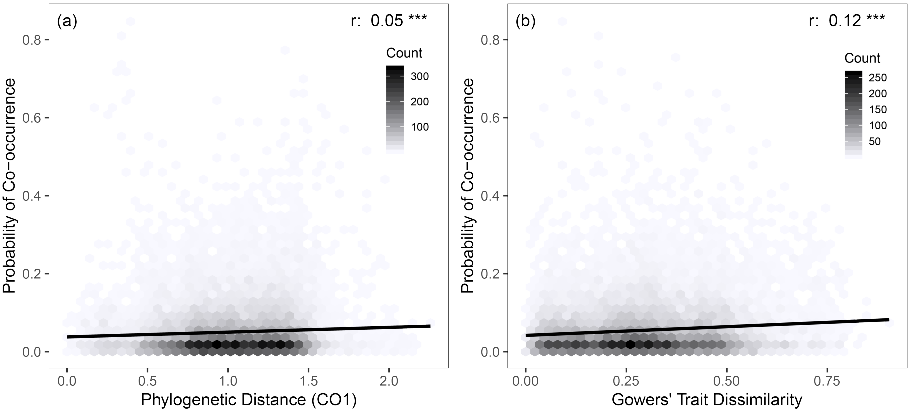

FIG. S4.1: **Hexagonal density plot showing co-occurrence probability against phylogenetic distance and trait dissimilarity at** 10 × 10.(a) Co-occurrence probability per species pair vs. Phylogenetic distance per species pair (CO1 gene). pair. (b) Co-occurrence probability per species pair vs. Gower's trait dissimilarity per species pair

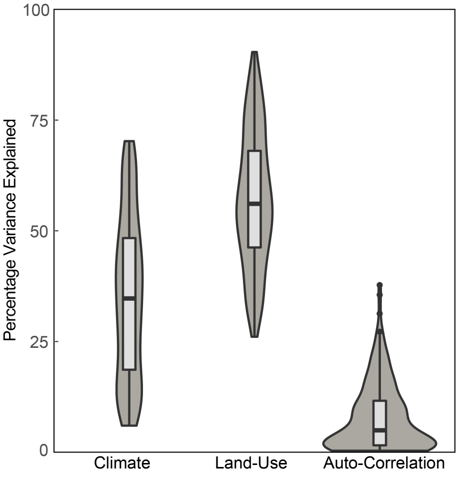

FIG. S4.2: **Violin and boxplots showing the distribution of variance explained by climate, land use and random spatial autocorrelation for all wild bee species (n=204).**

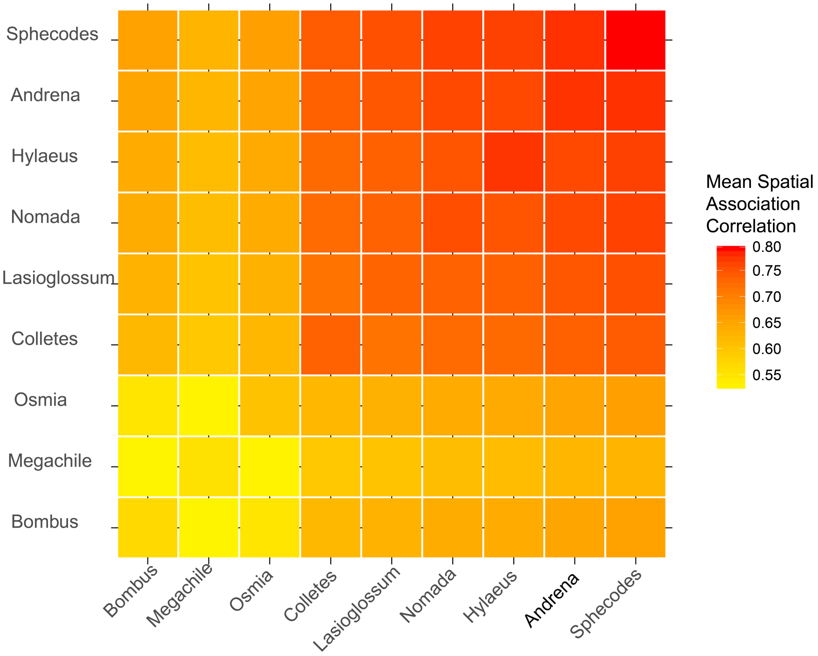

FIG. S4.3: **Mean spatial association correlation measured as a response to latent model factors between species of the nine most specious genera at 10×10 km.**

5 The interplay of climate and land use change affects the distribution of EU bumblebees

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5.1 Abstract

Bumblebees in Europe have been in steady decline since the 1900s. This decline is expected to continue with climate change as the main driver. However, at the local scale, land use and land cover (LULC) change strongly affects the occurrence of bumblebees. At present, LULC change is rarely included in models of future distributions of species. This study's objective is to compare the roles of dynamic LULC change and climate change on the projected distribution patterns of 48 European bumblebee species for three change scenarios until 2100 at the scales of Europe, and Belgium, Netherlands and Luxembourg (BENELUX). We compared three types of models: (1) only climate covariates, (2) climate and static LULC covariates and (3) climate and dynamic LULC covariates. The climate and LULC change scenarios used in the models include, extreme growth applied strategy (GRAS), business as might be usual and sustainable European development goals. We analysed model performance, range gain/loss and the shift in range limits for all bumblebees. Overall, model performance improved with the introduction of LULC covariates. Dynamic models projected less range loss and gain than climate-only projections, and greater range loss and gain than static models. Overall, there is considerable variation in species responses and effects were most pronounced at the BENELUX scale. The majority of species were predicted to lose considerable range, particularly under the extreme growth scenario (GRAS; overall mean: 64% ± 34). Model simulations project a number of local extinctions and considerable range loss at the BENELUX scale (overall mean: 56% ± 39). Therefore, we recommend species-specific modelling to understand how LULC and climate interact in future modelling. The efficacy of dynamic LULC change should improve with higher thematic and spatial resolution. Nevertheless, current broad scale representations of change in major land use classes impact modelled future distribution patterns.

5.2 Introduction

Recent scientific consensus suggests that we are facing a sixth mass extinction event, correlated strongly to anthropogenic factors (Ceballos et al. 2015). To avoid the dramatic loss of biodiversity and associated ecosystem services, immediate and thorough conservation efforts are required (Barnosky et al. 2011). An important role of biodiversity conservation research is to understand and estimate potential changes in biodiversity alongside changing abiotic and biotic conditions (Elith et al. 2010; Porfirio et al. 2014).

In an effort to understand these effects experts have produced scenarios of climate, and land use and land cover (LULC) change. Land use and land cover change scenarios use potential climate change, policy decisions and strategies to represent socio-economic developments which will inevitably shift land use and management (Rounsevell et al. 2005; van Vuuren et al. 2011; Verburg et al. 2006). Scientists have developed scenarios with the goal to evaluate the impact of environmental changes on biodiversity (Spangenberg et al. 2012). Their role in biodiversity analyses is to allow the production of dynamic land use variables which better reflect future habitat suitability for a species and may be useful to explain additional drivers of distributional changes alongside climate change. There is strong consensus that both climate and LULC change are important in driving the observed patterns of biodiversity declines (Luoto et al. 2007; Ostberg et al. 2015). Historically, LULC change has been the dominant cause of observed biodiversity changes and researchers expect that it will remain an ongoing threat to worldwide biodiversity (Millennium Ecosystem Assessment, 2005; Ostberg et al. 2015). Climate and land use change underlie a multitude of environmental pressures that may have a greater joint impact on biodiversity than when operating in isolation (Clavero et al. 2011; Mantyka-pringle et al. 2012). Therefore, models which exclude LULC change from modelling biodiversity in the future neglect a significant factor in potential drivers of species distribution change, even if these projections are coarse and at broad spatial scales.

Species distribution models (SDMs) represent a powerful tool for understanding patterns in biodiversity. They combine species occurrence data with environmental conditions to estimate the distribution of species in space and time (Elith & Leathwick 2009). Often used to project species distributions into unsampled areas, or areas of possible invasion, they also project species distributions into the future (Franklin 2010). The majority of future distribution models include only climate change variables and do not include LULC variables or use only LULC variables based on current conditions (static; Bellard et al. 2012; Titeux et al. 2016). At broad spatial scales, climate is expected to be the main constraint to species distributions, but at finer resolutions, the effect of LULC covariates increase; landscape-specific features that provide nesting and feeding resources occur at this finer scale (Luoto et al. 2007; Rahbek et al. 2007; Thuiller et al. 2004; Araújo & Lavorel 2004). Therefore, improved estimations of biodiversity change require detailed land use change scenarios (Titeux et al. 2016).

Even though studies recommend the inclusion of LULC variables to avoid producing unrealistic projections, few studies have used dynamic LULC covariates to model biodiversity patterns in the future. Reasons for this is that projections of LULC change are rarely available or only at coarse resolution and with few land use classes (Titeux et al. 2016). However, climate predictions offer similar limitations with resolution and parameters often not directly relevant to the habitat suitability of species. Interestingly, the studies that explicitly include dynamic LULC variables in the SDM process show considerable variation in the effect this has on species distribution patterns, specifically range change (Barbet-Massin et al. 2012b; Chytrý et al. 2012; Ficetola et al. 2010; Martin et al. 2013; Riordan & Rundel 2014; Sohl 2014; Wisz et al. 2008). The variation is most likely due to differences in species, spatial scale and explanatory variables included in these studies. Likewise, the performance of SDMs usually depends strongly on the modelling framework used, the species modelled, the distribution, quality and quantity of collection data, and the resolution of the species occurrence data and covariates (Aguirre-Gutierrez et al. 2013; Bellard et al. 2012; Harris et al. 2013; Warren & Seifert 2011). Testing the effect of dynamic LULC covariates with multiple species, different resolutions and covariates is essential to understand their role in SDMs (Martin et al. 2013).

In this study, we evaluate the effects of LULC change scenarios available for Europe, on the distributional changes projected by SDMs for 48 European bumblebee species projected onto Belgium, the Netherlands, and Luxembourg (BENELUX), and at the European scale. We use three land use change scenarios (business as might be usual [BAMBU], growth applied strategy [GRAS], sustainable European development goals [SEDG]) representing alternative socio-economic futures, which have been specifically developed to evaluate the impacts of environmental changes on biodiversity (Assessing LArge-scale environmental Risks with tested Methods (ALARM) Scenarios; Spangenberg et al. 2012). We expect to observe differences in the projected distributions produced by climate-only models vs. models which include LULC. We expect that the differences between static and dynamic LULC models will be less pronounced and species-specific, and will likely depend on the spatial scale and resolution at which the LULC covariates are projected (Luoto et al. 2007; Martin et al. 2013). Overall, we aim to illustrate the bias associated with using climate change-only scenarios when modelling bumblebees that land use change will undoubtedly affect. We also aim to show how presently available dynamic LULC projections affect the modelled distributions for multiple species. Following this important step, we discuss the extent to which our results provide improvements to land use change scenarios in development and the conservation implications of using such SDMs.

5.3 Materials and Methods

5.3.1 Target species

Our study group is the genus *Bombus*, for which we have detailed, long-term, biogeographical records for most of Europe, and which has shown significant decline in the last one hundred years (Biesmeijer et al. 2006; Carvalheiro et al. 2013; Kerr et al. 2015; Rasmont et al. 2005). Forty-eight European bumblebee species were included in the analysis (see Table S5.1). The species modelled share similar life histories, but exhibit vastly different ranges and distributions in Europe (Rasmont et al. 2015a). According to the IUCN Red List of threatened species, *Bombus* in Europe includes species of all threat levels (Nieto et al. 2014).

Climate change impacts have been modelled for the genus *Bombus* at the European scale, projecting severe declines and northerly shifts for the majority of the species (Rasmont et al. 2015a). However, loss of habitat for feeding and nesting resources has been cited as a major driver of past *Bombus* decline (Biesmeijer et al. 2006; Carvalheiro et al. 2013; Goulson et al. 2010; Williams & Osborne 2009). Therefore, climate might not necessarily be the only significant driver of change for this group over the next one hundred years. Furthermore, the distribution patterns of wild bee species are reported to be affected by change in major land use classes, particularly the presence of arable land (Aguirre-Gutiérrez et al. 2015; Senapathi et al. 2015).

5.3.2 Species presence data

This study includes bumblebee collection records from 22 European countries and multiple sources including professional and amateur scientists (see Fig S5.1). The data were collated as part of the EU FP7 project STEP (Potts et al. 2011), and is aggregated and available to view on the Atlas Hymenoptera webpage (Rasmont & Iserbyt 2013). We used records from 1970 until 2000, as these represent the 'current' period of climate data, which we used to train the species distribution models. We had 462,636 records available to use.

5.3.3 Spatial extent and resolution

The spatial extent was limited to the extent of the ALARM projections of European land use, which in turn limited the species collection records available to use (see Fig S5.1). Europe in the context of this study is defined as the European Union without Ireland, Romania, Bulgaria, Canary Islands and Cyprus, and including Norway and Switzerland. We created 5 × 5 km, 10 × 10 km and 20 × 20 km European grids for training the SDMs to project onto the BENELUX (Belgium, Netherlands and Luxembourg) region. We also created a 50 × 50 km European grid for training the SDMs to project onto the original spatial extent of Europe. All map projections use the European terrestrial references system 1989 (ETRS89).

5.3.4 Climate and Land Use/Land Cover Data

Variables of current climatic conditions were produced from monthly interpolated rainfall and temperature data from 1971 to 2000, at a 10 resolution (Fronzek et al. 2012, Mitchell et al. 2004). We considered 14 climate variables for the modelling process (see Table S5.2). However, because climate variables are often strongly correlated. Including all climate variables in the models would have added redundant information. Therefore, to avoid collinearities, we conducted a selection according to Pearson correlation coefficients (<0.7; Dormann et al. 2013). When two variables were highly correlated, we selected the variable that we estimated to have the greatest ecological relevance to *Bombus* species. We selected total annual growing degree-days (>5°C), which was correlated with other temperature variables, because it is linked to the presence of wildflowers and flowering crops, both important food sources for bumblebees. Furthermore, we chose water balance, which was correlated with the majority of other precipitation variables because it is representative not only of total precipitation, but has a direct link with temperature, making it an important influence for terrestrial vegetation (Gerten et al. 2004). Five climate variables were used as explanatory covariates in the model: average precipitation of the wettest month; total annual number of growing degree-days above 5°C; mean diurnal range (mean of monthly difference between daily maximum and minimum temperatures); annual temperature range (maximum temperature of warmest month–minimum temperature of coldest month); and annual water balance (mean monthly precipitation minus the monthly potential evapotranspiration; Gerten et al. 2004).

Each of the five climate variables was aggregated to the 50 × 50 km and 20 × 20 km grids, and downscaled to the 10 × 10 km and 5 × 5 km grids using bilinear interpolation (Randin et al. 2009). All spatial analyses were conducted using Rstatistics 3.3.2 (R Core Team 2017), the Raster package (version 2.5-2; Hijmans 2015) and ARCGIS 10.2 (ESRI 2016).

The future land use projections were built in congruence with a set of global change scenarios and associated climate change as part of the European ALARM project (Spangenberg et al. 2012). These climate scenarios were derived from a coupled Atmosphere-Ocean General Circulation Model (HadCM3; New et al.

1999) and include the scenarios as outlined in the IPCC Special Report on Emission Scenarios (IPCC 2001). We produced the same five climate variables in the current period for each of three scenarios of climate change (BAMBU, GRAS, SEDG) in 2050 and 2100 for the four grid resolutions.

- **'Business as Might Be Usual' (BAMBU)**—IPCC A2 scenario (see Spangenberg et al. 2012, for more information); mean projected temperature rise in Europe at 2100 is 4.7°C; an intermediate change scenario based on extrapolated current socioeconomic and policy decisions.
- **'Growth Applied Strategy' (GRAS)**—IPCC A1FI; mean projected temperature rise in Europe at 2100 is 5.6°C; a maximum change scenario driven by policies of deregulation and economic growth.
- **'Sustainable European Development Goal' (SEDG)**—IPCC B1 scenario; mean projected temperature rise in Europe at 2100 is 3.0°C; a moderate change scenario driven by economic, social and environmental policies, related to stabilizing atmospheric greenhouse gases emissions and stopping the loss of biodiversity.

Current land use was obtained from the Coordination of Information on the Environment (CORINE) Land Cover at 250 × 250 m resolution (Bossard et al. 2000). The CORINE classes were reclassified as six classes to match the future projections. We removed the class 'others' from our analysis because it represents diverse land use types and was inexplicable in an ecologically relevant context for bumblebee species. Future land use was obtained from the ALARM EU project downscaled to 250 × 250 m for each of the three scenarios for 2050 and 2100 (Dendoncker et al. 2006; Spangenberg et al. 2012). At each grid resolution, we determined the percentage cover for each land use covariate. The final five land use layers were: percentage cover arable land; percentage cover forest; percentage cover grassland; percentage cover permanent crops; and percentage cover urban.

The role of the covariates will be tested in three ways using three variable sets in the models: (1) Dynamic climate-only models, suggesting that only climate variables matter in the future distribution of bumblebee species. (2) Static land use and dynamic climate, suggesting that land use variables are important in delimiting species habitat suitability, but that their future change will be driven only by climate change and changes in land use are redundant. (3) Dynamic climate and dynamic land use, suggesting that future distribution patterns will be dependent on the interaction between changing climate and changing land use.

5.3.5 Species distribution modelling

We used a SDM approach to compare the role of dynamic land use data in the future distribution patterns of bumblebees. We modelled the distribution of 48 species using R (R Core Team 2017) with the *biomod2* package (version 3.3-3; Thuiller et al. 2013). We chose an ensemble modelling approach, which creates a consensus of the predictions of multiple algorithms and is an established method to account for projection variability (Thuiller 2014a). Even small differences between algorithms can lead to different projections of future distribution change. Ensemble modelling aims to limit the many uncertainties of forecast modelling and has become increasingly used in studies of biodiversity change (Thuiller 2014a).

We chose three algorithms to include in the ensemble model based on their previous performances with analogous collection data for a similar insect species group (Aguirre-Gutierrez et al. 2013). The three algorithms chosen were a generalized linear model, GLM (Nelder & Wedderburn 1972), with linear and quadratic effects, and stepwise selection based on the Akaike Information Criteria (AIC); a generalized boosted model, GBM (Friedman 2001), with 3,000 trees and five cross-validation folds; and Maximum Entropy Modelling (MAXENT; Phillips & Dudík 2008), with linear and quadratic features. We decided to choose simplicity and ecological clarity over model complexity by dropping detailed features, such as product, threshold, hinge and polynomial.

Models for each species were trained at multiple resolutions at the European scale; 5 × 5 km, 10 × 10 km, 20 × 20 km and 50 × 50 km. We had 462,636 records available to use; these were aggregated as unique species occurrences for each grid cell resolution. The number of occurrences per resolution is as follows: 67030 at 5 × 5 km, 49146 at 10 × 10 km, 30104 at 20 × 20 km and 21,162 at 50 × 50 km. We modelled 48 species (see Table S5.1) with at least 50 unique records, and for which there are no ongoing taxonomic debates surrounding their species definition (see Rasmont et al. 2015a). A number of occurrences in the database were not point level GPS coordinates, but were recorded as UTM grids of varying sizes. To be confident in the spatial accuracy of collection records we removed occurrences that were recorded as UTM grids larger than 1×1, km. As the sampling methods were diverse and non-systematic, there are likely spatial biases amongst the records. To deal with this potential spatial autocorrelation between closely sampled locations we selected a subset of points per species. A random starting observation was selected and all points in adjacent grid cells removed; this was then repeated for all remaining points. This produced a more even spread of observations and minimized the effects of heavy sampling at particular locations.

As true absences were not available (it is not possible to accurately say that a bee species is not present during sampling) we generated randomly distributed pseudo-absences for GBM and GLM and selected a background sample for MAXENT (Elith et al. 2011; Phillips et al. 2009). We used target-group sampling to select our background points (Mateo et al. 2010; Phillips et al. 2009). We specified that the background samples and pseudo-absences could only be selected from areas where other bumblebees have been recorded since 1970. This approach is more objective than taking the background and pseudo-absence samples from sites that have not been sampled, accounting for potential sampling bias (Elith et al. 2011; Phillips et al. 2009) and providing more accurate results (Mateo et al. 2010). To account for within algorithm variation we trained the models 10 times for each of the 48 species, the three algorithms, the three model hypotheses, and the four grid resolutions. This resulted in 360 models per species. We used a bootstrap approach where random subsets of 80% of the data were used for model training and the remaining 20% to produce Area Under the Curve (AUC) values to test model performance (Bahn & Mcgill 2013; Jiménez-Valverde & Lobo 2007). For each covariate included in the model, we calculated variable contribution as the change in correlation between the covariates and the response with and without the selected variable (Thuiller et al. 2015). We then produced an ensemble model for each of the three model hypotheses, creating a median representation of the predictions of the 10 runs and three algorithms together. We chose the median value as it is less sensitive to extreme values than the mean.

We projected the models trained at 5 × 5 km, 10 × 10 km and 20 × 20 km, onto BENELUX. BENELUX comprises no novel conditions under the scenarios (i.e., there are no conditions in BENELUX in 2100 that do not already occur within Europe). Therefore, no forecasting into unknown ecological space occurred (Fig S5.2). We also projected the data trained at 50 × 50 km onto the entire European study area. For each species we produced habitat suitability maps of the median ensemble predicted distribution. One map was produced for each of the three model types at 2050, and 2100 under the three change scenarios at the 4 grid resolutions. Habitat suitability maps were converted to binary presence absence maps using the values under which specificity and sensitivity is optimized (Thuiller et al. 2015).

5.3.6 Statistical analysis

Analyses were conducted on the ensemble model map projections of binary presence/absence. To compare the projected distributions of the three model hypotheses we measured the change in three distribution metrics. We calculated range change by looking at changes per species in areas of occupancy between the current and future periods. Specifically, we analysed the percentage of grid cells lost (present in the current period and absent in the future) by each species under the different scenarios and the percentage of grid cells gained (percentage of absent cells in the current period occupied in the future). To examine spatial shifts we took the centroid of the species range from the present (2000) and the future (2050 and 2100). A positive value indicates northerly shift and negative, a southerly shift.

To determine the role of the different models, (i.e. climate-only model [COM], dynamic LULC model [DLM] and static LULC model [SLM]), we created separate mixed effects models for each of the three metrics for both Europe and BENELUX projections. We included species as a random effect, as we were interested in how changes in distribution of the species vary across the different model types, periods and scenarios, and not in the inherent variation between species. Furthermore, to determine if our results are related to the structure of the data we also included the current range of the species as a covariate. Due to large numbers of zeros both range loss and range gain at the BENELUX scale were analysed with two separate mixed models: Bernouli distributed models of the probability of gain or loss and a linear mixed effects model of values given range loss/gain were projected.

Finally, in addition to presenting results for bumblebees as a group, we chose two species, *Bombus argillaceus* (Scopoli 1763; increasing in range) and *B. veteranus* (Fabricius 1793; decreasing in range), to look more closely at the difference between model projections with and without LULC covariates. We chose these two species as they are at opposite end of the spectrum of climate risk, both had high model performance values, both have a large number of collection records within Europe and we believe them to be representative of two futures, i.e. considerable range gain and considerable range loss, respectively (Rasmont et al. 2015a). The current distribution of *B. argillaceus* is in Southern and South Eastern Europe as well as Western Asia (Rasmont & Iserbyt 2013). In previous climate-only models of future conditions *B. argillaceu*s was projected to increase its range considerably in Western Europe (Rasmont et al. 2015a). *Bombus veteranus* exhibits an already patchy distribution in the plains of Northern Europe and has already declined in Belgium, shifting from an abundant species to one which is barely present (Rasmont & Iserbyt 2013). Under future climate-only projections *B. veteranus* is expected to decrease in range considerably (Rasmont et al. 2015a).

5.4 Results

5.4.1 Model training fit and variable contribution

For models trained on the current period, we assessed model fit using AUC scores. An AUC value below 0.5 indicates a model fit that is not better than random, values above indicate enhanced model fit. We used AUC values to compare the change in model fit per species with LULC vs. a COM (Fig 5.1). The mean AUC values for all species are above 0.7, indicating better than random model fit. For all 48 species, model fit improves by the addition of LULC covariates. A paired Wilcoxon rank sum test indicates that the mean difference between the AUC values of the models with LULC and the COMs is 0.013 ±0.004 (p value <.001).

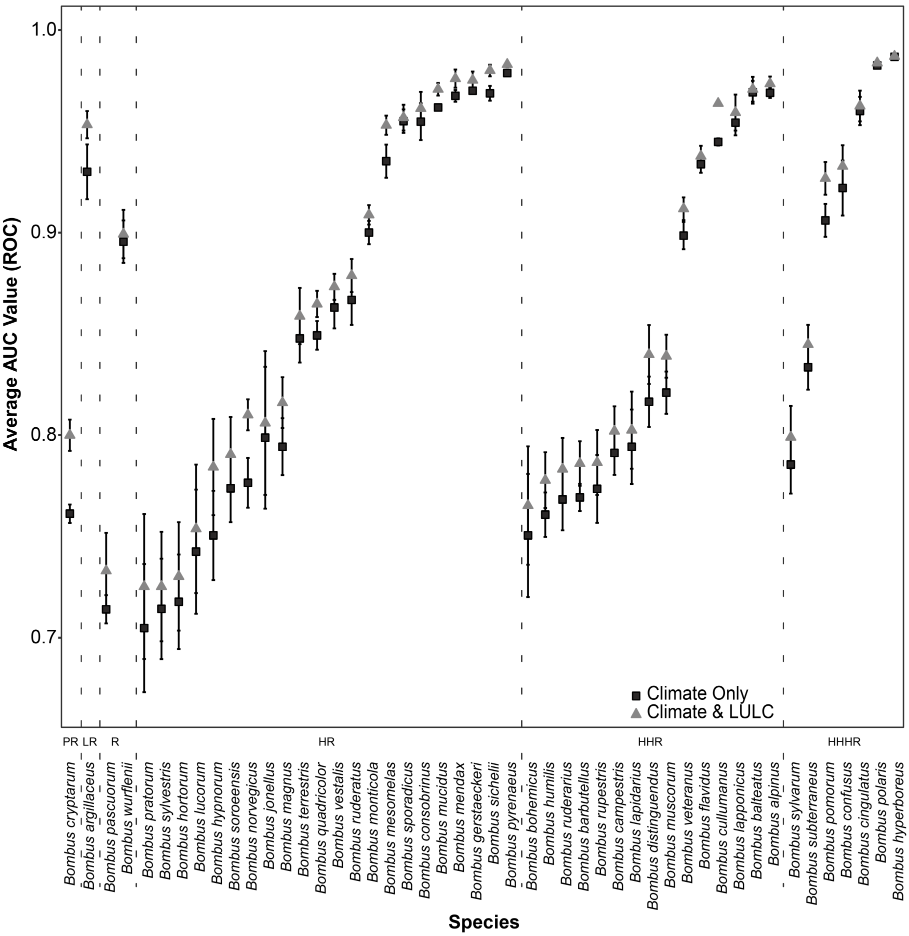

FIG. 5.1: **Area under the curve (AUC) statistics for median-ensemble-model performance visualized per species.** Black squares represent models with only climate covariates and grey triangles models with land use land cover (LULC) covariates and climate covariates. Groupings represent Climatic risk as calculated by the Climate Risk Atlas for Bumblebees (Rasmont et al. 2015a). Potential risk (PR), low risk (LR), Risk (R), high risk (HR), very high risk (HHR), extreme risk (HHHR).

We also compared the variable contributions of the different explanatory covariates included in the models (Fig 5.2). Climatic variables are the most important in explaining the current distribution of all species. The total annual number of growing degree-days was included amongst the four most important variables for 44 of the species modelled. The most important LULC covariate is the percentage cover of arable land but the percentage cover of forest is also important for a number of species (Fig 5.2). Overall LULC variables contribute 15% of total variable importance.

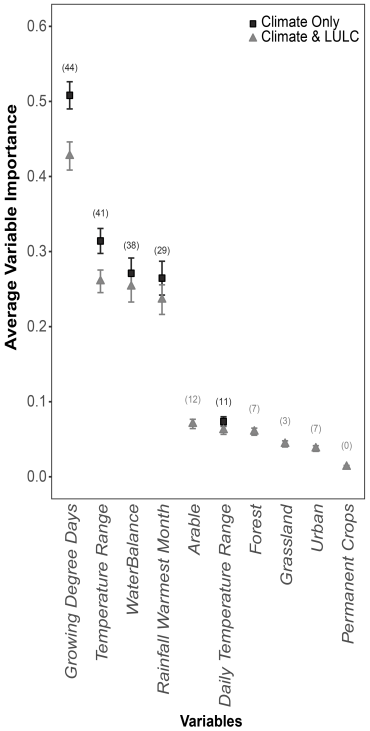

FIG. 5.2: **Average variable importance values and standard errors of all covariates included in the training models.** Black squares represent models with only climate covariates and grey triangles models with land use land cover (LULC) covariates and climate covariates. The numbers in the brackets represent the number of species for which this variable was one of the four most important variables.

5.4.2 The future of bumblebees projected at the BENELUX scale

Of the distribution change metrics analysed, the largest discrepancies were found in the projected range loss (Fig 5.3a,b). There is considerable variability between species and between scenarios but model type has a significant effect on the projections of whether species will lose range and how much range will be lost (Table

5.1). Overall species are more likely to lose range under DLMs than both COMs and SLMs ($p < .001$ and .002; Table 5.2). However, given range loss occurs (i.e. excluding species that showed no range loss) then greater loss is projected by COMs than both SLMs and DLMs (1.3%; $p < .001$; Table 5.2). However, this relationship is highly variable and species specific. Under COMs 11 species show greater mean range loss averaged across scenario and resolution, however, five species show greater range loss under DLMs (Fig 5.3a). The relationship between projected range loss of SLMs and DLMs, while not significant at the BENELUX scale, (Table 5.2) also appears to be species specific, with some species below the equal projection line, indicating greater range loss under DLMs (Fig 5.3b). There are no significant interactions between model type and other explanatory variables, suggesting a consistent effect of model type across scenarios, periods and resolutions (Table 5.1).

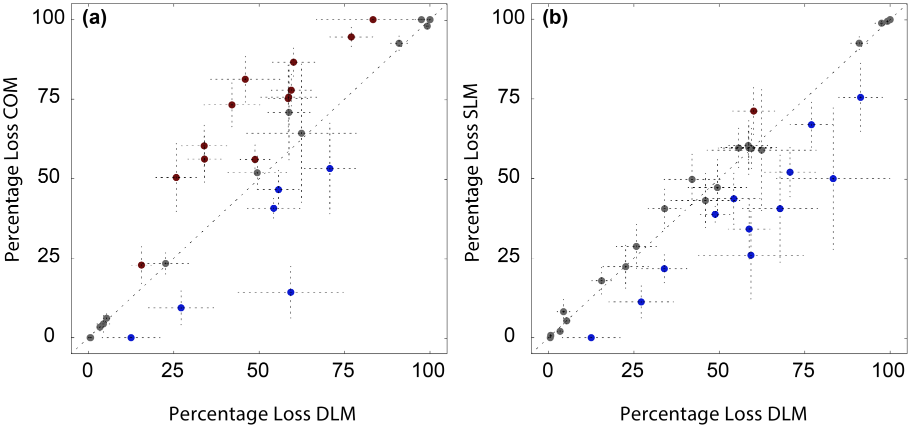

FIG. 5.3: **Comparison of percentage loss projections between model types for BENELUX 2000–2050.** (a) Climate-only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. (a) N = 36, (b) N = 38. Results are averaged across resolution 5 × 5, 10 × 10 and 20 × 20 km) and scenario (BAMBU, SEDG, GRAS), represented by standard error bars (dashed lines). The equal projection line (dashed line 0,0 to 100,100) represents the point at which the two model projections are equal. Red = above the equal projection line, Blue = below the equal projection line, Grey = overlapping the equal projection line.

Model type, period, scenario and resolution at which the modelling occurred significantly influence the probability of range gain (Table 5.1). Only 50% of species were projected to gain any range at all within BENELUX by 2100 (Fig 5.4a,b). The odds of range gain are significantly higher for DLM projections than for COM and SLM ($p < .0001$; Table 5.2). When range gain occurs there is no

Table 5.1: **Effects of SDM variability on the distributional change of bumblebees.**

	BENELUX (20 × 20, 10 × 10 **and** 5 × 5 **km**)					**Europe** (50 × 50 **km**)		
Explanatory variables	**Probability of Loss**	**Percentage Loss**	**Probability of Gain**	**Percentage Gain**	**Centroid Shift (km)**	**Percentage Loss**	**Percentage Gain**	**Centroid Shift (km)**
Single Terms								
Range Size Present Europe	-	**	-	-	-	***	***	***
Model Type (COM, DLM, SLM)	***	***	***	**	-	***	***	***
Period (2000-50, 2050-80)	-	***	***	***	***	***	***	***
Scenario (BAMBU, GRAS, SEDG)	***	***	***	***	***	***	-	***
Resolution (20 × 20, 10 × 10, 5 × 5 km)	-	***	***	_	-			
Two-way Interactions								
Range Size Present × Model Type	-	-	-	-	-	-	-	-
Range Size Present × Period	-	-	-	-	-	-	***	***
Range Size Present × Scenario	-	-	-	-	-	-	-	-
Range Size Present × Resolution	-	-	-	-	-			
Model Type × Period	-	-	***	-	-	-	-	-
Model Type × Scenario	-	-	-	-	-	-	-	-
Model Type × Resolution	-	-	-	-	-			
Period × Scenario	-	***	***	-	-	***	-	***
Period × Resolution	-	-	-	-	-			
Scenario × Resolution	-	-	-	-	-			
Degrees of Freedom	1706	1511	1617	726	1361	853	856	847

p-values: .01 ≤ p ≤ .05 = *, .001 ≤ p ≤ 0.01 = ** and <.001 = *** The most parsimonious models as chosen by Bayesian information criteria (BIC) for the percentage range loss, percentage range gain, and shift in the distributional centroid for 48 bumblebee species at European and BENELUX scales. The significance of each term included in the model is shown. The symbol "–" represents a variable not included in the best model. The random term for all models was '1 | species.' For a detailed version of the table see Supporting Table S5.3.

significant difference between COMs and DLMs, however, both projected significantly higher loss than SLMs (1.4 and 1.2%, $p < .0001$ & .03; Table 5.2). This can be visualized in Fig 5.4a, where variation between species is evenly distributed and clustered at zero and Fig 5.4b, where seven species have a considerably greater range gain under DLMs.

Period and scenario at which the modelling occurred significantly influence the directional shift of the distribution centroid ($p < .001$; Table 5.1). Model type did not significantly affect the projected shift.

5.4.3 The future of bumblebees projected at the European scale

At the European scale with lower spatial resolution (50 × 50 km), SLMs project significantly less range loss than both COMs and DLMs (2.9% and 1.7%; p = <.001 and .02, Table 5.2). Overall, all 48 species are projected to lose at least some

TABLE 5.2: **Pairwise comparisons between model types.**

	BENELUX (20 × 20, 10 × 10 **and** 5 × 5 **km**)					**Europe** (50 × 50 **km**)		
Contrasts	**Probability of Loss (Odds Ratio)**	**Percentage Loss**	**Probability of Gain (Odds Ratio)**	**Percentage Gain**	**Centroid Shift (km)**	**Percentage Loss**	**Percentage Gain**	**Centroid Shift (km)**
COM – DLM	0.13***	1.32***	0.30***	1.17	NA	1.17	1.62***	51.7***
COM – SLM	0.34***	1.32***	0.58*	1.45**	NA	2.91***	1.97***	48.2***
DLM – SLM	2.57**	1	1.93***	1.24*	NA	1.74*	1.21**	-3.5

p-values: .01 ≤ p ≤ .05 = *, .001 ≤ p ≤ .01 = ** and <.001 = *** Showing the fixed effect and the significance of the best models as chosen by Bayesian information criteria BIC. Null hypothesis tested: that the difference between contrasts is equal to 0. Values are averaged over other explanatory variables included in the model (see Table S5.3.)

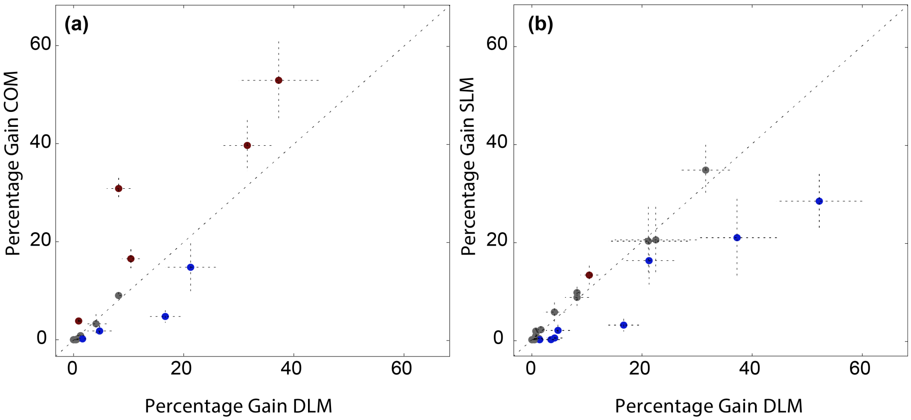

FIG. 5.4: **Comparison of percentage gain projections between model types for BENELUX 2000–2050.** (a) Climate-only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. (a) N = 25, (b) N = 35 bumblebee species in BENELUX for 2000–2050. Results are averaged across resolution (5 × 5, 10 × 10 and 20 × 20 km) and scenario (BAMBU, SEDG, GRAS), represented by standard error bars (dashed lines). The equal projection line (dashed line 0,0 to 70,70) represents the point at which the two model projections are equal. Red = above the equal projection line. Blue = below the equal projection line. Grey = overlapping the equal projection line.

range and the relationships between the different model types shows a strong linear correlation, but with considerable deviation from the assumption of the projections being equal (Fig 5.5a,b). Eighteen species are projected to lose greater range under COMs whilst fourteen species are projected to lose greater range under DLMs (Fig 5.5a). The relationship between DLMs and SLMs is clearer with a higher number of species below the equal protection line than above, which supports the significant effect found in the mixed models (1.21%, $p < .01$; Fig 5.5b and Table 5.1).

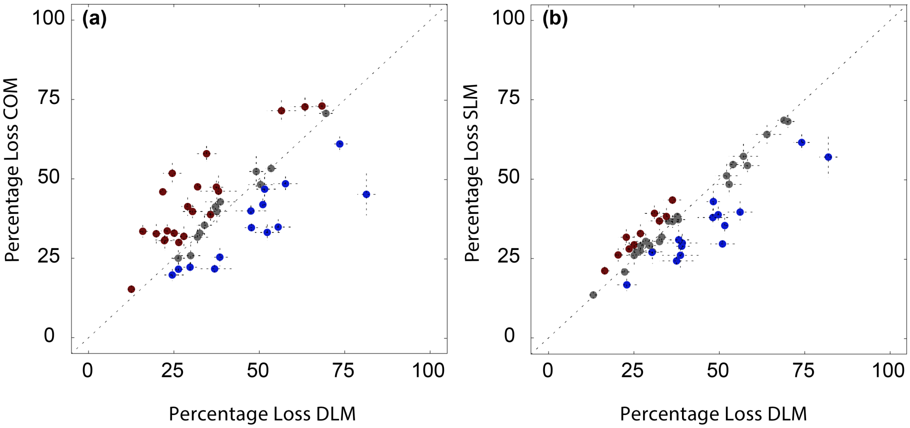

FIG. 5.5: **Comparison of percentage loss projections between model types at European Scale 2000–2050.** (a) Climate-only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. N = 48. 50 × 50 km resolution. Results are averaged across scenario (BAMBU, SEDG, GRAS), represented by standard error bars (dashed lines). The equal projection line (dashed line 0,0 to 100,100) represents the point at which the two model projections are equal. Red = above the equal projection line. Blue = below the equal projection line. Grey = overlapping the equal projection line.

At the European scale greater range gain is projected by COMs than SLMs and DLMs (2% and 1.6%; $p < .001$; Table 5.2). DLMs project greater range gain than SLMs (1.2%, p value = .01; Table 5.2). This relationship is visible in Fig 5.6a with the majority of species considerably above the equal projection line. The same pattern is observed for SLMs and DLMs, with 12 species below the equal projection line. The majority of species only illustrate modest range gain, and the differences between model types are emphasized when range gain is high (Fig 5.6a,b).

Centroid distributional shifts are greater under COMs than SLMs and DLMs (48.2 and 51.7 km; $p < .001$). There is no significant difference in centroid distributional shift between SLMs and DLMs (Fig 5.7).

5.4.4 The role of other explanatory variables in the mixed models

Scenario, period, and resolution are included in the majority of best models. The effect of these explanatory variables is consistent across the different distribution change measures and scales. The more extreme change scenario (GRAS) projects

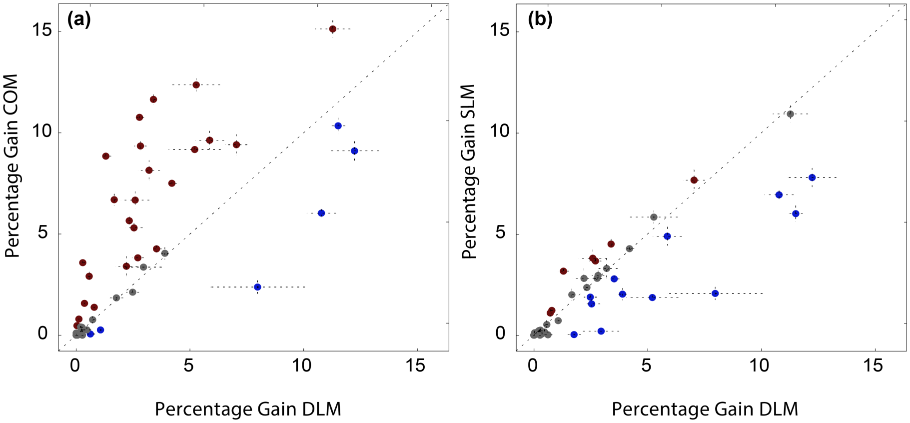

Fig. 5.6: **Comparison of percentage gain projections between model types at European Scale 2000–2050.** (a) Climate-only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. N = 48. 50 × 50 km resolution. Results are averaged across scenario (BAMBU, SEDG, GRAS), represented by standard error bars (dashed lines). The equal projection line (dashed line 0,0 to 15,15) represents the point at which the two model projections are equal. Red = above the equal projection line. Blue = below the equal projection line. Grey = overlapping the equal projection line.

greater loss and northern shift of the centroid than business as usual (BAMBU) and sustainable scenarios (SEDG). The probability of range gain is lowest under the GRAS scenario and the largest range gain occurs under SEDG. In the period 2000–2050 lower percentage range loss, and lower centroid shift were projected. The SEDG scenario showed a significant interaction with period with range loss and centroid shift much lower for the period 2050–2100. The effect of resolution at the BENELUX scale did not interact significantly with model type, however, overall lower range loss and greater gain occurs at the finer resolutions. Finally, the current size of the distribution was also included in some best models, at the European scale more widespread species lose less and gain more range (for full details of all models see Table S5.3 and Figs. S5.3–S5.10).

5.4.5 Focus on one atypical and one representative species

Bombus argillaceus is atypical compared to the majority of European bumblebees. It is one of only two species projected to increase in range under climate change. At the 5 × 5 km resolution *B. argillaceus* increases in range and latitude under all model types and scenarios. The projected range gain percentage is

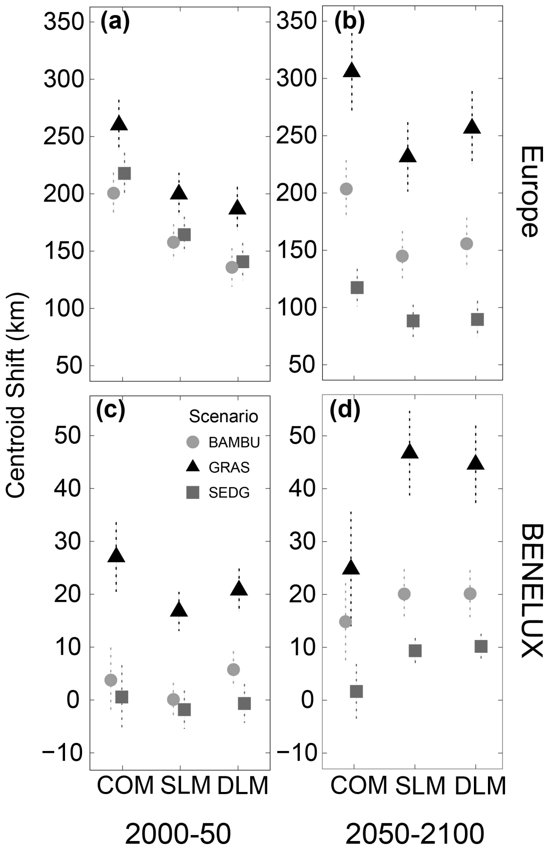

FIG. 5.7: **Mean and standard error of directional shift of species distribution centroid.** For Climate-only Models (COM), Dynamic Land Use Models (DLM) and Static Land Use Models (SLM) at Europe at 2050 (a) and 2100 (b) and BENELUX at 2050 (c) and 2100 (d) for three change scenarios (BAMBU, GRAS, SEDG).

larger for COMs (BAMBU: 16%, GRAS: 42%, SEDG: 14%; Fig 5.8a–c) than DLMs (9%, 34%, 7%; Fig 5.8d–f) or SLMs (10%, 36%, 10%; Fig 5.8g–i). At the BENELUX scale only new areas of habitat suitability are projected. At the European scale we observe that *B. argillaceus* is one of the few species to significantly increase in range. This range gain is much less under SLMs and DLMs than COMs. Under COMs *B. argillaceus* is projected to gain considerable range in the West and East of Europe (Fig 5.9). A large amount of the projected range loss is in areas with novel climatic conditions, making the predictions unreliable.

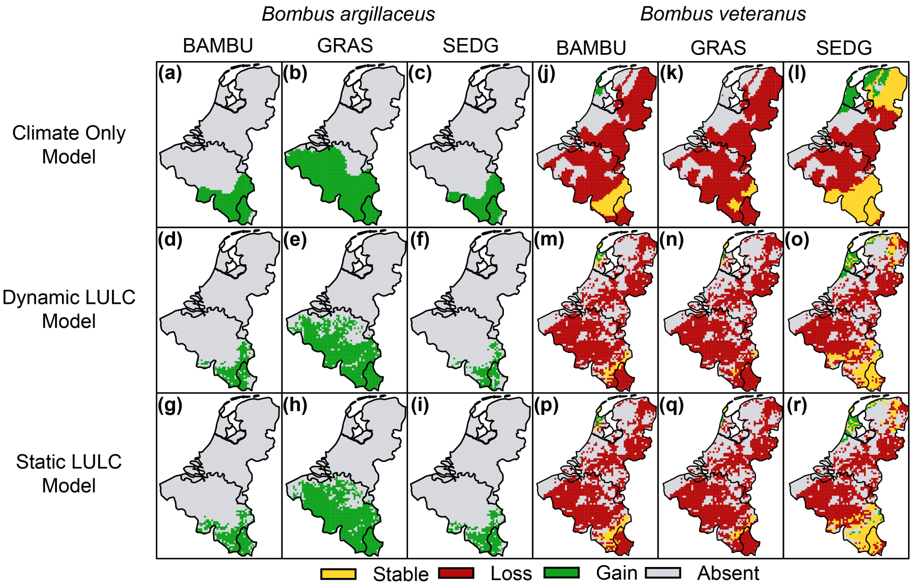

FIG. 5.8: **BENELUX maps showing** 5 × 5 **km resolution of change in habitat suitability between 2000 and 2100 for two species,** ***Bombus argillaceus*** **(a–i; atypical) and** ***Bombus veteranus*** **(j–r; representative of many species).** Habitat suitability change is shown for three future change scenarios (BAMBU, GRAS, and SEDG) and for three model types (Climate-only [a–c, j–l], Dynamic LULC [d–f, m–o], and Static LULC [g–i, p–r]). Yellow: cells that have remained as suitable habitat; Red: cells that were suitable in 2000 but unsuitable in 2100; Green: cells that were unsuitable in 2000 but suitable in 2100; Grey: cells that were never projected as suitable habitat.

Bombus veteranus is one of the numerous European bumblebee species projected to lose a large part of its suitable habitat under climate change; it is therefore representative of the majority of bumblebees in Europe. *Bombus veteranus* under BAMBU and GRAS is expected to lose almost its entire suitable habitat in BENELUX. The species is not projected to go extinct at 5 × 5 km resolution, but projections of the GRAS scenario show only a tiny pocket of remaining suitable habitat in South-east Belgium (Fig 5.8k,n,q). Significant gain is only projected under SEDG for COMs (25%; Fig 5.8l). At the European scale *B. veteranus* loses more range under COMs (54%, 67%, 38%; Fig 5.9j–l) than SLMs (32%, 50%, 19%; Figure 5.9p–r) and DLMs (40%, 55%, 26%; Fig 5.9m–o). *Bombus veteranus* is projected to expand into Northern Europe, further under COMs. Overall SLMs project more persistence in the landscape but less Northern shift. Finally, the centroid of the distribution of *B. veteranus* is projected to shift further North overall under DLMs than SLMs (BAMBU: +95 km, GRAS: +68 km SEDG: +98

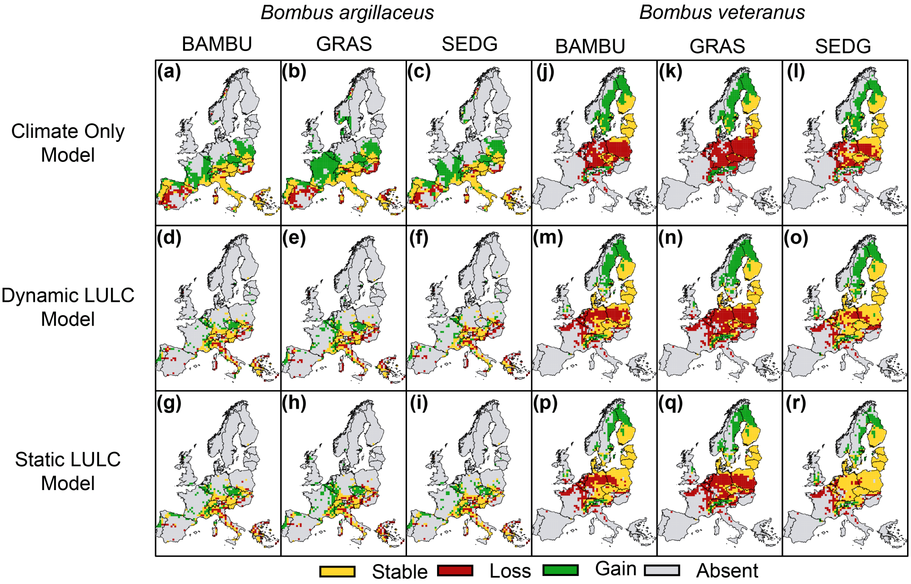

Fig. 5.9: **European maps showing** 50 × 50 **km resolution of change in habitat suitability between 2000 and 2100 for two species, *Bombus argillaceus* (a–i; atypical) and *Bombus veteranus* (j–r; representative of many species).** Habitat suitability change is shown for three future change scenarios (BAMBU, GRAS, and SEDG) and for three model types (Climate-only [a–c, j–l], Dynamic LULC [d–f, m–o], and Static LULC [g–i, p–r]). Yellow: cells that have remained as suitable habitat; Red: cells that were suitable in 2000 but unsuitable in 2100; Green: cells that were unsuitable in 2000 but suitable in 2100; Grey: cells that were never projected as suitable habitat.

km, Fig 5.9m–r).

5.5 Discussion

This study shows that incorporating dynamic LULC change scenarios, even those with low precision and few classes, can have significant effects on the projected distributions of bumblebee species. Species can only occur in a location at any time when a series of critical conditions are met, including both suitable climate and land use and land cover types that allow them to feed, grow, survive and reproduce. Therefore, it is surprising that the use of climate change projections is commonplace, whereas LULC change projections are rarely used in species forecasting (Titeux et al. 2016). We tested the effect of dynamic LULC variables on projecting future distribution changes for 48 European *Bombus* species in 2050 and 2100. *Bombus* being a genus for which change in major land use classes has affected historical distribution patterns (Aguirre-Gutiérrez et al. 2015; Senapathi et al. 2015).

5.5.1 Models including LULC compared to climate-only models

All models improved in fit (AUC) when adding LULC covariates. However, this refers to goodness-of-fit and does not necessarily mean greater predictive ability (Thuiller et al. 2004). A number of species are influenced by LULC covariates, in particular the percentage cover of arable land and forest. The results support research showing that using only climate covariates may over-represent the species range in the present (Luoto et al. 2007; Sohl 2014; Stanton et al. 2012). This is likely to misrepresent species range change as well as the shift of species range limits. The importance of LULC change is dependent on whether habitat requirements, namely nesting and feeding resources (Busch, 2006), can be adequately captured by the relationship between these six land use covariates and the climate change covariates. Therefore, we saw variation for bumblebees as they differ significantly in their landscape requirements (Goulson et al. 2010; Persson et al. 2015). A result unique to our study is that COMs (at the European scale) projected greater range loss and lower range gain than when land use covariates were included. This is in part due to greater range size in the present under COMs. However, there were also examples of areas that became suitable for certain bumblebees with the introduction of LULC covariates. These results suggest that for some species including LULC covariates, projects, on average, a wider bioclimatic envelope and is more likely to project persistence in the landscape. In other words LULC covariates, provide a habitat filter over the climate prediction. However, we did not observe the same pattern for all species, and there were species, which showed greater loss and gain with dynamic land use covariates. Overall, the relationship was highly variable (see Figs. S5.7–S5.10). This inconsistent relationship indicates that dynamic LULC model predictions are not simply a level up or down from climate-only models. Additionally, the introduction of LULC covariates projected an inability of most bumblebees to completely track Northern climate shifts, particularly into Scandinavia, supporting historical patterns (Kerr et al. 2015).

5.5.2 Models including dynamic LULC compared to static LULC models

Including static LULC change in SDMs is based on the incorrect assumption that LULC will not change in the future or that this change is negligible in comparison to climate change (Stanton et al. 2012). In this study, loss and gain of suitable habitat was more likely with dynamic LULC covariates. The distribution patterns of DLMs represent more variable suitable habitat conditions in time than SLMs under equivalent climate change, resulting in greater projected range loss and gain. However, this pattern varied between species and was more discernible for some over others. This variability is supported by other studies; including dynamic LULC covariates previously led to more accurate model predictions for invasive bullfrogs (Ficetola et al. 2010) and central European plants (Chytrý et al. 2012), but not so for a European butterfly species (Martin et al. 2013). Our multi-species study indicates that a number species show projected distribution changes under different model types, however, some do not show any. This, in and of itself, is not surprising as species differ in their dependency on specific characteristics of climate and land use. Therefore, including dynamic LULC covariates, even at coarse thematic resolution, can significantly alter the projected distributional changes of certain species.

5.5.3 Inclusion of LULC in models for individual species distribution projections

We focused on the projections of two species, *B. argillaceus* was atypical compared to the majority of species, demonstrating range. The results suggest that dynamic LULC limits the availability of suitable habitat in the North. Overall, this illustrates the necessity of dynamic LULC in prospective SDMs, and that change in major land use classes such as grassland and urban affect observed species range change under climate change. *Bombus veteranus* is representative of the patterns observed for many species. Climate drove the distribution but

LULC models projected extra areas of suitable habitat, which were rarely continuous and perhaps indicative of real world patterns. Fragmented suitable habitat increases the probability of losing local populations and decreases the probability of establishing new populations, both of which severely affect a species' tracking of global change.

5.5.4 LULC-inclusive models for forecasting and guiding conservation efforts

The importance of including LULC projections depends on the goals and desired outcomes of the modelling process. As a tool, SDMs explore unknown areas and periods where conditions may be suitable for species occurrence, observe the role of environmental covariates and influence conservation management (Franklin 2010). However, due to limitations in data availability and modelling methods their value to conservation and ability to predict occurrence should not be overestimated (Lobo 2016), particularly in the case of undersampled and geographically and taxonomically restricted insect data (De Palma et al. 2016). Regarding covariate influence, we observe that for at least some species dynamic LULC covariates significantly affect projected distributions. Regarding conservation management, variation between model types, model performance and projected distributions suggests that using DLMs to inform conservation practices would be suitable at the broad scale. The absence of dynamic LULC covariates could lead to significantly underfitted potential distributions for specific landscapes or species with implications for management. (Franklin 2013; Porfirio et al. 2014; Wright et al. 2015). Overall, species and purpose-specific approaches to covariate selection should be preferred.

5.5.5 The generation of dynamic LULC scenarios deserves more attention

The observed patterns strongly support the case for more detailed LULC change scenarios. This supports the conclusions of similar studies (Barbet-Massin et al. 2012b; Martin et al. 2013). The scenarios presented here intend to provide a platform on which to relate species conservation to socio-economic factors and policy decisions, they also aim to make it possible to assess which improvements at landscape level are needed to improve species persistence (Van Vuuren et al. 2011). However, it is likely that the LULC change maps produced by these scenarios will become superseded by updated, more detailed LULC change scenarios, linked to new climate change models. Finer resolution and more detailed classes would greatly improve LULC projections (Busch, 2006; Verburg et al. 2009). In the case of bumblebees, we know that to model wild bee species adequately we need ecologically relevant LULC covariates that represent local management (Aguirre-Gutiérrez et al. 2015; Marshall et al. 2015; Scheper et al. 2015). New scenarios should emphasize a relevance to biodiversity and land use management, for example, separating between natural-grassland and agricultural-grassland, and intensive and less intensive farming systems. While the incidence of and change in forest and arable land cover correlates with habitat suitability, this is an indirect effect. The coarseness of these classifications does not provide an adequate foundation to extract causal information or infer on the importance of land use management (Thuiller et al. 2004). Moreover, national and international policies, such as the CAP in Europe, tend not to change land cover per se (grassland remains grassland), but the management level and thus biodiversity value. For example, arable land cover is the most important LULC covariate for the majority of bumblebees as defined by the correlative variable importance values (see Table S5.1). However, the ecological significance of this importance could relate to agricultural intensification, pesticide use, availability of floral resources, or most likely, a combination of these factors.

5.5.6 Differences between the data sources

Among the 48 bumblebees modelled there are examples of polytypic species representing significant intraspecific variation (Rasmont 1983). For example, SDMs at subspecies level for *B. terrestris* performed differently from aggregated models with all subspecies as a single unit (Lecocq et al. 2016). We did not utilize this variation; we modelled the habitat requirements of each species using all available records. Occurrence points were selected to represent the highest resolution possible to model at 5 × 5 km resolution, and many points were removed. However, due to the nature of the data and the multitude of sources it is still likely that some point records were not accurately recorded, though we expect this number to be minimal (Duputié et al. 2014).

There were distinctions between the resolution of the climate and land use sources in the past and in the future. Due to the coarse nature of Atmosphere-Ocean General Circulation Models (AOGCMs) used to calculate the climate-change covariates they do not represent accurately fine scale effects (Fronzek et al. 2012). This means at the 10 × 10 and 5 × 5 km resolutions that fine-scale topographic effects of climate may be lost. This may result in a more homogeneous representation of climate at these resolutions, which may over-represent range size and connectivity. However, this is representative of climate data often used in studies of this type to model in the future, and in general climate is more homogeneous than land use, particularly at the BENELUX scale. To understand in detail the climate effects on biodiversity, fine scale climate change projections are required. The land-use change maps were downscaled to match the availability of current LULC data at European scale. However, the downscaling algorithm is likely to produce some clustering for the future LULC covariates (Dendoncker et al. 2006). Therefore, we focused on percentage cover covariates and it was not possible to include covariates of connectivity and edge effects, as they would not be comparable to present conditions. Furthermore, the land-use change models were created in congruence with climate variables; this means that present and future comparisons are valid at the different modelled resolutions (Rounsevell et al. 2006).

Finally, there are many methods for SDM and changes to the modelling algorithms, covariates and resolutions can affect the results (Aguirre-Gutierrez et al. 2013; Warren & Seifert 2011). We chose to use simplified algorithms in an ensemble modelling approach to account for this variation (Thuiller 2014a).

5.6 Concluding Remarks

This work represents a detailed analysis of the effect of dynamic LULC scenarios at different scales on the projected distributions of multiple species. We show species dependent responses to the effect of dynamic LULC, which demonstrates that these types of scenarios can play a significant role in projecting species distributions under climate change. Climate variables alone, whilst driving habitat suitability, are unlikely to project accurately the detailed distribution patterns of all species. Therefore, we advocate repeated use and testing of these available scenarios with multiple species. However, new scenarios and projections of LULC change at finer spatial and thematic resolutions that indicate management practices will be necessary to better assess biodiversity change in an uncertain future.

5.7 Acknowledgements

We acknowledge funding from the BELSPO (BELSPO; BR/132/A1/BELBEES). We specifically thank Leopoldo Castro, Centre Suisse de Cartographie de la Faune (CSCF/SZKF), Björn Cederberg, Gilles Mahé, Aulo Manino, for providing data and we thank all others who provided their data in the context of the STEP Project (`www.step-project.net`). We also thank Steve Donovan for his help in proofreading the manuscript. Finally, we thank the two anonymous reviewers who provided valuable comments and insights on a previous version of the manuscript.

5.8 Supporting Information

Tables

Table S5.1: **Average variable importance values across all resolutions for forty-eight bumblebee species.** Focus species highlighted gray.

Species	Arable	Rainfall Wettest Month	Forest	Growing Degree Days	Grassland	Diurnal Range	Permanent Crops	Annual Temp Range	Urban	Water Balance
Bombus alpinus	0.07	0.02	0.05	0.91	0.03	0.01	0	0.01	0.02	0.07
Bombus argillaceus	0.06	0.68	0.07	0.06	0.17	0.06	0.05	0.34	0.06	0.23
Bombus balteatus	0.06	0.02	0.01	0.84	0.01	0.02	0.01	0.07	0.01	0.01
Bombus barbutellus	0.05	0.32	0.07	0.37	0.02	0.05	0	0.43	0.05	0.7
Bombus bohemicus	0.02	0.01	0.04	0.73	0.02	0.06	0	0.23	0.04	0.05
Bombus campestris	0.07	0.1	0.04	0.43	0.04	0.02	0	0.11	0.07	0.22
Bombus cingulatus	0.1	0.11	0.02	0.5	0.01	0.01	0.01	0.46	0	0.06
Bombus confusus	0.05	0.22	0.05	0.23	0.05	0.16	0.01	0.27	0.04	0.25
Bombus consobrinus	0.1	0.13	0.1	0.83	0.02	0.15	0.02	0.23	0.02	0.15
Bombus cryptarum	0.05	0.19	0.15	0.37	0.22	0.15	0.04	0.22	0.02	0.07
Bombus cullumanus	0.03	0.15	0.04	0.14	0.04	0.38	0.14	0.55	0.02	0.77
Bombus distinguendus	0.05	0.03	0.05	0.74	0.04	0.07	0.02	0.03	0.03	0.07
Bombus flavidus	0.12	0.02	0.01	0.69	0.01	0.01	0	0.19	0.01	0.03
Bombus gerstaeckeri	0.21	0.78	0.05	0.18	0.12	0.03	0.01	0.09	0.02	0.22
Bombus hortorum	0.02	0.02	0.01	0.24	0.03	0.08	0	0.59	0.04	0.05
Bombus humilis	0.01	0.39	0.04	0.3	0.01	0.02	0	0.12	0.02	0.79
Bombus hyperboreus	0.09	0.23	0.01	0.97	0.03	0.02	0	0.02	0.1	0.04
Bombus hypnorum	0.1	0.01	0.2	0.22	0.01	0.06	0.01	0.51	0.17	0.18
Bombus jonellus	0.08	0.02	0.01	0.43	0.01	0.01	0.01	0.16	0	0.05
Bombus lapidarius	0.02	0.02	0.01	0.36	0.01	0.03	0	0.17	0.05	0.19
Bombus lapponicus	0.02	0.05	0.04	0.87	0.04	0.05	0.01	0.07	0.03	0.09
Bombus lucorum	0.02	0.09	0.03	0.48	0.01	0.12	0	0.44	0.06	0.05
Bombus magnus	0.12	0.07	0.03	0.23	0.04	0.1	0.03	0.68	0.02	0.44
Bombus mendax	0.21	0.76	0.14	0.21	0.1	0.02	0.02	0.16	0.05	0.19
Bombus mesomelas	0.08	0.66	0.11	0.19	0.13	0.01	0.02	0.26	0.02	0.25
Bombus monticola	0.09	0.57	0.1	0.38	0.03	0.2	0.01	0.34	0.01	0.19
Bombus mucidus	0.18	0.78	0.07	0.13	0.09	0.01	0.01	0.19	0.02	0.23
Bombus muscorum	0.06	0.03	0.27	0.4	0.02	0.06	0	0.25	0.01	0.15
Bombus norvegicus	0.02	0.02	0.09	0.39	0.02	0.01	0.02	0.45	0.13	0.02
Bombus pascuorum	0.04	0.01	0.08	0.22	0.04	0.17	0	0.49	0.11	0.11
Bombus polaris	0.05	0.2	0.01	0.86	0.03	0.01	0	0.05	0.01	0.11
Bombus pomorum	0.09	0.36	0.13	0.32	0.02	0.03	0.01	0.18	0.02	0.68
Bombus pratorum	0.14	0.03	0.17	0.3	0.12	0.15	0.01	0.46	0.18	0.19
Bombus pyrenaeus	0.19	0.87	0.06	0.32	0.05	0.08	0.02	0.12	0.02	0.29
Bombus quadricolor	0.14	0.26	0.04	0.65	0.06	0.02	0	0.49	0.01	0.19
Bombus ruderarius	0.04	0.24	0.04	0.45	0.03	0.04	0	0.11	0.02	0.59
Bombus ruderatus	0.04	0.21	0.02	0.12	0.01	0.01	0	0.11	0.01	0.89
Bombus rupestris	0.05	0.25	0.02	0.41	0.01	0.01	0.01	0.2	0.04	0.74
Bombus sichelii	0.07	0.76	0.1	0.35	0.09	0.07	0.03	0.16	0.02	0.27
Bombus soroeensis	0.11	0.33	0.03	0.51	0.1	0.01	0	0.25	0	0.1
Bombus sporadicus	0.04	0.02	0.01	0.43	0.02	0.04	0.01	0.53	0	0.01
Bombus subterraneus	0.02	0.26	0.03	0.34	0.02	0.09	0.01	0.31	0.01	0.8
Bombus sylvarum	0.1	0.21	0.03	0.25	0.02	0.01	0	0.1	0.02	0.66
Bombus sylvestris	0.02	0.01	0.07	0.4	0.01	0.04	0	0.25	0.1	0.19
Bombus terrestris	0	0.02	0.04	0.26	0.01	0.05	0	0.24	0.04	0.09
Bombus vestalis	0.04	0.01	0.01	0.43	0.03	0.01	0	0.14	0.04	0.09
Bombus veteranus	0.04	0.11	0.02	0.54	0.07	0.12	0.05	0.42	0.01	0.18
Bombus wurflenii	0	0.69	0.04	0.58	0.01	0.02	0	0.26	0.01	0.17

Table S5.2: **Climate covariate selection** All available climate variables and those selected for the modelling process.

Climate Variable	Final Model
Annual Mean Temperature	No
Average Annual Precipitation	No
Max Temperature Coldest Month	No
Max Temperature Warmest Month	No
Mean Diurnal Range	**Yes**
Mean Precipitation Driest Month	No
Mean Precipitation Wettest Month	**Yes**
Mean Temperature Coldest Month	No
Mean Temperature Warmest Month	No
Min Temperature Coldest Month	No
Min Temperature Warmest Month	No
Temperature Annual Range	**Yes**
Total Annual Growing Degree Days (>5°c)	**Yes**
Water Balance - Year Sum (Mean monthly precipitation - monthly PET)	**Yes**

Table S5.3: **Detailed Effects of SDM variability on the Distributional Change of Bumblebees.**The most parsimonious models as chosen by Bayesian information criteria (BIC) for the percentage range loss, percentage range gain, and shift in the distributional centroid for forty-eight bumblebee species at European and BENELUX scales. The random term for all models was '1 | species.' p-values: .01 ≤ p ≤ .05 = *, .001 ≤ p ≤ .01 = ** and <.001 = ***.

Percentage Loss EUROPE					
	Estimate	Std. Error	DF	t value	P(>|t|)
Intercept	50	2.59	144	19.29	<0.001 ***
Current Range Size EU	-0.47	0.06	412	-7.98	<0.001 ***
Model Type (DLM)	-1.17	0.68	823	-1.71	0.087
Model Type (SLM)	-2.91	0.68	824	-4.26	<0.001 ***
Scenario (GRAS)	6.07	0.96	815	6.34	<0.001 ***
Scenario (SEDG)	0.1	0.96	815	0.1	0.921
Period (2050-2100)	3.48	1.06	863	3.29	0.001 **
GRAS:2050-2100	5.44	1.36	818	4	<0.001 ***
SEDG:2050-2100	-16.68	1.36	815	-12.31	<0.001 ***
Percentage Gain EUROPE (log)					
	Estimate	Std. Error	DF	t value	P(>|t|)

Table S5.3 continued from previous page

Intercept	-2.8	0.42	126	-6.69	<0.001 ***
Current Range Size EU	0.09	0.01	566	9.8	<0.001 ***
Model Type (DLM)	-0.57	0.1	822	-5.51	<0.001 ***
Model Type (SLM)	-0.82	0.1	823	-7.94	<0.001 ***
Period (2050-2100)	0.78	0.17	843	4.66	<0.001 ***
Range Size: 2050-2100	-0.02	0.01	830	-4.15	<0.001 ***

Centroid Distributional Shift EUROPE

	Estimate	Std. Error	df	t value	Pr(>|t|)
Intercept	92.42	25.63	151	3.61	<0.001 ***
Current Range Size EU	3.52	0.62	275	5.68	<0.001 ***
Model Type (DLM)	-51.51	7.79	820	-6.61	<0.001 ***
Model Type (SLM)	-48.25	7.8	821	-6.19	<0.001 ***
Scenario (GRAS)	50.73	10.91	810	4.65	<0.001 ***
Scenario (SEDG)	9.59	10.91	810	0.88	0.379
Period (2050-2100)	37.59	15.42	832	2.44	0.015*
Range Size: 2050-2100	-0.33	0.41	831	-0.8	0.424
GRAS:2050-2100	41.39	15.56	815	2.66	0.008**
SEDG:2050-2100	-79.5	15.42	810	-5.16	<0.001 ***

Probability of Loss BENELUX (Bernouli)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	6.34	1.97	3.22	0.00129**
Model Type (DLM)	2.04	0.3	6.72	<0.001 ***
Model Type (SLM)	1.1	0.26	4.13	<0.001 ***
Scenario (GRAS)	0.72	0.29	2.46	0.0139*
Scenario (SEDG)	-0.54	0.26	-2.06	0.0390*

Percentage Loss BENELUX (log)

	Estimate	Std. Error	DF	t value	Pr(>|t|)
Intercept	4.25	0.27	104	15.6	<0.001 ***
Current Range Size EU	-0.02	0.01	1088	-3.25	0.001**
Model Type (DLM)	-0.28	0.05	1488	-5.41	<0.001 ***
Model Type (SLM)	-0.28	0.05	1488	-5.33	<0.001 ***
Scenario (GRAS)	0.34	0.07	1484	5.01	<0.001 ***
Scenario (SEDG)	-0.12	0.08	1515	-1.45	0.147
Period (2050-2100)	0.49	0.07	1485	6.92	<0.001 ***
Resolution (10km)	-0.33	0.05	1486	-6.63	<0.001 ***
Resolution (5km)	-0.48	0.05	1486	-9.6	<0.001 ***
GRAS:2050-2100	0.24	0.1	1484	2.44	0.015*
SEDG:2050-2100	-0.67	0.1	1485	-6.81	<0.001 ***

Probability of Gain BENELUX (Bernouli)

Table S5.3 continued from previous page

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-2.33	0.65	-3.61	0.538
Model Type (DLM)	1.61	0.29	5.5	<0.001 ***
Model Type (SLM)	0.24	0.28	0.86	0.386
Scenario (GRAS)	-0.83	0.27	-3.08	0.002**
Scenario (SEDG)	0.18	0.27	0.69	0.478
Period (2050-2100)	-2.19	0.4	-5.53	<0.001 ***
Resolution (10km)	1.95	0.22	8.96	<0.001 ***
Resolution (5km)	3.15	0.24	13.13	<0.001 ***
DLM: 2050-2100	-0.82	0.42	-1.96	0.048*
SLM: 2050-2100	0.62	0.41	1.51	0.132
GRAS:2050-2100	-0.52	0.41	-1.26	0.205
SEDG:2050-2100	1.52	0.38	3.97	<0.001 ***

Percentage Gain BENELUX (log)

	Estimate	Std. Error	DF	t value	Pr(>|t|)
Intercept	1	0.3	42	3.33	0.002
Model Type (DLM)	-0.16	0.11	706	-1.48	0.139
Model Type (SLM)	-0.37	0.11	704	-3.45	<0.001 ***
Scenario (GRAS)	0.09	0.11	702	0.81	0.421
Scenario (SEDG)	0.35	0.09	704	3.66	<0.001 ***
Period (2050-2100)	-0.84	0.09	705	-9.84	<0.001 ***

Centroid Distributional Shift BENELUX

	Estimate	Std. Error	DF	t value	Pr(>|t|)
Intercept	2.24	4.9	40	0.46	0.65
Scenario (GRAS)	19.16	2.54	1333	7.54	<0.001 ***
Scenario (SEDG)	-6.79	2.38	1334	-2.85	0.004**
Period (2050-2100)	12.51	2.03	1340	6.15	<0.001 ***

Figures

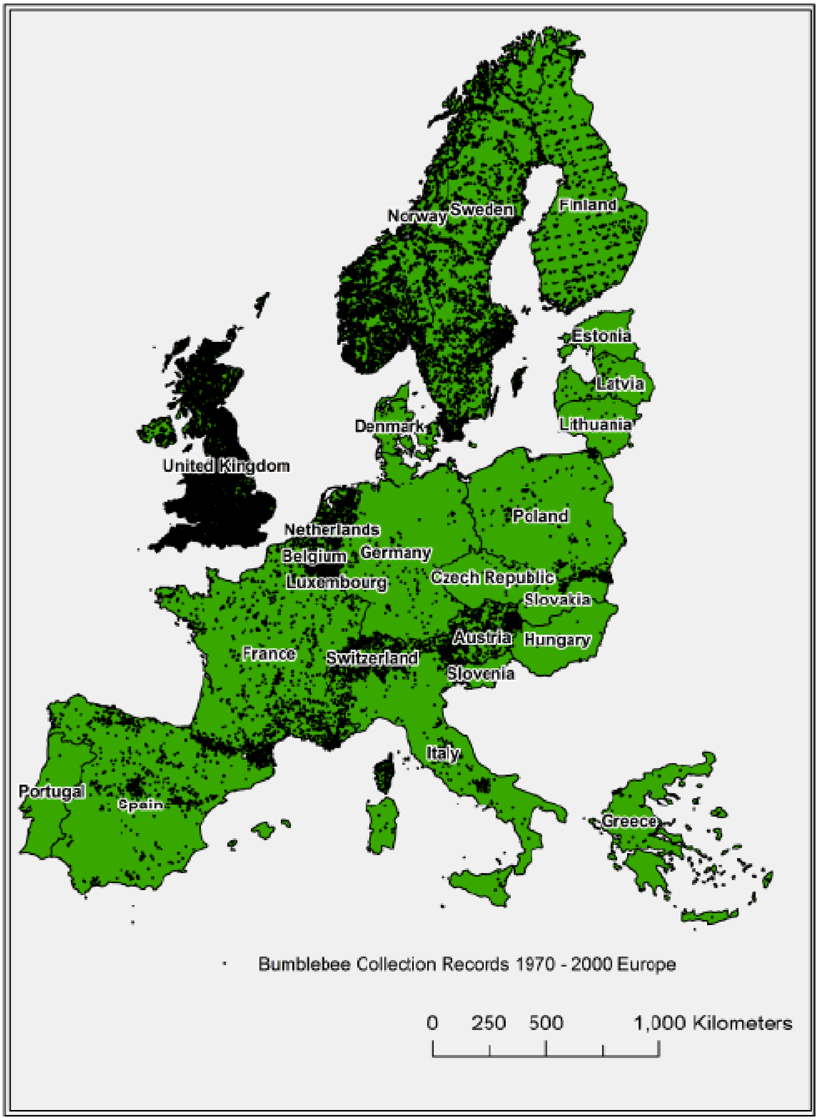

Fig. S5.1: **Extent of study area and Bumblebee collections (1970-2000).**

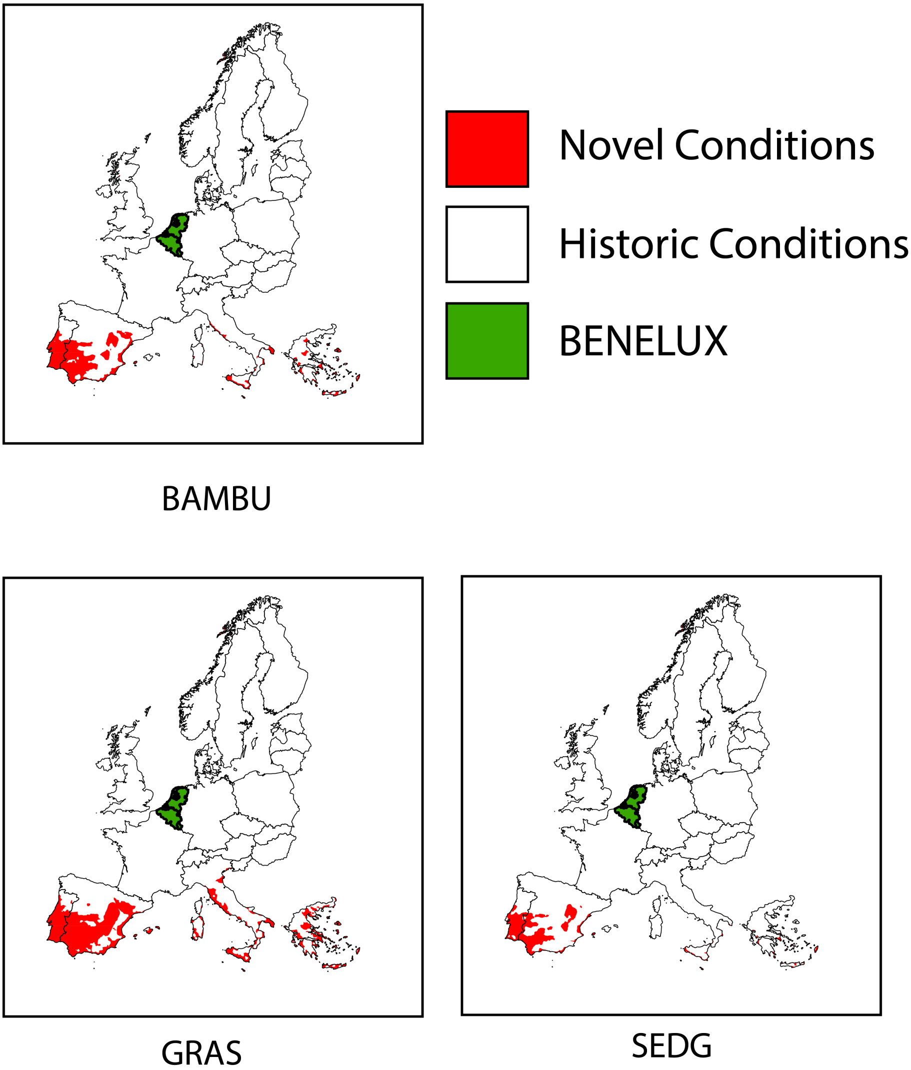

FIG. S5.2: **Novel climatic conditions present in 2100 that did not occur in Europe in 2000 for the 3 change scenarios (GRAS, BAMBU, SEDG).**

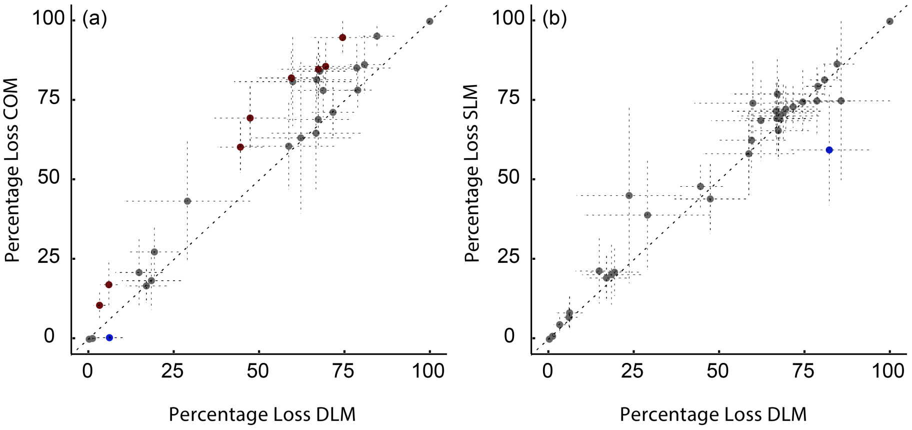

FIG. S5.3: **Comparison of percentage loss projections between model types for BENELUX 2050-2100.** (a) Climate Only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. Results are averaged across resolution (5 × 5, 10 × 10 and 20 × 20 km) and scenario (BAMBU, SEDG, GRAS) and represented by standard error bars (dashed lines). Red = above the no difference line, Blue = below the no difference line, Grey = overlapping the no difference line.

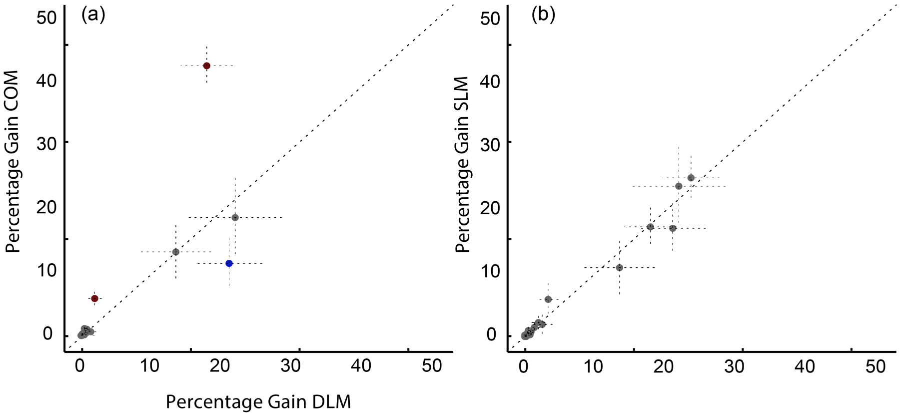

FIG. S5.4: **Comparison of percentage gain projections between model types for BENELUX 2050-2100.** (a) Climate Only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. Results are averaged across resolution (5 × 5, 10 × 10 and 20 × 20 km) and scenario (BAMBU, SEDG, GRAS) and represented by standard error bars (dashed lines). Red = above the no difference line, Blue = below the no difference line, Grey = overlapping the no difference line.

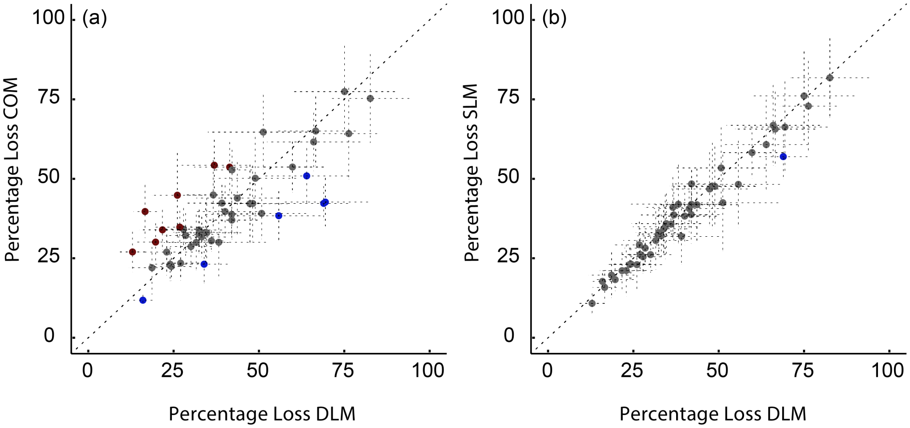

Fig. S5.5: **Comparison of percentage loss projections between model types for Europe 2050-2100.** (a) Climate Only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. Results are averaged across scenario (BAMBU, SEDG, GRAS) and represented by standard error bars (dashed lines). Red = above the no difference line, Blue = below the no difference line, Grey = overlapping the no difference line.

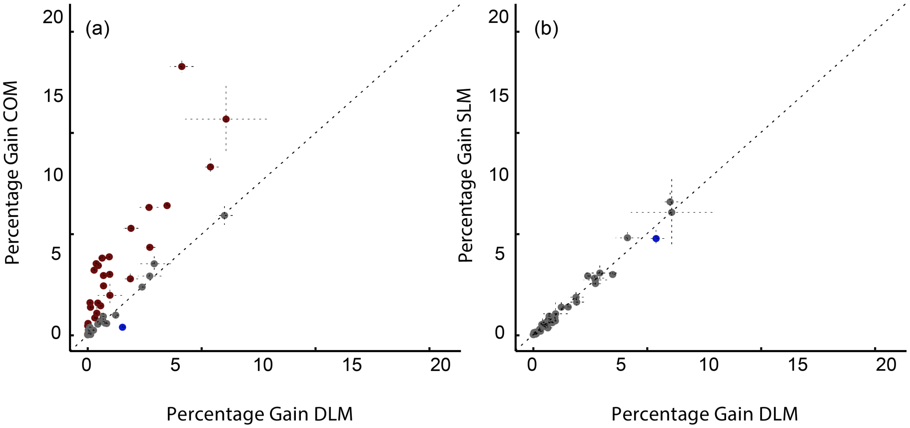

Fig. S5.6: **Comparison of percentage gain projections between model types for Europe 2050-2100.** (a) Climate Only Models (COM) and Dynamic Land Use Models (DLM) and (b) Static Land Use Models (SLM) and DLM. Results are averaged across scenario (BAMBU, SEDG, GRAS) and represented by standard error bars (dashed lines). Red = above the no difference line, Blue = below the no difference line, Grey = overlapping the no difference line.

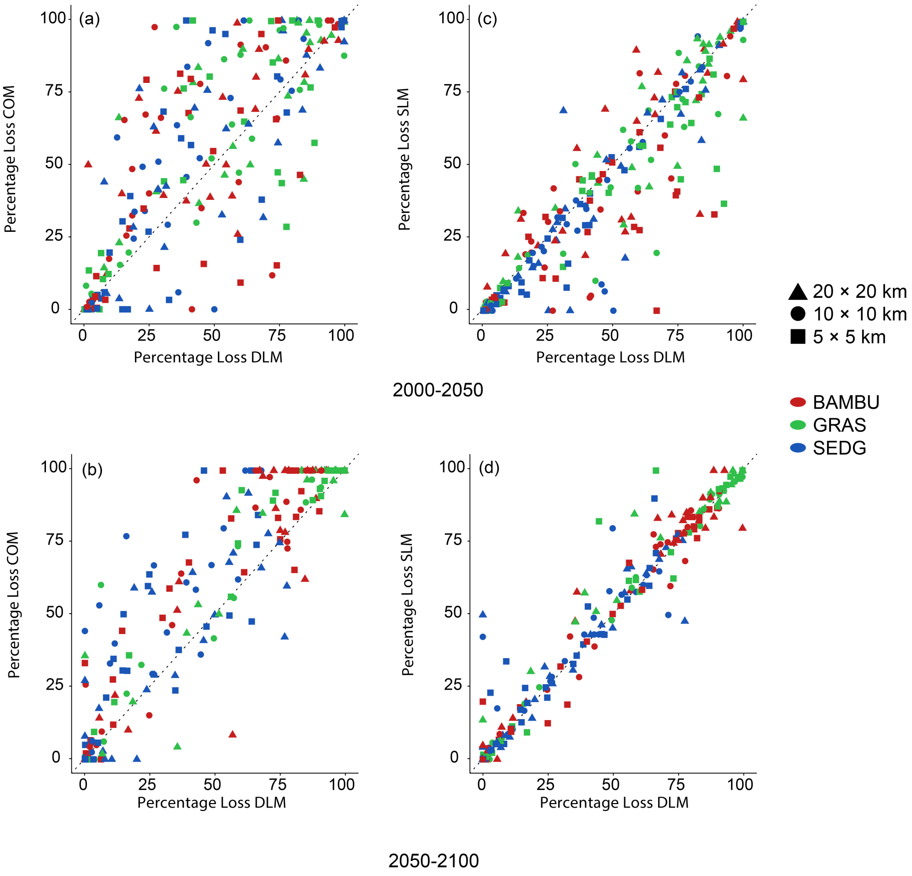

FIG. S5.7: **Comparison of percentage loss projections between model types for BENELUX.** Climate Only Models (COM) vs. Dynamic Land Use Models (DLM) for 2000-2050 (a) and 2050-2100 (b). Static Land Use Models (SLM) vs. DLM for 2000-50 (c) and 2050-2100 (d). Colours represent change scenarios (BAMBU, SEDG, GRAS) and shapes represent resolution (5 × 5, 10 × 10 and 20 × 20 km).

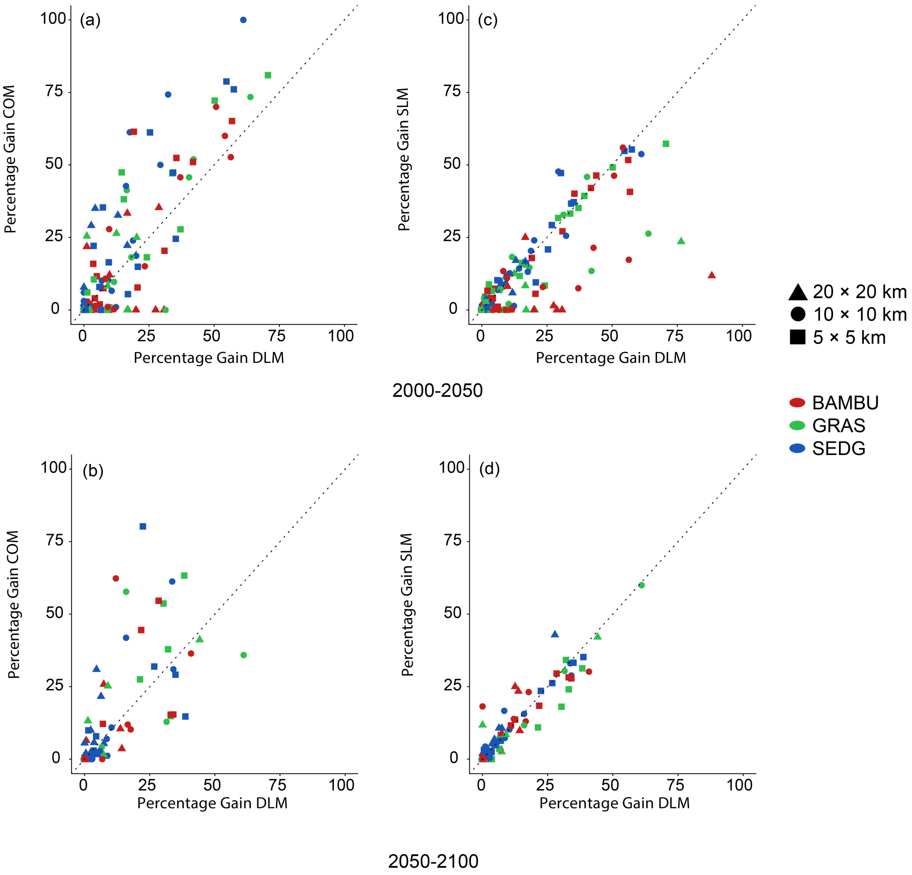

FIG. S5.8: **Comparison of percentage gain projections between model types for BENELUX.** Climate Only Models (COM) vs. Dynamic Land Use Models (DLM) for 2000-2050 (a) and 2050-2100 (b). Static Land Use Models (SLM) vs. DLM for 2000-50 (c) and 2050-2100 (d). Colours represent change scenarios (BAMBU, SEDG, GRAS) and shapes represent resolution (5 × 5, 10 × 10 and 20 × 20 km).

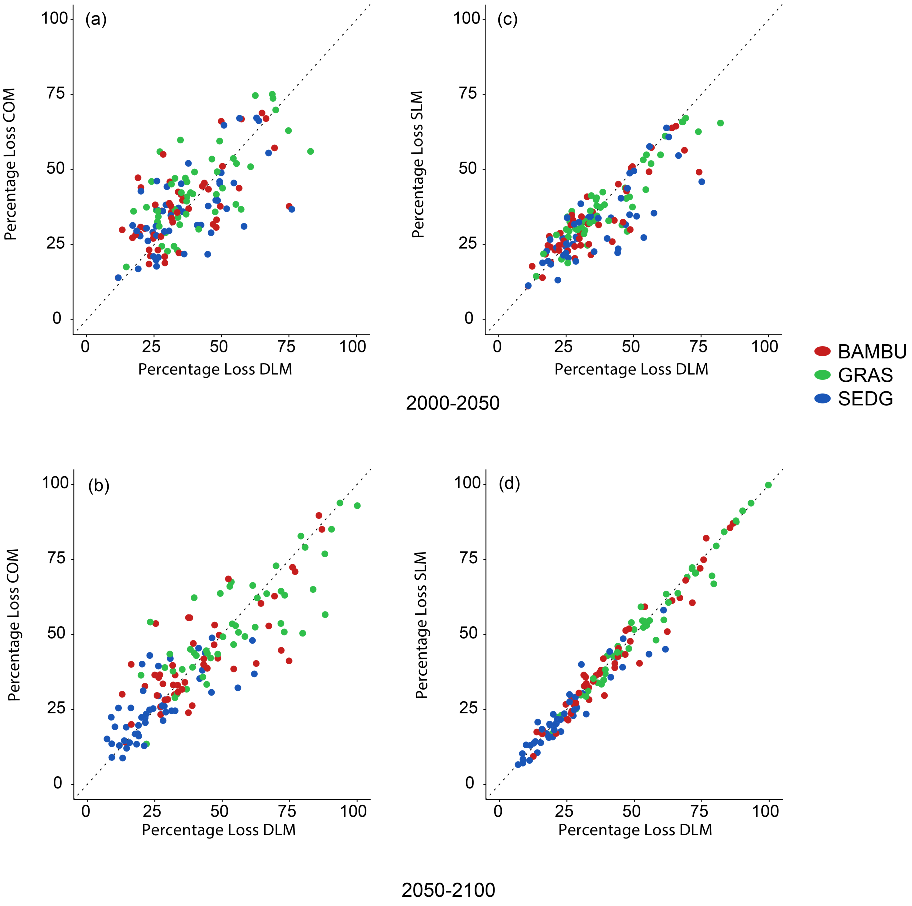

FIG. S5.9: **Comparison of percentage loss projections between model types for Europe.** Climate Only Models (COM) vs. Dynamic Land Use Models (DLM) for 2000-2050 (a) and 2050-2100 (b). Static Land Use Models (SLM) vs. DLM for 2000-50 (c) and 2050-2100(d). Colours represent change scenarios (BAMBU, SEDG, GRAS).

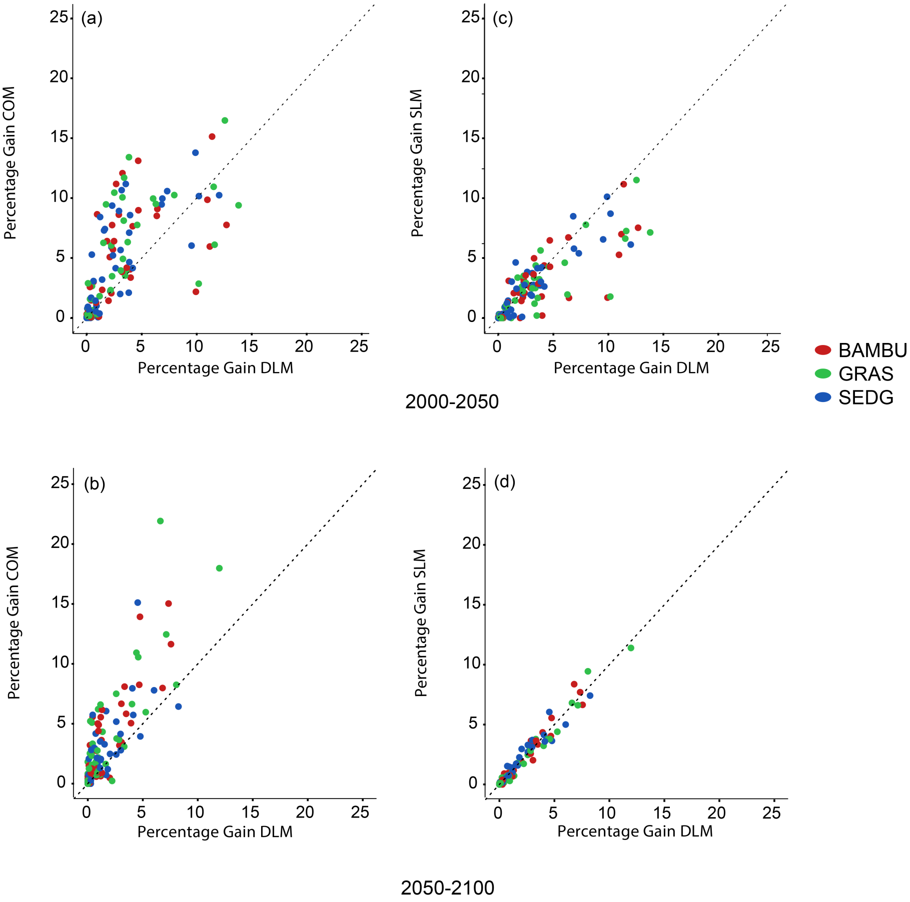

FIG. S5.10: **Comparison of percentage gain projections between model types for Europe.** Climate Only Models (COM) vs. Dynamic Land Use Models (DLM) for 2000-2050 (a) and 2050-2100 (b). Static Land Use Models (SLM) vs. DLM for 2000-50 (c) and 2050-2100(d). Colours represent change scenarios (BAMBU, SEDG, GRAS).

6 Pyrenees' bumblebees and butterflies shift in elevation over 115 years of climate and land use changes

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6.1 Abstract

Under climate change species are expected shift their geographic ranges polewards and to higher elevations. To quantify ongoing climate change effects long-term surveys of biodiversity are necessary. Few studies have looked at how species distribution within a community have shifted periods over a hundred years. In this study we compare the distribution of a plant-pollinator community 115 years apart. In 1889 Professor Julius MacLeod recorded the plant and plant visitors of Gavarnie-Gèdre, a commune in the Hautes-Pyrénées in the South France. In 2005-06 the same areas and plant communities were resampled, this time with a focus on the visitor community. Here we present the overall patterns and changes observed for the distribution of the bumblebee, day-flying Lepidoptera and plant community sampled in 1889 and in 2005-06. The composition of the community shows relative stability in species richness and many of the pollinator's and plants observed in both periods were found within the same interactions in both 1889 (40%) and 2005-06 (30%). We also observed clear shifts to higher elevations for the bumblebee and butterfly visitors and their visited plants. Bumblebees have shifted on average 168m, day-flying Lepidoptera 236m and the visited plants 227m further uphill. The region also shows significant warming in the past 115 years and the modelled historical land use maps suggests a shift in the tree line with an increase in forest at higher elevations. The results allow us to hypothesize that these observed increases in elevation are being driven by these environmental changes. Increases in temperature and loss of habitat may decrease the survival and size of pollinator populations at their range edges. Overall, observed and expected trends suggest that certain rare and/or specialist species may be forced to move even further uphill and potentially face extinction in the near future.

6.2 Introduction

Climate change is expected to increase temperatures globally particularly at high latitudes and elevations (IPCC 2014). Climate change can strongly impact the spatial distribution of biodiversity (Bellard et al. 2012; Pecl et al. 2017); species move polewards increasing in latitude (Bebber et al. 2013; Root et al. 2003; Sagarin et al. 1999), and at the same time species also track climate change by increasing in elevation where possible (Parmesan & Yohe 2003; Pounds et al. 1999; Walther et al. 2002). This leads to an increase in species richness at cooler latitudes and elevations and may result in species which dominate in warmer areas out-competing species from these cooler areas (Warren et al. 2001). Alongside these spatial shifts, species also show temporal shifts to climate change with many species altering their phenology and following the climate by being active earlier in the year (Menzel et al. 2006). The changing climate also interacts with land use/land cover (LULC) changes increasing the impact on biodiversity patterns. Shifts in elevation, in particular, are expected to be more apparent and quicker than shifts in latitude (Parmesan & Yohe 2003). Areas of high elevation often contain rapidly changing climate conditions across small stretches and therefore are easier for species to follow (Chen et al. 2011). Overall expected patterns of range change in high elevation include the extinction of populations at lower elevation and more species colonizing higher elevations. However, in practice, species from lower elevations may not adequately conceal the loss of high elevation species going extinct or shifting even higher, and this may result in the dominance of widespread species at all elevations (Wilson et al. 2007).

Bumblebees, butterflies and day-flying moths (day-flying Lepidoptera) are ideal representative groups to show how species distributions patterns in high-elevation areas have shifted over long time periods of climate and LULC change. Elevation gradients in alpine habitat provide in-situ opportunities to see how species adapt to changing environments (Körner 2007). Insects are likely to show physiological and behavioural responses to the conditions as elevation increases (Hodkinson 2005). Morphologically and physiologically, bumblebees are well adapted to alpine conditions (Dillon & Dudley 2014; Goulson 2010; Peat et al. 2005). Foraging behaviour of bumblebees also varies by elevation; species when foraging in the productive subalpine habitats were found to be more specialized than when foraging in more disturbed montane habitats or in less productive alpine habitats (Miller-Struttmann and Galen 2014). Bumblebees and butterflies, in high elevation habitats, are both known to increase developmental times and maximizing heat retention (Sømme 1989). Certain species of butterfly have dark wings which can be angled towards to the sun to improve heat absorption and are able to initiate flight at lower temperatures (MacLean et al. 2016). These adaptations allow these species to deal with colder temperatures; as temperatures in high-elevation areas increase these adaptations will be less essential to these species and may lead to lower survival rates at previously suitable elevations (Hodkinson 2005). Bumblebees and butterflies are also two groups that show considerable range loss and extinctions when modelled under future scenarios of climate and LULC change (Marshall et al. 2018; Rasmont et al. 2015a; Settele et al. 2008).

Previous studies have compared historical and modern surveys of species distributions in high elevation areas. The majority of studies show an increase in elevation over decades. For example in a 42-year time period moths on Mount Kinabalu, Borneo, shifted in elevation by an average 67m (Chen et al. 2009). Over a 35 year period in the Sierra Nevada Mountains, the majority of butterfly species shifted significantly higher in mean elevation, consistent with the climate warming in the area (Forister et al. 2010). Bird species in Peru shifted 49m in average elevation over a 41 year time period (Forero-Medina et al. 2011). Far greater elevation range change was observed over 35 years in butterflies of the Guadarrama mountains in central Spain, where on average species shifted 293m further up the elevation gradient (Wilson et al. 2007). In contrast in northern Sweden two surveys 60 years apart did not show a clear trend of insect species moving to higher elevations (Franzén and Öckinger 2012).

Many bumblebees, butterflies and moths cannot freely track climate, as they rely on plant species as a food source. Plant species have also shown significant increase in elevation in a number of areas; in Southern California plant species shifted in elevation on average by 65m over a 30 year period (Kelly and Goulden 2008); in western Europe comparing plant species mean elevation over the last 100 years shows an shifted on average by 29m per decade (Lenoir et al.

2008), and in southern Québec, vegetation has moved an average of 9m per decade (Savage and Vellend 2014). Due to the reliance of these insect species on plants you would expect that this interaction will also shift with climate change and that the pollinators will follow their preferred plants uphill. However, loss of spatial occurrence as well as phenological shifts may lead to mismatches in co-occurrence of bees and plants, as observed over 120 years of difference in Illinois (Burkle et al. 2013).

In this study we have the unique opportunity to compare an alpine community of bumblebees, day-flying Lepidoptera and the plants they visit in the Pyrenees, 115 years apart. Not only does this allow for the comparison of distinct groups but also to measure change over a far longer time period than equivalent studies. Specifically we will use observations of plant and plant–visitor communities documented in "De pyreneeënbloemen" made in 1889 (MacLeod 1891), and compare them to surveys conducted in the same areas in 2005-06. Specifically we aim to test three hypotheses: (1) that significant climate and land use changes occurred in the Pyrenees National Park in the last 115 years; (2) that the composition of the bumblebee, butterfly and plant community altered and/or shifted in mean elevation over 115 years; and (3) that bumblebee traits explain their observed elevation patterns and shifts.

6.3 Materials and Methods

6.3.1 Study area

We studied the long-term temporal changes of bumblebees and the plants they visit in the area of the commune Gavarnie-Gèdre in the Hautes-Pyrénées department of France, next to the border with Spain (Fig 6.1). The surveyed area is part of the Pyrenees National Park (est. 1967) located in the western part of the Pyrenees. The elevation in the national park ranges from approximately 1000m a.s.l to its maximum of 3298m a.s.l, the Vignemale Peak. The region straddles the borders of the Atlantic and Mediterranean biogeographic zones and therefore is home to broad and diverse biodiversity with a large quantity of endemic species (Feuillet and Sourp 2011). Whilst protected, the region is still home to settlements and agricultural land, with settlements usually at lower elevations and agricultural areas higher up the mountainside, up to 2000m (Mottet et al. 2006). Broadly, the vegetation of the region can be described as hay meadows and pine forest, with the tree line around 2200m (Crampe et al. 2007). Climatically the areas receives both oceanic and mountain climates with an average annual temperature of approximately 6.5°C and average annual rainfall of 1049mm.

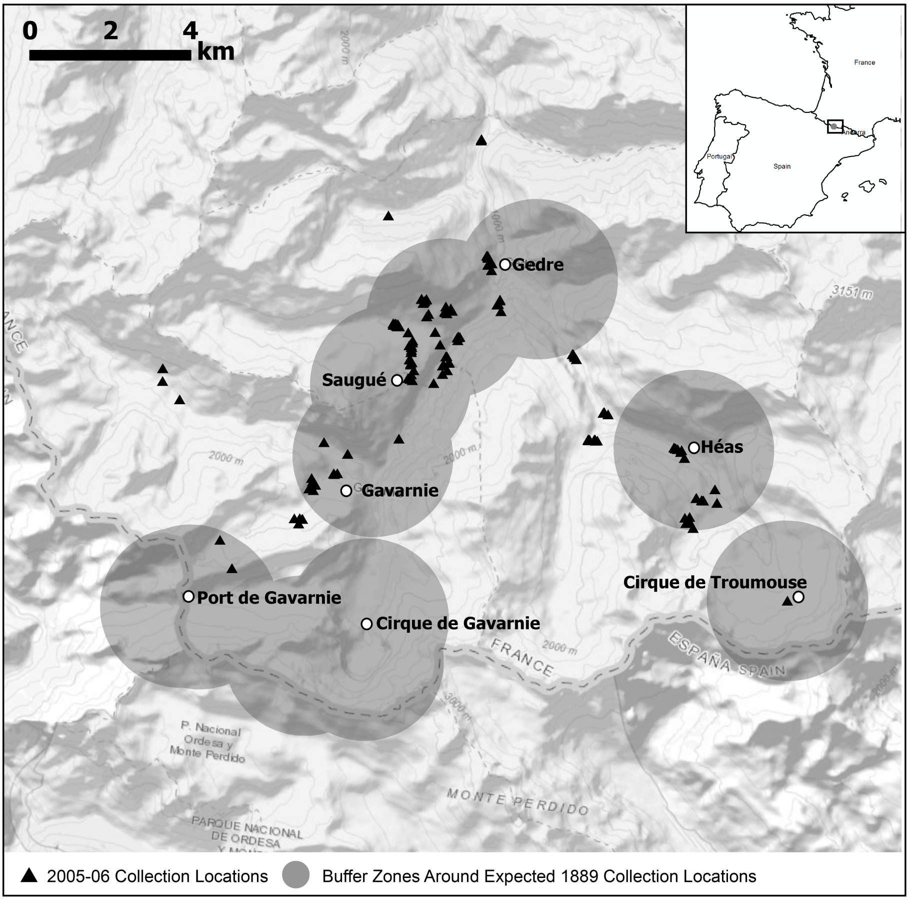


FIG. 6.1: **Locations of survey sites in 1889 and 2005-06 in the Pyrenees national park.** Grey circles represent the expected sampling locations in 1889. Black triangles represent exact sampling locations in 2005-06.

6.3.2 Bumblebee, Lepidoptera and plant surveys

We focused the study on wild bumblebees and large day-active Lepidoptera, as they are abundant in the historical surveys are well adapted to the high elevation region, well known, and relatively easy to survey and identify. In the 2005-06 survey, bumblebee species that were not identifiable in the field were collected and identified later by Stuart Roberts. Two separate surveys in the region, both conducted in August, were compared. Between the 5th and 31st of August 1889 biologist and naturalist Professor Julius Macleod sampled the plant and plant visitor communities. In 2005 (8th to 25th August) and 2006 (14th to 31st August) efforts were made to resample the same areas as MacLeod had visited, this time limiting the survey to the plant species with insect visitors recorded in 1889, with an increased focus on the visitors themselves and not the plants. Other plant species that were abundantly visited were also recorded.

6.3.3 1889 Collections

Between the 5th and 31st of August 1889 and the 8th of June to 3rd of July 1890 biologist and naturalist Professor Julius Macleod sampled the plant and plant visitor communities in the Luz Valley in the Pyrenees mountains in Southern France. Only the records collected in August were used in this study. Specifically he sampled plant communities in the areas of Gèdre (1000m), Cascade de Gavarnie (1500m), port de Gavarnie (2300m), cirque de Troumouse (2000m), the brêche de Roland (2800m), Saugué (1500m - 1650m) and Héas (1450m). These areas encompass elevations ranging from 1000m until 2800m above sea level (asl), plant visitors were found from 1000m to 2100m. He published an account of the plants and plant visitors he observed in 1891 in “De pyreneeënbloemen” (MacLeod 1891). The goal of MacLeod’s survey was to make a comparison of the floral community along habitat and elevation gradients in the Pyrenees specifically to compare to a similar study conducted in the Alps (Müller 1881). The collection of insect visitors to these plants was deliberate but incidental to the overall aim. Nonetheless, MacLeod collected and identified all insects visitors observed when surveying the plant community. MacLeod surveyed 263 separate plant species with 569 separate insect visitors. The bumblebees collected by MacLeod were identified by Professor Otto Schmiedeknecht.

A number of species names did not correspond with present day terminology and we used Schmiedeknecht's publication, Die Hymenopteren Mitteleuropas, to compare to the checklist of bumblebees from the Natural History Museum (Williams 2016), to determine the correct taxonomic names which would correspond with present day bumblebees (Schmiedeknecht 1907). The Lepidoptera collected by MacLeod where identified by Dr. Otto Staudinger. As with the bumblebees a number of the names attributed to occurrences do not coincide with modern day systematics and a comparison of historical name changes was made using the original publications of Staudinger (Staudinger 1871) and Butterflies and Moths of the World from the Natural History Museum (`http://www.nhm.ac.uk/our-science/data/butmoth/search/`). The plant species which were identified by MacLeod himself were compared using the "The Plant List", an online resource with historical synonyms of the majority of global plants (`http://www.theplantlist.org/`).

6.3.4 2005/06 Collections

In 2005 (8th to 25th August) and 2006 (14th to 31st August), two surveys were conducted to analyse the plant visitor community of the most visited plant species in the same areas that MacLeod sampled in 1889. The fundamental difference between the two surveys is the target organism. In 1889 the plant species were targeted for the survey and the visitors collected as seen. In 2005-06 the target was the plant visitors and a selection of plants was made, based on MacLeod's findings, to maximize sampling of the pollinator community. Therefore, direct comparisons of whole networks are not possible. At each location surrounding the area mentioned by Macleod for each of the plant species chosen a plot was made and observed for 15 minutes. During the 15 minutes observation window all flower visitors were either identified by sight but not caught, or caught and later identified by experts. The surface area of each plot was measured and its flower density was recorded. Other plant species with abundant visitors not observed in 1889 were also included. The altitude and GPS coordinates (WGS1984) for each plot were also recorded.

6.3.5 Climate Change

Climate data was generated using the software package ClimateEU (v4.63; Hamann et al. 2013). Climate provides minimum, maximum and mean temperature records and precipitation for sample locations with known elevation. We extracted these metrics at a 1 × 1km grid resolution for a 10km buffer surrounding the centroid of all collection records. We aggregated the values for decades by taking the mean value across all 10 years. Since the climate records available in the ClimateEU software start at 1900 we took the decade 1900 to 1910 as a proxy for the period 1885 to 1895. For the modern day records we also aggregated the data between 2000 and 2010 to the mean value of each metric across all 10 years. We then compared each of the temperature metrics using paired two sample t-tests to examine whether temperature and rainfall values were significantly different between the two periods, both annually and for August. We also calculated the annual mean temperature and the mean temperature of August for all years between 1900 and 2006 to test whether there was a significant trend in changing temperature. Due to the nature of the collection records, specifically that we do not have exact coordinates for the collection records in 1889 it is infeasible to directly test whether climate changes at specific sites have resulted in community changes, we therefore focus on climate changes at the regional scale.

6.3.6 Land Use/Land Cover Change

Land use/land cover (LULC) maps for the Pyrenees in 1889 were not available. To estimate LULC change in the area we used historic reconstruction maps for Europe (Fuchs et al. 2015). These maps represent modelled reconstructions of LULC in Europe from 1900 until 2010 using a combination of historical LULC data sources and a modelling approach called Historic Land Dynamics Assessment or HILDA (Fuchs et al. 2013). This resource provides a rough estimate of how the LULC in the study area has shifted in the past 110 years at a 1 × 1km grid resolution. We used LULC maps from two decades to show changes in the time periods of the surveys (1900 and 2010). Due the coarseness of the LULC data there were not enough grid cells to analyse the change in elevation in each 200m elevation zone. Therefore, we split the mountain into two regions of different elevation, 1000-1799m (Montane) and 1800-2299m (Sub-alpine) (Gómez et al.

2017). Chi-square tests were used to assess differences in the proportions of each LULC class at montane and subalpine elevations between the two time-periods. We also included a trend analysis of all decades to show how LULC changed over 110 years in our study area. The LULC classes available in the historic LULC maps include forests, grasslands, cultivated land, human settlements, water and other. The "other" category comprises the areas of ruderal vegetation, beaches, bare floors, rocks, and other parts of the landscape difficult to classify.

6.3.7 Community Change

For the bumblebee and day-flying Lepidoptera assemblages, we examine the change in proportion of the different species between the two time periods as well as describe the species that were not found in either of the two periods. We examine the changes in proportion at , 1000-1799m (Montane) and 1800-2299m (Sub-alpine) elevations. Due to differences in sampling intensity, protocol and target species between the two periods, we had to limit our community analysis to species of bumblebee, day-flying Lepidoptera and plants which were observed during both surveys.

6.3.8 Elevation Change

MacLeod's descriptions of his sampling locations are not clear enough to provide exact areas to attribute to the collection records. Therefore, as we do not know exactly where MacLeod sampled and potentially the location areas from both periods do not overlap exactly, we grouped the occurrences into elevation ranges rather than sites (elevation is provided by MacLeod for each observation). We split the occurrences into elevation ranges of 200m, i.e. from 1000-1200m to 2000-2200m. The number of occurrences collected at each elevation range are not uniform between the two time periods. Therefore to avoid any bias of oversampling at certain elevations we used the approach of Chen et al. (2009) to determine the average elevation of individuals in 1889 and in 2005-06. This entailed measuring the mean elevation of each species in each time period using three methods. The first method (m1) simply implies using all available occurrences in each time period to calculate the average elevations. The second method (m2) deals with the fact that certain species may make up a greater proportion of the species at one elevation range over another, therefore we took the weighted mean of each species based on its proportion in the six elevation classes. The final method (m3) recognizes that the sampling intensity in each elevation range is not equal in the two time periods. Therefore, at each elevation range the time period with the greater number of records was re-sampled to coincide with the time period with lower sampling intensity and then the mean elevation of each species was calculated. This was repeated 1000 times and the average of all mean values per species was used at the final value. For all three methods for each of the three groups we compared the elevation ranges in both periods to assess whether there was an increase or decrease in elevation overall and per species using t-tests or a Wilcoxon rank sum test when the sample means are not normally distributed.

6.3.9 Trait Responses

The traits of the bumblebees recorded in both periods were extracted from the “European bee traits database” (established by ALARM, `www.alarm-project.ufz.de`, and developed by STEP, `www.STEP-project.net`). We extracted traits relating to (1) habitat specialization, (1 to 8, number of habitat types where a species occurs); (2) feeding specialization (oligolectic, polylectic, no lectic status); (3) length of flight period (2 to 9 months); and (4) tongue length as measured by Obeso (1992) for bumblebee populations in the northern part of the Iberian Peninsula. We chose this resource for tongue lengths as it included all non-parasitic species from our study, comes from a geographically close region, and was measured as an average of individuals across an elevation gradient. We tested whether different trait had different relationships to elevation and elevation change between periods.

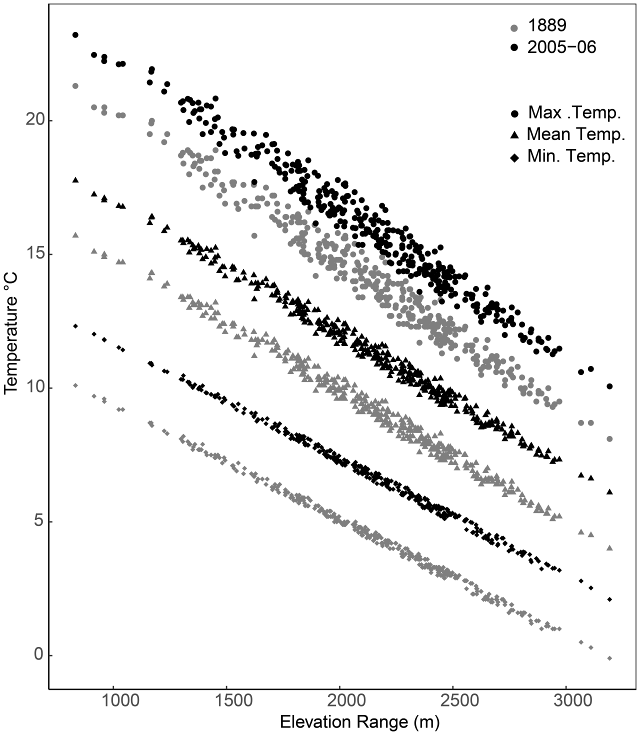


Fig. 6.2: **Difference in minimum, mean and maximum temperature changes in Luz Valley in August at different elevations between 1889 and 2005-06.**

6.4 Results

6.4.1 Climate Change

At the landscape level we observe considerable climate change between the two time periods. The mean annual temperature significantly increased by 0.02°C per year (f=2667, df=38802, p=<0.001; Fig S6.1). Furthermore, the average mean, minimum and maximum temperatures of August between the 1901-1910 and 2001-2010 show significant differences. The mean temperature increased on average by 2.1°C (t=1351.7, df=355, p=<0.001). The minimum temperature increased on average by 2.3°C (t=1210.1, df=355, p=<0.001) and the maximum temperature by 1.9°C (t=990.9, df=355, p=<0.001). The temperature also increased consistently at all elevations in the surrounding area. The increase is consistent from lower to higher elevations. Equivalent temperatures are all found higher in elevation in 2005-06. The equivalent average temperature in August is now on average 425m ±44m higher, the minimum 513m ±24m and the maximum 299m ±80m (Fig 6.2). Overall less change has occurred for the extreme maximum temperatures of August.

6.4.2 Land Use/Land Cover Change

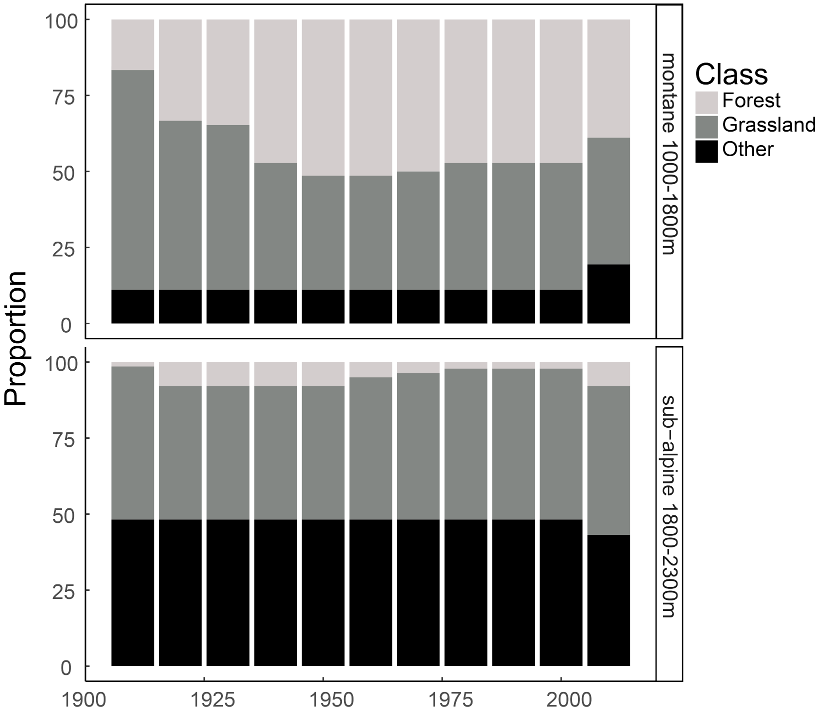


FIG. 6.3: **Land use change in Luz Valley between 1900 and 2010.** Reconstructed as part of the Historic Land Dynamics Assessment (HILDA; Fuchs et al. 2013; Fuchs et al. 2015).

Land use/land cover (LULC) data from 1889 in the region was not available so we used coarse LULC estimates from the year 1910 as a proxy. We calculated per elevation zone changes in the main LULC types for the surrounding study region. There are only three LULC classes at the broad thematic resolution of the LULC maps available for both time periods; (i) forest, (ii) grassland, and (iii) other land.

When split into montane (1000-1800m) and sub-alpine (1800-2300m) areas we observe a significant change in land use composition between the three classifications. In 1910 in montane elevations 16% of the LULC was forest, 72% grassland and 11% other, this changes to 38% forest, 42% grassland 19% other in 2010 (chi square: χ^2=13.9, df=2, p=<0.001; Fig 6.3). Sub-alpine LULC shows the same patterns with forest increasing from 1% to 8% and grassland increasing from 50% to 49%, other land changed slightly from 48% to 43% (χ^2=6.6, df=2, p=0.03, Fig 6.3).

6.4.3 Community Composition

The total number of bumblebee species found in 1889 was 16 and increased to 17 in 2005-06. Twelve species were found in both surveys (Fig 6.4). Unique to 1889 were *B. mendax*, *B. monticola*, *B. mucidus*, and *B. pratorum*. *Bombus mendax* and *B. mucidus* are singletons. On the other hand, *B. monticola* (2%) was found more abundantly. Singletons found in 2005-06 but not in 1889 include *B. rupestris*, *B. sylvarum*, and *B. sylvestris*. *Bombus bohemicus* (5%), *B. pyrenaeus* (2%) on the other hand were absent in 1889 and found with a moderately high abundance in 2005-06. In 1889, 47 species of butterfly or day flying moth were found, 16 of which were singletons. In 2005-06, 27 species were found, of which 7 were singletons. Nineteen species were found in both surveys, 11 of which had more than a single record in both periods (Fig 6.4). Species which were found abundantly in a single period include *Boloria pales* (6%), *Erebia tyndarus* (5%), *Parnassius apollo* (4%) in 1889, and *Issoria lathonia* (4%), *Thymelicus sylvestris* (4%) in 2005-06.

6.4.4 Elevation Shifts

We measured the change in elevation of the 12 bumblebee species present in both time periods using three different methods as explained above (Fig 6.5a). Overall using m1, bumblebee species shifted 206m up the mountain (paired t-test: t=4.59, df=11, p=<0.001, 95%CI = 107.3, 304.9). Of the 12 species 10 showed an shift in mean elevation. Using m2 we observed an overall mean shift of 147m upwards (t=2.56, df=11, p=0.026, 95%CI = 20.5, 273.2). Of the 12 species 9 showed a shift in elevation. Using m3 we observed an overall shift upwards of 151m (t=2.64,

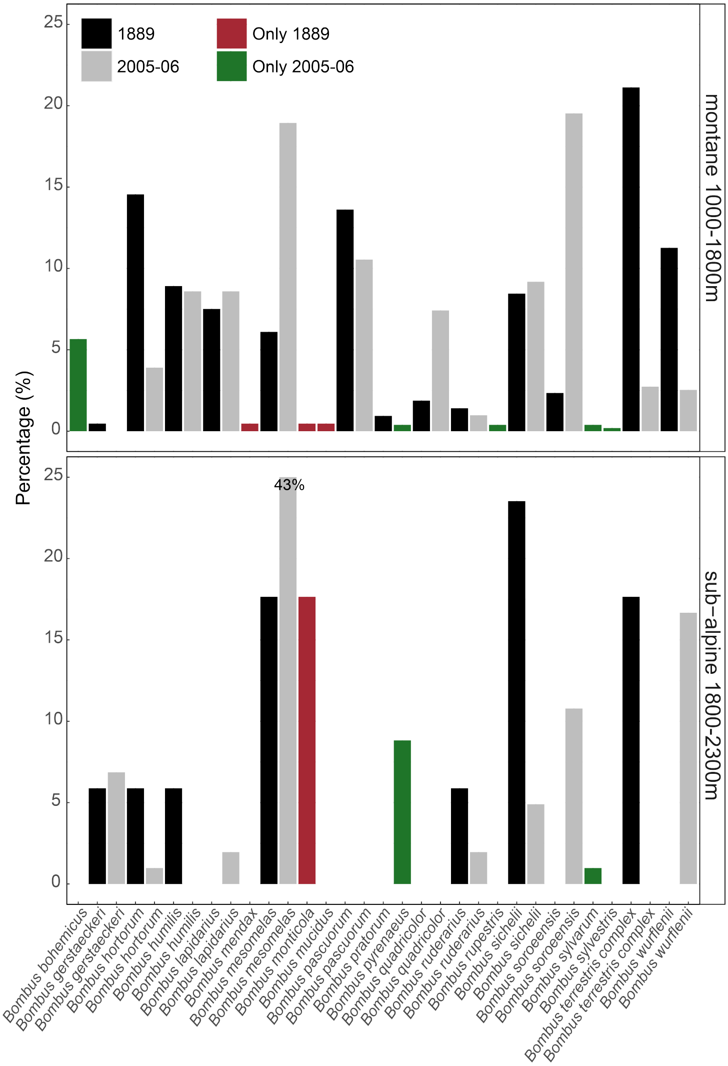


FIG. 6.4: **Relative abundance of bumblebee species in different elevation zones in 1889 and 2005-06.**Black: 1889, Grey: 2005-06, Red: unique to 1889 and Green: unique to 2005-06.

df=11, *p*=0.023, 95%CI = 24.9, 277). Of the 12 species 8 showed an shift in mean elevation under all three methods. The species that shifted the most in elevation were *B. wurflenii*, *B. gerstaeckeri* and *B. lapidarius*. Regardless of the method, all three species showed large shift in mean elevation. Depending on the three calculation methods *B. wurflenii* had an average elevation shift of between 333m and 446m with a minimum of 1000m and maximum of 1700m in 1889 and a minimum of 1491m and maximum of 2200m in 2005-06 (Fig 6.5a). *Bombus gerstaeckeri* had an average elevation shift of between 328m and 400m with a minimum of 1600m and maximum of 1900m in 1889 and a minimum of 2100m and maximum of 2200m in 2005-06. *Bombus lapidarius* shifted between 344 and 467m. The only species that shows a downhill trajectory between the time periods is *B. soroeensis*, which had an average elevation decrease of between -53m and -217m.

The change in elevation of the day-flying Lepidoptera found in both 1889 (n=164) and 2005-06 (n=138) surveys (Fig 6.5b) using m1 shows an overall shift in elevation of 262m (W=13, df=10, p=0.002, 95%CI=127.1, 398.2). Using m2 the the day-flying Lepidoptera show an overall a shift in elevation of 249m (W=26, df=10, p=0.03, 95%CI=57.8, 440.6). Finally, using m3 there was an overall shift of 198m (t=3.41, df=10, p=0.007, 95%CI = 68.2, 327). Of the 11 species 8 showed an shift in elevation under all three methods. The greatest shift of elevation was observed for *Colias croceus* Leiden (between 421m and 742m) and *Aglais urticae* (between 444m and 459m). The only species to show a consistent downhill trend in average elevation difference was *Macroglossa stellatarum* which decreased between 26m and 217m.

As mentioned before, we limited our analysis to the plants where bumblebee, butterfly and day flying moth species were found to be visiting in both time-periods (Fig 6.5c). Twenty-six plant species were observed for visitors in both time periods and 16 of these were recorded with bumblebee, butterfly and day moth visits more than once. Again, the majority of species showed an uphill trend comparing 1889 to 2005-06, m1 shows and overall shift of 243m (W=67.5, df=15, p=0.02, 95%CI= 151.9, 333.3). Using m2 the visited plants show an average of 225m movement uphill (W=74, df=15, p=0.04, 95%CI=120.5, 328.6). Finally, m3 shows an shift of 214m (W=64.5, df=15, p=0.02, 95%CI=128.7, 301.2). Thirteen of the 16 species displayed an uphill trend under all three methodologies. *Cirsium arvense* (between 497m and 521m), *Allium lusitanicum* (between 456m and 482m) and species of the *Aconitum* genus (between 386m and 476m) showed the greatest average shift in mean elevation. Not a single plant species measured show an overall downhill trend in mean elevation.

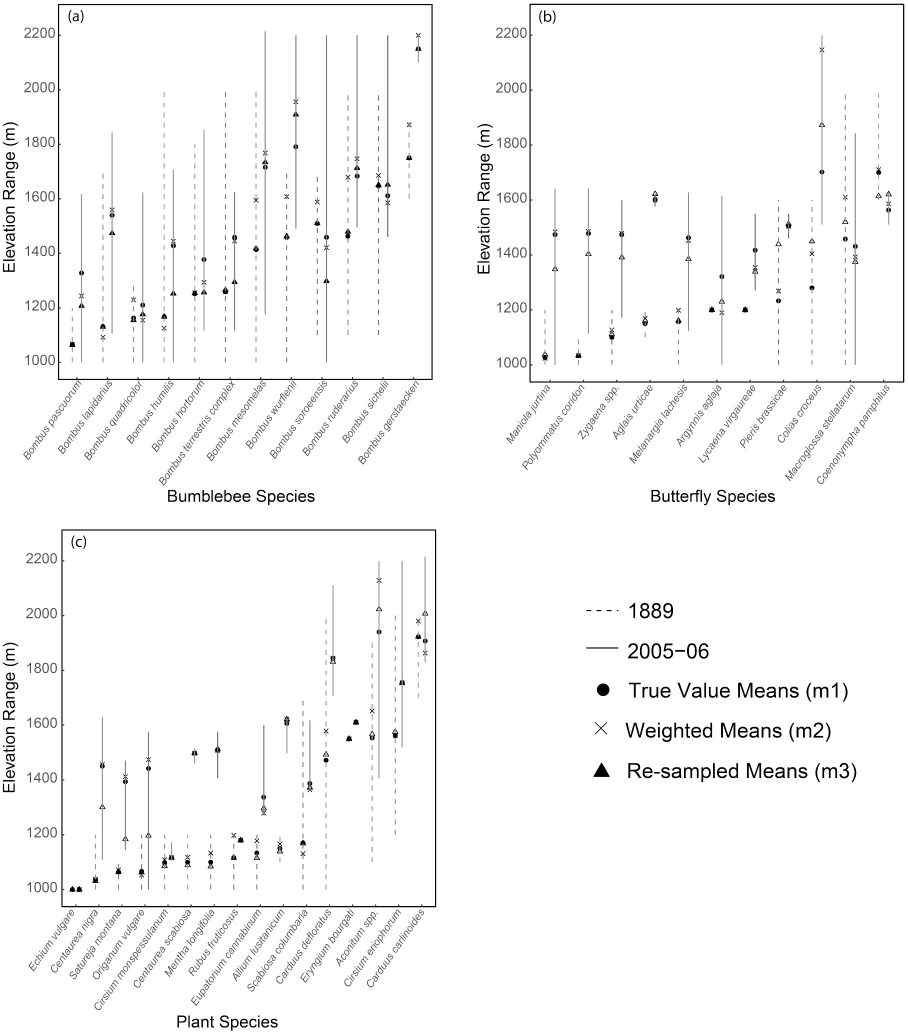


FIG. 6.5: **Elevation change between 1889 and 2005-06** For (a) bumblebees, (b) day-flying Lepidoptera and (c) their visited plants. Dashed line: 1889. Solid line: 2005-06. Shapes refer to different methods to calculate mean elevation shift: Circle: (m1) uses using all available occurrences in each time period to calculate the average elevations. Cross: (m2) weighted mean of each species based on its proportion in the six elevation classes (1000-1200, 1200-1400, 1400-1600, 1600-1800, 1800-2000, 2000-2200m). Triangles: (m3) in each elevation class the time period with the greater number of records was resampled to coincide with the time period with lower sampling intensity and then the mean elevation of each species was calculated.

6.4.5 Bumblebee Specialization

Habitat-specialist bumblebees were found much higher up the mountain than generalists and this relationship has a strong correlation in both time periods. We compared the re-sample means, as these represent the most conservative estimations of elevation shift. Pearson correlation coefficients were -0.53 in 1889 and -0.58 in 2005-06 (Fig 6.6). We also observe that specialists occur in higher elevations in 2005-06 than in 1889, but that the same comparison between generalists does not show a difference in elevation (Fig 6.6). There is also a weak relationship (Pearson r= -0.2) between elevation change and habitat specialization (Fig S6.2a). Overall, we do not see generalists higher up the mountain as hypothesized (Fig 6.6). Additionally, there is a high correlation between habitat specialization and number of flying months (Pearson r=0.79; Fig S6.2b) so we treat the two traits as similar, and therefore choose to show habitat specialization. We do not observe any clear patterns for tongue-length other than that *B. gerstaeckeri*, one of the species with the greatest shift in mean elevation, has a far longer tongue than all other species (see Obeso 1992; Fig S6.2c). *Bombus gerstaeckeri* also represents the only oligolectic bumblebee found in both periods. It is therefore found higher up the mountain (mean=1950m) in both periods than both the polylectic (1471m) and parasitic species (1224m; Fig S6.2d).

6.5 Discussion

In this study we compared two plant pollinator communities 115 years apart. We specifically tested three hypotheses; (1) that significant climate and land use changes occurred in the Pyrenees National Park in the last 115 years; (2) that the composition of the bumblebee, butterfly and plant community altered and/or shifted in mean elevation over 115 years; and (3) that bumblebee traits explain their observed elevation patterns and shifts.

Over 115 years of changes in the Gavarnie/Gedre region of the Hautes Pyrenees the community of bumblebees, day-flying Lepidoptera and the plants they visited were found to significantly increase their mean elevation. The bumblebee communities showed a stable trend in species richness over 115 years, with only

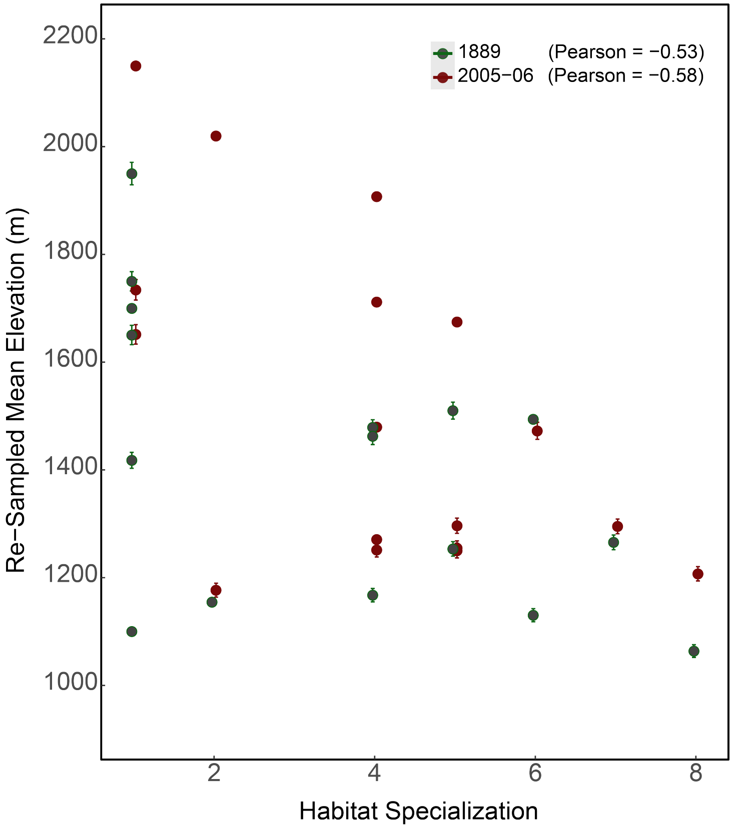


FIG. 6.6: **Mean elevation against species habitat specialization.** Elevation calculated using (m3), in each elevation class the time period with the greater number of records was re-sampled to coincide with the time period with lower sampling intensity and then the mean elevation of each species was calculated. Green:1889, Red:2005-06. Habitat specialization from 1-8 based on the number of different European biomes where the species has been found previously.

slight changes in species composition and proportions. The sampled butterfly and day flying moth community showed more significant differences between the two time periods but this is most likely explained by a different sampling intensity and focus on the smaller less conspicuous species in 1889. The upward shifts for all three groups suggest and average shift of approximately 200m and this is in line with similar studies of long-term elevation change of butterflies in other locations (Chen et al. 2009; Wilson et al. 2005; Wilson et al. 2007). For bumblebees on the other hand this study is one of the few studies to show a long-term elevation shifts for a bumblebee assemblage at one site. Franzen & Ockinger (2012) measured changed in bumblebee elevation in Sweden but observed no significant increase across 60 years. At the larger spatial scale Kerr et al. (2015) observed that in the US and Europe Southern species showed an overall increase in elevation of approximately 300m since 1974. This effect varied by species but the geographical effect of North versus South was stronger, with Northern species decreasing in elevation (Kerr et al. 2015). This supports the observed differences between this study and that by Franzen & Ockinger (2012) as the Pyrenees are far further south in Europe than the Swedish mountains of their study. In the Rocky Mountains in Colorado Pyke et al. (2016) find similar results when measuring the elevation increase of bumblebees between 1974 and 2007. As with our study they find that the elevation increase is not consistent for all species, with some species moving more than 400m and others showing no change at all. The shorter time period of the other studies on butterflies and the continental study of bumblebees show similar values in mean elevation increase for species which suggests that the majority of these changes may have occurred in the last 50 years and that the trend in elevation increase is not steady over time but has been triggered by particular changes later in the 20th century. For example climate changes since 1950 have occurred at a faster rate than those observed before the 1950s (IPCC 2014).

The majority of bumblebees species can forage over large distance and while they can occur at very high altitudes, they are generally not restricted to particular elevations across the whole range of species (Goulson 2010; Walther-Hellwig & Frankl 2003). However, in lower latitudes of the Northern hemisphere bumblebees can often be found to be restricted to high elevation mountain habitats (Vereecken 2017; Williams et al. 2009a). Therefore the decrease of a species at lower elevation and increase at higher elevations in areas such as the Pyrenees indicates that climate and/or land use/land cover (LULC) changes at lower elevations have restricted the availability of feeding and nesting resources and are driving species uphill (Parmesan & Yohe 2003; Pyke et al. 2016). The observed changes in the environment support the indication that the elevation increases are driven by changes in climate, LULC and floral resource availability. Equivalent minimum, mean and maximum temperatures have shifted between 300m and

500m uphill, the montane LULC of 1889 is closer to the LULC at the sub-alpine elevations in 2005-06 and the plants that were observed with bumblebee and day-flying Lepidoptera visitors in 1889 shifted in similar magnitudes uphill. It is therefore difficult to separate the drivers, and the results observed are most likely due to the interaction between all three changes. Climate changes provide more suitable agricultural areas higher up the mountain and both climate and LULC change shift the climatic niche of flowering plants uphill (Dale 1997; Lenoir et al. 2008). The variation observed between species would suggest that it is not only one consistent changing factor causing these changes in elevation.

Interestingly, the minimum and mean temperatures have changed more than the maximum temperature of August over the last 115 years, suggesting the absence of extreme heat wave conditions. Extreme temperatures during the flying period of the species can lead to significant decreases in abundance and potentially local extinctions of butterfly and bumblebee species (Parmesan et al. 2000; Rasmont & Iserbyt 2012; WallisDeVries et al. 2011). Our results suggest that the distributional shifts are driven by consistent changes in temperature over time rather than extreme conditions. However, this could change in the near future according to climate change predictions. However, as Pyke et al. (2016), we do not see an overall shift of bumblebee elevation that matches the upward shift in climate which we would be around 425m. The modelled climate change data shows that equivalent maximum temperatures in August have shifted less in elevation than the minimum and mean. This could lead to the hypothesis that bumblebees are more affected by extreme temperatures and therefore their distribution patterns are more likely to be affected by shift in the maximum temperature. This is in line with the hypothesis that heat waves are causing local extinctions in bumblebees (Rasmont & Iserbyt 2012). Climate change is predicted to have a significant influence on the distribution of bumblebees across Europe, with the majority of species expected to decline considerably in range (Rasmont et al. 2015a). High-elevation habitats are predicted to become increasingly important for maintaining the biodiversity of bumblebees and day-flying Lepidoptera, as they are likely to become refuges of colder temperatures that may no longer exist at lower elevations under different scenarios of climate change (Penado et al. 2016; Rasmont et al. 2015a; Settele et al. 2008). At a finer scale in the Swiss Alps the bumblebee community was predicted to not only lose range and increase in elevation but also to become more homogenized under climate change (Pradervand et al. 2014). We do not observe any clear indication of homogenization of the bumblebee community but if elevation increases continue, then the more generalist bumblebees will likely begin to occupy the same space as the more specialist species, which often results in the decline in abundance of specialist species (MacLean & Beissinger 2017). Fine scale species distribution models for plants in the Alps suggest that plant species will persist in high elevation areas under climate change and are unlikely to go extinct even under extreme scenarios (Randin et al. 2009). This suggests that bumblebees and the day-flying Lepidoptera in this region are unlikely to go extinct from a lack of feeding resources.

Furthermore, potential land use changes alongside climate change scenarios are likely to make these refuges even smaller and more important in a landscape context (Marshall et al. 2018). The results presented here suggest that this interaction between climate and LULC change has already caused distributional changes in pollinator communities. Due to climate warming, the tree line in woodland areas of the alps has shifted uphill (Gehrig-Fasel et al. 2007). This presented by an overall increase in forested area. In the Pyrenees this movement is less pronounced and the tree line movement seems to generally be driven by past anthropogenic disturbances (Ameztegui et al. 2016). Either way, movement of the tree line shifts important forage and nesting resources for wild pollinators further uphill. In the nearby commune of Villelongue, also in the Hautes-Pyrenees and the Pyrenees national park, pastures have increased from 4.9% to 25.8% of total surface area between 1950 and 2003 of which the majority was the conversion of meadows (Mottet et al. 2006). The data we have available from the late 19th and early parts of the 20th century do not allow us to analyse the quality of the grassland present at different time periods. However, the conversion of meadows to pasture removes necessary resources and will result in the decrease in populations of wild pollinators and is one of the main drivers of decline of wild pollinator populations worldwide (Potts et al. 2016b). In addition to this information in 2005 and 2006 there was significant grazing at lower elevations, which may explain the smaller number of species found at these elevations.

Climate and LULC change can both potentially explain the shifts observed and one of the key mechanism by which this occurs is the loss or movement of floral resources (Kennedy et al. 2013). Non-parasitic bumblebees provide pollination services to many wildflowers and range from generalist to specialist interactions with plant species; due to their temperament for cold conditions and large flowering range, bumblebees are vital pollinators for plants which exist in cold, unpredictable climates, and in fragmented habitats (Goulson 2010). A good example of this is the pollination services bumblebees provide in European mountain habitats including the Pyrenees (Iserbyt et al. 2008). Spatial mismatches and phenological shifts caused by climate change between plants and their pollinators will decrease the effectiveness of this service and in specialist cases will result in significant population declines (Burkle et al. 2013). As well as being specialized in feeding, species may be more or less specialized in the types of landscape they can survive in as well. This is likely to influence the response of species to environmental changes, habitat specialist butterflies in the UK showed that whilst half of generalist species increased their distributions, 89% of specialists decreased (Warren et al. 2001). We observe in general that specialist species are found higher up the mountain than generalists. The change in elevation is also greater for specialist species and very small for generalists. The plant-pollinator interactions of the consistent species suggest that there is considerable variation; particularly in the generalist pollinators in terms of what plants they visit. However, we do observe potential evidence that at least the persistent interactions may be shifting in unison, suggesting that the observed changes in pollinators is due to an interaction between climate, land use and plant distribution changes.

A potential exhibit of these different drivers in action can be observed in the species *B. gerstaeckeri*, a red listed vulnerable species and also the only feeding specialist of the observed assemblage (Nieto et al. 2014; Ponchau et al. 2006). The genus of species on which *B. gerstaeckeri* collects pollen is *Aconitum*. In the surveys *Aconitum* also showed an increase in elevation of approximately 400m. This suggests that *B. gerstaeckeri* has been driven to higher elevations to maintain access to its solitary food source. This narrow diet is likely to significantly increase the vulnerability of bumblebees to drivers of decline (Rasmont & Mersch 1988; Williams et al. 2009b). Additionally, *B. gerstaeckari* prefers sub-alpine woody habitats, and therefore movements in the tree line will shift suitable habitat (Rasmont et al. 2015b). Species specialized in high-elevation areas are likely to suffer greater from climate change than others (Dirnböck et al. 2011). *Aconitum*spp. are deep flowers and *B. gerstaeckeri* has a far longer tongue than any of the other bumblebee species (Obeso 1992). Previous studies with *B. gerstaeckeri* have implicated the lower ratio of queens to workers compared to other bumblebees which feed on *Aconitum* spp. as a potential example of its vulnerability (Ponchau et al. 2006). These factors combined explain why we see a large change for this species. The other species to show a large increase is *B. wurflenii*, which is classified on the red list as least concern but does show a decreasing trend (Nieto et al. 2014; Rasmont et al. 2015c). *Bombus wurflenii* is also known to feed on *Aconitum* spp. (Ponchau et al. 2006), and was found visiting it in high numbers in both time periods. It has also been observed in other studies to show a tendency towards feeding specialization (Kämper et al. 2016). Continued monitoring in the region and other areas is therefore a must. The only bumblebee species to show a decrease in elevation is *B. soroeensis*, which is defined as high altitude species in southern Europe (Williams et al. 2007). This is an unexpected result, and should be explored in more detail. Surveys of *B. sorooensis* from other high elevation areas should be examined to see if the species is decreasing in mean elevation across its extent.

Repeated surveys offer the unique opportunity to quantify how communities have changed over time. However, comparing a study from the 19th century brings with it its own exceptional challenges when comparing to studies using modern day research techniques. From the published account of the surveys in 1889 and 1890 it is difficult to know the intensity of the insect visitor sampling when we know that the focus of the study was on plant diversity in the region. Furthermore, the age of the work provides a number of taxonomical difficulties and many names used in 1889 were later changed (see Table S6.1). We would hesitate to draw any conclusion related to declines or extinction of the butterfly and particularly the day flying moth species because of this taxonomic difference and the less targeted sampling in 2005-06. There is also a discrepancy in the sampling intensity at different elevations, we have used statistical methods to account for this, but any comparison with 1889 will be limited by MacLeod's sampling intensity. Overall to draw more conclusions for what is happening in this region there is a necessity of repeated sampling, these snapshots can only reveal limited information (Dawson et al. 2011). A future sampling of the entire plant and insect community would allow for a more robust comparison, showing both long-term change in multiple groups and being able to compare short and long-term changes for groups such as the bumblebees. A particular focus of different months would also be useful, for example *B. pratorum* has been found regularly in the region in recent times suggesting that its presence in August 1889 and absence in August 2005-06 is potentially due to phenological shifts, as rarely would *B. pratorum* still be flying so late in the season. The current datasets from 2005-06 are focused on August and do not allow an estimate of phenological shifts, future surveys should therefore encompass June and July as well.

Significant climate and land use changes have occurred in the Pyrenees National Park in the last 115 years. This has not caused significant species losses but has altered the distribution patterns of the bumblebee and day-flying Lepidoptera community. Many species show an increase in elevation that corresponds to these changes as well as shifts in the elevation of their preferred plant species. We also see that specialist species are found higher up the mountain and may be more vulnerable to change. Overall, this indicates that there are likely complex interactions between climate, land use and plant distribution changes, however the results clearly indicate that specialist species in these habitat are at risk of significantly declining in range if these changes persist.

6.6 Supporting Information

Tables

TABLE S6.1: **Name changes of bumblebees, day-flying Lepidoptera and plants.** From the original 1889 and/or 2005-06 classification to the accepted classification in the present day.

Bumblebees	
Original	**Final**
Bombus agrorum	*Bombus mesomelas*
Bombus agrorum var. pascuarum	*Bombus pascuorum*
Bombus alticola	*Bombus sichelii*
Bombus mastrucatus	*Bombus wurflenii*
Bombus pomorum var. elegans	*Bombus pomorum*
Bombus rajellus	*Bombus ruderarius*
Bombus soroënsis var. laetus	*Bombus soroeensis*
Bombus variabilis	*Bombus humilis*
Bombus lapponicus	*Bombus monticola*

Plants	
Original	**Final**
Allium fallax	*Allium lusitanicum*
Allium montana	*Allium lusitanicum*
Carduus carlinifolius	*Carduus defloratus*
Carduus medius	*Carduus defloratus*
Cirsium lanceolatum	*Cirsium vulgare*
Galeopsis pyrenaica	*Galeopsis ladanum*
Galeopsis angustifolia	*Galeopsis ladanum*
Mentha sylvestris	*Mentha longifolia*
Parnassia rotundifolia	*Parnassia palustris*

Day-flying Lepidoptera	
Original	**Final**
Agrotis decora	*Euxoa decora*
Agrotis ocellina	*Chersotis ocellina*
Argynnis euphrosine	*Boloria euphrosyne*
Argynnis pales	*Boloria pales*
Botys nigrata	*Pyrausta nigrata*
Botys purpuralis var. ostrinalis	*Pyrausta purpuralis*
Callimorpha hera	*Euplagia quadripunctaria*
Choreutis pretiosana	*Tebenna pretiosana*
Colias edusa	*Colias croceus*
Epinephele janira	*Maniola jurtina*
Erebia lappona	*Erebia pandrose*
Erebia stygne	*Erebia meolans*
Hercyna phrygialis	*Metaxmeste phrygialis*
Ino statices var.	*Adscita statices*
Leucophasia sinapsis	*Leptidea sinapis*
Lycaena aegon	*Plebejus argus*
Lycaena astrarche	*Aricia cramera*
Lycaena bellargus	*Polyommatus bellargus*
Lycaena corydon	*Polyommatus coridon*
Lycaena hylas	*Polyommatus dorylas*
Lycaena icarus	*Polyommatus icarus*
Melanargia galathea	*Melanargia lachesis*
Melitaea dictymna	*Melitaea diamina*
Nemeobius lucina	*Hamearis lucina*
Nisoniades tages	*Erynnis tages*
Pararge maera var. adrasta	*Lasiommata maera*
Plusia gamma	*Autographa gamma*
Polyomnatus virgaureae	*Lycaena virgaureae*
Rhodecera rhamni	*Gonepteryx rhamni*
Satyrus alcyone	Hipparchia alcyone
Simaethis oxyacanthella	*Anthophila fabriciana*
Sphinx convolvuli	*Agrius convolvuli*
Syrichthus alveus	*Pyrgus alveus*
Syrichthus malvae	*Pyrgus malvae*
Syrichthus sao	*Spialia sertorius*
Syrichthus serratulae	*Pyrgus serratulae*
Tancalia leeuwenhoeckella	*Pancalia leuwenhoekella*
Thecla rubi	*Callophrys rubi*
Vanessa antiopa	*Nymphalis antiopa*
Vanessa Io	*Aglais io*
Vanessa urticae	*Aglais urticae*
Venilia macularia	*Pseudopanthera macularia*

Figures

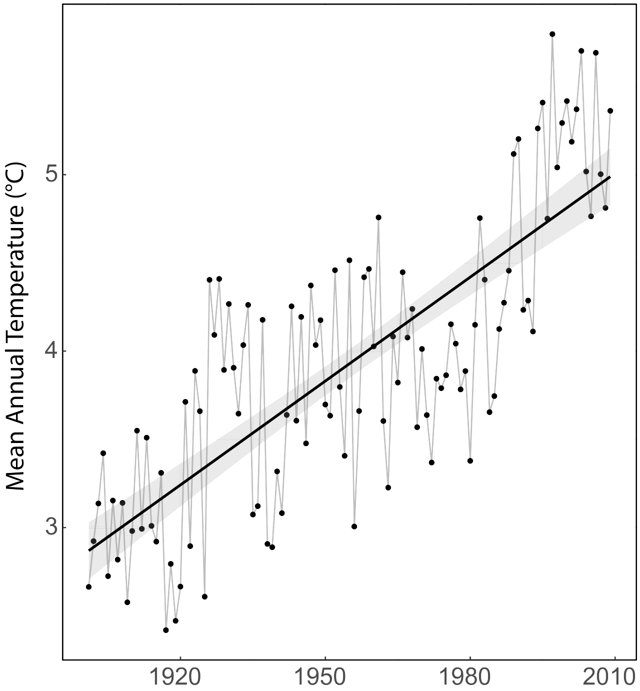


Fig. S6.1: **Mean annual temperature trends between 1900-2010.** Line represents linear relationship with 95% confidence interval.

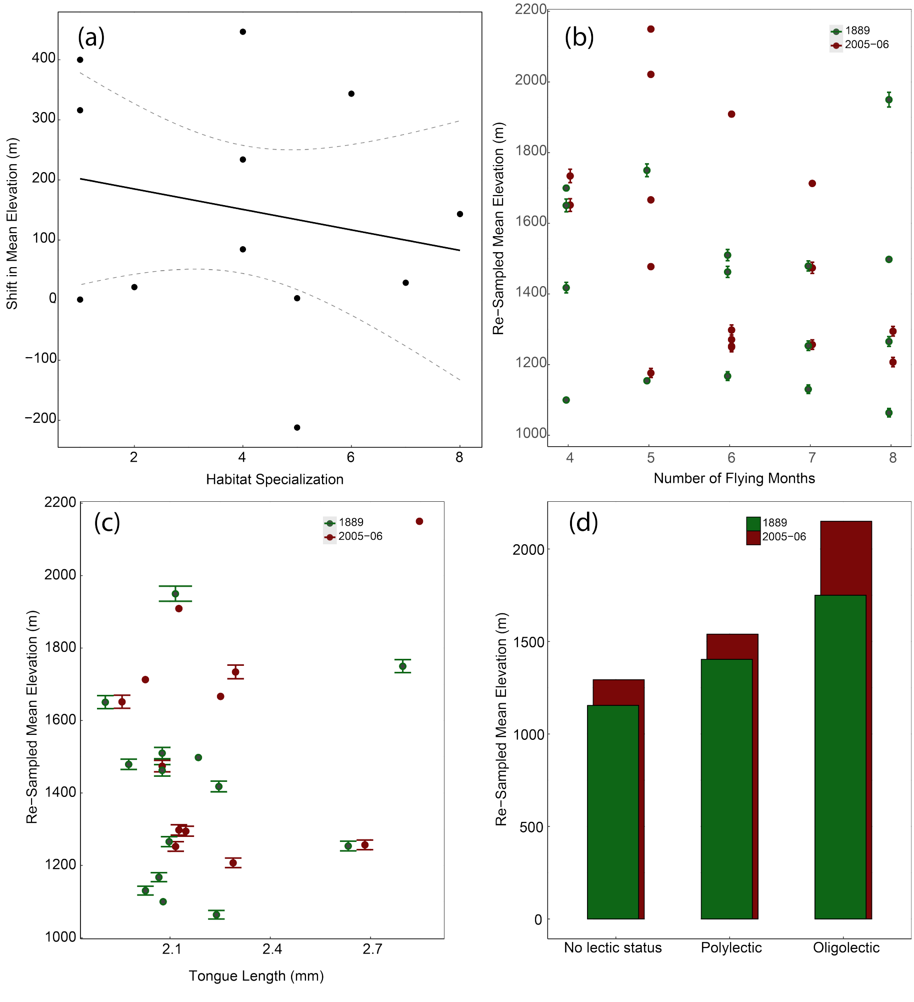
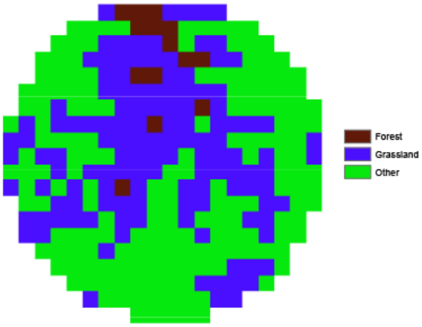
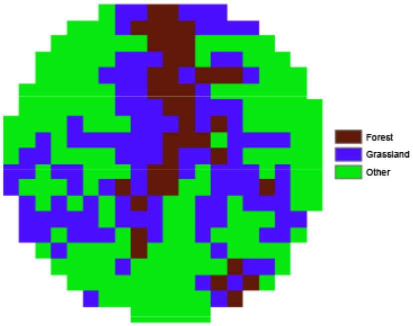


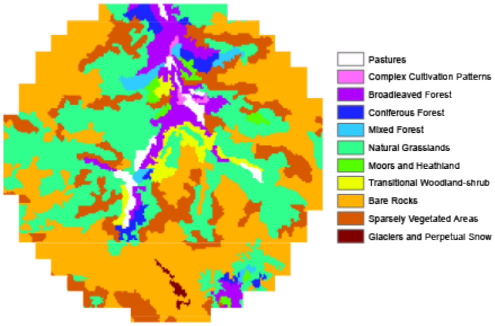
FIG. S6.2: **Mean elevation and elevation changes versus species traits.** (a) Change in elavation against habitat specialisation. Habitat specialization from 1-8 based on the number of different European biomes where the species has been found previously. Dotted line represents 95% confidence interval of linear fit.(b) Mean elevation against number of flying months. (c) Mean elevation against tongue length. Tongue length measurements taken from Obeso, (1992). (d) [Mean elevation against lectic status. No lectic status represents the parasitic species. *Bombus gerstaeckeri* is the only oligolectic species. Change in elevation and mean elevation calculated using (m3), in each elevation class the time period with the greater number of records was re-sampled to coincide with the time period with lower sampling intensity and then the mean elevation of each species was calculated. Green:1889, Red:2005-06.



HILDA 1910



HILDA 2010



CORINE 2006

FIG. S6.3: **Land use/land cover (LULC) maps Gedre/Gavarnie Pyrenees National Park, 1910, 2006, 2010** (a) HILDA modelled LULC for 1910; (b) Hilda modelled LULC for 2010; (c) actual LULC from 2006, CORINE

7 General Discussion

L. Marshall

7.1 Overview

The study of the distribution of biodiversity in space and time is a fundamental aspect of ecology, evolutionary biology and conservation. Understanding these patterns can provide information on where species are distributed globally, population trends (increasing or decreasing), threat of extinction, the role of these species in the ecosystem, and the best ways to protect these species (Patterson 1994; Shaffer et al. 1998; Rodrigues et al. 2004; Pimm et al. 2014). The study of biodiversity distributions and conservation increases in significance when coupled with large-scale, rapid global change. Anthropogenic climate and land use/land cover (LULC) change has already fundamentally affected global biodiversity and is expected to continue to do so in the future (Thomas et al. 2004; Millennium Ecosystem Assessment 2005; Barnosky et al. 2011; Bellard et al. 2012; Newbold et al. 2015; Newbold et al. 2016). This creates an urgency to comprehend where species are distributed, what factors affect this distribution, how is this distribution likely to change and what can we do to ensure the continued existence of these species. These themes form the backbone of this thesis and have been explored for wild bee species at different spatial and temporal scales in Europe. Due to the impacts of climate and LULC changes in the past and future, we have focused on these two factors as drivers of wild bee distribution patterns **The general objective of this thesis was to examine how LULC and climate conditions impact the diversity and distribution patterns of wild bee species at different spatial and temporal scales.** In this discussion we will explore the results of the four separate scientific chapters together in terms of how they explore and test the three aims we proposed in the introduction. Specifically, to (1) test the efficacy of using statistical modelling tools to understand wild bee distributions in the present and future and suggest how to improve these methods; (2) provide novel understanding of how wild bee community assemblages are structured at large geographical scales and what drives this structure; and (3) quantify and compare how past, present, and future changes to wild bee and specifically, bumblebee distributions are expected to be influenced by LULC and climate changes.

In summary, related to the first aim, we show that based on the restricted extent and unequal species coverage of available wild bee collection data, robust methods to predict distribution patters are required. We used species distribution models (SDM) for this purpose. We show that, when applied to wild bees, SDM performance varies depending on the agricultural landscape where species are collected and on the traits of the modelled species (chapter 3). We show that incorporating co-occurrence between wild bee species improves model performance (chapter 4) and that incorporating LULC change variables also improves model performance in the present and results in significant differences in projected distributions for bumblebees in the future (chapter 5).

We focused on the second aim in chapter 4, and show clearly that habitat filtering explains the majority of wild bee assemblage patterns but that there is unexplained variation shared between species. Furthermore, we show that habitat filtering patterns show a clear phylogenetic signal, but that it is not explained by traits.

Finally, for the third aim we show that the interaction between climate and LULC projections for future do not affect all bumblebee species equally (chapter 5); and that changes in LULC and climate have occurred simultaneously in the Pyrenees forcing certain species to move towards higher elevations (chapter 6).

The general discussion is structured into three sections; firstly we explore the relevance of the results of the four chapters concerning the current literature and state of the art in ecology, biodiversity and conservation fields. Secondly, we expand upon the relevance and describe the implications of this thesis from a scientific point of view but also its implications to society in general. Finally we take the aforementioned relevance and implications, and formulate proposals and recommendations for future research.

7.2 Relevance

7.2.1 Modelling distribution patterns

The approaches available to estimate and predict how and where species are distributed have proliferated since the beginning of the century. Species distribution models (SDMs) are an excellent example of these approaches as they specifically provide the opportunity for researchers to combine occurrence records and, environmental and biotic variables to produce estimate of distribution patterns (Guisan & Thuiller 2005; Elith & Leathwick 2009). These methods are constantly being improved and applied to different problems. Many questions surround the use of SDMs at all stages of the model building and interpretation stages. A common question with SDMs is, what are the appropriate environmental covariates to use when constructing SDMs? Early SDMs and the majority of prospective SDMs used climate variables to delimit species distributions (Araújo & Guisan 2006; Elith & Leathwick 2009; Titeux et al. 2016). We support a long-term consensus of studies that indicate the importance of including LULC variables alongside climate variables to better capture the environmental niche of species, especially in areas with few climate extremes such as the Netherlands (Pearson et al. 2004; Araújo & Pearson 2005; Del Barrio et al. 2006; Luoto et al. 2007; Titeux et al. 2009; Clavero et al. 2011). However, this is not only shown at the smaller scale of the Netherlands, where LULC variables explain the majority of the variation in wild bee habitats (chapter 4), but also at the larger European scale, where model performance increases with the addition of LULC variables and significantly affects projected outcomes (chapter 5). The improvements to satellite technology and algorithms for classifying LULC, and its changes, has increased the availability of high resolution LULC maps for many parts of the globe (Kuemmerle et al. 2013; Congalton et al. 2014; He et al. 2015; Almeida et al. 2016; Gómez et al. 2016). Furthermore, this data is increasingly more accessible. Investments into ‘big data’ create online platforms for geodata and there has been progress in encouraging researchers to publish data sources (Costello 2009; Hampton et al. 2013). Satellite data and social mapping data is also increasingly more accessible (Hu et al. 2016; Reiche et al. 2016). Consequently, combined with open access software, the analysis of this data is more streamlined (Reichman et al. 2011). Therefore, there is little reason to focus purely on climate envelope modelling when trying to predict species distribution patterns.

Another issue around SDM construction concerns the importance of ecological/biotic factors in SDMs and the methods available to include them. The consensus states that SDMs with only environmental covariates are missing interspecific interactions, a fundamental aspect of ecology (Kissling et al. 2011; Wisz et al. 2012). We show that even over a relatively large geographic extent co-occurrence between species are a small but significant part of the niche variation observed in wild bee species in the Netherlands (chapter 4). Together with the results from Araújo et al. (2013) our results provide evidence against the Eltonian noise hypothesis[1], we show that biotic interactions might have a noticeable effect at large resolutions and across large extents. Furthermore, our study uses state-of-the-art methods which can provide estimates of biotic interactions based on co-occurrence patterns and does not rely on a priori knowledge of how species interact (Wisz et al. 2012; Ovaskainen et al. 2015; Ovaskainen et al. 2017). The results presented are summarized at the national scale but it would be possible to look deeper into the data and begin to extract specific species pairs that show strong positive or negative correlations. The logical next step is then to begin to hypothesize on the mechanisms behind these positive interactions and potentially incorporate these mechanisms in models accounting for these ecological interactions. For example, the mechanism behind the interaction between bee hosts and bee parasites is clear (Giannini et al. 2013). However, the mechanism behind why two species outcompete each other for resources (Godsoe & Harmon 2012; Meineri et al. 2012) or mechanisms of potential facilitative interactions are likely more complex (Gutiérrez et al. 2005; Heikkinen et al. 2007). However complicated these interactions may be, trying to understand the mechanisms of why SDMs improve when species are modelled together is a necessary step to improve the efficacy of SDMs. Another way of potentially incorporating the interactions between species is to model functional groups rather than individual species (Kissling et al. 2011). However, as we observe in chapter 3 there is still

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[1] The ‘Eltonian noise hypothesis’ is the hypothesis that large spatial extents and low resolutions, found in many geographic sources, are too coarse grained for biotic interactions between species to influence a species distribution (Soberón & Nakamura 2009).

considerable variation in model performance not explained when species are aggregated to functional trait groups and the results of chapter 4 show that the traits presently available for wild bees may not be suitable for modelling functional groups at this stage.

As SDMs have proliferated as a tool in ecology, the validation and interpretation of models has become increasingly important. It is therefore necessary to ask how effective are SDMs when applied to different species in different locations? In chapter 3 we show clearly that using a simple measure of model performance - habitat suitability in areas where independent collections were conducted - that the ability to predict habitat suitability can vary considerably depending on the location and the species functional group modelled. Furthermore, we even show that the method used to collect species can influence the performance of species distribution models, indicating that certain techniques may increase the likelihood of a species occurrence in a training or testing dataset. This shows clearly the inherent uncertainty in SDMs, an aspect which can never be removed and should be clear in the methodology used and any resulting model interpretation (Araújo et al. 2005; Buisson et al. 2010). How the species model is interpreted should relate directly to the original goal of the model (Guillera-Arroita et al. 2015). For example, in chapter 5 we create projected futures for bumblebees under different scenarios using different selections of covariates, the specific purpose of these models was not to predict the exact locations of bumblebees in 2050 and 2100, the aim was to observe how covariate selection altered projections of distribution patterns in the future. Therefore, we would hesitate to use the predictions to draw conclusions on actual distributions of bumblebees in Europe in 2050 or 2100, i.e. if the resulting maps were to be used to influence conservation practices either by selecting high risk areas, areas of future refuges, or predicting species extinctions (Sinclair et al. 2010; Ochoa-Ochoa et al. 2016), then they should be re-modelled with this specific goal and using the information obtained from the results of chapter 5 to limit the amount of uncertainty. (Sinclair et al. 2010; Ochoa-Ochoa et al. 2016). In chapter 4 on the other hand we have far less uncertainties in the hierarchical modelling of species communities (HMSC) model. As expected when modelling an entire community of species, performance varies according to the species. However, we include high resolution variables, species co-occurrence and we are not using the model to predict into unknown space but only to find patterns within the model training boundaries, therefore we feel more confident on the relevance of the conclusions reached regarding assemblage distributions and conservation recommendations.

Prospective modelling in the age of rapid global change is an important tool but one which comes with a number of caveats. As mentioned prospective modelling has widespread uncertainties in all aspects of the modelling process (Bellard et al. 2012), including the collection of species records in the present (particularly for insects; Lobo 2016), the models used to predict climate or LULC change (Dendoncker et al. 2008; IPCC 2014; Alexander et al. 2017), the algorithms used to train the models (Aguirre-Gutierrez et al. 2013), and the methods used to simplify and visualize the projections (Jiménez-Valverde & Lobo 2007; Calabrese et al. 2014). All these uncertainties could imply that these methods should not be used at all and only introduce noise to an already complicated and discordant conservation biology field. We believe that this is not the case and, that even with these uncertainties, prospective modelling shows an upward trend in use and quality, and has become a useful addition to conservation during the last decades, given that uncertainties are clearly discussed (Porfirio et al. 2014). This correlates strongly with the improvements to occurrence data quality, variable selection (Austin & Van Niel 2011), increases in the availability and number of approaches (Pacifici et al. 2015), improved climate change projections (Kay et al. 2015; Fick & Hijmans 2017) and more recently LULC models (De Rosa et al. 2016; Alexander et al. 2017), and an overall more robust and critical SDM field. Our study in chapter 5 is therefore an important stepping stone in this trend, as we show clearly that the inclusion of even coarse LULC change projections will result in significant differences when modelling the distribution patters of some bumblebees at the European and BENELUX scales. However, in all the aspects mentioned and including our study many improvements are still possible to increase the usefulness of prospective models of biodiversity patterns.

Land use/land cover change projections must improve. We clearly show that greater thematic resolution of LULC classes influences the modelled predictions of wild bees distributions. In chapter 4 we show that specific LULC classes such as sandy areas, natural grasslands and heathland appear from the models as fundamental LULC types, which support a specific diversity of wild bees. In comparison to the LULC covariates in the present for the Netherlands, the LULC change covariates used in chapter 5 are more thematically coarse. Aggregated classes such as grassland and arable eliminate the nuance of the interaction between wild bees and LULC. However we show that these classes do influence bumblebee distributions even without this nuance. Therefore, the next step requires high resolution LULC change models built using scenarios that include these important LULC classes. We show that while these coarse LULC classes may influence bumblebees, solitary bees are often more specialized and forage in a smaller range and therefore these coarse classes are likely to be inappropriate to model their distributions. These improvements to LULC change models are expected and different methods that will maintain high thematic resolution have been proposed (Rickebusch et al. 2011; Verburg et al. 2011). This means that the work shown in chapter 5 can and should be repeated. As improvements are made to the quality of occurrence, and climate and LULC change models then the same questions proposed here should be revisited with the long-term aim to obtain useful predictions of distribution patterns to influence the conservation of wild bees.

Prospective modelling of biodiversity with SDMs suffers from the same criticism as all SDMs, namely that several elements of the species biology are not taken into account. In particular the dispersal ability of a species and its phenotypic plasticity are important factors for prospective modelling. Whether or not a species will establish in an area depends on the environmental conditions of that area, i.e. if the climate conditions are suitable for the physiology of the species and the LULC offers necessary resources. This aspect is captured by a SDM. However, regardless of whether a habitat is suitable, a species is limited to areas that it can successfully reach based upon its dispersal capabilities. This is a difficult aspect to measure for many species. In chapter 5 we partially account for it by treating bumblebee species with two extremes, either complete dispersal or no dispersal. Our results also tentatively suggest that maybe LULC can act as a proxy for dispersal showing increased limitations for the Northern movement of bumblebees. However, the absence of dispersal in our models is a strong limitation especially as we know that bumblebees are not equivalent in their dispersal capabilities (Darvill et al. 2010; Lepais et al. 2010). This is a fundamental aspect of prospective modelling that needs to be accounted for (Dormann 2007). Including dispersal ability has been shown to improve plant abundance models, especially alongside co-occurrence (Boulangeat et al. 2012) but this requires a priori knowledge of both inter and intra-specific variation in dispersal ability or at least an accurate method to estimate it. Furthermore, the dispersal capabilities of the populations at the leading edge of the range are more important than those across the whole range (Fordham et al. 2012). There are no clear estimates of short-term dispersal capability for the majority of bumblebees, only across evolutionary time periods (Williams et al. 2017).

Alongside dispersal capabilities, a significant assumption of prospective SDMs is that species ecology and behaviour are static and that their relationship to the environment is in equilibrium and will not change in the future (Araújo & Pearson 2005). This is inherently incorrect as we know that species can exhibit significant intraspecific variation and are capable of adapting to changing conditions (Bellard et al. 2012). Therefore, the plasticity and evolution of species is a vital aspect to prospective modelling. For example preliminary work into heat tolerances of bumblebees would provide a more mechanistic view to whether future climate conditions would be suitable for a species (Martinet et al. 2015), and would not rely entirely on the current climate distribution of the species to estimate this tolerance. Early results suggest significant differences between species with a widespread common species such as *B. lucorum* tolerating consistent high temperatures for a long period of time and an alpine species, *B. alpinus*, showing much lower tolerance (Martinet et al. 2015). Other insect species have shown the potential to increase their upper thermal limits (Hoffmann et al. 2013). As with dispersal, knowing the phenotypic plasticity of populations at the leading edges of the range is most important. The plasticity of these populations is likely to strongly influence the persistence of the species under changing conditions (Valladares et al. 2014). However, the speed at which climate change is occurring may negatively impact even the most adaptable species (Gunderson & Stillman 2015). We propose that the true effectiveness of prospective biodiversity scenarios made using SDMs will not be realized until actual knowledge of species behaviour and ecology is consistently incorporated into prospective modelling frameworks.

7.2.2 Community Assembly

Assembly Patterns

Species demonstrate a large amount of intraspecific variation and this may influence their responses to changing conditions. However, species do not exist in isolation and form interacting assemblages, communities and ecosystems. Therefore, to fully appreciate how changing conditions will affect species we need to analyse how and where groups of species form and specifically what factors drive these assemblages. A long-term and ongoing debate in community ecology and biogeography centers around whether a species range is defined by its environment and its physiological and ecological requirements or whether it responds to its interactions with other species representing assembly rules, including competition and facilitation (Cody et al. 1975; Connor & Simberloff 1979). In chapter 4 we quantified and described the factors that influence the assemblages of wild bees in the Netherlands. The results show that the relationship with the environment drives the majority of the patterns observed but that species co-occurrence explains additional variation in the observed distributions of wild bees. The relationship between different wild bee species was estimated during the modelling process and no prior knowledge of competitive or facilitative interactions was included.

Biotic interactions in species assembly has been shown to be an important factor in separating the realized niche, actual space an organism inhabits, from the fundamental niche, environmental conditions in which the species can survive (Hutchinson 1957). The single species SDMs used in chapters 3 and 5 use only covariates which estimate the fundamental niche of the wild bees, i.e. climate and LULC conditions, while in chapter 4 we explored the co-occurrence structure of wild bee assemblages, a closer estimate of the realized niche. The results from chapter 4 indicate that there are aspects of the community assemblages of wild bees that we do not capture when looking at the fundamental niche alone. Due to limitations on data quality and availability the models run in chapter 4 were limited to a resolution of 10 × 10 km. The effects of species interaction, particularly competition, on community assembly are likely to be more visible at finer resolutions (Araújo & Rozenfeld 2014; Thuiller et al. 2015). This might indicate why we observe only positive interactions between wild bee species, which could be a landscape resources shared by the species but not captured exactly at the resolution modelled and with the covariates selected. Furthermore, we see a similarity in niche for closely related species but co-occurrence is not significantly more likely. At finer resolutions both geographically and in thematic resolution of LULC covariates we might expect to see a more clear representation of the community including competitive interactions between wild bee species around nesting or floral resources. We would also need to test the role of phylogenetic relatedness at finer resolution, to see if the correlation between habitat filtering and phylogenetic relatedness persists and whether we can see more clearly if closely related species actually co-occur more or less than expected by chance. We would hypothesize that competitive interactions, at the fine scale, are likely to be greater for closely related species than distantly related species.

Chapter 6 also includes community patterns and tentatively explores whether mutualistic interactions between species (plants and pollinators) lead to similar responses to environmental changes. There is also a large body of literature which suggests that facilitative interactions between species are more apparent in community assembly in stressful conditions, such as high elevation habitats where extreme environmental conditions may be responsible for delimiting species (Bertness & Callaway 1994; Michalet 2005; Cavieres et al. 2016; D'Amen et al. 2017). There is also evidence that as these extreme conditions increase the likelihood of facilitative interactions then the likelihood of competitive interactions may decrease (Callaway et al. 2002; He et al. 2013). While we do not specifically test this hypothesis we see evidence that the community from 1889 has not shifted in unison over 115 years but specific species of bumblebees, day-flying Lepidoptera and wild flowers have shifted. However, the results do suggest that plants and pollinators may have shifted together. The facilitative interaction between plants and pollinators may also explain the influence of the positive co-occurrence between wild bee species observed in chapter 4.

Role of traits in distribution patterns

Another way to group and define communities is based on the traits found in different assemblages. Trait based ecology has been a steadily growing field in response to the limitations of purely taxonomic approaches. The application of trait-based ecology to terrestrial arthropods is often a necessity because of extreme diversity found in the phylum (Wong et al. 2018). In the case of globally diverse groups like wild bees the results presented in this thesis could be applicable in other areas of the globe. Specifically, the hope is that well-studied areas with a less diverse fauna, i.e. the Netherlands, could produce results and patterns that at the trait level could be transferred and applicable to areas with a more diverse and less well-studied wild bee fauna. However, we would hesitate to say that the results of our studies that include traits are sufficient to allow us to predict wild bee responses to the environment in the Netherlands, let alone for other locations. This hesitation stems from the fact that it is difficult to determine whether observed patterns in the relationship between traits and distribution modelling or habitat filtering are processes that are inherent to the group of wild bees or if they are a response to the factors driving the patterns of distribution. A potential cause of this is that we do not define, a priori, the traits that may present a greater response to the different, for example we could have hypothesised that nesting traits and feeding traits may show a clearer relationship with environmental drivers than traits related to demography. The incompletely supported assumptions associated with trait-based plant ecology are transferable to trait-based insect or bee ecology as well. Namely, we do not have a clear picture of whether wild bee functional traits link to actual measurements of fitness. We also do not take into account intra-specific variation in traits and the degree to which functional traits show a general measurable relationship to environmental conditions is not always supported (Shipley et al. 2016).

In chapter 3, we see that wild bee species can be grouped together based on their traits and that highly specialized bees are likely to be better captured by SDMs in agricultural locations and large generalists less so. However the distinction we made when grouping species could always be extended. In the case of chapter 3 we see clearly that bumblebees are separated into their own functional trait group but even within the bumblebees distinctions can be made based on, for example, their degree of habitat and feeding specialization. In chapter 6 we see that elevation distributions are linked to the habitat specialization of bumblebees. This is reinforced by the results of chapter 4, where we see that species are structured taxonomically in their responses to LULC and climate defined habitats/'niches' but that the included traits do not capture this adequately. This implies that our selection of traits is not an efficient proxy for the patterns shared by taxonomically similar species. In other words, these traits are not sufficiently phylogenetically conserved[2] (Freckleton et al. 2002). One explanation as to why we do not see a strong pattern from shared functional traits is that maybe these traits do not actually have a high degree of functionality and consequently do not influence evolutionary history of the species enough to have an observable effect (Shipley et al. 2016). Trait responses can differ significantly to phylogenetic responses if the trait shows a weak phylogenetic signal. This has been observed for diversity losses and its relationship to body size in mammals (Fritz & Purvis 2010). This is supported by results of wild bee diversity losses in Europe, which were more or less extreme depending on whether phylogenetic, functional or species diversity was measured (De Palma et al. 2017). Furthermore the sensitivity of wild bee species to LULC was explained in part by species traits but this was not consistent across LULC types (De Palma et al. 2015). Therefore, our attempt to relate niche characteristics to sets of similar traits may be somewhat too complex for the traits we had available to us.

We hypothesize that traits more closely related to actual feeding behaviour and flower choice would result in clearer relationships with habitat suitability and distribution patterns. One such example would be actual tongue length of wild bees which is highly related to the flowers visited (Obeso 1992; Michener 2000). In chapter 6 we use tongue-length of the different bumblebee species and the species with the longest tongue and most specialized feeding habit was one of the species to most shift in elevation. Furthermore, wild bees differ in their methods to collect and store pollen, for example bumblebees use a corbicula, a basket like structure on the tibia to store pollen while many solitary bees

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[2] Phylogenetically conserved indicates how far back in time a trait is found among all organisms in a clade. A highly phylogenetically conserved trait is shared by organisms in larger, older clades, whereas a trait which is less phylogenetically conserved is shared among organism in smaller clades (Martiny et al. 2012).

use a set of dense hairs called scopa (Michener 2000). The location and complexities of these structures can differ a lot between species and can help species avoid competition, for both plants and bees (Michener 2000; Ruchisansakun et al. 2016). Nesting habit could also be expanded from the modest classifications used in this thesis. Greater information on the actual substrate used would more closely resemble landscape requirements (Cane 1991). These traits may better capture the difference and similarity between species that separate them at the finest scale.

7.2.3 Land Use/Land Cover and Climate Effects

The availability of nesting and feeding resources is what defines the suitability of a landscape for wild bees. These necessary conditions can occur at an incredibly fine scale and be highly species specific (Michener 2000). This degree of accuracy when estimating and predicting LULC from aerial photographs and satellite images is not yet feasible. Therefore, we have to use more broadly defined LULC as proxies for wild bee suitable habitat. The limitation of the thematic resolution of LULC increases when we analyse the past and the future instead of the present. In chapters 3 and 4 we had access to present day LULC maps which allow for a number of specific LULC classes. We show that specific natural habitats are of extreme importance for distinct wild bee species and assemblages. Natural and semi-natural habitats act as a source of wild bees for crop pollination services (Öckinger & Smith 2006; Garibaldi et al. 2011; Klein et al. 2012; Le Féon et al. 2013; Kleijn et al. 2015), however the inherent value of these areas for maintaining a high or distinctive biodiversity are less well studied. We show in chapter 4 that, by looking at occurrence records collected within these semi-natural habitat types, they can account for distinct assemblages of wild bees. The results illustrate the relevance of using a nationwide database of wild bee occurrences and not being limited to surveys from particular habitat types. Additionally, conservation of wild bees often focuses on the improvement to already intensively managed landscapes (Goulson 2003a; Winfree 2010; Kleijn et al. 2018). Whereas we show that the diversity of wild bees in the Netherlands would only be conserved adequately if the unique semi-natural habitat types are maintained. The species which contribute to this uniqueness are often not included among the most abundant crop pollinators (Kleijn et al. 2015), however, these species may influence the behaviour and effectiveness of the more abundant pollinators and their role in crop pollination may change across temporal and geographic scales (Garbialdi et al. 2013; Winfree et al. 2018). Often these rarer species have highly specialized interactions with their habitat, which results in them being more accurately modelled by SDMs in chapter 3.

For the past and future the available thematic resolution of the LULC covariates is significantly lower than for the present. This is because the scenarios were developed to examine the principle LULC classes of Europe, resulting in 6 classes (See section 2.2.2; Rounsevell et al. 2006). This means we are less able to focus on particular habitat use and instead examine how climate and LULC changes over time may influence wild bee distribution patterns. Potts et al. (2016b) in their assessment report of the current state of pollinator and pollinations conclude that “there remain relatively few published assessments of the combined effect of land use and climate change on pollinators and pollination”. With this thesis we make a contribution to fill this gap. Specifically, regarding the interaction and connectedness between the two drivers we show clearly that, even at low thematic and spatial resolution, the inclusion of LULC change alongside climate change results in significantly different future projections for certain bumblebee species. We observe that incorporating LULC change does not only influence the distribution patterns within the climate envelope already defined by the model, but also that for certain bumblebee species LULC change can either enhance or mask the effects of climate change. Clavero et al. (2011) find similar results; they show that the present climate range occupied by Catalan breeding birds significantly differs depending on the LULC occupied, therefore any changes to the LULC would also directly affect the climate range of the community. The results presented in this thesis reinforce the importance of LULC as an indicator of habitat suitability for wild bees but more importantly emphasize the necessity to include LULC changes in future biodiversity scenarios because not only does LULC change alter the distribution patterns within a climate range, it may also result in a shift of the full projected range. In general the interaction between climate and LULC changes suggests smaller ranges for bumblebees in the future. Therefore, the results can be added to the list of studies showing that biodiversity loss is greater when the interaction between LULC and climate change is included in future scenarios (Jetz et al. 2007; Barbet-Massin et al. 2012b; Riordan & Rundel 2014; Sohl 2014; Visconti et al. 2016). The dialogue around this subject should therefore shift from whether or not to include LULC change covariates, to how to produce better LULC change projections with a clear temporal dimension for use in biodiversity scenarios (de Chazal & Rounsevell 2009; Titeux et al. 2016).

We also observe in chapter 6 that in a 115-year period both significant LULC and climate changes can occur. Therefore, when looking at a snapshot of two single years it becomes difficult to separate the drivers of the observed shift in wild pollinators. Ongoing climate changes and LULC changes are difficult to separate and are likely to be interactive. Climate changes are likely to influence LULC changes and vice versa. However, in chapter 6 we see evidence that climate change and elevation shifts are occurring together. This matches a number of other studies which suggest climate change may be driving the observed shifts in elevation in mountainous areas (Chen et al. 2009; Franzén & Öckinger 2012). However, aspects such as deforestation or land abandonment in mountains may result in precipitation or temperature increases (Fairman et al. 2011; Payne et al. 2017), therefore, as we observed for the future, the changes affecting wild bees are unlikely to be occurring in isolation. For an area like the Netherlands which does not have climate extremes but does have a long history of LULC changes we see that the majority of the variation in wild bee niches is explained by LULC rather than climate, this is unlikely to be consistent in areas where the climate varies to a greater degree across smaller geographic areas, such as mountainous areas. Our results show, based on the responses of wild bees, that the influence of LULC and climate will not be consistent at different geographic and temporal scales, however we can confidently state that climate is unlikely to be the only important driver of biodiversity change.

7.3 Implications

The results presented in this thesis can be expanded upon to provide implications for research and society in general. We separate the implications of this thesis into three main areas (1) methodological, (2) wild bee research and (3) wild bee conservation. We outline here how our understanding of these areas has increased or changed based on the results presented in the thesis.

7.3.1 Methodological

Chapters 3, 4 and 5 reinforce the idea that the realized niche of species is unlikely to be accounted for by the climatic envelope alone. This implies that when modelling species distributions researchers should take into account more aspects of the habitat requirements and the ecology of the species they are modelling. Therefore, when available LULC covariates should be included along with species interactions. The main implication of chapter 5 is that LULC variables, even when of low thematic resolution, will be important when defining the present day 'niche' of species and changes to those LULC classes will result in different projected futures for the bees. We hope therefore that the results presented will encourage researchers looking at biodiversity scenarios in the future to include LULC change projections.

However, the results also imply that from a modelling perspective a one size fits all approach is likely not suitable and researchers should implement species-specific modelling where applicable. Adapting a modelling approach per species is time consuming but fitting multiple models and including a priori information of the species ecology will improve modelling performance. For example, mountainous bumblebees may be adequately modelled with climate covariates but a widespread parasitic bumblebee will be better modelled taking into account the range of its host (Suhonen et al. 2015, 2016). Unfortunately, as we show in chapter 4 if we want to estimate co-occurrence importance for many species it is not possible to have a species by species modelling process, and therefore some models may be of low performance. An ideal situation for modelling wild bees would involve having a clear understanding of the mechanisms driving their distributions. Specifically, that would involve knowing a priori the relationship between the fine scale environmental conditions, the interactions with other species (bees and other organisms) and the direction of these interactions, facilitative or restrictive. Overall, this represents a technical and analytical barrier to modelling a group of species. The best model for a species will always include all the parameters relevant to its specific niche, however, to model a group of species it is necessary to use a subset of important, shared parameters. This means that when modelling multiple species we increase the ability to compare between species but at the same time are likely to decrease in model accuracy per species.

The results from chapter 3 additionally imply that whilst using independent collections to test model performance is the ideal situation (Elith & Leathwick 2009), this is not easily accomplished with wild bees. Model performance differs depending on the methods used to collect species with pan traps and transect netting resulting in different collections. It is well known that different collections methods result in different estimates of a wild bee community (Westphal et al. 2008) and therefore our research implies that to ensure sampling of the rarest and most specialized species, for a testing or training dataset, sampling intensity should be high and expertise is required.

7.3.2 Wild bee research

Wild bee communities are difficult to sample in their entirety, small, specialized bees which are active for only a short part of the year can easily be missed when sampling (Westphal et al. 2008). Therefore, an implication of this thesis and potential limitation is the indication that more wild bee occurrence records are required to obtain a detailed overview of all wild bee diversity. Models are made to deal with incomplete databases of occurrences but generally the conclusions and results will be improved if the models are trained with more detailed surveys (Braunisch & Suchant 2010). Even in well-sampled areas such as the Netherlands and other part of Western Europe there remain many wild bee species for which we do not have a clear enough picture of their distribution and habitat requirements. In chapters 3 and 4 when we select species based on a certain number of records in recent years we are limited to a Dutch wild bee fauna of 193 or 204 species of an expected approximately 300-350 species (Peeters et al. 2012). This implies that the methods and conclusions presented in this thesis may be irrelevant for the rarest and possibly most endangered species. There is no simple solution to this issue as the rarest species are difficult to observe regularly and cannot be sampled in large numbers. This indicates why there are few long-term studies of wild bee decline and the majority are from North America or Europe (Potts et al. 2016b). One way to improve this is to find and repeat more historical studies. Our results from chapter 6 imply that we can observe interesting changes in communities when repeating historical studies and that more effort should be made to find and digitize old collections, particularly in countries outside of North America and Europe. However, there is certainly a positive trend associated with the number of collection records, and technological advancements are improving their quantity and accuracy. This thesis illustrates the importance of long-term records of species distribution patterns. The results presented would not be possible without having the presence of large databases of species records (Shaffer et al. 1998).

However, even with an imperfect database of wild bee collection records the results presented have clear implications regarding wild bee research. The results of chapter 5 imply that bumblebee species in Europe are likely to have smaller ranges and more fragmented habitats in the future if LULC change projections are included alongside climate changes. This more pessimistic projection of the future also indicates that the assumption that bumblebee species will disperse further north at their northern boundaries, as presented in climate only projections (Rasmont et al. 2015a), may be unrealistic. Combined with the results of chapter 6, that support the conclusion that some southern European bumblebees are increasing in elevation (Kerr et al. 2015), we can conclude that distribution patterns of bumblebees are not easily grouped together and that to be able to adequately conserve them we must account for greater gradation in their relationships with the environment and each other. This is supported by chapter 4's conclusion, that for all wild bees multiple factors affect the community assemblage structure and conservation groupings. In other words the results of this thesis illustrate clearly the complexities of wild bee distribution patterns and indicate that future research should focus on these complexities.

7.3.3 Conservation of wild bees

The results presented in this thesis provide some clear implication related to the conservation of wild bee species. Wild bee conservation is a topic that has been brought into focus in recent years as more information of honeybee declines and wild bee declines and their potential causes permeates everyday news. This evidence is often distorted in the mainstream media; honey bees and pesticides are often given the majority of focus when they represent only a single species and a single driver (Vanbergen & The Insect Pollinators Initiative 2013; Geldmann & González-Varo 2018). We hope that the results in this thesis illustrate the subtleties of wild bee distribution patterns and their conservation requirements. However, it is clear that it is an unrealistic goal to collect and monitor all populations in a certain area. Therefore, we need to find ways to group species together and simplify the complexity whilst still maintaining precise directed conservation initiatives. The models in chapter 4 provide assemblages which can be considered as conservation units at the Dutch scale. These assemblages correspond to particular habitat types that can be, and in many cases are already, conserved. These areas are rarely conserved with the direct goal of conserving wild bees, but for other aspects of biodiversity and ecosystem services. The results imply that they are home to unique wild bee assemblages and therefore monitoring wild bee populations and making this information accessible could provide additional support to the efficacy of these conservation measures. In chapter 5 this is reinforced as we see that when accounting for LULC change, areas of particular importance for wild bees become smaller, demonstrating that these models may indicate refuges for bumblebees in the future when using the correct information at the appropriate scale.

The clearest conclusions concerning distribution patterns at a species level are found for more specialized species. In chapter 3 the distributions of habitat and feeding specialists are better accounted for using SDMs than more generalist groups. We also see that in chapter 4 the species that define assemblages are often specialized in certain habitats and in chapter 6 we see that elevation patterns in bumblebees are correlated with a species degree of habitat specialization. These results imply that specialized species could be useful as indicator taxa for conservation. In other words these species should be monitored, and increases and decreases in their ranges and abundances may indicate overall well-being of the wild bee community (Carignan & Villard 2002). Lõhmus and Runnel (2018) however advise against putting too much value in indicator taxa, they show the value of an indicator can vary depending on survey effort and that covariation between species may not be a sufficient factor to justify an indicator species. Additionally, chapter 4 results imply that phylogenetic relationships may also be used to conserve species. For example species of the same genera may have similar environmental requirements and protecting these requirements could benefit the entire genera of wild bees.

7.4 Future Research

The results presented in the thesis indicate a number of research avenues that warrant exploration in the future. These avenues concern both methodological and applied research. We show clearly in this thesis that including LULC within SDMs improves our ability to predict wild bee distributions. However, the coarse LULC included in chapters 5, and 6 and even the higher thematic resolution LULC in chapters 3 and 4 still only act as a substitute for the actual mechanisms which cause a wild bee to be present in one location and not another. Therefore, using remotely sensed and mapped LULC and LULC change models, which are both continually improving in accuracy and resolution (Congalton et al. 2014), we should be constantly testing and comparing our predictions of species distribution with LULC maps of different thematic resolution. The current detail of LULC maps for the present and future are not equivalent in number of classes. For the future we should be using LULC change models which incorporate variables similar to those used in chapter 4, we know that more specific LULC classes such as heathland, dunes, and the separation of agricultural and semi-natural grasslands are important, therefore we should use models which project how these habitat types may change in the future. Direct future research that we hope to engage in will build on the results of chapter 5 and use LULC change projections with higher thematic resolution to model bumblebee distribution patterns until 2050 for Belgium. This includes using maps of how agricultural land use at the parcel level is likely to shift (Beckers et al. 2018) as well as how fine scale natural land cover elements may change in the future in Belgium (Vanderhaegen et al. 2015). Furthermore, we aim to explore not only the effect of higher thematic resolution on Bumblebees but also sweat bees (family: Halictidae). Sweat bees include a number of solitary wild bee and are often smaller and more specialized (Michener 2000). Therefore, they are likely to have a finer scale relationship with LULC covariates and we aim to test if they respond differently from bumblebees in the future when modelled with higher thematic resolution.

The current need is for clearer separation not only in LULC categories but also accounting for variation in quality and management of certain LULC classes. For example, organic farms often support a higher wild bee diversity (Holzschuh et al. 2008; Happe et al. 2018), and oil seed rape is an important food source for wild bee as it is a late-season, mass-flowering crop (Westphal et al. 2003). Being able to include and compare organic fields to conventional fields, or late season and early season crops, may provide a greater accuracy when predicting wild bee distributions. Therefore, next research steps should look at comparing SDMs that include land use management against models which only include LULC.

The methodology used in this thesis is focussed around statistical modelling techniques where we have examined the relationships and response of many species to differences and changes in explanatory factors. However, there is a clear role for process based models to deal with the research needs identified in this thesis. Specifically, we identify that a greater understanding of morphological, physiological, and behavioural knowledge of wild bee species would provide key information to concentrate the statistical/correlative models within a predefined range of possibilities. Statistical models would clearly benefit from greater understanding of the traits, fitness components and habitat requirements of wild bees (Kearney & Porter 2009). For example, standard operative environmental temperature models [3].can be used to estimate the thermal biology of insects and allows for the comparison of thermal stress in different environments (Dzialowski 2005; Kearney & Porter 2009). These models have previously been used to test activity levels diurnally for Euglossine bees (Armbruster & Berg

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[3] "Standard operative temperature relates heat loss from an animal in a complex thermal environment to a reference laboratory environment" (Dzialowski 2005)

1994). However, these models also require realistic ranges of species environmental conditions for calibration, in this case more correlative models can be useful in providing these limits (Dzialowski 2005). Additionally, the knowledge of clear biotic interactions, for example wild bees which feed exclusively on one plant species or parasite bees with a single host could lead to more process based correlative models, where the species dependent on the other is modelled only with the known range of its food source or host.

Agent-based models which examine behavioural and physiological responses at the individual level can provide Agent-based models have only very recently been applied to wild bee species. Becher et al. (2018) has produced a model for six bumblebee species which can simulate colony dynamics and foraging within a spatially explicit landscape. The outputs from these models for these six species could provide additional information regarding the carrying capacity of certain habitats and fine scale dispersal. This information can either support or contradict habitat suitability maps from SDMs by indicating the type of habitats which can support a greater number of colonies. Furthermore, when high-resolution pesticide maps are available for correlative modelling these models could provide a priori estimates on pesticide exposure allow the statistical model to limit the response of species to within their known ranges. In the future however, a key requirement to be able to use more process based models would be to move away from the focus on model bee species, such as *A. mellifera* and *B. terrestris* and conduct more physiological and behavioural experiments on non-managed wild bees.

There is also the possibility of the results presented here providing useful information for process based models. For example the results presented in chapter 4 provide estimates of species pairs that share a response to an unknown latent factor, these correlations could be used to estimate and assume a priori interactions between species. Furthermore, where we observe a strong relationship between a particular habitat and species this information could provide additional support to process based models of habitat use among wild bees.

Furthermore, new technologies such as LiDAR provide three-dimensional representations of the landscape in the form of vegetation structure (Bergen et al.

2009; He et al. 2015). In the future it would be interesting to explore the ability of vegetation structure, as a covariate, to accurately model wild bee abundance. We would hypothesis that, when correctly calculated, covariates of vegetation structure may be able to distinguish between similar LULC classes of differing quality. The effectiveness of vegetation structure covariates, to model diversity, has been shown for butterflies in the Netherlands (Aguirre-Gutiérrez et al. 2017b).

Higher resolution of land use classes that capture the fine scale differences at the landscape level relates directly to another area that needs to be explored for wild bee distribution modelling. Specifically, that all bee species visit flowering plants as a food resource. High-resolution information of wildflower occurrences exists for many locations. A simple first examination of the importance of wild flowers for wild bees would involve SDMs using plant distributions at the family or genera level to predict wild bees patterns, as has been shown for specialist wild bees in Brazil (Giannini et al. 2013). A more complex analysis would build upon the results of chapter 4. It would be possible to use the HMSC framework to examine the role of co-occurrence and predict not only wild bee assemblages, but also whole communities of plants and pollinators. This could even be extended to include below ground co-occurrence with arbuscular mycorrhizal fungi species; which have been shown to minimize disruptions in plan-pollinator communities (Bennett & Cahill Jr 2018). Modelling whole communities increases the link to ecosystem functioning and potentially estimating services in unknown areas. The next step would be to model the distributions of co-occurring species concurrently, and project these models on to future conditions to improve accuracy and usefulness of biodiversity scenarios.

The results from chapter 4 also demonstrate the importance of accounting for wild bee interactions when trying to interpret community assembly patterns. Our results imply that there is still a large amount of work necessary to determine what is driving these positive interactions. Are the positive interactions driven by a shared resource at coarser spatial resolutions? Are there competitive interactions at finer scales? Therefore, research into wild bees needs to take interactions between wild bee species into account. A first step would be to see if we are capable of modelling the interactions between hosts and parasites accurately. This has been shown somewhat for bumblebees but remains a significant gap for other wild bees (Giannini et al. 2013; Suhonen et al. 2015, 2016). Host parasite relationships often demonstrate significant chemical similarities (Michener 2000), and therefore are likely to be a more essential factor for the distribution of the two species than shared environmental conditions. The knowledge about wild bees and their parasites is often imprecise and parasites may have multiple hosts and vice versa. Therefore, a first step would be to focus on highly specialized host parasite relationships, testing if the latent effects in the HMSC framework capture these relationships and then modelling the species in conjunction. Finally, a number of papers have observed that biotic interactions, and in particular facilitation, between species is likely to be stronger in severe environments (Bertness & Callaway 1994; Callaway et al. 2002; Michalet 2005; He et al. 2013; Cavieres et al. 2016; D'Amen et al. 2017), therefore we propose to repeat the analysis in chapter 4 for species communities (including flowering plants) across a more extreme abiotic gradient for example a habitat similar to that explored in chapter 6. The majority of the studies that show these patterns are focused on plants and evidence from pollinator assemblages or a plant-pollinator community would represent novel research.

In this thesis we focus on the interaction between LULC and climate change as drivers of wild bee decline. We know that there are a number of other drivers, including pesticide use, pathogens and invasive species (Potts et al. 2010; Vanbergen & The Insect Pollinators Initiative 2013). Future research should address the multiple effects of all drivers in combination including their impacts on wild bee declines but also there interactions and additive effects (Potts et al. 2010). These goals are limited by the quality of the data, and whilst there is widespread collection data as well as LULC and climate maps, we do not have access to long-term data regarding genetic diversity of bees, pesticide use or disease prevalence and the data available is often geographically restricted (Maebe et al. 2016; Schoonvaere et al. 2018). Detailed data mining and analysis is required to find sufficient data to look at the interaction between multiple drivers at sufficiently large spatial and temporal scales.

Finally, a fundamental research step in the future involves collecting more data on wild bee occurrence, particularly from under-sampled areas. One way to improve occurrence data is by using high quality citizen science data. The work presented in this thesis depends on large quantities of high quality occurrence data and utilized databases with a number of citizen science records. The cryptic morphology of many wild bee species means that citizen science effort will never be 100% accurate (Williams 2007; Carolan et al. 2012). However, alongside high quality photos and experts to verify collections there is the potential to produce far more records than are currently available. Citizen scientists are also a vital resource for digitizing historical collections (Beaman & Cellinese 2012). Historic collections are necessary for examining diversity and distribution trends over time, including pollinators (Bartomeus et al. 2018). Future studies search the literature for historical wild bee collections from areas that have not been sampled in recent times, such as the study conducted by MacLeod presented in chapter 6 (MacLeod 1891). There are many historical records in museums or even recorded in old publications that are yet to be digitized (Scoble 2010). Combining these records with modern wild bee monitoring schemes could provide datasets they will be incredibly useful in answering question regarding changes to the diversity and distribution of wild bees throughout history.

7.5 Final Conclusion

The overall objective of this thesis was to examine how land use/land cover (LULC) and climate conditions affect the diversity and distribution patterns of wild bee species at different spatial and temporal scales. In this thesis we explored the impact of LULC and climate alongside other factors using historical records and statistical techniques to show how present day distributions of wild bees in the Netherlands can be modelled and how bumblebees may show changes in diversity and distribution due to climate and LULC changes. Our results indicate that species distribution models (SDMs) vary in their accuracy depending on the wild bee species and locations being predicted. However, wild bees do not occur in isolation from each other and we observed that combining wild bee species together in a joint SDM (JSDM) approach shows significant positive patterns of co-occurrence that explain additional variation of wild bee distributions to that explained by environmental conditions alone, and in turn that there are phylogenetic groupings that influence the distribution of wild bees. This indicates a complex system, which rejects the idea that wild bees can be conserved as a single homogeneous group. The influence of LULC on present day wild bee distributions in the Netherlands, imply that LULC covariates are of importance in explaining changes in diversity and distribution of wild bees over time as well. We tested this for the future at broad temporal and geographic scales showing that dynamic LULC covariates significantly affect the projected distribution patterns of European bumblebees under different scenarios modelled until 2100, often resulting in even more restricted distributions. At a finer geographical scale but also over a long time period (1889 -2005-06) we see that high elevation populations of bumblebees and their host plants exhibit an overall shift uphill that is associated with measured climate changes and directional LULC changes, but that some species have shifted dramatically while others did not shift at all. Throughout all four studies we see that specialized species often respond differently than more generalist wild bee species, frequently showing clearer statistical trends. Furthermore, there are species-specific differences that can be difficult to capture using traits or phylogenetic relatedness.

Considering these studies collectively we are able to show the importance of historical collections for measuring trends in biodiversity, as well as providing advice for conserving wild bees. In conclusion this thesis has explored a set of distinct questions united by the common theme of modelling wild bees and their interactions with the environment through space and time. These results are not exhaustive but provide evidence to fill gaps in the knowledge of wild bee distributions. The results also provide clear opportunities for future research including more detailed information on wild bee dispersal, preferences, and interactions and to examine the drivers of decline together and not in isolation. Wild bees are declining and face a number of threats, we hope that the results presented here can in a small way influence the conservation of wild bee species and ensure the persistence of high diversity wild bee communities which have an intrinsic worth as well as provide important benefits to society.

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A – Appendix

A.1 Nederland Zoemt

Nederland Zoemt is a project from LandschappenNL, Naturalis Biodiversity Center, IVN and Natuur & Milieu with the aim of *"structurally increasing the food and nesting resources for wild bees in the Netherlands"*. A specific objective of the project was to create region-specific advise for monitoring and protecting wild bees. These advises should be usable across the country by local governments, educational facilities, contractors, green workers and gardeners. Furthermore, these plans should be used in conjuction with citizen science monitoring programs and an application outlining the suitable bee plants present in the Netherlands. The best way to implement these advises was to create them at the municipality level.

During my PhD we produced a wild bee advise document for each of the 388 municipalities in the Netherlands. The wild bee occurrence data from Chapters 3 and 4 were used to create a list of all species which have been found in a municipality since 2000. This list was then extended using species distribution models (SDMs) to show which 'extra' species have suitable habitat within the municipality. Each SDM is projected onto current conditions and each projection produces a map of suitable habitat at the scale of the Netherlands. These habitat suitability maps are then simplified into presence absence maps by creating a threshold which converts areas of high suitability to a one and areas of low suitability to a zero. We then published a map showing areas of high and low wild bee habitat suitability for the whole municipality. Furthermore, for each municipality we made a list of 'special' species (rare species with a clear ecological role) which have been found previously, and give clear guidelines for their management. Finally, the document contains general management advise for wild bees applicable across the country.

An example document for the municipality of Leiden is presented below. All muncipality documents are avaiable to download at `www.nederlandzoemt.nl`.

Advies voor Leiden

Suggesties voor het verbeteren van de leefomgeving voor wilde bijen in jouw gemeente

Dit advies is specifiek voor jouw gemeente opgesteld binnen het project Nederland Zoemt. Hierin geven we een beeld van de bijen die in jouw gemeente gevonden zijn of zouden kunnen voorkomen en van de bijenhotspots in de gemeente. Daarnaast geven we suggesties voor het verbeteren van de leefomgeving voor wilde bijen. Om dit advies op te stellen is gebruik gemaakt van waarnemingen die tussen 2000 en 2017 zijn gedaan door heel Nederland. Dit advies is een mooi begin om bijvriendelijke gemeente te worden. Als je nog aanvullend advies of monitoring uit wil voeren, vind je hier de partijen om bij aan te kloppen.

De wilde bijen in Leiden

Kennis over bijen in Nederland komt van verschillende databronnen, waarbij niet elke gemeente even goed onderzocht is. In jouw gemeente zijn 613 **waarnemingen** gedaan[1] van in totaal 68 **verschillende** soorten (achteraan dit document vind je daar een lijst van). Bij goed beheer voorspellen wij dat de leefomgeving potentieel voor 87 **soorten** geschikt is. Hieronder staat een overzicht van wilde bijen groepen die gevonden zijn, en het totaal aantal wilde bijen groepen die bij goed beheer voor zouden kunnen komen (potentieel).

Soortgroep	Gevonden	Potentieel
Behangersbijen	3	3
Bloedbijen	3	5
Bonte viltbijen	0	0
Dikpootbijen	1	1
Ertsbijen	0	0
Groefbijen	10	11
Hommels	8	11
Houtbijen	1	1
Kegelbijen	0	0
Klokjesbijen	1	1
Langhoornbijen	0	0
Maskerbijen	3	5
Metselbijen	2	5
Mortelbijen	1	1
Pluimvoetbij	1	1
Roetbijen	0	0
Rouwbijen	1	1
Sachembijen	1	2
Slobkousbijen	1	1
Tronkenbijen	1	1
Tubebijen	1	1
Viltbijen	0	0
Wespbijen	9	11
Wol en Harsbijen	1	1
Zandbijen	17	22
Zijdebijen	2	2
Totaal	68	87

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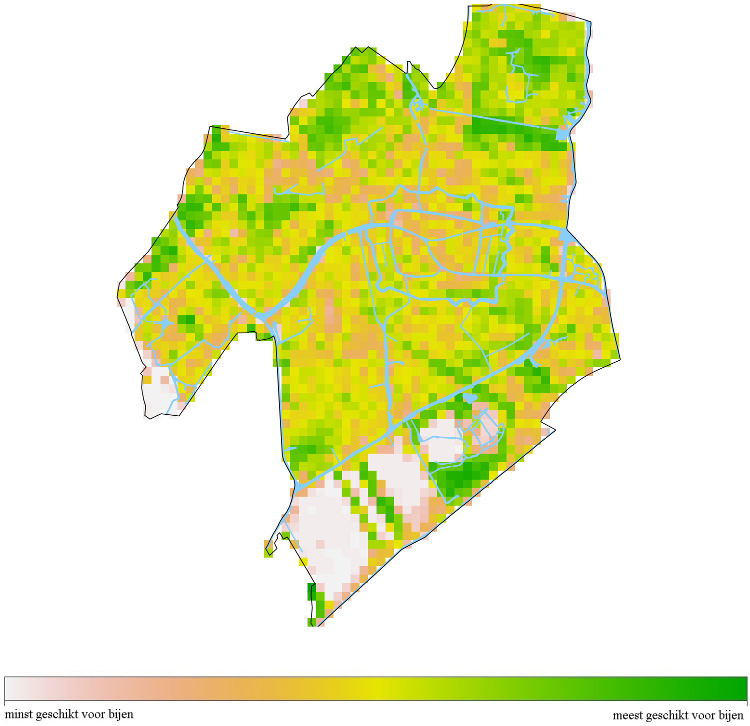
[1] Er zijn niet in elke gemeente evenveel waarnemingen gedaan. Als hier weinig waarnemingen staan, wil dit zeker niet zeggen dat er in jouw gemeente weinig soorten voorkomen, het kan ook zijn dat er weinig waarnemers actief zijn.

Bijenhotspots in Leiden

Onderstaande kaart voorspelt voor jouw gemeente hoe geschikt de omgeving is voor wilde bijen. De voorspelling is gedaan op basis van het landschapstype en klimaatdata. De groene stukken hebben de hoogste potentie voor bijen, terwijl de witte stukken volgens onze modellen minder geschikt zijn. Het instandhouden en uitbreiden van de groene stukken is van groot belang voor de wilde bijen. Daarnaast liggen er op de witte plekken dus kansen voor verbetering, bijvoorbeeld door bijvriendelijke planten te plaatsen, het beheer aan te passen en de agrarische sector te betrekken.

Mogelijk onderneemt jouw gemeente al veel actie in bepaalde gebieden, maar zie je dit niet terug op de kaart. Dat komt omdat wij in onze landschapsanalyses deze lokale initiatieven niet mee hebben kunnen nemen.



Speciale soorten in Leiden

Voor de wilde bijensoorten hieronder heeft jouw gemeente een speciale verantwoordelijkheid, omdat deze relatief vaak gevonden zijn en een relatief groot deel van het geschikte gebied voor deze soort in deze gemeente valt. Door rekening te houden met de wensen van deze soorten kan de gemeente sterk bijdragen aan het behoud van deze soorten voor Nederland.

1. Lichte wilgenzandbij (*Andrena mitis*): Nestelt op open, zandige plekken. Is afhankelijk van wilgen als voedselbron met name Grauwe wilg en Schietwilg, De soort kan gevonden worden tussen mrt-jun.
2. Fluitenkruidbij (*Andrena proxima*): Afhankelijk van dolle kervel, fluitenkruid en zevenblad. Te vinden op heide en ruderale, voedselrijke graslanden. Ze nestelen op begroeide plekken. De soort kan gevonden worden tussen apr-aug.
3. Roodbuikje (*Andrena ventralis*): Leeft van wilgen en maakt haar nest in zanderige, lichtbegroeide grond. Nest en wilgen moeten in een straal van maximaal 210m van elkaar zijn. De soort kan gevonden worden tussen mrt-mei.
4. Grote klokjesbij (*Chelostoma rapunculi*): Nestelt in bestaande gaatjes, bijvoorbeeld gemaakt door keverlarven. Is volledig afhankelijk van bloemen uit de klokjes familie. De soort kan gevonden worden tussen mei-aug.
5. Wormkruidbij (*Colletes daviesanus*): Is afhankelijk van bloemen uit de composietenfamilie, met name boerenwormkruid en jacobskruiskruid. Ze kunnen zelf nestelplaatsen maken in de grond, maar kunnen ook in bijenhotels met gaatjes van 6mm nestelen. De soort kan gevonden worden tussen jun-sep.
6. Resedamaskerbij (*Hylaeus signatus*): Is afhankelijk van reseda en nestelt in holle stengels. De soort kan gevonden worden tussen mei-sep.
7. Klokjesdikpoot (*Melitta haemorrhoidalis*): Is afhankelijk van de klokjesfamilie en nestelt in de grond. De soort kan gevonden worden tussen jun-sep.

Aan de slag met bijvriendelijk beheer

Wil je je gemeente bijvriendelijker maken? Dat kan door te zorgen dat er altijd voedsel en nestgelegenheid voor wilde bijen aanwezig is, het liefst op korte afstand van elkaar (max. 200m). We beschrijven hieronder beknopt hoe de gemeente daarvoor kan zorgen.

Voedsel

Bijen zie je vaak druk van bloem naar bloem vliegen. Dat doen ze voor de nectar die dient als brandstof en voor het stuifmeel (pollen) dat essentieel is als voedsel voor de larven. De mate waarin bloemen waarde hebben voor bijen verschilt per soort. Sommige bijen zijn gespecialiseerd op één of enkele planten terwijl andere soorten minder kritisch zijn. Over het algemeen geldt: hoe groter de diversiteit hoe meer soorten bijen. Bloeiende bomen, heesters en struiken zijn goede opties om aan te planten in perken, denk daarbij aan bramen, mei- of sleedoorn, inheemse wilgen en lindes, maar bijvoorbeeld ook Spaanse aak. Andere vaste planten zijn rozen, klokjes, salie, lupine, et cetera. Vermijd bij gekweekte planten de cultivars met gevulde bloemen (zoals bij rozen vaak het geval is), die leveren nauwelijks stuifmeel en nectar. Bij het zaaien van kruidachtige planten heeft het gebruik van lokale soorten de voorkeur. Dat kan bijvoorbeeld door maaisel afkomstig van een kruidenrijke plek in de buurt op een nieuwe plek neer te leggen. Sommige planten zoals wilde peen, pastinaak, rode klaver, duizendblad, paardenbloem en akkerdistel kunnen in heel Nederland gebruikt worden. In het voorjaar kunnen bloeiende bolgewassen van belang zijn voor hommels. Kijk hier voor nog meer voorbeelden van geschikte planten voor wilde bijen. Bijen kunnen niet alleen geholpen worden met het aanplanten van bijvriendelijke planten maar ook door het niet weghalen van spontaan opgekomen planten. Zo kunnen hondsdraf en dovenetel die spontaan onder een heg zijn opgekomen belangrijk zijn voor hommels.

Nestgelegenheid

De eisen die worden gesteld aan nestgelegenheid verschillen per soort (kijk hier voor meer informatie). Een deel van de soorten nestelt in de grond en graaft daar gangetjes. Andere soorten nestelen bovengronds in door kevers gemaakte gaten in hout of holle stengels van bijvoorbeeld braam, riet of afgestorven kruiden. Op veel plekken is een groot deel van de grond bedekt met tegels, grind of houtsnippers en worden afgestorven stengels in het najaar verwijderd. Het achterwege laten van bodembedekking en het laten staan van kruiden in de winter zijn eenvoudige manieren om nestgelegenheid voor bijen te vergroten. Veel soorten maken hun nest bij voorkeur op plaatsen waar niet al te dichte vegetatie wordt afgewisseld met stukjes onbedekte bodem. Over het algemeen geldt: hoe meer variatie, hoe meer bijen. Het is ook mogelijk om actief nestgelegenheid aan te bieden in de vorm van bijenhotels. Kijk hier voor instructies voor het maken van een bijenhotel. Dat is goed voor de bijen maar ook leuk voor iedereen die bijen graag een keer van dichtbij aan het werk wil zien. Een groot, professioneel bijenhotel plaatsen kan natuurlijk ook. Bij www.bijenhotelkopen.nl hebben ze verschillende typen die veel nestgelegenheid bieden. Met een informatiebord kun je bewoners bewust maken van het belang van bijen en wat er in de stad voor bijen gedaan kan worden. Een andere mogelijkheid om actief nestgelegenheid aan te bieden is het maken van een bijenheuvel, een grotendeels onbegroeide heuvel van klei of zand op een zonnige plek. Door de bult weer vrij te maken en de zijkanten af te steken als deze eenmaal begroeid is geraakt, kan de heuvel elk jaar weer ruimte bieden aan bijen. Hommels maken wat grotere nesten, bijvoorbeeld in oude muizenholen. Rommelige en ruige vegetatie langs randen van heggen biedt goede nestplek voor hommels.

Beheer

Na het aanplanten of zaaien is goed beheer van groot belang. Bijen hebben doorlopend bloeiende planten nodig en maaien moet daarom gefaseerd gebeuren. Probeer daarbij minimaal 15% van het oppervlak te laten staan. Maai het liefst na de bloei en maximaal 2 keer per jaar. Verder is het belangrijk dat maaisel afgevoerd wordt om te zorgen dat de grond schraler wordt en grassen niet te dominant worden. Probeer klepelen te vermijden, dit is niet goed voor alle dieren en planten. Ook is het van belang niet te zware machines te gebruiken om zo de bodemstructuur te behouden en de nesten in de bodem niet teveel te beschadigen. Kijk hier voor nog meer tips voor goed maaibeheer.

Lijst met gevonden soorten in Leiden

Witbaardzandbij	*Andrena barbilabris*	Tronkenbij	*Heriades truncorum*
Tweekleurige zandbij	*Andrena bicolor*	Gewone maskerbij	*Hylaeus communis*
Goudstaartzandbij	*Andrena carantonica*	Tuinmaskerbij	*Hylaeus hyalinatus*
Goudpootzandbij	*Andrena chrysosceles*	Resedamaskerbij	*Hylaeus signatus*
Wimperflankzandbij	*Andrena dorsata*	Gewone geurgroefbij	*Lasioglossum calceatum*
Grasbij	*Andrena flavipes*	Breedkaakgroefbij	*Lasioglossum laticeps*
Vosje	*Andrena fulva*	Gewone smaragdgroefbij	*Lasioglossum leucopus*
Roodgatje	*Andrena haemorrhoa*	Matte bandgroefbij	*Lasioglossum leucozonium*
Gewone dwergzandbij	*Andrena minutula*	Ingesnoerde groefbij	*Lasioglossum minutissimum*
Lichte wilgenzandbij	*Andrena mitis*	Langkopsmaragdgroefbij	*Lasioglossum morio*
Viltvlekzandbij	*Andrena nitida*	Gewone franjegroefbij	*Lasioglossum sexstrigatum*
Vroege zandbij	*Andrena praecox*	Biggenkruidgroefbij	*Lasioglossum villosulum*
Fluitenkruidbij	*Andrena proxima*	Gewone slobkousbij	*Macropis europaea*
Witkopdwergzandbij	*Andrena subopaca*	Tuinbladsnijder	*Megachile centuncularis*
Grijze rimpelrug	*Andrena tibialis*	Gewone behangersbij	*Megachile versicolor*
Doornkaakzandbij	*Andrena trimmerana*	Grote bladsnijder	*Megachile willughbiella*
Roodbuikje	*Andrena ventralis*	Bruine rouwbij	*Melecta albifrons*
Grote wolbij	*Anthidium manicatum*	Klokjesdikpoot	*Melitta haemorrhoidalis*
Gewone sachembij	*Anthophora plumipes*	Roodzwarte dubbeltand	*Nomada fabriciana*

Tuinhommel	*Bombus hortorum*	Gewone wespbij	*Nomada flava*
Boomhommel	*Bombus hypnorum*	Gewone kleine wespbij	*Nomada flavoguttata*
Steenhommel	*Bombus lapidarius*	Kortsprietwespbij	*Nomada fucata*
Veldhommel	*Bombus lucorum*	Roodsprietwespbij	*Nomada fulvicornis*
Akkerhommel	*Bombus pascuorum*	Smalbandwespbij	*Nomada goodeniana*
Weidehommel	*Bombus pratorum*	Donkere wespbij	*Nomada marshamella*
Vierkleurige koekoekshommel	*Bombus sylvestris*	Signaalwespbij	*Nomada signata*
Grote koekoekshommel	*Bombus vestalis*	Geelzwarte wespbij	*Nomada succincta*
Lathyrusbij	*Chalicodoma ericetorum*	Rosse metselbij	*Osmia bicornis*
Grote klokjesbij	*Chelostoma rapunculi*	Gedoornde slakkenhuisbij	*Osmia spinulosa*
Wormkruidbij	*Colletes daviesanus*	Pantserbloedbij	*Sphecodes gibbus*
Duinzijdebij	*Colletes fodiens*	Gewone dwergbloedbij	*Sphecodes miniatus*
Pluimvoetbij	*Dasypoda hirtipes*	Dikkopbloedbij	*Sphecodes monilicornis*
Roodpotige groefbij	*Halictus rubicundus*	Geelgerande tubebij	*Stelis punctulatissima*
Parkbronsgroefbij	*Halictus tumulorum*	Blauw zwarte houtbij	*Xylocopa violacea*