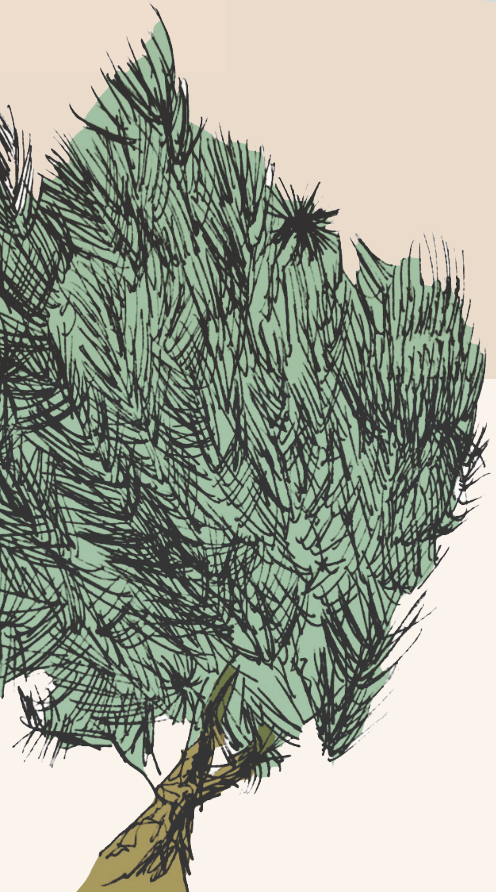

Jesús Aguirre Gutiérrez

Biodiversity responses to climate and land-use change: a historical perspective

2015

Biodiversity responses to climate and land-use change:

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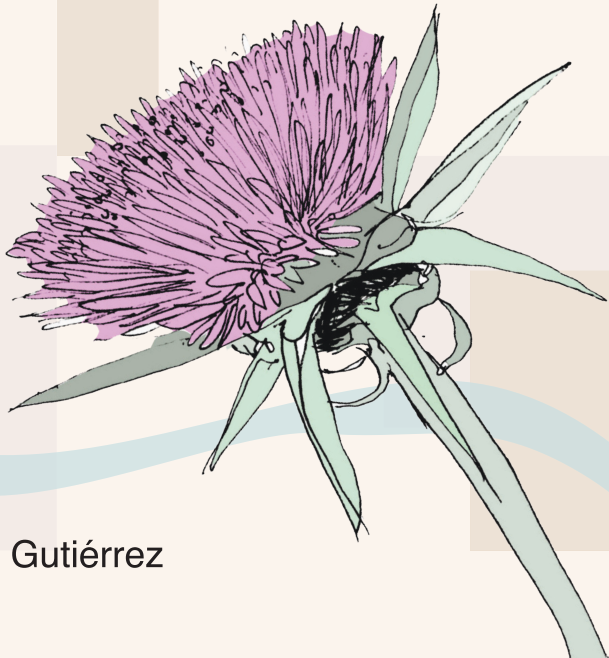

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A historical perspective

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A historical perspective

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Faculteit der Natuurwetenschappen, Wiskunde en Informatica

To my two greatest adventures
on this earth

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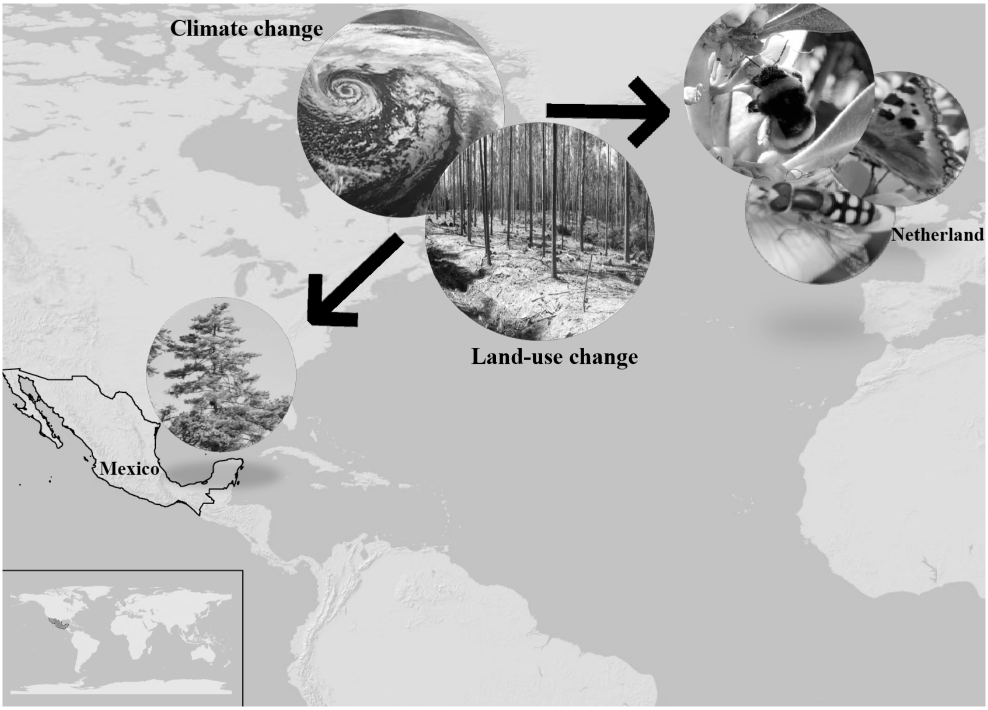
1

Introduction and thesis outline

J. Aguirre-Gutiérrez



Global environmental impacts on biodiversity

There are probably between 5 to 11 million of eukaryotic species on earth (Mora *et al*., 2011; Cardinale *et al*., 2012; Costello *et al*., 2013) of which, according to calculations of Mora *et al*. (2011), 86% of terrestrial species and 91% of marine species are yet to be discovered. This is challenging as it means that at most we have a basic idea of what biodiversity really is, where it is and how it interlinks to make ecosystems function.

Notwithstanding our lack of knowledge, we are certain that it is currently facing alarming declines (Hooper *et al*., 2012; Cardinale *et al*., 2012), with for example ~20% of the known vertebrates, invertebrates and plants classified as being threatened with extinction (Hoffmann *et al*., 2010; Brummitt & Bachman, 2010; Collen *et al*., 2012). This is in addition to all species that we still do not know, many of which we may never know before they go extinct. Recent scenarios of expected species extinctions also point in the same direction with high number of species committed to extinction in the near future (Pereira *et al*., 2010). This is a dramatic trend, inevitably leading to loss of genes, species, species traits, unique functions and ultimately whole systems and with that our capacity to respond to future environmental changes (Bellard *et al*., 2012; Cardinale *et al*., 2012).

Much of the research carried out in the field of ecology and biodiversity conservation addresses the processes and impacts of biodiversity loss. The focus ranges from identification of the main drivers of biodiversity loss to how these drivers act and interact to limit the distribution of biodiversity around the globe (e.g. Kennedy *et al*., 2013; Newbold *et al*., 2015). Some of the main drivers that can force species to local or global extinction and cause the modification of the original species distributions are habitat loss, habitat fragmentation and changes in climatic conditions. These drivers can act alone or in parallel, however when acting together they may have stronger and more deleterious effects (Jetz *et al*., 2007; Fox *et al*., 2014). While biodiversity can respond to the pressure of such drivers by for example adapting to the new environmental conditions (requiring many generation cycles, hence this a slow process), a more immediate response involves the colonization of new suitable areas resulting in shifts in their distributional ranges (Lenoir & Svenning, 2015). These geographic shifts in species distribution may in turn alter the community structure and species interactions, e.g. through the arrival of species previously absent from the area and migration of local species in order to follow more suitable conditions (Lurgi *et al*., 2012), thereby disrupting the balance of ecosystems. As a result, ecosystems and their functioning may change, as well as the services and goods we obtain from nature (e.g. timber, protection against soil erosion, clean air and water, among others) (DeFries *et al.*, 2004).

As climatic and land use related drivers have been classified as main factors for biodiversity loss and limiting species distributions around the world, in the following sections I discuss their importance and some of the mechanisms by which they drive biodiversity changes globally.

Climate effects on biodiversity

While climate changes cyclically, the rate at which it has changed during the last 100 years has no precedent, with two main periods of fast warming during the last century, 1910–1945 and from 1976 to the present (Walther *et al*., 2002). Besides temperature increases, precipitation regimes have changed, and extreme weather events have become more common.

Earth surface temperature has risen considerably during the last century and is expected to continue to rise during the 21st century (Fig. 1). The mean global surface temperature is expected to increase by at least 1 °C and the increases in average temperatures are expected to be stronger in the tropics and subtropics than in mid latitude regions (Kirtman *et al*., 2013). These changes are expected to cause more extreme heat waves, with an increase in the number of warm days and nights. Consequently, decreases in the snow cover and tinning of the arctic ice cover is also projected to occur in the near future, having devastating effects not only for local but also for global biodiversity in terrestrial and marine ecosystems (Post *et al*., 2013).

Changes in precipitation regimes are expected to vary across the globe with increases in average precipitation expected at high and mid latitudes, but with decreases expected in the tropics and subtropics (Fig. 2) (Kirtman *et al*., 2013). Extreme precipitation events have already become more apparent recently and are expected to continue increasing in number and intensity, especially in North America and Europe (Kirtman *et al*., 2013). In central and northern Europe substantial increases in winter precipitation are expected during this century, meanwhile more extreme summer precipitation events are expected in the northeastern regions accompanied with substantial decreases in precipitation events in the southern European areas (Beniston *et al*., 2007). The effects of the observed and expected modifications in precipitation

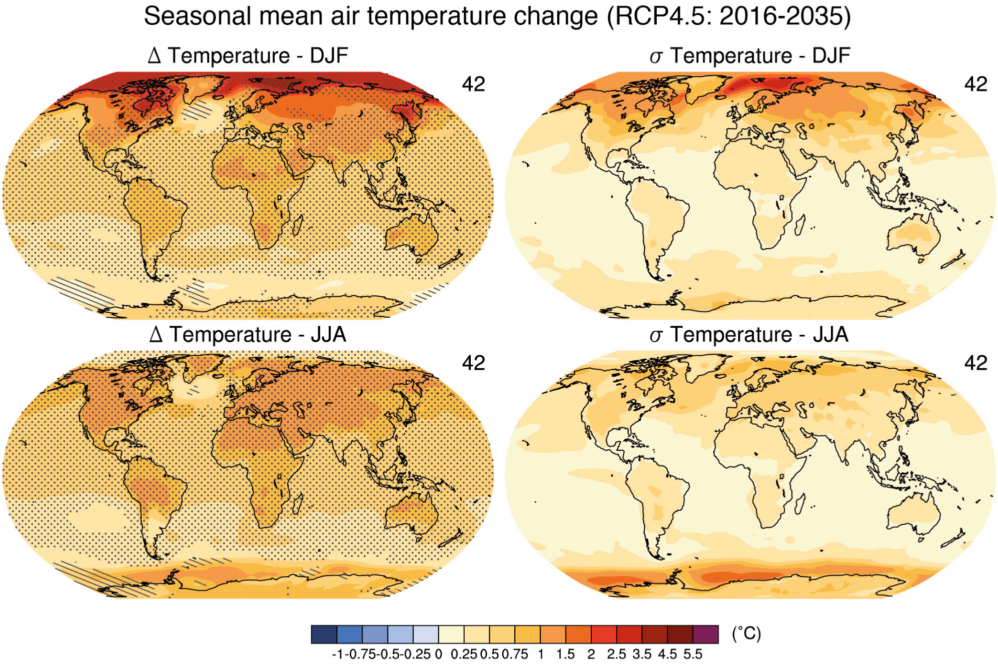


Figure 1. CMIP5 multi-model ensemble mean of projected changes in December, January and February and June, July and August surface air temperature for the period 2016–2035 relative to 1986–2005 under RCP4.5 scenario (left panels). The right panels show an estimate of the model-estimated internal variability (standard deviation of 20-year means). Hatching in left-hand panels indicates areas where projected changes are small compared to the internal variability (i.e., smaller than one standard deviation of estimated internal variability), and stippling indicates regions where the multi-model mean projections deviate significantly from the simulated 1986–2005 period (by at least two standard deviations of internal variability) and where at least 90% of the models agree on the sign of change. The number of models considered in the analysis is listed in the top-right portion of the panels; from each model one ensemble member is used. See Box 12.1 in Chapter 12 of the IPCC report (Stocker *et al.*, 2013) for further details and discussion. Technical details are in Annex I (Stocker *et al.*, 2013). Figure and legend taken from Stocker *et al.* (2013).

conditions on biodiversity are still largely unclear. However, modifications of ecosystem services provision are expected across the globe (Huxman *et al.*, 2004), e.g. through the modification of the species composition in such ecosystems (e.g. Hély *et al.*, 2006; Martinho *et al.*, 2007; Lindner *et al.*, 2010).

Changes in the earth's temperature and in the precipitation intensity can have highly deleterious effects on biodiversity, forcing changes in the species distributions globally and thus affecting ecosystem functioning (Knapp *et al.*, 2008; Wu *et al.*, 2011). The recent rapid modifications in various climatic conditions raise important concerns about our ability to conserve natural resources and points to the need for robust tools and frameworks that help investigate how species will respond to future global environmental changes and what our role is for mitigating such impacts on biodiversity.

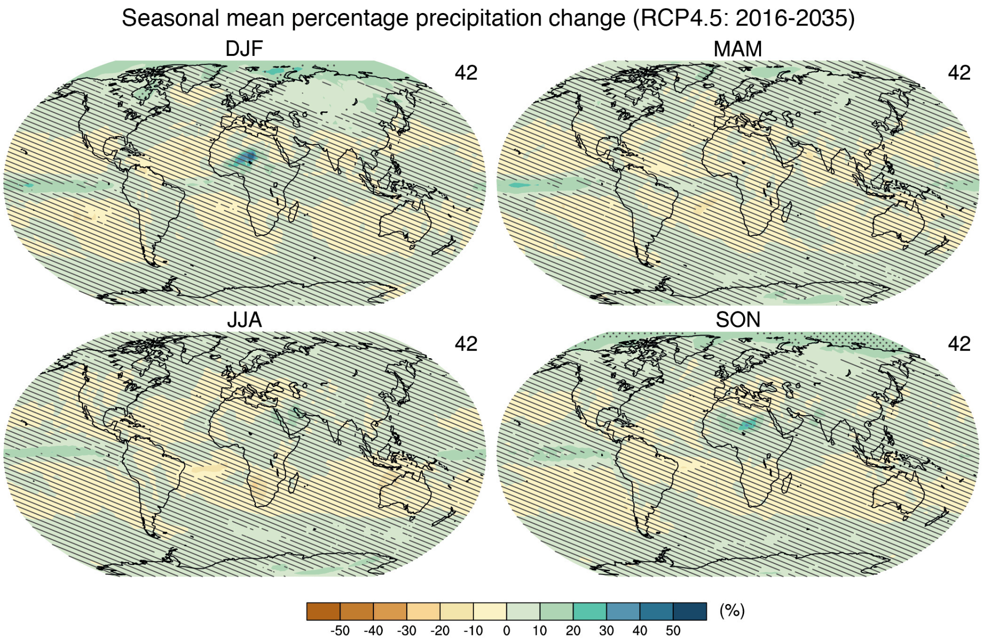


Figure 2. CMIP5 multi-model ensemble mean of projected changes (%) in precipitation for 2016–2035 relative to 1986–2005 under RCP4.5 for the four seasons. The number of CMIP5 models used is indicated in the upper right corner. Hatching and stippling as in Figure 1 (from Kirtman *et al*., 2013). DJF: December-January-February. MAM: March-April-May. JJA: June-July-August. SON: September-October-November. Figure and legend taken from Stocker *et al*., (2013).

Land use effects on biodiversity

Human population growth has direct impacts on the surrounding environment as it increases the requirements for food and commodities, which in turn put more pressure on natural resources (Foley *et al*., 2005). Therefore, human population growth has been classified as the ultimate driver accelerating species extinctions (Pimm *et al*., 2014). This increasing pressure is globally reflected in more changes in land use (see Fig. 3 for an example on global deforestation) (DeFries *et al*., 2004). Land-use changes often bring about the loss of habitats and their fragmentation, i.e. the breaking apart of a habitat per se (Fahrig, 2003). After habitat loss and fragmentation occur they often create

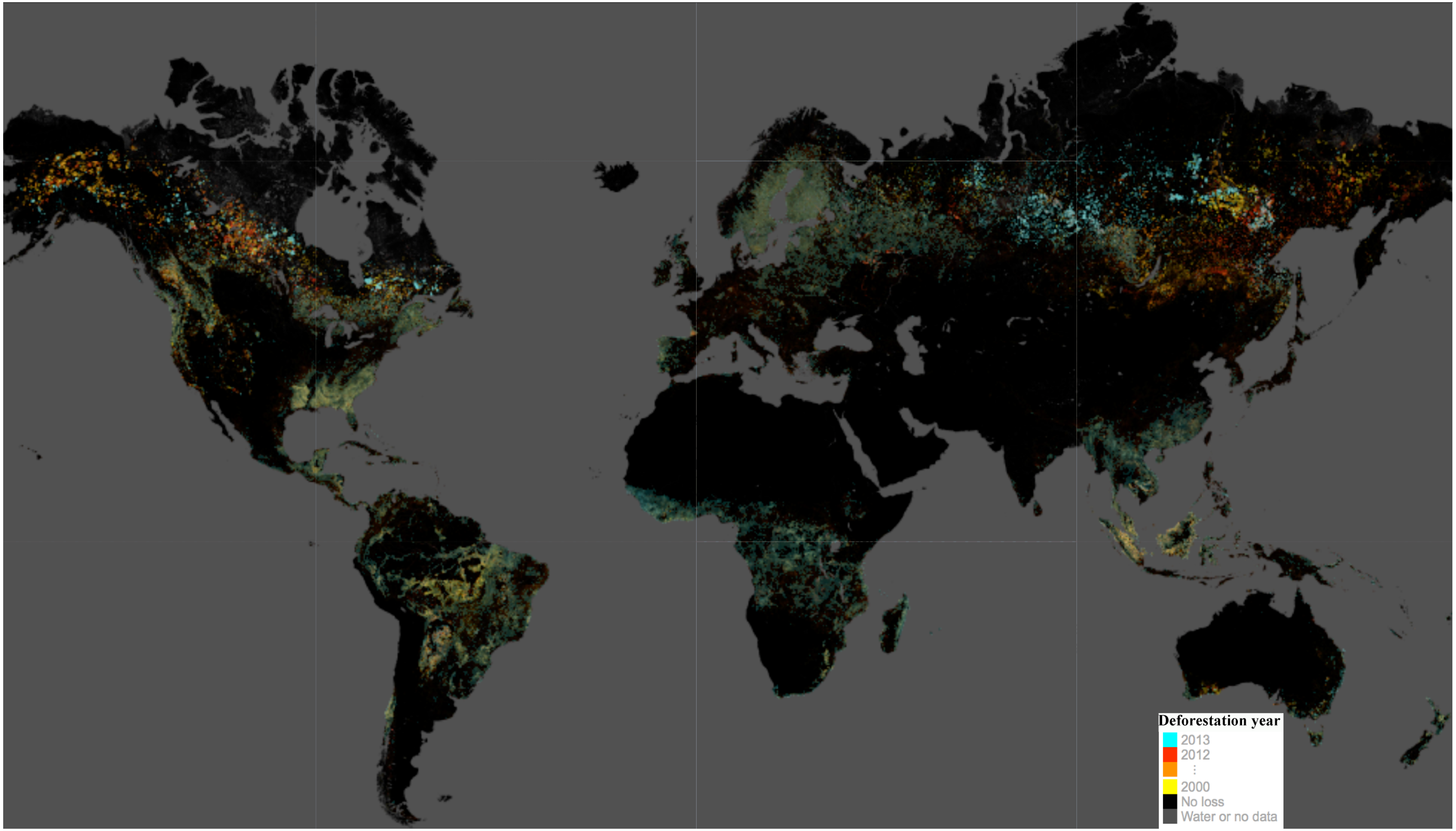


Fig. 3. The world deforestation across the years from 2000 to 2013. Different coloured pixels represent areas that have been deforested along this 13 years period. Map modified from Hansen *et al*. (2013).

a new set of different landscape conditions to which local species are not adapted, which may also leave local species in disadvantage against invasive ones (Thuiller, 2007), often leading to their local extinction (Vellend *et al*., 2006; Kuussaari *et al*., 2009). During the last century global biodiversity has experienced alarming declines due to direct and indirect effects of these two drivers of change (Krauss *et al*., 2010; Meyfroidt & Lambin, 2011). However, not only global but also local biodiversity changes are of pivotal importance as it is local biodiversity patterns that most ecosystems services rely on (Newbold *et al*., 2015). This is of particular importance as landscape level land use modifications have already caused high local species richness losses (above 20% loss) in many areas in the world, with the number of regions experiencing this level of biodiversity loss expected to double by the year 2100 (Newbold *et al*., 2015).

The amount and quality of suitable habitat remaining after land use changes are the major landscape characteristics limiting species distributions at local as well as global scales (e.g. Gibbons *et al*., 2000; Mortelliti *et al*., 2010). These landscape characteristics can delimit the potential distribution of species across the landscape by, between others, modifying the resource availability and the species mortality risks (Watling *et al*., 2011). Landscapes with high amounts of natural areas are of particular importance for the maintenance of biodiversity and their services (Thuiller, 2007; Kennedy *et al*., 2013). It has been shown that landscapes with higher amount of natural habitat and in general higher heterogeneity (of natural habitats) can maintain higher levels of biodiversity than managed and more homogeneous landscapes (e.g. Benton *et al*., 2003; Fischer *et al*., 2006). However, it is important to keep in mind that in the context of species distributions not only the amount of suitable habitat in the landscape is of importance for the presence and subsistence of a given species, but also its dispersal capabilities and the interaction with other organisms (Guisan & Thuiller, 2005). Consequently, the amount of suitable habitat in the landscape is only one indication of the suitability of a given landscape for the occurrence of a species.

Habitat fragmentation may also disrupt the arrival of new species and their persistence in a landscape by modifying the microclimatic conditions, resource availability and the arrangement of habitat patches in the surrounding landscape matrix (Ewers & Didham, 2006). Especially the area of suitable habitat, the proximity of habitat patches and the amount of edges present in the landscape after a fragmentation event are some of the main drivers of local biodiversity (Fahrig, 2003). The area of remaining patches has been shown to limit the species distribution and persistence as bigger patches may maintain higher biodiversity levels than smaller ones given the availability of resources (Fahrig, 2003; Ewers & Didham, 2006). In this context the proximity of suitable habitat patches plays a major role, particularly when the surrounding matrix is inhospitable: the closer these habitat patches are, the higher the probability of inter-patch dispersal and thus of species survival. The fragmentation in a given landscape invariably creates areas with higher amounts of edges, which have been shown to produce negative effects on biodiversity by mainly modifying the microclimatic condition and the vegetation structure of a habitat patch in a given landscape (Fahrig, 2003). These modifications may create a reshuffling of biodiversity in the edge regions favouring species adapted to the new abiotic condition and thus bringing about possible new biotic interactions in those regions and causing changes in the local community structure (Kupfer *et al.*, 2006). However, not all edges in a given area may have negative effects on biodiversity (e.g. acting as functional barriers), for example, those created between natural and managed systems, which may increase local biodiversity by favouring the dispersal of organisms between the different land use classes (Kuefler *et al.*, 2010). The positive or negative impact of the edge effects ultimately depends on the organism under consideration as edges may have a positive impact on organism that depend on multiple habitat types for survival but may negatively impact single habitat species that require more stable habitat conditions (e.g. Fonderflick *et al.*, 2013).

During the last century agricultural expansion has been a major cause of habitat loss and fragmentation. The total amount of agricultural land around the world increased from 34% in 1960 to almost 39% in 2011 (FAO, 2015), and the forest area, which covered about 3.8 billion ha in the 1990 (30% of total land area), has decreased by ~ 2% by the year 2005, meaning a loss of 66.4 million ha in a period of only 15 years (FAO *et al.*, 2012). Given the rates at which we are losing natural habitats, and in general biodiversity, and the increasing amount of managed land around the world it is imperative to understand how species respond to these habitat modifications. We can do this not only by investigating present species responses to the pressure of these drivers, but also analysing their historical responses (Poschlod *et al.*, 2005; e.g. Hermy & Verheyen, 2007). Because historical data are lacking for most regions and taxa, most studies analysing species responses to historical land use drivers use the space for time substitution approach and compare current landscapes that vary in landscape features (e.g. Brosi *et al.*, 2008; Uehara-Prado & Freitas, 2009), mostly at small spatial scales (Benedick *et al.*, 2006; Taki *et al.*, 2010). In this way it is assumed that the comparison of recent landscapes that differ in landscape characteristics represents the processes than have taken place in a specific location across time, which may not be always the case possibly leading to wrong conclusions. Therefore, studies that use real historical data are of pivotal importance mainly because recent observed species distributions may not be the result of recent environmental changes but of past changes in these conditions.

Species Distribution Modelling as a tool to analyse historical-to-present and forecast future impacts of climatic and land-use changes on biodiversity

Species can respond to changes in environmental conditions by colonization of more suitable habitats (Lenoir & Svenning, 2015). As a result of the recent changes in climatic and land use condition across the globe we have already observed patterns of species range modifications and species distributional shifts (Parmesan & Yohe, 2003; Chen *et al*., 2011). Given the expected future changes in environmental conditions it seems certain that biodiversity will continue to adapt to these modifications by changing their distributional ranges (Pereira *et al*., 2010). Different sets of tools have been developed in order to investigate recent and future species responses to these changes in environmental conditions, making it also possible to analyse the modifications in the species distributions by comparing their ranges across different time periods (e.g. Guisan & Thuiller, 2005; Warren *et al*., 2010; Rangel *et al*., 2010).

Species Distribution Models (SDMs, Guisan & Thuiller, 2005), also known as Ecological Niche Models (ENMs, Soberón & Nakamura, 2009), are an important tool for analysing species distributions. SDMs are correlative models that investigate the relationship between species occurrences and the underlying environmental conditions in those locations, obtaining in this way an insight into the geographical and ecological niche space in which the species are distributed (Fig. 4) (Elith & Leathwick, 2009). The species-environment relationship is then projected into the same or other study areas with the present environmental conditions in order to analyse current species distributions. These can also be forecasted to investigate, for example, the effects of future climate and land-use change on the distribution of biodiversity (Thuiller *et al*., 2005; e.g. Schweiger *et al*., 2012).

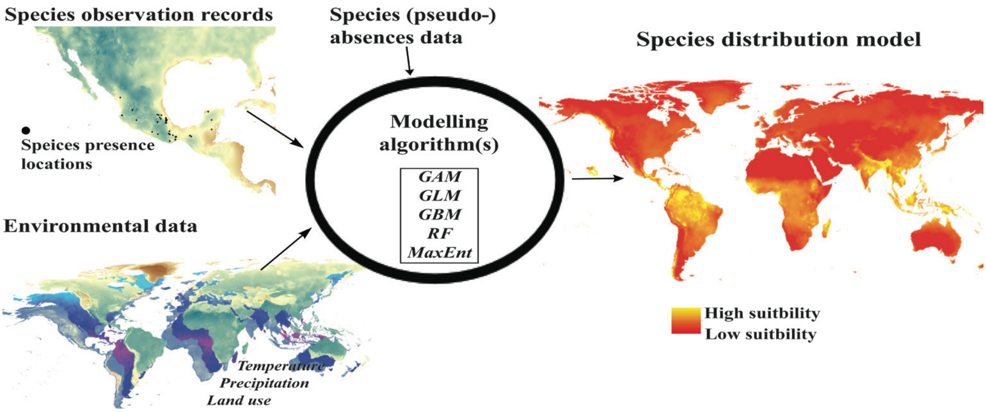


Fig. 4. Schematization of the process and data needed for constructing species distribution models. The main data needed are information on species presence locations, environmental information of the condition where the species occur and information of where the species does not occur, in case this is not available then pseudo-absences can be generated. These data form then the input for the different modelling algorithms, which in turn will develop the model predicting of habitat suitability for the species in the projected geographic area.

Historical to present and future projections of species distributions are used as a primary resource for biodiversity conservation planning (Guisan *et al.*, 2013), as for the selection of protected areas (Hannah *et al.*, 2007; Marshall *et al.*, 2014), to investigate possible effects of invasive species on local biodiversity (Jiménez-Valverde *et al.*, 2011; Buckland *et al.*, 2014) and for the creation of biodiversity adaptation and mitigation plans, among others. However, there are assumptions that have to be considered before drawing conclusions for biodiversity conservation, as are the lack of species interaction and dispersal limitation information included during the modelling protocol (Guisan & Thuiller, 2005; Franklin, 2010).

SDMs are often applied to model single species distributions; however, they can also be used to model multiple species as to investigate the species richness of a given location (Dubuis *et al.*, 2011; Guisan & Rahbek, 2011). This can be accomplished in different ways, however, the most common are first modelling single species and stacking their projected distributions either as binary (presence-absence) predictions, thus obtaining an indication of the number (richness) and identity (composition) of the species present in a given location (Dubuis *et al.*, 2011; D'Amen *et al.*, 2015); or by stacking their habitat suitability values. In this last option a threshold for setting a binary prediction is not needed, in which case higher values for a pixel would point to (possible) higher species richness. However, with this method the species identity information is lost (Dubuis *et al*., 2011). There are other possibilities as to model species richness directly, or using macro ecological models, which need a different data input and to comply with different model assumptions. More insight into these techniques can be found in Calabrese *et al*. (2014) and Distler *et al*. (2015).

There is a plethora of algorithms and platforms for constructing SDMs, each one of those with their specific formulations and features for selecting environmental correlates and with different output criteria (Thuiller *et al*., 2009). It has been shown that in some cases different algorithms may render different modelling results, which can affect the conclusions that one can derive from a given modelling exercise (Elith & Graham, 2009). Specifically, while one model can predict high suitability for a species in a given location, in an extreme case another may predict a medium or low suitability, making it difficult to extrapolate these predictions to other areas or time periods (Thuiller, 2004; Thuiller, 2014). Besides the between-algorithm variation also models constructed for the same species and with the same algorithm but with different sets of data can render different predictions (within-algorithm variation). Because of this it has been suggested that the ensemble of different models can be used as a viable and more robust option than the single model approach when modelling species distributions (Thuiller, 2014). However, there is still not consensus on which algorithms may perform best depending on the species data characteristics, e.g. the spatial distribution and amount of the species data available. We tackle this question in Chapter 2 of this thesis.

SDMs are a powerful tool for biodiversity conservation and for predicting future effects of climate and land-use changes on species distributions. However, the accuracy and usability of SDM predictions will always depend on the quality of the data (species and environmental) used when constructing such models and on the specific assumptions of the modelling algorithm (Elith & Graham, 2009). Thus one of the first steps to carry out when constructing SDMs should be to define the objective of such model and analyse the quality and accuracy of the data that will be used in the modelling protocol (Araújo & Peterson, 2012). When analysing the final model, its assumptions should also be discussed in light of the purpose for which it was created, e.g. were dispersal limitation and biotic interactions taken into account? The awareness of the strengths and caveats of these models may help us understand better what we are modelling and the meaning of the results. Considering this will allow for a more realistic inference of the impacts of present and future environmental changes on biodiversity.

Thesis outline

In this thesis I investigate how global biodiversity change drivers, particularly climate change and land use modifications, shape biodiversity distributions over time. More specifically, in Chapter 2 I analyse which species distribution modelling algorithms render more robust predictions of habitat suitable for the modelled species. Moreover, I investigate which of these algorithms are more constant in their predictions across model repetitions and for which set of spatial and environmental conditions. I investigate the between and within model variability when constructing SDMs for species with different number of record locations, from rare to common, and with a varied geographic distribution (Aguirre-Gutiérrez *et al*., 2013). Based on these results a more informed selection of the modelling algorithms for constructing SDMs can be made, which may finally result on more robust model projections of species distribution and their drivers. The results of this chapter form the basis of the choices of modelling approaches for subsequent chapters.

In Chapter 3 I apply the knowledge of the most robust and best performing algorithms for fitting SDMs based in our results from Chapter 2 (Aguirre-Gutiérrez *et al*., 2015). In this chapter a SDM framework using one of the best performing algorithms is applied in order to predict the distribution and analyse the ecological niche similarities between closely related Mexican white pine taxa, which range from southern United States to Mexico and Central America. Closely related taxa may be difficult to differentiate even with morphological and genetic analysis. Another technique that can be use in order to obtain estimates of similarity between taxa is comparing their ecological niches. Here we use SDMs to extract the species ecological niches to then compare them.

In Chapter 4 I investigate whether the relative importance of climate (temperature and precipitation) and land use (habitat composition, fragmentation and spillover potential) as drivers of species distributions has changed over time. Models of species distributions often assume that the importance of such drivers in the present will be the same in the future, and current models base their forecasting on this assumption in order to detect future impacts of environmental changes. However, this may not be always the case as climate and land use are unlikely to change in parallel, suggesting that the importance of such drivers for biodiversity distributions could be non-constant across time. I use data for bees, butterflies and hoverflies collected between 1951 and the present to address this question.

Functional traits can be described as species characteristics related to their morphology, physiology, structure, phenology and behaviour, that are relevant for the organism in order to respond to environmental modifications (Díaz *et al*., 2013; Violle *et al*., 2007). Species can shift their distribution in pursuit of favourable environments, however, these spatial modifications may be determined by the species specific trait characteristics used as response to the pressures of these drivers. In Chapter 5 I firstly investigate the areal range changes, latitudinal and longitudinal shifts that bee, butterfly and hoverfly species have experienced since the last half of this century and then investigate if and to what extent these spatial modifications are related to specific species trait characteristics.

In Chapter 6 I investigate how past and present changes in landscape characteristics, related to habitat composition and fragmentation, impact the distribution and richness of biodiversity. I do this by analysing a dataset of bee, butterfly and hoverfly species richness changes recorded between the year 1900 and the present. Land use maps from different time periods are used to extract the original conditions of the landscape before changes occurred and also the changes that occurred in a given landscape across time.

The synthesis presented in Chapter 7 brings the results from the different chapters together and relates these to the effects of environmental changes on the distribution of biodiversity from a historical and present time perspective. Specifically, it is discussed how historical and present changes in environmental conditions may determine the present species distributions and what this means for the analysis of species response to future climatic and land use changes. During the synthesis I focus on these aspects and analyse future prospects of research within this realm.

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2

Fit-for-purpose: Species distribution model performance depends on evaluation criteria – Dutch hoverflies as a case study

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Abstract

Understanding species distributions and the factors limiting them is an important topic in ecology and conservation, including in nature reserve selection and predicting climate change impacts. While Species Distribution Models (SDM) are the main tool used for these purposes, choosing the best SDM algorithm is not straightforward as these are plentiful and can be applied in many different ways. SDM are used mainly to gain insight in 1) overall species distributions, 2) their past-present-future probability of occurrence and/or 3) to understand their ecological niche limits (also referred to as ecological niche modelling). The fact that these three aims may require different models and outputs is, however, rarely considered and has not been evaluated consistently. Here we use data from a systematically sampled set of species occurrences to specifically test the performance of Species Distribution Models across several commonly used algorithms. Species range in distribution patterns from rare to common and from local to widespread. We compare overall model fit (representing species distribution), the accuracy of the predictions at multiple spatial scales, and the consistency in selection of environmental correlations all across multiple modelling runs. As expected, the choice of modelling algorithm determines model outcome. However, model quality depends not only on the algorithm, but also on the measure of model fit used and the scale at which it is used. Although model fit was higher for the consensus approach and Maxent, Maxent and GAM models were more consistent in estimating local occurrence, while RF and GBM showed higher consistency in environmental variables selection. Model outcomes diverged more for narrowly distributed species than for widespread species. We suggest that matching study aims with modelling approach is essential in Species Distribution Models, and provide suggestions how to do this for different modelling aims and species' data characteristics (i.e. sample size, spatial distribution).

Introduction

Understanding current and predicting future distributions of species is pivotal for ecology and for implementation of biodiversity conservation and policy measures (e.g. International Union for Conservation of Nature -IUCN Red Lists; reserve selection). One of the most common methods used to gain insight in species distributions and environmental niches is Species Distribution Modelling (Guisan & Thuiller, 2005), which is also referred to as ecological niche modelling (see discussions on terminology in (Elith & Leathwick, 2009; McInerny & Etienne, 2012; Peterson & Soberón, 2012; Warren, 2012; Higgins *et al*., 2012). SDM identifies locations with suitable (a)biotic conditions for species occurrences, based on climatological, environmental and/or biotic correlates (Soberón & Nakamura, 2009). A broad range of algorithms (Franklin, 2009, Peterson *et al*., 2011) and platforms (i.e. BIOMOD, ModEco, OpenModeller; Thuiller *et al*., 2009; Guo Q & Liu, 2010; Souza Muñoz *et al*., 2009) can be used to fit the models, each with unique features, such as different variable selecting techniques or methods for selecting (pseudo) absences (Elith *et al*., 2006; Elith &Graham, 2009; Pearson *et al*., 2006; Segurado *et al*., 2006). Consequently, the best fitted model depends not only on presence data available, but also strongly on the modelling approach (Buisson *et al*., 2010; Barve *et al*., 2011). SDMs are used mainly to (1) gain insight in species' overall distribution (i.e. Bidinger *et al*., 2012; Machado-Machado, 2012), (2) obtain predicted occurrences for specific locations (i.e. Raes *et al*., 2009; Rodríguez-Soto *et al*., 2009) or (3) understand niche limits of species (i.e. Peterson & Soberón, 2012; Beale *et al*., 2008; Veloz *et al*., 2012; Saupe *et al*., 2012). Several studies point to the need to evaluate and validate SDMs and perform in-depth analyses of the impact of algorithm selection and within algorithm consistency of predictions to generate more meaningful models (Elith & Leathwick, 2009; Araújo & Peterson, 2012). For example, using virtual species, Saupe *et al*. (2012) found that the distribution of the species data used for model training with regard to the environmental conditions available influences modelling results. Wisz *et al*. (2008) showed that model accuracy (AUC values) depends on the algorithm used, reinforcing the need to assess performance of different modelling techniques (Araújo & Guisan, 2006), including consensus methods (that integrate the predictions of several algorithms) (Marmion *et al*., 2009). Lastly, Zimmermann *et al*. (2010) showed how SDM can be tailored to satisfy different aims and improve prediction accuracy. However, our screening of recent papers using SDM (see Table S1 in Supplementary material) shows that studies modelling a single species tend to use one algorithm, whereas studies modelling multiple species tend to use multiple algorithms, generally without clear explanation of the reasons for algorithms selection criteria. The 19 algorithms used in a set of 42 recent papers (Table S1) occur in both, single and multi-species studies, with Maxent (Maximum entropy) and GLM (Generalized Linear Models) being two of the most common ones. However, none of these studies analyse the advantages/ disadvantages of selecting one or more algorithms, being still unclear whether species-specific features such as level of rarity, geographic spread or a combination of both, affect model fit (but see Table S1).

Here we investigate which species distribution modelling algorithms perform most consistently when: (1) evaluating overall model fit; (2) evaluating spatial predictions of species occurrence at patch, landscape and regional scales; and (3) identifying environmental factors as important correlates of species occurrence. We test these three aspects for a group of well-sampled hoverfly species in the Netherlands, that are selected such that they include rare to common and local to widespread species.

Methods

Species data and selection

We used presence-only records for Dutch hoverflies (Diptera: Syrphidae) in the Netherlands from the European Invertebrate Survey (EIS, 2012) collected during the last ten years (2000-2010). This database contains more than 400, 000 records of 328 species over a time span of 200 years for the entire country (Fig. S1). For the species selection we first characterised all species in terms of occupancy (rare to common, based on the number of 1 km2 cells occupied) and spatial distribution (narrowly distributed to widespread). Spatial distribution measure was calculated as the longest distance found within the 3d quartile of distances between all recorded locations for that species. We chose the 3th quartile distance as it may better represent the records distribution in geographic space, avoiding any outlier present in the last quartile. We then extracted a total of 16 species that clearly belonged to one of the following four groups: narrowly distributed and rare (NR), narrowly distributed and common (NC), widely distributed and rare (WR), and widely distributed and common (WC). The selected species ranged in number of records from 6 to 2094 and in spatial distribution from 3.2 to 238.4 Km 3rd quartile distance (Table S2).

Environmental data used for modelling

We obtained bioclimatic data from WorldClim (Hijmans *et al*., 2005), as its variables render biologically meaningful estimates representing annual trends in seasonality and extreme/limiting factors. We did not include additional environmental variables, as our objective was not an in-depth study of the ecology of the hoverfly species but rather of the consistency of performance of the different algorithms. The selected species covered most of the range in environmental space of the Netherlands (Fig. S2). To reduce co-linearity between predictors (Guisan & Thuiller, 2005), we only retained variables with a Pearson's pair-wise correlation coefficient <|0.7|. When two variables were highly correlated we chose the one least correlated to others, leading to a total of nine climatic and one topographic variables with a spatial resolution of 1 km2 selected for the construction of the species distribution models (Table S3).

Modelling algorithms

We fitted species distribution models (SDM) using six commonly used algorithms (see Table S1): four machine learning methods, Artificial Neural Networks (ANN; Ripley, 1996), Generalized Boosted Models (GBM; Ridgeway, 1999; Friedman, 2001), Random Forests (RF; Breiman, 2001) and Maximum Entropy modelling (Maxent; Phillips *et al.*, 2006); and two regression methods, Generalized Additive Models (GAM; Hastie, 1990), Generalized Linear Models (GLM; McCullagh, 1989). We did not use "true absence" data, using instead a random or a given sample of background points as pseudo-absences. These algorithms have been applied for modelling environmental relationships for a wide range of species (Franklin, 2009; Thuiller *et al.*, 2009; Elith *et al.*, 2006; Wisz *et al.*, 2008; Phillips *et al.*, 2006; Mateo *et al.*, 2010). We used the BIOMOD package (Thuiller *et al.*, 2009) (v. 1.1-7.00) for R (R Development Core Team, 2011) for all selected algorithms, except Maxent, for which we used the Maximum Entropy Modelling software MaxEnt (v3.3.3e, www.cs.princeton.edu/~schapire/maxent/). We followed default settings recommended by Thuiller . (2010) (for BIOMOD) and Phillips and Dudik (Phillips & Dudik, 2008) (MaxEnt) for fitting the models. As every run within the ANN algorithm can render different results we selected the best weight decay and the number of units in the hidden layer by carrying out five-fold cross-validation runs. The GAM models were run with a spline function with three degrees of smoothing. The GBM models were constructed by fitting 5000 trees and five cross-validations in order to identify the number of trees that produced most accurate predictions. GLM's were generated by using polynomial terms with the step wise procedure and using the Akaike Information Criterion (AIC) for model selection. For RF models 500 trees were used as the building criterion following other studies that have implemented the algorithm successfully with these settings (see Elith & Leathwick, 2009; Scarnati *et al.*, 2009; Garzón *et al.*, 2008; Lawler *et al.*, 2006). MaxEnt was run with the auto-features option and the logistic output format was used as this has proven to be the appropriate method in an extensive multispecies study carried out by Phillips and Dudik (2008) . Finally, a consensus ensemble approach (Araújo & New, 2007), hereafter "Consensus approach", was applied using the BIOMOD platform models generated by GLM, GAM, GBM, RF and ANN. The Consensus approach is thought to offer more robust predictions for the potential and realized distribution of species than single algorithms (Araújo & New, 2007). Maxent is not integrated in BIOMOD v1.1-7.00, and therefore it was not part of the Consensus approach. The Consensus approach implementation consisted of the ensemble of the 10 model repetitions x 5 modelling algorithms = 50 output maps. We used the Receiving Operating Characteristic (ROC) of the area under de curve mean method (Hanley & McNeil, 1982) to create consensus maps (Thuiller *et al.*, 2009). In this method, after converting the outputs to binary predictions using their correspondent thresholds that maximize the sensitivity and specificity of the models (Jiménez-Valverde & Lobo, 2007), every cell for which more than half of the models predicted a presence, was considered a presence, the other cells were assigned as absence. All single modelling algorithms were run for the 16 hoverfly species. For each species and algorithm ten replicate runs were applied (two species had only 6 and 8 number of occurrence records and for these respectively 6 and 8 replicate runs were conducted).

Modelling process

To generate the species distribution models, all modelling algorithms used in this study required the input of (pseudo)absences (BIOMOD) or background points (MaxEnt) (Mateo *et al.*, 2010; Phillips *et al.*, 2009; Barbet-Massin *et al.*, 2012). Pseudo-absences were randomly selected locations where the focal species was not present but other hoverfly species had been found (more than 9000 Km2 cells conforming the total species modelled and available for generation of pseudo absences). This approach is more objective and realistic than taking pseudo-absences from sites that have not been sampled at all, accounting for the possible sampling bias (Raes & ter Steege, 2007; Elith *et al.*, 2011) , and likely providing more accurate results (Mateo *et al.*, 2010; Phillips *et al.*, 2009). For every species, the presence records were randomly partitioned in 75% for training and 25% for testing and were the same for all algorithms but Maxent, which was run in a separated platform. This random partitioning was repeated ten times to obtain a robust estimate for the algorithm's performance (Franklin, 2009). We generated and compared a total of 1078 models for the

16 selected species (16 species x 7 algorithms (incl. consensus) X 6-10 cross-validation runs).

Evaluation of results across modelling algorithms

Comparing the quality and accuracy of SDMs is generally achieved by comparing prediction success, however, this represents a limited view of the models accuracy (Wiens, 1989). Therefore, we evaluate the SDMs in three different ways: a) comparing the Area Under the Curve (AUC) values to assess differences in the general model fit, b) comparing the geographical consistency of the maps produced by each of the algorithms to assess the spatial congruence in presence and absence predictions; and c) comparing the contribution of the various environmental variables to the different models to assess the consistency of variable selection and contribution between runs within algorithm. Together these assessments provide a more robust and better evaluation of the performance of the different algorithms and insight into general model fit (a), spatial congruence of the maps (b) and the species' niche characterisation (c).

Comparing model fit across algorithms: AUC

To obtain a measure of the accuracy of the constructed SDMs the AUC of the ROC has been used. This measure is not only threshold independent but also evaluates both the false-positive error rate and the true positive rate in order to obtain a measure for the accuracy of the constructed model. AUC values range from 0 to 1, with values below 0.5 representing a model that is not better than random and values of 1 represent models that are highly accurate (Scarnati *et al.*, 2009). For our AUC evaluations, we obtained the AUC values from each of the models created by the 10 repetitions for each species and per algorithm, including the consensus approach. Although this metric has been highly criticized in some recent studies (Raes *et al.*, 2009; Jiménez-Valverde, 2012), it is still the most applied measure of accuracy for SDMs and that is why we considered it for our analysis. Moreover, one of the aims of this paper is to show that other accuracy measures, such as consistency of spatial predictions and of environmental variables selection may render different results compared to AUC.

Geographical consistency of predicted distributions

Species occurrence maps are the end product of most SDM. However, models with similar AUC values do not necessarily predict occurrences in the same locations. To assess how consistent the spatially explicit predictions of presence and absence are within and between algorithms, we calculated the similarity of the maps produced in replicate runs and compared similarity across algorithms. The SDM map similarity was assessed by creating the binary predictions (presence/absence maps) for each run using the threshold that minimizes the difference between sensitivity and specificity for each of the models (Jiménez-Valverde & Lobo, 2007). Next, the 10 presence-absence maps were compared pair-wise (45 comparisons) to obtain map similarity values per algorithm per species.

Spatial accuracy can be evaluated at different scales (Borcard *et al.*, 2004; Kraft & Ackerly, 2010). Analyzing patterns at different spatial scales is a common procedure, i.e. the ecological neighbour theory of Addicott *et al.* (1987) or the work of Wiens (1989), and relevant to identify the ecological process and spatial needs of the species. For example, the relationship between plant diversity and ecosystem functioning was found to be scale dependent (Díaz & Cabido, 2001; de Bello *et al.*, 2010).

We apply three different statistics incorporated in the Map Comparison Kit (Visser & de Nijs, 2006) to assess geographical patterns at different scales from the binary SDM output maps. For evaluations at small scale (single cell: 1km2) we used Cohen's Kappa statistic (Cohen, 1960). For medium scale evaluations, we used the Improved Fuzzy Kappa (Hagen-Zanker, 2009), which also takes values of surrounding cells into account (radius of neighbourhood of 4 cells). For large scale similarity we used the Fuzzy Global Matching (Hagen-Zanker, 2006), which evaluates overlap in patches of cells by taking into account their area of intersection, area of disagreement and the size of the patch. The latter two metrics make use of the fuzzy set theory to extract similarity values (Hagen-Zanker, 2009).

Consistency in environmental variables used to predict distributions

To evaluate the consistency in the strength assigned to each of the environmental variables in cross-validation SDM runs, we estimated the importance values of each variable per algorithm per species, as described by Thuiller *et al.* (2010). To obtain consistency values for each variable per model, species and algorithm we calculated the absolute difference between each of the importance values obtained for each of the 10 model runs and the average variable importance (average of the 10 model runs). We refer to this as the "deviance from average variable contribution". A high deviance indicates a high variance in variable importance across runs. This analysis was not performed for the consensus approach as it is composed of all BIOMOD algorithms and a combined variable contribution value cannot be defined in a meaningful way for an ensemble model.

Overall analysis of results

We used Linear Mixed Effects Models (LME) (Bolker *et al*., 2009) to investigate the possible effect of algorithm, the number of records and their spatial distribution on the attained AUC values, the geographic prediction similarity (Kappa, Improved Fuzzy Kappa and Fuzzy Global Matching) and the environmental variable contributions.

We fitted the LME in the R platform using the "nlme" package (Pinheiro *et al*., 2012). To improve the normality of the data a logit transformation was applied to the response variables AUC and Map similarity and a log transformation to the DFAC values. We used the number of records, spatial distribution of the records (upper value of 3rd quartile distance) and the algorithm as the fixed effects and the species as the random effect for the AUC and Map similarity. To account for the non-independence of the predictions generated based on the data from a given species, species identity was included as a random effect. Finally, we evaluated the consistency in variable contribution to the SDMs with a LME that included the environmental variable and algorithm as fixed effects and species as a random effect.

Results

Comparing model fit across algorithms: AUC

AUC values differed significantly between algorithms (Fig. S3) and significantly declined with increasing number of records (Fig. 1). The Consensus approach obtained the highest AUC values, independently of the number of records and the spatial distribution. The next best models in terms of model fit were Maxent and GAM, which had significantly higher AUC values than GLM, GBM, RF, especially at low numbers of records, while ANN performed significantly worse (Table 1). Spatial distribution did not significantly affect model fit (only weakly for Maxent. Table 1, Table S4).

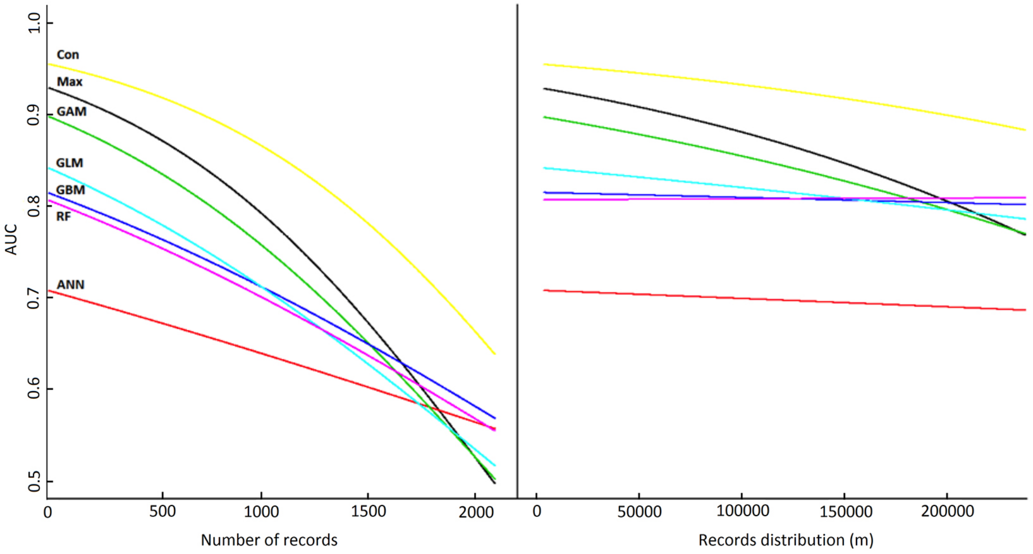


Figure 1. Effect of records availability and spatial distribution on model fit. Effect of records availability and spatial distribution on model fit based on the AUC evaluation of the different algorithms. For the AUC evaluation, we present the back-transformed mean values estimated using Linear Mixed Effect models for each algorithm. The first column presents the results with relation to the number of records and the second with relation to the records distribution.

Geographical consistency of predicted distributions

The spatial scale at which maps were compared strongly affected the spatial congruence within algorithms. At the largest scale (Fuzzy global matching comparison, "FGM") all algorithms rendered high spatial congruence across model runs, while spatial congruence was lower at medium scale (Improved Fuzzy Kappa comparison, "IFK") and again lower when individual (1km2) cells were compared (Kappa comparison) (Fig. 2). This is expected, because the first two methods buffer against small mismatches between maps (Hagen-Zanker, 2009). For all algorithms except ANN, spatial congruence was not significantly affected by number of records or spatial distribution of the data (at small and medium scales, Table 1). ANN spatial congruence improved with increasing number of records (small and medium scales) and wider distribution (all scales) of the data.

At small scale (i.e. using the Kappa statistic), Maxent and GAM produced the highest spatial consistency. RF, GBM, GLM and the Consensus approach performed similarly when number of records was high but significantly worse at low number of records (Fig. 2, Kappa panel). ANN models produced the lowest spatial consistency at both small and medium spatial scale, at the latter scale joined by a poorly performing Consensus approach. At medium spatial scale, Maxent rendered the highest spatial consistency values, but as above several other algorithms, GAM, GBM, GLM and RF, were not significantly worse (Fig. 2, IFK panel, Table 1, Table S6). GBMs and RF performed better than the other algorithms at large spatial scale (with all rendering high map similarities; Fig. 2 FGM panel, Table 1, Table S7). This improvement may, however, be due to overfitting as they mostly predict small presence patches matching closely to the locations where the training records are found (example for RF in Fig. S4).

Environmental consistency of predicted distributions

There were significant differences in how consistently algorithms assign importance to environmental variables between different runs (Table 1, Table S8). GBM and RF were the most consistent algorithms, followed by Maxent, while ANN, GAM and GLM rendered significantly higher variability across runs (Fig. 3). Variable assignment was often less consistent at small sample sizes (for ANN, GAM, GLM and RF; Fig. S5). The spatial distribution of the data affected the consistency in variable importance assignment for all algorithms for at least one variable (Fig. S6).

Discussion

Species distribution modelling is currently the main method for predicting species distributions, which in turn may guide conservation management actions. SDM can be implemented using a range of different algorithms, whose performances are analysed in this study in three different but complementary ways, by comparing model fit, consistency of spatial predictions and consistency of the selection of environmental variables. We show that depending on the research objectives, number of records and spatial distribution of such records the most suitable algorithm will vary.

The model fit

The decline of model fit (AUC) with increasing number of records is expected when using pseudo-absences or background data because the maximum attainable AUC value decreases with number of records (maximum AUC= (1-area occupied)/2) (Phillips *et al.*, 2006; Raes & ter Steege, 2007; Bean *et al.*, 2012). For comparisons of model fit between species the (bias corrected) null

Table 1. Results of the Linear Mixed Effect models for the AUC, Kappa, IFK, FGM and DFAC (deviance from average variable contribution). The significance of the pairwise algorithms comparisons, their interaction with the number of records and spatial distribution is presented. The positive and negative signs apply for the first algorithm being compared against the second. For the first four measures the positive sign points to algorithms that render higher values -better fits and maps similarities. In the DFAC, the negative signs point to a more consistent algorithm as it renders lower deviances than the second. Max= Maxent, Con= Consensus approach; ns= no significant; na= not applicable. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported.

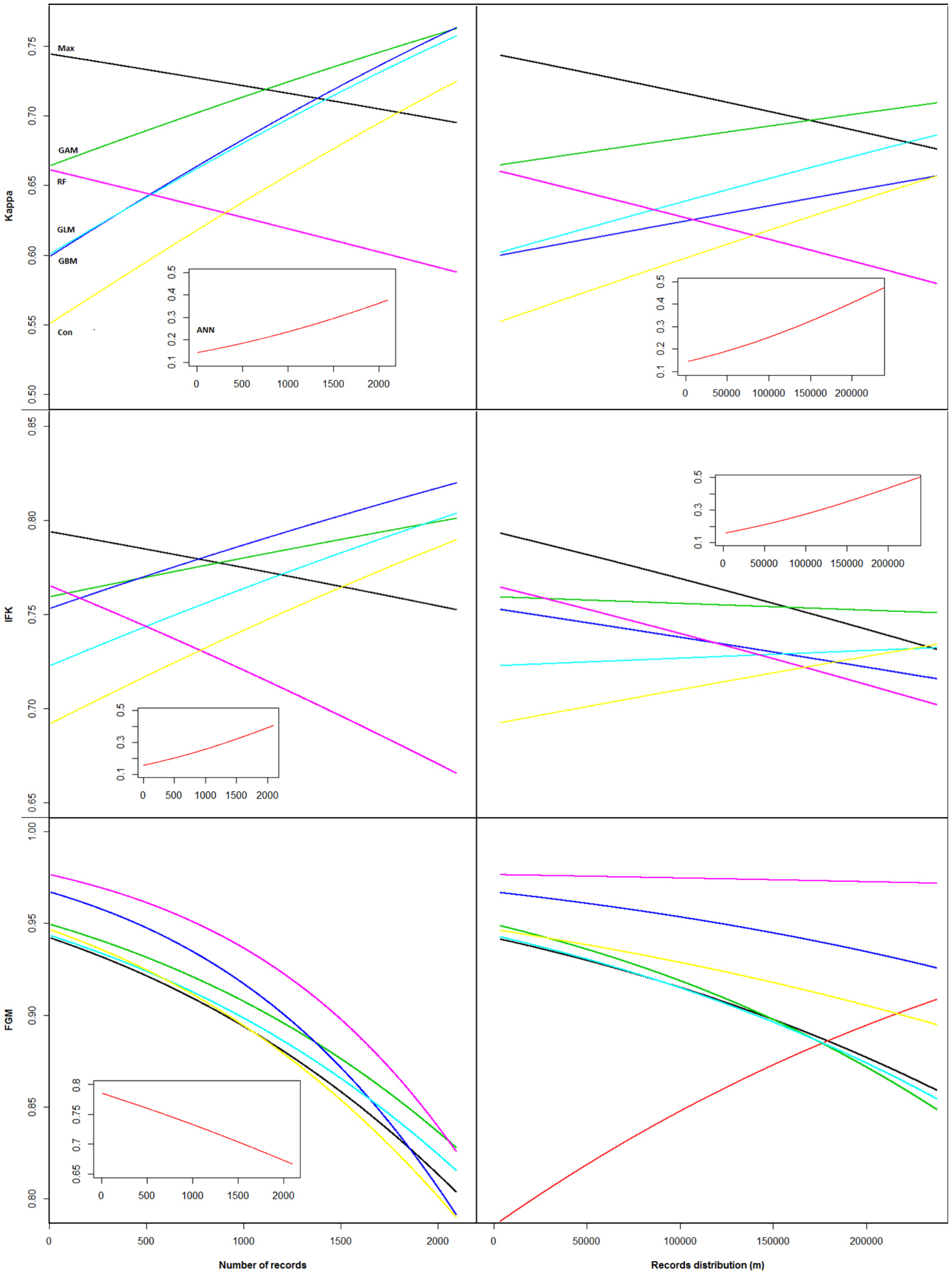
Algorithms	AUC	Kappa	IFK	FGM	DFAC
Max vs ANN	(+) ***	(+) ***	(+) ***	(+) ***	(-) ***
Max vs GAM	ns	ns	ns	ns	(-) ***
Max vs GBM	(+) ***	(+) ***	ns	(-) ***	(+) ***
Max vs GLM	(+) ***	(+) ***	ns	ns	(-) ***
Max vs RF	(+) ***	ns	ns	(-) ***	(+) ***
Max vs Con	(-) *	(+) ***	(+) **	ns	na
ANN vs GAM	(-) ***	(-) ***	(-) ***	(-) ***	(+) ***
ANN vs GBM	(-) **	(-) ***	(-) ***	(-) ***	(+) ***
ANN vs GLM	(-) ***	(-) ***	(-) ***	(-) ***	ns
ANN vs RF	(-) *	(-) ***	(-) ***	(-) ***	(+) ***
ANN vs Con	(-) ***	(-) ***	(-) ***	(-) ***	na
GAM vs GBM	(+) ***	ns	ns	(-) ***	(+) ***
GAM vs GLM	(+) *	ns	ns	ns	(-) ***
GAM vs RF	(+) ***	ns	ns	(-) ***	(+) ***
GAM vs Con	(-) ***	(+) *	ns	ns	na
GBM vs GLM	ns	ns	ns	(+) ***	(-) ***
GBM vs RF	ns	ns	ns	(-) **	(+) ***
GBM vs Con	(-) ***	ns	ns	(+) ***	na
GLM vs RF	ns	ns	ns	(-) ***	(+) ***
GLM vs Con	(-) ***	ns	ns	ns	na
RF vs Con	(-) ***	(+) *	ns	(+) ***	na
Max vs Records	(-) ***	ns	ns	(-) **	na
ANN vs Records	ns	(+) *	(+) *	ns	na
GAM vs Records	(-) ***	ns	ns	(-) **	na
GBM vs Records	(-) *	ns	ns	(-) ***	na
GLM vs Records	(-) **	ns	ns	(-) **	na
RF vs Records	(-) *	ns	ns	(-) ***	na
Con vs Records	(-) ***	ns	ns	(-) ***	na
Max vs Distribution	(-) *	ns	ns	(-) *	na
ANN vs Distribution	ns	(+) ***	(+) **	(+) *	na
GAM vs Distribution	ns	ns	ns	(-) **	na
GBM vs Distribution	ns	ns	ns	ns	na
GLM vs Distribution	ns	ns	ns	(-) *	na
RF vs Distribution	ns	ns	ns	ns	na
Con vs Distribution	ns	ns	ns	ns	na

model approach would be more appropriate (Raes & ter Steege, 2007), but here we only compared model fit within species.

As in other studies (Marmion *et al*., 2009; Lomba *et al*., 2010), the Consensus approach rendered the best overall model fit, probably because presence predictions are strictly limited to cells for which the majority of the models in the ensemble predict a presence. However, considering only AUC scores as an evaluation method for model performance may not always be the best approach (Wiens, 1989), as AUC is not indicative of geographical and environmental consistency of a model (see below). Even though the Consensus approach produced good general fits, its drawbacks become apparent when using other performance measures (Table 2).

Maxent's better performance in comparison to the other "single" algorithms might be partly due to how the environmental variables and their interactions are modelled, i.e. incorporating progressively more mathematical complexity of the model when more data are available (Phillips *et al*., 2006; Elith *et al*., 2011). It also seems that generative methods in general (Maxent, but also RF and GBM) render better results with small sample sizes, maybe due to faster convergence to their higher asymptotic error than discriminative methods (Ng & Jordan, 2002). In comparison, discriminative methods such as GLM and GAM improve their accuracy as the number of records increases and may even surpass results offered by generative methods at large sample sizes (see Fig. 1 at around 1700 records). However, for most taxa and regions, data availability rarely reaches the point where advantages of discriminative methods can be benefitted from (Phillips *et al*., 2009; Ponder *et al*., 2010). Finally, thanks to its regularization procedure, Maxent models are less likely to overfit the data (Phillips *et al*., 2006; Elith *et al*., 2011), than RF and GBM models (as shown in Fig. S4, and other recent studies, (Elith & Graham, 2009; Oliver *et al*., 2012).

Figure 2. (next page) **Effect of records availability and spatial distribution on geographical consistency.** Effect of records availability and spatial distribution on geographical consistency of the different algorithms. For each spatial scale (small scale –Kappa; medium scale – IFK; and large scale - FGM), we present the back-transformed mean values estimated using Linear Mixed Effect models for each algorithm. The first column presents the results with relation with the number of records and the second with relation with the records distribution. For clarity of comparisons, ANN results are presented separately whenever its values were much lower than those obtained for other algorithms. See Tables 1 and S5 for further statistical information.


Kappa
IFK
FGM
Max
GAM
RF
GLM
GBM
Con
ANN
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
0.90
0.95
1.00
0.1
0.2
0.3
0.4
0.5
0.65
0.7
0.75
0.8
0
500
1000
1500
2000
50000
100000
150000
200000
Number of records
Records distribution (m)

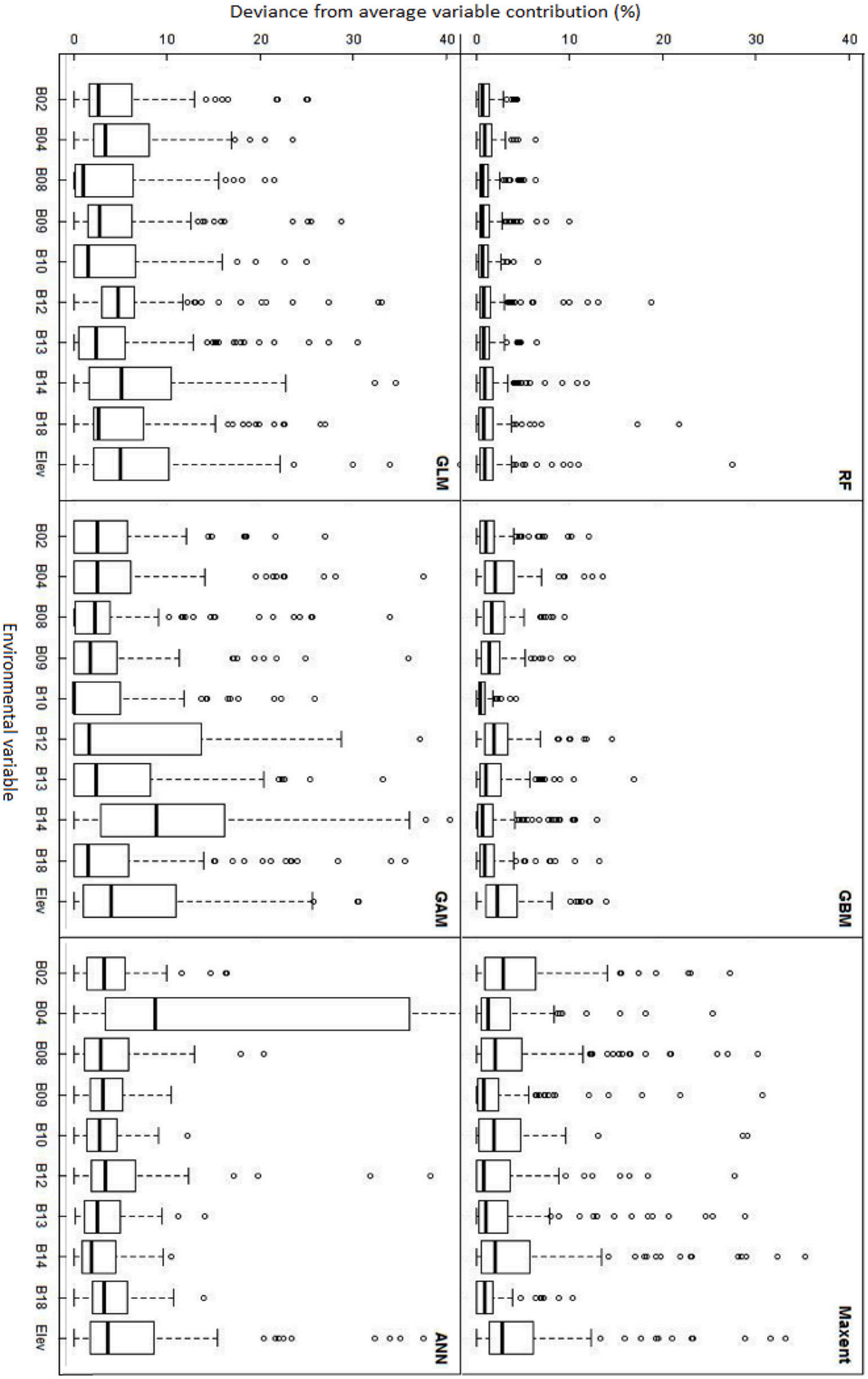
Obtaining geographically consistent predicted distributions

Our results show that a high AUC value is not necessarily associated with a high spatial accuracy of the models (e.g. for Consensus approach in our study). However, algorithms with low AUC values produced very inconsistent spatial predictions (see Figs. 1 and 3). Moreover, the accuracy of the occurrence predictions depended on the spatial scale used. Here we used scales that roughly represent small (sub) populations (1km2 cell comparison), landscape level patterns (several km2 area) or regional populations. If we focus on small and medium scale geographic processes, Maxent, GAM and RF models attain the best results predicting consistently the same geographic areas across repetitions (Fig. 2, Kappa and IFK panels). This result suggests that these algorithms are preferable when modelling species that are narrowly distributed and from which not many record locations are available. However, at larger spatial scales all algorithms produce highly accurate and largely similar results (with the exception of ANN), RF and GBM obtaining only slightly better results (Fig. 2, FGM panel). This suggests that when focusing on processes occurring at regional or country scale, RF and GBM algorithms might be preferable. However, due to their tendency to overfit (Fig. S4), the usefulness of these algorithms for temporal or spatial extrapolation is limited.

How consistent are SDM algorithms when selecting significant environmental variables?

From the six algorithms, RF and GBM were the most consistent when selecting the environmental factors that are considered to limit the species distributions (Fig. 3). However, these algorithms tend to under-predict the species range because of overfitting the models to the training data, which is apparent by the poor predictions of the test data, as shown by the low AUC values (Fig. 1). In such cases these algorithms only detect part of the realized niche of the species and underestimate the areas that the species could potentially inhabit.

Figure 3. (next page) **Consistency of the variables' contribution to the model. Variability of the contribution of each environmental variable (i.e. deviance from the average variable contribution to the model) for each algorithm.** In the Y axis higher deviance represents a lower consistency in the contribution values given by the algorithm to the different variables across runs. The values for variable "B04" in the ANN algorithm go to 80% and other variables present outliers going beyond the 40 %, however, for plotting convenience we show only the deviance up to the 40%. See Table 1 and Tables S8 and S9 for further statistical information.


Deviance from average variable contribution (%)
0
10
20
30
40
Environmental variable
B02
B04
B08
B09
B10
B12
B13
B14
B18
Elev
GLM
RF
GAM
GBM
ANN
Maxent

Therefore, if we are only interested in the environmental niche of a species these two algorithms provide better results in our evaluation. However, there are other algorithms that performed almost as good in the consistent selection of environmental variables, while not highly overfitting the data (e.g. Maxent, see also AUC evaluation). These might be a good option for a more consistent selection of the species' important environmental variables.

Implications for species distribution modelling

Setting the aim of the SDM exercise beforehand is key for obtaining appropriate SDMs (Araújo & Peterson, 2012). SDM studies are performed with different main aims in mind (e.g. estimating potential general distribution, obtaining past, present or future spatial predictions, environmental niche characterization, summarized in Table 2). Our study clearly shows that depending on the objective of the study different algorithms should be selected for SDM. For example, if a conservation practitioner needs to know what the likelihood is of a species occurring in a small nature reserve then using a model with a high spatial congruence and high fit is essential. On the other hand, if one wants to understand the environmental conditions that most likely limit a species' distribution, an algorithm with high consistency in variable strength assessment is more important. If one would be interested in a balance between the above then yet another algorithm might be preferred. In our analysis Maxent obtained some of the best results across evaluation criteria and might thus be a good starting point from among the readily available modelling options (Table 2), whereas for specific questions several other algorithms give similar quality results or might be preferred, e.g. RF for consistency in environmental variable selection.

Our results are representative of the currently implemented versions of the different algorithms and it is likely that future changes in coding the algorithms may lead to performance improvements. Moreover, while these results are only representative for the set of conditions present in the study area (The Netherlands) and caution must be taken in extrapolating our findings to areas that are substantially different, the extent and high quality of the database here used (Netherlands hoverfly database, where pseudo-absences selected for the models are likely closely related to real absences), allowed us to select the species with variable distribution patterns following objective criteria, thus making it possible to carry out algorithms comparisons with real instead of virtual data. Further work is needed to corroborate our results for areas with broader spatial and environmental range.

Table 2. Summary of the algorithms' performance across analyses and the different aims for which they attain better results (for more details see Figs. 1-3).

Algorithm	Model fit -AUC values	Binary predictions similarity	Consistency in Environmental Variables selection	Observations
Consensus approach	High	Low at fine scale Medium at medium scale Medium at coarse scale	NA*	-Good for high model fit for narrow, wide, small and big sample sizes. It is not the best option for similarity in spatial distribution.
Maxent	High	High at fine scale High at medium scale Medium at coarse scale	Medium to high	-High scores for narrow and moderately wide distribution of records, also good for small and moderately big sample sizes (up to around 1700 records).
GAM	Medium	Medium at fine scale Medium at medium scale Medium at coarse scale	Low	-For narrow and moderately wide distribution of records, also good for small and moderately big sample sizes (around 1400 records).
GBM	Low	Low at fine scale Medium at medium scale High at coarse scale	High	-Obtains higher scores than others for common and widespread records. Obtains lower scores with small and narrow records' distribution.
GLM	Low	Low at fine scale Medium at medium scale Medium at coarse scale	Low	-Preferred for common and widespread records although not the best in any comparison metric. Obtains lower scores with small and narrow records' distribution.
RF	Low	Medium at fine scale Medium at medium scale High at coarse scale	High	-Good for common and widespread record. Obtains lower scores with small and narrow records' distribution. Similar to GBM
ANN	Very low	Very low at fine scale Very low at medium scale Very low at coarse scale	Low	-Not better than other in most of the comparisons. It produces low scores across analysis.

*Not Available for this method.

Conclusion

While species distribution modelling is commonly used to inform and guide conservation actions, until now no extensive evaluation of the quality of the many available methods was available (Elith & Leathwick, 2009; Araújo & Guisan, 2006). While current species distribution modelling studies commonly select modelling algorithm haphazardly, mainly based on AUC accuracy, our results show that performance is different between algorithms; no single algorithm was performing best for all evaluation metrics (model fit, geographical consistency and environmental niche). We show that a high model fit does not necessarily translate into highly consistent spatial (i.e. consensus approach) or environmental niche predictions, highlighting the need of a priori matching of study aims with modelling approach. We designed a modelling workflow (Fig. 4), that one may follow to select the most suitable modelling algorithm(s) and/or approaches for a given aim (e.g. determining the range of spatially restricted species, or identifying algorithms that produce more consistent models for environmental variables selection, given more certainty during analysis of the species' ecological niche). Such framework is applicable to different species datasets taking into account variation in several important characteristics of species distributions (level of rarity and spatial extent).

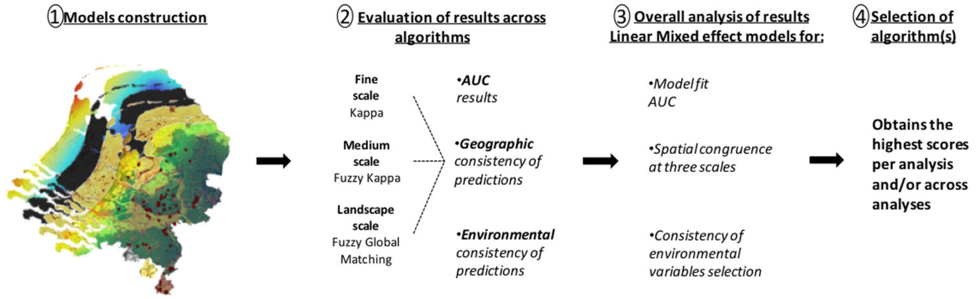


Figure 4. SDM's analysis framework. Framework for analysing the algorithms adequacy for modelling our species distribution by means of model fit, binary predictions similarity and selection of variables importance. These results are analysed across algorithms by means of Linear Mixed Effects models (LME), which will aid in the selection of the most suitable algorithm for modelling our species distributions.

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Supplementary material

Table S1. (next page) **Different approaches for producing SDMs are exemplified by the large variety of algorithms used.** In 42 publications from 2012 containing the words "Species Distribution Models" in the title for 2012 (ISI Web of Knowledge, until 26/06/2012) the studies used 19 different algorithms. These studies focus on different aspect of the modelling process (with the "*" symbol).

Author	Title	Year	Modelling Single species	Modelling Multi species	Effect of number records	Effect of records distribution	Interested in Environmental variables	Algorithm(s) used
Adhikari, D. Barik, S. K. Upadhaya, K.	Habitat distribution modelling for reintroduction of Ilex khasiana Purk, a critically endangered tree species of northeastern India	2012	*	-	-	-	-	Maxent
Ashcroft, Michael B. French, Kristine O. Chisholm, Laurie A.	A simple post-hoc method to add spatial context to predictive species distribution models	2012	-	*	-	-	-	Maxent
Babar, Shilpa Amarnath, Giriraj Reddy, C. S. Jentsch, Anke Sudhakar, S.	Species distribution models: ecological explanation and prediction of an endemic and endangered plant species (Pterocarpus santalinus L.f.)	2012	*	-	-	-	-	GARP MAXENT BIOCLIM
Barbet-Massin, Morgane Jiguet, Frederic Albert, Cecile Helene Thuiller, Wilfried	Selecting pseudo-absences for species distribution models: how, where and how many?	2012	-	*	*	-	-	GLM GAM MARS MDA CTA BRT RF
Bateman, Brooke L. VanDerWal, Jeremy Johnson, Christopher N.	Nice weather for bettongs: using weather events, not climate means, in species distribution models	2012	-	*	-	-	*	Maxent
Bean, William T. Stafford, Robert Brashares, Justin S.	The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models	2012	*	-	*	-	-	Maxent
Bentlage, Bastian Shcheglovitova, Mariya	NichePy: modular tools for estimating the similarity of ecological niche and species distribution models	2012	-	*	-	-	-	RF ENFA Ensemble of models
Bidinger, K. Loetters, S. Roedder, D. Veith, M.	Species distribution models for the alien invasive Asian Harlequin ladybird (Harmonia axyridis)	2012	*	-	-	-	*	Maxent

Bonthoux, Sebastien Balent, Gerard	**Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape**	**2012**	-	*	-	-	-	**GLM** **GAM** **ANN** **BRT** **MDA** **RF** **MARS**
Foltete, Jean-Christophe Clauzel, Celine Vuidel, Gilles Tournant, Pierline	Integrating graph-based connectivity metrics into species distribution models	2012	*	-	-	-	-	GLM
Freeman, Elizabeth A. Moisen, Gretchen G. Frescino, Tracey S.	Evaluating effectiveness of down-sampling for stratified designs and unbalanced prevalence in Random Forest models of tree species distributions in Nevada	2012	-	-	*	-	-	RF
Gomez-Rodriguez, Carola Bustamante, Javier Diaz-Paniagua, Carmen Guisan, Antoine	Integrating detection probabilities in species distribution models of amphibians breeding in Mediterranean temporary ponds	2012	-	*	-	-	*	GLM
Hanberry, B. B. He, H. S. Dey, D. C.	Sample sizes and model comparison metrics for species distribution models	2012	-	*	*	-	-	RF
Hassall, Christopher	Predicting the distributions of under-recorded Odonata using species distribution models	2012	-	*	*	-	*	GLM
Heikkinen, Risto K. Marmion, Mathieu Luoto, Miska	Does the interpolation accuracy of species distribution models come at the expense of transferability?	2012	-	*	-	-	-	GAM MARS GLM MAXENT ANN GBM RF GARP CTA MDA

Heinanen, Stefan Erola, Johnny von Numers, Mikael	**High resolution species distribution models of two nesting water bird species: a study of transferability and predictive performance**	**2012**	-	*	-	-	*	**Maxent**
Hijmans, Robert J.	Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model	2012	-	*	-	-	-	BIOCLIM MAXENT
Illoldi-Rangel, Patricia Rivaldi, Chissa-Louise Sissel, Blake Trout Fryxell, Rebecca Gordillo-Perez, Guadalupe Rodriguez-Moreno, Angel Williamson, Phillip Montiel-Parra, Griselda Sanchez-Cordero, Victor Sarkar, Sahotra	Species distribution models and ecological suitability analysis for potential tick vectors of lyme disease in Mexico.	2012	-	*	-	-	-	Maxent
Jimenez-Valverde, Alberto	Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling	2012	*	-	-	-	-	GLM
Kamino, Luciana H. Y. Stehmann, Joao Renato Amaral, Silvana De Marco, Paulo, Jr. Rangel, Thiago F. de Siqueira, Marinez F. De Giovanni, Renato Hortal, Joaquin	Challenges and perspectives for species distribution modelling in the neotropics	2012	-	*	*	-	*	BIOCLIM GAM GARP MARS EED ANN
Loe, Leif Egil Bonenfant, Christophe Meisingset, Erling L. Mysterud, Atle	Effects of spatial scale and sample size in GPS-based species distribution models: are the best models trivial for red deer management?	2012	*	-	*	-	-	GLM

Loehle, Craig	**Relative frequency function models for species distribution modeling**	**2012**	-	*	-	-	-	**RFF**
Lundy, Mathieu G. Buckley, Daniel J. Boston, Emma S. M. Scott, David D. Prodoehl, Paulo A. Marnell, Ferdia Teeling, Emma C. Montgomery, W. Ian	Behavioural context of multi-scale species distribution models assessed by radio-tracking	2012	*	-	-	-	*	GLM
Machado-Machado, Elia Axinia	Empirical mapping of suitability to dengue fever in Mexico using species distribution modeling	2012	*	-	-	-	*	Maxent
Mateo, Ruben G. Felicisimo, Angel M. Pottier, Julien Guisan, Antoine Munoz, Jesus	Do Stacked Species Distribution Models Reflect Altitudinal Diversity Patterns?	2012	-	*	-	-	-	BRT GLM MARS GARP GMD Maxent Ensemble of models
Matin, Shafique Chitale, Vishwas Sudhir Behera, Mukunda Dev Mishra, Birupakshya Roy, Partha Sarathi	Fauna data integration and species distribution modelling as two major advantages of geoinformatics-based phytobiodiversity study in today's fast changing climate	2012	-	*	-	-	-	Maxent
Meynard, Christine N. Kaplan, David M.	The effect of a gradual response to the environment on species distribution modeling performance	2012	*	-	-	-	*	GLM BRT
Oliver, Tom H. Gillings, Simon Girardello, Marco Rapacciuolo, Giovanni Brereton, Tom M. Siriwardena, Gavin M. Roy, David B. Pywell, Richard Fuller, Robert J.	Population density but not stability can be predicted from species distribution models	2012	-	*	-	-	-	GAM ANN RF MAXENT

Parra-Quijano, M. Iriondo, J. M. Torres, E.	**Improving representativeness of genebank collections through species distribution models, gap analysis and ecogeographical maps**	**2012**	-	*	-	-	-	**GLM**
Royle, J. Andrew Chandler, Richard B. Yackulic, Charles Nichols, James D.	Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions	2012	-	-	-	-	-	Maxent
Saupe Erin E., Barve Vijay, Myers Corinne E., Soberón Jorge, Barve Narayani,, et al.	Variation in niche and distribution model performance: The need for a priori assessment of key causal factors	2012	-	*	-	*	*	BIOCLIM DOMAIN GAM GARP Maxent
Sindt, Anthony R. Pierce, Clay L. Quist, Michael C.	Fish Species of Greatest Conservation Need in Wadeable Iowa Streams: Current Status and Effectiveness of Aquatic Gap Program Distribution Models	2012	-	*	-	-	-	CTA
Stanton, Jessica C. Pearson, Richard G. Horning, Ned Ersts, Peter Akcakaya, H. Resit	Combining static and dynamic variables in species distribution models under climate change	2012	-	*	-	-	*	Maxent
Tisseuil, C. Vrac, M. Grenouillet, G. Wade, A. J. Gevrey, M. Oberdorff, T. Grodwohl, J. -B. Lek, S.	Strengthening the link between climate, hydrological and species distribution modeling to assess the impacts of climate change on freshwater biodiversity	2012	-	*	-	-	*	BRT

Torres, Natalia M. De Marco Junior, Paulo Santos, Thiago Silveira, Leandro de Almeida Jacomo, Anah T. Diniz-Filho, Jose A. F.	**Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics**	**2012**	*****	**-**	**-**	**-**	**-**	**BIOLCIM GARP MAXENT GBM RF MD DOMAIN CTA MARS MDA ANN**
Tyberghein, Lennert Verbruggen, Heroen Pauly, Klaas Troupin, Charles Mineur, Frederic De Clerck, Olivier	Bio-ORACLE: a global environmental dataset for marine species distribution modelling	2012	*	-	-	-	*	Maxent
Vaclavik, Tomas Kupfer, John A. Meentemeyer, Ross K.	Accounting for multi-scale spatial autocorrelation improves performance of invasive species distribution modelling (iSDM)	2012	*	-	-	-	*	GLM Maxent
Vaclavik, Tomas Meentemeyer, Ross K	Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion	2012	*	-	-	-	-	ENFA
Vanhatalo, Jarno Veneranta, Lari Hudd, Richard	Species distribution modeling with Gaussian processes: A case study with the youngest stages of sea spawning whitefish (Coregonus lavaretus L. s.l.) larvae	2012	*	-	-	-	*	GLM
Vasconcelos, Tiago S. Rodriguez, Miguel A. Hawkins, Bradford A.	Species distribution modelling as a macroecological tool: a case study using New World amphibians	2012	-	*	*	-	-	BIOCLIM OM_GARP MAXENT
Veloz, Samuel D. Williams, John W. Blois, Jessica L. He, Feng Otto-Bliesner, Bette Liu, Zhengyu	No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models	2012	-	*	-	-	*	BRT MARS MARS-COM GAM GLM Ensemble of models

Williams-Tripp, M. D'Amico, F. J. N. Page, C. Bertrand, A. Nemoz, M. Brown, J. A.	**Modeling Rare Species Distribution at the Edge: The Case for the Vulnerable Endemic Pyrenean Desman in France**	**2012**	*	-	-	-	*	**GLM**

*Focus; -Not important. ANN: Artificial Neural Networks; BIOCLIM: Bioclimatic Envelope; BRT: Boosted Regression Trees; CTA: Classification Tree; DOMAIN: Multivariate distance; GMD: Gower's Metric; EED: Euclidean Environmental Distance; ENFA: Ecological Niche Factor Analysis; Ensemble: Ensemble of models; GAM: Generalized Additive Models; GARP: Genetic Algorithm for Rule-set Production; GBM: Generalized Boosting Models; GLM: Generalized Linear Models; MARS: Multivariate Adaptive Regression Splines; Maxent: Maximum Entropy; MD: Mahalanobis Distance; MDA: Mixture Discriminant Analysis; RF: Random Forest; RFF: Relative Frequency Function.

Table S2. Description of the species data used for fitting the models.

Species	Number of records	Distance (Km)
Brachyopa bicolor	19	165.36
Brachyopa scutellaris	81	160.65
Brachyopa testacea	22	74.95
Chalcosyrphus piger	21	83.20
Cheilosia chrysocoma	43	162.32
Cheilosia lenis	11	16.75
Chrysotoxum cautum	346	119.69
Eristalinus aeneus	127	238.35
Eupeodes corollae	1578	15.12
Helophilus trivittatus	2094	3.29
Lejogaster tarsata	100	142.41
Lejops vittata	8	29.73
Melanostoma scalare	1512	33.58
Microdon devius	6	48.00
Platycheirus immarginatus	10	219.69
Psilota atra	12	39.51

*Distance represents the 3$^{th.}$ quartile distance between the most separated record locations for the focus species.

Table S3. Environmental variables used for fitting the SDM.

Name	**Description**	**Unit**	**Mean**	**Range**	**Std. Dev.**
B02	Mean Diurnal Range	°C	6.3	4.9 – 7.8	8.6
B04	Temperature Seasonality	°C	5.4	5 – 5.7	0.1
B08	Mean Temperature of Wettest Quarter	°C	11.5	3.4 – 17.3	4.2
B09	Mean Temperature of Driest Quarter	°C	6.9	3.4 – 11.2	2.8
B10	Mean Temperature of Warmest Quarter	°C	16.3	15.3 - 17.3	0.6
B12	Annual Precipitation	mm	824.7	723 - 983	63.9
B13	Precipitation of Wettest Month	mm	82.5	71 - 94	6.9
B14	Precipitation of Driest Month	mm	55.5	40 - 71	9.2
B18	Precipitation of Warmest Quarter	mm	231.6	194 - 272	22.2
Elevation	Elevation range	masl	109	-8 - 300	72.6

The data has a resolution of ≈1 km^2 (Hijmans et al. 2005, http://www.worldclim.org).

Table S4. Statistical results of the Linear Mixed Effect models for the AUC values between algorithms and their interaction with the number of records and spatial distribution.

Algorithms	Estimate	z value	Pr(>|z|)
Max vs ANN	1.6890	10.6090	<0.01***
Max vs GAM	0.3988	2.5060	0.2087
Max vs GBM	1.0940	6.8710	<0.01***
Max vs GLM	0.9014	5.6630	<0.01***
Max vs RF	1.1460	7.1990	<0.01***
Max vs Con	-0.4769	-2.9960	0.0596.
ANN vs GAM	-1.2900	-8.1040	<0.01***
ANN vs GBM	-0.5950	-3.7380	<0.01**
ANN vs GLM	-0.7873	-4.9460	<0.01***
ANN vs RF	-0.5428	-3.4100	0.0165*
ANN vs Con	-2.1660	-13.6050	<0.01***
GAM vs GBM	0.6948	4.3650	<0.01***
GAM vs GLM	0.5026	3.1570	0.0366*
GAM vs RF	0.7471	4.6940	<0.01***
GAM vs Con	-0.8757	-5.5020	<0.01***
GBM vs GLM	-0.1922	-1.2080	0.9555
GBM vs RF	0.0523	0.3280	1
GBM vs Con	-1.5710	-9.8670	<0.01***
GLM vs RF	0.2445	1.5360	0.8299
GLM vs Con	-1.3780	-8.6590	<0.01***
RF vs Con	-1.6230	-10.1950	<0.01***
Max vs records	-0.0012	-5.1640	<0.01***
ANN vs records	-0.0003	-1.3120	0.9267
GAM vs records	-0.0010	-4.3280	<0.01***
GBM vs records	-0.0006	-2.4080	0.2579
GLM vs records	-0.0008	-3.2080	0.0317*
RF vs records	-0.0006	-2.4140	0.2537
Con vs records	-0.0012	-4.9600	<0.01***
Max vs distance	0.0000	-2.6830	0.1378
ANN vs distance	0.0000	-0.2010	1
GAM vs distance	0.0000	-1.8910	0.5998
GBM vs distance	0.0000	-0.1700	1
GLM vs distance	0.0000	-0.7300	0.999
RF vs distance	0.0000	0.0260	1
Con vs distance	0.0000	-2.0140	0.51

The estimates are the values as obtained in the mixed model without being logit back-transformed. Max= Maxent, Con= Consensus approach; Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported.

Table S5. Statistical results of the Linear Mixed Effect models for the maps similarity values at the finer scale (Kappa) between algorithms and their interaction with the number of records and their spatial distribution.

Algorithms	Estimate	z value	Pr(>|z|)
Max vs ANN	2.8590	20.0740	<0.01***
Max vs GAM	0.3869	2.7170	0.127
Max vs GBM	0.6669	4.6830	<0.01***
Max vs GLM	0.6600	4.6350	<0.01***
Max vs RF	0.3995	2.8050	0.1013
Max vs Con	0.8643	6.0690	<0.01***
ANN vs GAM	-2.4720	-17.3570	<0.01***
ANN vs GBM	-2.1920	-15.3920	<0.01***
ANN vs GLM	-2.1990	-15.4390	<0.01***
ANN vs RF	-2.4590	-17.2690	<0.01***
ANN vs Con	-1.9950	-14.0050	<0.01***
GAM vs GBM	0.2799	1.9660	0.5448
GAM vs GLM	0.2731	1.9180	0.5798
GAM vs RF	0.0126	0.0890	1
GAM vs Con	0.4774	3.3520	0.0196*
GBM vs GLM	-0.0068	-0.0480	1
GBM vs RF	-0.2673	-1.8770	0.6096
GBM vs Con	0.1974	1.3860	0.9001
GLM vs RF	-0.2605	-1.8290	0.6443
GLM vs Con	0.2043	1.4340	0.88
RF vs Con	0.4648	3.2630	0.0268*
Max vs records	-0.0001	-0.5660	0.9999
ANN vs records	0.0006	2.9870	0.0627
GAM vs records	0.0002	1.1230	0.9721
GBM vs records	0.0004	1.7810	0.6779
GLM vs records	0.0003	1.6890	0.7397
RF vs records	-0.0001	-0.7260	0.999
Con vs records	0.0004	1.7680	0.6867
Max vs distance	0.0000	-0.7530	0.9987
ANN vs distance	0.0000	3.8090	<0.01**
GAM vs distance	0.0000	0.4760	1
GBM vs distance	0.0000	0.5600	0.9999
GLM vs distance	0.0000	0.8470	0.9964
RF vs distance	0.0000	-0.7870	0.9981
Con vs distance	0.0000	1.0070	0.9868

The estimates are the values as obtained in the mixed model without being logit back-transformed. Max= Maxent, Con= Consensus approach; Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported.

Table S6. Statistical results of the Linear Mixed Effect models for the maps similarity values at the medium scale (Improved Fuzzy Kappa) between algorithms and their interaction with the number of records and their spatial distribution.

Algorithms	Estimate	z value	Pr(>|z|)
Max vs ANN	3.0180	21.0680	<0.01***
Max vs GAM	0.2000	1.3960	0.8929
Max vs GBM	0.2337	1.6310	0.771
Max vs GLM	0.3915	2.7330	0.12
Max vs RF	0.1673	1.1680	0.9623
Max vs Con	0.5407	3.7750	<0.01**
ANN vs GAM	-2.8180	-19.6720	<0.01***
ANN vs GBM	-2.7840	-19.4370	<0.01***
ANN vs GLM	-2.6260	-18.3350	<0.01***
ANN vs RF	-2.8510	-19.9000	<0.01***
ANN vs Con	-2.4770	-17.2940	<0.01***
GAM vs GBM	0.0337	0.2350	1
GAM vs GLM	0.1915	1.3370	0.9154
GAM vs RF	-0.0327	-0.2280	1
GAM vs Con	0.3407	2.3780	0.2692
GBM vs GLM	0.1578	1.1020	0.9741
GBM vs RF	-0.0664	-0.4630	1
GBM vs Con	0.3070	2.1430	0.4146
GLM vs RF	-0.2242	-1.5650	0.8102
GLM vs Con	0.1492	1.0420	0.9823
RF vs Con	0.3734	2.6070	0.1643
Max vs records	-0.0001	-0.4970	1
ANN vs records	0.0006	2.7130	0.1261
GAM vs records	0.0001	0.5110	1
GBM vs records	0.0002	0.8380	0.9964
GLM vs records	0.0002	0.9470	0.991
RF vs records	-0.0002	-1.0330	0.9832
Con vs records	0.0002	1.0780	0.9775
Max vs distance	0.0000	-0.7120	0.999
ANN vs distance	0.0000	3.4450	0.0138*
GAM vs distance	0.0000	-0.0940	1
GBM vs distance	0.0000	-0.3930	1
GLM vs distance	0.0000	0.0990	1
RF vs distance	0.0000	-0.6660	0.9995
Con vs distance	0.0000	0.4240	1

The estimates are the values as obtained in the mixed model without being logit back-transformed. Max= Maxent, Con= Consensus approach; Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported.

Table S7. Statistical results of the Linear Mixed Effect models for the maps similarity values at the coarser scale (Fuzzy Global Matching) between algorithms and their interaction with the number of records and their spatial distribution.

Algorithms	Estimate	z value	Pr(>|z|)
Max vs ANN	1.4940	15.9990	<0.001***
Max vs GAM	-0.1440	-1.5420	0.81365
Max vs GBM	-0.5910	-6.3300	<0.001***
Max vs GLM	-0.0231	-0.2480	1
Max vs RF	-0.9389	-10.0560	<0.001***
Max vs Con	-0.0857	-0.9180	0.99159
ANN vs GAM	-1.6380	-17.5410	<0.001***
ANN vs GBM	-2.0850	-22.3290	<0.001***
ANN vs GLM	-1.5170	-16.2460	<0.001***
ANN vs RF	-2.4330	-26.0550	<0.001***
ANN vs Con	-1.5790	-16.9170	<0.001***
GAM vs GBM	-0.4470	-4.7880	<0.001***
GAM vs GLM	0.1209	1.2940	0.92416
GAM vs RF	-0.7949	-8.5140	<0.001***
GAM vs Con	0.0582	0.6240	0.99959
GBM vs GLM	0.5679	6.0820	<0.001***
GBM vs RF	-0.3479	-3.7260	0.00486**
GBM vs Con	0.5053	5.4120	<0.001***
GLM vs RF	-0.9158	-9.8090	<0.001***
GLM vs Con	-0.0626	-0.6710	0.99925
RF vs Con	0.8532	9.1380	<0.001***
Max vs records	-0.0007	-3.5260	0.00996**
ANN vs records	-0.0003	-1.5410	0.8148
GAM vs records	-0.0007	-3.4830	0.01229*
GBM vs records	-0.0010	-5.2310	<0.001***
GLM vs records	-0.0006	-3.3910	0.01626*
RF vs records	-0.0010	-5.5500	<0.001***
Con vs records	-0.0007	-3.9620	0.00215**
Max vs distance	0.0000	-2.4560	0.22236
ANN vs distance	0.0000	2.4970	0.20312
GAM vs distance	0.0000	-3.0250	0.0523
GBM vs distance	0.0000	-2.1470	0.40086
GLM vs distance	0.0000	-2.6080	0.15775
RF vs distance	0.0000	-0.4670	0.99997
Con vs distance	0.0000	-1.8400	0.61951

The estimates are the values as obtained in the mixed model without being logit back-transformed. Max= Maxent, Con= Consensus approach. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported.

Table S8. Statistical results of the Linear Mixed Effects models for the deviance from the average environmental variable contribution values between algorithms without separating by variable (environmental variable nested in species).

Algorithms	Estimate	z value	Pr(>|z|)
Max vs ANN	-0.4294	-16.0850	<1e-07***
Max vs GAM	-0.2503	-9.3770	<1e-07***
Max vs GBM	0.1603	6.0040	<1e-07***
Max vs GLM	-0.4268	-15.9870	<1e-07***
Max vs RF	0.3840	14.3870	<1e-07***
ANN vs GAM	0.1791	6.7080	<1e-07***
ANN vs GBM	0.5897	22.0890	<1e-07***
ANN vs GLM	0.0026	0.0990	1
ANN vs RF	0.8134	30.4720	<1e-07***
GAM vs GBM	0.4106	15.3810	<1e-07***
GAM vs GLM	-0.1764	-6.6090	<1e-07***
GAM vs RF	0.6344	23.7640	<1e-07***
GBM vs GLM	-0.5870	-21.9910	<1e-07***
GBM vs RF	0.2238	8.3830	<1e-07***
GLM vs RF	0.8108	30.3730	<1e-07***

A significant P value points to a significance difference between the deviance values presented by each algorithm. Higher estimates mean a higher deviance an thus a less consistent modelling algorithm. The estimates are the values as obtained in the mixed model without being log back-transformed. Max= Maxent; Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. Corrected Tukey's P values reported. See Table S9 for a per variable comparison results between algorithms.

Table S9. Statistical results of the Linear Mixed Effect models results for the deviance from the average environmental variable contribution values between algorithms for the same variable.

Algorithm	Env. Variable	Estimate	z value	Pr(>|z|)
ANN-Max	B02	0.0308	0.3470	0.9993
ANN-Max	B04	1.4344	16.1480	**<0.001*** **
ANN-Max	B08	0.1548	1.7430	0.5033
ANN-Max	B09	0.5731	6.4520	**<0.001*** **
ANN-Max	B10	0.1873	2.1090	0.2825
ANN-Max	B12	0.6494	7.3110	**<0.001*** **
ANN-Max	B13	0.3506	3.9460	**0.0011** **
ANN-Max	B14	-0.1361	-1.5320	0.6435
ANN-Max	B18	0.8251	9.2880	**<0.001*** **

Table S9 - continued

Algorithm	Env. Variable	Estimate	z value	Pr(>|z|)
GAM-ANN	Elevation	0.0226	0.2540	0.9999
GAM-Max	B02	-0.1685	-1.8970	0.4039
GAM-Max	B04	0.3135	3.5290	**0.00558****
GAM-Max	B08	-0.0750	-0.8440	0.9593
GAM-Max	B09	0.2196	2.4720	0.1322
GAM-Max	B10	-0.2076	-2.3370	0.1794
GAM-Max	B12	0.5548	6.2450	**<0.001*****
GAM-Max	B13	0.2332	2.6250	0.09128.
GAM-Max	B14	0.7881	8.8720	**<0.001*****
GAM-Max	B18	0.5982	6.7340	**<0.001*****
GAM-Max	Elevation	0.2469	2.7800	0.0609
GBM-ANN	B02	-0.6102	-6.8700	**<0.001*****
GBM-ANN	B04	-1.2910	-14.5330	**<0.001*****
GBM-ANN	B08	-0.3318	-3.7350	**0.0025****
GBM-ANN	B09	-0.4538	-5.1090	**<0.001*****
GBM-ANN	B10	-0.7768	-8.7440	**<0.001*****
GBM-ANN	B12	-0.4163	-4.6860	**<0.001*****
GBM-ANN	B13	-0.4310	-4.8520	**<0.001*****
GBM-ANN	B14	-0.4282	-4.8210	**<0.001*****
GBM-ANN	B18	-0.7059	-7.9460	**<0.001*****
GBM-ANN	Elevation	-0.4516	-5.0830	**<0.001*****
GBM-GAM	B02	-0.4109	-4.6260	**<0.001*****
GBM-GAM	B04	-0.1700	-1.9130	0.3939
GBM-GAM	B08	-0.1020	-1.1480	0.8610
GBM-GAM	B09	-0.1003	-1.1290	0.8693
GBM-GAM	B10	-0.3819	-4.2990	**<0.001*****
GBM-GAM	B12	-0.3216	-3.6210	**0.0039****
GBM-GAM	B13	-0.3136	-3.5300	**0.0056****
GBM-GAM	B14	-1.3525	-15.2250	**<0.001*****
GBM-GAM	B18	-0.4790	-5.3920	**<0.001*****
GBM-GAM	Elevation	-0.4741	-5.3370	**<0.001*****
GBM-Max	B02	-0.5794	-6.5230	**<0.001*****
GBM-Max	B04	0.1435	1.6150	0.5884
GBM-Max	B08	-0.1770	-1.9920	0.3467
GBM-Max	B09	0.1193	1.3430	0.7608
GBM-Max	B10	-0.5894	-6.6360	**<0.001*****
GBM-Max	B12	0.2331	2.6240	0.09152.
GBM-Max	B13	-0.0804	-0.9050	0.9453

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Algorithm	Env. Variable	Estimate	z value	Pr(>|z|)
GBM-Max	B14	-0.5643	-6.3530	**<0.001*****
GBM-Max	B18	0.1192	1.3420	0.7610
GBM-Max	Elevation	-0.2272	-2.5580	0.1079
GLM-ANN	B02	0.0720	0.8110	0.9657
GLM-ANN	B04	-0.8617	-9.7010	**<0.001*****
GLM-ANN	B08	-0.2798	-3.1500	**0.0202***
GLM-ANN	B09	0.1219	1.3720	0.7439
GLM-ANN	B10	-0.1539	-1.7330	0.5099
GLM-ANN	B12	0.1946	2.1910	0.2420
GLM-ANN	B13	0.0350	0.3940	0.9988
GLM-ANN	B14	0.5900	6.6420	**<0.001*****
GLM-ANN	B18	0.1287	1.4490	0.6970
GLM-ANN	Elevation	0.1269	1.4290	0.7095
GLM-GAM	B02	0.2714	3.0550	**0.0273***
GLM-GAM	B04	0.2593	2.9180	**0.0409***
GLM-GAM	B08	-0.0500	-0.5630	0.9933
GLM-GAM	B09	0.4754	5.3510	**<0.001*****
GLM-GAM	B10	0.2410	2.7130	0.0728.
GLM-GAM	B12	0.2893	3.2560	**0.0142***
GLM-GAM	B13	0.1524	1.7160	0.5212
GLM-GAM	B14	-0.3342	-3.7620	**0.0024****
GLM-GAM	B18	0.3556	4.0030	**<0.001*****
GLM-GAM	Elevation	0.1044	1.1750	0.8490
GLM-GBM	B02	0.6823	7.6800	**<0.001*****
GLM-GBM	B04	0.4292	4.8320	**<0.001*****
GLM-GBM	B08	0.0520	0.5850	0.9920
GLM-GBM	B09	0.5757	6.4810	**<0.001*****
GLM-GBM	B10	0.6229	7.0120	**<0.001*****
GLM-GBM	B12	0.6109	6.8770	**<0.001*****
GLM-GBM	B13	0.4660	5.2460	**<0.001*****
GLM-GBM	B14	1.0183	11.4630	**<0.001*****
GLM-GBM	B18	0.8345	9.3950	**<0.001*****
GLM-GBM	Elevation	0.5785	6.5120	**<0.001*****
GLM-Max	B02	0.1028	1.1580	0.8569
GLM-Max	B04	0.5727	6.4470	**<0.001*****
GLM-Max	B08	-0.1250	-1.4070	0.7228
GLM-Max	B09	0.6950	7.8240	**<0.001*****
GLM-Max	B10	0.0334	0.3760	0.9990

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Table S9 - continued

Table S9 - continued

Algorithm	Env. Variable	Estimate	z value	Pr(>|z|)
GLM-Max	B12	0.8440	9.5010	**<0.001*** **
GLM-Max	B13	0.3856	4.3400	**<0.001*** **
GLM-Max	B14	0.4540	5.1100	**<0.001*** **
GLM-Max	B18	0.9538	10.7370	**<0.001*** **
GLM-Max	Elevation	0.3513	3.9540	**0.0010** **
RF-ANN	B02	-0.7983	-8.9860	**<0.001*** **
RF-ANN	B04	-1.7411	-19.6000	**<0.001*** **
RF-ANN	B08	-0.7283	-8.1990	**<0.001*** **
RF-ANN	B09	-0.7105	-7.9980	**<0.001*** **
RF-ANN	B10	-0.6778	-7.6310	**<0.001*** **
RF-ANN	B12	-0.8074	-9.0890	**<0.001*** **
RF-ANN	B13	-0.6479	-7.2930	**<0.001*** **
RF-ANN	B14	-0.3920	-4.4130	**<0.001*** **
RF-ANN	B18	-0.7494	-8.4360	**<0.001*** **
RF-ANN	Elevation	-0.8816	-9.9240	**<0.001*** **
RF-GAM	B02	-0.5990	-6.7430	**<0.001*** **
RF-GAM	B04	-0.6201	-6.9800	**<0.001*** **
RF-GAM	B08	-0.4985	-5.6120	**<0.001*** **
RF-GAM	B09	-0.3570	-4.0190	**<0.001*** **
RF-GAM	B10	-0.2829	-3.1850	**0.0181***
RF-GAM	B12	-0.7128	-8.0240	**<0.001*** **
RF-GAM	B13	-0.5305	-5.9720	**<0.001*** **
RF-GAM	B14	-1.3162	-14.8170	**<0.001*** **
RF-GAM	B18	-0.5226	-5.8830	**<0.001*** **
RF-GAM	Elevation	-0.9041	-10.1780	**<0.001*** **
RF-GBM	B02	-0.1880	-2.1170	0.2784
RF-GBM	B04	-0.4501	-5.0670	**<0.001*** **
RF-GBM	B08	-0.3965	-4.4630	**<0.001*** **
RF-GBM	B09	-0.2567	-2.8900	**0.0445***
RF-GBM	B10	0.0990	1.1140	0.8759
RF-GBM	B12	-0.3911	-4.4030	**<0.001*** **
RF-GBM	B13	-0.2169	-2.4420	0.1421
RF-GBM	B14	0.0363	0.4080	0.9986
RF-GBM	B18	-0.0436	-0.4910	0.9970
RF-GBM	Elevation	-0.4300	-4.8410	**<0.001*** **
RF-GLM	B02	-0.8703	-9.7970	**<0.001*** **
RF-GLM	B04	-0.8793	-9.8990	**<0.001*** **
RF-GLM	B08	-0.4485	-5.0490	**<0.001*** **

Table S9 - continued

Algorithm	Env. Variable	Estimate	z value	Pr(>|z|)
RF-GLM	B09	-0.8324	-9.3700	<0.001***
RF-GLM	B10	-0.5239	-5.8980	<0.001***
RF-GLM	B12	-1.0020	-11.2800	<0.001***
RF-GLM	B13	-0.6829	-7.6870	<0.001***
RF-GLM	B14	-0.9820	-11.0550	<0.001***
RF-GLM	B18	-0.8781	-9.8850	<0.001***
RF-GLM	Elevation	-1.0085	-11.3530	<0.001***
RF-Max	B02	-0.7675	-8.6400	<0.001***
RF-Max	B04	-0.3066	-3.4520	0.0073**
RF-Max	B08	-0.5735	-6.4560	<0.001***
RF-Max	B09	-0.1374	-1.5460	0.6341
RF-Max	B10	-0.4905	-5.5220	<0.001***
RF-Max	B12	-0.1580	-1.7790	0.4795
RF-Max	B13	-0.2973	-3.3470	0.0105*
RF-Max	B14	-0.5281	-5.9450	<0.001***
RF-Max	B18	0.0757	0.8520	0.9580
RF-Max	Elevation	-0.6572	-7.3980	<0.001***

A significant P-value points to a significance difference between the deviance values with higher values meaning a higher deviance and thus a less consistent modelling algorithm. The estimates are the values as obtained in the mixed model without being log back-transformed. Max= Maxent; Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05. Corrected Tukey’s P values reported.

Note 1:

*For questions about specific models and/or algorithms formula please contact the author for correspondence.

*More information about the species database can be obtained contacting directly the European Invertebrate Survey – The Netherlands, PO Box 9517, 2300 RA Leiden, The Netherlands; http://www.eis-nederland.nl.

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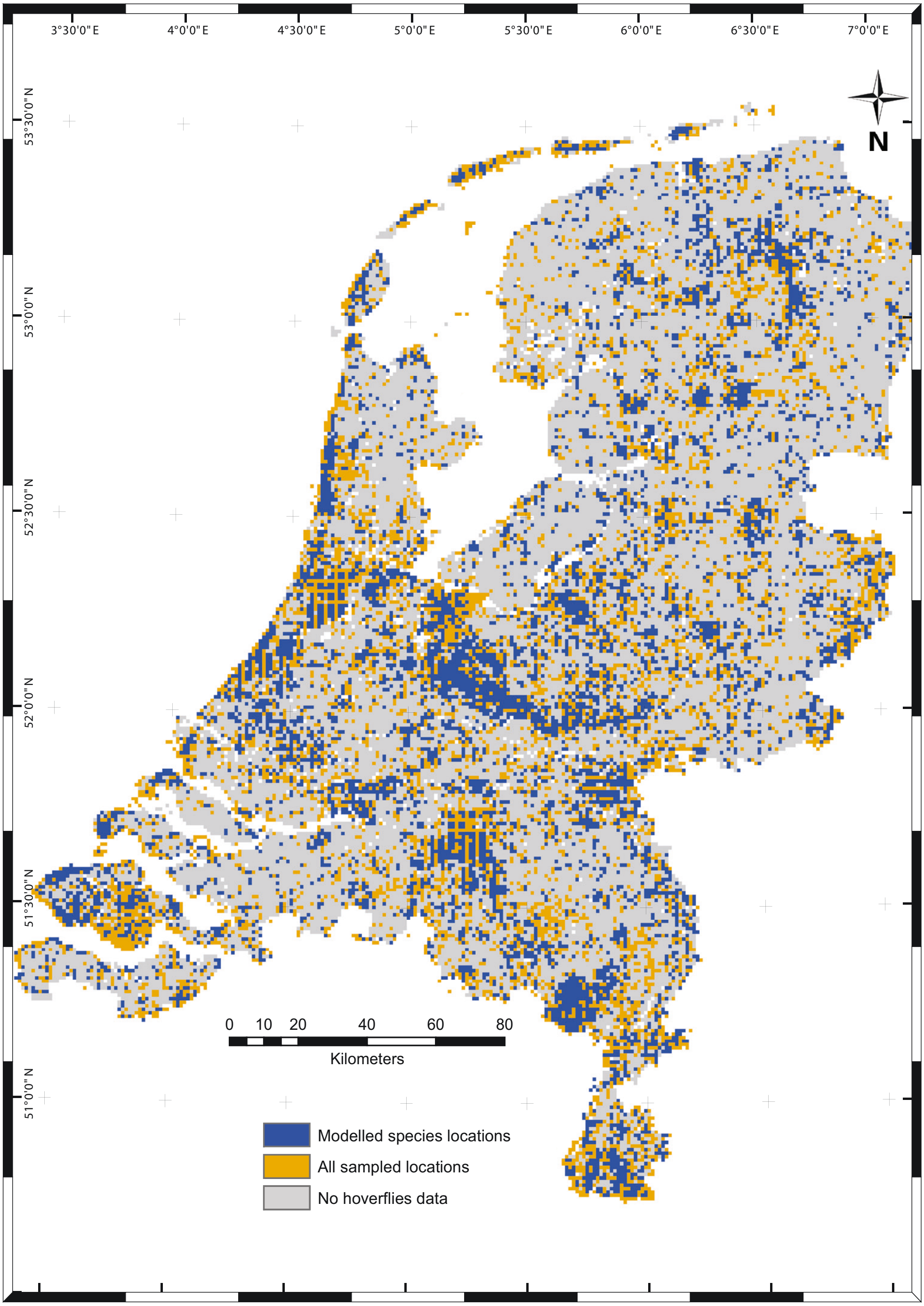

Figure S1. Distribution of the records locations of hoverfly species in the Netherlands. All the localities where hoverflies hove been found are represented by the orange colour. Blue represents the distribution of the locations for the species modelled in this study.

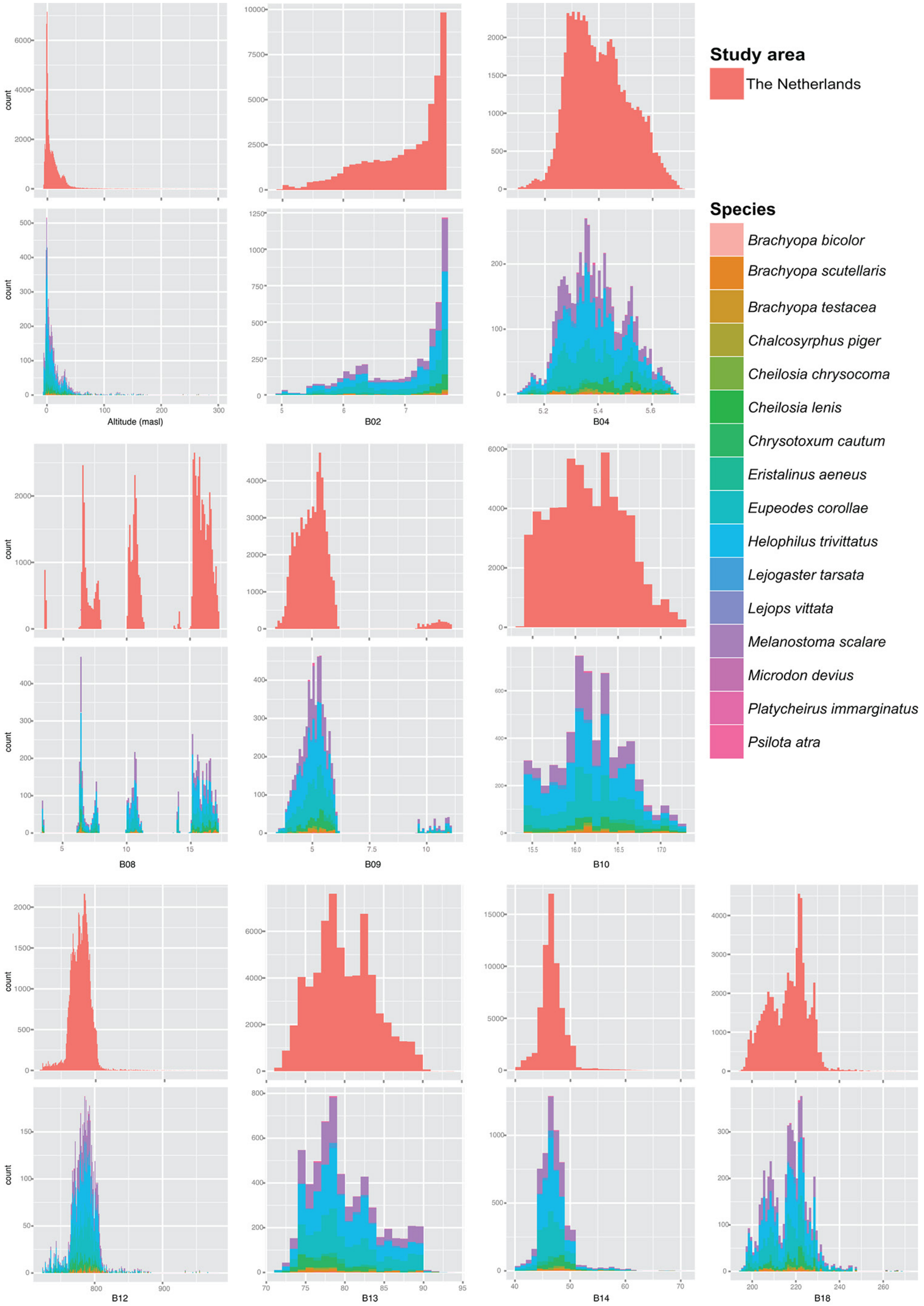

Figure S2. Representation of the environmental space occupied by the modelled species (for the 10 environmental variables used, in different colours representing the species) and the available environmental conditions in the complete study area (graphs in red colour). The selected species cover the vast majority of Netherlands environmental space. The “x” axis represents the range of values for the environmental variable and the “y “axis represents the counts of cells with those conditions. For reference to the variables names and units see Table S3.

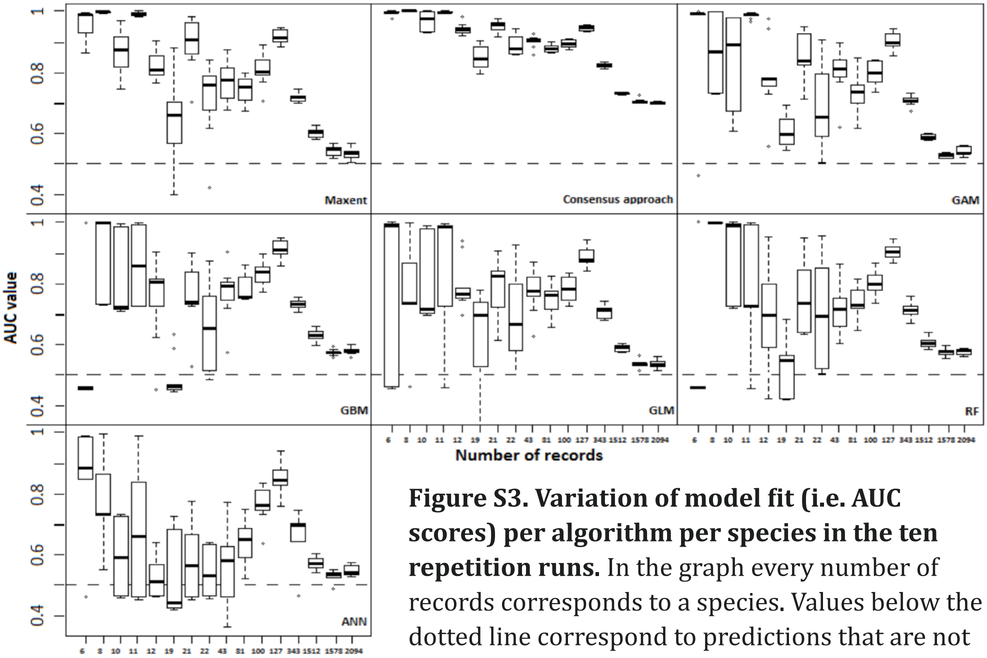

Figure S3. Variation of model fit (i.e. AUC scores) per algorithm per species in the ten repetition runs. In the graph every number of records corresponds to a species. Values below the dotted line correspond to predictions that are not better than random. See Table 1 and S4 for further details.

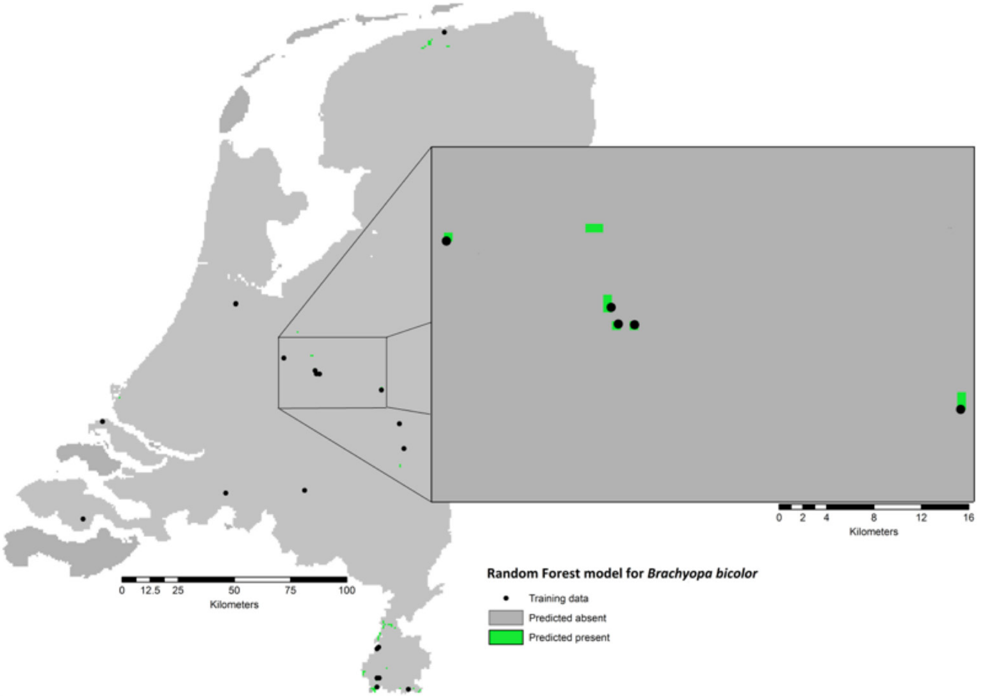

Figure S4. Example of the data overfitting problematic for one of the RF models. Cells in green represent areas predicted as presences and in grey are the areas predicted as absences, the black dots represent presence records used during the training of the models. The overfitting occurs and the “presences” predictions are mostly constrained to the training records locations.

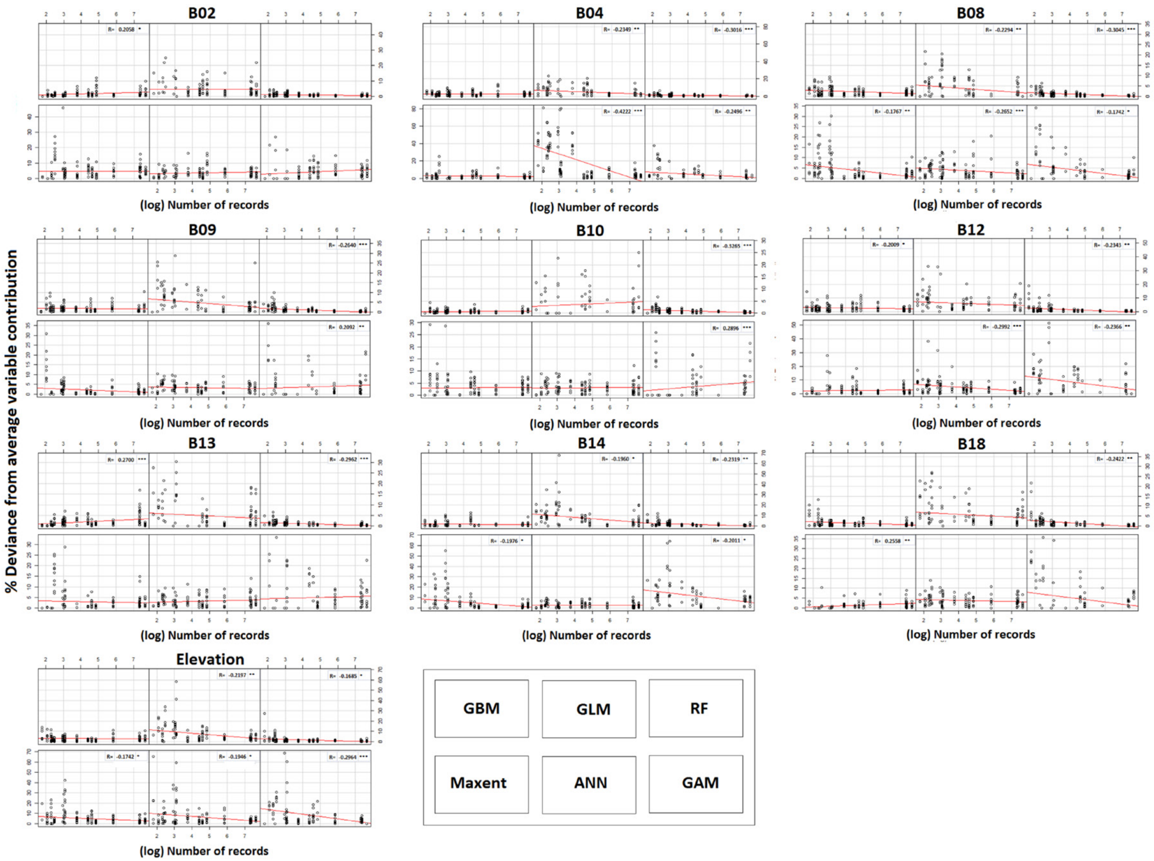

Figure S5. Deviance from the average variable contribution per variable and algorithm depending on the number of records. ***R*** represents the correlation values between these two variables. Only significant correlations are presented. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

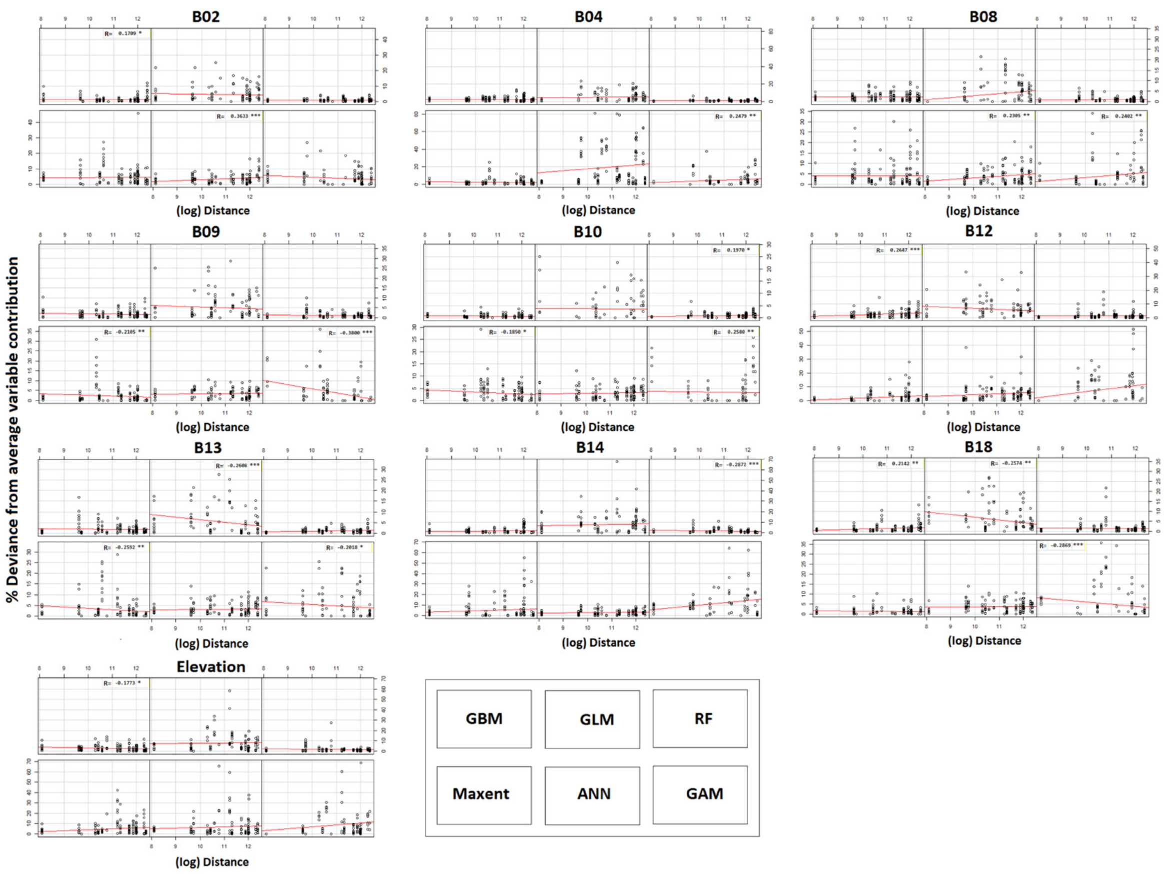

Figure S6. Deviance from the average variable contribution per variable depending on the records' spatial distribution. ***R*** represents the correlation values between these two variables. Only significant correlations are presented. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05.

3

Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines

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Abstract

In the face of global environmental change, identifying the factors that shape the ecological niches of species and understanding the mechanisms behind them can help draft effective conservation plans. The differences in the ecological factors that shape species distributions may then help to highlight differences between closely-related taxa. We investigate the applicability of ecological niche modelling and the comparison of species distributions in ecological niche space to detect areas with priority for biodiversity conservation, and to analyse differences in the ecological niche spaces used by closely-related taxa. As location we use the United States of America, Mexico and Central America. We apply ordination and ecological niche modelling techniques to assess the main environmental drivers of the distribution of Mexican white pines (Pinus: Pinaceae). Furthermore, we assess the similarities and differences of the ecological niches occupied by closely related taxa. We analyse whether Mexican white pines occupy similar or equivalent ecological niches. We found that all the studied taxa presented different responses to the environmental factors, resulting in a unique combination of niche conditions. Our stacked habitat suitability maps highlighted regions in southern Mexico and northern Central America as highly suitable for most species and thus with high conservation value. By quantitatively assessing the niche overlap, similarity and equivalency of Mexican white pines, our results prove that the distribution of one species cannot be implied by the distribution of another, even if these taxa are considered closely related. The fact that each Mexican white pine is constrained by a unique set of environmental conditions, and thus their non-equivalence of ecological niches, has direct implications for conservation as this highlights the inadequacy of one-fits all type of conservation measure.

Introduction

The conservatism of ecological niches (sensu Grinnell, 1917) has become an issue of concern given the expected impacts of climate change on biodiversity (Thomas *et al.,* 2004; Chen *et al.,* 2011; Araújo *et al.,* 2013). This has prompted the development of new tools to assess how the ecological niche of species can shrink/contract, expand or persist, in environmental and geographic space, anticipating the effects of global climate change (Warren *et al.,* 2010; Peterson, 2011; Broennimann *et al.,* 2012). Understanding how the ecological niche of species will change can be used to implement or guide conservation actions, especially in biodiversity-rich areas (Guisan *et al.,* 2013).

Species groups that are highly diverse and present a varied set of ecological adaptations along an environmental gradient may be of importance for understanding ecological niche differences and to prepare mitigation actions against global change impacts. The plant family Pinaceae (Farjon, 2008) includes 11 genera and 228 species around the world, and has a centre of diversity in North and Central America. The genus *Pinus* has its centre of diversity in Mexico with 49 of the 120 recognized species inhabiting habitats from alpine tree line elevations to lowland sea level (Gernandt & Pérez-de la Rosa, 2014). Particularly the taxa in the subgenus *Strobus*, commonly known as the Mexican white pines, are highly important on a global scale because the ecological processes in which they are involved (e.g., carbon sequestration, soil nutrient retention and cycling, ecosystem structure) and because of their provision of ecosystem services in the form of wood, resin and pulp (Richardson, 1998). Moreover, this subgenus contains taxa that have been classified as 'closely related' (Bruederle *et al.,* 2001). There is no general agreement on the taxonomic status of some Mexican white pines, even after recent morphological and phylogenetic studies (Price *et al.,* 1998; Castro-Félix *et al.,* 2008; Tomback & Achuff, 2010). For instance, *Pinus* strobiformis and *P. ayacahuite* were formerly classified as the same species (Perry, 1991; Farjon & Styles, 1997; Bruederle *et al.,* 2001). This highlights the ongoing problems with cryptic species, problems that are not unique to taxonomy but also to biogeography and conservation studies (Bickford *et al.,* 2007; Pfenninger & Schwenk, 2007).

The development of ecological niche models (ENMs; Soberón &

Nakamura, 2009), also referred to as species distribution models (Guisan & Thuiller, 2005; Araújo & Peterson, 2012), has facilitated the extraction of ecological niche characteristics that can assist taxonomic delineations and biodiversity conservation (Raxworthy *et al.,* 2007; Blair *et al.,* 2013).

In this study we analyse how the species-specific responses to environmental factors and the differences between distributions in ecological niche space can aid future species conservation plans and in the ongoing debate on differentiation between closely related taxa of the subgenus *Strobus*. To this end we use ENM and ordination techniques to characterize the ecological niches of Mexican white pine taxa and to quantify similarities between them. First, we identify the main environmental variables that constraint their distributions. We then use the information on their environmental constraints to generate a 'global' habitat suitability map for Mexican white pines to highlight hotspots of habitat suitability to inform conservation planning. We also, assess whether different Mexican white pine taxa share the same ecological niche space. Finally, we discuss how differences in the distribution of ecological niche spaces and the species-specific responses to environmental factors may inform conservation plans. Following the niche conservatisms assumption (e.g., Kozak & Wiens, 2006; Rödder & Lötters, 2009), we would expect more genetically closely-related species to share more of their environmental niche space, resulting in high ecological niche space overlap, high similarity and high spatial overlap. Meanwhile with niche divergence as a speciation mechanism, we would expect the ecological niches of closely related species to differ significantly (Rice *et al.,* 2003; Jakob *et al.,* 2010). Due to the similarities in morphological and physiological characteristics between the Mexican white pines, we expect their ecological niches to be similar. However, due to the different adaptations to different environments we expect ecological niches to be non-equivalent.

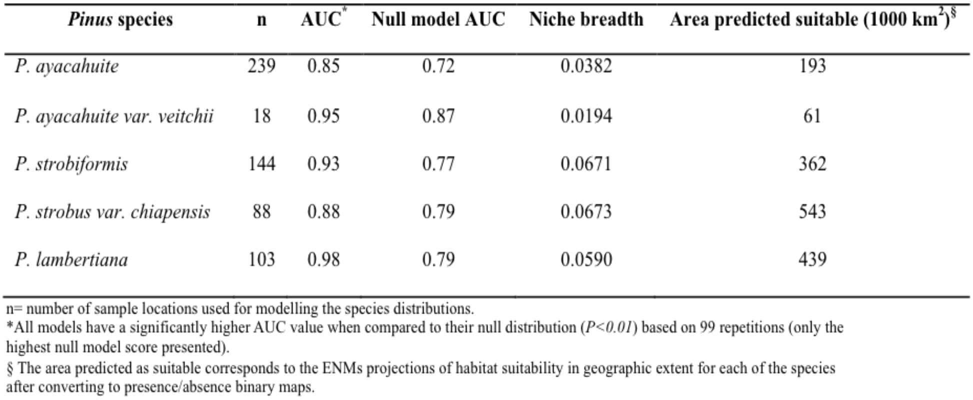
Methods

Study area and species data

The study area includes the native distribution of Mexican white pines, extending from the southern United States of America (USA) into Central America (Perry, 1991), and covers approximately 15 million km2, comprising a wide variety of biomes, with an elevation gradient ranging from sea level to more than 5450 masl.

We selected five Mexican white pine taxa (genus *Pinus*, subgenus *Strobus*, section *Strobus*, subsection *Strobi*. Little and Critchfield, 1969): *P. strobiformis* Engelm, *P. ayacahuite* Ehrenb. ex Schltdl., *P. ayacahuite* var. *veitchii* (Roezl) Shaw, *P. lambertiana* Dougl., *P. strobus* var. *chiapensis* (Martínez). We were not able to include *P. flexilis* var. *reflexa* Engelm because of the low number of available sample locations (<5). Except for *P. lambertiana*, all white pine taxa in our study have their main geographic distribution in Mexico. The current distributions of *P. strobiformis* and *P. lambertiana* extend further north into the USA, while *P. strobus* var. *chiapensis* and *P. ayacahuite* extend further south into Central America. We obtained species presence data from the University of Guadalajara Herbarium (IBUG, 2013), the National Commission for the Knowledge and Use of Biodiversity (CONABIO, 2013), the Global Biodiversity Information Facility (GBIF, 2013) and the Conifers database (Farjon, 2013a) collected during the last 30 years. After removing duplicates and screening for incomplete meta-information we obtained a total of 593 presence records for the five pine taxa (Table 1).

Table 1. Ecological niche models evaluation by their AUC and null model results.



Pinus species	n	AUC*	Null model AUC	Niche breadth	Area predicted suitable (1000 km^2)§
P. ayacahuite	239	0.85	0.72	0.0382	193
P. ayacahuite var. veitchii	18	0.95	0.87	0.0194	61
P. strobiformis	144	0.93	0.77	0.0671	362
P. strobus var. chiapensis	88	0.88	0.79	0.0673	543
P. lambertiana	103	0.98	0.79	0.0590	439

n= number of sample locations used for modelling the species distributions.
*All models have a significantly higher AUC value when compared to their null distribution (*P<0.01*) based on 99 repetitions (only the highest null model score presented).
§ The area predicted as suitable corresponds to the ENMs projections of habitat suitability in geographic extent for each of the species after converting to presence/absence binary maps.

Environmental data

We selected environmental data related to different eco-physiological constraints of the pine taxa. We obtained annual trends in extreme limiting conditions related to precipitation and temperature from WorldClim (Hijmans *et al.,* 2005). The selected variables presented Pearson's correlation ≤ 0.70 (Dormann *et al.,* 2013) and had a resolution of 1 km2 (Table 2). We included the mean temperature of coldest quarter (°C) and isothermality (the quotient of mean diurnal and annual temperature ranges), given the reported different preferences in temperature of the taxa in the genus *Pinus* (Perry, 1991; Farjon & Styles, 1997). These climatic variables relate to temperature extremes, which are one of the main constraints to the distribution of vegetation (van Zonneveld *et al.,* 2009; Linares & Tiscar, 2010). We included the annual precipitation (mm) and precipitation seasonality (mm) as these variables have been shown to directly influence the development and survival of pine taxa (Sáenz-Romero *et al.,* 2006; Sánchez-Salguero *et al.,* 2012). We also included topographic and soil characteristics, namely elevation (masl), slope (degrees), soil pH and percentage carbon content (% weight) (FAO *et al.,* 2012; INEGI, 2014). The soil characteristics may facilitate or limit the growth of different pine taxa (Galindo-Jaimes *et al.,* 2002). Elevation was included as different pine taxa tend to be found at different elevation ranges (Gernandt & Pérez-de la Rosa, 2014). We also included solar radiation (kW/m2) (CCAFS, 2014), and the Normalized Difference Vegetation Index (NDVI) as an average for the 1980-2010 period (IRI, 2013) which has been shown to increase the accuracy of model predictions for vegetation mapping (Papeş *et al.,* 2012; Rocchini, 2013). In our study, NDVI is used to help in the delimitation of the actual distribution of vegetation.

Ecological Niche Modelling

To analyse the spatial distribution of Mexican white pines and identify key environmental variables that constrain the species distributions we used ENMs. Based on a previous study (Aguirre-Gutiérrez *et al.,* 2013), we selected maximum entropy modelling as implemented in MaxEnt (Phillips *et al.,* 2006). We used the auto-features settings and the logistic output format in MaxEnt because these options have proven to be appropriate for extensive multi-species studies (Phillips & Dudik, 2008). We used the target group approach, as suggested by Mateo et al. (2010) and Elith et al. (2011), when extracting background points for MaxEnt as it has performed with higher accuracy than other methods (i.e., random selection). In this approach the collection localities where other Mexican white pine species have been found but where the species being modelled was not present where used as background locations. As suggested by Elith et al. (2011) this approach provides also the advantage of accounting for possible records selection biases. We used the null model approach of Raes and ter Steege (2007) to test the significance of our model predictions. The null model approach tests the area under the curve (AUC) value of the receiver-operating characteristic of the species niche model against a null distribution of 99 repetitions. The null distribution was generated from the sample localities of the target group. Added advantage of testing against a null-model is that all collection localities can be used for model calibration.

Table 2. Percentage of variable contribution to the model construction, derived from the permutation importance analysis from MaxEnt. Top three ranking variables printed in bold. The results represented the drop in AUC after the values from the focus variable are permuted and the model is re-evaluated and compared to the original model. This drop is standardized and converted to percentage contribution. For each *Pinus* taxon, the three variables with the highest contributions are presented in bold.

Variable	*P. ayacahuite*	*P. ayacahuite var. veitchii*	*P. strobiformis*	*P. strobus var. chiapensis*	*P. lambertiana*
Isothermality	**39.3**	1.3	4.8	**28.2**	**16.9**
Mean temperature of coldest quarter	2.2	0.4	2.4	**16.3**	7.0
Annual precipitation	7.2	0.1	2.5	**21.0**	0.5
Precipitation seasonality	**8.1**	**66.2**	3.9	13.6	**28.5**
Elevation	**35.8**	**28.1**	**49.0**	13.3	2.2
NDVI	2.9	**2.8**	**6.7**	2.5	0.8
Slope	0.6	0.2	2.8	2.3	1.1
Solar radiation	0.3	0.0	**24.8**	1.1	**40.0**
Soil total organic carbon	1.5	0.2	0.3	1.4	1.7
Soil pH	1.9	0.8	2.9	0.3	1.3

The models of Mexican white pines were projected on the study area to identify suitable habitats for their distribution and conservation. To assess the importance of the different environmental variables in our models, we used the permutation importance values rendered by MaxEnt and their ecological response curves (Phillips & Dudik, 2008).

Calculating niche characteristics: breadth, overlap, equivalency and similarity

We calculated ecological niche characteristics to assess the degree of shared environmental niche space between Mexican white pines. We obtained the niche breadth of each species (i.e., the amount of ecological niche space available to the different pine species) by applying the Levins' inverse concentration metric (Levins, 1968). The niche breadth ranges from 0, when all but one grid cell has non-zero suitability, to 1 when all the grid cells in the study area are equally suitable (Mandle *et al.,* 2010). Therefore, species with a wider environmental distribution render higher niche breadth values.

The assessment of niche overlap allows quantifying the niche shared by the Mexican white pines. In this study, niche overlap between pairs of Mexican white pines was computed by means of the Schoener's D statistic directly from ecological niche space (Schoener, 1968; Warren *et al.,* 2008). The value of D ranges between 0, when two species have no overlap in the environmental space, and 1 when two species share the same environmental space.

We used the niche equivalence test to assess whether the ecological niches of pairs of Mexican white pines are significantly different from each other and if the two niche spaces are interchangeable. We performed the niche equivalence test by comparing the niche overlap values (D) of pairs of Mexican white pines to a null distribution of 100 overlap values. We determined non-equivalence of ecological niches if the niche overlap value of the species being compared was significantly lower than the overlap values from the null distribution ($P \leq 0.05$).

The test for niche equivalence is conservative as it only assesses if the two species are identical in their niche space by using their exact locations and does not consider the surrounding space. Therefore, we also performed a niche similarity test, which assesses if the ecological niches of any pair of species are more different than expected by chance, accounting for the differences in the surrounding environmental conditions in the geographic areas where both species are distributed (Warren et al. 2010). A significant difference from the niche similarity test would not only indicate differences in the environmental niche space the two species occupy, but also that these differences are not due to the environmental conditions that are geographically available.

To extract the ecological niche space occupied by each Mexican white pine species and to quantify niche overlap, equivalence and similarity we used an ordination technique that applies kernel smoothers to the species presences in environmental space for the selection, combination and weighting of environmental variables (Broennimann *et al.,* 2012). We specified a division of the environmental space into a grid of 100 x 100 cells, in which each cell corresponds to a unique vector of the available environmental conditions in the study area. The number of occurrences per species can be bias and not represent the total distribution of the species in environmental space; this might result in an underestimation of their density in some of the cells and overestimation in others. Because of this possibility of over- and under-estimations, a kernel density function is applied for the smoothing density of occurrences for each of the cells in environmental space, thus obtaining a better indication of the environmental conditions suitable for each species. Further details about the kernel density estimator and its parameters can be found in Broennimann et al. (2012). We implemented this approach by means of a principal component analysis that is calibrated on the entire environmental space present in the study area (hereafter referred to as "PCA-ent"). All analyses were performed in the R platform (R Development Core Team, 2014).

Results

Responses to environmental gradients

The distributions of Mexican white pines are underpinned by their different responses to the environment (Fig. 1; Table 2). The distributions of all Mexican white pines were mainly constrained by a combination of isothermality, precipitation seasonality, elevation and solar radiation. Highly suitable areas for *P. ayacahuite* were found at high elevations (≈2000 m) and high isothermality (≈0.95), both of these variables being the most important predictors of its distribution. For *P. ayacahuite* var. *veitchii* the suitability increased along with both, precipitation seasonality and elevation. The distribution of *P. strobiformis* was mainly constrained by elevation and, to a lesser extent by solar radiation (Table 3). *P. strobiformis* showed an optimum suitability at altitudes between 2500 and 3000 meters and at radiation of around 15 kW/m2. Isothermality was an important environmental factor constraining the distribution of *P. strobus* var. *chiapensis*, with highest suitability at values of ≈0.90. Annual precipitation was also a main constraint for the distribution of *P. strobus* var. *chiapensis*, with suitability sharply increasing at initial increments of precipitation. Finally, *P. lambertiana* was mainly constrained by the solar radiation and precipitation seasonality, areas with radiation around 13-14 kW/m2 and with a variation in precipitation of ≈ 60 mm showing highest suitability. Unlike expected, none of the Mexican white pines were strongly constrained by soil factors. Most of the pine taxa had responses to soil variables that rarely overpassed suitability estimates of 0.5.

White pines distribution and hotspots

We developed ecological niche models for each of the five Mexican white pine taxa (Fig. 2). Although, P. aycahuite var. *veitchii* was modelled using only 18 presence records, the null-model protocol we applied suggests that our results are significantly better than expected by a random model. In fact, all our ENMs performed significantly better than expected by chance alone ($P<0.01$; Table 1).'Stacking' of the five distribution models resulted in a map model with centres of high environmental suitability for Mexican white pines (Fig. 2a). Centres of high suitability were located on the Mexican trans-volcanic belt and on the mountain chain connecting southern Mexico and Guatemala. Additional hotspots were found on the Mexican occidental and south-eastern mountain chains, and on the central-southern areas of Mexico, with only a narrow area in northern Mexico highlighted as highly suitable for most taxa (Fig. 2a).

Ecological niche properties

The analysis of ecological niche properties rendered a PCA-ent with the first axis mainly loaded by isothermality, solar radiation and average temperature of coldest quarter, explaining 32.3% of the total variation in environmental conditions for the taxa in the study area (Fig. 3). The second axis explained about 28% of the variation and was loaded by soil pH, annual precipitation, elevation and NDVI variables.

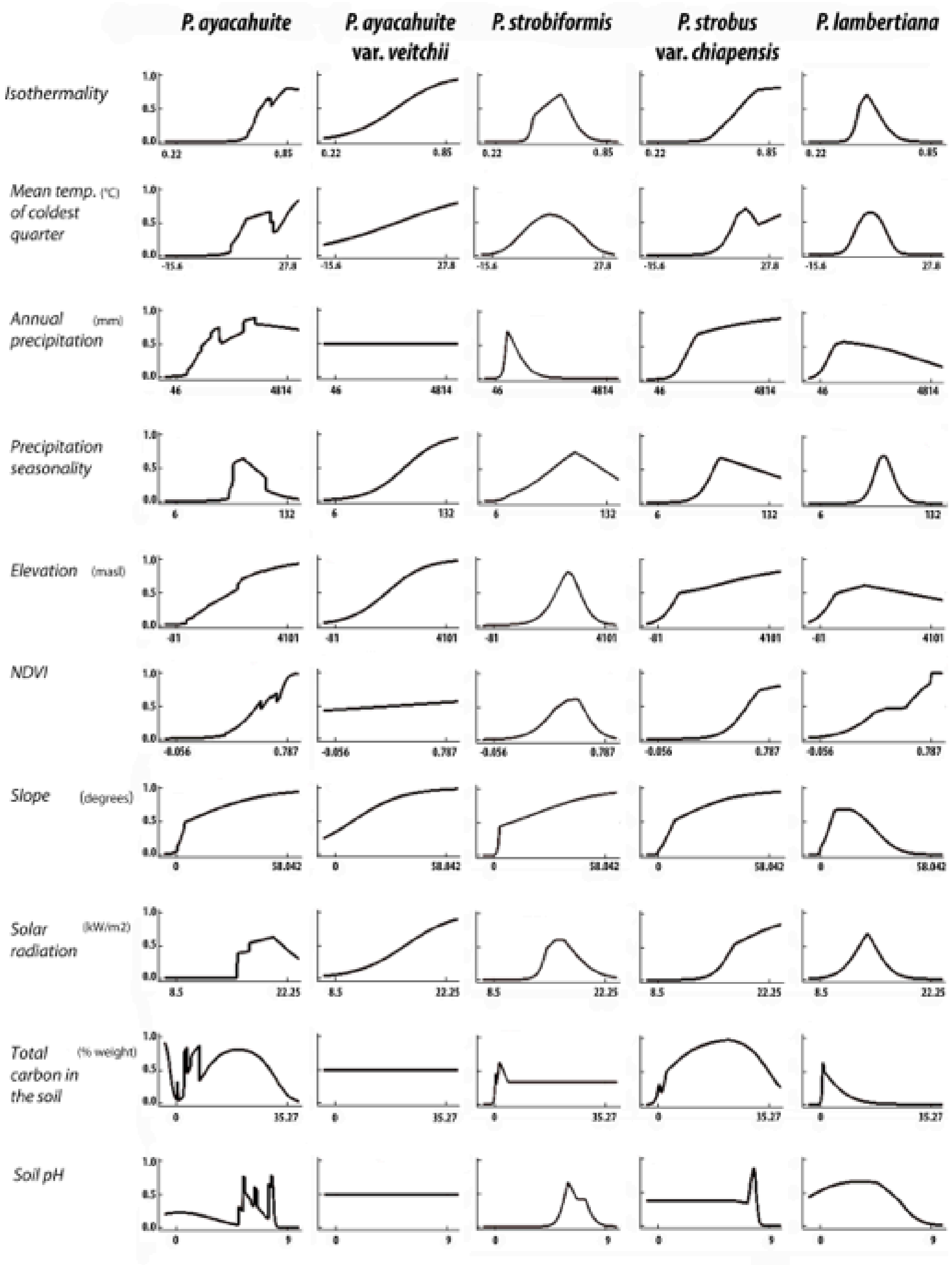


Figure 1. The ecological response curves for each of Mexican white pine. The response curves are based on the ENMs. Response curves show the ranges in environmental conditions that are more favourable for the distribution of the species. The x-axis of the variables represents their ranges for the complete study area, while the y-axis represents the predicted suitability of the focus variable when all of the other variables are set to their average. In Table 2, we highlight the three most relevant variables for each species.

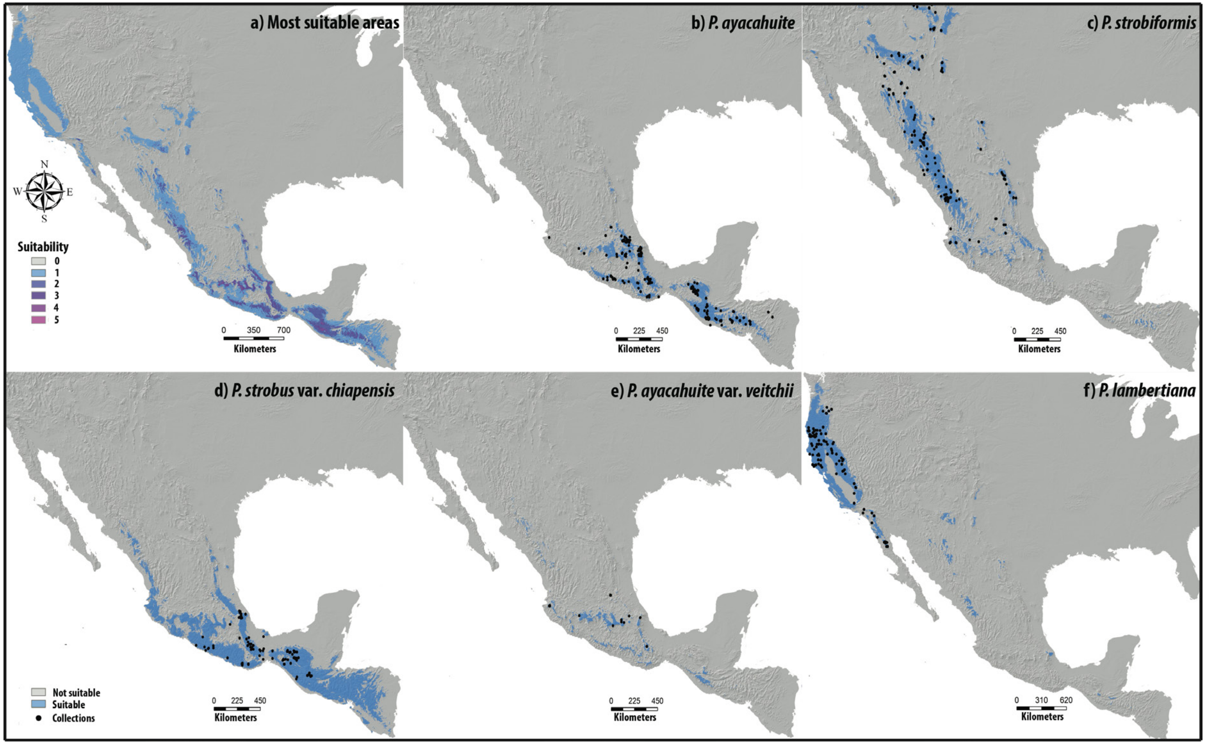


Figure 2. Distribution models for the five Mexican white pines representing the areas in geographic space with high environmental suitability. Panel a) presents the results from an ensemble of the five niche models, highlighting regions of shared habitat suitability. Value of 0 indicates an area that is not suitable and 5 and area with high habitat suitability for the five Mexican white pine taxa. For panels b) to f) the blue colour represents the areas that have high habitat suitability after applying the 10 percentile presence threshold criteria to the models' suitability scores, e.g. 10% of the most extreme presence observations in environmental niche space are forced outside the predicted presence area because they may represent errors in the 'presence' recordings or outliers in the environmental space (Tinoco et al., 2009). Black dots represent the sample/presence locations.

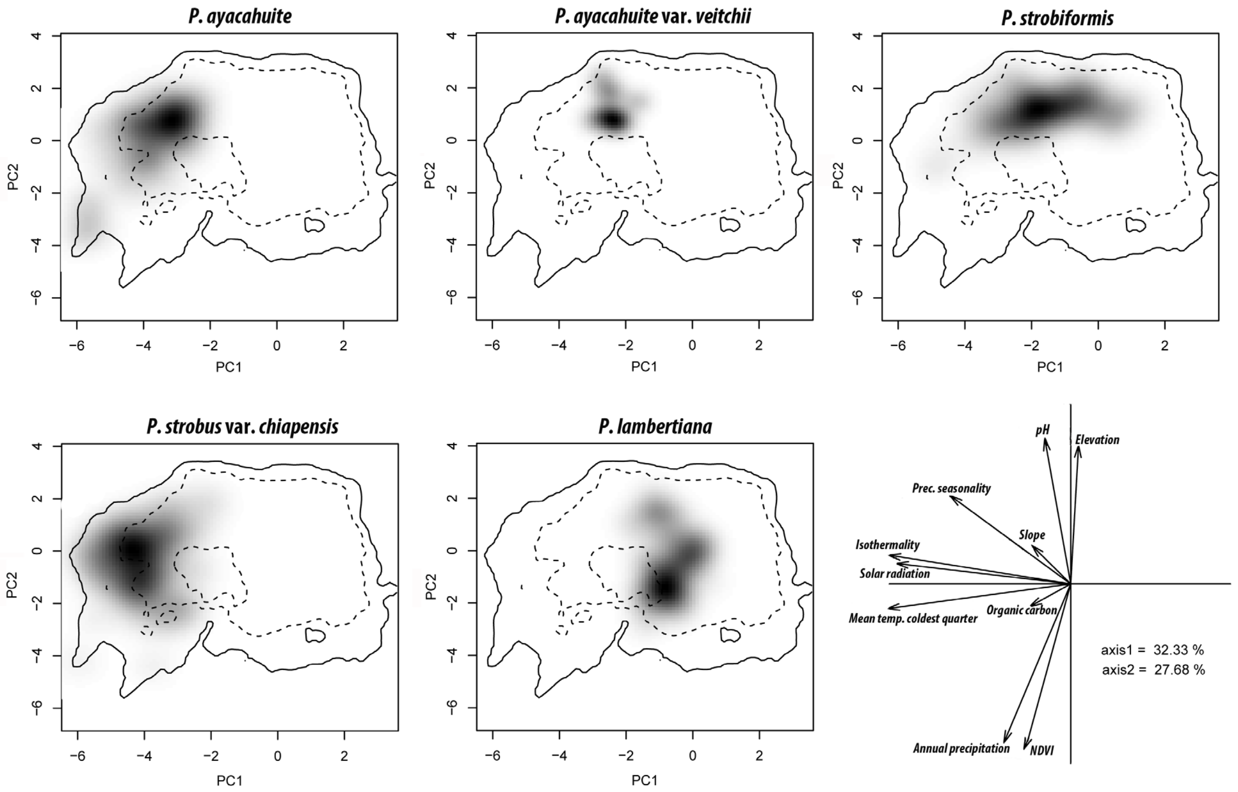


Figure 3. Ecological niche of the five analysed Mexican white pines in environmental space produced by the principal component analysis method (PCA-ent). The PCA-ent results represent the niche of the species in the two main axes with the environmental conditions of the complete study area. For each species the grey-to-black shading represents the grid-cell density of the species' occurrences (black being the highest density). The first dashed line represent the 50% of the available environment and the solid line represents the 100%. The last panel presents the contribution of variables for loading the main PCA-ent axes and the percentage of inertia explained by axes one and two.

Niche breadth and overlap

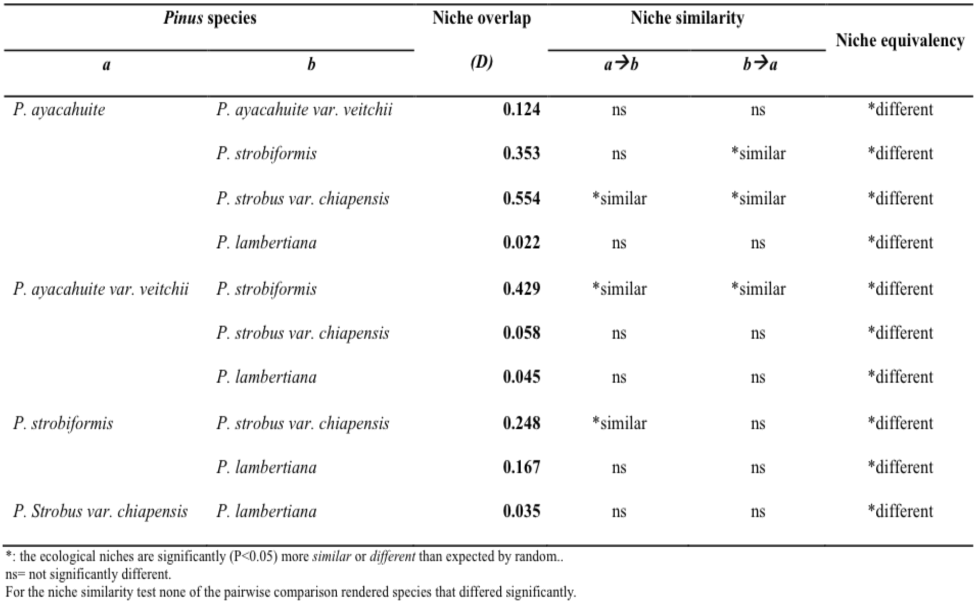
The results from the niche breadth assessment showed a high variation in environmental suitability for Mexican white pines (Table1). The highest niche breadth we found was 0.0673 for *P. strobus* var. *chiapensis*, which also presented the broadest distribution of suitable habitat (see "Area predicted suitable" in Table 1). The niche breadth for *P. strobiformis* was also similarly high (0.0671), however this species had a narrower distribution of suitable habitat than *P. strobus* var. *chiapensis*. *P. lambertiana* presented a niche breadth smaller than that of *P. strobus* var. *chiapensis*, while, the niche breadth of *P. ayacahuite* was almost half of that of *P. strobiformis* (Table 1). *P. ayacahuite* var. *veitchii*, exhibited both the narrowest distribution of suitable habitat and the lowest niche breadth—three times smaller than that of the *P. strobus* var. *chiapensis* (Table 1).

Niche overlap results suggest a great variability in the environmental space inhabited by the different Mexican white pines (Table 3; Fig. 3). Some species, such as *P. ayacahuite* and *P. lambertiana*, occupy considerably different environmental niches. Even closely-related taxa such as *P. ayacahuite* and its variety *P. ayacahuite* var. *veitchii*, also differed in their occupied niche space (Fig. 3; Table 3). All niche overlap values are presented in Table 3.

Niche equivalency and similarity

For all possible pairwise comparisons between Mexican white pines the null hypothesis of the niche equivalency test was rejected (Table 3). On the other hand, in our analysis of niche similarity the null hypothesis held for all pairs of Mexican white pines ('Niche similarity' in Table 3). For some pairs of Mexican white pines the niche similarities were higher than expected by chance, e.g., *P. ayacahuite* with *P. strobus* var. *chiapensis*, and *P. ayacahuite* var. *veitchii* with *P. strobiformis*. The environmental niches of *P. ayacahuite* and *P. strobus* var. *chiapensis* were not statistically different ($P>0.05$), exhibiting 55% of geographic overlap (Table 3). Other pairs of pine taxa shared niche spaces that were more similar than expected by chance, but only in one direction, e.g., *P. strobiformis* with P. ayacahuite, and *P. strobiformis* with *P. strobus* var. *chiapensis*. This suggests that the ecological niche of *P. strobiformis* was more similar than expected by chance to the one of *P. ayacahuite* but not vice-versa. The same is true for *P. strobiformis*, whose ecological niche was more similar to the one of *P. strobus* var. *chiapensis* but not vice-versa. Combined with our results from niche equivalency, our findings highlight how the ecological niches of the Mexican white pine species although similar, are not identical.

Table 3. Ecological niche comparisons for the Mexican white pines. Niche overlap values are presented for the comparisons of niche similarity and equivalency of species a with species b. All of the comparisons between the Mexican white pines highlight the non-equivalency of their ecological niches.



***Pinus* species**		**Niche overlap**	**Niche similarity**		**Niche equivalency**
a	***b***	***(D)***	***a*→*b***	***b*→*a***	
P. ayacahuite	*P. ayacahuite var. veitchii*	**0.124**	ns	ns	*different
	P. strobiformis	**0.353**	ns	*similar	*different
	P. strobus var. chiapensis	**0.554**	*similar	*similar	*different
	P. lambertiana	**0.022**	ns	ns	*different
P. ayacahuite var. veitchii	*P. strobiformis*	**0.429**	*similar	*similar	*different
	P. strobus var. chiapensis	**0.058**	ns	ns	*different
	P. lambertiana	**0.045**	ns	ns	*different
P. strobiformis	*P. strobus var. chiapensis*	**0.248**	*similar	ns	*different
	P. lambertiana	**0.167**	ns	ns	*different
P. Strobus var. chiapensis	*P. lambertiana*	**0.035**	ns	ns	*different

*: the ecological niches are significantly (P<0.05) more *similar* or *different* than expected by random..
ns= not significantly different.
For the niche similarity test none of the pairwise comparison rendered species that differed significantly.

Discussion

We have identified the environmental constraints for the distribution of Mexican white pines by applying state-of-the-art ecological niche modelling and ordination techniques. The identification of the main environmental constrains of the present distribution of species is key for current conservation actions and when investigating the impacts of future climate change on biodiversity. The wide distribution of Mexican white pines in the American continent underlines the variety of environmental conditions to which they are adapted and also may reflect on the physiological differences between them. This is particularly important as the physiology of pine trees may limit their distribution across environmental gradients, however, more physiologically oriented models (see Prentice *et al.,* 1992; Pearson & Dawson, 2003) should be applied in order to test this for the Mexican white pines.

Moreover, we observed that the variables reflecting climate-extreme characteristics play an important role when investigating current species distributions, as found in our variable importance analysis, and may also render insights when investigating future species distributions responses to climate change and future conservation actions (Zimmermann *et al.,* 2009).

The environment shaping the distribution of Mexican white pines

The environmental factors shaping the distribution of the Mexican white pines varied considerably. The two more northerly-distributed pine species, *P. strobiformis* and *P. lambertiana*, were highly constrained by solar radiation and temperature (Table 3). This is as expected, for these species as they inhabit the northernmost regions of the distribution of Mexican white pines, where low-temperatures winters last long and where access to light and heat are some of the main constrains for the survival and distribution of plant species (Maravilla *et al.,* 2004; Weiss *et al.,* 2004).

Isothermality is the quotient of the differences between the daily and annual temperature ranges. Presence at high values of isothermality may indicate that the species prefers areas where the differences in daily temperature across the day and night are greater than those across the year. The importance of isothermality for the distribution of different Mexican white pines shown in our models is supported by the great variation in daily and seasonal temperatures found across their distributional range (e.g., the mountain range in the state of Chihuahua Mexico in comparison to central and southern Mexico). In the northern areas, where *P. strobiformis* and part of *P. lambertiana* have their main distribution, the daily temperatures fluctuations appear to be smaller than the great variation in temperature observed across the year, meanwhile southern Mexico and Central America regions (where *P. ayacahuite* and *P. strobus* var. *chiapensis* are mainly distributed) present higher daily temperature variation in comparison to that found across the year (Maravilla *et al.,* 2004; Weiss *et al.,* 2004).

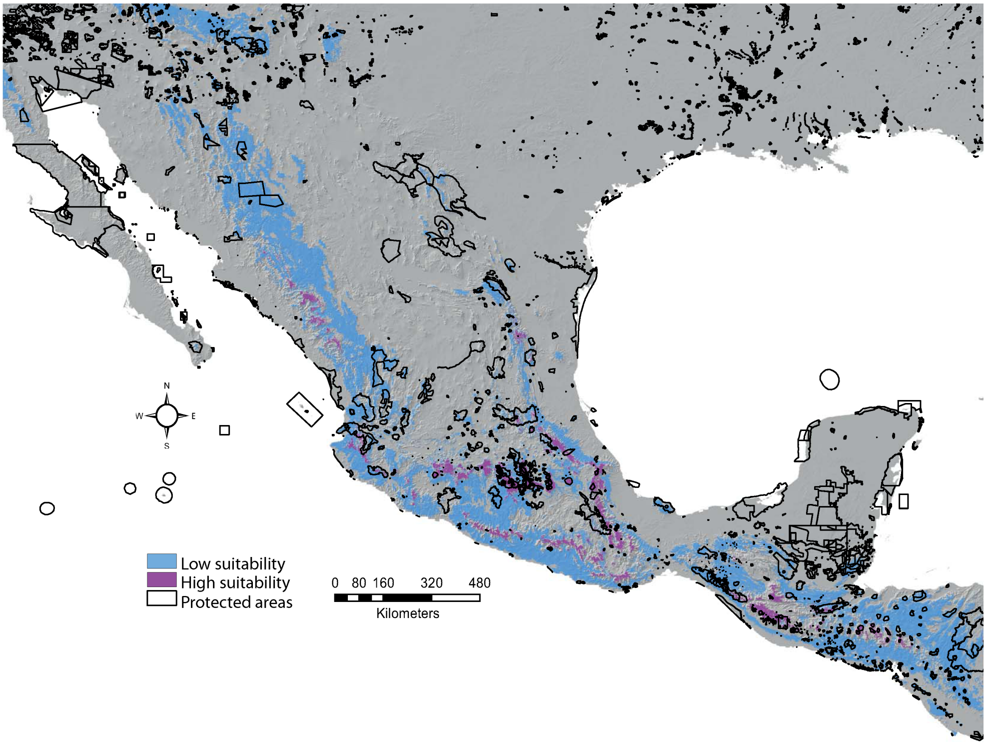
The potential distribution of Mexican white pines obtained from our ENMs, are in accordance with previously outlined ranges (Perry *et al.,* 1998), rendering the added value of been spatial explicit models and of delineating the differences in ecological niche space conditions that shape the species distribution. Our results build upon previous knowledge, improving the differentiation of the ecological niche ranges and highlighting the different habitats for each Mexican white pine. Specifically, areas where *P. ayacahuite* (Fig. 2b) and *P. strobus* var. *chiapensis* (Fig. 2d) are both found are of particular importance as the latter is considered endangered under the IUCN (International Union for Conservation of Nature) Red List categories and the populations of the former are declining (Thomas & Farjon, 2013). We have shown a wider environmental niche space for *P. strobus* var. *chiapensis* than for other species (Fig. 3). The populations of *P. strobus* var. *chiapensis* have decreased in the past years (Thomas & Farjon, 2013). Some of the main threats identified for *P. strobus* var. *chiapensis* are high deforestation rates, land conversion to agriculture, the introduction of exotic species (e.g., *Casuarina equisetifolia* L. and *Cupressus lusitanica* Miller), and the fragmentation of populations (del Castillo *et al.,* 2009; Thomas & Farjon, 2013). Our results highlight opportunities for the re-introduction and implementation of new management plans for *P. strobus* var. *chiapensis* in areas with high habitat suitability (Fig. 2d). The ENM of *P. strobiformis* indicates a centre of distribution in north-western Mexico and south-west of the USA and highlight areas from which not presence records have been collected (Fig. 2c). These areas present opportunities to cross-reference our assessments on ecological niche modelling for this species.

Pine species with wide spatial distribution and large niche breadth, such as *P. strobiformis* and *P. strobus* var. *chiapensis* (Table 1; Figs. 2c and 2d), may better endure some effects from climatic changes (Thomas, 2011). However, although they are widely distributed this might not safeguard them from direct anthropogenic impacts as deforestation (e.g., Barsimantov & Navia Antezana, 2012; Vidal *et al.,* 2014). Our projections of habitat suitability for *P. strobiformis* showed a geographical overlap with *P. ayacahuite* var. *veitchii* in the trans-volcanic belt of central Mexico (Figs. 2c and 2e). This is not surprising as this region has been classified as a centre of diversity of the genus in Mexico and is where the major geographic divisions between the *P. ayacahuite*, its variety *veitchii* and *P. strobiformis* occur (Perry, 1991; Gernandt & Pérez-de la Rosa, 2014). This highlights the importance of the trans-volcanic belt as an area of high potential for biodiversity conservation (Fig. 2).

The only white pine species whose range did not overlap with other white pines was *P. lambertiana*, (Fig. 2f). For *P. lambertiana*, suitable habitat was also projected in small locations where it has not been previously recorded in southern USA (Fig. 2f). For *P. lambertiana*, these areas might not yet been populated because of the long distance to the main distributional range in California (Kinloch Jr & Dulitz, 1990), or given any restricting biological interactions and environmental or anthropogenic barriers (Pearson & Dawson, 2003; Keith *et al.,* 2011).

The highlighted suitability hotspots areas (Fig. 2a) are of singular importance as it has been shown that most species of the genus *Pinus* in Mexico are not adequately protected by the currently proposed network of natural protected areas (Aguirre-Gutiérrez & Duivenvoorden, 2010). This is corroborated by our results that show that from a total area of 985568 km2 predicted as suitable at least for one white pine species only 12% is inside declared/official protected areas (Fig. 4). Furthermore, from the 49717 km2 predicted as highly suitable for most Mexican white pine species only 10966 km2 are currently under protection (Fig. 4). The highlighted hotspots regions are crucial to delimitate networks of protected areas and safeguard the centre of diversity of the Mexican white pines.

Fig. 4. (next page) **Location of the suitable areas for Mexican white pines. We focus on Mexico and Central America because most of the suitable areas are found in this region.** Blue areas represent areas that are suitable for at least one or two of the Mexican white pine species. In purple we present the areas suitable for three or more of Mexican white pine species. The areas delineated with black lines represent the official network of protected areas (IUCN and UNEP-WCMC 2014).



The niche overlap, equivalency and similarity

Given the wide variation in environmental conditions where white pines species occur, it is perhaps not surprising that niche overlap between Mexican white pines was low. The low niche overlap values between *P. ayacahuite* and *P. lambertiana*, and between the latter and *P. strobus* var. *chiapensis*, are also reflected on their different environmental constrains (Farjon *et al.,* 1997; Richardson, 1998)

In our analysis we show how the ecological niches of Mexican white pines are not interchangeable: our assessment of niche equivalency rejected the null hypothesis that the ecological niches of all species pairs are equivalent. This shows why it is not accurate to imply niche characteristics for one species based on the niche of another—even for these considered 'closely related' pine species. The niche similarity results suggest that Mexican white pines share more characteristics of their environmental niche spaces than randomly expected. Together, the findings above are not contradictory but suggest a tight link between these pine species, which share environmental niche spaces, thus corroborating they are closely related but still different taxa. The observed similarities in ecological niche space between Mexican white pines suggest that they have similar environmental constrains but that a different set of variables within this environmental niche space restrict their distribution. Further taxonomic analyses that take information on ecological niche similarity and equivalency into account, as well as morphological and molecular information, are needed to generate a comprehensive classification scheme for the Mexican white pines.

Implications for a broader context

The differences in environmental constrains shown in our study offers insights on the ecological niches of Mexican white pines as well as on individual impacts that on-going changes in climatic conditions may likely have on them. This is an important issue as an increase in temperature from 1.8 to 4.0 °C, and a reduction in precipitation up to 20% are expected in the "worst case" climate change scenario for the regions of Central America to northern Mexico (Solomon *et al.,* 2007). Changes in climatic conditions will have a direct effect on the distribution of the Mexican white pines whose ranges are strongly constrained by temperature and precipitation (Gomez-Mendoza & Arriaga, 2007; Chen *et al.,* 2011). Nonetheless, to comprehensively assess the impacts of climate change, ENMs need to consider not only climatic information of the future conditions but also integrate the species dispersal mechanisms, crucial biological interactions and barriers for dispersion.

Information on niche breadth has direct implications in planning conservation actions, as widely distributed species might be less vulnerable to localized anthropogenic exploitation (Bellard *et al.,* 2012; Mantyka-pringle *et al.,* 2012). Conservation actions for the Mexican white pines can include protection of current forest stands, reintroduction of species in deforested/disturbed areas and increasing the connectivity between forested patches of pine populations. Furthermore, considering the effects of habitat fragmentation and land-use change on forest biodiversity is pivotal as these pressures can have delayed and long-term negative impacts (extinction debt, Tilman *et al.,* 1994) that need to be accounted for if conservation plans are to be successful (Gonzalez, 2013). Particularly, the narrow distribution of *P. ayacahuite* var. *veitchii* is likely at risk given logging actions and the intense urban activities that are expanding into the trans-volcanic belt area (Farjon, 2013b). There are few protected areas along or close to the Mexican trans-volcanic belt, though most of them are small and scattered (Fig. 4). Some of the main protected areas are the “Zempoala - La Bufa" national park, the “Sierra de Manantlan” and the “Monarch butterfly” reserve. These reserves represent important areas that can act as reservoirs of pines diversity, however, even in the Monarch butterfly reserve that has high protection status, current logging actions and land conversion continue their negative impact on biodiversity (Navarrete *et al.,* 2011). Still, protected areas and social awareness seem to be a main asset for the conservation of biodiversity and particularly of the Mexican white pines.

Conclusions

The significant differences in ecological niche spaces we have shown also reflect the reported taxonomic divisions among Mexican white pines (Syring *et al.,* 2007; del Castillo *et al.,* 2009). Differences in environmental constrains of the different Mexican white pine species are also reflected on the niche similarity, overlap and equivalency results. Based on these differences our results support the taxonomic division between the P. ayacahuite–*P. strobiformis* complex.

Several drivers of declines of pine species around the world have been discussed in recent work (Richardson *et al.,* 2007), and Mexican white pines are among the most threatened of pine taxa. Deforestation for agriculture and wood extraction are key drivers of the alarming decline of taxa in this group (i.e., Richardson *et al.,* 2007; Navarrete *et al.,* 2011; Vidal *et al.,* 2014) and thus of their unique genetic diversity (Farjon et al. 1997). Reduced genetic diversity will reduce the ability of these pines to respond to changing environmental conditions, making it imperative to protect remaining populations. Current and future conservation actions, not only for the Mexican white pines but also for other taxa, could benefit from insights derived from knowledge of the role of environmental variables in shaping the ecological niche of focus species. In this context, effective conservation actions must take into account intrinsic requirements of different species and the main environmental drivers that shape their distributions. Different conservation interventions may be required even for closely-related taxa (e.g., *P. ayacahuite* and the *veitchii* variety). Insights from this study should be useful for improving the on-going conservation actions to mitigate the declining trends in the populations of Mexican white pines by directing re-introductions and guiding the establishment of effective networks of protected areas.

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4

The importance of climate in setting species range limits has increased in recent decades

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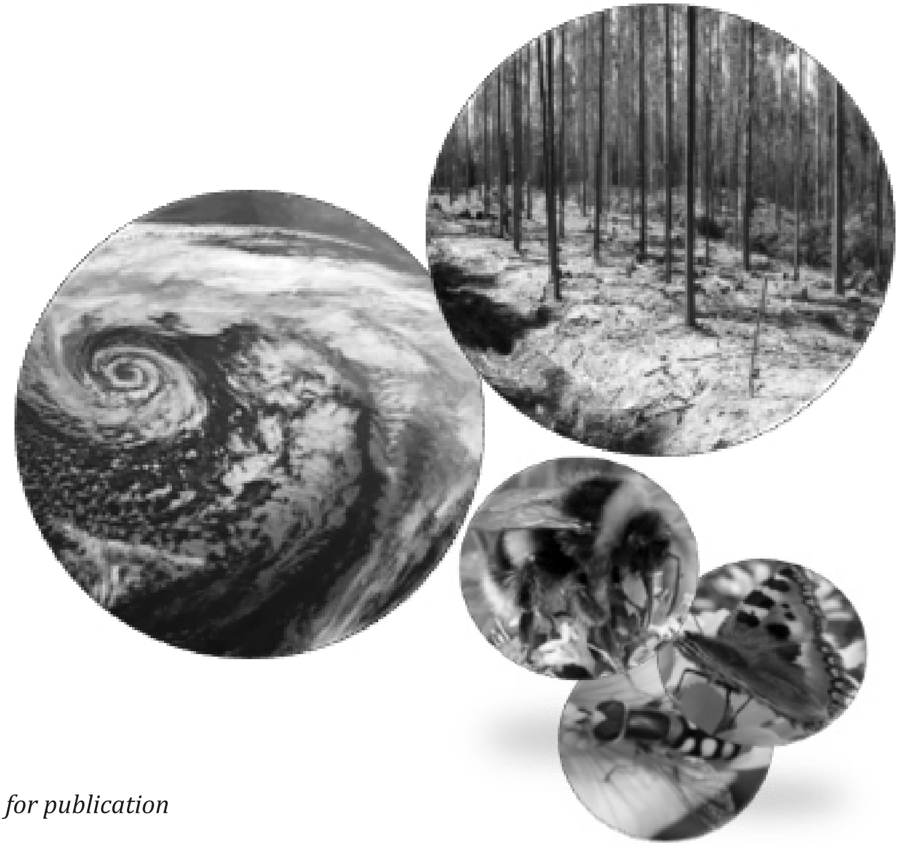

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Abstract

Climate and land use changes are two main drivers of biodiversity change, and predicting their impact on species distributions is key to manage ongoing and future global change. However, methods such as species distribution models that are commonly used to forecast such changes assume that the importance of abiotic factors in delimiting species distributions remains constant over time. Here, we use spatially-explicit historical data on climate, land use and species occurrences to test whether the importance of different climatic and land use drivers for setting species geographic range limits has changed over a period of more than 60 years (1951–2014). We modelled the distribution of a total of 470 pollinator species (bees, butterflies and hoverflies) in three different time periods (1951–1970, 1971–1990, 1998–2014) across the Netherlands. We then assessed the importance of several climate (precipitation, temperature) and land use variables (landscape composition, habitat fragmentation, and spillover potential) in setting species geographic range limits over time. Results suggest that land use variables, especially landscape composition, had a constantly high importance in limiting geographic distributions of all pollinator species across time. In contrast, importance values of climatic factors tended to be generally lower than those of land use variables across all pollinator groups. However, the importance of temperature in setting range limits of bees and hoverflies has significantly increased in recent times. Given the projected increases in temperature over the next decades, our results suggest that predictions of future species range changes may underestimate the role of climate in setting range limits. This might be particularly true in regions where —similarly to the Netherlands— large-scale land-use changes have mostly ceased, but temperature change remains rapid.

Introduction

Recent rapid changes in climatic conditions (e.g. temperature and precipitation; McCain and Colwell 2011) have raised considerable concerns over their effect on biodiversity (e.g. Thomas et al. 2004). For instance, changes in temperature (Sala et al. 2000, Dawson et al. 2011) and the increase of extreme weather events (Hansen et al. 2012) can lead to important changes in biodiversity around the globe. Moreover, during the last century biodiversity has experienced alarming declines and functional shifts due to the effects of land-use changes such as habitat loss (Meyfroidt and Lambin 2011), habitat fragmentation (Krauss et al. 2010), and land use intensification (Tscharntke et al. 2005). Climate and land use are therefore considered key drivers of biodiversity loss today, and particularly when combined, they can reduce suitable habitats for species and disrupt ecological interactions, potentially driving species to extinction (Hegland et al. 2009, Fox et al. 2014).

Climate and land-use changes are unlikely to change in parallel (Fox et al. 2014). For example, the rate of temperature rise increased in recent decades (Hansen et al. 2012), while for several highly industrialized countries major habitat changes were more intense in the past (Fuchs et al. 2014). Consequently, the importance of such drivers for biodiversity dynamics may vary over time. However, many tools (e.g. species distribution models, SDMs; Thuiller 2004) used to analyse the effects of climate and land use on biodiversity and to forecast species range shifts under potential future global change are based on projections of present-day species responses to different climatic and land use drivers. Such projections assume that species distributions are in equilibrium with current environmental conditions and that relationships between abiotic factors and species occurrences remain constant over time (Dormann 2007). This assumption is likely to affect the performance and reliability of SDMs, especially under non-equilibrium conditions (Eskildsen et al. 2013). It is therefore crucial to evaluate whether the importance of global change drivers and their effects on species distributions remain constant over time. A key limitation for such evaluations is that future empirical data are not available against which projections can be validated. However, the availability of historical information on biodiversity and environmental factors across the same spatial domain allows exploring the dynamics of such relationships.

Here, we use a unique set of spatially-explicit species occurrence records of several groups of flower visitors (bees, hoverflies, and butterflies), in the following referred to as "pollinators", and environmental data from the Netherlands since 1951 to the present to investigate whether the importance of climate (temperature and precipitation) and land use (landscape composition, habitat fragmentation and spillover potential) as drivers of species distributions has changed over time. Pollinator's accessibility to feeding and nesting resources greatly depend on landscape patterns (Winfree et al. 2011, Oliver et al. 2012). Therefore, we expect landscape composition and habitat fragmentation to pose a generally high influence on species distributions. Given that most large-scale land-use changes in the studied region have occurred before the 1990s (Harms et al. 1987, EEA -European Environment Agency 2010), and that pronounced changes in precipitation regimes and temperature have been recorded in recent time (Klein Tank 2004, Ligtvoet et al. 2013), we expect that climate might have become more relevant to species distributions in recent decades.

Methods

Study region and time periods

The Netherlands has been intensely sampled for biodiversity since the early 19th century, with high-quality species distribution data being available at the country level across several decades. Moreover, in the last century the Netherlands has experienced major changes in climate (KNMI, 2014) and land use conditions (Knol et al. 2004, Hazeu et al. 2010). The fact that major changes in both of these conditions have occurred in the study area over the last century makes this region particularly suitable for analysing the impacts of these drivers on biodiversity distributions. All three aspects (biodiversity, climate and land use) are well documented with spatially explicit data across more than 50 years. After the Second World War (i.e. during 1950–1970), the Netherlands has suffered rapid habitat loss and pronounced agricultural intensification with an associated increase in pesticide use (Harms et al. 1987). After 1990, there was an increasing investment in conservation measures and agro-environmental schemes, especially since the turn of the millennium (Kleijn and Sutherland 2003). The Netherlands has also experienced important changes in climate, including important increases in average temperature over the last century (~1.7°C; Ligtvoet et al. 2013), which may greatly affect the distribution of pollinators (Kjøhl et al. 2011), with the most rapid warming been experienced during the last 20 years (Klein Tank 2004). This increase in temperature is twice the global average (Van Oldenborgh et al. 2009), and increases of up to 5°C are expected during the forthcoming century (Ligtvoet et al. 2013). Moreover, important changes in the temporal distribution and amount of precipitation have been observed in the Netherlands, with the average annual winter precipitation increasing by ca. 20% (Klein Tank 2004, Ligtvoet et al. 2013). Furthermore, although the Netherlands covers a relatively small spatial extent, it shows strong variation in climatic conditions along its latitudinal and longitudinal gradients. For instance, the first warm day (above 20°C) occurs up to 20 days earlier in the southeaster part than in the northwest. There is also less precipitation and higher evapotranspiration in the coastal zone, resulting in higher probabilities of drought in these areas in comparison to inland eastern locations (Ligtvoet et al. 2013). Based on these observed changes in climate and land use we binned the occurrence records (see below) into three distinct time periods (TP1: 1951–1970, TP2: 1971–1990, TP3: 1998–2014) and analysed whether the responses of species distributions to environmental conditions have changed over time.

Species distribution data

We included three key pollinator taxa in our study: bees (Hymenoptera: Apoidea), hoverflies (Diptera: Syrphidae) and butterflies (Lepidoptera: Papilionoidea and Hesperioidea). Presence records for each species across the three time periods were obtained for bees and hoverflies from the European Invertebrate Survey (EIS-Nederland, www.eis-nederland.nl) and for butterflies from the Dutch National Database of Flora and Fauna (NDFF, www.ndff.nl). Experts from the EIS and the NDFF have extensively assessed the quality of species identification and location accuracy of all species' presence records that we included in our study. More details about the quality evaluation can be found in www.ndff.nl/validatie.

All species occurrence records were compiled at a resolution of 5 × 5 km grid cells to accommodate the higher uncertainty in geographic coordinates of the older records relative to the higher location accuracy of the more recent records. Accurate distribution models can be obtained with small sample sizes depending on the species prevalence in the study area (van Proosdij et al*. In press*). In our study we included all species that were present in at least five 5 × 5 km grid cells and only those that were represented in each of the three time periods. This allowed us to analyse a total of 470 pollinator species, including 207 bee species, 61 butterfly species, and 202 species of hoverflies (see Table S1). From a total of 1820 landscapes (5 × 5 km grid cells) in the Netherlands, 914 had records for bees in TP1, 894 for butterflies, and 1094 for hoverflies. In TP2, bees were present in 972 landscapes, butterflies in 1484, and hoverflies in 1376. In TP3, bees were sampled in 1346 landscapes, butterflies in 1655, and hoverflies in 1592 landscapes (see Fig. S1 for the spatial distribution of the sampled landscapes across time).

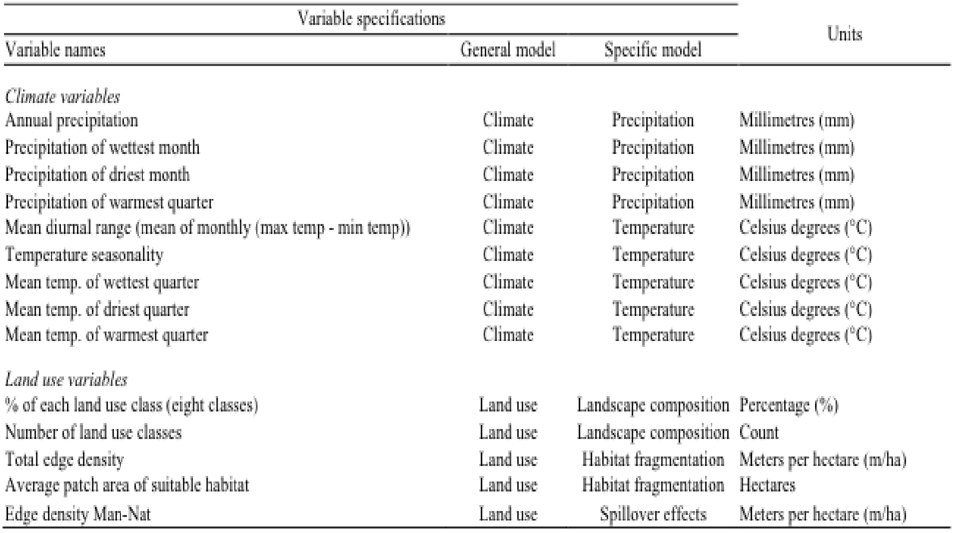
Climatic data

We obtained climate data for the Netherlands on maximum, minimum and average values of temperature and precipitation from the project "ClimateEU: historical and projected climate data for Europe" (Wang et al. 2012). Climatic data were obtained at the same resolution as the land use and species distribution data (5 × 5 km grid cells). These data were then used to calculate the 19 bioclimatic variables described in Hijmans et al. (2005). To avoid colinearity, when two variables were highly correlated (Pearson's correlation ≥ |0.75|), we only selected the variable that was thought to delimit strongly the distribution of insects, e.g. those that capture extreme conditions during the year (e.g. temperature of warmest quarter of the year instead of mean annual temperature). These variables have, as supported by other studies (e.g. Kjøhl et al*.* 2011), important impacts on the distribution and persistence of pollinators (see Table 1).

Land use data

Land use data were obtained from the geo-information department of Wageningen University (www.wageningenur.nl) with an original resolution of 25 × 25 m pixels. The land use map for the oldest time period (TP1) is based on topographic cartography and the newer maps (TP2-TP3) are based on remote sensing imagery, all of them with high land use classification accuracy ranging from 85–98% (Knol et al. 2004, Hazeu et al. 2010). The land use maps were obtained for the years 1960 (representing TP1), 1980 (TP2) and 2008 (TP3), which represent central points in time for each of the time periods for which the species data was obtained (see above). As land use data from more recent time periods had more detailed information on land use classes than data from older time periods, the land use maps were reclassified to derive eight consistent land use types that were representative for all three time periods: agriculture, grassland, forest, moors/peat, sandy soils, swamps, urban and water. Based on these reclassified land use maps, for each 5 × 5 km grid cell (Table 1) and for each time period, we then calculated a total of twelve land use metrics. These land use metrics have previously been shown to impact species richness of pollinators (see Aguirre-Gutiérrez et al. *In press*). The calculated metrics characterize three major aspects of landscape and habitat structure (Tscharntke et al. 2012): landscape composition (nine metrics), habitat fragmentation (two metrics) and spillover potential (one metric) (see below).

Table 1. Variables used in species distribution models and their grouping for subsequent analyses in linear mixed models. For the 'general model', environmental variables were grouped into either climate or land use. For the 'specific model', variables were grouped into five finer divisions of climate (temperature and precipitation) or land use (landscape composition, habitat fragmentation and spillover).



Variable specifications			Units
Variable names	General model	Specific model	
Climate variables			
Annual precipitation	Climate	Precipitation	Millimetres (mm)
Precipitation of wettest month	Climate	Precipitation	Millimetres (mm)
Precipitation of driest month	Climate	Precipitation	Millimetres (mm)
Precipitation of warmest quarter	Climate	Precipitation	Millimetres (mm)
Mean diurnal range (mean of monthly (max temp - min temp))	Climate	Temperature	Celsius degrees (°C)
Temperature seasonality	Climate	Temperature	Celsius degrees (°C)
Mean temp. of wettest quarter	Climate	Temperature	Celsius degrees (°C)
Mean temp. of driest quarter	Climate	Temperature	Celsius degrees (°C)
Mean temp. of warmest quarter	Climate	Temperature	Celsius degrees (°C)
Land use variables			
% of each land use class (eight classes)	Land use	Landscape composition	Percentage (%)
Number of land use classes	Land use	Landscape composition	Count
Total edge density	Land use	Habitat fragmentation	Meters per hectare (m/ha)
Average patch area of suitable habitat	Land use	Habitat fragmentation	Hectares
Edge density Man-Nat	Land use	Spillover effects	Meters per hectare (m/ha)

For landscape composition, the nine metrics reflected the percentage of each land use type per grid cell (eight metrics) as well as the total number of land use classes per grid cell (one metric). The latter was included as a proxy of spatial heterogeneity, which can influence the turnover of pollinator species assemblages (Tscharntke et al. 2012). Habitat fragmentation was represented by two metrics: the average area of suitable habitat patches and total edge density. Following the evaluation of habitat suitability for pollinators from Vogiatzakis et al. (2015), we classified the land use classes, grassland, moors/peat, forest and sandy soils as 'suitable habitat', and agriculture, urban, water and swamps as 'non-suitable habitat'. For total edge density, we calculated the density of edges between all land use types in a grid cell. Finally, we used one metric to characterize species spillover potential, i.e. the potential for movements of organisms across managed and natural systems (Rand et al. 2006). Here, the proximity and existence of edges between managed and (semi-) natural systems plays a key role. We therefore calculated the edge density between managed and (semi-) natural systems. We considered the land use types grassland and agriculture as (intensively-) managed and moors/peat, forest, swamps and sandy soils as (semi-) natural systems. Urban and water were not taken into account in this calculation.

All calculations of land use metrics were carried out in R (Development Core Team, http://cran.r-project.org) with the "SDMTools" package.

Changes in climatic and land use conditions over time

We quantified the changes in abiotic conditions that took place in the Netherlands between consecutive time periods (TP1–TP2, TP2–TP3). We also analysed the overall changes that occurred between the first and last period (TP1–TP3). The changes were calculated as the post-period minus the pre-period value (e.g. TP3-TP1) for each climatic and land use variable. After obtaining the change values we used a student's *t*-test (Box 1987) to investigate if significant changes in climatic and land use conditions indeed occurred.

Species distribution models

For each bee, butterfly and hoverfly species in each time period (TP1, TP2 and TP3), we fitted SDMs using the maximum entropy modelling approach with

MaxEnt (Phillips et al. 2006). MaxEnt is a machine learning technique that has been extensively used for modelling large data sets of species in locations with varied sets of environmental conditions, rendering high model accuracy (Elith and Leathwick 2009, Marshall et al*.* *In press*). We selected MaxEnt after an in-depth comparison with other algorithms for a wide range of species with different sample sizes and spatial distribution of their recording locations in our study area (Aguirre-Gutiérrez et al*.* 2013). This comparison showed that MaxEnt was one of the best performing algorithms with high model sensitivity and specificity. We therefore use MaxEnt as the model algorithm here. In MaxEnt, we allowed to fit more complicated models (use of different features types) depending on the number of records available as described in Phillips and Dudik (2008) and Elith et al. (2011). In MaxEnt the term "features" refers to a set of transformations applied to the original variables, depending on the number of records included in the model (Elith et al. 2011). Following Phillips and Dudick (2008), we fitted only linear features for species with less than 10 available presence records; linear and quadratic features for species with the number of available records between 10 and 14 records; and linear, quadratic and hinge features (i.e. functions for piecewise linear splines) for species with 15 to 79 records. For species with more than 80 records the product (of all pair-wise combinations of covariates) and threshold features (involving a simple step fitted function) were added. More in-depth explanations of the MaxEnt modelling and feature types can be found in Elith et al. (2011).

As species sampling collections are usually geographically biased (e.g. Merow et al*.* 2013), this can also generate environmental gradient selection bias. We accounted for this, as suggested by Phillips et al. (2009) and Mateo et al. (2010), by only extracting background information from those collection localities where species from the same pollinator group had been sampled. This method, called "target group", has proven to considerably increase model performance (Phillips and Dudik, 2008). Moreover, this approach aids to account for possible sampling and environmental selection biases because the modelled data contains the same collection bias as the data used for the background selection (Elith et al. 2011). To account for the within algorithm model variation, we computed SDMs for each species using ten repetitions with a bootstrap approach where 80% of the data was used for training and 20% for model testing. We then used the area under the curve (AUC) value of the receiver-operating characteristic to summarize model performance (Hanley and McNeil 1982). However, AUC values are constrained by the fraction of the geographic area covered by the species, and are often low for species with large sample sizes and increase as the number of sampling records decreases (Phillips et al*.* 2006, van Proosdij et al*. In press*). To account for between-model variability and to avoid basing our model selection on AUC values alone, we obtained an ensemble model for each species by averaging the suitability scores across the ten model repetitions and used this average value in subsequent analysis.

In order to investigate the importance of the different environmental drivers for delimiting species distributions, we obtained two different evaluation metrics: the “permutation importance” and the “percentage contribution” (Phillips 2006). These metrics have been successfully applied in other studies (e.g. Sobek-Swant et al*.* 2012, Tellería et al*.* 2012, Gallardo and Aldridge 2013, Quillfeldt et al*.* 2013). For the “permutation importance”, the values of the focus variable are randomly permuted on the training presence and background data. The model is then re-evaluated on the permuted data and the change in the model’s AUC is calculated. Large changes in AUC value indicate that the model is highly dependent on the specific variable and thus has a higher importance for defining the final model. For the “percentage contribution”, the importance value of each variable depends on the specific path taken by the algorithm to obtain the optimal model. During each model iteration MaxEnt identifies which environmental variables contribute for the model fitting process by detecting the change in model gain after modifying the coefficient for a single feature (Phillips 2006). MaxEnt then assigns the change in model gain to the environmental variable that the feature depended on in order to obtain its final contribution. For the final values for each of the two evaluation metrics (permutation importance and percentage contribution) we averaged the results of the ten model repetitions. The obtained importance values were used as a measure of how strongly a species distribution is limited by a specific environmental driver and then applied to assess if and how the importance of such drivers varied between the three time periods analysed (see below).

Environmental drivers limiting pollinator distributions across time

We used a linear mixed effects model (Zuur et al. 2009) to test whether climatic and land use variables (Table 1) had similar importance in limiting species distributions in different time periods. We performed two analyses. In the first mixed model ('general model'), we aggregated the various SDM predictor variables into two general classes: climate or land use (Table 1). The importance values were then used as response variable and the type of environmental variable (climate or land use), pollinator group and time period as well as their interaction as explanatory variables. In the second mixed model ('specific model'), we evaluated in more detail which of the climate or land use variables were important for each pollinator group. Hence, we repeated the mixed model analysis, but used a finer subgrouping of environmental variables by aggregating them into five groups: precipitation, temperature, landscape composition, habitat fragmentation and spillover potential (Table 1). This allowed us to assess which specific types of climate and land use variables have the strongest effects on limiting pollinator distributions. In both mixed models we used species identity as a random effect.

Several of the importance values of environmental variables were equal to zero. To deal with the high number of zeros, we applied a zero-inflated model approach which combines a Binomial and Gaussian model (see Carvalheiro et al. 2014). First, we compared the probability of the environmental variables to have an effect on species distribution using a Binomial model (variable equal 0: no importance; 1: importance >0%). Second, we compared the strength of the effect of those environmental variables that had an effect (i.e. with importance values >0) using a Gaussian model. For the Gaussian model the importance values were $\log_e$-transformed to normalize the residuals. In both, the Gaussian and the Binomial models, we used mixed models with species identity as a random effect. We also tested for significant differences between pollinator groups and time periods by performing post-hoc pairwise comparison tests (TukeyHSD). The analyses were repeated for both the permutation importance and the percentage contribution variable importance values from MaxEnt.

All mixed models were implemented using the "lme4" package and the multiple comparison tests using the “multcomp” package with the “glht” function in the R platform (http://cran.r-project.org).

Results

Changes in abiotic conditions over time

All climatic variables showed significant changes between the first (1951–1970) and the last (1998–2014) time period (Fig. 1; Table S2). While annual precipitation increased (<20 mm on average), all other precipitation-related variables showed negative changes (Fig. 1). All temperature-related variables, with the exception of temperature seasonality, showed increases between 0.2 (mean diurnal range) to 3.8 °C (mean temperature of driest quarter) (Fig. 1).

Concerning land use composition, all land use classes (except sandy soils and water) showed significant changes in their amount between the first and last time period (Fig. 1; see Table S2). Forest, swamps and urban classes increased in their percentage in the landscape whereas agriculture, grasslands and moors/peat decreased (Fig. 1). As for variables related to fragmentation, the average patch area of suitable habitats in the landscape also presented significant declines of up to 90 ha on average (Fig. 1). The total amount of edges in the landscape and the edges between natural and managed systems also increased significantly, and the number of land use classes in the landscape increased by 1.5 on average over this time period (Fig. 1; Table S2).

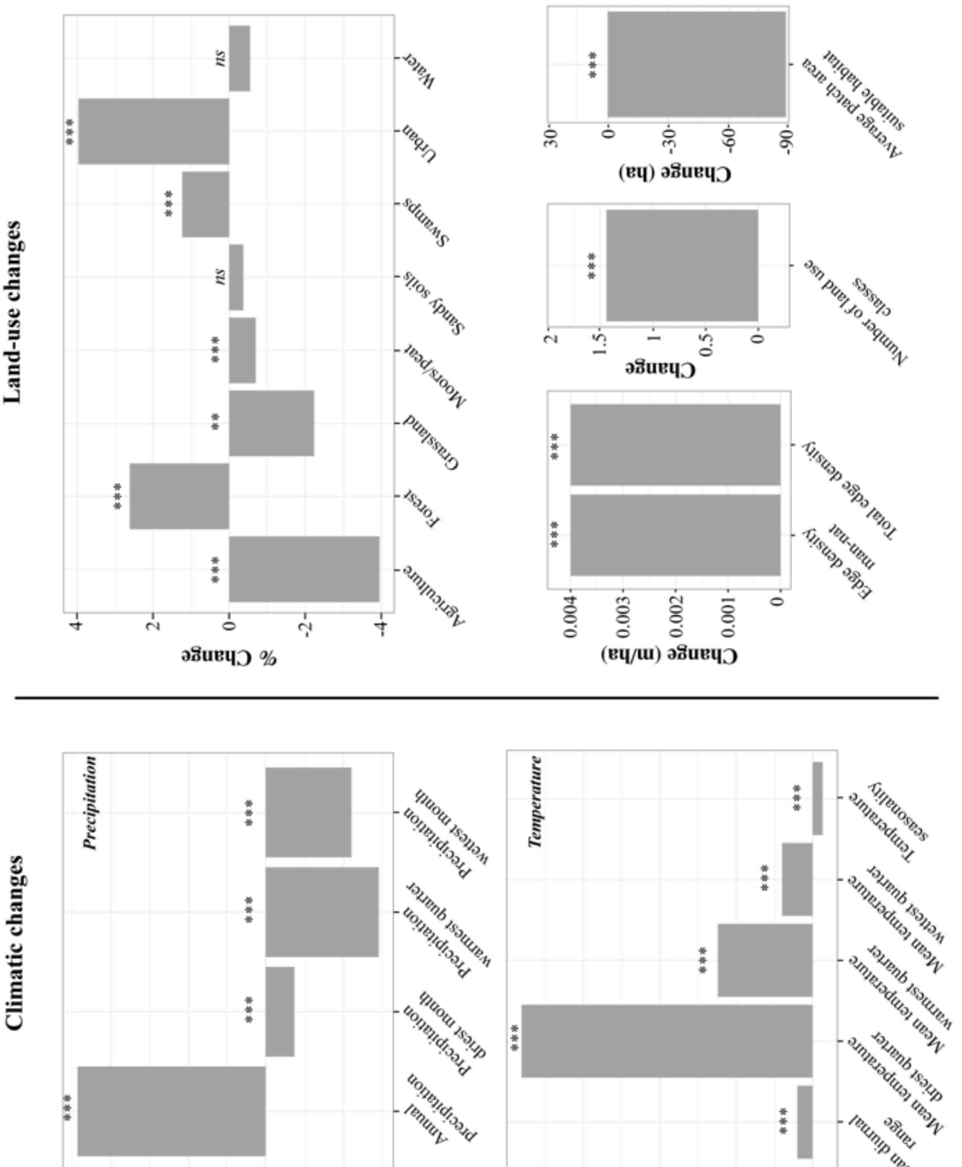


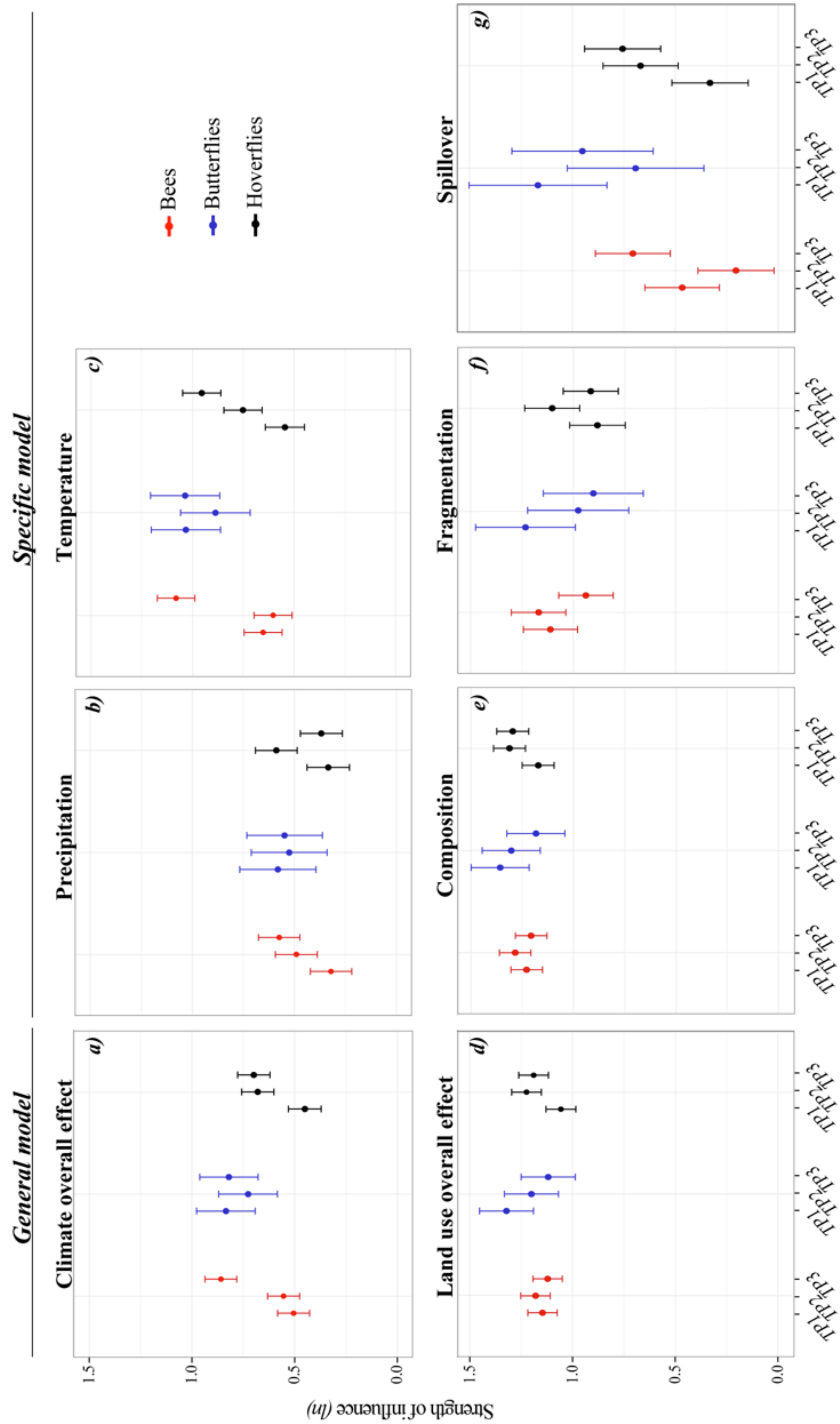
Figure 1. **Changes in climatic and land use conditions in the Netherlands between the first (TP1, 1951–1970) and the last (TP3, 1998–2014) time period.** The asterisk above the bars represents whether a significant change has occurred or not. Significance levels: ***P < 0.001; **P < 0.01; *P < 0.05; *ns*: not significant. For statistical details see Table S2.

Absolute importance of climate and land use in limiting pollinator distributions across time

The analyses with the permutation variable importance (Fig. 2; Tables S5–S8) and the percentage variable contribution gave similar results (see Fig. S2 and Tables S3–S4, for the results using the "percentage contribution" evaluation for the strength of the effect). The only exception was for precipitation for which a slight decrease in importance over time was detected using the percentage contribution and an increase over time with the permutation importance. The different results for the precipitation variables may be caused by a higher correlation within this group of variables, to which the percentage contribution metrics is known to be susceptible. Given the overall similarity of the result, we only present the analysis from the Gaussian model for the permutation importance in the main text, as it analyses the "strength" each environmental variable has in limiting species distributions, and the results from all other analyses in the supplementary material.

In all time periods, climate was an important and statistically significant factor limiting the distributions of pollinators (Fig. 2a; Tables S5–S6). This was true for both precipitation (Fig. 2b) and temperature (Fig. 2c) although temperature tended to have higher importance values than precipitation (Supplementary material, Tables S7–S8). Compared to climate, the overall effect of land use for limiting species distributions was higher (Fig 2d vs. Fig. 2a). Among the specific land use variables, landscape composition was the strongest variable and spillover the weakest, with habitat fragmentation showing intermediate effects (Fig. 2e–g; Tables S7–S8). These effects were largely consistent across pollinator groups (Fig. 2).

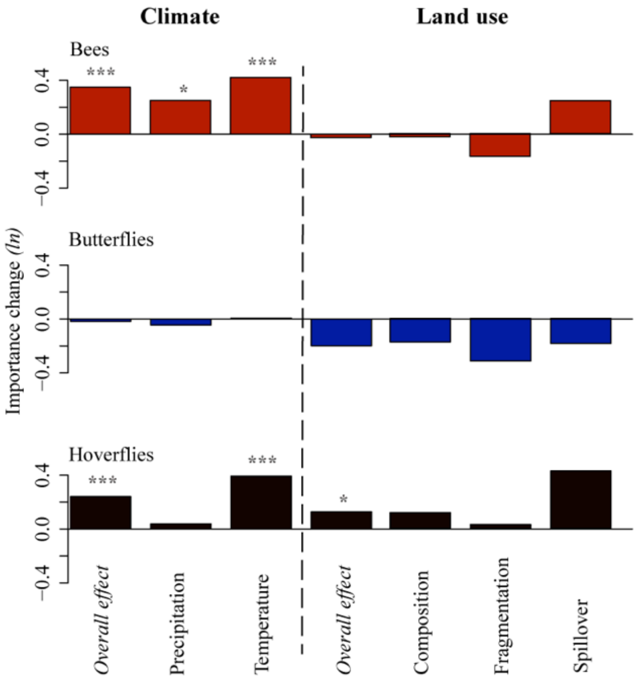
Figure 2. (next page) **Absolute importance of climate (a–c) and land use (d–g) for limiting species distributions of different pollinator groups (bees, butterflies and hoverflies) across time (periods: TP1, 1951–1970; TP2, 1971–1990; TP3, 1998–2014).** Values illustrate the average importance values ± 95% confidence intervals of variables that have an influence on species distributions of each pollinator group ("strength" of environmental variables, Gaussian model). For both climate and land use we present the overall effect ('general model') and the effect of the more detailed classes of environmental variables ('specific model') (compare Table 1). For statistical details see Tables S6 and S8.


General model
Specific model
Climate overall effect
Precipitation
Temperature
Land use overall effect
Composition
Fragmentation
Spillover
a)
b)
c)
d)
e)
f)
g)
Bees
Butterflies
Hoverflies
Strength of influence (ln)
1.5
1.0
0.5
0.0
TPP1
TPP2
TPP3

Relative changes in the importance of climate and land use

Overall, importance of climate (Fig. 2a) in setting range limits increased through time for bees and hoverflies (Fig. 3; Fig. S3 and Table S6). For these two pollinator groups, this overall shift in the importance of climate was mostly due to the effect of temperature (Fig. 3). Precipitation showed a significant increase in importance between T1 and T3 for bees (Fig. 3) whereas for hoverflies this only occurred between T1 and T2 (Fig. 2b). This effect was not found for precipitation with the “percentage contribution” evaluation (Fig. S2). Butterflies did not show such trends in the importance of climate (Fig. 2a–c). In contrast to climate, the overall importance of land use did not significantly change across pollinator groups and land use variables in most cases (Fig. 3). The importance of habitat fragmentation and spillover potential presented overall decreases and increases respectively, however, these were not significant (Fig. 3). Land use, especially landscape composition and habitat fragmentation, remained of constantly high importance through time (Fig. 2d–f).

Figure 3. Relative changes in the importance of climatic and land use drivers for bee, butterfly and hoverfly distributions between the first (TP1, 1951–1970) and the last (TP3, 1998–2014) time period. The different climatic variables (left of dotted line) and land use variables (right of dotted line) correspond to Fig. 2. The importance change is expressed as *ln*-transformed values based on the (Gaussian) linear mixed models results from Fig. 2. The asterisk above the bars represent a significant change occurred. Significance levels: ***P < 0.001; **P < 0.01; *P < 0.05. For statistical details see Tables S6 and S8.



Discussion

Using spatially-explicit historical data (1951–2014) of climate, land use and species occurrences, we investigated if the importance of climatic and land use drivers for limiting species distributions has changed over time. Our results show that the importance of land use variables such as landscape composition and habitat fragmentation has been constantly high whereas climatic factors tended to have lower importance in setting species geographic range limits. However, climatic drivers, especially temperature, became significantly more important over time, and temperature became even as important as habitat composition during recent decades.

The non-constant importance of climatic variables (especially temperature) for limiting species distributions of Dutch bees and hoverflies over the last >60 years could be related to the observed recent increase in temperature in the study area (Fig. 1; KNMI 2014). Given the current projections of future climate change (Diez et al. 2012), these findings suggest that climate may play an even larger role for limiting species distributions in the future. For butterflies, the importance of climate was constantly high which could be explained by interactions between small-scale changes in habitat condition and climate. Many butterfly species depend on warm microclimatic conditions for larval development (WallisDeVries and Van Swaay 2006). Increases in temperature lead to milder winters, which could enhance opportunities for the development of butterflies. However, when associated with the high nitrogen deposition, such mild winters increase plant productivity, which reduces opportunities for developing caterpillars to absorb solar heat (WallisDeVries and Van Swaay 2006). Hence, the interplay between changes in climatic conditions and land use may result in counter-intuitive changes in local habitat conditions.

Within temperate regions such as the Netherlands, rapid changes in temperature and precipitation as well as increases in extreme weather events may have strong effects on population dynamics of pollinators (WallisDeVries et al. 2011, Rasmont et al. 2015). Since SDM methods assume that currently observed occurrence-climate relationships persist in the future, the variable importance of climatic variables here detected can have important implications for the interpretation of species range projections based on

SDMs. Thus, future species range projections based on SDMs alone may severely underestimate the role that climate plays in setting future species range limits. Other more trait-based or mechanistic approaches might then be appropriate for analysing future species responses to climate changes (Pacifici et al. 2015).

The relative importance of climate and land use can depend on spatial scale, i.e. extent and grain size. For instance, climate measured at coarse grid cell resolutions might mostly describe the countrywide trends in climatic conditions (Ligtvoet et al. 2013) and thus its probable impact on species distributions at broad spatial scale can be analysed. Measures of the microclimatic conditions at the patch level (fine-scale) may render further insights into the local distribution patterns of species (Suggitt et al. 2011), and thus of the climate change impacts at fine-scale, however, these measures are not readily available at the country or global levels, making it difficult to include them in large scale analysis. Landscape characteristics might, however, mostly modify species distributions locally. Our result that climatic conditions, especially temperature-related variables, become increasingly important drivers of species distributions in the study area agree with the observed physical changes in these drivers across time (Klein Tank 2004, Ligtvoet et al. 2013). We detected significant changes in the importance of climatic conditions for driving the species distributions of pollinators across the last >60 years, even at the spatial extent of the Netherlands. We expect that such effects might even be more pronounced across larger regions with stronger variation in these conditions (e.g. countries/regions that cover a broader spatial extent). However, further research is needed to test whether the temporal change in the importance of climate and land use as range-limiting factors varies at different spatial extents and grain sizes.

Like in other highly industrialized countries the major land-use changes in the Netherlands have occurred in earlier time periods (~1950). However, small changes in land use conditions have still occurred in the Netherlands during the last half-century (Fig. 1). Nevertheless, land use, especially landscape composition, remains of high importance for limiting species distributions even in recent times. This result reflects the high importance of habitat availability (here represented by landscape composition) and accessibility (here represented by habitat fragmentation and spillover) for pollinators. Indeed, climatically suitable areas might not be occupied by species if habitat conditions remain unsuitable (Oliver et al. 2012). Hence, the high importance of habitat fragmentation (i.e. habitat patch area and edge density) in our study is most likely linked to the impact that fragmentation has on pollinator's access to feeding and nesting resources, including indirect effects on microclimatic conditions in the surrounding landscape (Steffan-Dewenter 2003, Ries et al. 2004).

The effects of habitat spillover were weaker than those of landscape composition and habitat fragmentation, but they represent also accentuated changes in importance values across time periods (bees and hoverflies; Fig. 2 and Fig. 3). Highly homogeneous areas (e.g. intensive agricultural lands) are among the most common habitats in the study region. Hence, an increasing amount of edges between managed and natural systems (surrogate of spillover potential) may be becoming a major driver for the exchange of organism in the landscape between different land use classes. These findings on spillover effects are highly relevant for conservation and management of ecosystem services worldwide because landscapes dominated by large extensions of agricultural fields have become the rule in most industrialized countries (Foley et al. 2005, EEA -European Environment Agency 2010). In high-biodiversity countries with expanding agriculture/economy, the future impacts of land-use changes on biodiversity may even be more pronounced than in highly industrialized countries were major land-use changes have already ceased decades ago (Sala et al. 2000).

Our historical analysis supports the view that land use drivers (especially landscape composition and habitat fragmentation) have been most important in limiting pollinator distributions across time (Oliver et al. 2012, Warren et al. 2001). However, we also show that climate drivers, particularly temperature, have currently reached a similar importance than landscape composition in limiting species distributions (see Fig. 2 and Fig. 3). This suggests that ongoing and future climate change could overpass the impacts of land use modifications on biodiversity (Leadley et al. 2010). This change in the importance of drivers is likely related to the fact that in our study region most major land-use changes have already ceased several decades ago (e.g. Bouma et al. 1998, Knol et al. 2004). In contrast, changes in climatic conditions such as increases in annual temperatures and a higher frequency of extreme weather events have occurred during recent decades (Hansen et al. 2012). Hence, our results are most likely transferable to other highly industrialized countries in temperate regions.

Concluding remarks

Projections of the potential future impacts of climate and land-use changes on biodiversity often assume that the importance of drivers for limiting species distributions remains constant over time (Dormann 2007). However, our historical analysis shows that the importance of environmental drivers can vary substantially. More specifically, we show that the importance of temperature has strongly increased in recent time periods, which raises concerns over the use of SDMs fitted with current environmental predictors to project future species distributions under climate change. Given the current and projected rapid changes in temperature and other climate conditions in the near future (Rogelj et al. 2012), the effect of climate is likely to equal or overpass the effects of changes in land use conditions (see Leadley et al. 2010), especially in regions where large-scale land-use changes have mostly ceased. A more in depth exploration of the (non-)constancy of climate versus land use for limiting species distributions requires further testing, e.g. with historical data for other taxa or in other areas such as tropical and arctic regions. This would help to disentangle whether and to what extent the results found in this study can be extended to other taxonomic and functional groups and biomes.

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Supplementary material

Table S1 (next page) Species list for the three focal pollinator groups. The number of records available in each of three time periods (TP1, TP2, TP3) is provided.

Group	Species name	Number of presence records*		
		TP 1	TP2	TP3
Bees	*Andrena angustior*	53	51	72
Bees	*Andrena apicata*	30	27	29
Bees	*Andrena argentata*	28	17	19
Bees	*Andrena barbilabris*	136	157	249
Bees	*Andrena bicolor*	30	45	169
Bees	*Andrena bimaculata*	13	9	28
Bees	*Andrena carantonica*	91	104	241
Bees	*Andrena cineraria*	47	54	151
Bees	*Andrena clarkella*	47	87	146
Bees	*Andrena chrysosceles*	36	50	185
Bees	*Andrena dorsata*	37	33	167
Bees	*Andrena falsifica*	10	13	6
Bees	*Andrena flavipes*	74	85	381
Bees	*Andrena florea*	23	26	81
Bees	*Andrena fucata*	43	77	80
Bees	*Andrena fulvida*	21	12	23
Bees	*Andrena fulvago*	12	9	17
Bees	*Andrena fuscipes*	120	89	132
Bees	*Andrena fulva*	81	123	268
Bees	*Andrena gravida*	36	19	57
Bees	*Andrena haemorrhoa*	118	190	442
Bees	*Andrena hattorfiana*	26	15	22
Bees	*Andrena helvola*	13	21	58
Bees	*Andrena humilis*	39	34	40
Bees	*Andrena labialis*	26	17	49
Bees	*Andrena lapponica*	29	25	38
Bees	*Andrena labiata*	22	26	66
Bees	*Andrena lathyri*	9	8	12
Bees	*Andrena minutula*	42	79	117
Bees	*Andrena minutuloides*	6	11	13
Bees	*Andrena mitis*	19	28	46
Bees	*Andrena nigriceps*	23	18	23
Bees	*Andrena nigroaenea*	75	93	127
Bees	*Andrena nitida*	77	71	219
Bees	*Andrena ovatula*	56	37	71
Bees	*Andrena pilipes*	39	15	13
Bees	*Andrena praecox*	64	79	157
Bees	*Andrena proxima*	15	13	88
Bees	*Andrena ruficrus*	40	35	35
Bees	*Andrena semilaevis*	31	29	29
Bees	*Andrena subopaca*	79	134	219
Bees	*Andrena synadelpha*	7	23	40
Bees	*Andrena tibialis*	55	37	95
Bees	*Andrena vaga*	41	40	245
Bees	*Andrena varians*	53	54	36

Bees	*Andrena ventralis*	21	31	119
Bees	*Andrena wilkella*	51	53	78
Bees	*Anthidium manicatum*	31	43	171
Bees	*Anthidium punctatum*	12	14	25
Bees	*Anthidium strigatum*	22	24	81
Bees	*Anthophora furcata*	23	24	46
Bees	*Anthophora plumipes*	39	49	151
Bees	*Anthophora quadrimaculata*	15	21	20
Bees	*Anthophora retusa*	22	12	12
Bees	*Bombus bohemicus*	70	56	90
Bees	*Bombus campestris*	90	37	196
Bees	*Bombus cryptarum*	20	11	16
Bees	*Bombus hortorum*	76	62	232
Bees	*Bombus humilis*	33	7	10
Bees	*Bombus hypnorum*	46	50	295
Bees	*Bombus jonellus*	35	22	93
Bees	*Bombus lapidarius*	115	53	511
Bees	*Bombus lucorum*	82	67	305
Bees	*Bombus magnus*	30	18	46
Bees	*Bombus muscorum*	66	14	38
Bees	*Bombus norvegicus*	20	21	26
Bees	*Bombus pascuorum*	165	108	657
Bees	*Bombus pratorum*	89	83	436
Bees	*Bombus ruderarius*	57	10	89
Bees	*Bombus sylvestris*	62	81	170
Bees	*Bombus terrestris*	97	85	490
Bees	*Bombus vestalis*	36	25	115
Bees	*Bombus veteranus*	44	7	6
Bees	*Ceratina cyanea*	12	13	18
Bees	*Chelostoma campanularum*	36	44	53
Bees	*Chelostoma distinctum*	19	10	6
Bees	*Chelostoma florisomne*	50	43	76
Bees	*Chelostoma rapunculi*	55	55	106
Bees	*Coelioxys elongata*	10	6	11
Bees	*Coelioxys inermis*	30	25	52
Bees	*Coelioxys mandibularis*	29	22	46
Bees	*Coelioxys quadridentata*	23	15	11
Bees	*Colletes cunicularius*	42	52	188
Bees	*Colletes daviesanus*	72	84	193
Bees	*Colletes fodiens*	31	62	142
Bees	*Colletes halophilus*	7	16	57
Bees	*Colletes impunctatus*	5	8	5
Bees	*Colletes marginatus*	16	30	35
Bees	*Colletes succinctus*	46	58	100
Bees	*Dasypoda hirtipes*	89	78	277
Bees	*Epeoloides coecutiens*	14	8	82
Bees	*Epeolus cruciger*	44	44	129
Bees	*Epeolus variegatus*	18	30	117

Table S1 (*continued*)

Bees	*Eucera longicornis*	25	14	8
Bees	*Halictus confusus*	61	64	111
Bees	*Halictus rubicundus*	102	138	204
Bees	*Halictus tumulorum*	73	126	290
Bees	*Heriades truncorum*	61	60	135
Bees	*Hylaeus annularis*	44	52	58
Bees	*Hylaeus brevicornis*	61	84	76
Bees	*Hylaeus communis*	92	169	236
Bees	*Hylaeus confusus*	65	134	166
Bees	*Hylaeus gibbus*	63	89	83
Bees	*Hylaeus hyalinatus*	64	135	142
Bees	*Hylaeus pectoralis*	17	25	21
Bees	*Hylaeus pictipes*	20	35	24
Bees	*Hylaeus punctulatissimus*	10	12	17
Bees	*Hylaeus rinki*	12	11	13
Bees	*Hylaeus signatus*	22	69	60
Bees	*Lasioglossum albipes*	91	83	91
Bees	*Lasioglossum brevicorne*	19	14	18
Bees	*Lasioglossum calceatum*	179	206	394
Bees	*Lasioglossum fratellum*	8	20	18
Bees	*Lasioglossum fulvicorne*	51	53	67
Bees	*Lasioglossum laticeps*	14	25	32
Bees	*Lasioglossum lativentre*	25	7	12
Bees	*Lasioglossum leucopus*	62	91	130
Bees	*Lasioglossum leucozonium*	138	176	313
Bees	*Lasioglossum lucidulum*	21	32	77
Bees	*Lasioglossum malachurum*	22	24	41
Bees	*Lasioglossum morio*	37	65	206
Bees	*Lasioglossum minutissimum*	24	51	80
Bees	*Lasioglossum nitidiusculum*	30	17	8
Bees	*Lasioglossum nitidulum*	20	24	33
Bees	*Lasioglossum parvulum*	28	32	19
Bees	*Lasioglossum pauxillum*	17	28	74
Bees	*Lasioglossum prasinum*	49	61	28
Bees	*Lasioglossum punctatissimum*	81	80	103
Bees	*Lasioglossum quadrinotatum*	13	7	12
Bees	*Lasioglossum quadrinotatulum*	47	45	46
Bees	*Lasioglossum rufitarse*	49	48	12
Bees	*Lasioglossum sabulosum*	14	24	49
Bees	*Lasioglossum semilucens*	27	28	56
Bees	*Lasioglossum sexstrigatum*	132	166	226
Bees	*Lasioglossum sexnotatum*	40	21	87
Bees	*Lasioglossum tarsatum*	21	15	15
Bees	*Lasioglossum villosulum*	103	153	176
Bees	*Lasioglossum xanthopus*	17	10	26
Bees	*Lasioglossum zonulum*	75	86	132
Bees	*Macropis europaea*	61	133	196
Bees	*Megachile analis*	5	13	10

Table S1 (*continued*)

Bees	*Megachile centuncularis*	74	75	173	Bees	*Nomada goodeniana*	52	63	140
Bees	*Megachile circumcincta*	48	27	27	Bees	*Nomada integra*	23	6	10
Bees	*Megachile ericetorum*	21	19	83	Bees	*Nomada lathburiana*	47	37	181
Bees	*Megachile lapponica*	43	55	25	Bees	*Nomada leucophthalma*	25	34	72
Bees	*Megachile leachella*	39	32	57	Bees	*Nomada marshamella*	62	91	159
Bees	*Megachile ligniseca*	16	7	46	Bees	*Nomada obscura*	5	5	6
Bees	*Megachile maritima*	29	16	20	Bees	*Nomada panzeri*	59	99	124
Bees	*Megachile versicolor*	34	44	105	Bees	*Nomada ruficornis*	85	127	248
Bees	*Megachile willughbiella*	49	67	226	Bees	*Nomada rufipes*	137	126	138
Bees	*Melecta albifrons*	22	18	38	Bees	*Nomada sheppardana*	66	108	154
Bees	*Melitta haemorrhoidalis*	32	35	63	Bees	*Nomada signata*	49	59	98
Bees	*Melitta leporina*	21	25	67	Bees	*Nomada similis*	15	17	19
Bees	*Melitta nigricans*	15	10	72	Bees	*Nomada striata*	39	16	38
Bees	*Melitta tricincta*	12	8	19	Bees	*Nomada succincta*	76	84	145
Bees	*Nomada alboguttata*	69	97	167	Bees	*Osmia aurulenta*	10	8	16
Bees	*Nomada bifasciata*	27	12	31	Bees	*Osmia caerulescens*	52	46	65
Bees	*Nomada fabriciana*	44	56	148	Bees	*Osmia claviventris*	28	32	40
Bees	*Nomada ferruginata*	20	30	88	Bees	*Osmia cornuta*	27	34	66
Bees	*Nomada flavoguttata*	49	82	156	Bees	*Osmia leaiana*	19	18	15
Bees	*Nomada flavopicta*	31	32	67	Bees	*Osmia leucomelana*	28	21	45
Bees	*Nomada flava*	115	150	272	Bees	*Osmia niveata*	36	22	28
Bees	*Nomada fucata*	36	41	160	Bees	*Osmia rufa*	81	129	337
Bees	*Nomada fulvicornis*	45	20	48	Bees	*Osmia uncinata*	6	10	34
Bees	*Nomada fuscicornis*	24	8	23	Bees	*Panurgus banksianus*	64	77	72

Table S1 (*continued*)

Bees	*Panurgus calcaratus*	68	71	147
Bees	*Sphecodes albilabris*	21	24	174
Bees	*Sphecodes crassus*	37	44	114
Bees	*Sphecodes ephippius*	53	51	120
Bees	*Sphecodes ferruginatus*	12	9	11
Bees	*Sphecodes geoffrellus*	41	82	92
Bees	*Sphecodes gibbus*	46	60	107
Bees	*Sphecodes hyalinatus*	12	8	7
Bees	*Sphecodes longulus*	29	59	94
Bees	*Sphecodes marginatus*	25	35	52
Bees	*Sphecodes miniatus*	39	88	142
Bees	*Sphecodes monilicornis*	95	106	234
Bees	*Sphecodes pellucidus*	63	98	184
Bees	*Sphecodes puncticeps*	33	48	67
Bees	*Sphecodes reticulatus*	25	46	97
Bees	*Sphecodes rubicundus*	7	5	30
Bees	*Stelis breviuscula*	25	18	27
Bees	*Stelis ornatula*	19	11	11
Butterflies	*Aglais urticae*	237	1171	1518
Butterflies	*Anthocharis cardamines*	174	620	1226
Butterflies	*Apatura iris*	19	49	58
Butterflies	*Aphantopus hyperantus*	182	551	845
Butterflies	*Araschnia levana*	240	825	1340
Butterflies	*Argynnis aglaja*	51	38	44
Butterflies	*Argynnis niobe*	54	48	53
Butterflies	*Argynnis paphia*	46	36	95
Butterflies	*Boloria aquilonaris*	9	14	10
Butterflies	*Boloria selene*	125	99	61
Butterflies	*Callophrys rubi*	154	287	421
Butterflies	*Carterocephalus palaemon*	46	69	116
Butterflies	*Celastrina argiolus*	239	737	1418
Butterflies	*Coenonympha pamphilus*	319	1090	1058
Butterflies	*Coenonympha tullia*	66	56	12
Butterflies	*Colias croceus*	268	168	864
Butterflies	*Colias hyale*	188	162	401
Butterflies	*Cupido minimus*	5	6	5
Butterflies	*Erynnis tages*	26	5	8
Butterflies	*Gonepteryx rhamni*	238	982	1389
Butterflies	*Hesperia comma*	106	132	116
Butterflies	*Heteropterus morpheus*	10	27	26
Butterflies	*Hipparchia semele*	195	368	347
Butterflies	*Hipparchia statilinus*	8	10	8
Butterflies	*Inachis io*	206	1136	1552
Butterflies	*Issoria lathonia*	195	123	299
Butterflies	*Lasiommata megera*	250	1048	1346
Butterflies	*Leptidea sinapis*	17	7	30
Butterflies	*Limenitis camilla*	83	141	109
Butterflies	*Lycaena dispar*	24	24	18

Table S1 (*continued*)

Table S1 (*continued*)

Butterflies	*Lycaena phlaeas*	309	953	1380
Butterflies	*Lycaena tityrus*	166	254	263
Butterflies	*Maculinea alcon*	93	137	100
Butterflies	*Maniola jurtina*	296	869	1356
Butterflies	*Melanargia galathea*	14	18	11
Butterflies	*Melitaea athalia*	49	21	24
Butterflies	*Neozephyrus quercus*	128	377	686
Butterflies	*Nymphalis antiopa*	61	38	374
Butterflies	*Nymphalis polychloros*	64	68	43
Butterflies	*Ochlodes faunus*	224	636	927
Butterflies	*Papilio machaon*	129	181	882
Butterflies	*Pararge aegeria*	183	559	1433
Butterflies	*Pieris brassicae*	223	1038	1524
Butterflies	*Pieris napi*	249	1067	1542
Butterflies	*Pieris rapae*	255	1179	1555
Butterflies	*Plebeius agestis*	121	201	532
Butterflies	*Plebeius argus*	164	246	333
Butterflies	*Plebeius optilete*	7	11	5
Butterflies	*Polygonia c-album*	166	451	1444
Butterflies	*Polyommatus coridon*	28	7	6
Butterflies	*Polyommatus icarus*	261	855	1359
Butterflies	*Polyommatus semiargus*	19	8	10
Butterflies	*Pontia daplidice*	36	10	48
Butterflies	*Pyrgus malvae*	86	72	64
Butterflies	*Pyronia tithonus*	177	498	823
Butterflies	*Satyrium ilicis*	114	145	108
Butterflies	*Thecla betulae*	41	49	77
Butterflies	*Thymelicus lineola*	179	672	1316
Butterflies	*Thymelicus sylvestris*	125	395	551
Butterflies	*Vanessa atalanta*	342	1089	1558
Butterflies	*Vanessa cardui*	265	864	1539
Hoverflies	*Anasimyia contracta*	20	50	43
Hoverflies	*Anasimyia interpuncta*	45	110	175
Hoverflies	*Anasimyia lineata*	148	296	312
Hoverflies	*Anasimyia transfuga*	53	98	101
Hoverflies	*Baccha elongata*	98	190	269
Hoverflies	*Brachyopa insensilis*	5	13	10
Hoverflies	*Brachyopa pilosa*	12	43	70
Hoverflies	*Brachyopa scutellaris*	22	64	64
Hoverflies	*Brachypalpoides lentus*	25	94	134
Hoverflies	*Brachypalpus laphriformis*	7	28	54
Hoverflies	*Ceriana conopsoides*	11	14	49
Hoverflies	*Chalcosyrphus nemorum*	32	114	223
Hoverflies	*Chamaesyrphus lusitanicus*	8	8	8
Hoverflies	*Cheilosia albipila*	30	144	189
Hoverflies	*Cheilosia ranunculi*	147	375	586
Hoverflies	*Cheilosia barbata*	13	11	7
Hoverflies	*Cheilosia bergenstammi*	37	60	183

Hoverflies	*Cheilosia canicularis*	6	13	24
Hoverflies	*Cheilosia carbonaria*	10	22	36
Hoverflies	*Cheilosia chrysocoma*	14	26	39
Hoverflies	*Cheilosia cynocephala*	11	53	56
Hoverflies	*Cheilosia fraterna*	46	64	111
Hoverflies	*Cheilosia grossa*	24	68	85
Hoverflies	*Cheilosia illustrata*	19	28	324
Hoverflies	*Cheilosia impressa*	61	102	208
Hoverflies	*Cheilosia latifrons*	32	81	44
Hoverflies	*Cheilosia lenis*	6	17	9
Hoverflies	*Cheilosia longula*	26	24	19
Hoverflies	*Cheilosia mutabilis*	28	22	27
Hoverflies	*Cheilosia pagana*	154	329	679
Hoverflies	*Cheilosia proxima*	19	48	130
Hoverflies	*Cheilosia scutellata*	63	47	83
Hoverflies	*Cheilosia semifasciata*	12	35	65
Hoverflies	*Cheilosia urbana*	29	37	33
Hoverflies	*Cheilosia uviformis*	19	27	14
Hoverflies	*Cheilosia variabilis*	45	124	199
Hoverflies	*Cheilosia velutina*	14	33	24
Hoverflies	*Cheilosia vernalis*	94	146	209
Hoverflies	*Chrysogaster cemiteriorum*	22	12	14
Hoverflies	*Chrysogaster solstitialis*	29	84	152
Hoverflies	*Chrysogaster virescens*	7	11	37
Hoverflies	*Chrysotoxum arcuatum*	33	82	36
Hoverflies	*Chrysotoxum bicinctum*	66	179	209
Hoverflies	*Chrysotoxum cautum*	70	185	261
Hoverflies	*Chrysotoxum festivum*	56	123	108
Hoverflies	*Chrysotoxum octomaculatum*	19	23	6
Hoverflies	*Chrysotoxum vernale*	55	96	63
Hoverflies	*Chrysotoxum verralli*	6	13	22
Hoverflies	*Criorhina asilica*	17	32	25
Hoverflies	*Criorhina berberina*	46	123	200
Hoverflies	*Criorhina floccosa*	6	17	51
Hoverflies	*Criorhina pachymera*	5	14	32
Hoverflies	*Criorhina ranunculi*	5	9	19
Hoverflies	*Dasysyrphus albostriatus*	112	245	344
Hoverflies	*Dasysyrphus hilaris*	55	127	31
Hoverflies	*Dasysyrphus pauxillus*	5	17	15
Hoverflies	*Dasysyrphus pinastri*	29	94	22
Hoverflies	*Dasysyrphus tricinctus*	106	169	204
Hoverflies	*Dasysyrphus venustus*	89	227	255
Hoverflies	*Didea alneti*	11	38	34
Hoverflies	*Didea fasciata*	51	144	173
Hoverflies	*Didea intermedia*	35	76	89
Hoverflies	*Epistrophe eligans*	80	239	370
Hoverflies	*Epistrophe flava*	10	47	16
Hoverflies	*Epistrophe grossulariae*	40	142	130

Table S1 (*continued*)

Table S1 (*continued*)

Hoverflies	*Epistrophe nitidicollis*	72	219	243
Hoverflies	*Episyrphus balteatus*	260	559	1173
Hoverflies	*Eristalinus aeneus*	30	63	99
Hoverflies	*Eristalinus sepulchralis*	201	516	726
Hoverflies	*Eriozona syrphoides*	8	8	7
Hoverflies	*Eristalis abusiva*	139	342	443
Hoverflies	*Eristalis anthophorina*	28	46	20
Hoverflies	*Eristalis arbustorum*	315	600	994
Hoverflies	*Eristalis horticola*	142	363	687
Hoverflies	*Eristalis intricaria*	248	496	655
Hoverflies	*Eristalis nemorum*	208	394	872
Hoverflies	*Eristalis pertinax*	199	554	1073
Hoverflies	*Eristalis similis*	22	54	74
Hoverflies	*Eristalis tenax*	217	498	1135
Hoverflies	*Eumerus funeralis*	34	99	101
Hoverflies	*Eumerus ornatus*	11	9	8
Hoverflies	*Eumerus sogdianus*	15	28	18
Hoverflies	*Eumerus strigatus*	71	164	185
Hoverflies	*Eupeodes goeldlini*	12	41	24
Hoverflies	*Eupeodes corollae*	254	445	816
Hoverflies	*Eupeodes latifasciatus*	66	180	301
Hoverflies	*Eupeodes lapponicus*	21	79	79
Hoverflies	*Eupeodes luniger*	70	204	387
Hoverflies	*Eupeodes nielseni*	5	19	21
Hoverflies	*Ferdinandea cuprea*	37	116	175
Hoverflies	*Helophilus hybridus*	80	243	370
Hoverflies	*Helophilus pendulus*	321	690	1123
Hoverflies	*Helophilus trivittatus*	202	463	959
Hoverflies	*Heringia heringi*	17	44	36
Hoverflies	*Lejogaster metallina*	149	270	288
Hoverflies	*Lejogaster tarsata*	39	93	75
Hoverflies	*Leucozona laternaria*	31	43	16
Hoverflies	*Leucozona lucorum*	33	53	80
Hoverflies	*Lejops vittata*	11	9	7
Hoverflies	*Megasyrphus erratica*	18	78	58
Hoverflies	*Melanostoma mellinum*	310	604	993
Hoverflies	*Melanostoma scalare*	134	346	702
Hoverflies	*Melangyna cincta*	52	161	207
Hoverflies	*Melangyna lasiophthalma*	18	75	70
Hoverflies	*Melangyna quadrimaculata*	12	37	18
Hoverflies	*Melangyna umbellatarum*	41	95	121
Hoverflies	*Meligramma guttata*	29	57	54
Hoverflies	*Meligramma triangulifera*	27	102	77
Hoverflies	*Merodon equestris*	63	258	307
Hoverflies	*Microdon analis*	12	34	52
Hoverflies	*Microdon devius*	5	5	5
Hoverflies	*Melanogaster aerosa*	12	19	13
Hoverflies	*Melanogaster hirtella*	136	297	454

Hoverflies	*Melanogaster nuda*	43	112	97
Hoverflies	*Meliscaeva auricollis*	99	176	307
Hoverflies	*Meliscaeva cinctella*	99	176	147
Hoverflies	*Myathropa florea*	165	488	978
Hoverflies	*Heringia brevidens*	5	32	15
Hoverflies	*Heringia pubescens*	19	64	24
Hoverflies	*Heringia vitripennis*	71	103	49
Hoverflies	*Neoascia geniculata*	42	61	26
Hoverflies	*Neoascia interrupta*	10	50	32
Hoverflies	*Neoascia meticulosa*	32	100	113
Hoverflies	*Neoascia obliqua*	5	18	45
Hoverflies	*Neoascia podagrica*	249	430	502
Hoverflies	*Neoascia tenur*	72	226	269
Hoverflies	*Orthonevra brevicornis*	10	27	26
Hoverflies	*Orthonevra geniculata*	7	21	19
Hoverflies	*Orthonevra intermedia*	8	23	40
Hoverflies	*Orthonevra nobilis*	14	10	11
Hoverflies	*Parhelophilus consimilis*	10	15	11
Hoverflies	*Parhelophilus frutetorum*	28	71	134
Hoverflies	*Parhelophilus versicolor*	67	148	225
Hoverflies	*Paragus haemorrhous*	34	111	215
Hoverflies	*Paragus pecchiolii*	6	6	18
Hoverflies	*Parasyrphus annulatus*	9	64	52
Hoverflies	*Parasyrphus lineolus*	34	106	31
Hoverflies	*Parasyrphus malinellus*	27	58	35
Hoverflies	*Parasyrphus punctulatus*	81	160	160
Hoverflies	*Parasyrphus vittiger*	60	67	10
Hoverflies	*Pelecocera tricincta*	13	16	39
Hoverflies	*Pipizella viduata*	95	160	272
Hoverflies	*Pipizella virens*	8	11	7
Hoverflies	*Pipiza austriaca*	35	37	14
Hoverflies	*Pipiza bimaculata*	34	115	121
Hoverflies	*Pipiza fenestrata*	24	24	12
Hoverflies	*Pipiza lugubris*	19	40	68
Hoverflies	*Pipiza luteitarsis*	15	33	18
Hoverflies	*Pipiza noctiluca*	57	123	176
Hoverflies	*Pipiza quadrimaculata*	22	50	6
Hoverflies	*Platycheirus albimanus*	194	394	726
Hoverflies	*Platycheirus ambiguus*	12	15	9
Hoverflies	*Platycheirus angustatus*	117	228	319
Hoverflies	*Platycheirus clypeatus*	244	509	670
Hoverflies	*Platycheirus discimanus*	8	10	6
Hoverflies	*Platycheirus fulviventris*	81	213	148
Hoverflies	*Platycheirus immarginatus*	14	30	13
Hoverflies	*Platycheirus manicatus*	68	89	60
Hoverflies	*Platycheirus peltatus*	223	365	329
Hoverflies	*Platycheirus scambus*	151	292	202
Hoverflies	*Platycheirus scutatus*	172	321	412

Table S1 (*continued*)

Hoverflies	*Pyrophaena granditarsa*	156	262	295
Hoverflies	*Pyrophaena rosarum*	48	65	178
Hoverflies	*Rhingia campestris*	235	516	814
Hoverflies	*Riponnensia splendens*	5	8	12
Hoverflies	*Scaeva pyrastri*	177	282	505
Hoverflies	*Scaeva selenitica*	69	235	416
Hoverflies	*Sericomyia lappona*	6	13	13
Hoverflies	*Sericomyia silentis*	61	77	258
Hoverflies	*Sphaerophoria batava*	37	114	149
Hoverflies	*Sphaerophoria fatarum*	23	38	15
Hoverflies	*Sphaerophoria interrupta*	21	18	37
Hoverflies	*Sphaerophoria philanthus*	17	38	40
Hoverflies	*Sphaerophoria rueppelli*	27	71	105
Hoverflies	*Sphaerophoria scripta*	189	434	931
Hoverflies	*Sphaerophoria taeniata*	26	33	46
Hoverflies	*Sphaerophoria virgata*	6	39	18
Hoverflies	*Sphegina clunipes*	30	47	61
Hoverflies	*Sphegina elegans*	15	21	24
Hoverflies	*Syritta pipiens*	277	567	1028
Hoverflies	*Syrphus ribesii*	231	523	866
Hoverflies	*Syrphus torvus*	163	317	449
Hoverflies	*Syrphus vitripennis*	239	410	596
Hoverflies	*Temnostoma bombylans*	13	35	130
Hoverflies	*Temnostoma vespiforme*	14	36	78
Hoverflies	*Triglyphus primus*	17	33	24
Hoverflies	*Trichopsomyia flavitarsis*	11	29	21
Hoverflies	*Trichopsomyia lucida*	8	21	14
Hoverflies	*Tropidia scita*	122	295	464
Hoverflies	*Volucella bombylans*	131	212	461
Hoverflies	*Volucella pellucens*	109	261	514
Hoverflies	*Volucella zonaria*	12	49	374
Hoverflies	*Xanthogramma citrofasciatum*	14	17	25
Hoverflies	*Xanthogramma pedissequum*	39	106	258
Hoverflies	*Xanthandrus comtus*	33	53	120
Hoverflies	*Xylota abiens*	24	24	24
Hoverflies	*Xylota florum*	36	37	8
Hoverflies	*Xylota meigeniana*	7	16	6
Hoverflies	*Xylota segnis*	153	346	700
Hoverflies	*Xylota sylvarum*	57	136	221
Hoverflies	*Xylota tarda*	18	36	34
Hoverflies	*Xylota xanthocnema*	10	31	31

*The number of presence records represents the number of 5 x 5 km grid cells for which the species was reported at least once during the period analysed.

Table S1 (*continued*)

Environmental variable	Average value			Standard deviation			TP1 vs	P-value	TP2 vs	P-value	TP1 vs	P-value
	P1	P2	P3	P1	P2	P3	*t*		*t*		*t*	
Mean diurnal range	7.05	7.09	7.25	0.67	0.71	0.75	1.81	0.06	6.06	<0.001	8.02	<0.001
Temperature seasonality	5.79	5.54	5.66	0.13	0.12	0.14	-56.09	<0.001	26.81	<0.001	-27.66	<0.001
Mean temp. of wettest quarter	15.45	8.99	15.85	0.68	4.24	2.06	-61.58	<0.001	59.57	<0.001	7.54	<0.001
Mean temp. of driest quarter	5.79	5.27	9.60	1.78	1.50	1.97	-9.06	<0.001	71.55	<0.001	58.76	<0.001
Mean temp. of warmest quarter	15.92	16.14	17.16	0.36	0.49	0.45	14.66	<0.001	63.11	<0.001	88.32	<0.001
Annual precipitation	803.90	753.74	828.20	25.14	16.93	21.82	-67.66	<0.001	110.24	<0.001	29.84	<0.001
Precipitation of wettest month	102.28	78.40	91.18	5.96	4.53	4.86	-130.5	<0.001	78.64	<0.001	-59.09	<0.001
Precipitation of driest month	44.84	41.54	41.13	2.91	2.62	3.45	-34.5	<0.001	-3.87	<0.001	-33.65	<0.001
Precipitation of warmest quarter	253.40	198.85	238.78	11.70	11.69	11.48	-	<0.001	99.67	<0.001	-36.46	<0.001
Average patch area of suitable habitat	104.97	76.32	16.61	354.79	210.36	113.3	-2.76	<0.01	9.94	<0.001	-9.43	<0.001
Total edge density	0.019	0.018	0.023	0.008	0.007	0.011	-3.92	<0.001	15.95	<0.001	11.73	<0.001
Edge density managed-natural systems	0.007	0.008	0.011	0.004	0.003	0.005	4.27	<0.001	15.29	<0.001	18.37	<0.001
Number of land use classes	6.28	6.42	7.72	1.21	0.95	0.75	3.69	<0.001	42.87	<0.001	40.36	<0.001
Grassland	42.23	43.16	40.00	26.26	25.90	20.35	1	0.31	-3.82	<0.001	-2.67	<0.01
Agriculture	31.41	27.82	27.46	25.01	24.99	22.31	-4.03	<0.001	-0.42	0.66	-4.68	<0.001
Moors/peat	2.04	1.38	1.34	6.32	5.07	4.68	-3.23	<0.01	-0.23	0.81	-3.53	<0.001
Forest	8.53	10.14	11.14	13.92	14.42	14.23	3.19	<0.01	1.95	0.05	5.2	<0.001
Urban	6.94	10.22	10.90	7.69	10.87	10.13	9.82	<0.001	1.8	0.07	12.39	<0.001
Water	6.97	5.47	6.42	15.46	10.24	10.70	-3.22	<0.01	2.56	0.01	-1.16	0.25
Swamps	0.20	0.16	1.43	0.70	0.44	5.80	-1.88	0.05	8.67	<0.001	8.37	<0.001

Table S2. Changes in environmental conditions related to climate and land use across the Netherlands. Comparisons were carried with a Student t-tests for changes between time period TP1 and TP2 and time period T2 and TP3.

Environmental	Group	Period	Estimate	z-value	P-value
Climate	B	P2	0.71	18.22	<0.01
Climate	B	P3	0.74	19.00	<0.01
Climate	B	P4	0.88	22.76	<0.01
Climate	BU	P2	0.87	12.27	<0.01
Climate	BU	P3	0.70	9.79	<0.01
Climate	BU	P4	0.68	9.55	<0.01
Climate	H	P2	0.65	16.47	<0.01
Climate	H	P3	0.71	18.14	<0.01
Climate	H	P4	0.71	18.01	<0.01
Land use	B	P2	1.05	29.56	<0.01
Land use	B	P3	1.04	29.43	<0.01
Land use	B	P4	1.05	29.58	<0.01
Land use	BU	P2	1.16	17.80	<0.01
Land use	BU	P3	1.03	15.86	<0.01
Land use	BU	P4	0.96	14.78	<0.01
Land use	H	P2	0.95	26.52	<0.01
Land use	H	P3	1.15	32.03	<0.01
Land use	H	P4	1.10	30.78	<0.01
Climate vs Land use	B	P2	-0.34	-8.40	<0.01
Climate vs Land use	B	P3	-0.30	-7.47	<0.01
Climate vs Land use	B	P4	-0.17	-4.16	<0.01
Climate vs Land use	BU	P2	-0.29	-3.86	<0.01
Climate vs Land use	BU	P3	-0.34	-4.53	<0.01
Climate vs Land use	BU	P4	-0.28	-3.82	<0.01
Climate vs Land use	H	P3	-0.44	-10.66	<0.01
Climate vs Land use	H	P4	-0.40	-9.70	<0.01
Climate	B vs H	P2	0.06	1.03	1.00
Climate	H vs BU	P2	-0.22	-2.76	0.18
Climate	B vs BU	P2	-0.17	-2.07	0.67
Climate	B vs H	P3	0.03	0.51	1.00
Climate	H vs BU	P3	0.01	0.16	1.00
Climate	B vs BU	P3	0.04	0.51	1.00
Climate	B vs H	P4	0.17	3.17	0.06
Climate	H vs BU	P4	0.03	0.32	1.00
Climate	B vs BU	P4	0.20	2.47	0.35
Land use	B vs H	P2	0.09	1.87	0.81
Land use	H vs BU	P2	-0.21	-2.80	0.16
Land use	B vs BU	P2	-0.11	-1.54	0.96
Land use	B vs H	P3	-0.10	-2.08	0.66
Land use	H vs BU	P3	0.11	1.51	0.97
Land use	B vs BU	P3	0.01	0.10	1.00
Land use	B vs H	P4	-0.06	-1.10	1.00
Land use	H vs BU	P4	0.14	1.86	0.82
Land use	B vs BU	P4	0.08	1.12	1.00
Climate	B	P1 vs P3	-0.17	-4.01	<0.01
Climate	BU	P1 vs P3	0.19	2.43	0.38
Climate	H	P1 vs P3	-0.06	-1.28	0.99
land use	B	P1 vs P3	0.00	-0.04	1.00
land use	BU	P1 vs P3	0.20	2.85	0.15

Table S3. Multiple comparison analysis (Tukey HSD test) of the strength of the effect of an environmental variable (general Gaussian model) for driving the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the "percentage contribution" variable importance values. For this "general model" the first 18 rows show whether climate or land use have an effect on the species distributions of different pollinator groups. The next nine rows present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following 18 rows present the results of comparisons between different pollinator groups for each climate or land use variable. The last six rows present the results for the comparisons between the first and last period of the analysis for each variable and pollinator group. Adjusted Tukey's P-values are reported.

Environmental variables	Group	Period	Estimat	z-value	P-value
Composition	B	P2	1.14	29.73	<0.01
Composition	B	P3	1.18	30.74	<0.01
Composition	B	P4	1.16	30.25	<0.01
Composition	BU	P2	1.21	17.10	<0.01
Composition	BU	P3	1.12	15.87	<0.01
Composition	BU	P4	1.05	14.92	<0.01
Composition	H	P2	1.06	27.30	<0.01
Composition	H	P3	1.23	31.86	<0.01
Composition	H	P4	1.17	30.29	<0.01
Fragmentation	B	P2	0.95	13.94	<0.01
Fragmentation	B	P3	1.09	15.92	<0.01
Fragmentation	B	P4	0.79	11.64	<0.01
Fragmentation	BU	P2	0.97	7.72	<0.01
Fragmentation	BU	P3	0.84	6.67	<0.01
Fragmentation	BU	P4	0.74	5.89	<0.01
Fragmentation	H	P2	0.83	11.99	<0.01
Fragmentation	H	P3	0.89	12.93	<0.01
Fragmentation	H	P4	0.94	13.63	<0.01
Precipitation	B	P2	0.59	11.61	<0.01
Precipitation	B	P3	0.76	14.79	<0.01
Precipitation	B	P4	0.43	8.43	<0.01
Precipitation	BU	P2	0.62	6.54	<0.01
Precipitation	BU	P3	0.47	5.00	<0.01
Precipitation	BU	P4	0.42	4.44	<0.01
Precipitation	H	P2	0.76	14.58	<0.01
Precipitation	H	P4	0.31	5.96	<0.01
Spillover	B	P2	0.41	4.42	<0.01
Spillover	B	P3	-0.31	-3.23	0.17
Spillover	B	P4	0.55	5.85	<0.01
Spillover	BU	P2	1.14	6.55	<0.01
Spillover	BU	P3	0.65	3.81	0.02
Spillover	BU	P4	0.60	3.45	0.09
Spillover	H	P2	0.20	2.05	0.98
Spillover	H	P3	0.87	9.21	<0.01
Spillover	H	P4	0.78	8.22	<0.01
Temperature	B	P2	0.80	16.88	<0.01
Temperature	B	P3	0.72	15.24	<0.01
Temperature	B	P4	1.23	26.32	<0.01
Temperature	BU	P2	1.08	12.47	<0.01
Temperature	BU	P3	0.88	10.15	<0.01
Temperature	BU	P4	0.89	10.27	<0.01
Temperature	H	P2	0.56	11.65	<0.01
Temperature	H	P3	0.69	14.51	<0.01
Temperature	H	P4	1.02	21.41	<0.01
Composition vs	B	P2	0.19	2.73	0.55
Composition vs	B	P2	0.54	10.03	<0.01
Composition vs Spillover	B	P2	0.73	7.65	<0.01
Composition vs	B	P2	0.34	6.78	<0.01
Fragmentation vs	B	P2	0.35	4.52	<0.01
Fragmentation vs Spillover	B	P2	0.54	4.85	<0.01
Fragmentation vs	B	P2	0.15	2.00	0.99

Table S4. Multiple comparison analysis (Tukey HSD test) of the strength of an environmental variable (specific Gaussian model) or driving the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the "percentage contribution" variable importance values. For this "specific model" the first 45 rows show whether the specific climatic or land use variables have an effect on the species distributions of different pollinator groups. In rows 46 to 135 present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following rows (136 to 180) show if climate or land use related variables show a difference in their effect between different pollinator groups. Lastly, rows 181 to 225 show if the strength of the effect of the same environmental variable for driving the species distributions of each pollinator group has changed over time. Adjusted Tukey's P-values are reported.

Precipitation vs	B	P2	-0.20	-3.32	0.13
Spillover vs Temperature	B	P2	-0.38	-3.89	0.02
Composition vs	B	P3	0.09	1.29	1.00
Composition vs	B	P3	0.41	7.52	<0.01
Composition vs Spillover	B	P3	1.48	15.37	<0.01
Composition vs	B	P3	0.46	9.08	<0.01
Fragmentation vs	B	P3	0.32	4.08	<0.01
Fragmentation vs Spillover	B	P3	1.39	12.45	<0.01
Fragmentation vs	B	P3	0.37	4.85	<0.01
Precipitation vs Spillover	B	P3	1.07	10.44	<0.01
Precipitation vs	B	P3	0.05	0.76	1.00
Spillover vs Temperature	B	P3	-1.02	-10.21	<0.01
Composition vs	B	P4	0.37	5.20	<0.01
Composition vs	B	P4	0.73	13.36	<0.01
Composition vs Spillover	B	P4	0.61	6.41	<0.01
Composition vs	B	P4	-0.07	-1.47	1.00
Fragmentation vs	B	P4	0.36	4.60	<0.01
Fragmentation vs Spillover	B	P4	0.24	2.21	0.93
Fragmentation vs	B	P4	-0.44	-5.84	<0.01
Precipitation vs Spillover	B	P4	-0.12	-1.14	1.00
Precipitation vs	B	P4	-0.80	-13.19	<0.01
Spillover vs Temperature	B	P4	-0.69	-6.92	<0.01
Composition vs	BU	P2	0.24	1.86	1.00
Composition vs	BU	P2	0.59	5.89	<0.01
Composition vs Spillover	BU	P2	0.07	0.38	1.00
Composition vs	BU	P2	0.13	1.41	1.00
Fragmentation vs	BU	P2	0.35	2.42	0.81
Fragmentation vs Spillover	BU	P2	-0.17	-0.85	1.00
Fragmentation vs	BU	P2	-0.11	-0.80	1.00
Precipitation vs Spillover	BU	P2	-0.52	-2.78	0.50
Spillover vs Temperature	BU	P2	0.06	0.34	1.00
Composition vs	BU	P3	0.28	2.19	0.94
Composition vs	BU	P3	0.65	6.48	<0.01
Composition vs Spillover	BU	P3	0.47	2.68	0.59
Composition vs	BU	P3	0.25	2.64	0.63
Fragmentation vs	BU	P3	0.37	2.53	0.72
Fragmentation vs Spillover	BU	P3	0.18	0.91	1.00
Fragmentation vs	BU	P3	-0.04	-0.28	1.00
Precipitation vs Spillover	BU	P3	-0.18	-0.98	1.00
Precipitation vs	BU	P3	-0.40	-3.62	0.05
Spillover vs Temperature	BU	P3	-0.22	-1.23	1.00
Composition vs	BU	P4	0.31	2.42	0.82
Composition vs	BU	P4	0.63	6.33	<0.01
Composition vs Spillover	BU	P4	0.45	2.51	0.75
Composition vs	BU	P4	0.17	1.78	1.00
Fragmentation vs	BU	P4	0.32	2.22	0.93
Fragmentation vs Spillover	BU	P4	0.13	0.65	1.00
Fragmentation vs	BU	P4	-0.15	-1.07	1.00
Precipitation vs Spillover	BU	P4	-0.19	-0.99	1.00
Precipitation vs	BU	P4	-0.47	-4.19	<0.01
Spillover vs Temperature	BU	P4	-0.28	-1.52	1.00
Composition vs	H	P2	0.23	3.19	0.19
Composition vs	H	P2	0.30	5.46	<0.01
Composition vs Spillover	H	P2	0.86	8.80	<0.01
Composition vs	H	P2	0.50	9.69	<0.01
Fragmentation vs	H	P2	0.07	0.91	1.00
Fragmentation vs Spillover	H	P2	0.63	5.57	<0.01
Fragmentation vs	H	P2	0.27	3.51	0.07
Precipitation vs Spillover	H	P2	0.56	5.39	<0.01
Precipitation vs	H	P2	0.20	3.19	0.19

Table S4 (*continued*)

Table S4 (*continued*)

Composition vs	H	P3	0.34	4.83	<0.01
Composition vs	H	P3	0.50	9.05	<0.01
Composition vs Spillover	H	P3	0.37	3.80	0.02
Composition vs	H	P3	0.55	10.69	<0.01
Fragmentation vs	H	P3	0.15	1.95	0.99
Fragmentation vs Spillover	H	P3	0.02	0.19	1.00
Fragmentation vs	H	P3	0.20	2.63	0.64
Precipitation vs Spillover	H	P3	-0.13	-1.30	1.00
Precipitation vs	H	P3	0.05	0.76	1.00
Spillover vs Temperature	H	P3	0.18	1.79	1.00
Composition vs	H	P4	0.24	3.30	0.13
Composition vs	H	P4	0.86	15.64	<0.01
Composition vs Spillover	H	P4	0.39	4.00	0.01
Composition vs	H	P4	0.16	3.13	0.23
Fragmentation vs	H	P4	0.63	7.92	<0.01
Fragmentation vs Spillover	H	P4	0.15	1.36	1.00
Fragmentation vs	H	P4	-0.08	-1.00	1.00
Precipitation vs Spillover	H	P4	-0.47	-4.60	<0.01
Precipitation vs	H	P4	-0.70	-11.44	<0.01
Spillover vs Temperature	H	P4	-0.23	-2.28	0.90
Composition	H vs B	P2	-0.08	-1.46	1.00
Composition	H vs BU	P2	-0.15	-1.83	1.00
Composition	B vs BU	P2	-0.07	-0.84	1.00
Composition	H vs B	P3	0.06	1.06	1.00
Composition	H vs BU	P3	0.11	1.40	1.00
Composition	B vs BU	P3	0.06	0.69	1.00
Composition	H vs B	P4	0.01	0.27	1.00
Composition	H vs BU	P4	0.12	1.51	1.00
Composition	B vs BU	P4	0.11	1.33	1.00
Fragmentation	H vs B	P2	-0.12	-1.20	1.00
Fragmentation	B vs BU	P2	-0.02	-0.13	1.00
Fragmentation	H vs B	P3	-0.20	-2.02	0.98
Fragmentation	H vs BU	P3	0.05	0.37	1.00
Fragmentation	B vs BU	P3	0.25	1.74	1.00
Fragmentation	H vs B	P4	0.15	1.51	1.00
Fragmentation	H vs BU	P4	0.20	1.40	1.00
Fragmentation	B vs BU	P4	0.05	0.38	1.00
Precipitation	H vs B	P2	0.16	2.25	0.92
Precipitation	H vs BU	P2	0.14	1.31	1.00
Precipitation	B vs BU	P2	-0.02	-0.22	1.00
Precipitation	H vs B	P3	-0.03	-0.39	1.00
Precipitation	H vs BU	P3	0.26	2.46	0.79
Precipitation	B vs BU	P3	0.29	2.72	0.55
Precipitation	H vs B	P4	-0.12	-1.67	1.00
Precipitation	H vs BU	P4	-0.11	-1.00	1.00
Precipitation	B vs BU	P4	0.01	0.13	1.00
Temperature	H vs B	P2	-0.24	-3.51	0.07
Temperature	H vs BU	P2	-0.52	-5.23	<0.01
Temperature	B vs BU	P2	-0.28	-2.85	0.44
Temperature	H vs B	P3	-0.03	-0.43	1.00
Temperature	H vs BU	P3	-0.19	-1.90	0.99
Temperature	B vs BU	P3	-0.16	-1.61	1.00
Temperature	H vs B	P4	-0.22	-3.28	0.15
Temperature	H vs BU	P4	0.13	1.30	1.00
Temperature	B vs BU	P4	0.35	3.53	0.07
Spillover	H vs B	P2	-0.21	-1.60	1.00
Spillover	H vs BU	P2	-0.94	-4.74	<0.01
Spillover	B vs BU	P2	-0.73	-3.69	0.04
Spillover	H vs B	P3	1.17	8.79	<0.01
Spillover	H vs BU	P3	0.22	1.10	1.00

Table S4 (*continued*)

Spillover	H vs B	P4	0.24	1.77	1.00
Spillover	H vs BU	P4	0.18	0.90	1.00
Spillover	B vs BU	P4	-0.06	-0.29	1.00
Precipitation	B	P2 vs P3	-0.17	-2.65	0.63
Precipitation	B	P2 vs P4	0.16	2.52	0.74
Precipitation	B	P3 vs P4	0.33	5.15	<0.01
Precipitation	BU	P2 vs P3	0.15	1.23	1.00
Precipitation	BU	P2 vs P4	0.20	1.68	1.00
Precipitation	BU	P3 vs P4	0.05	0.45	1.00
Precipitation	H	P2 vs P3	0.02	0.33	1.00
Precipitation	H	P2 vs P4	0.45	6.86	<0.01
Precipitation	H	P3 vs P4	0.43	6.54	<0.01
Temperature	B	P2 vs P3	0.08	1.36	1.00
Temperature	B	P2 vs P4	-0.44	-7.63	<0.01
Temperature	B	P3 vs P4	-0.52	-9.00	<0.01
Temperature	BU	P2 vs P3	0.20	1.90	0.99
Temperature	BU	P2 vs P4	0.19	1.80	1.00
Temperature	BU	P3 vs P4	-0.01	-0.10	1.00
Temperature	H	P2 vs P3	-0.13	-2.22	0.93
Temperature	H	P2 vs P4	-0.46	-7.81	<0.01
Temperature	H	P3 vs P4	-0.33	-5.63	<0.01
Composition	B	P2 vs P3	-0.04	-0.90	1.00
Composition	B	P2 vs P4	-0.02	-0.49	1.00
Composition	B	P3 vs P4	0.02	0.41	1.00
Composition	BU	P2 vs P4	0.15	1.97	0.99
Composition	BU	P3 vs P4	0.07	0.88	1.00
Composition	H	P2 vs P3	-0.18	-4.09	<0.01
Composition	H	P2 vs P4	-0.11	-2.68	0.59
Composition	H	P3 vs P4	0.06	1.41	1.00
Fragmentation	B	P2 vs P3	-0.14	-1.54	1.00
Fragmentation	B	P2 vs P4	0.15	1.71	1.00
Fragmentation	B	P3 vs P4	0.29	3.25	0.16
Fragmentation	BU	P2 vs P3	0.13	0.77	1.00
Fragmentation	BU	P2 vs P4	0.23	1.37	1.00
Fragmentation	BU	P3 vs P4	0.10	0.59	1.00
Fragmentation	H	P2 vs P3	-0.06	-0.66	1.00
Fragmentation	H	P2 vs P4	-0.11	-1.18	1.00
Fragmentation	H	P3 vs P4	-0.05	-0.53	1.00
Spillover	B	P2 vs P3	0.72	5.58	<0.01
Spillover	B	P2 vs P4	-0.14	-1.06	1.00
Spillover	B	P3 vs P4	-0.85	-6.62	<0.01
Spillover	BU	P2 vs P3	0.49	2.06	0.98
Spillover	BU	P2 vs P4	0.53	2.23	0.92
Spillover	BU	P3 vs P4	0.05	0.20	1.00
Spillover	H	P2 vs P3	-0.67	-5.15	<0.01
Spillover	H	P2 vs P4	-0.59	-4.48	<0.01
Spillover	H	P3 vs P4	0.08	0.65	1.00

Environmental	Group	Period	Estimat	z-value	P-value
Climate	B	TP1	4.54	19.58	<0.01
Climate	B	TP2	4.12	18.57	<0.01
Climate	B	TP3	5.07	20.48	<0.01
Climate	BU	TP1	5.38	11.97	<0.01
Climate	BU	TP2	5.41	12.01	<0.01
Climate	BU	TP3	5.96	12.03	<0.01
Climate	H	TP1	3.79	17.72	<0.01
Climate	H	TP2	4.96	20.4	<0.01
Climate	H	TP3	4.79	20.18	<0.01
Land use	B	TP1	5.83	21.82	<0.01
Land use	B	TP2	5.55	21.87	<0.01
Land use	B	TP3	5.80	21.85	<0.01
Land use	BU	TP1	6.55	12.47	<0.01
Land use	BU	TP2	6.01	12.8	<0.01
Land use	BU	TP3	5.94	12.81	<0.01
Land use	H	TP1	5.11	21.57	<0.01
Land use	H	TP2	6.20	21.28	<0.01
Land use	H	TP3	5.87	21.76	<0.01
Climate vs Land use	B	TP1	-1.29	-6.08	<0.01
Climate vs Land use	B	TP2	-1.42	-7.63	<0.01
Climate vs Land use	B	TP3	-0.73	-3.23	0.04
Climate vs Land use	BU	TP1	-1.17	-2.49	0.29
Climate vs Land use	BU	TP2	-0.59	-1.45	0.95
Climate vs Land use	BU	TP3	0.02	0.05	1
Climate vs Land use	H	TP1	-1.32	-8.03	<0.01
Climate vs Land use	H	TP2	-1.24	-4.83	<0.01
Climate	B vs H	TP1	0.74	2.67	0.19
Climate	H vs BU	TP1	-1.59	-3.38	0.02
Climate	B vs BU	TP1	-0.84	-1.78	0.81
Climate	B vs H	TP2	-0.84	-2.85	0.12
Climate	H vs BU	TP2	-0.45	-0.94	1
Climate	B vs BU	TP2	-1.29	-2.74	0.16
Climate	B vs H	TP3	0.28	0.92	1
Climate	H vs BU	TP3	-1.17	-2.25	0.46
Climate	B vs BU	TP3	-0.89	-1.7	0.86
Land use	B vs H	TP1	0.72	2.23	0.47
Land use	H vs BU	TP1	-1.44	-2.62	0.21
Land use	B vs BU	TP1	-0.72	-1.29	0.98
Land use	B vs H	TP2	-0.65	-1.84	0.77
Land use	H vs BU	TP2	0.19	0.37	1
Land use	B vs BU	TP2	-0.46	-0.91	1
Land use	B vs H	TP3	-0.07	-0.19	1
Land use	H vs BU	TP3	-0.07	-0.14	1
Land use	B vs BU	TP3	-0.14	-0.27	1
Climate	B	P1 vs	-0.53	-2.83	0.14
Climate	BU	P1 vs	-0.58	-1.33	0.99
Climate	H	P1 vs	-0.99	-6.01	<0.01
Land use	B	P1 vs	0.02	0.10	1
Land use	BU	P1 vs	0.61	1.27	0.99
Land use	H	P1 vs	-0.76	-3.37	0.03

Table S5. Multiple comparison analysis (Tukey HSD test) of the probability of an environmental variable having an effect (general Binomial model) on the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the “permutation importance” variable importance values. For this “general model” the first 18 rows show whether climate or land use have an effect on the species distributions of different pollinator groups. The next nine rows present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following 18 rows present the results of comparisons between different pollinator groups for each climate or land use variable. The last six rows present the results for the comparisons between the first and last period of the analysis for each variable and pollinator group. Adjusted Tukey’s P-values are reported.

Environmental	Group	Period	Estimate	z-value	P-value
Climate	B	TP1	0.51	12.72	<0.01
Climate	B	TP2	0.55	13.87	<0.01
Climate	B	TP3	0.86	21.73	<0.01
Climate	BU	TP1	0.83	11.46	<0.01
Climate	BU	TP2	0.73	9.99	<0.01
Climate	BU	TP3	0.82	11.3	<0.01
Climate	H	TP1	0.45	11.07	<0.01
Climate	H	TP2	0.68	16.97	<0.01
Climate	H	TP3	0.70	17.43	<0.01
Land use	B	TP1	1.15	31.44	<0.01
Land use	B	TP2	1.18	32.34	<0.01
Land use	B	TP3	1.12	30.76	<0.01
Land use	BU	TP1	1.32	19.7	<0.01
Land use	BU	TP2	1.20	17.86	<0.01
Land use	BU	TP3	1.12	16.64	<0.01
Land use	H	TP1	1.06	28.55	<0.01
Land use	H	TP2	1.22	33.21	<0.01
Land use	H	TP3	1.19	32.24	<0.01
Climate vs Land use	B	TP1	-0.64	-16.14	<0.01
Climate vs Land use	B	TP2	-0.63	-15.68	<0.01
Climate vs Land use	B	TP3	-0.26	-6.64	<0.01
Climate vs Land use	BU	TP1	-0.49	-6.69	<0.01
Climate vs Land use	BU	TP2	-0.47	-6.5	<0.01
Climate vs Land use	BU	TP3	-0.30	-4.11	<0.01
Climate vs Land use	H	TP1	-0.61	-14.88	<0.01
Climate vs Land use	H	TP2	-0.54	-13.62	<0.01
Climate vs Land use	H	TP3	-0.49	-12.24	<0.01
Climate	B vs H	TP1	0.05	0.97	1
Climate	H vs BU	TP1	-0.38	-4.61	<0.01
Climate	B vs BU	TP1	-0.33	-3.97	<0.01
Climate	B vs H	TP2	-0.13	-2.22	0.49
Climate	H vs BU	TP2	-0.05	-0.57	1
Climate	B vs BU	TP2	-0.17	-2.08	0.61
Climate	B vs H	TP3	0.16	2.84	0.13
Climate	H vs BU	TP3	-0.12	-1.46	0.96
Climate	B vs BU	TP3	0.04	0.47	1
Land use	B vs H	TP1	0.09	1.72	0.86
Land use	H vs BU	TP1	-0.26	-3.46	0.02
Land use	B vs BU	TP1	-0.18	-2.3	0.44
Land use	B vs H	TP2	-0.04	-0.84	1
Land use	H vs BU	TP2	0.02	0.32	1
Land use	B vs BU	TP2	-0.02	-0.26	1
Land use	B vs H	TP3	-0.07	-1.31	0.99
Land use	H vs BU	TP3	0.07	0.92	1
Land use	B vs BU	TP3	0.0002	0.04	1
Climate	B	P1 vs	-0.35	-8.32	<0.001
Climate	BU	P1 vs	0.01	0.19	1
Climate	H	P1 vs	-0.25	-5.71	<0.001
Land use	B	P1 vs	0.02	0.68	1
Land use	BU	P1 vs	0.20	3.02	0.08
Land use	H	P1 vs	-0.13	-3.6	0.01

Table S6. Multiple comparison analysis (Tukey HSD test) of the strength of the effect of an environmental variable (general Gaussian model) for driving the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the "permutation importance" variable importance values. For this "general model" the first 18 rows show whether climate or land use have an effect on the species distributions of different pollinator groups. The next nine rows present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following 18 rows present the results of comparisons between different pollinator groups for each climate or land use variable. The last six rows present the results for the comparisons between the first and last period of the analysis for each variable and pollinator group. Adjusted Tukey's P-values are reported.

Environmental variables	Group	Period	Estimate	z-value	P-value
Precipitation	B	TP1	4.56	16.7	<0.01
Precipitation	B	TP2	4.00	15.91	<0.01
Precipitation	B	TP3	4.72	16.87	<0.01
Precipitation	BU	TP1	5.16	10	<0.01
Precipitation	BU	TP2	5.57	9.99	<0.01
Precipitation	BU	TP3	5.95	9.8	<0.01
Precipitation	H	TP1	4.04	16.01	<0.01
Precipitation	H	TP2	4.88	16.89	<0.01
Precipitation	H	TP3	4.39	16.57	<0.01
Temperature	B	TP1	4.57	17.5	<0.01
Temperature	B	TP2	4.33	17.17	<0.01
Temperature	B	TP3	5.53	17.63	<0.01
Temperature	BU	TP1	6.01	10.43	<0.01
Temperature	BU	TP2	5.66	10.58	<0.01
Temperature	BU	TP3	6.26	10.23	<0.01
Temperature	H	TP1	3.67	15.74	<0.01
Temperature	H	TP2	5.10	17.84	<0.01
Temperature	H	TP3	5.43	17.68	<0.01
Composition	B	TP1	5.86	19.38	<0.01
Composition	B	TP2	6.03	19.64	<0.01
Composition	B	TP3	6.19	19.41	<0.01
Composition	BU	TP1	7.08	11.11	<0.01
Composition	BU	TP2	6.68	11.65	<0.01
Composition	BU	TP3	6.63	11.73	<0.01
Composition	H	TP1	5.44	20.29	<0.01
Composition	H	TP2	6.48	18.77	<0.01
Composition	H	TP3	6.28	19.29	<0.01
Fragmentation	B	TP1	6.07	11.11	<0.01
Fragmentation	B	TP2	5.37	13.2	<0.01
Fragmentation	B	TP3	5.55	12.89	<0.01
Fragmentation	BU	TP1	6.93	6.33	<0.01
Fragmentation	BU	TP2	5.14	8.22	<0.01
Fragmentation	BU	TP3	6.17	7.5	<0.01
Fragmentation	H	TP1	4.62	13.81	<0.01
Fragmentation	H	TP2	5.95	11.86	<0.01
Fragmentation	H	TP3	5.61	12.64	<0.01
Spillover	B	TP1	5.30	9.78	<0.01
Spillover	B	TP2	4.07	11.1	<0.01
Spillover	B	TP3	4.89	10.66	<0.01
Spillover	BU	TP1	5.42	6.27	<0.01
Spillover	BU	TP2	6.14	5.67	<0.01

Table S7. Multiple comparison analysis (Tukey HSD test) of the probability of an environmental variable having an effect (specific Binomial model) on the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the "permutation importance" variable importance values. For this "specific model" the first 45 rows show whether the specific climatic or land use variables have an effect on the species distributions of different pollinator groups. In rows 46 to 135 present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following rows (136 to 180) show if climate or land use related variables show a difference in their effect between different pollinator groups. Lastly, rows 181 to 225 show if the probability of the same environmental variable on having an effect on each pollinator group has changed over time. Adjusted Tukey's P-values are reported.

Spillover	BU	TP3	4.18	6.36	<0.01
Spillover	H	TP1	4.45	10.93	<0.01
Spillover	H	TP2	5.75	9.14	<0.01
Spillover	H	TP3	4.68	10.81	<0.01
Precipitation vs Temperature	B	TP1	-0.01	-0.02	1
Precipitation vs Temperature	B	TP2	-0.33	-1.59	1
Precipitation vs Temperature	B	TP3	-0.81	-2.68	0.59
Precipitation vs Temperature	BU	TP1	-0.84	-1.5	1
Precipitation vs Temperature	BU	TP2	-0.09	-0.16	1
Precipitation vs Temperature	BU	TP3	-0.31	-0.46	1
Precipitation vs Temperature	H	TP1	0.37	1.86	1
Precipitation vs Temperature	H	TP2	-0.21	-0.75	1
Precipitation vs Temperature	H	TP3	-1.04	-3.63	0.05
Precipitation vs Spillover	B	TP1	-0.73	-1.38	1
Precipitation vs Spillover	B	TP2	-0.07	-0.2	1
Precipitation vs Spillover	B	TP3	-0.17	-0.37	1
Precipitation vs Spillover	BU	TP1	-0.26	-0.3	1
Precipitation vs Spillover	BU	TP2	-0.57	-0.52	1
Precipitation vs Spillover	BU	TP3	1.77	2.42	0.81
Precipitation vs Spillover	H	TP1	-0.41	-1.07	1
Precipitation vs Spillover	H	TP2	-0.86	-1.37	1
Precipitation vs Spillover	H	TP3	-0.29	-0.69	1
Composition vs Precipitation	B	TP1	1.30	4.53	<0.01
Composition vs Precipitation	B	TP2	2.03	7.5	<0.01
Composition vs Precipitation	B	TP3	1.47	4.77	<0.01
Composition vs Precipitation	BU	TP1	1.92	3.08	0.25
Composition vs Precipitation	BU	TP2	1.12	1.88	0.99
Composition vs Precipitation	BU	TP3	0.68	1.08	1
Composition vs Precipitation	H	TP1	1.41	6.05	<0.01
Composition vs Precipitation	H	TP2	1.59	4.62	<0.01
Composition vs Precipitation	H	TP3	1.88	6.17	<0.01
Composition vs Temperature	B	TP1	1.29	4.72	<0.01
Composition vs Temperature	B	TP2	1.70	6.29	<0.01
Composition vs Temperature	B	TP3	0.66	1.96	0.99
Composition vs Temperature	BU	TP1	1.08	1.61	1
Composition vs Temperature	BU	TP2	1.03	1.79	1
Composition vs Temperature	BU	TP3	0.37	0.59	1
Composition vs Temperature	H	TP1	1.77	8.29	<0.01
Composition vs Temperature	H	TP2	1.38	4.04	0.01
Composition vs Temperature	H	TP3	0.84	2.48	0.77
Composition vs Fragmentation	B	TP1	-0.21	-0.37	1
Composition vs Fragmentation	B	TP2	0.66	1.57	1
Composition vs Fragmentation	B	TP3	0.65	1.44	1
Composition vs Fragmentation	BU	TP1	0.15	0.13	1
Composition vs Fragmentation	BU	TP2	1.55	2.34	0.87
Composition vs Fragmentation	BU	TP3	0.46	0.55	1
Composition vs Fragmentation	H	TP1	0.83	2.6	0.67
Composition vs Fragmentation	H	TP2	0.52	0.97	1
Composition vs Fragmentation	H	TP3	0.67	1.42	1
Composition vs Spillover	B	TP1	0.56	1.01	1
Composition vs Spillover	B	TP2	1.96	5.15	<0.01
Composition vs Spillover	B	TP3	1.30	2.71	0.56
Composition vs Spillover	BU	TP1	1.66	1.8	1
Composition vs Spillover	BU	TP2	0.55	0.5	1
Composition vs Spillover	BU	TP3	2.45	3.53	0.06
Composition vs Spillover	H	TP1	0.99	2.53	0.73
Composition vs Spillover	H	TP2	0.73	1.11	1
Composition vs Spillover	H	TP3	1.60	3.47	0.08
Fragmentation vs Precipitation	B	TP1	1.50	2.81	0.47
Fragmentation vs Precipitation	B	TP2	1.37	3.61	0.05
Fragmentation vs Precipitation	B	TP3	0.82	1.95	0.99
Fragmentation vs Precipitation	BU	TP1	1.77	1.63	1

Table S7 (*continued*)

Fragmentation vs Precipitation	BU	TP2	-0.43	-0.66	1
Fragmentation vs Precipitation	BU	TP3	0.22	0.26	1
Fragmentation vs Precipitation	H	TP1	0.58	1.88	0.99
Fragmentation vs Precipitation	H	TP2	1.07	2.13	0.96
Fragmentation vs Precipitation	H	TP3	1.22	2.84	0.44
Fragmentation vs Temperature	B	TP1	1.50	2.83	0.45
Fragmentation vs Temperature	B	TP2	1.04	2.74	0.53
Fragmentation vs Temperature	B	TP3	0.01	0.03	1
Fragmentation vs Temperature	BU	TP1	0.92	0.83	1
Fragmentation vs Temperature	BU	TP2	-0.52	-0.83	1
Fragmentation vs Temperature	BU	TP3	-0.08	-0.1	1
Fragmentation vs Temperature	H	TP1	0.95	3.22	0.17
Fragmentation vs Temperature	H	TP2	0.86	1.71	1
Fragmentation vs Temperature	H	TP3	0.18	0.39	1
Fragmentation vs Spillover	B	TP1	0.77	1.09	1
Fragmentation vs Spillover	B	TP2	1.31	2.81	0.47
Fragmentation vs Spillover	B	TP3	0.65	1.17	1
Fragmentation vs Spillover	BU	TP1	1.51	1.18	1
Fragmentation vs Spillover	BU	TP2	-1.00	-0.88	1
Fragmentation vs Spillover	BU	TP3	2.00	2.18	0.94
Fragmentation vs Spillover	H	TP1	0.17	0.37	1
Fragmentation vs Spillover	H	TP2	0.21	0.28	1
Fragmentation vs Spillover	H	TP3	0.93	1.7	1
Spillover vs Temperature	B	TP1	0.73	1.39	1
Spillover vs Temperature	B	TP2	-0.26	-0.78	1
Spillover vs Temperature	B	TP3	-0.64	-1.36	1
Spillover vs Temperature	BU	TP1	-0.58	-0.65	1
Spillover vs Temperature	BU	TP2	0.48	0.44	1
Spillover vs Temperature	BU	TP3	-2.08	-2.83	0.45
Spillover vs Temperature	H	TP1	0.78	2.08	0.97
Spillover vs Temperature	H	TP2	0.65	1.04	1
Spillover vs Temperature	H	TP3	-0.75	-1.69	1
Precipitation	H vs B	TP1	-0.52	-1.54	1
Precipitation	H vs BU	TP1	-1.12	-2.06	0.97
Precipitation	B vs BU	TP1	-0.60	-1.09	1
Precipitation	H vs B	TP2	0.88	2.52	0.73
Precipitation	H vs BU	TP2	-0.69	-1.14	1
Precipitation	B vs BU	TP2	-1.57	-2.7	0.57
Precipitation	H vs B	TP3	-0.33	-0.95	1
Precipitation	H vs BU	TP3	-1.56	-2.45	0.79
Precipitation	B vs BU	TP3	-1.23	-1.91	0.99
Temperature	H vs B	TP1	-0.90	-2.84	0.44
Temperature	H vs BU	TP1	-2.34	-3.93	0.01
Temperature	B vs BU	TP1	-1.44	-2.39	0.83
Temperature	H vs B	TP2	0.77	2.2	0.94
Temperature	H vs BU	TP2	-0.56	-0.98	1
Temperature	B vs BU	TP2	-1.33	-2.37	0.85
Temperature	H vs B	TP3	-0.10	-0.25	1
Temperature	H vs BU	TP3	-0.83	-1.26	1
Temperature	B vs BU	TP3	-0.73	-1.1	1
Composition	H vs B	TP1	-0.41	-1.1	1
Composition	H vs BU	TP1	-1.64	-2.46	0.78
Composition	B vs BU	TP1	-1.22	-1.8	1
Composition	H vs B	TP2	0.44	1.02	1
Composition	H vs BU	TP2	-0.21	-0.33	1
Composition	B vs BU	TP2	-0.65	-1.05	1
Composition	H vs B	TP3	0.08	0.19	1
Composition	H vs BU	TP3	-0.36	-0.57	1
Composition	B vs BU	TP3	-0.44	-0.71	1
Fragmentation	H vs B	TP1	-1.45	-2.32	0.88
Fragmentation	H vs BU	TP1	-2.31	-2.05	0.98
Fragmentation	B vs BU	TP1	-0.87	-0.72	1

Table S7 (*continued*)

Fragmentation	H vs B	TP2	0.58	0.92	1
Fragmentation	H vs BU	TP2	0.81	1.04	1
Fragmentation	B vs BU	TP2	0.23	0.33	1
Fragmentation	H vs B	TP3	0.06	0.11	1
Fragmentation	H vs BU	TP3	-0.56	-0.62	1
Fragmentation	B vs BU	TP3	-0.63	-0.69	1
Spillover	H vs B	TP1	-0.84	-1.27	1
Spillover	H vs BU	TP1	-0.97	-1.04	1
Spillover	B vs BU	TP1	-0.13	-0.13	1
Spillover	H vs B	TP2	1.68	2.36	0.86
Spillover	H vs BU	TP2	-0.39	-0.32	1
Spillover	B vs BU	TP2	-2.07	-1.84	1
Spillover	H vs B	TP3	-0.21	-0.35	1
Spillover	H vs BU	TP3	0.50	0.65	1
Spillover	B vs BU	TP3	0.72	0.92	1
Precipitation	B	TP1 vs TP2	0.56	2.4	0.82
Precipitation	B	TP1 vs TP3	-0.16	-0.62	1
Precipitation	B	TP2 vs TP3	-0.73	-3.02	0.3
Precipitation	BU	TP1 vs TP2	-0.40	-0.74	1
Precipitation	BU	TP1 vs TP3	-0.79	-1.32	1
Precipitation	BU	TP2 vs TP3	-0.38	-0.61	1
Precipitation	H	TP1 vs TP2	-0.84	-3.28	0.14
Precipitation	H	TP1 vs TP3	-0.35	-1.52	1
Precipitation	H	TP2 vs TP3	0.49	1.83	1
Temperature	B	TP1 vs TP2	0.24	1.08	1
Temperature	B	TP1 vs TP3	-0.97	-3.39	0.1
Temperature	B	TP2 vs TP3	-1.20	-4.34	<0.01
Temperature	BU	TP1 vs TP2	0.35	0.6	1
Temperature	BU	TP1 vs TP3	-0.25	-0.39	1
Temperature	BU	TP2 vs TP3	-0.60	-0.98	1
Temperature	H	TP1 vs TP2	-1.42	-6.03	<0.01
Temperature	H	TP1 vs TP3	-1.76	-6.74	<0.01
Temperature	H	TP2 vs TP3	-0.34	-1.1	1
Composition	B	TP1 vs TP2	-0.17	-0.53	1
Composition	B	TP1 vs TP3	-0.34	-1.01	1
Composition	B	TP2 vs TP3	-0.16	-0.5	1
Composition	BU	TP1 vs TP2	0.40	0.6	1
Composition	BU	TP1 vs TP3	0.45	0.69	1
Composition	BU	TP2 vs TP3	0.05	0.09	1
Composition	H	TP1 vs TP2	-1.03	-3.15	0.21
Composition	H	TP1 vs TP3	-0.83	-2.71	0.57
Composition	H	TP2 vs TP3	0.20	0.53	1
Fragmentation	B	TP1 vs TP2	0.69	1.11	1
Fragmentation	B	TP1 vs TP3	0.52	0.81	1
Fragmentation	B	TP2 vs TP3	-0.17	-0.34	1
Fragmentation	BU	TP1 vs TP2	1.79	1.57	1
Fragmentation	BU	TP1 vs TP3	0.76	0.6	1
Fragmentation	BU	TP2 vs TP3	-1.04	-1.17	1
Fragmentation	H	TP1 vs TP2	-1.34	-2.51	0.74
Fragmentation	H	TP1 vs TP3	-0.99	-2.08	0.97
Fragmentation	H	TP2 vs TP3	0.34	0.57	1
Spillover	B	TP1 vs TP2	1.23	2.07	0.97
Spillover	B	TP1 vs TP3	0.40	0.61	1
Spillover	B	TP2 vs TP3	-0.83	-1.62	1
Spillover	BU	TP1 vs TP2	-0.71	-0.56	1
Spillover	BU	TP1 vs TP3	1.25	1.3	1
Spillover	BU	TP2 vs TP3	1.96	1.7	1
Spillover	H	TP1 vs TP2	-1.29	-1.86	1
Spillover	H	TP1 vs TP3	-0.23	-0.43	1
Spillover	H	TP2 vs TP3	1.07	1.51	1

Table S7 (*continued*)

Environmental variables	Group	Period	Estimate	z-value	P-value
Precipitation	B	TP1	0.32	6.19	<0.01
Precipitation	B	TP2	0.49	9.36	<0.01
Precipitation	B	TP3	0.57	11.11	<0.01
Precipitation	BU	TP1	0.58	6.1	<0.01
Precipitation	BU	TP2	0.53	5.54	<0.01
Precipitation	BU	TP3	0.55	5.8	<0.01
Precipitation	H	TP1	0.33	6.32	<0.01
Precipitation	H	TP2	0.59	11.28	<0.01
Precipitation	H	TP3	0.37	7	<0.01
Temperature	B	TP1	0.65	13.66	<0.01
Temperature	B	TP2	0.60	12.59	<0.01
Temperature	B	TP3	1.08	22.86	<0.01
Temperature	BU	TP1	1.03	11.85	<0.01
Temperature	BU	TP2	0.89	10.16	<0.01
Temperature	BU	TP3	1.04	11.91	<0.01
Temperature	H	TP1	0.55	11.08	<0.01
Temperature	H	TP2	0.75	15.64	<0.01
Temperature	H	TP3	0.95	19.93	<0.01
Composition	B	TP1	1.23	31.29	<0.01
Composition	B	TP2	1.28	32.74	<0.01
Composition	B	TP3	1.21	30.76	<0.01
Composition	BU	TP1	1.36	18.81	<0.01
Composition	BU	TP2	1.30	18.04	<0.01
Composition	BU	TP3	1.18	16.38	<0.01
Composition	H	TP1	1.17	29.45	<0.01
Composition	H	TP2	1.31	33.07	<0.01
Composition	H	TP3	1.30	32.66	<0.01
Fragmentation	B	TP1	1.11	16.47	<0.01
Fragmentation	B	TP2	1.17	17.26	<0.01
Fragmentation	B	TP3	0.94	13.86	<0.01
Fragmentation	BU	TP1	1.23	9.94	<0.01
Fragmentation	BU	TP2	0.98	7.75	<0.01
Fragmentation	BU	TP3	0.90	7.25	<0.01
Fragmentation	H	TP1	0.88	12.75	<0.01
Fragmentation	H	TP2	1.10	16.15	<0.01
Fragmentation	H	TP3	0.91	13.37	<0.01
Spillover	B	TP1	0.47	5.06	<0.01
Spillover	B	TP2	0.21	2.18	0.94
Spillover	B	TP3	0.71	7.62	<0.01

Table S8. Multiple comparison analysis (Tukey HSD test) of the strength of an environmental variable (specific Gaussian model) for driving the distribution of pollinator species (bees, B, butterflies, BU and hoverflies, H), across the three time periods (TP) analysed using the "permutation importance" variable importance values. For this "specific model" the first 45 rows show whether the specific climatic or land use variables have an effect on the species distributions of different pollinator groups. In rows 46 to 135 present the results for comparisons between climate and land use variables for each pollinator group and time period separately. The following rows (136 to 180) show if climate or land use related variables show a difference in their effect between different pollinator groups. Lastly, rows 181 to 225 show if the strength of the effect of the same environmental variable for driving the species distributions of each pollinator group has changed over time. Adjusted Tukey's P-values are reported.

Spillover	BU	TP1	1.17	6.84	<0.01
Spillover	BU	TP2	0.69	4.09	<0.01
Spillover	BU	TP3	0.95	5.44	<0.01
Spillover	H	TP1	0.33	3.51	0.07
Spillover	H	TP2	0.67	7.19	<0.01
Spillover	H	TP3	0.76	8.03	<0.01
Precipitation vs Temperature	B	TP1	-0.33	-5.54	<0.01
Precipitation vs Temperature	B	TP2	-0.11	-1.87	1
Precipitation vs Temperature	B	TP3	-0.51	-8.51	<0.01
Precipitation vs Temperature	BU	TP1	-0.45	-4.12	<0.01
Precipitation vs Temperature	BU	TP2	-0.36	-3.31	0.13
Precipitation vs Temperature	BU	TP3	-0.49	-4.48	<0.01
Precipitation vs Temperature	H	TP1	-0.21	-3.41	0.1
Precipitation vs Temperature	H	TP2	-0.16	-2.7	0.57
Precipitation vs Temperature	H	TP3	-0.59	-9.69	<0.01
Precipitation vs Spillover	B	TP1	-0.15	-1.47	1
Precipitation vs Spillover	B	TP2	0.28	2.81	0.47
Precipitation vs Spillover	B	TP3	-0.13	-1.33	1
Precipitation vs Spillover	BU	TP1	-0.59	-3.2	0.18
Precipitation vs Spillover	BU	TP2	-0.17	-0.92	1
Precipitation vs Spillover	BU	TP3	-0.40	-2.16	0.95
Precipitation vs Spillover	H	TP1	0.00	0.02	1
Precipitation vs Spillover	H	TP2	-0.08	-0.8	1
Precipitation vs Spillover	H	TP3	-0.39	-3.83	0.02
Composition vs Precipitation	B	TP1	0.91	16.96	<0.01
Composition vs Precipitation	B	TP2	0.79	14.7	<0.01
Composition vs Precipitation	B	TP3	0.63	11.84	<0.01
Composition vs Precipitation	BU	TP1	0.78	7.9	<0.01
Composition vs Precipitation	BU	TP2	0.78	7.95	<0.01
Composition vs Precipitation	BU	TP3	0.64	6.51	<0.01
Composition vs Precipitation	H	TP1	0.84	15.32	<0.01
Composition vs Precipitation	H	TP2	0.72	13.42	<0.01
Composition vs Precipitation	H	TP3	0.93	17.11	<0.01
Composition vs Temperature	B	TP1	0.58	11.59	<0.01
Composition vs Temperature	B	TP2	0.68	13.68	<0.01
Composition vs Temperature	B	TP3	0.12	2.54	0.72
Composition vs Temperature	BU	TP1	0.32	3.58	0.05
Composition vs Temperature	BU	TP2	0.42	4.58	<0.01
Composition vs Temperature	BU	TP3	0.15	1.62	1
Composition vs Temperature	H	TP1	0.63	12.27	<0.01
Composition vs Temperature	H	TP2	0.56	11.23	<0.01
Composition vs Temperature	H	TP3	0.34	6.85	<0.01
Composition vs Fragmentation	B	TP1	0.12	1.7	1
Composition vs Fragmentation	B	TP2	0.12	1.68	1
Composition vs Fragmentation	B	TP3	0.27	3.89	0.02
Composition vs Fragmentation	BU	TP1	0.12	0.99	1
Composition vs Fragmentation	BU	TP2	0.33	2.56	0.71
Composition vs Fragmentation	BU	TP3	0.28	2.21	0.93
Composition vs Fragmentation	H	TP1	0.29	4.11	<0.01
Composition vs Fragmentation	H	TP2	0.21	3.01	0.3
Composition vs Fragmentation	H	TP3	0.38	5.47	<0.01
Composition vs Spillover	B	TP1	0.76	8.16	<0.01
Composition vs Spillover	B	TP2	1.08	11.33	<0.01
Composition vs Spillover	B	TP3	0.50	5.34	<0.01
Composition vs Spillover	BU	TP1	0.19	1.11	1
Composition vs Spillover	BU	TP2	0.61	3.57	0.06
Composition vs Spillover	BU	TP3	0.23	1.32	1
Composition vs Spillover	H	TP1	0.84	8.79	<0.01
Composition vs Spillover	H	TP2	0.64	6.85	<0.01
Composition vs Spillover	H	TP3	0.54	5.68	<0.01
Fragmentation vs Precipitation	B	TP1	0.79	10.32	<0.01
Fragmentation vs Precipitation	B	TP2	0.68	8.79	<0.01

Table S8 (*continued*)

Fragmentation vs Precipitation	B	TP3	0.36	4.74	<0.01
Fragmentation vs Precipitation	BU	TP1	0.65	4.63	<0.01
Fragmentation vs Precipitation	BU	TP2	0.45	3.17	0.2
Fragmentation vs Precipitation	BU	TP3	0.35	2.52	0.74
Fragmentation vs Precipitation	H	TP1	0.55	6.97	<0.01
Fragmentation vs Precipitation	H	TP2	0.51	6.64	<0.01
Fragmentation vs Precipitation	H	TP3	0.55	7.03	<0.01
Fragmentation vs Temperature	B	TP1	0.46	6.2	<0.01
Fragmentation vs Temperature	B	TP2	0.57	7.6	<0.01
Fragmentation vs Temperature	B	TP3	-0.14	-1.94	0.99
Fragmentation vs Temperature	BU	TP1	0.20	1.47	1
Fragmentation vs Temperature	BU	TP2	0.09	0.64	1
Fragmentation vs Temperature	BU	TP3	-0.13	-0.99	1
Fragmentation vs Temperature	H	TP1	0.34	4.42	<0.01
Fragmentation vs Temperature	H	TP2	0.35	4.7	<0.01
Fragmentation vs Temperature	H	TP3	-0.04	-0.54	1
Fragmentation vs Spillover	B	TP1	0.64	5.96	<0.01
Fragmentation vs Spillover	B	TP2	0.96	8.75	<0.01
Fragmentation vs Spillover	B	TP3	0.23	2.13	0.96
Fragmentation vs Spillover	BU	TP1	0.07	0.33	1
Fragmentation vs Spillover	BU	TP2	0.28	1.42	1
Fragmentation vs Spillover	BU	TP3	-0.05	-0.24	1
Fragmentation vs Spillover	H	TP1	0.55	4.96	<0.01
Fragmentation vs Spillover	H	TP2	0.43	3.98	0.01
Fragmentation vs Spillover	H	TP3	0.16	1.44	1
Spillover vs Temperature	B	TP1	-0.19	-1.92	0.99
Spillover vs Temperature	B	TP2	-0.40	-4.01	0.01
Spillover vs Temperature	B	TP3	-0.38	-3.85	0.02
Spillover vs Temperature	BU	TP1	0.13	0.75	1
Spillover vs Temperature	BU	TP2	-0.19	-1.1	1
Spillover vs Temperature	BU	TP3	-0.09	-0.47	1
Spillover vs Temperature	H	TP1	-0.21	-2.14	0.96
Spillover vs Temperature	H	TP2	-0.08	-0.85	1
Spillover vs Temperature	H	TP3	-0.20	-2.02	0.98
Precipitation	H vs B	TP1	0.01	0.19	1
Precipitation	H vs BU	TP1	-0.25	-2.26	0.91
Precipitation	B vs BU	TP1	-0.26	-2.4	0.83
Precipitation	H vs B	TP2	0.10	1.33	1
Precipitation	H vs BU	TP2	0.06	0.59	1
Precipitation	B vs BU	TP2	-0.04	-0.32	1
Precipitation	H vs B	TP3	-0.21	-2.8	0.48
Precipitation	H vs BU	TP3	-0.18	-1.66	1
Precipitation	B vs BU	TP3	0.03	0.25	1
Temperature	H vs B	TP1	-0.11	-1.57	1
Temperature	H vs BU	TP1	-0.49	-4.87	<0.01
Temperature	B vs BU	TP1	-0.38	-3.82	0.02
Temperature	H vs B	TP2	0.15	2.18	0.94
Temperature	H vs BU	TP2	-0.14	-1.37	1
Temperature	B vs BU	TP2	-0.28	-2.85	0.43
Temperature	H vs B	TP3	-0.13	-1.88	1
Temperature	H vs BU	TP3	-0.08	-0.82	1
Temperature	B vs BU	TP3	0.04	0.45	1
Composition	H vs B	TP1	-0.06	-1	1
Composition	H vs BU	TP1	-0.19	-2.25	0.92
Composition	B vs BU	TP1	-0.13	-1.57	1
Composition	H vs B	TP2	0.03	0.49	1
Composition	H vs BU	TP2	0.01	0.1	1
Composition	B vs BU	TP2	-0.02	-0.23	1
Composition	H vs B	TP3	0.09	1.61	1
Composition	H vs BU	TP3	0.11	1.37	1
Composition	B vs BU	TP3	0.02	0.28	1
Fragmentation	H vs B	TP1	-0.23	-2.37	0.85

Table S8 (*continued*)

Fragmentation	H vs BU	TP1	-0.35	-2.47	0.78
Fragmentation	B vs BU	TP1	-0.12	-0.86	1
Fragmentation	H vs B	TP2	-0.07	-0.69	1
Fragmentation	H vs BU	TP2	0.13	0.89	1
Fragmentation	B vs BU	TP2	0.19	1.35	1
Fragmentation	H vs B	TP3	-0.02	-0.24	1
Fragmentation	H vs BU	TP3	0.01	0.09	1
Fragmentation	B vs BU	TP3	0.04	0.25	1
Spillover	H vs B	TP1	-0.13	-1.02	1
Spillover	H vs BU	TP1	-0.84	-4.28	<0.01
Spillover	B vs BU	TP1	-0.70	-3.61	0.05
Spillover	H vs B	TP2	0.46	3.49	0.08
Spillover	H vs BU	TP2	-0.02	-0.13	1
Spillover	B vs BU	TP2	-0.49	-2.51	0.75
Spillover	H vs B	TP3	0.05	0.37	1
Spillover	H vs BU	TP3	-0.20	-0.98	1
Spillover	B vs BU	TP3	-0.24	-1.24	1
Precipitation	B	TP1 vs TP2	-0.17	-2.66	0.61
Precipitation	B	TP1 vs TP3	-0.25	-4.02	0.01
Precipitation	B	TP2 vs TP3	-0.08	-1.32	1
Precipitation	BU	TP1 vs TP2	0.06	0.48	1
Precipitation	BU	TP1 vs TP3	0.03	0.29	1
Precipitation	BU	TP2 vs TP3	-0.02	-0.20	1
Precipitation	H	TP1 vs TP2	-0.25	-3.96	0.01
Precipitation	H	TP1 vs TP3	-0.03	-0.52	1
Precipitation	H	TP2 vs TP3	0.22	3.45	0.09
Temperature	B	TP1 vs TP2	0.05	0.87	1
Temperature	B	TP1 vs TP3	-0.43	-7.62	<0.00
Temperature	B	TP2 vs TP3	-0.48	-8.48	<0.01
Temperature	BU	TP1 vs TP2	0.15	1.41	1
Temperature	BU	TP1 vs TP3	0.00	-0.04	1
Temperature	BU	TP2 vs TP3	-0.15	-1.45	1
Temperature	H	TP1 vs TP2	-0.21	-3.57	0.06
Temperature	H	TP1 vs TP3	-0.41	-7.11	<0.00
Temperature	H	TP2 vs TP3	-0.20	-3.59	0.05
Composition	B	TP1 vs TP2	-0.06	-1.36	1
Composition	B	TP1 vs TP3	0.02	0.53	1
Composition	B	TP2 vs TP3	0.08	1.89	0.99
Composition	BU	TP1 vs TP2	0.05	0.7	1
Composition	BU	TP1 vs TP3	0.17	2.28	0.9
Composition	BU	TP2 vs TP3	0.12	1.58	1
Composition	H	TP1 vs TP2	-0.14	-3.33	0.13
Composition	H	TP1 vs TP3	-0.12	-2.95	0.35
Composition	H	TP2 vs TP3	0.02	0.38	1
Fragmentation	B	TP1 vs TP2	-0.06	-0.66	1
Fragmentation	B	TP1 vs TP3	0.17	1.96	0.99
Fragmentation	B	TP2 vs TP3	0.23	2.61	0.65
Fragmentation	BU	TP1 vs TP2	0.26	1.58	1
Fragmentation	BU	TP1 vs TP3	0.33	2.04	0.98
Fragmentation	BU	TP2 vs TP3	0.07	0.45	1
Fragmentation	H	TP1 vs TP2	-0.22	-2.45	0.79
Fragmentation	H	TP1 vs TP3	-0.03	-0.36	1
Fragmentation	H	TP2 vs TP3	0.19	2.11	0.97
Spillover	B	TP1 vs TP2	0.26	2.06	0.98
Spillover	B	TP1 vs TP3	-0.24	-1.91	0.99
Spillover	B	TP2 vs TP3	-0.50	-3.94	0.01
Spillover	BU	TP1 vs TP2	0.47	2.06	0.98
Spillover	BU	TP1 vs TP3	0.22	0.92	1
Spillover	BU	TP2 vs TP3	-0.26	-1.1	1
Spillover	H	TP1 vs TP2	-0.34	-2.65	0.62
Spillover	H	TP1 vs TP3	-0.42	-3.31	0.13
Spillover	H	TP2 vs TP3	-0.09	-0.69	1

Table S8 (*continued*)

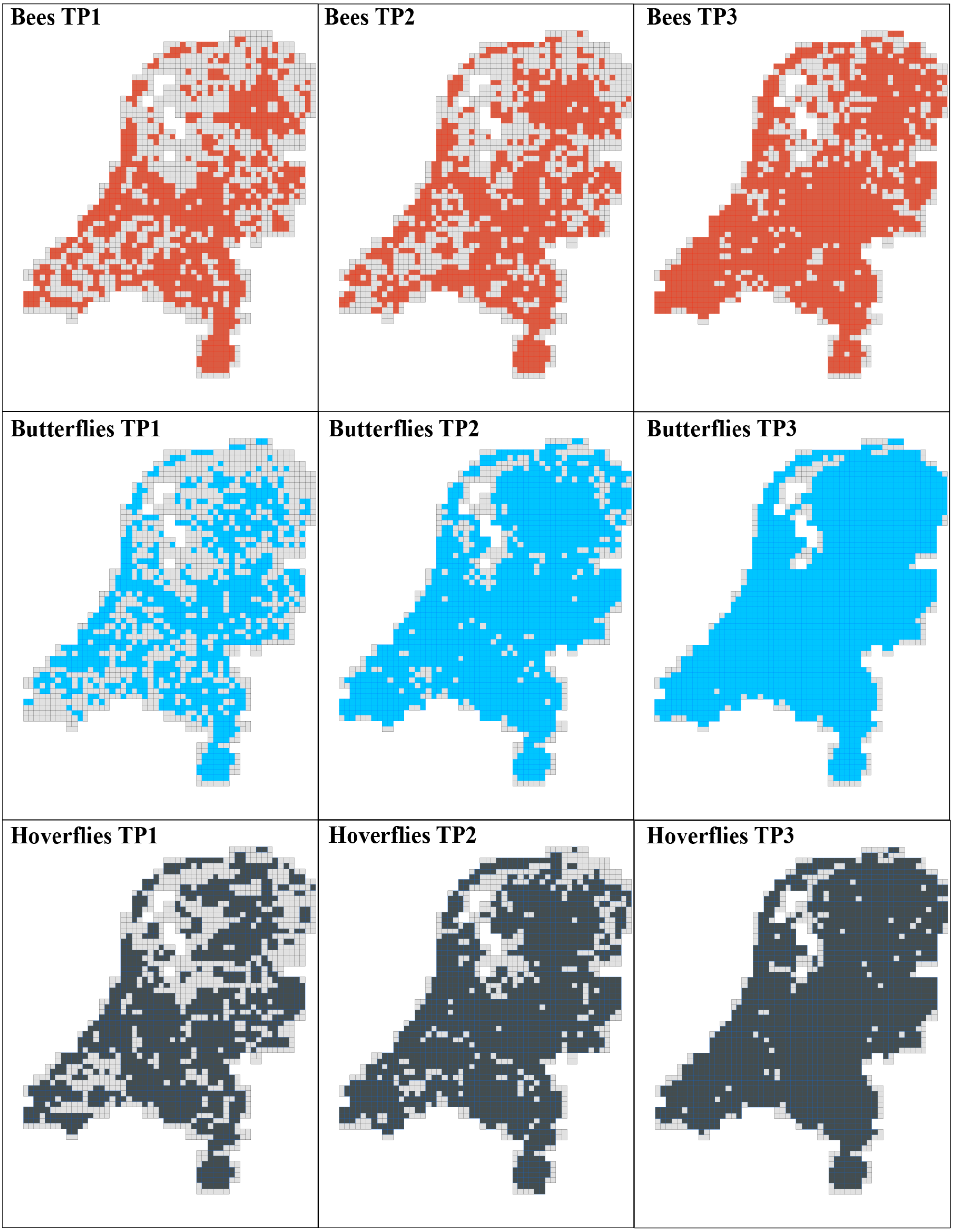

Figure S1. The distribution of the 5 × 5km landscapes (each cell in the map) in the Netherlands. Grey cells represent landscapes where no species were collected. Coloured cells represent landscapes where species were collected. The information is given for each of the three time periods analysed (TP1: 1951–1970, TP2: 1971–1990, TP3: 1998–2014) and for the three pollinator groups.

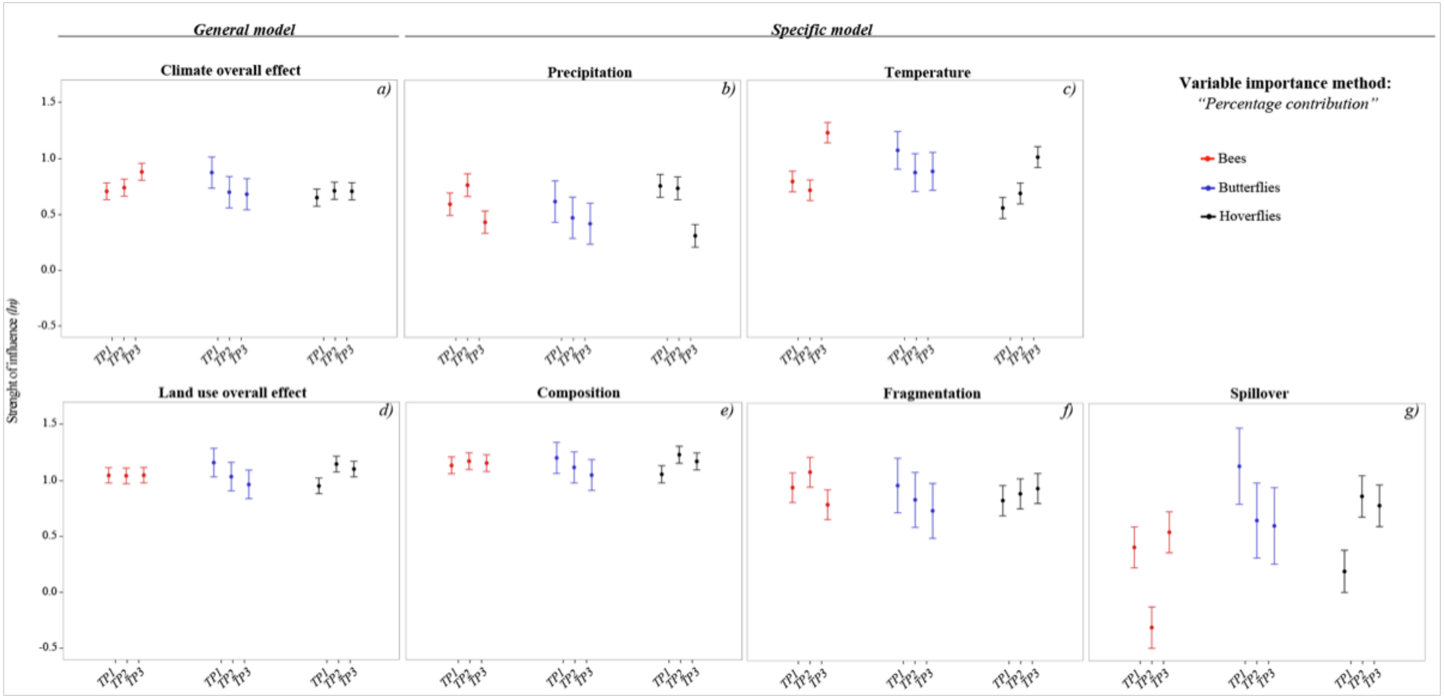

Figure S2. Extra analysis of variable importance with the "percentage contribution" evaluation criteria from MaxEnt. The absolute importance of climate (a–c) and land use (d–g) for limiting species distributions of different pollinator groups (bees, butterflies and hoverflies) across time (periods: TP1, 1951–1970; TP2, 1971–1990; TP3, 1998–2014). Values illustrate the average importance values ± 95% confidence intervals of variables that have an influence on species distributions of each pollinator group ("strength" of environmental variables, Gaussian model). For both climate and land use we present the overall effect ('general model') and the effect of the more detailed classes of environmental variables ('specific model'). The results show a similar pattern than the results obtained with the "Permutation Importance" method, except for Precipitation from which a weak decrease in importance across time is observed. For statistical details see Tables S3–S4.

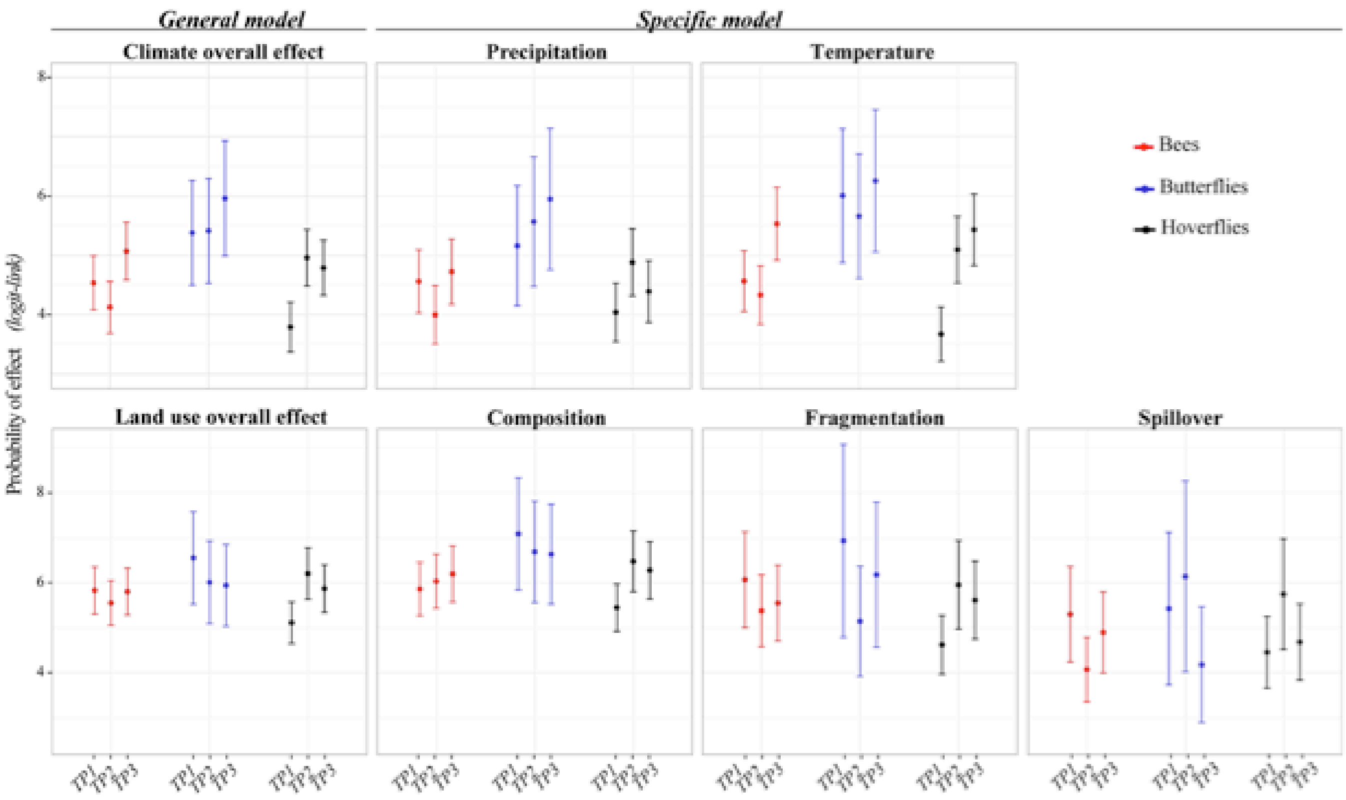

Figure S3. Importance of climate (upper row) and land use (lower row) for limiting species distributions of different pollinator groups (bees, butterflies and hoverflies) across time (periods: TP1, 1951–1970; TP2, 1971–1990; TP3, 1998–2014). Values illustrate the average importance ± 95% confidence intervals of variables that have an influence on species distribution of each pollinator group (Binomial model). For both climate and land use we present the overall effect (general model) and the effect of the more detailed classes of environmental variables (specific model). For statistical details see Tables S5 and S7.

5

Functional traits of pollinators explain contrasting range shifts related to climate and land use change

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Abstract

Changes in climate and land use can have important impacts on population persistence. Species respond to such environmental modifications by adapting to new conditions or by shifting their geographic distribution towards more suitable areas. However, the latter might be constrained by species' functional traits, that influence their ability to colonize or thrive in a habitat and to persist in the face of environmental changes. This study aims to test whether functional traits related to dispersal, reproduction, habitat use, and feeding can help predict how pollinator species respond to environmental changes and we use the Netherlands as our test site. We modelled species distributions from 470 pollinator species (bees, butterflies and hoverflies) using climate and land use data and analysed whether species traits (flight period, voltinism, habitat specialization, and larval food preference) of pollinators can explain areal range changes as well as latitudinal and longitudinal shifts over a period of more than 60 (1951–1970 vs. 1998–2014). Our results show that functional traits can help predict the extent (i.e. areal range changes) as well as the direction of pollinator range shifts (i.e. latitudinal or/and longitudinal) driven by environmental changes. However, taxonomic groups (e.g. bees and butterflies) may respond in contrasting manners given these environmental pressures and depending on their functional trait characteristics (e.g. dispersal, reproduction, habitat use, and feeding). For example while bees with greater habitat specialisation expanded more than generalists, for butterflies habitat generalists showed higher range expansions than habitat specialists. The majority of species (77–88%) expanded their ranges and shifted towards northern latitudes (22 ± 34 km for bees; 17.5 ± 25 km for butterflies; 19 ± 34 km for hoverflies), most bees shifted towards the west and butterflies towards the east. Bees mostly presented westwards shifts (14 ± 30 km) while butterflies showed predominant eastwards shifts (11 ± 21 km). Hoverflies did not show pronounced longitudinal shifts, and larval food preferences were key to explain their geographic range changes. Generalisations of species responses to climate and land use changes should not be made, responses greatly varying across and within taxa. Accounting for the species response traits when investigating future impacts of climate and land use changes on biodiversity can help predict biodiversity changes. Such information can improve biodiversity conservation and management

measures in face of global environmental changes.

Introduction

Changes in climate and land use can have severe effects on species distributions, which ultimately may also affect humanity by disrupting the supply of ecosystem services (e.g. pollination, carbon storage, clean water supplies, pest control, Lawler *et al.*, 2014; Mace *et al.*, 2012) . Around the world, changes in climate have intensified over the last decades with significant changes in precipitation patterns and increases in the occurrence of extreme weather events (Dawson *et al.*, 2011; Hansen *et al.*, 2012; IPCC, 2014) . Moreover, major and rapid land use changes have taken place during the first half of the century (~1950), e.g. in north-western (NW) Europe where habitat loss, agricultural expansion, and increases in the use of pesticides have been pronounced (Harms et al., 1987). In more recent decades, most large-scale land-use changes have ceased in such regions (Harms *et al.*, 1987; European Environmental Agency, 2011) , but highly modified landscapes and increases in nitrogen deposition levels remain key challenges for managing and conserving biodiversity (Sala *et al.*, 2000; Xiankai *et al.*, 2008; Steffen *et al.*, 2015) .

Changes in climate and land use conditions have resulted in observable shifts of species geographic ranges, including range contractions or range expansions and major changes in their north-south and east-west distributional extents (Lenoir & Svenning, 2015), and substantial biodiversity declines (Krauss *et al.*, 2010; Meyfroidt & Lambin, 2011; Fox *et al.*, 2014) . For conservation programmes to be effective, an in-depth understanding of how different drivers affect biodiversity is needed. However, it largely remains unclear how these drivers impinge on functional aspects of biodiversity, e.g. whether and how functional groups respond differently in the face of global environmental change (Thuiller *et al.*, 2006; Eskildsen *et al.*, 2015) .

Species have different functional traits, i.e. morphological, physiological, phenological, or behavioural characteristics that constrain their response to the environment ('response traits') and/or their effects on ecosystem properties ('effect traits') (Díaz & Cabido, 1997; Díaz *et al.*, 2013; Mori *et al.*, 2013) . Hence, the ability of species to modify their geographic distributions in response to changes in the surrounding environment may be limited or constrained by their functional traits (Flynn *et al.*, 2009; Bellard *et al.*, 2012; Díaz *et al.*, 2013) , leading to changes in functional diversity within a community (Thuiller *et al.*, 2006). This can in turn affect ecosystem functioning by the modifications in species richness or the species identity (Lavorel, 2013). Establishing the relationship between species distributional changes and functional traits is therefore of primary importance for ecologist and conservation biologists in the face of ongoing and expected future global change. To date, however, the importance of multiple functional traits for the long-term changes in species richness and population persistence remains underexplored.

Insect pollinators are key for ecosystem functioning, 60–80% of wild plants benefiting from animal pollination (Kremen *et al.*, 2007) . Moreover, they are especially sensitive to climate and land use modifications, which have been recognised as two of the main drivers of biodiversity homogenisation and pollinator loss around the world (Potts *et al.*, 2010; Giannini *et al.*, 2012; Carvalheiro *et al.*, 2013) . In Europe, only after 1990 more environmentally friendly policies have been implemented in order to counteract the effects these drivers of change on biodiversity (Kleijn & Sutherland, 2003) . These policies have been directed to increase (semi-) natural habitats (e.g. grasslands and forest) and also, in the case of agri-environmental schemes, to increase the feeding and nesting resources for insect biodiversity in agricultural landscapes (Kleijn *et al.*, 2001) . These policies may ameliorate the negative effects of climate and land use changes on insect pollinators, potentially explaining in part the slowing down of pollinator diversity declines detected in NW-Europe (Carvalheiro *et al.*, 2013) . However, it is still not clear if some species benefit more than others, and how functional traits determine the response of these pollinators to climate land-use change over longer periods of time.

Here, we investigate how response traits of flower-visiting insects (i.e. bees, butterflies and hoverflies; in the following referred to as ‘pollinators’) relate to changes in species distributions over a period of more than 60 years in the Netherlands. Habitat loss and fragmentation have been shown to be main determinants of pollinator distributions (Potts *et al.*, 2010; González-Varo *et al.*, 2013). Therefore, given that major land-use changes already ceased decades ago, and the increased investment in biodiversity friendly practices, we expect that pollinator species have expanded their ranges over the studied period. In particular, species habitat use (i.e. degree of habitat specialisation) and feeding habits (i.e. larval food preferences) might be key determinants of population persistence in a landscape given their relation with nesting and feeding resource availability (e.g. Clavel *et al.*, 2010; Weiner *et al.*, 2014) . Hence, we expect that these functional traits determine the extent of species range changes. More specifically, we predict that habitat generalists and species that do not depend on a few rare feeding resources have increased their distributional extent more than other more specialised species. Finally, owing to the increases in temperature and precipitation change during the last half-century (van Oldenborgh & Van Ulden, 2003; Klein Tank, 2004) , we expect that observed range shifts along latitude and longitude might be related with traits that enable species to reach faster any suitable areas in more distant locations over time More specifically we expect that range shifts are more accentuated for large-bodied species, with longer flight periods and more generations per year.

Methods

Study region and time periods

Our study region, the Netherlands, is located in NW-Europe, and has a temperate climate with cold winters (average minimum temperature of -1°C) and warm summers (average maximum temperature of 24°C) (KNMI, 2014). The most prominent land use systems are agriculture, which occupies almost half of the national territory, plus urban areas (Hazeu *et al.*, 2010). Biodiversity in the Netherlands has been intensely sampled since the early 19th century. The area has experienced major changes in climate (KNMI, 2014), and land use has been registered for more than 100 years (Hazeu *et al.*, 2010; Knol *et al.*, 2004). Moreover, strong modifications of biogeochemical flows have occurred in the last century, including major changes in phosphorus and nitrogen cycling (Steffen *et al.*, 2015). We grouped all data into two main time periods based on the observed changes in climate conditions given the increases in temperature and extreme weather events along the last half-century. Moreover TP1 was centred in the 1960 given the observed changes in land use conditions that occurred around that time period with high habitat fragmentation levels and land use changes to more anthropogenic habitats, as agriculture and urban areas (Hazeu *et al.*, 2010; Knol *et al.*, 2004). These two periods correspond to years for which land use data of high accuracy were available (see the land use data section below). These two time periods were centred on the years for which the land use data were available (1960, 2008), and encompassed a 10 years before and after for the species distribution data in period 1 (1951–1970) and a 10 years and 7 after for period 2 (1998–2014). We used these two time periods to analyse spatial changes in pollinator species distributions from the past to the present.

Species distribution data

Three important flower visitor taxa (in the following referred to as 'pollinators') were considered in our study: bees (Hymenoptera: Apoidea), butterflies (Lepidoptera: Papilionoidea and Hesperioidea), and hoverflies (Diptera: Syrphidae). The occurrence records for each species were obtained for bees and hoverflies from the European Invertebrate Survey (EIS-Nederland, www.eis-nederland.nl) and for butterflies from the Dutch National Database of Flora and Fauna (NDFF, www.ndff.nl). The quality of species identification and the location accuracy of occurrence records has been assessed by the EIS and the NDFF (see www.ndff.nl/validatie). Since older species occurrence records have usually a higher uncertainty in their geographic location than newer records, we accounted for this uncertainty by compiling all occurrence records at a relatively coarse resolution of 5 × 5 km grid cells. We included only species that were present (1) in at least five 5 × 5 km grid cells, (2) in each of the two time periods, and (3) in the gap period (1971–1997). The latter was done to represent all species that have been present in the study area since the 1950s. This guarantees robust species-environment responses in the modelling process (see below) and allowed analysing the distribution patterns of a total of 207 bee species, 61 butterfly species, and 202 species of hoverflies (Table S1).

Species distribution modelling

For constructing species distribution models (SDMs) we obtained various climate and land use data that can have an impact on the survival and distribution of pollinators. For climate, maximum, minimum and average values of temperature and precipitation per grid cell were obtained from the project “ClimateEU: historical and projected climate data for Europe” (Wang *et al.*, 2012). Climatic data were extracted at the same resolution as the species distribution data (5 × 5 km grid cells) and then used to calculate the 19 bioclimatic variables as described in Hijmans *et al.,* (2005). After correlation analyses of all bioclimatic variables we selected four precipitation-related variables (all in mm) and five temperature related-variables (all in °C): annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation of warmest quarter, mean diurnal temperature range, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter and mean temperature of warmest quarter. These climate variables showed low to intermediate correlation coefficients (Pearson’s correlation $\leq |0.75|$) among each other.

Land use data were obtained from the geo-information department of Wageningen University (www.wageningenur.nl) for both time periods at an original resolution of 25 × 25 m. Both land use maps for period 1 and 2 had a high land use classification accuracy (~95% and 85% respectively) (Hazeu *et al.*, 2010; Knol *et al.*, 2004). The land use maps were obtained for the years 1960 (representing period1) and 2008 (period 2), which both are the central points in each time period for which the species data were aggregated. The newer land use map had a higher thematic resolution than the older land use map. Hence, both maps were reclassified to make land use types consistent between time periods. Eight land use types were extracted: agriculture, grassland, forest, moors/peat, sandy soils, swamps, urban and water. Based on these reclassified land use maps for each 5 × 5 km grid cell and time period we calculated a total of twelve land use metrics that have been shown to impact the distribution and richness of pollinators (see Aguirre-Gutiérrez *et al.*, In press): % of each land use class (eight classes), number of land use classes, total edge density (m/ha), average patch area of suitable habitat (ha) and the edge density between managed and natural systems (m/ha). These metrics characterized three major aspects of landscape and habitat structure (Tscharntke *et al.*, 2012): landscape composition (nine metrics), habitat fragmentation (two metrics) and spillover potential (one metric) (see below).

For landscape composition, the calculated metrics reflected the percentage of each land use type per grid cell (eight land use types) as well as the total number of land use classes per grid cell (one metric). The total number of land use classes was included as a proxy of spatial heterogeneity, which can influence the turnover of pollinator species assemblages (Tscharntke *et al.,* 2012). We represented habitat fragmentation with two metrics: the average area of suitable habitat patches and total edge density (total length of edges per hectare). For the former, we classified the land use classes grassland, moors/peat, forest and sandy soils as suitable habitat, and agriculture, urban, water and swamps as non-suitable habitat (Vogiatzakis *et al.*, 2015). For the latter, we calculated the density of edges between all land use types in a grid cell. We used one additional metric to characterize species spillover potential, i.e. the potential for movements of organisms across managed and natural systems (Rand *et al.*, 2006). For this, we considered the land use types grassland and agriculture as (intensively-) managed, and the land use types moors/peat, forest, swamps and sandy soils as (semi-)natural systems. We then calculated the edge density between these two systems. Urban and water were not taken into account in this calculation. All calculations of land use metrics were carried out in R (Development Core Team, http://cran.r-project.org) with the "SDMTools" package.

With the data on species occurrences, climate and land use we constructed SDMs for each bee, butterfly and hoverfly species for both period 1 and 2 using MaxEnt (Phillips *et al.*, 2006). MaxEnt is a machine learning modelling technique with high model accuracy that has been extensively used for modelling large sets of species in locations with contrasting environmental conditions (Elith & Graham, 2009). We selected MaxEnt after comparing it with other SDM algorithms (generalized boosting models, generalized linear models, random forest, artificial neural networks) for modelling a range of species with different sample sizes and different geographic distributions within the same study area, as it was one of the best performing algorithms with high model sensitivity and specificity (see Aguirre-Gutiérrez *et al.*, 2013). In MaxEnt, we allowed more complicated models (use of different features types) depending on the number of records available as described in Phillips & Dudik (2008) and Elith et al., (2011). As species sampling collections are often geographically biased, this can also create bias in the environmental gradient selection. To account for this, we followed Phillips *et al.,* (2009) and Mateo *et al.,* (2010) and only extracted background information for the SDMs from those collection localities where species from the same pollinator group had been sampled. This procedure has been shown to greatly increase model performance (“target group approach”) (Phillips *et al.*, 2009; Mateo *et al.*, 2010)It aids to account for possible sampling and environmental selection biases because the modelled data contains the same collection bias as the data used for the background selection (Elith *et al.*, 2011). In order to account for within algorithm model variation, we computed SDMs for each species using ten repetitions with a bootstrap approach where 80% of the data was used for training and 20% for model testing. Model performance per species was summarized with the area under the curve (AUC) values of the receiver-operating characteristic (Hanley & McNeil, 1982). AUC is a common measure of SDM performance and values range from 0 to 1, with higher scores often though to refer to higher model accuracy(but see Raes & ter Steege, 2007). However, recently it has been shown that these values are constrained by the fraction of the geographic area covered by each species, often with low AUC values for species with big sample sizes and hence a decrease in AUC values as the number of sampling records increases, which could influence the selection of models based only on AUC values (Phillips *et al.*, 2006; Raes & ter Steege, 2007). Given this and to avoid basing the model selection on AUC values alone we obtained an ensemble model for each species by averaging the suitability scores across ten model repetitions and used this ensemble model in subsequent analysis. We applied the MaxEnt logistic output format (Phillips & Dudik, 2008) to convert the ensemble suitability maps into binary maps (presence-absence) using the threshold that maximises the sensitivity and specificity of the model (Jiménez-Valverde & Lobo, 2007). These binary distribution maps were then used to analyse the spatial changes in pollinator distributions (see below).

Spatial changes in pollinator species distributions

We quantified three different aspects of spatial range changes based on modelled species distributions between the two time periods: (1) areal range changes (contractions and expansions), (2) latitudinal range shifts, and (3) longitudinal range shifts.

Areal range changes were calculated between time periods as the percentage gain or the percentage loss in geographic range size of each species using the “biomod2” R package (http://cran.r-project.org). We used linear models with Gaussian error structure to test if areal range changes of pollinator groups differed significantly from zero and between time periods. Using the pollinator group (bees, butterflies and hoverflies) as explanatory variable. To normalize residuals, we used the natural log of the ratio of areal range change as response variable. We then used a post-hoc pairwise comparison test (TukeyHSD) to assess whether the three pollinator groups differed significantly in areal range changes between the two time periods.

To assess latitudinal and longitudinal range shifts (north-south, east-west) for each species of the three pollinator groups, we used the centroids of the predicted (binary) species distribution maps for period 1 and 2 and calculated the difference in latitudinal and longitudinal location (in kilometres). This was done using the directional distribution tool in ArcGIS (v10.1 ESRI Redlands, CA). Values of zero reflect no change in the latitudinal or longitudinal midpoint of a species geographic range between periods, values above zero indicate range shifts towards northern or eastern locations, and values below zero represent range shifts towards southern or western locations. We applied Students *t*-tests for each pollinator group to quantify whether differences in latitudinal or longitudinal midpoints differed significantly between the two time periods.

Species traits and geographic distributions

To analyse if pollinator species traits can explain changes in species distributions, we compiled information on traits related to the pollinators susceptibility to climatic and land-use changes. The traits can therefore be considered as response traits *sensu* Díaz *et al.* (2013). For each pollinator group, a total of five functional traits were considered (Table 1). Traits related to species responses to land use change were habitat specialization (specialists or generalists) and food larval preference (bees: lectic status; butterflies: larval host plant specialization and Ellenberg nitrogen value of host plant; hoverflies: larval food type, animals or others). For traits related to species responses to climate change we considered flying period (number of weeks of flight) and voltinism (number of generations per year). We also considered body size, a trait that influences dispersal ability and hence may affect how species respond to both land use and climate changes. These traits were selected to capture several key aspects of species' life histories (dispersal, reproduction, habitat use and feeding habits). Traits were obtained for bees from S. P. Roberts from the “ALARM” project (www.alarmproject.net), for butterflies from Bink (1992), WallisDeVires (2014) and van Swaay *et al.,* (2006), and for hoverflies from the “Syrph the Net” database (Speight *et al.*, 2000) and Reemer *et al.,* (2009). For the Ellenberg nitrogen value of host plants for butterflies we gathered information on the larval host plant use published in the North European literature on butterflies (Geraedts, 1986; Heath & Emmet, 1989; Eliasson et al., 2005). Based on this information and the Ellenberg nitrogen indicator values, describing the soil fertility conditions and nitrogen preferences of larval host plants (Ellenberg et al., 1991; Fujita et al., 2013), we calculated an average Ellenberg nitrogen indicator value of host plants used by each butterfly species (Table 1).

Table 1. Functional traits of pollinators (bees, butterflies, hoverflies) and their relation to global change drivers. The related global change driver refers to either climate and/or land use which is expected to have a stronger relation with the given trait that mediates the response of the species.

Pollinator group	Trait	Trait category	Type	Related driver	Units	Description
All groups	Flight period	Dispersal	Continuous	Climate	Count	Number of flying weeks per year
All groups	Body size	Dispersal	Continuous	Climate / Land use	Millimetres	The specific measure of body size varies per pollinator group and we hereafter referred to it as ‘body size’. Measured as the intertegular distance for bees, wing size for butterflies, and body length for hoverflies.
All groups	Voltinism	Reproduction	Categorical	Climate	Univoltine or multivoltine	Number of generations per year. The number of life cycles that a species completes during a year. Univoltine species have one generation per year whereas multivoltine species have two or more generations per year.
All groups	Habitat specialisation	Habitat use	Categorical	Land use	Specialist or generalist	For bees, specialist species have only one habitat type and generalists more than one. The butterfly classification was made by distinguishing between anthropogenic (agricultural and urban) and (semi-)natural habitats shown on the biotope classification of European butterflies according to CORINE habitats. Generalist butterflies are species predominantly associated with anthropogenic habitats and specialists with (semi-)natural habitats. For hoverflies, habitat specialisation refers to the macro-habitats (CORINE land use) where the adult hoverflies are found, as specified in Speight et al. (2000).
All groups	Larval food preference	Feeding	Categorical	Land use	Non-polyphagous or polyphagous for bees. For butterflies the values range from 1 to 4; animals vs. other for hoverflies	For bees, their lectic preference is used, which is related to pollen and nectar resources. Non-polyphagous bees correspond to mono and oligolectic species. For butterflies, smaller values represent species that feed on one or few plant species and species with higher value feed on a varied range of plant species. For hoverflies, larval food is categorised according to whether they feed on living animals or other, which refers to plants and/or organic matter.
Butterflies	Larval food preference	Feeding	Continuous	Land use	Ellenberg nitrogen value	Nitrogen value of host plants. The values are based on information obtained for the larval host plant use and the Ellenberg nitrogen indicator values, describing the soil fertility conditions and nitrogen preferences of larval host plants.

*1: S.P.M. Roberts. Compilation of trait data of European bees from published sources (see www.alarmproject.net); 2: Bink (1992); 3: WallisDeVires (2014); 4: Speight *et al.*, (2000); 5: Reemer *et al.*, (2009); 6: Van Swaay *et al.*, (2006); 7: Geraerdts (1986); 8: Heath and Emmet (1989); 9: Eliasson *et al.*, (2005); 10: Ellenberg *et al.*, (1991); 11: Fujita *et al.*, (2013).

To analyse if and to what extent functional traits can explain the species areal range changes and latitudinal and longitudinal shifts we applied multivariate linear models with a Gaussian error structure. As range changes and latitudinal and longitudinal shifts may depend on the initial range size (number of occupied 5 × 5 km cells) of a species (i.e. in period 1), we included this as a control explanatory variable in all models. We further tested for all two-way interactions between predictor variables because combinations of functional traits may be involved in species responses to climate and land use modifications. To normalize residuals, we used the natural log of the ratio of areal range change, and the latitudinal as well as the longitudinal centroid shifts as response variables. All continuous explanatory variables were standardized and centred before analysis. We selected the most parsimonious model based on the Bayesian Information Criteria (smallest BIC) using the R package "MuMIn" (Barton, 2014). For comparison, we also kept all candidate models with BIC Δ< 2.Where relevant, we also show the results of the second best model (see results section). Model selection based on the BIC criteria was chosen because the number of degrees of freedom was very high and, in comparison to AIC, this method penalizes more complex models by excluding terms that only explain very reduced amounts of data variability (Johnson & Omland, 2004; Aho *et al.*, 2014).

Results

SDM performance

The implemented SDMs mostly showed fair to good AUC values. Overall, AUC values in period 1 (1951–1970, see Table S1) ranged from 0.62 to 0.98 (average of 0.82±0.08 SD) across all species. AUC values for period 2 (1998–2014) had a similar average of 0.80 (±0.11 SD), but a slightly wider range from 0.5 (three widely distributed butterfly species) to 0.99. AUC values are generally dependent on the number of records and hence the lowest values were commonly obtained for species with large sample sizes. AUC values also increased with a decreasing number of records decreased (*Pearson's coefficient* -0.73 for period 1 and -0.82 for period 2). Thus, lower AUC values did not point towards less well performing models, which were also supported by visual inspection of the species distribution maps and the species record locations.

Spatial changes in pollinator species distributions

Initial range sizes of all species covered <25% of the study area. Most species expanded their distributional range from period 1 (1951–1970) to period 2 (1998–2014) (Fig. 1a). For bees, about 83% of the species showed range expansions, 16% range contractions, and 1% no change. For butterflies, 77% of the species expanded their ranges and 23% showed range contractions. For hoverflies, 87.5% of the species showed range expansions and 12.5% range contractions. Overall, range size changes of hoverflies were significantly more accentuated than those of the two other pollinator groups (Fig. 1a; statistical details in Table S2).

Beyond areal range changes, the three pollinator groups also showed substantial latitudinal and longitudinal range shifts (Fig. 1b and Fig. 1c). From period 1 to period 2, all three pollinator groups shifted significantly northwards (Fig. 1b, Table S3), with an average of 22 ± 34 km for bees (mean ± SD), 17.5 ± 25 km for butterflies, and 19 ± 34 km for hoverflies. Longitudinal range shifts were less pronounced than latitudinal ones (Fig. 1c). However, bees shifted significantly westwards (on average 14 ± 30 km; Table S3) and butterflies significantly eastwards (on average 11 ± 21 km). Hoverflies showed, on average, no statistically significant longitudinal shifts (Table S3).

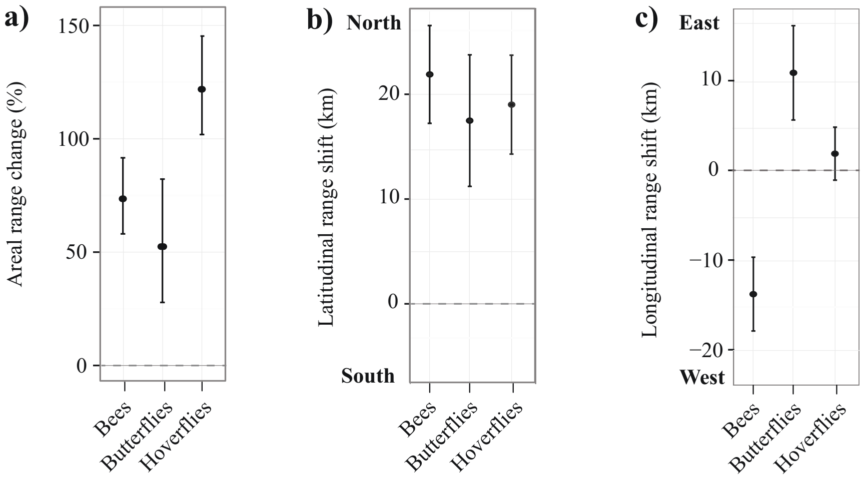


Figure 1. Spatial changes in species distributions of pollinators (bees, butterflies, hoverflies) between period 1 (1951–1970) and period 2 (1998–2014). Three aspects of species distributional changes are captured. (a) Areal range

changes (% change in geographic range size between period 1 and 2); (b) latitudinal range shifts (latitudinal change of the range centroid between periods, with positive values representing northward shifts and negative values southwards shifts, in km); (c) longitudinal range shifts (longitudinal change of the range centroid between periods, with positive values representing eastward shifts and negative values westward shifts, in km). For all spatial range changes, the mean ± 95% confidence interval across all species within a pollinator group is presented. Statistical tests of differences among pollinator groups and time periods are given in Table S2–S3.

Species traits and geographic distributions

Areal range changes were mostly explained by traits related to habitat specialisation, larval feeding habits, body size and flight period (Fig. 2, Table 2 and Table S4). Habitat specialization influenced species distributional changes of all three pollinator groups (Figs. 2a–c). However, the direction of the effect differed among groups. While for butterflies, more specialised species showed range contractions whereas generalists showed range expansions (Fig. 2b), bees with greater habitat specialisation expanded more than generalists (Fig. 2a). For hoverflies, areal range changes depended on species' initial range sizes: specialists expanded slightly more than generalists but only if species had small initial range sizes (Fig. 2c; Fig. S2; Table 2 and Table S4). For species with large initial ranges no differences were found between generalists and specialists. Larval feeding habits only affected the patterns of change for hoverflies. For this group, species with larvae feeding on animals presented greater areal range expansions than species feeding on other resources such as plants and organic matter (Fig. 2d). This effect was however constrained by the length of their flight period; species with longer flight periods generally showed more accentuated range expansions than species with shorter flight seasons. Body size also played an important role for hoverfly's areal range changes with large-bodied species showing on average more areal range expansions than small-bodied species (Fig. 2e).

Table 2. (next page) **Best models obtained during the analyses of areal range changes, latitudinal and longitudinal shifts and their relation to the species functional traits of pollinators (bees, butterflies, hoverflies).** For a detail version of the table see Table S4.

	Pollinator group	Best models	Explanatory variables selected					Adj. R²	BIC	Δ BIC
Areal range change	*Bees*	*1*	H	IR	–	–	–	0.23	273.1	
		2	–	IR	–	–	–	0.21	274.2	1.1
	Butterflies	*1*	H	–	–	–	–	0.38	130.3	
	Hoverflies	*1*	F × LFP	IR × H	S	–	–	0.37	305.1	
		2	F × LFP	IR	S	H	–	0.34	305.3	0.2
Latitudinal shift	*Bees*	*1*	IR	–	–	–	–	0.05	-404.2	
		2	IR	S	–	–	–	0.07	-403.7	0.5
	Butterflies	*1*	F × ND	H × ND	H × IR	–	–	0.40	-170.6	
		2	H × ND	H × IR	–	–	–	0.32	-168.8	1.7
	Hoverflies	*1*	V × LFP	IR	–	–	–	0.21	-452.6	
Longitudinal shifts	*Bees*	*1*	–	–	–	–	–	–	-143.4	
		2	F	–	–	–	–	0.02	-142.5	1
		3	V	–	–	–	–	0.02	-142.1	1.3
	Butterflies	*1*	F × V	F × H	F × IR	V × IR	–	0.45	-119.3	
		2	F × V	F × H	F × IR	V × IR	H × IR	0.47	-118.8	0.5
		3	F × V	–	–	–	–	0.26	-117.7	1.6
		4	F × V	F × H	F × IR	–	–	0.39	-117.4	1.9
	Hoverflies	*1*	LFP	IR	–	–	–	0.08	-240	

F: Flying period; LFP: Larval food preference; H: Habitat; ND: Larval food preference related to Ellenberg nitrogen value of diet; S: Body size; V: Voltinism; IR: Initial range.

Latitudinal shifts also depended on species functional traits. However, the role of the traits greatly varied between groups (Fig. 3; Table 2). For bees, body size was the only trait that influenced latitudinal range shifts (Fig. 3a; Table 2, see 2nd best model). Small-bodied bee species presented shifts towards higher latitudes that were slightly more pronounced than those detected for large-bodied species (Fig. 3a). For butterflies and hoverflies, larval food preferences often influenced their latitudinal shifts, although its effect depended on other traits (Table 2). For butterfly species that had generalists habitat preferences, species whose larvae feed on nitrophilous plants (plants adapted to high nitrogen conditions) had stronger shifts towards northern locations than species feeding on non-nitrophilous plants . However, if species were specialized in a given habitat, the trend was reverse, species feeding on non-nitrophilous plants having more accentuated northward shifts (Fig. 3b). The effect of larval feeding habits also interacted with flight period: for butterfly species feeding on non-nitrophilous plants, species with shorter flight periods had more accentuated shifts towards southern locations (Fig. 3b). For species feeding on nitrophilous plants the length of the flight period had little effect. For hoverflies, the influence of larval food preferences depended on voltinism (Fig. 3c): univoltine species with larval feeding on plants and other organic matter presented stronger shifts towards northern locations than hoverfly species feeding on animals. This pattern was not evident multivoltine hoverflies (Fig. 3c). Initial range size also influenced butterfly patterns of change, with habitat specialists with large range sizes shifting more towards northern locations than species with small range sizes (Table S4).

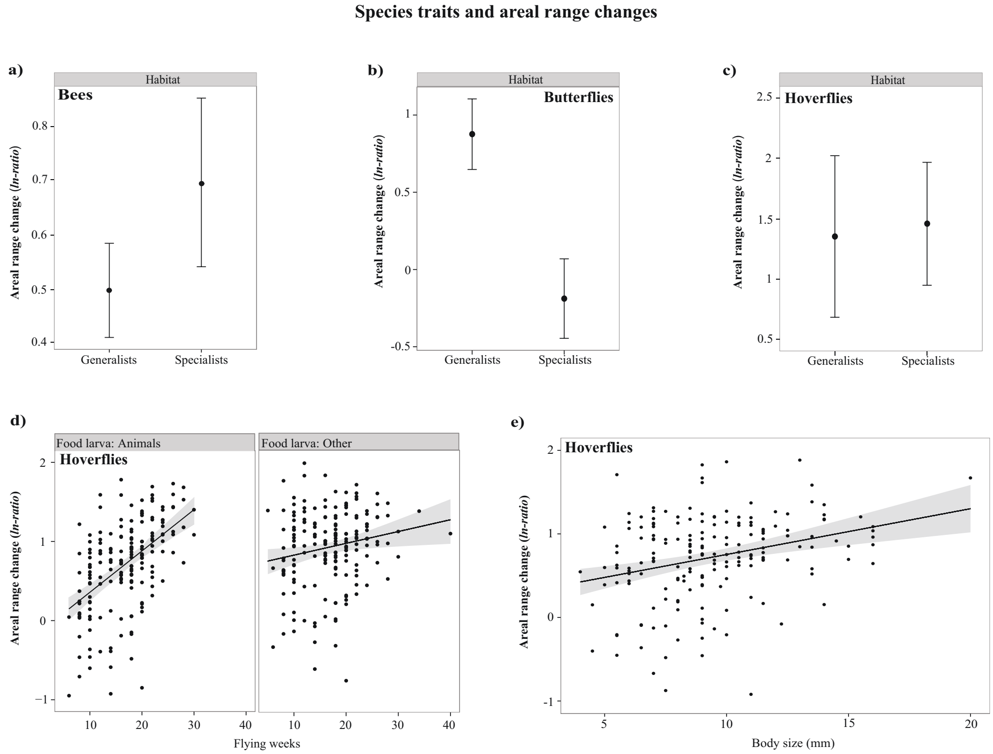


Figure 2. Relation between species traits and areal range changes of pollinators (bees, butterflies, hoverflies). (a) Bee habitat specialists have on average larger areal range expansions than generalists. (b) Butterflies show an opposite trend, with habitat generalists presenting range expansions and habitat specialists range contractions. c) Hoverfly habitat specialists presented a mild stronger areal range expansion than generalists, however, this difference with generalists is not as strong as for bees and butterflies (mean ± 1SD shown only for species with small initial ranges, first quartile of the data, for comparison purposes with bees and butterflies; See Table S2 for the full data plot). (d, e) Hoverfly's areal range changes depend on larval food, length of flight period, and adult body size. Areal range changes of hoverflies with larval feeding on animals are more strongly dependent on length of flight period than species with larval feeding on other resources (d). Large-bodied hoverfly species increase their range size more strongly than small-bodied species (e). For all plots the average prediction ± 95% confidence intervals are shown. For statistical details see Table S4.

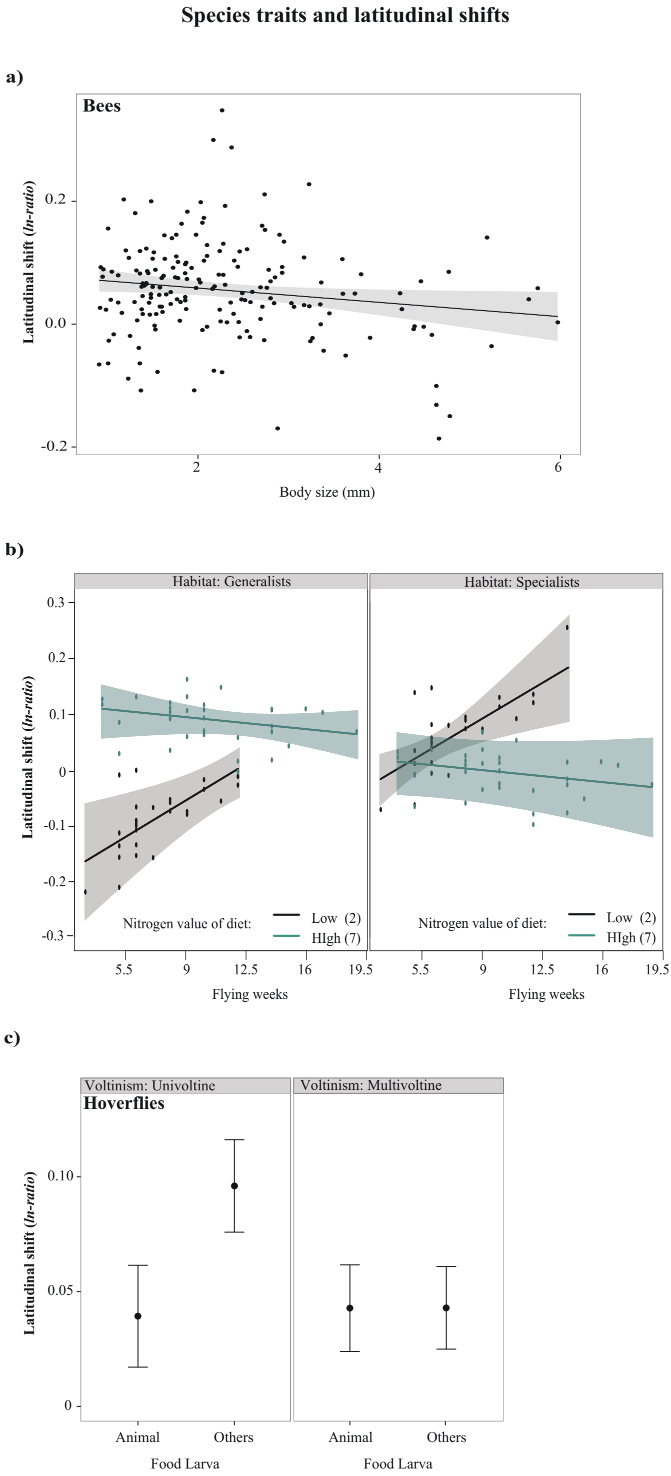
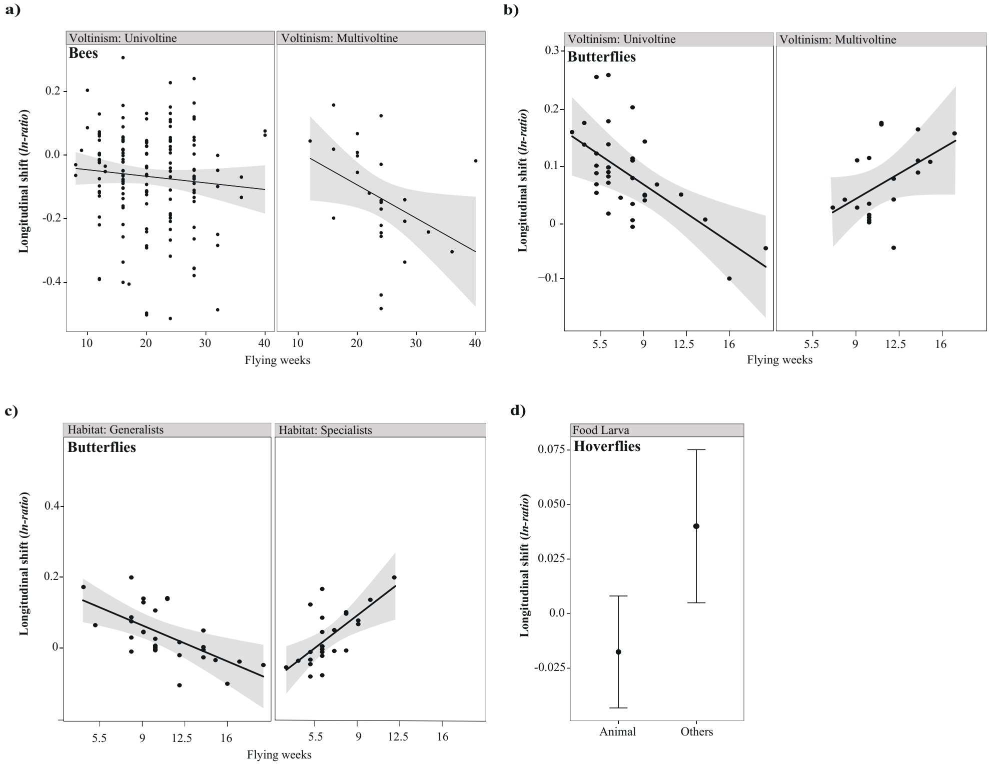


Figure 3. Relation between species traits and latitudinal range shifts of pollinators (bees, butterflies, hoverflies). (a) Effect of bee body size on latitudinal range shift, with smaller species shifting more towards northern locations than larger species. (b) Butterfly latitudinal range shifts depend on habitat use and larval host plant use. Habitat generalists with larval host plants that have high nitrophily values and habitat specialists with larva host plants that show low nitrogen levels shifted towards more northern latitudes. Moreover, butterfly species with shorter flight periods show stronger shifts towards southern latitudes than species with longer flight periods, but only when larval host plants have low nitrophily values. (c) Finally, hoverfly's latitudinal range shifts depend on voltinism and larval food plants, with univoltine species that have larval feeding on other resources than animals presenting more northwards shifts than animal feeder species. For butterflies the partial residual (i.e. residuals after removing the effect of all other variables) are shown. For all plots the average prediction ± 95% confidence intervals are shown. For statistical details see Table S4.

Longitudinal range shifts were also influenced by several traits: the length of the flight period, voltinism, habitat specialisation and larval feeding habits (Table 2 and Table S4). Bees with longer flight periods and with multiple generations per year presented on average stronger shifts towards western locations than univoltine species with shorter flight periods (Fig. 4a). For butterflies the opposite trend was found, , i.e. species with long flight periods had stronger shifts towards eastern locations than species with short flight periods (Fig. 4b). The effect of flight period length was also constrained by habitat specialisation (Fig. 4c) and initial range size of butterfly species (Table 2). Butterfly habitat generalists with short flight periods as well as habitat specialists with long flight periods showing stronger shifts towards eastern locations (Fig. 4c). Butterfly species with longer flight period and large initial range sizes expanded more towards the east than other butterfly species (Table S4). Moreover, univoltine butterfly species with larger initial ranges presented stronger shifts towards the east than multivoltine species (Table S4). For hoverflies, larval feeding preferences were the most important trait to explain longitudinal range shifts (Fig. 4d; Table 2). Hoverfly species with larval feeding on animals tended to shift towards the west whereas species feeding on other sources (plants/organic material) tended to shift towards the east (Fig. 4d). Initial range size also played a role, with large-ranging hoverflies showing stronger shifts towards eastern locations (Table S3 and Table S4).

Fig. 4. (next page) **Relation between species traits and longitudinal range shifts of pollinators (bees, butterflies, hoverflies).** (a) Multivoltine bee species with longer flight periods show stronger shifts towards western locations than univoltine species. (b) Butterflies responded in the opposite direction than bees, with multivoltine species that have longer flight periods shifting towards more eastern locations, and univoltine species with longer flight periods shifting towards more western locations. (c) Butterfly habitat specialists increased their shifts towards eastern locations as their flight period increased and habitat generalists showed no shifts or shifts towards the west with increases in flight period. (d) Finally, hoverfly species with larva feeding on plants and other organic material shifted towards eastern locations whereas species with larval feeding on animals shifted towards more western locations. For statistical details see Table S4.

Species traits and longitudinal shifts



Discussion

Recent studies have suggested that pollinator diversity recovered during recent decades in NW-Europe (Carvalheiro *et al.*, 2013). Subsequent studies have evaluated the role of specific climatic and land use drivers on pollinator species long term patterns of change (e.g. Aguirre-Gutierrez et al. *in press*; Aguirre-Gutierrez et al. *in prep.*). However, the role that the species traits play in the responses of biodiversity to climatic and land use changes is still far from being clearly understood (Parmesan *et al.*, 2013). In this study we use detailed information on species occurrence, climate and land use and show that functional traits can help predict the extent as well as the direction of pollinator species range changes driven by environmental changes. We show that following our expectations species with initial narrow distributions (IR) increased their ranges during this last half century. This has been probably as a result of the increase in biodiversity conservation policies adopted in the Netherlands, and in general in

NW-Europe, during the last decades. Moreover, we show that both, habitat use and feeding habits related traits can explain the observed patterns in areal range changes and geographic shifts of the three pollinator groups but that their responses can be contrasting (e.g. between bees and butterflies). The impacts of body size, flight period and voltinism varied per pollinator group and often interacted with other traits. Below we discuss the details and the ecological implications of our findings.

Species traits and areal range changes

Our findings show pronounced pollinator range expansions (50–70% for bees and butterflies, and of more than 100% for many hoverflies) over the whole time period here analysed (>60 years). Other studies as in Carvalheiro *et al.,* (2013) have shown a pattern of decreases in species losses or even increases in pollinator diversity for the study area. Our study allows us to go further than only detecting patterns of change of species distributions but also evaluate in detail which species in each pollinator group are responsible for the observed change distribution patterns.

Areal range changes of bees were on average more accentuated for species with greater habitat specialisation (Fig. 2a), for hoverflies this depended on the initial range size (Fig. S1) and for butterflies this occurred for generalist species. More specialized species tend to have a smaller range, and are hence more likely to increase their ranges than the most widely distributed species (generalists) (Table 2 and Table S4; Fig. S2). However, the effect of specialization was significant over and above the effect of size of initial range, indicating that when comparing species with similar initial ranges, specialised species expanded more than generalist species. This suggests that habitat resources for specialist species have become more widely available along the last half century, while habitat resources for generalist species have been kept relatively constant. Indeed, in the Netherlands forest cover has increased generating a varied source of nesting and feeding habitats along the forest structure gradient (shrub–trees), which has positive impacts on the bee composition favouring specialist species (Grundel *et al.*, 2010). This has been also shown to have positive impacts on hoverflies, especially on saproxylic species (Reemer etl al. 2005). The fact that for butterflies more generalist species have increased more their ranges points to also increases in the anthropogenic habitats, e.g. urban areas, which have come more readily available in the study area.

Our results show average areal range expansions for hoverflies, a pattern also that started to be observed already by past studies (Reemer *et al.*, 2003). Hoverflies areal changes were particularly influenced by traits that are related with dispersal ability, such as length of flight period and body size. The positive effect of flight period length and body size was expected given that these species can reach distant suitable habitats more easily, and given their longer flight periods, may be more adapted to a wider range of climatic conditions (Sullivan *et al.*, 2000; Chown & Gaston, 2010). Indeed, species with shorter flight period have a higher risk of suffering declines (Sullivan *et al.*, 2000). However, the positive effect of length of flight period was mostly detected for species whose larvae feed on animals in comparison to species with larva feeding on plants or organic matter (Fig. 2d). These increases may be partially explained by the continuous in the availability of crop fields along the latitudinal gradient of the Netherlands from which aphid eaters may specially benefit. Other (semi-) natural (e.g. floral) feeding resources have become more fragmented in the landscape mainly driven by the increases in intensive agriculture and urban areas (Jongman, 2002), which could also explain the marginal effects on other hoverflies species.

Species traits and latitudinal shifts

Given the ongoing increases in temperature (Klein Tank, 2004; IPCC, 2014), latitudinal shifts are expected for several biodiversity groups (Chen *et al.*, 2011). The three pollinator groups presented average northward range shifts of 17.5–22 km since the 1950s. These results suggests that climatic drivers, especially those related to changes in temperature, may be highly important for setting current species limits in their latitudinal range (Lenoir & Svenning, 2015). Moreover, it has been suggested that climatic drivers may become more important in the future for limiting species distributions (Diez *et al.*, 2012). Given that most strong land use changes have already occurred in the study are in past decade (Harms *et al.*, 1987; European Environmental Agency, 2011), the effects of changes in climatic conditions seem to pose one of the main threats for pollinators.

Latitudinal shifts in bees were explained by their body size, meanwhile for butterflies and hoverflies were explained by larval food preferences, the flight period and habitat specialisation (for butterflies) and voltinism (hoverflies) (see Fig. 3). The species body size is a proxy for dispersal ability (Chown & Gaston,

2010) , and so it expectable that larger species with higher mobility are able to respond faster to increases in temperature. Our findings, however, show the opposite with larger species (e.g. bumblebee species) having on average weaker shifts in contrast to smaller species, which tended to move more towards northern locations. This result might be explained by the fact that larger species tend to have higher energy efficiency and higher tolerance against starvation (Hoiss *et al.*, 2012) , although this remains controversial (see Chown & Gaston, 2010) . Moreover, bigger species tend to have longer foraging distances, thus these may not be as affected by changes in local landscape conditions given their capacity to maintain a longer distance between their feeding and nesting resources in comparison to smaller species (Greenleaf *et al.*, 2007) . The lack of an effect of body size on butterflies and hoverflies (but see range changes for hoverflies) may be due to the distance to their feeding and nesting resources, as these are not as restrictive as for bees, which are central place foragers that need both the feeding and nesting resources at short distances.

The importance of larval food preferences related to the nitrophily of host plants of butterflies partly explained their latitudinal, however this effect was dependent on the length of their flight period and their habitat specialisation. Previous studies show that nitrogen deposition is a major driver of biodiversity change (Xiankai *et al.*, 2008) and that for butterflies it can disrupt the distribution of species adapted to nutrient poor environments by affecting their rates of development and their reproductive potential (Throop & Lerdau, 2004; Wallisdevries & Van Swaay, 2006; Turlure *et al.*, 2013). The increases in nitrogen deposition and also the increase of nitrophilous plants in the study area (Tamis *et al.*, 2005). Similarly to what was suggested by previous studies (e.g. Öckinger *et al.*, 2006; Wallisdevries & Van Swaay, 2006; Weiss, 1999) we observed that butterfly's latitudinal shifts were mostly related to the affinity of their host plants to habitats rich in nitrogen and that for these species the length of their flight period had a weak effect on latitudinal shifts. Moreover, habitat generalists moved north but mostly species that are associated with highly nitrophilous plants. The shifts presented by these butterfly species are thus likely due to the expansions of their host plants in the Netherlands and surrounding areas and as shown by the habitat generalists, these shifts may be closely related to the expansion of anthropogenic habitats (Tamis *et al.*, 2005; Van Landuyt *et al.*, 2008). Investigating the spatial distribution of the butterfly host plants and including nitrogen deposition information would render further insight as to what extent nitrogen deposition per se is driving the distribution of butterfly communities.

As with butterflies, hoverfly latitudinal shifts were explained by the larval food preferences, however these depended on the number of generations of the species along the year. The fact that larva feeding on other resources, as plant and organic material, mostly shifted northwards implies that their feeding resources have become more widely available in those locations. As shown by Reemer *et al.,* (2005), this may be the case for a great part of the species (e.g. saproxylic hoverflies) in the Netherlands. Moreover, it has been shown that temperature has a direct effect on the species development (Kiritani, 2006), favouring the multivoltine species to increase their number of generations (Tobin *et al.*, 2008), thus explaining the observed difference in our study between univoltine and multivoltine species.

Species traits and longitudinal shifts

Range shifts along longitude have been less investigated than latitudinal range shifts (Lenoir & Svenning, 2015). However, our study shows that despite latitudinal shifts being more accentuated than longitudinal shifts (Fig. 1b and Fig. 1c), the latter were still substantial. Longitudinal shifts were mostly explained by the length of the flight period and their voltinism for both bees and butterflies, but interestingly with opposite trends. Multivoltine bees with longer flight periods tended to shift towards western locations meanwhile butterflies tended to shift towards the east. It has been suggested that species with short flight periods in the year may be more vulnerable to climatic and land-use changes than species with longer flight periods (Nilsson *et al.*, 2008). Longer flight periods may enhance the species winter survival by rendering access to more feeding resources in longer periods across the year and accelerating developmental rate (Kiritani, 2006; Robinet & Roques, 2010). Moreover, it has been shown that multivoltine species with longer flight periods, which may start earlier during the year, profit from increases in temperature given the acceleration in developmental rates by producing more generations during the year (Robinet & Roques, 2010). Thus the effect of voltinism and the length of the flight period may be in principle related to both, changes in climatic conditions, e.g. changes in continentally in the Netherlands, and also to land-use modifications. Specially, the western areas have become of primary importance for bees, which are central place foragers, requiring heterogeneous landscapes with feeding resources but also with suitable nesting locations within relatively short distances (Gathmann & Tscharntke, 2002; Murray *et al.*, 2009). These conditions seem to have become more readily available in the west of the country given the high levels of agricultural landscapes and also the increases in landscape fragmentation (e.g. given increases in urban areas) in comparison to the eastern locations (see Table S5 for a general view of these changes). The shifts of butterflies towards eastern locations may indicate changes in distributions of their host plants (Krauss *et al.*, 2004; Dennis *et al.*, 2004) given the increases in species adapted to nutrient rich and decreases of those adapted to nutrient poor conditions in and around the study area (Tamis *et al.*, 2005; Van Landuyt *et al.*, 2008). Moreover, this may also be the result of changes in land use in the study area, as more (semi-)natural environments preferred by butterflies have become less accessible in the west part of the country, where a greater part of the intensive arable agricultural area is located (Diogo *et al.*, 2013). This may also explain the fact that most specialists butterflies, which are associated to (semi-)natural habitats have shifted towards eastern locations.

Hoverflies did not present overall shifts in their longitudinal distribution as a group; however, this is the result of almost half of the species presenting shifts towards the west (98 species) and the others towards the opposite direction (104 species). The distribution and amount of agriculture in the landscape may also explain the shifts presented by hoverflies (e.g. Jauker *et al.*, 2009), as animal feeding larva shifted towards the west, where, as mentioned before, more agriculture landscapes, and thus feeding resources, especially for aphid feeders, have become largely available. Hence the small longitudinal shifts observed for hoverflies as a whole may be explained by this dichotomy in shifts of animal feeders (west) against plant/organic material feeders (east).

Concluding remarks and future prospects

Biodiversity conservation programmes often assume that responses of one or few species groups (e.g. of insects) would represent how general biodiversity responds to drivers of biodiversity change, e.g. climate and land use (Caro & O'Doherty, 1999; Ozaki *et al.*, 2006). However, this may not be always the case as much of the responses to such drivers may be constrained by the species, or group specific, functional traits (Díaz *et al.*, 2013). Understanding how species' ecological and life history traits are associated with distributional responses to climate and land-use change can help to improve conservation actions by accounting for the functional capacity of the species to respond to these changes. In our study we show that information on species traits can help predict the areal range changes and latitudinal and longitudinal shifts related to climatic and land use changes. Moreover, we show that traits involved in the different spatial distribution changes may vary between pollinator groups and that in some cases they can respond in opposite direction (e.g. see traits involved in longitudinal shifts for bees and butterflies). The relation between the spatial changes detected for butterflies and the nitrophily of their host plants are of primary concern given the documented increases of nitrogen deposition in the Netherlands and western Europe in general during the last decades and its impact on biodiversity (Xiankai *et al.*, 2008; Feest *et al.*, 2014). Importantly the fact that all groups showed shifts towards northern latitudes greatly underlines the role that climatic changes may have setting species range limits, raising concerns about further impacts of changes in climatic conditions on the distribution of biodiversity. Given the observed species geographic shifts and their areal range changes within the study area it is essential to investigate how these may impact the protection status of the species and also if, how and to what extent the ecosystem functions (i.e. pollination of wild plants) and services (i.e. pollination of crops) they provide have been disrupted in the past or are likely to be disrupted in the future. Our results raise concerns about the efficacy of general conservation actions that do not account for these differential responses across (pollinator) groups and highlight the restricted value of one-fits-all type of conservation measure.

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Supplementary material

Table S1. (next page) **List of species from the three pollinator groups included in the analyses.** The number of records available in each time periods (TP1, TP2) used during the MaxEnt modelling is provided. The AUC value represents the model accuracy (see methods) for each species and time period.

roup	Species name	Number of presence records		MaxEnt model AUC		Areal	Latitudinal change (km)	Longitudinal change
		TP1	TP2	TP1	TP2	TP1-TP2		
Bees	*Andrena angustior*	53	72	0.86	0.80	168.29	73.99	12.90
Bees	*Andrena apicata*	30	29	0.78	0.90	-2.63	15.54	-20.17
Bees	*Andrena argentata*	28	19	0.88	0.85	-47.69	41.27	-21.22
Bees	*Andrena barbilabris*	136	249	0.76	0.72	114.55	1.30	-14.50
Bees	*Andrena bicolor*	30	169	0.84	0.80	340.00	63.41	-62.62
Bees	*Andrena bimaculata*	13	28	0.70	0.86	4.35	16.71	4.93
Bees	*Andrena carantonica*	91	241	0.76	0.73	120.51	25.02	-19.78
Bees	*Andrena chrysosceles*	36	185	0.86	0.80	164.29	23.77	-32.72
Bees	*Andrena cineraria*	47	151	0.81	0.78	103.03	37.26	0.51
Bees	*Andrena clarkella*	47	146	0.82	0.78	31.92	14.21	0.32
Bees	*Andrena dorsata*	37	167	0.84	0.81	59.84	-1.62	-22.79
Bees	*Andrena falsifica*	10	6	0.80	0.90	-57.14	31.18	3.58
Bees	*Andrena flavipes*	74	381	0.80	0.73	124.53	20.06	-32.63
Bees	*Andrena florea*	23	81	0.96	0.92	255.56	33.73	-91.54
Bees	*Andrena fucata*	43	80	0.75	0.78	230.36	56.21	-2.69
Bees	*Andrena fulva*	81	268	0.78	0.86	285.19	63.25	21.98
Bees	*Andrena fulvago*	12	17	0.95	0.95	28.21	-3.28	5.17
Bees	*Andrena fulvida*	21	23	0.80	0.71	147.42	9.98	-23.22
Bees	*Andrena fuscipes*	120	132	0.81	0.87	32.67	31.03	5.49
Bees	*Andrena gravida*	36	57	0.83	0.87	83.56	21.45	-13.20
Bees	*Andrena haemorrhoa*	118	442	0.75	0.64	192.17	15.49	-24.11
Bees	*Andrena hattorfiana*	26	22	0.93	0.94	-14.29	9.36	-0.33
Bees	*Andrena helvola*	13	58	0.94	0.83	825.00	109.38	-61.86
Bees	*Andrena humilis*	39	40	0.88	0.89	45.78	31.99	8.56
Bees	*Andrena labialis*	26	49	0.92	0.88	159.57	3.29	-70.65
Bees	*Andrena labiata*	22	66	0.85	0.81	247.27	39.54	-21.78
Bees	*Andrena lapponica*	29	38	0.81	0.90	192.59	-9.67	-16.29
Bees	*Andrena lathyri*	9	12	0.97	0.95	67.44	55.93	0.64
Bees	*Andrena minutula*	42	117	0.87	0.82	52.56	47.24	-23.98

Table S1

Bees	*Andrena minutuloides*	6	13	0.90	0.93	625.00	15.17	8.28
Bees	*Andrena mitis*	19	46	0.88	0.89	247.22	71.70	-35.84
Bees	*Andrena nigriceps*	23	23	0.86	0.88	-8.93	-5.12	-21.21
Bees	*Andrena nigroaenea*	75	127	0.77	0.78	-3.68	36.93	-4.02
Bees	*Andrena nitida*	77	219	0.82	0.72	31.03	15.15	18.47
Bees	*Andrena ovatula*	56	71	0.86	0.85	6.67	26.26	9.86
Bees	*Andrena pilipes*	39	13	0.82	0.95	18.18	10.90	3.59
Bees	*Andrena praecox*	64	157	0.73	0.75	45.58	15.72	7.36
Bees	*Andrena proxima*	15	88	0.87	0.84	153.85	54.16	-63.93
Bees	*Andrena ruficrus*	40	35	0.84	0.88	-16.91	-51.44	-23.01
Bees	*Andrena semilaevis*	31	29	0.82	0.94	-8.24	33.83	12.43
Bees	*Andrena subopaca*	79	219	0.76	0.73	100.00	20.93	-31.74
Bees	*Andrena synadelpha*	7	40	0.98	0.85	566.67	131.52	-2.65
Bees	*Andrena tibialis*	55	95	0.81	0.78	31.77	40.14	-12.35
Bees	*Andrena vaga*	41	245	0.82	0.75	110.00	32.78	6.92
Bees	*Andrena varians*	53	36	0.78	0.71	-18.94	54.38	-11.26
Bees	*Andrena ventralis*	21	119	0.87	0.80	218.46	11.83	-9.73
Bees	*Andrena wilkella*	51	78	0.79	0.79	105.22	24.31	-20.90
Bees	*Anthidium manicatum*	31	171	0.89	0.77	256.45	45.25	-35.71
Bees	*Anthidium punctatum*	12	25	0.84	0.94	29.17	63.85	-29.19
Bees	*Anthidium strigatum*	22	81	0.90	0.88	262.16	10.50	13.84
Bees	*Anthophora furcata*	23	46	0.89	0.85	152.08	43.13	-60.22
Bees	*Anthophora plumipes*	39	151	0.84	0.82	135.71	10.25	-40.20
Bees	*Anthophora*	15	20	0.89	0.98	20.00	-18.52	24.73
Bees	*Anthophora retusa*	22	12	0.83	0.75	94.74	18.70	16.22
Bees	*Bombus bohemicus*	70	90	0.80	0.73	0.00	-8.38	-32.47
Bees	*Bombus campestris*	90	196	0.78	0.77	58.59	-1.56	-55.38
Bees	*Bombus cryptarum*	20	16	0.81	0.66	278.18	17.44	53.20
Bees	*Bombus hortorum*	76	232	0.78	0.74	118.49	18.49	-22.19
Bees	*Bombus humilis*	33	10	0.87	0.81	-48.81	41.11	21.58
Bees	*Bombus hypnorum*	46	295	0.81	0.74	67.83	-45.09	-50.32

Table S1 (*continued*)

Bees	*Bombus jonellus*	35	93	0.77	0.82	198.33	-63.88	-26.07
Bees	*Bombus lapidarius*	115	511	0.79	0.66	126.09	-17.12	-17.94
Bees	*Bombus lucorum*	82	305	0.79	0.69	154.84	-2.07	-36.03
Bees	*Bombus magnus*	30	46	0.79	0.90	248.89	-13.60	-12.58
Bees	*Bombus muscorum*	66	38	0.73	0.92	20.00	28.85	-6.29
Bees	*Bombus norvegicus*	20	26	0.82	0.77	119.51	18.79	-50.28
Bees	*Bombus pascuorum*	165	657	0.70	0.59	125.00	-3.83	-21.34
Bees	*Bombus pratorum*	89	436	0.76	0.66	157.72	30.67	-44.32
Bees	*Bombus ruderarius*	57	89	0.79	0.94	-5.56	-65.47	-141.69
Bees	*Bombus sylvestris*	62	170	0.75	0.74	111.11	21.88	-33.21
Bees	*Bombus terrestris*	97	490	0.75	0.65	140.67	1.33	-2.67
Bees	*Bombus vestalis*	36	115	0.88	0.75	220.00	56.94	-0.15
Bees	*Bombus veteranus*	44	6	0.77	0.95	-63.03	-83.93	-113.42
Bees	*Ceratina cyanea*	12	18	0.86	0.94	-34.69	5.66	13.82
Bees	*Chelostoma*	36	53	0.90	0.87	110.61	35.24	-13.65
Bees	*Chelostoma distinctum*	19	6	0.97	0.97	-35.71	8.73	2.86
Bees	*Chelostoma florisomne*	50	76	0.86	0.81	91.30	30.42	-20.99
Bees	*Chelostoma rapunculi*	55	106	0.86	0.81	96.70	43.16	-4.47
Bees	*Coelioxys elongata*	10	11	0.78	0.68	-25.27	-26.52	-101.50
Bees	*Coelioxys inermis*	30	52	0.80	0.83	126.09	20.80	-72.77
Bees	*Coelioxys mandibularis*	29	46	0.86	0.94	83.33	-8.72	-32.87
Bees	*Coelioxys*	23	11	0.81	0.90	-29.49	133.50	41.85
Bees	*Colletes cunicularius*	42	188	0.79	0.74	234.85	-24.22	42.01
Bees	*Colletes daviesanus*	72	193	0.80	0.74	61.15	48.77	-9.06
Bees	*Colletes fodiens*	31	142	0.84	0.80	190.20	-9.36	-30.68
Bees	*Colletes halophilus*	7	57	0.97	0.95	125.93	-10.11	14.76
Bees	*Colletes impunctatus*	5	5	0.91	0.90	242.86	-44.67	-57.20
Bees	*Colletes marginatus*	16	35	0.70	0.84	1.16	2.08	47.67
Bees	*Colletes succinctus*	46	100	0.82	0.89	44.44	60.60	27.24
Bees	*Dasypoda hirtipes*	89	277	0.79	0.76	87.01	30.22	-2.86
Bees	*Epeoloides coecutiens*	14	82	0.89	0.87	-15.73	46.38	15.98

Table S1 (*continued*)

Bees	*Epeolus cruciger*	44	129	0.78	0.86	182.09	18.57	8.70
Bees	*Epeolus variegatus*	18	117	0.79	0.82	142.62	10.04	-17.75
Bees	*Eucera longicornis*	25	8	0.94	0.76	89.13	6.07	11.30
Bees	*Halictus confusus*	61	111	0.83	0.81	57.14	27.05	15.88
Bees	*Halictus rubicundus*	102	204	0.75	0.76	107.00	56.38	-10.11
Bees	*Halictus tumulorum*	73	290	0.74	0.71	125.00	15.04	-48.92
Bees	*Heriades truncorum*	61	135	0.83	0.78	32.76	47.02	-9.13
Bees	*Hylaeus annularis*	44	58	0.82	0.85	11.97	-26.29	13.43
Bees	*Hylaeus brevicornis*	61	76	0.81	0.80	46.34	-11.42	22.97
Bees	*Hylaeus communis*	92	236	0.75	0.76	19.07	22.15	-8.42
Bees	*Hylaeus confusus*	65	166	0.81	0.78	52.25	34.28	-0.36
Bees	*Hylaeus gibbus*	63	83	0.75	0.78	125.96	30.25	-5.04
Bees	*Hylaeus hyalinatus*	64	142	0.80	0.81	73.50	2.53	1.19
Bees	*Hylaeus pectoralis*	17	21	0.81	0.93	-74.71	-17.39	-35.60
Bees	*Hylaeus pictipes*	20	24	0.90	0.83	29.11	32.67	11.17
Bees	*Hylaeus*	10	17	0.88	0.88	91.58	6.18	-6.65
Bees	*Hylaeus rinki*	12	13	0.79	0.90	-66.14	123.57	46.68
Bees	*Hylaeus signatus*	22	60	0.86	0.83	172.00	14.36	21.01
Bees	*Lasioglossum albipes*	91	91	0.69	0.79	-31.22	66.44	28.12
Bees	*Lasioglossum*	19	18	0.80	0.89	-41.94	51.78	-3.66
Bees	*Lasioglossum*	179	394	0.68	0.70	127.97	2.45	-34.57
Bees	*Lasioglossum fratellum*	8	18	0.98	0.91	88.89	32.21	24.14
Bees	*Lasioglossum*	51	67	0.87	0.84	150.62	34.63	-8.67
Bees	*Lasioglossum laticeps*	14	32	0.94	0.88	571.43	70.80	10.54
Bees	*Lasioglossum lativentre*	25	12	0.87	0.96	-8.93	-26.98	8.66
Bees	*Lasioglossum leucopus*	62	130	0.80	0.77	43.75	36.86	35.84
Bees	*Lasioglossum*	138	313	0.74	0.70	138.28	42.64	-11.59
Bees	*Lasioglossum lucidulum*	21	77	0.87	0.76	157.14	37.69	-8.94
Bees	*Lasioglossum*	22	41	0.95	0.89	90.32	30.11	-18.77
Bees	*Lasioglossum*	24	80	0.86	0.74	271.80	-27.91	28.30
Bees	*Lasioglossum morio*	37	206	0.91	0.78	329.03	58.22	-72.44

Table S1 (*continued*)

Bees	*Lasioglossum*	30	8	0.89	0.78	55.81	68.30	-46.56
Bees	*Lasioglossum nitidulum*	20	33	0.91	0.89	86.05	38.60	-13.12
Bees	*Lasioglossum parvulum*	28	19	0.88	0.87	-11.32	-7.32	20.87
Bees	*Lasioglossum pauxillum*	17	74	0.87	0.86	506.67	72.11	-56.23
Bees	*Lasioglossum prasinum*	49	28	0.78	0.90	-30.82	20.35	8.61
Bees	*Lasioglossum*	81	103	0.77	0.84	5.10	16.26	-10.91
Bees	*Lasioglossum*	47	46	0.86	0.84	18.56	35.64	-14.46
Bees	*Lasioglossum*	13	12	0.77	0.81	20.37	27.97	0.65
Bees	*Lasioglossum rufitarse*	49	12	0.81	0.80	-19.60	-50.63	-22.89
Bees	*Lasioglossum*	14	49	0.74	0.89	25.95	10.09	14.14
Bees	*Lasioglossum*	27	56	0.88	0.78	71.83	24.50	-47.26
Bees	*Lasioglossum*	40	87	0.92	0.82	102.44	39.81	-11.41
Bees	*Lasioglossum*	132	226	0.71	0.72	65.81	11.57	-11.28
Bees	*Lasioglossum tarsatum*	21	15	0.81	0.96	41.18	8.53	-56.87
Bees	*Lasioglossum*	103	176	0.76	0.76	60.19	29.07	-17.19
Bees	*Lasioglossum*	17	26	0.92	0.93	75.68	108.49	-43.36
Bees	*Lasioglossum zonulum*	75	132	0.83	0.77	28.67	59.07	-12.59
Bees	*Macropis europaea*	61	196	0.81	0.76	-6.56	16.59	2.63
Bees	*Megachile analis*	5	10	0.62	0.89	196.55	-14.94	-6.98
Bees	*Megachile*	74	173	0.77	0.81	35.66	-10.90	-66.84
Bees	*Megachile circumcincta*	48	27	0.73	0.85	-16.28	14.38	-24.09
Bees	*Megachile ericetorum*	21	83	0.94	0.85	459.38	-16.94	-72.56
Bees	*Megachile lapponica*	43	25	0.82	0.74	-42.57	34.19	-12.99
Bees	*Megachile leachella*	39	57	0.90	0.92	56.92	-7.13	-34.54
Bees	*Megachile ligniseca*	16	46	0.82	0.88	-8.49	-8.57	-24.10
Bees	*Megachile maritima*	29	20	0.89	0.99	-52.38	40.93	-5.40
Bees	*Megachile versicolor*	34	105	0.84	0.79	133.33	12.25	-5.53
Bees	*Megachile willughbiella*	49	226	0.73	0.72	221.25	21.45	2.52
Bees	*Melecta albifrons*	22	38	0.86	0.80	173.53	86.87	-16.65
Bees	*Melitta*	32	63	0.85	0.86	240.00	91.77	1.34
Bees	*Melitta leporina*	21	67	0.77	0.89	262.50	6.52	-120.04

Table S1 (*continued*)

Bees	*Melitta nigricans*	15	72	0.81	0.84	92.31	43.13	-14.69
Bees	*Melitta tricincta*	12	19	0.96	0.86	4.55	32.97	-57.40
Bees	*Nomada alboguttata*	69	167	0.80	0.77	14.71	14.08	-11.48
Bees	*Nomada bifasciata*	27	31	0.91	0.91	-28.41	36.74	0.11
Bees	*Nomada fabriciana*	44	148	0.84	0.82	60.61	24.04	-30.50
Bees	*Nomada ferruginata*	20	88	0.83	0.80	155.26	-3.87	-20.89
Bees	*Nomada flava*	115	272	0.79	0.70	161.61	18.92	-19.73
Bees	*Nomada flavoguttata*	49	156	0.82	0.78	37.39	14.32	-36.42
Bees	*Nomada flavopicta*	31	67	0.87	0.83	135.39	17.65	-75.25
Bees	*Nomada fucata*	36	160	0.88	0.82	125.30	28.40	-34.43
Bees	*Nomada fulvicornis*	45	48	0.87	0.77	27.42	80.85	-53.10
Bees	*Nomada fuscicornis*	24	23	0.90	0.91	17.31	70.90	-18.02
Bees	*Nomada goodeniana*	52	140	0.81	0.78	34.33	52.39	8.13
Bees	*Nomada integra*	23	10	0.79	0.68	51.35	5.94	7.33
Bees	*Nomada lathburiana*	47	181	0.80	0.81	61.72	30.39	3.23
Bees	*Nomada*	25	72	0.78	0.82	300.00	46.25	0.99
Bees	*Nomada marshamella*	62	159	0.74	0.76	81.58	34.23	-38.58
Bees	*Nomada obscura*	5	6	0.84	0.96	150.00	-96.62	-9.15
Bees	*Nomada panzeri*	59	124	0.77	0.78	0.00	12.21	-30.16
Bees	*Nomada ruficornis*	85	248	0.80	0.75	176.09	32.59	-3.85
Bees	*Nomada rufipes*	137	138	0.79	0.86	14.89	44.08	10.16
Bees	*Nomada sheppardana*	66	154	0.82	0.79	92.86	16.71	12.50
Bees	*Nomada signata*	49	98	0.86	0.79	197.59	5.16	-31.28
Bees	*Nomada similis*	15	19	0.91	0.90	-5.26	52.88	-5.63
Bees	*Nomada striata*	39	38	0.83	0.83	54.00	19.44	8.53
Bees	*Nomada succincta*	76	145	0.81	0.80	-9.14	26.01	-11.39
Bees	*Osmia aurulenta*	10	16	0.90	0.96	15.56	-73.35	0.74
Bees	*Osmia caerulescens*	52	65	0.82	0.80	106.93	17.15	-6.51
Bees	*Osmia claviventris*	28	40	0.86	0.85	90.00	28.33	6.60
Bees	*Osmia cornuta*	27	66	0.90	0.78	100.00	-0.11	-40.11
Bees	*Osmia leaiana*	19	15	0.89	0.67	168.75	24.07	22.10

Table S1 (*continued*)

Bees	*Osmia leucomelana*	28	45	0.89	0.79	90.91	27.53	-8.42
Bees	*Osmia niveata*	36	28	0.92	0.85	51.28	1.20	1.30
Bees	*Osmia rufa*	81	337	0.78	0.68	152.54	23.72	-22.03
Bees	*Osmia uncinata*	6	34	0.82	0.90	281.82	69.42	9.07
Bees	*Panurgus banksianus*	64	72	0.83	0.82	1.17	47.42	8.91
Bees	*Panurgus calcaratus*	68	147	0.80	0.83	73.04	40.89	25.20
Bees	*Sphecodes albilabris*	21	174	0.92	0.80	294.00	-37.36	61.02
Bees	*Sphecodes crassus*	37	114	0.78	0.74	55.91	-39.61	-52.29
Bees	*Sphecodes ephippius*	53	120	0.78	0.81	9.09	-3.62	5.95
Bees	*Sphecodes ferruginatus*	12	11	0.98	0.90	172.00	20.06	3.29
Bees	*Sphecodes geoffrellus*	41	92	0.81	0.76	61.39	-7.36	-24.52
Bees	*Sphecodes gibbus*	46	107	0.85	0.79	106.32	58.27	21.75
Bees	*Sphecodes hyalinatus*	12	7	0.98	0.97	26.32	27.30	9.19
Bees	*Sphecodes longulus*	29	94	0.77	0.78	408.57	31.00	-14.04
Bees	*Sphecodes marginatus*	25	52	0.75	0.79	404.76	-29.33	-21.75
Bees	*Sphecodes miniatus*	39	142	0.80	0.76	47.13	10.04	-40.05
Bees	*Sphecodes monilicornis*	95	234	0.72	0.75	40.00	18.57	-34.36
Bees	*Sphecodes pellucidus*	63	184	0.77	0.77	107.08	9.13	-7.93
Bees	*Sphecodes puncticeps*	33	67	0.82	0.78	42.73	7.66	-46.92
Bees	*Sphecodes reticulatus*	25	97	0.85	0.78	157.35	54.59	-27.12
Bees	*Sphecodes rubicundus*	7	30	0.94	0.85	227.27	66.11	-12.26
Bees	*Stelis breviuscula*	25	27	0.90	0.79	25.00	40.55	-7.52
Bees	*Stelis ornatula*	19	11	0.82	0.83	115.49	-0.85	25.45
Butterflies	*Aglais urticae*	237	1518	0.67	0.50	213.22	44.71	38.15
Butterflies	*Anthocharis*	174	1226	0.73	0.58	422.22	39.31	12.78
Butterflies	*Apatura iris*	19	58	0.90	0.88	59.74	40.07	17.72
Butterflies	*Aphantopus*	182	845	0.74	0.68	231.80	21.37	29.65
Butterflies	*Araschnia levana*	240	1340	0.76	0.55	230.32	57.51	2.85
Butterflies	*Argynnis aglaja*	51	44	0.80	0.91	71.13	9.56	23.87
Butterflies	*Argynnis niobe*	54	53	0.86	0.97	-28.09	24.40	-2.98
Butterflies	*Argynnis paphia*	46	95	0.87	0.77	265.71	47.05	0.77

Table S1 (*continued*)

Butterflies	*Boloria aquilonaris*	9	10	0.98	0.98	4.76	-6.75	0.11
Butterflies	*Boloria selene*	125	61	0.74	0.88	11.94	32.61	-0.42
Butterflies	*Callophrys rubi*	154	421	0.81	0.81	122.77	3.74	0.47
Butterflies	*Carterocephalus*	46	116	0.88	0.94	11.69	9.73	-1.70
Butterflies	*Celastrina argiolus*	239	1418	0.71	0.53	241.36	40.77	0.23
Butterflies	*Coenonympha*	319	1058	0.63	0.61	141.00	57.59	30.26
Butterflies	*Coenonympha tullia*	66	12	0.88	0.98	-81.58	56.88	3.65
Butterflies	*Colias croceus*	268	864	0.71	0.62	57.88	-16.59	-1.88
Butterflies	*Colias hyale*	188	401	0.75	0.66	74.31	17.10	20.13
Butterflies	*Cupido minimus*	5	5	0.98	0.88	-60.00	20.98	0.41
Butterflies	*Erynnis tages*	26	8	0.92	0.95	118.75	-46.54	-51.31
Butterflies	*Gonepteryx rhamni*	238	1389	0.70	0.54	140.85	36.71	17.90
Butterflies	*Hesperia comma*	106	116	0.78	0.91	23.13	58.13	23.71
Butterflies	*Heteropterus*	10	26	0.88	0.97	-69.03	-35.53	-3.38
Butterflies	*Hipparchia semele*	195	347	0.71	0.83	30.80	9.87	-9.59
Butterflies	*Hipparchia statilinus*	8	8	0.98	0.99	-86.96	-18.15	-2.07
Butterflies	*Inachis io*	206	1552	0.68	0.51	125.23	12.28	16.13
Butterflies	*Issoria lathonia*	195	299	0.70	0.78	43.89	-5.89	-3.65
Butterflies	*Lasiommata megera*	250	1346	0.67	0.55	364.07	58.40	28.17
Butterflies	*Leptidea sinapis*	17	30	0.81	0.89	-5.46	-1.75	-1.29
Butterflies	*Limenitis camilla*	83	109	0.81	0.89	-22.42	18.13	24.32
Butterflies	*Lycaena dispar*	24	18	0.98	0.93	-35.42	-9.41	1.76
Butterflies	*Lycaena phlaeas*	309	1380	0.66	0.53	131.82	1.64	14.13
Butterflies	*Lycaena tityrus*	166	263	0.78	0.87	40.39	29.68	12.23
Butterflies	*Maculinea alcon*	93	100	0.82	0.92	-16.13	1.67	-0.74
Butterflies	*Maniola jurtina*	296	1356	0.66	0.56	228.22	16.13	34.73
Butterflies	*Melanargia galathea*	14	11	0.85	0.87	8.16	-29.80	9.75
Butterflies	*Melitaea athalia*	49	24	0.85	0.98	-70.27	11.56	-15.00
Butterflies	*Neozephyrus quercus*	128	686	0.76	0.72	301.26	-6.78	6.66
Butterflies	*Nymphalis antiopa*	61	374	0.83	0.72	161.49	50.77	-26.14
Butterflies	*Nymphalis polychloros*	64	43	0.76	0.78	-38.13	8.03	-7.68

Table S1 (*continued*)

Butterflies	*Ochlodes faunus*	224	927	0.70	0.65	184.02	12.21	15.60
Butterflies	*Papilio machaon*	129	882	0.77	0.66	350.71	6.90	9.01
Butterflies	*Pararge aegeria*	183	1433	0.72	0.52	361.41	31.82	18.28
Butterflies	*Pieris brassicae*	223	1524	0.69	0.51	224.35	28.66	5.31
Butterflies	*Pieris napi*	249	1542	0.69	0.51	107.79	18.33	27.21
Butterflies	*Pieris rapae*	255	1555	0.67	0.50	144.98	29.86	33.74
Butterflies	*Plebeius agestis*	121	532	0.80	0.74	120.83	-6.65	19.49
Butterflies	*Plebeius argus*	164	333	0.78	0.85	44.24	13.25	0.57
Butterflies	*Plebeius optilete*	7	5	0.93	0.96	-75.00	-0.71	9.64
Butterflies	*Polygonia c-album*	166	1444	0.80	0.53	160.91	32.75	-9.03
Butterflies	*Polyommatus coridon*	28	6	0.95	0.92	-15.39	-12.03	15.51
Butterflies	*Polyommatus icarus*	261	1359	0.71	0.53	145.02	7.19	3.00
Butterflies	*Polyommatus*	19	10	0.94	0.96	-62.07	-39.26	-10.74
Butterflies	*Pontia daplidice*	36	48	0.78	0.70	92.06	30.22	87.25
Butterflies	*Pyrgus malvae*	86	64	0.76	0.87	12.34	17.46	17.17
Butterflies	*Pyronia tithonus*	177	823	0.77	0.70	150.00	26.96	20.62
Butterflies	*Satyrium ilicis*	114	108	0.80	0.90	8.43	12.91	-1.51
Butterflies	*Thecla betulae*	41	77	0.87	0.94	144.44	35.30	-0.80
Butterflies	*Thymelicus lineola*	179	1316	0.74	0.55	236.32	40.80	70.44
Butterflies	*Thymelicus sylvestris*	125	551	0.79	0.70	352.38	29.62	7.38
Butterflies	*Vanessa atalanta*	342	1558	0.66	0.51	15.54	52.61	59.10
Butterflies	*Vanessa cardui*	265	1539	0.66	0.50	37.50	39.34	23.11
Hoverflies	*Anasimyia contracta*	20	43	0.87	0.73	27.03	23.96	-25.13
Hoverflies	*Anasimyia interpuncta*	45	175	0.82	0.76	65.94	35.87	17.22
Hoverflies	*Anasimyia lineata*	148	312	0.74	0.72	85.07	9.98	13.97
Hoverflies	*Anasimyia transfuga*	53	101	0.81	0.79	19.73	19.50	6.31
Hoverflies	*Baccha elongata*	98	269	0.80	0.75	81.88	2.55	-20.20
Hoverflies	*Brachyopa insensilis*	5	10	0.95	0.87	335.71	121.21	-28.55
Hoverflies	*Brachyopa pilosa*	12	70	0.95	0.84	473.91	51.57	-9.09
Hoverflies	*Brachyopa scutellaris*	22	64	0.85	0.89	376.74	23.88	3.92
Hoverflies	*Brachypalpoides lentus*	25	134	0.88	0.81	300.00	45.83	-8.23

Table S1 (*continued*)

Hoverflies	*Brachypalpus*	7	54	0.92	0.89	573.91	109.28	-1.89
Hoverflies	*Ceriana conopsoides*	11	49	0.76	0.87	124.74	63.72	-20.03
Hoverflies	*Chalcosyrphus*	32	223	0.90	0.79	224.64	52.67	-16.16
Hoverflies	*Chamaesyrphus*	8	8	0.97	0.87	134.78	-93.76	51.72
Hoverflies	*Cheilosia albipila*	30	189	0.86	0.76	215.71	42.72	-14.35
Hoverflies	*Cheilosia barbata*	13	7	0.95	0.96	37.50	5.88	8.78
Hoverflies	*Cheilosia*	37	183	0.86	0.80	386.96	-20.02	24.59
Hoverflies	*Cheilosia canicularis*	6	24	0.96	0.96	412.50	35.98	7.79
Hoverflies	*Cheilosia carbonaria*	10	36	0.88	0.85	17.86	29.93	-27.01
Hoverflies	*Cheilosia chrysocoma*	14	39	0.90	0.85	-26.39	85.68	14.36
Hoverflies	*Cheilosia cynocephala*	11	56	0.92	0.78	75.00	36.38	-12.35
Hoverflies	*Cheilosia fraterna*	46	111	0.77	0.77	73.68	22.37	16.64
Hoverflies	*Cheilosia grossa*	24	85	0.89	0.81	287.69	0.86	33.46
Hoverflies	*Cheilosia illustrata*	19	324	0.88	0.78	978.95	13.32	-47.33
Hoverflies	*Cheilosia impressa*	61	208	0.82	0.76	132.74	37.13	-18.20
Hoverflies	*Cheilosia latifrons*	32	44	0.74	0.80	61.18	0.33	-7.57
Hoverflies	*Cheilosia lenis*	6	9	0.92	0.99	225.00	4.42	2.31
Hoverflies	*Cheilosia longula*	26	19	0.87	0.89	-47.87	-23.92	20.80
Hoverflies	*Cheilosia mutabilis*	28	27	0.82	0.80	6.25	25.88	-10.37
Hoverflies	*Cheilosia pagana*	154	679	0.73	0.63	236.05	30.86	5.02
Hoverflies	*Cheilosia proxima*	19	130	0.88	0.87	438.89	31.15	-16.24
Hoverflies	*Cheilosia ranunculi*	147	586	0.75	0.63	175.57	26.96	1.18
Hoverflies	*Cheilosia scutellata*	63	83	0.85	0.88	46.46	-14.06	-20.84
Hoverflies	*Cheilosia semifasciata*	12	65	0.95	0.87	275.61	63.09	0.59
Hoverflies	*Cheilosia urbana*	29	33	0.84	0.82	-1.02	20.69	24.22
Hoverflies	*Cheilosia uviformis*	19	14	0.91	0.77	159.18	81.84	-5.35
Hoverflies	*Cheilosia variabilis*	45	199	0.89	0.81	281.43	47.65	-39.36
Hoverflies	*Cheilosia velutina*	14	24	0.93	0.88	68.63	44.40	60.18
Hoverflies	*Cheilosia vernalis*	94	209	0.74	0.75	88.74	9.25	-10.32
Hoverflies	*Chrysogaster*	22	14	0.91	0.99	-42.42	-4.52	0.96
Hoverflies	*Chrysogaster solstitialis*	29	152	0.83	0.83	497.73	63.51	-11.85

Table S1 (*continued*)

Hoverflies	*Chrysogaster virescens*	7	37	0.95	0.87	500.00	69.03	42.99
Hoverflies	*Chrysotoxum arcuatum*	33	36	0.86	0.92	17.44	5.72	-5.94
Hoverflies	*Chrysotoxum bicinctum*	66	209	0.84	0.81	62.07	22.43	6.83
Hoverflies	*Chrysotoxum cautum*	70	261	0.85	0.79	133.57	35.07	3.41
Hoverflies	*Chrysotoxum festivum*	56	108	0.83	0.80	65.19	24.34	11.24
Hoverflies	*Chrysotoxum*	19	6	0.91	0.98	-79.17	-10.44	-0.69
Hoverflies	*Chrysotoxum vernale*	55	63	0.86	0.88	-14.10	25.91	6.01
Hoverflies	*Chrysotoxum verralli*	6	22	0.96	0.88	232.43	47.70	10.63
Hoverflies	*Criorhina asilica*	17	25	0.83	0.89	160.42	79.81	14.30
Hoverflies	*Criorhina berberina*	46	200	0.86	0.79	187.32	34.17	1.12
Hoverflies	*Criorhina floccosa*	6	51	0.90	0.84	1109.09	89.07	-14.36
Hoverflies	*Criorhina pachymera*	5	32	0.78	0.92	566.67	68.22	-10.47
Hoverflies	*Criorhina ranunculi*	5	19	0.88	0.91	500.00	35.42	12.50
Hoverflies	*Dasysyrphus*	112	344	0.82	0.74	250.00	21.10	-6.58
Hoverflies	*Dasysyrphus hilaris*	55	31	0.80	0.90	-45.69	9.75	6.24
Hoverflies	*Dasysyrphus pauxillus*	5	15	0.91	0.83	2225.00	-25.74	99.07
Hoverflies	*Dasysyrphus pinastri*	29	22	0.88	0.80	-34.78	-8.89	11.84
Hoverflies	*Dasysyrphus tricinctus*	106	204	0.79	0.82	104.05	19.46	-6.91
Hoverflies	*Dasysyrphus venustus*	89	255	0.76	0.77	58.46	7.49	12.91
Hoverflies	*Didea alneti*	11	34	0.89	0.81	-5.10	8.55	-8.16
Hoverflies	*Didea fasciata*	51	173	0.82	0.84	135.92	-12.61	-28.02
Hoverflies	*Didea intermedia*	35	89	0.86	0.82	132.05	-5.51	5.49
Hoverflies	*Epistrophe eligans*	80	370	0.81	0.73	150.00	8.87	-20.52
Hoverflies	*Epistrophe flava*	10	16	0.87	0.83	40.98	-13.55	-8.08
Hoverflies	*Epistrophe grossulariae*	40	130	0.83	0.83	308.70	40.11	-21.09
Hoverflies	*Epistrophe nitidicollis*	72	243	0.80	0.75	40.10	11.15	-4.49
Hoverflies	*Episyrphus balteatus*	260	1173	0.65	0.54	152.09	-17.74	16.00
Hoverflies	*Eriozona syrphoides*	8	7	0.86	0.91	-36.36	30.18	2.69
Hoverflies	*Eristalinus aeneus*	30	99	0.95	0.90	107.32	34.94	28.57
Hoverflies	*Eristalinus sepulchralis*	201	726	0.70	0.60	107.08	41.17	16.93
Hoverflies	*Eristalis abusiva*	139	443	0.76	0.66	146.63	17.78	29.61

Table S1 (*continued*)

Hoverflies	*Eristalis anthophorina*	28	20	0.89	0.92	-58.28	-9.21	11.54
Hoverflies	*Eristalis arbustorum*	315	994	0.65	0.55	87.16	-9.29	13.95
Hoverflies	*Eristalis horticola*	142	687	0.78	0.65	202.78	1.66	-13.87
Hoverflies	*Eristalis intricaria*	248	655	0.68	0.63	148.52	16.76	21.16
Hoverflies	*Eristalis nemorum*	208	872	0.71	0.58	400.00	23.62	14.46
Hoverflies	*Eristalis pertinax*	199	1073	0.72	0.55	252.69	-6.34	-8.62
Hoverflies	*Eristalis similis*	22	74	0.82	0.76	325.00	23.49	21.30
Hoverflies	*Eristalis tenax*	217	1135	0.70	0.55	208.43	5.29	17.32
Hoverflies	*Eumerus funeralis*	34	101	0.86	0.86	169.51	-24.79	20.65
Hoverflies	*Eumerus ornatus*	11	8	0.97	0.93	177.27	41.77	6.83
Hoverflies	*Eumerus sogdianus*	15	18	0.94	0.86	-41.73	17.02	-8.36
Hoverflies	*Eumerus strigatus*	71	185	0.70	0.79	51.35	82.94	55.63
Hoverflies	*Eupeodes corollae*	254	816	0.67	0.59	86.43	-0.44	14.49
Hoverflies	*Eupeodes goeldlini*	12	24	0.81	0.84	117.31	-85.64	27.39
Hoverflies	*Eupeodes lapponicus*	21	79	0.83	0.84	489.47	50.46	-25.64
Hoverflies	*Eupeodes latifasciatus*	66	301	0.75	0.72	147.75	38.08	-5.33
Hoverflies	*Eupeodes luniger*	70	387	0.78	0.73	191.91	-7.05	-0.13
Hoverflies	*Eupeodes nielseni*	5	21	0.76	0.86	239.39	-9.61	-37.49
Hoverflies	*Ferdinandea cuprea*	37	175	0.90	0.76	247.62	25.31	-29.74
Hoverflies	*Helophilus hybridus*	80	370	0.76	0.67	115.85	-14.26	-4.40
Hoverflies	*Helophilus pendulus*	321	1123	0.65	0.53	90.78	15.68	15.92
Hoverflies	*Helophilus trivittatus*	202	959	0.69	0.56	144.19	-2.51	19.54
Hoverflies	*Heringia brevidens*	5	15	0.89	0.67	2937.50	87.85	-41.81
Hoverflies	*Heringia heringi*	17	36	0.76	0.82	164.00	65.97	-34.34
Hoverflies	*Heringia pubescens*	19	24	0.89	0.87	19.67	-10.13	-25.34
Hoverflies	*Heringia vitripennis*	71	49	0.78	0.75	-4.62	12.70	-5.06
Hoverflies	*Lejogaster metallina*	149	288	0.76	0.71	132.02	42.47	3.30
Hoverflies	*Lejogaster tarsata*	39	75	0.85	0.85	94.95	-17.37	-2.23
Hoverflies	*Lejops vittata*	11	7	0.84	0.99	-92.05	88.47	58.59
Hoverflies	*Leucozona laternaria*	31	16	0.82	0.86	252.83	-4.79	18.11
Hoverflies	*Leucozona lucorum*	33	80	0.91	0.82	157.90	40.11	-5.48

Table S1 (*continued*)

Hoverflies	*Megasyrphus erratica*	18	58	0.85	0.87	232.08	-79.58	-19.11
Hoverflies	*Melangyna cincta*	52	207	0.83	0.79	105.51	11.72	-5.69
Hoverflies	*Melangyna*	18	70	0.82	0.82	471.43	40.23	-22.50
Hoverflies	*Melangyna*	12	18	0.89	0.95	28.89	44.94	-13.39
Hoverflies	*Melangyna*	41	121	0.86	0.81	113.95	28.16	7.25
Hoverflies	*Melanogaster aerosa*	12	13	0.92	0.91	296.77	-13.47	25.27
Hoverflies	*Melanogaster hirtella*	136	454	0.73	0.68	170.55	11.84	22.97
Hoverflies	*Melanogaster nuda*	43	97	0.85	0.77	93.10	9.97	8.30
Hoverflies	*Melanostoma*	310	993	0.62	0.56	170.91	-4.93	15.85
Hoverflies	*Melanostoma scalare*	134	702	0.71	0.64	317.65	0.92	13.87
Hoverflies	*Meligramma guttata*	29	54	0.92	0.87	104.92	42.07	-8.93
Hoverflies	*Meligramma*	27	77	0.90	0.85	545.24	36.38	-26.34
Hoverflies	*Meliscaeva auricollis*	99	307	0.78	0.72	143.36	-2.98	-8.79
Hoverflies	*Meliscaeva cinctella*	99	147	0.84	0.82	18.61	24.14	5.52
Hoverflies	*Merodon equestris*	63	307	0.82	0.75	128.77	8.00	24.40
Hoverflies	*Microdon analis*	12	52	0.81	0.87	161.29	30.50	2.95
Hoverflies	*Microdon devius*	5	5	0.94	0.70	250.00	-2.87	-0.81
Hoverflies	*Myathropa florea*	165	978	0.73	0.58	216.67	2.49	-4.69
Hoverflies	*Neoascia geniculata*	42	26	0.89	0.87	51.35	14.64	26.46
Hoverflies	*Neoascia interrupta*	10	32	0.68	0.80	5.71	30.07	-30.48
Hoverflies	*Neoascia meticulosa*	32	113	0.82	0.77	136.07	70.75	-1.26
Hoverflies	*Neoascia obliqua*	5	45	0.93	0.87	1008.33	-22.64	11.95
Hoverflies	*Neoascia podagrica*	249	502	0.67	0.67	120.86	10.60	10.56
Hoverflies	*Neoascia tenur*	72	269	0.78	0.74	72.02	-8.28	6.23
Hoverflies	*Orthonevra brevicornis*	10	26	0.91	0.81	127.50	47.93	16.30
Hoverflies	*Orthonevra geniculata*	7	19	0.93	0.82	-20.00	-6.72	-2.00
Hoverflies	*Orthonevra intermedia*	8	40	0.69	0.83	329.63	117.71	27.55
Hoverflies	*Orthonevra nobilis*	14	11	0.97	0.96	229.41	19.45	3.34
Hoverflies	*Paragus haemorrhous*	34	215	0.75	0.80	387.27	38.12	14.22
Hoverflies	*Paragus pecchiolii*	6	18	0.93	0.97	273.68	8.95	-1.62
Hoverflies	*Parasyrphus annulatus*	9	52	0.93	0.92	63.74	-1.99	2.16

Table S1 (*continued*)

Hoverflies	*Parasyrphus lineolus*	34	31	0.80	0.87	74.29	-8.37	10.97
Hoverflies	*Parasyrphus malinellus*	27	35	0.90	0.89	92.73	5.64	-4.24
Hoverflies	*Parasyrphus*	81	160	0.86	0.84	2.37	10.32	-1.15
Hoverflies	*Parasyrphus vittiger*	60	10	0.84	0.88	-9.52	-8.50	29.66
Hoverflies	*Parhelophilus*	10	11	0.81	0.87	1022.22	-2.44	36.09
Hoverflies	*Parhelophilus*	28	134	0.87	0.77	240.82	82.14	-10.96
Hoverflies	*Parhelophilus*	67	225	0.82	0.75	95.75	-4.85	9.73
Hoverflies	*Pelecocera tricincta*	13	39	0.94	0.96	-22.86	-15.59	11.60
Hoverflies	*Pipiza austriaca*	35	14	0.87	0.90	-17.14	-28.22	7.92
Hoverflies	*Pipiza bimaculata*	34	121	0.83	0.80	91.84	73.09	20.52
Hoverflies	*Pipiza fenestrata*	24	12	0.82	0.84	92.16	14.97	37.03
Hoverflies	*Pipiza lugubris*	19	68	0.80	0.83	178.67	34.28	-5.67
Hoverflies	*Pipiza luteitarsis*	15	18	0.82	0.85	14.46	22.21	-19.36
Hoverflies	*Pipiza noctiluca*	57	176	0.81	0.82	64.57	23.08	-23.89
Hoverflies	*Pipiza quadrimaculata*	22	6	0.92	0.87	-82.20	-119.93	-5.69
Hoverflies	*Pipizella viduata*	95	272	0.78	0.77	63.25	8.81	-27.25
Hoverflies	*Pipizella virens*	8	7	0.97	0.97	77.78	-3.99	6.84
Hoverflies	*Platycheirus albimanus*	194	726	0.76	0.62	156.48	11.37	8.12
Hoverflies	*Platycheirus ambiguus*	12	9	0.86	0.85	38.89	72.34	-15.41
Hoverflies	*Platycheirus*	117	319	0.80	0.68	64.87	47.24	34.74
Hoverflies	*Platycheirus clypeatus*	244	670	0.70	0.61	84.85	16.94	19.35
Hoverflies	*Platycheirus*	8	6	0.91	0.80	-52.50	-4.17	-18.56
Hoverflies	*Platycheirus fulviventris*	81	148	0.78	0.80	22.30	-11.39	17.68
Hoverflies	*Platycheirus*	14	13	0.87	0.73	-39.41	-79.68	-55.25
Hoverflies	*Platycheirus manicatus*	68	60	0.76	0.84	81.25	-19.87	-22.63
Hoverflies	*Platycheirus peltatus*	223	329	0.69	0.70	44.04	12.93	26.62
Hoverflies	*Platycheirus scambus*	151	202	0.73	0.77	97.89	10.21	7.70
Hoverflies	*Platycheirus scutatus*	172	412	0.75	0.67	207.09	24.87	11.54
Hoverflies	*Pyrophaena*	156	295	0.73	0.74	113.46	7.50	-5.26
Hoverflies	*Pyrophaena rosarum*	48	178	0.91	0.81	69.12	27.07	-11.55
Hoverflies	*Rhingia campestris*	235	814	0.69	0.60	235.63	19.75	44.97

Table S1 (*continued*)

Hoverflies	*Riponnensia splendens*	5	12	0.90	0.94	2150.00	27.52	8.05
Hoverflies	*Scaeva pyrastri*	177	505	0.71	0.66	122.17	5.82	-13.44
Hoverflies	*Scaeva selenitica*	69	416	0.77	0.69	245.08	15.37	0.29
Hoverflies	*Sericomyia lappona*	6	13	0.81	0.88	1009.09	27.03	56.15
Hoverflies	*Sericomyia silentis*	61	258	0.81	0.80	50.46	-2.85	-10.08
Hoverflies	*Sphaerophoria batava*	37	149	0.81	0.86	163.27	-45.80	3.48
Hoverflies	*Sphaerophoria fatarum*	23	15	0.82	0.88	105.81	-5.00	22.34
Hoverflies	*Sphaerophoria*	21	37	0.83	0.94	165.39	6.85	-18.99
Hoverflies	*Sphaerophoria*	17	40	0.82	0.91	-34.02	-2.03	18.63
Hoverflies	*Sphaerophoria*	27	105	0.83	0.83	127.63	39.76	19.30
Hoverflies	*Sphaerophoria scripta*	189	931	0.70	0.57	133.95	-1.37	10.70
Hoverflies	*Sphaerophoria*	26	46	0.82	0.78	159.21	48.54	43.82
Hoverflies	*Sphaerophoria virgata*	6	18	0.85	0.95	-41.76	62.90	0.23
Hoverflies	*Sphegina clunipes*	30	61	0.92	0.85	494.60	44.16	-26.37
Hoverflies	*Sphegina elegans*	15	24	0.86	0.92	39.66	17.60	10.76
Hoverflies	*Syritta pipiens*	277	1028	0.68	0.54	187.69	-0.43	31.98
Hoverflies	*Syrphus ribesii*	231	866	0.69	0.58	139.52	-3.95	-3.07
Hoverflies	*Syrphus torvus*	163	449	0.74	0.69	171.60	-8.33	-9.23
Hoverflies	*Syrphus vitripennis*	239	596	0.69	0.64	102.36	-24.89	-1.58
Hoverflies	*Temnostoma*	13	130	0.93	0.81	411.63	84.36	-33.19
Hoverflies	*Temnostoma*	14	78	0.87	0.86	348.39	71.79	-26.21
Hoverflies	*Trichopsomyia*	11	21	0.70	0.75	73.13	32.84	-11.91
Hoverflies	*Trichopsomyia lucida*	8	14	0.85	0.92	220.00	51.28	-25.71
Hoverflies	*Triglyphus primus*	17	24	0.85	0.90	-21.77	43.30	-25.90
Hoverflies	*Tropidia scita*	122	464	0.73	0.67	112.50	7.76	18.27
Hoverflies	*Volucella bombylans*	131	461	0.75	0.71	255.56	30.31	-3.69
Hoverflies	*Volucella pellucens*	109	514	0.78	0.70	186.67	0.79	-17.43
Hoverflies	*Volucella zonaria*	12	374	0.87	0.76	694.44	48.99	-32.11
Hoverflies	*Xanthandrus comtus*	33	120	0.73	0.74	75.26	10.28	-13.65
Hoverflies	*Xanthogramma*	14	25	0.93	0.95	39.68	45.14	-3.52
Hoverflies	*Xanthogramma*	39	258	0.89	0.80	198.29	23.89	-17.84

Table S1 (*continued*)

Hoverflies	*Xylota abiens*	24	24	0.91	0.81	98.88	14.17	4.85
Hoverflies	*Xylota florum*	36	8	0.87	0.73	71.88	-7.02	22.60
Hoverflies	*Xylota meigeniana*	7	6	0.95	0.93	-24.00	-2.46	-5.81
Hoverflies	*Xylota segnis*	153	700	0.74	0.64	164.07	11.78	-19.25
Hoverflies	*Xylota sylvarum*	57	221	0.86	0.78	193.83	26.82	-17.88
Hoverflies	*Xylota tarda*	18	34	0.94	0.80	211.63	28.46	-5.77
Hoverflies	*Xylota xanthocnema*	10	31	0.93	0.91	240.00	57.80	-5.85

*The number of presence records represents the number of 5 x 5 km grid cells for which the species was reported at least once during the period analysed.

Table S1 (*continued*)

Comparisons	Group	Coefficient	Std. Error	z-value	P-value
TP 1 to 2	B	0.55	0.05	11.28	<0.001
TP 1 to 2	BU	0.42	0.09	4.67	<0.001
TP 1 to 2	H	0.8	0.05	16.09	<0.001
Range Δ TP 1 vs 2	B vs BU	0.13	0.10	1.28	0.54959
Range Δ TP 1 vs 2	B vs H	-0.25	0.07	-3.52	0.00255
Range Δ TP 1 vs 2	BU vs H	-0.38	0.10	-3.65	0.0016

Adjusted Tukey's *P-values* reported; Δ: Change.

Table S2. Comparisons of areal range changes of pollinators across time. In “Comparisons”, TP refers to the time periods between which areal range changes are compared (TP 1 = 1951–1970; TP 2 = 1998–2014). “Group” represents the pollinator group, bees (B), butterflies (BU) and hoverflies (H). The first three rows test if there was a significant change between the areal range size of TP1 and TP2 for each pollinator group. The last three rows test whether the areal range changes significantly differs among pollinator groups. The coefficients from the linear models are presented.

Table S3. Results of the comparison of shifts in the midpoints of species distributions per pollinator group for the whole study period, TP1–TP2 (TP 1 = 1951–1970; TP 2 = 1998–2014). A Student *t*-test was used to investigate if the overall changes in the centroids of the species geographic ranges differed significantly from zero (no change) within each pollinator group.

Group	Latitude *t*	P-value	Longitude *t*	P-value
Bees	4.99	<0.001	-4.99	<0.001
Butterflies	2.01	0.04	2.21	0.03
Hoverflies	4.46	<0.001	0.79	0.43

Table S4. (next page)**Detailed results of best model to explain the relation between species functional traits of three pollinator groups (bees, butterflies, hoverflies) and areal range changes, latitudinal and longitudinal shifts, respectively.** The starting model contained areal range change, latitudinal or longitudinal shift values as response variable and all two way interactions between functional traits as predictors (including also the starting range size). After model selection, only models with BIC Δ <2 were kept. The level of the factorial variable to which the coefficient refers to is shown between brackets. Coefficients and standard errors are provided for each model.

Areal range change			**M1±SE**	**M2±SE**	**M3±SE**	**M4±SE**
	Bees	Intercept	0.49±0.04	0.56±0.03		
		H (specialists)	0.19±0.07			
		IR	-0.27±0.03	-0.25±0.03		
		Adj. R^2	0.23	0.2		
	Butterflies	Intercept	0.88±0.12			
		H (specialists)	-1.06±0.17			
		Adj. R^2	0.38			
	Hoverflies	Intercept	0.72±0.06	0.71±0.05		
		S	0.15±0.03	0.17±0.03		
		F	0.31±0.06	0.32±0.06		
		LFP (other)	0.21±0.07	0.23±0.07		
		IR	-0.30±0.04	-0.33±0.04		
		H (specialists)	-0.48±0.16	-0.12±11		
		F × LFP (other)	-0.22±0.07	-0.25±0.07		
		H (specialists) × IR	-0.58±0.19			
		Adj. R^2	0.37	0.34		
Latitudinal shifts						
	Bees	Intercept	0.05±0.005	0.05±0.005		
		IR	-0.01±0.005	-0.01±0.005		
		S		-0.01±0.005		
		Adj. R^2	0.04	0.06		
	Butter	Intercept	0.02±0.01	0.03±0.01		
		F	0.03±0.01			
		ND	0.06±0.01	0.04±0.01		
		H (specialists)	0.02±0.02	-0.01±0.02		
		IR	-0.003±0.01	-0.004±0.01		
		F × ND	-0.03±0.01			
		H (specialists) × ND	-0.10±0.02	-0.05±0.02		
		H (specialists) × IR	0.03±0.01	0.04±0.01		
		Adj. R^2	0.40	0.32		
	Hoverflies	Intercept	0.04±0.009			
		LFP (other)	0.0001±0.01			
		V (univoltine)	-0.003±0.01			
		IR	-0.02±0.005			
		LFP (other) × V (univoltine)	0.05±0.02			
		Adj. R^2	0.21			

Longitudinal shifts						
	Bees	Intercept	-0.07±0.01	-0.07±0.01	-0.13±0.03	
		F		-0.02±0.01		
		V (univoltine)			0.06±0.03	
		Adj. R^2	0	0.02	0.01	
	Butter	Intercept	0.04±0.02	0.04±0.02	0.03±0.02	0.03±0.02
		F	0.04±0.02	0.04±0.02	0.09±0.02	0.04±0.02
		V (univoltine)	0.02±0.02	0.01±0.02	0.002±0.02	0.03±0.02
		H (specialists)	0.03±0.03	0.02±0.02		0.01±0.03
		IR	-0.01±0.02	-0.01±0.02		0.02±0.01
		F × V (univoltine)	-0.1±0.03	-0.10 ±0.02	-0.09±0.03	-0.09±0.03
		F × H (specialists)	0.14±0.03	0.14±0.03		0.12±0.03
		F × IR	0.05±0.01	0.05±0.02		0.04±0.01
		V (univoltine) × IR	0.06±0.02	0.09±0.03		
		H (specialists) × IR		-0.05 ±0.03		
		Adj. R^2	0.45	0.47	0.26	0.40
	Hoverflies	Intercept	-0.01±0.01			
		LFP (other)	0.06±0.02			
		IR	0.03±0.008			
		Adj. R^2	0.08			

F: Flying period; LFP: Larval food preference; H: Habitat; ND: Larval food preference related to Ellenberg nitrogen value of diet; S: Size; V: Voltinism; IR: Initial range.

M1–M4: Coefficients of the best models obtained; SE: standard error.

Table S5. The environmental variables included in the analyses and their changes across time across the Netherlands. Comparisons were carried with a *Student t-tests* for changes between time period TP1 and TP2.

Environmental variable	Average value		Standard deviation		TP1 vs TP2	P-value
	TP1	TP2	TP1	TP2	*t*	
Mean diurnal range	7.05	7.25	0.67	0.75	8.02	<0.001
Temperature seasonality	5.79	5.66	0.13	0.14	-27.66	<0.001
Mean temp. of wettest quarter	15.45	15.85	0.68	2.06	7.54	<0.001
Mean temp. of driest quarter	5.79	9.6	1.78	1.97	58.76	<0.001
Mean temp. of warmest quarter	15.92	17.16	0.36	0.45	88.32	<0.001
Annual precipitation	803.9	828.2	25.14	21.82	29.84	<0.001
Precipitation of wettest month	102.28	91.18	5.96	4.86	-59.09	<0.001
Precipitation of driest month	44.84	41.13	2.91	3.45	-33.65	<0.001
Precipitation of warmest quarter	253.4	238.78	11.7	11.48	-36.46	<0.001
Average patch area of suitable habitat	104.97	16.61	354.79	113.3	-9.43	<0.001
Total edge density	0.019	0.023	0.008	0.011	11.73	<0.001
Edge density managed-natural systems	0.007	0.011	0.004	0.005	18.37	<0.001
Number of land use classes	6.28	7.72	1.21	0.75	40.36	<0.001
Grassland	42.23	40	26.26	20.35	-2.67	<0.01
Agriculture	31.41	27.46	25.01	22.31	-4.68	<0.001
Moors/peat	2.04	1.34	6.32	4.68	-3.53	<0.001
Forest	8.53	11.14	13.92	14.23	5.2	<0.001
Urban	6.94	10.9	7.69	10.13	12.39	<0.001
Water	6.97	6.42	15.46	10.7	-1.16	0.25
Swamps	0.2	1.43	0.7	5.8	8.37	<0.001
Sandy soils	1.68	1.31	9.1	7.23	-1.26	0.21

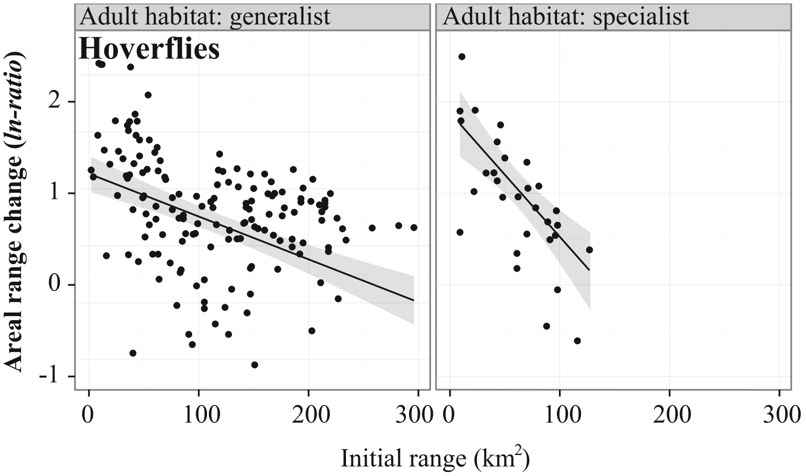

Fig. S1. Effect of habitat specialisation on hoverflies depended on the initial range size of the species. Range expansions were on average more accentuated for species with greater habitat specialisation and smaller initial ranges.

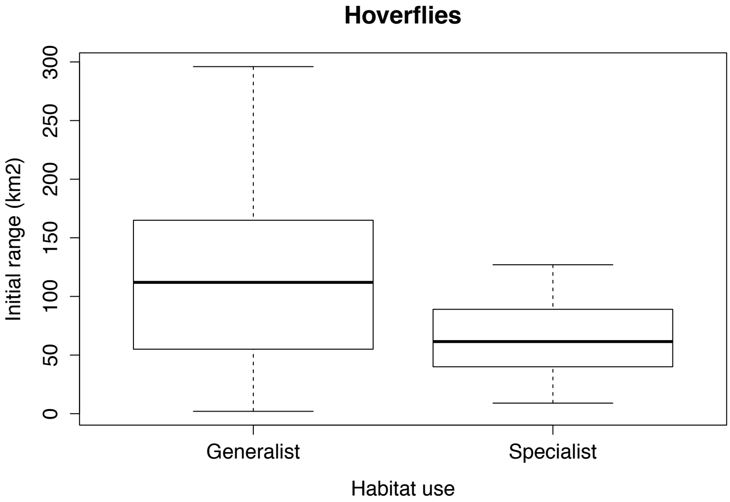

Figure S2. Summary of the initial range size for hoverfly habitat generalists and specialists.

6

Susceptibility of pollinators to ongoing landscape changes depends on landscape history

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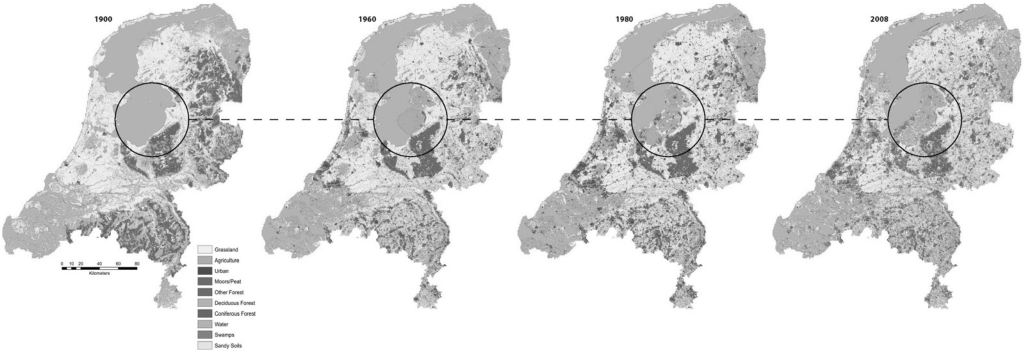

Diversity and Distributions, In Press.

Abstract

Pollinators play an important role in ecosystem functioning, affecting also crop production. Their decline may hence lead to serious ecological and economic impacts, making it essential to understand the processes that drive pollinator shifts in space and time. Land-use changes are thought to be one of the most important drivers of pollinators' loss, and there is increasing investment on pollinator-friendly landscape management. However, it is still unclear if landscape history of a given region influences on how pollinator communities respond to further landscape modification. Using geographically explicit historical landscape and pollinator data from the Netherlands, we evaluated how species richness changes of three important pollinator groups (bees, hoverflies and butterflies) are affected by landscape changes related to habitat composition, fragmentation and species spillover potential, and if such effects depend on the historical characteristics of the landscape. Our results show that the effect of landscape changes varied between different pollinator groups. While bumblebee richness benefited from increases in edges between managed and natural systems, other bees benefited from increases in landscape heterogeneity and hoverfly richness was fairly resistant to land-use changes. We found that for the majority of the pollinators past landscape characteristics conditioned the more recent pollinator richness changes. Landscapes, which had historically more suitable habitat, were more susceptible to display hoverfly declines (caused by drivers not considered in this study). Landscapes, which had historically greater spillover potential, were more likely to suffer butterfly richness declines and the bumblebee assemblages were more susceptible to the effects of fragmentation. The diversity of responses of the pollinator groups suggest that multispecies approaches that take group-specific responses to land-use change into account are highly valuable. These findings emphasize the limited value of a one-size-fits-all biodiversity conservation measure and highlight the importance of considering landscape history when planning biodiversity conservation actions.

Introduction

There is increasing concern about the status and trends of pollinators across the globe (Potts *et al.,* 2010, Winfree, 2013). Pollinators play an important role for the functioning of ecosystems and are essential for crop production (Vanbergen & The Insect Pollinators Initiative, 2013, Garibaldi *et al.,* 2013). However, they have suffered accentuated declines over the past century (Biesmeijer *et al.,* 2006, Carvalheiro *et al.,* 2013), only showing some subtle signs of recovery in some regions in recent years (Carvalheiro *et al.,* 2013). Understanding the processes that have led to shifts in pollinator diversity is essential to develop better conservation measures that stop declines and restore pollinator communities.

While there is a great diversity of potential drivers of pollinator loss (Potts *et al.,* 2010), global land-use intensification and landscape fragmentation are among the prime suspects (Winfree *et al.,* 2009). Because historical data are lacking for most regions and taxa, most studies that aim to evaluate the impacts of landscape changes compare current landscapes that vary in landscape features (e.g. Brosi *et al.,* 2008; Uehara-Prado & Freitas, 2009). Most of these studies assess shifts at small spatial scales and focus on a limited type of landscapes (Benedick *et al.,* 2006; Taki *et al.,* 2010). Studies using a space-for-time substitution approach assume that comparing recent landscapes that differ in fragmentation and composition represents the processes that have taken place in a specific location across time. However, this is unlikely to be generally true, as the original state of the landscape could be guiding the responses of the remaining biodiversity (Kuussaari *et al.,* 2009). For example, locations that have been subjected to rapid historical landscape changes may have species communities more susceptible to extinctions presenting also an extinction debt (delayed loss of biodiversity after habitat loss and/or fragmentation events) (Tilman *et al.,* 1994), than locations that have experienced changes at slower peace through time. Therefore, the loss of a given fraction of natural habitat may have a stronger impact on locations that were already deprived of natural habitat. Moreover, (re)colonization patterns that determine in situ biodiversity may also depend on the original state of the landscape and such effects might then not be apparent in short-term studies. Evaluating if and to what extent landscape history conditions species responses to changes in the landscape characteristics is, therefore, crucial for the improvement of biodiversity conservation actions.

Given that different pollinator groups (e.g. bees, hoverflies, butterflies) differ in their needs for habitat and feeding resources and also in their life history and dispersal capabilities (Fründ *et al.,* 2010), it is expected that the responses of pollinators to fragmentation and habitat loss will vary between groups. However, landscape management practices that aim to slow biodiversity loss are usually based on the responses of single species groups (Fleishman *et al.,* 2000), suggesting a one-size-fits-all type of biodiversity conservation measure, an approach that has been challenged by recent biodiversity conservation studies (Maes & Dyck, 2005; Gerlach *et al.,* 2013).

Different hypotheses concerning the effect of landscape modification on pollinators have been proposed (Tscharntke *et al.,* 2012). However, these are based on evidence from space for time substitution studies (e.g. Hendrickx *et al.,* 2007). In this study, using historical and current landscape and pollinator information, and thus not relying on the space for time substitution, we analyse the impacts that changes in habitat composition and fragmentation during the last 100 years in the Netherlands have had on the species richness changes of the different pollinator groups. We further analyse if these impacts are similar across pollinator groups and if landscape history (i.e. landscape conditions before changes occurred) conditions the species responses to these impacts.

Landscapes with higher amount of suitable habitat and higher diversity of habitats are likely to present higher diversity of food resources and contain a more diverse pollinator assemblage (e.g. β-diversity hypothesis; see Tscharntke et al. 2012). Therefore, it is expected that increases in habitat heterogeneity and in the amount of suitable habitat are positively related to changes in pollinator species richness (hypothesis 1). Moreover, while landscape fragmentation is generally perceived as having negative effects on biodiversity (Potts *et al.,* 2010) (hypothesis 2), the increase in length of edges, specially between (semi) natural and managed systems may increase the interactions between organisms, and thus, increase the functional connectivity, thus helping to maintain high local biodiversity (Bianchi *et al.,* 2006; Kuefler *et al.,* 2010). It is hence expected that the increase in edges between managed and natural land-use classes, a proxy for potential species spillover effects (Blitzer *et al.,* 2012), favours the local species richness (hypothesis 3). Additionally high spatial heterogeneity of communities (at local and landscape scale) may reduce the negative local effects of fragmentation or loss of suitable habitat (e.g. landscape insurance hypotheses, see (Tscharntke *et al.,* 2012), being important to consider interactive effects between different landscape parameters.

Methods

Species data

This study uses data from a previous study of Carvalheiro *et al.* (2013) which has applied a combination of interpolation and extrapolation techniques to species accumulation curves to deal with the unstandardized nature of historical collections and estimated richness changes of three important Dutch pollinator groups (bees, butterflies and hoverflies) for three time comparisons: 1930–1949 vs. 1950–1969 (TC1), 1950–1969 vs. 1970–1989 (TC2) and 1970–1989 vs. 1990–2009 (TC3). In the study of Carvalheiro *et al.* (2013) the bee and hoverfly data were obtained from the European Invertebrate Survey (EIS-Nederland, http://www.eis-nederland.nl) and the butterfly data from the Dutch National Database of Flora and Fauna (NDFF, www.ndff.nl). For and in depth explanation on how species richness changes were calculated and more details about the species richness data and methods see Carvalheiro *et al.* (2013). The focal area of this study, the Netherlands, has been intensely sampled for biodiversity since the early 19th century and is an area that has experienced major well-documented changes in land-use (Knol *et al.,* 2004; Hazeu *et al.,* 2010). Here we used such detailed information on land-use and test if land-use change explains the patterns of pollinator richness changes detected by Carvalheiro *et al.,* (2013). As in Carvalheiro *et al.* (2013) the bumblebees (Apidae, Bombini) were separated from other bees (hereafter referred to as non-bumblebees) due to their recognized high vulnerability (Williams & Osborne, 2009) and different trait characteristics (highly-social, large bees with a large foraging range). A total of 40 landscapes (10x10 km each) for bumblebees, 144 for non-bumblebees, 432 for butterflies and 402 for hoverflies were used (Fig. S1).

Land-use data

We obtained land-use data for the years 1900 (at 50 × 50 meters resolution), 1960, 1980 and 2008 (each at 25 × 25 meters resolution), with a high land-use classification accuracy ranging from 84.8 to 98 % (Knol *et al.,* 2004; Hazeu *et al.,* 2010). Based on those land-use maps, for each 10x10 km cell ('landscapes') for which we had species richness change values, we calculated land-use changes between the following periods: 1900 vs. 1960 (LP1), 1960 vs. 1980 (LP2), and 1980 vs. 2008 (LP3). We assumed land-use data from LP1, LP2 and LP3 to be representative of the time comparisons TC1, TC2 and TC3, respectively, because most of the species' sampling period was covered by the land-use change period. These time periods are also associated with very different trends in land-use change. During LP1 the Netherlands suffered intensive and rapid habitat loss, while during LP2 there was great agriculture intensification and associated increase in pesticides use (Harms *et al.,* 1987; Geiger *et al.,* 2010). During LP3 there was an increase in investment on conservation measures and agri-environmental schemes (Kleijn & Sutherland, 2003; European Environmental Agency, 2010; European Environmental Agency, 2011). For each time comparison we calculated several metrics of landscape composition and fragmentation and their changes (explained below).

To standardize land cover type classifications between maps, the land-use classes were reclassified to match the oldest map classes (1900). This resulted in 10 final land-use classes for the four maps (Fig. S2; see Table S1 in Supporting Information). The resulting land-use maps were then used for the extraction of the fragmentation and composition variables for each 10 × 10 km landscape cell as described below.

Landscape composition and fragmentation metrics

In our study, we identified several landscape variables related to composition and fragmentation mentioned by Tscharntke et al. (2012) which include the ones most commonly used in recently empirical published work (Table S2).

We selected two variables related to habitat composition: the percentage of suitable habitat (PSH) present in each 10x10 km cell, and the number of land-use classes (patch richness: PR). To calculate PSH, land-use suitability values were generated by expert opinion (Vogiatzakis *et al.,* 2014) and were applied equally to all pollinator groups (Table S1). Although these values were not created for the Netherlands but for the United Kingdom, this is the best approximation currently available for the land-use classes in our study area. Following these values we classified the land-use classes Grassland, Moors/Peat, Deciduous/Mixed forest and Sandy soils as suitable habitat, and Agriculture, Coniferous forest, Urban, Water and Swamps as non-suitable habitat. Due to the excessive management of Dutch grasslands (e.g. high fertilizers input), their suitability is likely lower today than it was before the 70's (Oenema *et al.,* 2012). Despite the difference in grassland suitability between periods grassland was always considered suitable as this habitat still has substantial feeding and nesting resources for pollinators in comparison to other agricultural habitats (Hegland *et al.,* 2001; Öckinger & Smith, 2007). In addition, we have at present, no objective way to assess grassland suitability change. Agriculture was considered not suitable as in the Netherlands it mostly refers to highly intensified monocultures. To calculate patch richness (PR), we used the number of land-use classes, and we consider this variable a surrogate for spatial heterogeneity of species assemblages (β-diversity hypothesis; Tscharntke *et al.,* 2012).

As landscape fragmentation is a complex process, we divided the fragmentation variables into two groups. The first group included two variables representing habitat configuration per se: proximity between suitable habitat patches (Proximity); and average weighted mean patch area of suitable habitat patches (PA, where a smaller value represents more fragmentation). The second group included edge density in the total landscape (ED). However, the edges between managed and natural systems may enhance functional connectivity (i.e. edges between differently managed systems) instead of acting as functional barriers (Kuefler *et al.,* 2010), and can be seen as a surrogate for landscape spillover effects. Therefore, we also calculated the edge density between managed and natural systems (ED Man-Nat) and analysed its affects separately from the total edge density. When calculating the edge density between managed and natural systems we considered the Grassland and Agriculture classes as (intensively) managed and the Moors, Peat, the Forest types, Swamps and Sandy soils as (semi-)natural systems. All spatial analyses were carried out in ArcGis (v10, Esri

Redlands, CA, USA). The landscape fragmentation and edge metrics were obtaining using Fragstats v4 (McGarigal *et al.,* 2012).

Statistical analysis

All statistical analyses were carried out in the R platform (R Development Core Team, 2014). For each of the landscape metrics described above we calculated the land-use changes (Δ) that occurred in each time period (LP1, LP2 and LP3). The land-use change data for each time period was calculated as the log of the ratio between the post period and the pre period landscape value (e.g. for LP1, pre period equals 1900 and post period equals 1960). As we also wanted to test if the historical characteristics of the landscape conditioned the effect of such land-use changes, we also considered information of the original state of the landscape as a separate variable, hereafter referred to as T1 (i.e. for TC1 we included fragmentation and composition values in 1900, for TC2 we included the fragmentation and composition values in 1960 and for TC3 the values of 1980). We then analysed the impact of landscape fragmentation and composition on bumblebees, non-bumblebees, butterflies and hoverflies species' richness changes, with linear mixed effects models using the "lme4" R package (Bates *et al.,* 2014). As we sometimes have data from the same location in more than one time period (see Fig. S1), to account for the non-independence of the predictions generated based on the data from a given location and period of time we used the time comparison analysed (TC1, TC2, TC3) and landscape ID (cell location) as random effects. Including time comparison as a fixed effect would allow us to explore in more detail the dynamics of biodiversity changes in the study region. However, the objective of our study is to detect general patterns of responses of the different pollinator groups to land use modification, so that they can be extrapolated to other regions where man-driven landscape changes occurred in different time periods.

For all the species groups we created a general initial model that included all the interactions between the fragmentation and composition variables for the original state (T1) and land-use change values (Table S3). We then selected the most parsimonious model (smallest Bayesian Information Criterion, BIC) by applying a model selection procedure using the R package "MuMIn" (Barton, 2014). The species richness change data was transformed to a log-ratio and the landscape variables were centred and standardised before analyses (*z* scores; Gelman, 2008). Given that landscapes closer to each other may present similar species richness changes we first tested for any spatial autocorrelation using the Morans *I* test with the R package "spdep" (Bivand, 2014), and no significant effects were found. After analysis, we confirmed the applicability of our linear mixed effects model to the data as the residuals of fitted models were approximately normally distributed with no indication of over dispersion or heteroscedasticity.

Results

Effect of changes in habitat heterogeneity and in the amount of suitable habitat

The increase in habitat diversity (i.e. diversity of land-use classes) positively impacted one pollinator group (Table 1), the non-bumblebees, where richness increased with habitat heterogeneity (Table 1a; Fig. 1a).

Table 1. Results of the mixed models analysing the species richness changes as function of landscape composition and fragmentation. Details about the original starting model are presented in Table S3. The final model for each species group analysed was the best model (lowest BIC) after model selection. We also present the second best model and its BIC value for comparison purposes.

	Terms	Coefficient	SE	BIC	2nd best BIC	2nd best model
a) Non-bumblebees	Δ PR	0.1257	0.0357	-23.2	-22.8	Null
b) Hoverflies	PSH T1	-0.0730	0.0230	-104	-100.7	Δ PA + PSH T1
c) Bumblebees	ED Man-Nat T1	0.1439	0.0914	22	25	ED Man-Nat T1 + Δ PA + Δ PA × ED Man-Nat T1
	Δ PA	-0.0917	0.0677			
	Δ ED Man-Nat	0.2482	0.0825			
	Δ PA × ED Man-Nat T1	-0.4599	0.2009			
d) Butterflies	ED Man-Nat T1	-0.0656	0.0255	22.5	22.6	ED T1

Composition and fragmentation variables descriptors= PR: Number of land-use classes in the landscape; ED Man-Nat: Edge density between managed and natural habitat; ED: Total edge density in the landscape; PA: patch's area; PSH: Percentage of suitable habitat in the landscape. Δ: Change; T1: Time 1 or original landscape state. SE= standard error. All two-way combinations of terms were tested, but only the terms included in the two best models are listed.

Although most landscapes in the Netherlands (our 10 × 10 km cells) have experienced decreases or increases over the last century between -20% and +20 % (Fig. S3), contrary to expectations none of the pollinator groups were affected by changes in the amount of suitable habitat (Table 1). However, hoverfly richness changes were conditioned by the amount of suitable habitat in the original landscape (Table 1b): landscapes that contained low amounts of suitable habitat in the original state were more likely to show subsequent species richness increases than landscapes with abundant suitable habitat in the original state (Fig. 1b).

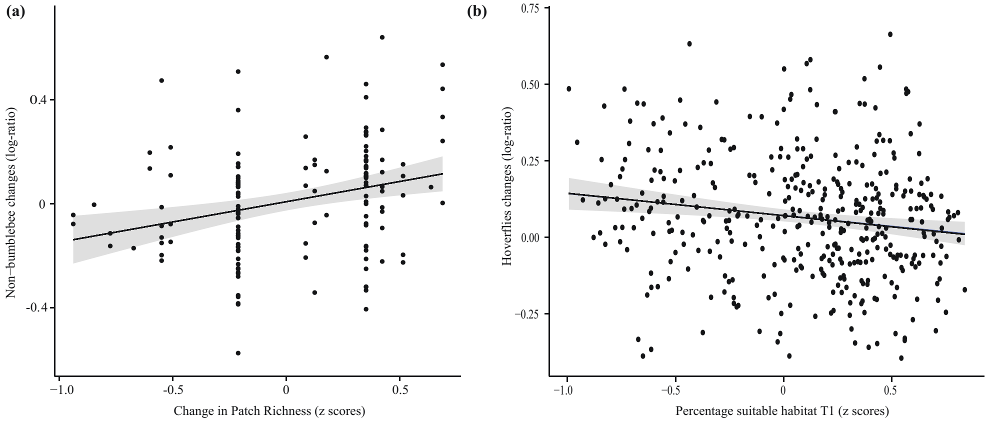

Figure 1. The effects of habitat composition on pollinator species richness changes. a) Effect of habitat heterogeneity (Δ PR) on non-bumblebees. Landscapes that increased in heterogeneity presented higher species richness than more homogeneous landscapes; b) Effect of the percentage of suitable habitat on hoverflies. Landscapes with high percentage (T1) presented significantly lower species richness changes than low percentage ones. For all plots the values of the centred-standardized explanatory variables are presented. Grey bands represent the 95% confidence interval.

Effect of changes in landscape fragmentation

The pollinators' responses to fragmentation differed among the different groups. In landscapes that had originally a high spillover potential (i.e. where edge density between managed and natural areas was high in T1) changes in the average patch area had an effect on bumblebees: declines in richness were more accentuated in areas where patch area increased (Table 1c; Fig 2a). In landscapes with a high average patch area species richness loss was more likely with increases in the density of these edges. Other groups were not significantly affected by changes in fragmentation level (i.e. changes in proximity between patches of suitable habitat or total edge density). However, responses of butterflies to other landscape characteristics (or to other drivers) were conditioned by the original state of fragmentation in the landscape (ED T1, in model 2). Landscapes with higher amount of edges in the original state were significantly more likely to suffer decreases in butterfly species richness (Table 1d; Fig. 2b).

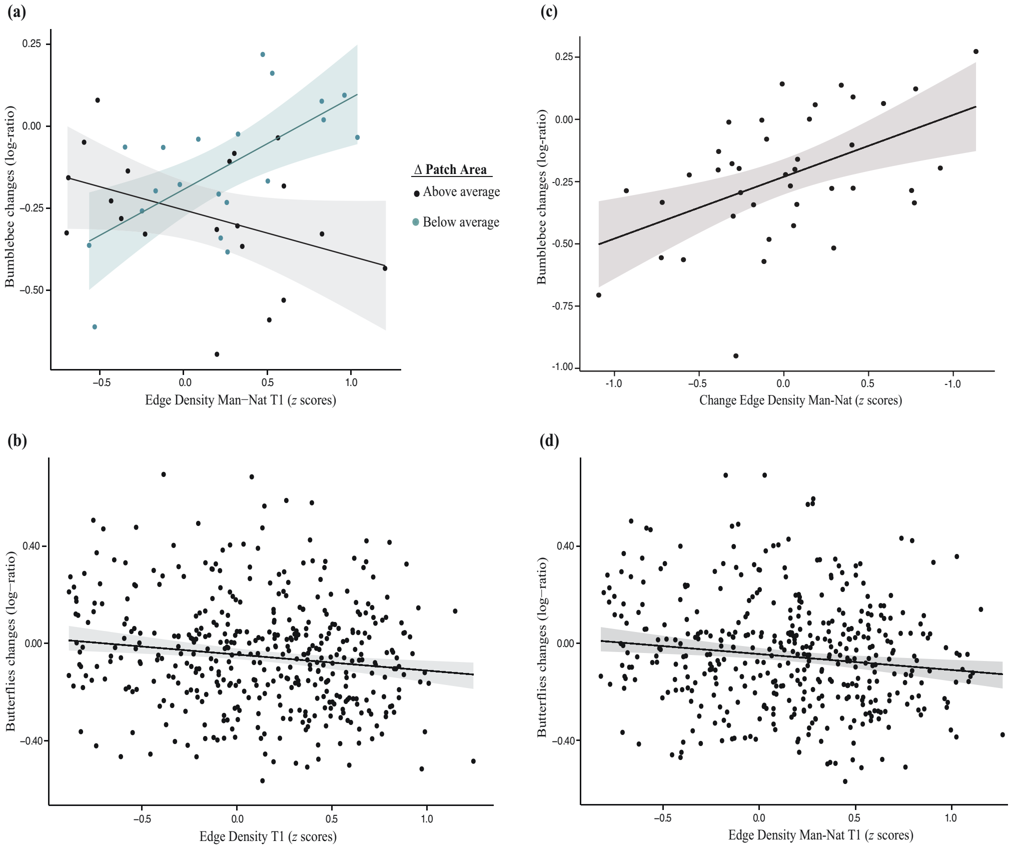

Figure 2. The effects of fragmentation and edges for spillover effects on pollinator species richness changes. a) Effect of the interaction between the edge density of managed and natural systems (T1) and the change in patch area on bumblebees. Increases in richness occurred in landscapes with originally more of these edges and smaller patches. Light colours represent negative or below the average Δ Patch Area. Dark colours represent positive above average Δ Patch Area; b) The effect of the total edge amount in the landscape (T1) on butterfly species richness changes. Landscapes with high densities of total edge were more likely to experience negative species richness changes of butterflies; c) Effects of changes in edge density between managed and natural systems on species richness of bumblebees. Landscapes with higher edge densities were more likely to increase their bumblebee

species richness; d) Effects of edge between managed and natural systems (T1) on species richness of butterflies. Landscapes with higher densities were more likely to decrease their butterfly species richness. For bumblebees the partial residual (i.e. residuals after removing the effect of all other variables) are shown. For all plots the values of the centred-standardized explanatory variables are presented. Grey bands represent the 95% confidence interval.

Effect of changes in the density of edges between managed and natural habitats, a proxy for potential species spillover effects

Bumblebees were the only group of pollinators affected by changes in edge density between managed and natural systems (ED Man-Nat; Fig. 2c). Increases in ED Man-Nat led to significant increases in species richness of bumblebees (Table 1c). Moreover, for bumblebees the effects of fragmentation (i.e. patch area) described above depended on the original density ED Man-Nat (i.e. of edges which potentiate spillover effects). In landscapes with originally high spillover potential, increases in patch area led to more accentuated declines (Fig. 2a). Richness changes in butterflies were also conditioned by the original spillover potential. For this group, species richness increases were more likely to occur in landscapes with originally less edge density between managed and natural systems, conversely, landscapes with originally higher density of these edges were more likely to present species richness declines (Fig. 2d).

Discussion

Anthropogenic landscape changes are one of the main drivers of biodiversity loss (González-Varo *et al.,* 2013). Most studies evaluating the impacts of such changes focus on a limited number of species and compare current landscapes with different levels of habitat modification, mostly comparing extremes (i.e. use space for time substitution) (Winfree, 2013). While this approach allowed the development of important ecological approaches on the impacts of landscape changes (Tscharntke *et al.,* 2012), long-term datasets based on a large number of species are needed to better understand the role of the landscapes' history on ongoing patterns of species changes. Here we use a long-term datasets (>100 years) on pollinator richness change and land-use changes and show that changes in species richness were closely linked to landscape historical changes (diversity of habitats, patches' area and potential for spillover effects between managed and natural systems), but that such effects largely depended on the original state of the landscape before changes occurred (Table 2).

Table 2. Summary results for the composition and fragmentation hypothesis analysed. Hypothesis one analyses the effects of landscape composition on biodiversity. Hypothesis two focuses on the effects of landscape fragmentation and hypothesis three on the edges between managed and natural systems, a proxy for spillover effects. The results are group dependent. There is a predominant effect of the original state of the landscape on the pollinator species richness changes.

Group	**Landscape state**	**Hypothesis 1 -Composition effects**		**Hypothesis 2 -Fragmentation effects**		**Hypothesis 3 - Fragmentation spillover effects**
		> Suitable habitat → > Species richness	> Habitat heterogeneity → > Species richness	<Patch area, Proximity; > Edges → < Species richness	> Edges→ < Species richness	> Edges MAN-NAT → > Species richness
Bumblebees	T1					*Positive*
	Δ			*Negative*		*Positive*
Non-bumblebees	T1					
	Δ		*Positive*			
Butterflies	T1				*Negative*	*Negative*
	Δ					
Hoverflies	T1	*Negative*				
	Δ					

T1: Original landscape state; Δ: Changes; SR: Species richness; >: Higher; <: Lower; →: Then. Positive and Negative: direction of the effect.

Effect of changes in habitat heterogeneity and in the amount of suitable habitat

We expected that increases of the amount of suitable habitat and of the diversity of habitats would lead to increases the pollinator species richness (β-diversity hypothesis; Tscharntke et al. 2012). Contrary to our expectations, none of the studied pollinator groups were affected by changes in the amount of suitable habitat (Table 2). This result could be related to the fact that most of the species' data comes from recent time periods (last two periods; Fig. S1), a time during which the available natural habitat was already very reduced in the Netherlands (e.g. by loss of natural habitat to agricultural and urban landscapes; Fig. S2) and during which agricultural practices had already generated highly homogenous areas. Therefore, recent species responses might not be due to recent but to past changes in the landscape conditions, suggesting that extinction-colonization debt may be important (Bommarco *et al.,* 2014). Furthermore, in this study we defined Grassland, Moors/Peat, Deciduous/Mixed forest and Sandy soils as suitable habitats, and it is possible that pollinator species which resisted to the accentuated changes which occurred before 1980 are able to make use and sustain their populations in areas that we considered unsuitable (e.g. urban areas or agricultural landscapes).

Hoverflies were not affected by any of the landscape change characteristics considered by this study. This suggests that other drivers may be the most important for hoverflies (e.g. climate, other landscape characteristics). However, changes in richness of this group were conditioned by the original amount of suitable habitat in the landscape. This was expected as the majority of the Dutch syrphid species (around 2/3) present a close association with scrub and forest habitats (Reemer 2005), and the area of such habitats used to be smaller at the beginning of the second half of the 20th century. The fact that landscapes with higher amounts of suitable habitat (included forested areas) were less likely to experience further increases in hoverfly richness suggests that such areas already contained well-established populations and thus great increases in species richness were not possible. Moreover, hoverflies not only benefit from forested areas but also some of them (around 20-30 common species) greatly benefit, at the larval stage, from managed areas where prey is abundant (i.e. aphids in crop fields; Reemer et al. 2009), areas that in our study were not classified as suitable habitat.

The suitability of a habitat for pollinators depends on the availability of floral and nesting/reproduction resources, and hence on the characteristics of the landscape, such as habitat heterogeneity (Kremen *et al.,* 2007; Batáry *et al.,* 2011). The results of this study show that the effects of changes in habitat heterogeneity were mild, with only non-bumblebees increasing with the amount of habitat land-use classes available. However, these results show that higher diversity of habitats tend to contain a more diverse pollinator assemblage that more homogeneous areas (Table2). It is possible that landscapes with higher habitat heterogeneity have more diverse vegetation structures providing the diversity of feeding and nesting resources required by multiple bee species (Garibaldi *et al.,* 2014). Thus increasing the heterogeneity of land-use classes, for example by means of adding natural or semi-natural elements to more homogeneous landscapes, may improve the species richness levels of bees in these areas (Kremen *et al.,* 2007). Furthermore, this habitat improvement could especially benefit species that have different feeding preferences at different life stages and seasons of the year (Kohler *et al.,* 2008), and which without this habitat improvement seem to be particularly threatened.

Landscape fragmentation and spillover effects

In human-dominated areas, highly fragmented habitats (e.g. fragmented forest, urban areas) and mosaics of highly homogeneous landscapes, (e.g. areas with intensive agriculture), are the rule. While fragmentation of suitable habitat may negatively affect biodiversity (Fahrig, 2003), in homogeneous landscapes dispersal of organisms between patches of different land-use, i.e. spillover effect, becomes highly important as this may increase resource availability, generate stable ecological processes and facilitate ecosystem functioning (Kremen *et al.,* 2007; Blitzer *et al.,* 2012). However, depending on the scale and on the study taxa, this may in turn reduce the overall beta diversity, (e.g. Loreau, 2000; Clough *et al.,* 2007). Furthermore, these ecological processes may be reinforced in landscapes where habitat area and proximity between suitable habitats is increased (Sabatino *et al.,* 2010).

In our study the effect of changes in landscape fragmentation (reduction in patch area) on pollinators' richness was only evident for bumblebees (Table 1 and Table 2). The fact that fragmentation was associated with increased in bumblebee richness in landscapes where originally the density of edges between managed and natural systems was high was unexpected (Fig. 2a). However, this fragmentation-spillover outcome is logical if further fragmentation occurred in areas with already high amounts of managed and natural areas and thus with high species richness (given spillover potential already in place), facilitating in this manner additional potential spillover effects. The positive effect of these edges is further emphasized by the increase in species richness of bumblebees also in landscapes that experienced increases (change) in edge density between the managed and natural systems. Thus the edges between managed and natural systems become essential as they can potentiate the movement of species across different habitats (spillover effects; Table 2), and may facilitate the access to the diversified vegetation structures provided by a matrix of diversified patches of habitats that bumblebee communities need for feeding and nesting (Lye *et al.,* 2009). The access to these diversified resources is of primary importance for bumblebees since it has been shown that landscape resources diversity (e.g. given by higher levels of managed-natural areas) and not resources density drives bumblebee species distribution and foraging behaviour at the patch and landscape level (Jha and Kremen, 2013).

While butterflies richness changes were not associated with the patterns of fragmentation change, we found significant effects of the original landscape state (T1) of total edge density and spillover potential (Fig. 2b and Fig. 2d) (see also Tscharntke *et al.,* 2008; Lucey & Hill, 2012). However, our results suggest that landscapes that were originally more fragmented (high ED T1 and ED Man-Nat T1) were more likely to suffer butterfly species losses (Table 1d, first and second model). This may be because the amount of edges in the landscape may interfere with the habitats' (micro)climatic conditions (Ries *et al.,* 2004), which are vital for the survival of many butterflies, particularly specialist species (Ries & Debinski, 2001; WallisDeVries & Van Swaay, 2006). Furthermore, these responses suggest a possible delayed effect (T1 effects) on the recent butterflies communities and implies that recent butterfly richness may still be highly determined by the past landscape characteristics. Therefore it is possible that recent butterfly populations from more fragmented landscapes are more susceptible to local extinction (Sang *et al.,* 2010).

The lack of a significant effect of habitat fragmentation on hoverfly richness changes could be due to their high mobility, and non-dependence of larvae on flower resources (Jauker *et al.,* 2009) making them less dependent on the surrounding landscape configuration and more resilient to habitat changes (Schweiger *et al.,* 2005). The lack of fragmentation effects on non-bumblebees species was unexpected as these depend on small-scale landscape characteristics (Steffan-Dewenter *et al.,* 2002; Holzschuh *et al.,* 2007). However, it is possible that weak fragmentation effects on this group had been counteracted by increases in feeding and nesting resources availability created along habitat margins (Jauker *et al.,* 2009).

Implications for conservation and landscape management

Most studies analysing the changes in insect biodiversity in response to environmental changes focus on single species groups, e.g. butterflies, as insect biodiversity indicators (e.g. Fleishman *et al.,* 2000). The single-group approach has recently been challenged emphasising the need for a multi-group monitoring approach (e.g. Maes & Dyck, 2005; Gerlach *et al.,* 2013). However, butterflies tend to be the first choice because, as this group has historically caught the attention of conservationists and species are easily recognizable, data availability is greater than in other taxa. Butterflies are indeed one of the most sensitive pollinator groups (Carvalheiro *et al.,* 2013). However, here we show that responses of butterflies are not always representative for responses of other insect groups (e.g. responses of butterflies to ED Man-Nat but not of hoverflies, and the fact that contrary to non-bumblebees, butterflies were not affected by changes in habitat heterogeneity; see Table 2). Consequently, conservation measures aiming to restore pollinator populations and/or pollination functioning might be more effective when taking a broader range of pollinator responses into account.

While we analyse richness changes from three time periods from 1900 to 2009, the majority of the data originates from the most recent periods, post 1960 (Fig. S1). Large-scale landscape changes in the Netherlands occurred mostly before 1980 (Fig. S2), with some increases in forest area occurring in recent time periods. Therefore, it is possible that for most of the landscapes analysed and for some pollinator groups concurrent landscape changes were not large enough to cause significant changes in species richness. Moreover, the lack of higher resolution of our historical species data (10 × 10 km) could in principle lead to lower power to detect effects of our much more accurate landscape data on species richness changes. However, despite these limitations, our study found that for all studied groups landscape history influenced the way communities responded to landscape changes. The conditions of a given landscape in the previous time period (our T1) can be seen as a snapshot of a dynamic landscape in the past and may itself represent a landscape in flux. Therefore, the results of this study alert for the potential extinction or colonization debts in studies when no effects of recent landscape changes are detected (see also Bommarco *et al.,* 2014). Results from studies that implement the space-for-time substitution approach are likely to reflect a mix of responses to the past landscape (the 'original state') and to recent change in that landscape. In these studies strong biodiversity responses might be observed in landscapes where past and present changes occurred in the same direction (e.g. continued fragmentation or deforestation), whereas weak biodiversity responses may occur in landscapes where past and recent changes went in opposite directions (e.g. past deforestation now shifted to reforestation). The results of our study show clearly that attempts to counteract future species richness loss should consider both historical and present landscape conditions. Future monitoring schemes will be essential to determine to what extent present communities still carry signatures of past conditions, and what the time window of the responses is.

Land-use variables used in this study explained a relatively small part of the variance observed in species richness changes. This suggests that other drivers might also be important, such as climatic conditions, uses of pesticides, increases in the levels of nitrogen deposition, presence of pathogens and competition between species (Potts *et al.,* 2010; WallisDeVries, 2014). Further work on the conservation of insect pollinators that includes this information would be highly valuable.

Although species richness can be seen as a simple biodiversity indicator, it has been shown to be highly correlated to the functions biodiversity provides e.g. pollinator assemblages with higher richness were found to be associated with higher levels of pollination services delivery (Garibaldi *et al.,* 2013). Furthermore, species composition changes might have more important impacts on ecosystem functioning than species richness changes per se. Thus, further analysis incorporating changes observed in species composition, functional diversity and community homogenization across time and space would help unravelling the impact of these changes on ecosystem functioning and provide important insights for biodiversity conservation in these human-dominated landscapes.

Concluding remarks

Using historic data on Dutch pollinators and landscape changes covering more than 100 years, this study reveals striking differences in how pollinators responded to landscape characteristics. While some pollinators benefited from increased landscape heterogeneity (non-bumblebees), others depended mostly on landscape fragmentation levels and the potential for spillover effects (bumblebees). Strikingly, for the majority of the pollinators the historical landscape characteristics have conditioned their pattern of species richness changes during the last century in the Netherlands. This suggests that recent species responses to landscape modification are constrained by the past landscape conditions and that future pollinator responses to further landscape changes may be dependent on the recent landscape characteristics.

It is thus evident that conservation approaches must include information about the original state of the landscape, as this might condition the effects that such conservation actions could have on biodiversity and also on the ecosystem services it provides.

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Supplementary material

Table S1. Land-use classes in the Netherlands used in the study.The suitability values per class were assigned in a scale ranging from 0 (no suitable) to 5 (highly suitable). We present the per land-use average suitability values given by 13 experts in the species groups analysed as presented in Vogiatzakis et al. (2014).

Land-use class	*Suitability value*
Sandy soils	3.6
Grassland	3.5
Moors/Peat	3.2
Deciduous Forest	2.8
Mixed Forest	2.5
Agricultural	2.3
Coniferous Forest	1.9
Urban	1.6
Water	0.6
Swamps	0.2

Vogiatzakis I.N., Stirpe M.T., Rickebusch S., Metzger M., Xu G., Rounsevell, M, Bommarco R., Potts, S.G. (2014) Rapid assessment of historic, future and current habitat quality for biodiversity around UK Natura 2000 sites. *Environmental Conservation,* in press.

Table S2. (next page) **Summary of the most relevant studies for our analysis related to the impacts of landscape composition and configuration on pollinators.** We obtained these studies by means of a search in the ISI Web of Knowledge with the following data entrance: "Title=(land use cover change* bumblebee OR land use cover change* butterflies OR land use cover change* hoverflies). The search also included the following: "Title=(landscape* OR fragmentation* OR cover change*) AND Title=(pollinators* OR butterflies* OR hoverflies* OR Bees*)". The search was carried out on the 23th. of November 2012 and we only included studies from the year 2001 onwards. We do not include review papers in this table, for that check the references in the main document.

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Aguirre et al.	2010	Effects of forest fragmentation on assemblages of pollinators and floral visitors to male- and female-phase inflorescences of Astrocaryum mexicanum (Arecaceae) in a Mexican rain forest	Patch size.	Fragmentation had no effect on species richness but negatively affected Shannon's diversity index. Forest fragmentation correlates with changes in the composition of flower visitors Found reduction in the abundance of pollinators.
Benedick et al.	2006	Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments	Patch size; Isolation; Percentage of vegetation cover; Tree height; Tree density.	Species richness in forest remnants was significantly positively related to remnants size and significantly negatively related to isolation.
Berg et al.	2011	Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape	Proportion of landscape of forest/(arable fields + forest); Sum of proportion of landscape of all open habitats.	Power-line corridors highly important for the butterflies distribution. The surrounding habitat effects were weaker than the local effects. Forested landscapes contained higher abundance of low and intermediate mobility species.
Brosi et al.	2008	The effects of forest fragmentation on bee communities in tropical countryside.	Patch size; Patch shape; Isolation; Landscape context (proportion of forest and pasture).	No effect of forest variables on bee diversity and abundance. Strong changes in bee community composition because of the forest variables. Contrasting responses to habitat fragmentation from different bee groups.
Chaplin-Kramer et al.	2011	A meta-analysis of crop pest and natural enemy response to landscape complexity	Percentage of natural habitat; Percentage of non-crop habitat; Percentage of crop area; Habitat diversity; Distance to natural habitat and amount of linear features.	None of the landscape metrics produced a significant response in pests. Positive response in natural enemies to landscape complexity metrics but not to percentage crop and landscape diversity. Landscape complexity is highly important.
Cozzi et al.	2007	How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands?	Patch area; Proportion of forest land; Management type.	Matrix is important but not as much as fragmentation and management type.

Table S2

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Ekroos & Kuussaari	2012	Landscape context affects the relationship between local and landscape species richness of butterflies in semi-natural habitats	Arable field cover.	Local factors are more important than landscape factors in determining local species richness. Local species richness was limited by landscape factors in intensively cultivated landscapes.
Flick et al.	2012	Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada	Patch density; Patch richness; Amount of butterfly habitat.	Butterfly species richness was higher in landscapes with more butterfly habitat and higher patch density. Butterfly abundance was higher in landscapes with lower patch richness.
Greenleaf & Kremen	2006a	Wild bee species increase tomato production but respond differently to surrounding land use in Northern California.	Distance between focus field and natural habitat; Proportion of natural habitat; Proportion of agricultural habitat.	The natural habitat must be close enough to fields in order to have an increase in production effect. Wild bees response differently to the surrounding land use.
Greenleaf & Kremen	2006b	Wild bees enhance honey bees' pollination of hybrid sunflower	Farm management type; Proximity to natural habitat; Proportion of natural habitat.	Proximity to natural habitat and crop-planting practices within the vicinity of the field explained significant variation in pollination services.
Hannon & Sisk	2009	Hedgerows in an agri-natural landscape: Potential habitat value for native bees	Habitat types (hedgerows, woodlands, fields, woodlot).	Hedgerows and woodland had a significant positive effect on native bees.
Hatfield & Lebuhn	2007	Patch and landscape factors shape community assemblage of bumble bees, Bombus spp. (Hymenoptera : Apidae), in montane meadows	Meadow area; Area to perimeter ratio; Composition of floral resources; Meadow wetness index; Livestock grazing; Proportion of the surrounding matrix that is meadow habitat; Elevation.	Percent meadow and Meadow wetness impacted positively the richness and diversity, grazing had a negative effect.
Herrando & Pa	2004	Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors	Climatology; Topography; Vegetation structure; Proportion of built-up areas; Proportion of agricultural area.	Human disturbance had a deleterious effect. Vegetation variables had almost no effect.

Table S2 (*continued*)

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Holzschuh et al.	2010	How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids?	Edge density; Proportion of non-crop habitats; Proportion of grassland; Proportion of forest; Farming system (organic vs. conventional).	High proportions of conventionally managed and large crop fields threaten pollination. Bees were enhanced by high proportions of non-crop habitat in the landscape.
Jauker et al.	2009	Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat	Type of matrix surrounding the focal area.	The grassland cover amount is important (positively related) for wild bees. Hoverflies were not impacted by grassland cover amount. Responses differ between the groups analysed.
Kennedy et al.	2013	A global quantitative synthesis of local and landscape effects on wild bee pollinators in agro-ecosystems.	Nesting and floral resources within foraging distances, patch shape, inter patch connectivity, habitat aggregation, farm management.	Diversified and organic fields benefit bee richness and abundance. High-quality surrounding land cover is also important. Landscape configuration effects were weak.
Kivinen et al.	2007	Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes	Annual temperature sum above 5C; Mean temperature of the coldest month; Land cover classes.	Climate is a fundamental driver for butterfly species richness. Species richness of declining butterflies was positively related to the amount of grasslands. Positive contribution of small-scale agriculture and mix with forest mosaic. Strong positive effect of species richness of stable butterflies with the amount of deciduous and mixed forests. Negative relationship with the amount of grasslands. reflect the fact that the majority of stable butterflies are associated with forest edges and clearings.
Krauss et al.	2003	How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies?	Area; Isolation index; Landscape diversity index; Percentage grassland in the landscape.	Butterfly species increased with habitat area. Generalists showed a significant increase with landscape diversity
Krauss et al.	2010	Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels.	Connectivity; Patch size (current); Landscape area (current); Past patch area; Past landscape area.	The patch area is important together with connectivity.

Table S2 (*continued*)

Table S2 (*continued*)

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Kremen et al.	2007	Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change	Patch area; Species nesting type; Floral resources; Local presence of bare ground; Potential nesting cavities; Steeply sloping ground; Plants with pithy stems; Pre-existing holes; Matrix surrounding the focal area.	Bee abundance and species richness is positively related with the abundance and richness of flowering plants. Reduced landscape diversity is associated with the decreased of bee abundance at the community level. Larger pollinators were more sensitive to land-use change.
Kremen et al.	2002	Crop pollination from native bees at risk from agricultural intensification.	Type of agriculture (organic/inorganic); Distance to closest oak woodland and chaparral habitat (near vs far)	Agricultural intensification reduced the diversity and abundance of native bees.
Kremen et al.	2004	The area requirements of an ecosystem service: crop pollination by native bee communities in California.	Proportion of areas of Upland, Riparian and Wild habitat at different radii; Toxicity index; Farm management type; Field size.	Native bees were positively related to the proportion of natural habitat close to farms. Stability increased with increasing natural habitat area.
Krewenka et al.	2011	Landscape elements as potential barriers and corridors for bees, wasps and parasitoids	Grass strips measure; Isolation	Semi-natural habitats act as sources of bee and wasp diversity. Grass strips act as sinks and not as corridors when high quality patches are nearby.
Lentini et al.	2012	Supporting wild pollinators in a temperate agricultural landscape: Maintaining mosaics of natural features and production	Percentage of flowering ground cover; Percentage of native ground cover Trees; Land use in adjacent field; Proportion of conservation land; Proportion of infrastructure; Average rainfall.	Areas closer to conservation reserves and further from infrastructure will support more diverse bee communities. Tree cover and the matrix quality are important variables important for the abundance of individual species.

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Lütolf et al.	2009	History Matters: Relating Land-Use Change to Butterfly Species Occurrence	Farm size; Proportion of agricultural area; Proportion of arable land; Proportion of intensively cultivated grasslands; Proportion of orchards area; Proportion of Wetlands; Proportion of livestock; Proportion of residential building.	For dry grassland species, the variables related to change rate are more important than state variables. Small-to-large farm transformation has positive effects on persistence of two groups of butterfly species.
Mandelik et al.	2012	Complementary habitat use by wild bees in agro-natural landscapes	Field type (agriculture, forest, old fields); Species richness and abundance of blooming plants; Air temperature; Wind velocity; Cloud cover.	Natural forest presented a low number of bees (most commonly visitors of non-crop plants). Old fields are an important system feature in arable landscapes that can maintain pollination services.
Montero-Castaño & Vilà	2012	Impact of landscape alteration and invasions on pollinators: a meta-analysis	Fragment size; Nature of the surrounding matrix (disturbed versus non-disturbed or continuous); Distance to other fragments of same cover type; Continuity; Matrix disturbance.	Disturbance of the surrounding matrix is negatively related to pollinator visitation rates. Matrix is more important than fragment size. Responses of pollinators vary among taxa and ecosystem types.
Öckinger et al.	2012a	The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies	Patch area; Patch isolation; Index of land use in the landscape matrix (ratio forest/(forest + arable land); Matrix composition around focus area.	There were general effects of the matrix land use across landscapes. Increasing the matrix quality can render positive results for butterflies.
Öckinger et al.	2012b	Landscape matrix modifies richness of plants and insects in grassland fragments	Patch area; Isolation; Percentage of different LULC classes in the landscape.	Patch area impacts positively species richness, while isolation negatively but only for hoverflies. The matrix effect is variable.

Table S2 (*continued*)

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Ricketts, T. H.	2001	The Matrix Matters: Effective Isolation in Fragmented Landscapes	Land use/cover types in the matrix.	The matrix and the isolation between patches is highly important as it might have negative impacts.
Schüepp et al.	2011	Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies	Amount of woody habitat in the landscape; Isolation; Percentage of open area near-natural habitats in the landscape; Altitude; Local temperature; Humidity.	Both, habitat amount at the landscape level and patch connectivity are important predictors for wasps, bees and other insects.
Schweiger et al.	2005	Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales	Proportion of semi-natural elements (‘green veining’); Landscape diversity (number of green veining habitat types); Area weighted mean proximity index of green veining elements.	Connectivity between suitable patches is one of the most important predictors for arthropod species richness and changes.
Soga & Koike	2012	Life-history traits affect vulnerability of butterflies to habitat fragmentation in urban remnant forests	Patch area; Shape; Isolation; Distance to closest forest patch.	The host plant type, host plant range, voltinism, and adaptability to the matrix affect the effect of habitat fragmentation on butterflies.
Steffan-Dewenter	2003	Importance of Habitat Area and Landscape Context for Species Richness of Bees and Wasps in Fragmented Orchard Meadows	Patch area; Connectivity; Matrix importance value.	Species richness increased with habitat area. Mutualistic bees are more affected by the area amount. Connectivity highly influential for habitat specialists. Generalist benefit from a more heterogeneous matrix.
Steffan-Dewenter et al.	2002	Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds	Proportion of semi-natural habitat; Landscape type (simple/modified).	Solitary bees richness is higher with the increase of the proportion of semi-natural habitat but only in small patches. Honeybees get higher species richness values in simple habitats.

Table S2 (*continued*)

Author(s)	Year	Title	Summary of metrics used	Relevant findings
Summerville & Crist	2001	Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera)	Fragmentation treatment; Area remaining.	The area remaining is classified as an important predictor. Patch quality (i.e. floral resources) compensates for patch size Rare species may be especially vulnerable to fragmentation.
Taki et al.	2010	Effects of landscape metrics on Apis and non-Apis pollinators and seed set in common buckwheat	Area of forest cover; Area of forest and grassland cover.	Abundances of native honeybees, and wild non-honeybee insects were significantly related to the area variables
Thomas et al.	2001	The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes	Habitat quality; Patch area; Patch isolation.	Within habitat quality and site isolation are both important for persistence. Habitat quality is more important than patch area or isolation.
Tscheulin et al.	2011	Influence of landscape context on the abundance and diversity of bees in Mediterranean olive groves	Suitability; Mean patch area of each land cover; Total area of each land cover; Number of patches of each land cover; Mean patch perimeter of each land cover; Mean patch perimeter-area ratio of each land cover.	Small bees are impacted at smaller scales than larger bees. The responses vary depending on the taxa analysed.
Uehara-Prado & Freitas	2009	The effect of rainforest fragmentation on species diversity and mimicry ring composition of ithomiine butterflies	Forest type (Pristine forest and fragmented forest).	Forest type causes different responses. Forest fragmentation affects the composition of the ithomiine mimicry rings.
Uehara-prado et al.	2007	Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape	Forest type (Pristine forest and fragmented forest).	Butterflies species richness differ depending on the fragmentation status. The responses may sometimes be detected at species and subfamily levels.
Van Dyck Hans et al.	2009	Declines in Common, Widespread Butterflies in a Landscape under Intense Human Use	Vegetation types: open dunes, heathland, semi-natural grassland, farmland, urban area, and woodland.	Decline in abundance of the common species in vegetation types outside nature reserves, including farm- land, urban areas, and woodland

Table S2 (*continued*)

Table S2 (*continued*)

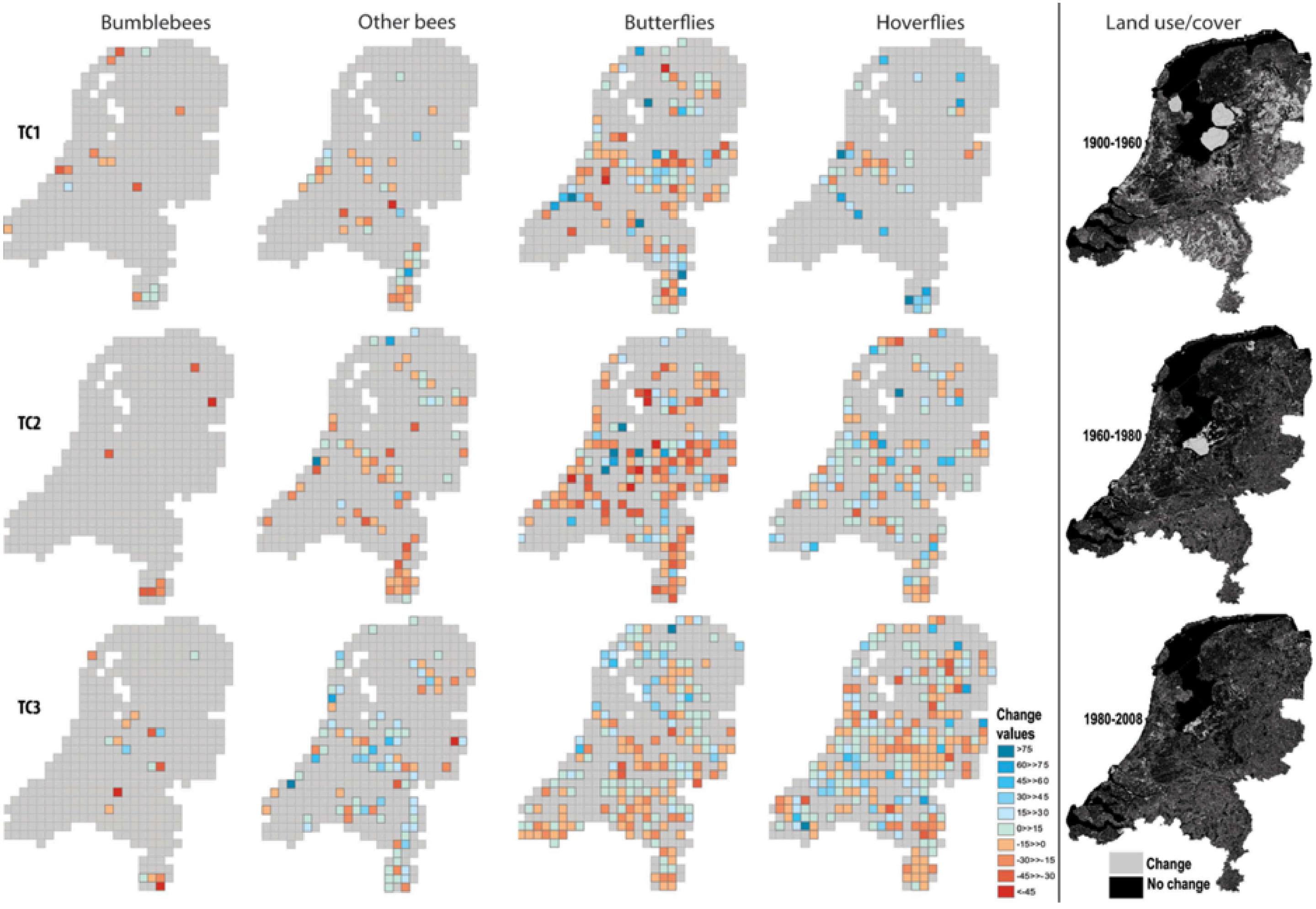
Author(s)	Year	Title	Summary of metrics used	Relevant findings
Watson et al.	2011	Forested Landscapes Promote Richness and Abundance of Native Bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin Apple Orchards	Proportional area of landscape and habitat categories in different radius.	Forests near apple orchards increase the numbers and diversity of bees
Westphal et al.	2003	Mass flowering crops enhance pollinator at a landscape scale densities	Mass flowering crops; Distance to semi-natural habitats.	Bumblebee were positively related to the availability of mass flowering crops. The mass flowering crops are not an effective determinants for bumblebees when grown at small local scales.
Williams M. R.	2010	Habitat resources, remnant vegetation condition and area determine distribution patterns and abundance of butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia	Area; Connectivity; Vegetation condition; Habitat resources.	Area and vegetation condition are the dominant determinants of species presence.
Winfree et al.	2008	Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA.	Proportion of woodland; Distance to the nearest patch of woodland; Farm management (organic\conventional); Floral availability related variables.	There weren't strong associations between land-use intensity and wild bee visitation to crops. Solitary species were positively associated with the abundance of weedy flowers in the farm field.
Winfree et al.	2009	A meta-analysis of bees’ responses to anthropogenic disturbance	Loss and/or fragmentation of habitat surrounding the study site: Agriculture area, Logging, Grazing, Fire, Pesticide use, Tillage.	There was a significant negative effect of anthropogenic disturbance on the abundance and species richness of wild, unmanaged bees. Bee abundance and richness declined significantly only for habitat loss.

Table S3. The General model implementation. Forward and backwards stepwise model selection was applied to the general starting model containing the below specified terms. All two-way interactions between the T1 and change terms were tested. Landscape ID (geographic location of the cell) and Period (1,2,3) were included as random effects.

T1 terms	**Change terms**	**Random terms**
ED Man-Nat T1	Δ Proximity	Landscape ID
ED T1	Δ PR	Time period
Patch Area T1	Δ ED Man-Nat	
PR T1	Δ ED	
Proximity T1	Δ Patch Area	
PSH T1	Δ PSH	

Fragmentation and composition variables descriptors= Proximity: Proximity index between patches of suitable habitat; PR: Number of land-use classes in the landscape; ED Man-Nat : Edge density between managed and natural systems; ED: Total edge density in the landscape; PA: average weighted mean patch's area of suitable habitat; PSH: Percentage of suitable habitat in the landscape. Δ: Change; T1: Time 1 or original landscape state.

Figure S1. (next page) **Changes in richness of several important pollinator groups in the Netherlands and the changes in land-use for the same areas.** In the left side the maps with cells (10x10km) for which we have values of species changes, for each three time comparisons of species richness and pollinator groups. Species richness comparisons, TC1: 1930–1949 vs. 1950–1969; TC2: 1950–1969 vs. 1970–1989; TC3: 1970–1989 vs. 1990–2009. Blue colours represent positive species richness changes while red colours represent negative changes. The right side of the image contains the maps presenting the areas in the Netherlands that experienced changes (grey) in land-use and the ones that did not experience changes (black) for the three time periods analysed.


Bumblebees
Other bees
Butterflies
Hoverflies
Land use/cover
TC1
TC2
TC3
1900-1960
1960-1980
1980-2008
Change values
>75
60>>75
45>>60
30>>45
15>>30
0>>15
-15>>0
-30>>-15
-45>>-30
<-45
Change
No change

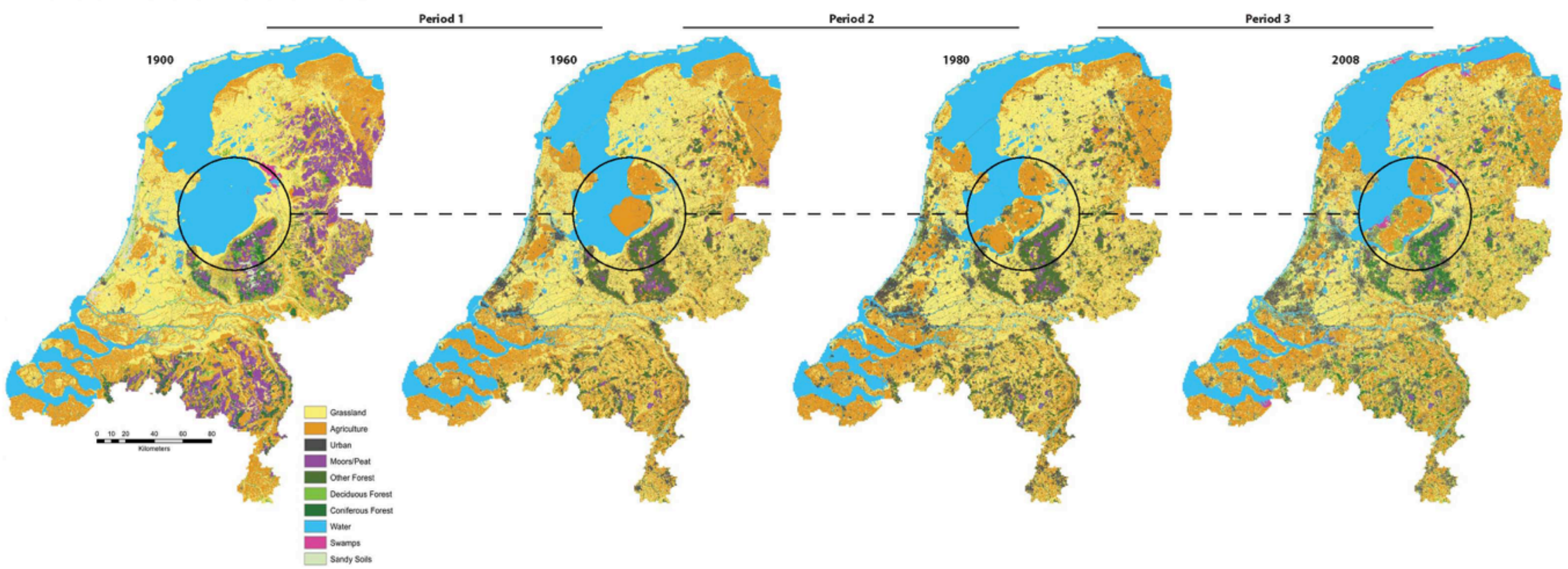


Figure S2. The distribution of the ten land-use classes present in the study area for the three time periods analysed after the land-use classes reclassification process. The circles linked by the dotted line enclose some of the most noticeable changes in land-use in the study area. These changes are represented in the first period by the conversion of a water environment to a firm land one (mostly agriculture), and followed in the next periods by changes to other land-use classes. For a more specific description of the land-use types see Table S1, Knol et al. (2004) and Hazeu et al. (2010)

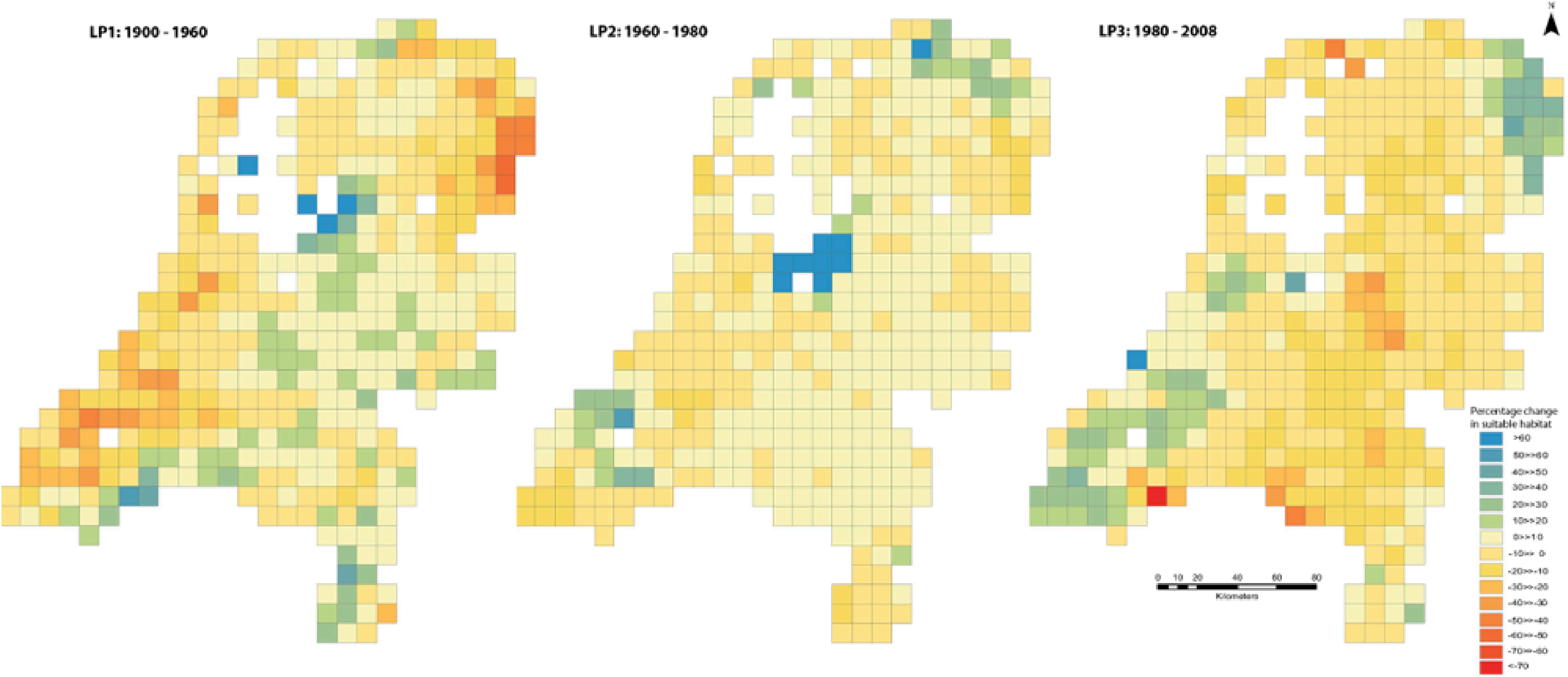


Figure S3. The changes in the percentage of suitable habitat in the landscape between the periods analysed. Most of the landscapes experienced changes in the amount of suitable habitat ranging from the +20% to -20% in the three periods. During period one most of the negative changes took place in the western of the country and also in the northeast areas. In period two there were still losses of suitable habitat in these areas but to a lesser degree, also showing the increases of suitable habitat in the centre of the country where a polder was established. Especially during period three the amount of suitable habitat has declined considerably in the central-south region of the country. However, in this period important increases in suitable habitat have occurred, mostly in the same areas that during period one had experienced important suitable habitat declines.

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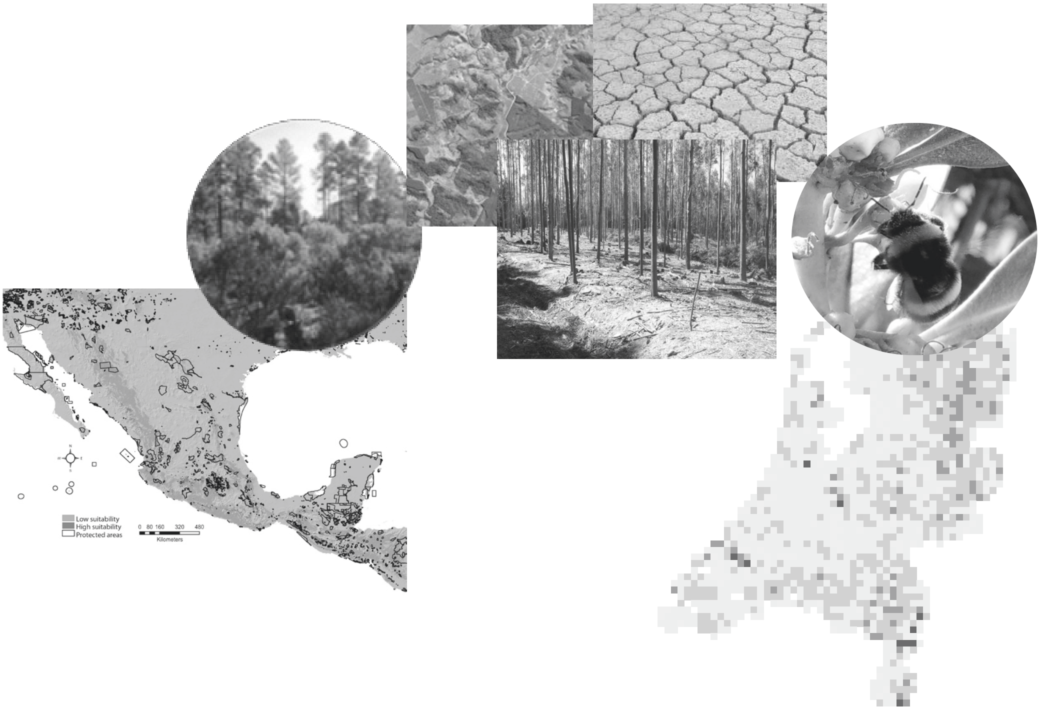
7

Synthesis:

Species distributions, ecological niches and the impacts of climate and land-use changes on species range limits

J. Aguirre-Gutiérrez



Where and how biodiversity is distributed around the globe has been investigated for centuries (Darwin, 1859; Patterson, 1994; Shaffer *et al.,* 1998; Wallace, 1869). This research field has produced a wealth of information and insight on the factors determining species distributions and the functions species carry out in ecosystems (e.g. Gamfeldt *et al.,* 2013; Nelson *et al.,* 2009). Moreover, research on the distribution of biodiversity locally and globally has proven directly applicable for nature conservation actions (e.g. Rodrigues *et al.*, 2004).

One of the main problems in studying species distributions is the lack of detailed distribution data and even more from old time periods (e.g. before 1950). Collecting such data requires enormous effort and has only been done for some iconic or local species, often only in part of their full distribution. Novel techniques have been applied to these historical species distribution data for investigating changes in biodiversity across time, as for instance in the work of Carvalheiro *et al.* (2013), however, this only renders a partial picture of these biodiversity changes. Consequently, methods that can robustly predict (global) species distributions based on a limited amount of species locations data as input are very important in this field. These methods should be able to capture, in an accurate manner, the environmental characteristics that limit species distributions (Chapter 2). These methods can then be used for a variety of applications including detection of current species distributions within protected areas (Bagchi *et al.,* 2013; Hannah, 2008), analysis of the pathways and impact of alien species invasions (Buckland *et al.,* 2014; Giovanelli *et al.,* 2008), investigating ecosystem services delivery under climate change scenarios (Polce *et al.* 2013; polce *et al.* 2014) or the investigation of differences in the ecological niches of closely-related taxa (e.g. Chapter 3).

In the following sections, I will summarize how the biodiversity responses to environmental change from past to present presented in this thesis contribute to the field of biodiversity conservation, and how this can help predict future biodiversity distributions in a context of global environmental change. Lastly I will present the implications of my results in the context of biodiversity conservation and discuss some of the future research prospects within the field.

Predicting species distributions across time

Since the beginning of the decade there has been a great investment in the development of approaches that can estimate where species are distributed and how their ranges are delimited by biotic and abiotic conditions. This has led to a boom in novel methods and frameworks to which we refer to as "Species distribution models", "Ecological Niche models" or "Habitat suitability models" (Franklin *et al.,* 2009; Peterson *et al.,* 2011). From these methods we have to decide on the modelling algorithm and framework. How or on what should we, as conservation biologists and ecologists, base our selection? Are all algorithms rendering the same answers? The decisions taken at this stage determine the results we get and thus the conclusions we draw.

In this thesis, I show that the performance of different modelling algorithms for predicting the distribution of a set of systematically selected data of species occurrences (rare to common and narrow to widespread species) varies significantly (Chapter 2). Some of these algorithms present significantly more accurate results than others, particularly MaxEnt or an ensemble of model predictions (Chapter 2). I show that these differences in outputs are maintained even when analysing landscapes across different spatial scales, and that algorithms also differ in how they attribute the importance of environmental drivers when delimiting the species distributions (Chapter 2). The differences in attribution of the drivers' importance is of main concern as it can lead to different conclusions on how drivers of change define the distribution of each species and thus on how different species (groups) can be protected. We should ideally opt for algorithms that are consistent in their predictions across modelling repetitions (low within algorithm variability) and spatial scales, and that have high accuracy in their predictions without being constrained by the species data characteristics (number of records and their spatial distribution).

Furthermore, I show that algorithms such as MaxEnt and an ensemble of model predictions are among the best options for modelling species distributions as they render high model fit and are consistent in their outputs (Chapter 2). However, although the ensemble of models often renders projections with high accuracy, these are also often difficult to interpret in regard to the assessment of how important are the environmental variables for delimiting species range limits given that they are an ensemble of predictions from different algorithm. Although the study presented in Chapter 2 focuses on the Netherlands, which has a relatively small area and homogeneous landscape characteristics, the results obtained are in line with others carried out in different locations and with different environmental conditions (e.g. Elith *et al.,* 2006). The high performance of species distribution models constructed with the MaxEnt algorithm for the Mexican white pines in the American continent (Chapter 3) also confirms our findings. Besides MaxEnt, an ensemble of model predictions has become appealing in recent years as it can capture the variability presented by the different algorithms into a more robust prediction (Thuiller, 2014). However, the construction of model ensemble also implies the selection of the method to obtain the final projection, e.g. average of predictions across modelling algorithms, median of predictions, consensus approach, mean of predictions weighted by the model accuracy, among others, which also needs an in-depth evaluation as different model ensemble methods may vary in their final output.

Although much research has been carried out in the field of species distribution modelling, more is needed to better understand how factors such as biotic interactions (Giannini *et al.,* 2013), species dispersal capacity (Boulangeat *et al.,* 2012), and their plasticity for adapting to changing environments (instead of modifying their distributions) (Eckhart *et al.,* 2011) may impact the model predictions. Incorporating this information in a satisfactory manner into the species distribution modelling protocol would enhance our knowledge of how biodiversity may respond to future environmental changes.

Climate and land use change set the limits of species distributions across time

Climatic and land-use changes are two of the main drivers of species distribution changes globally (Newbold *et al.,* 2015; Wu *et al.,* 2011). Modifications in each of these drivers can cause the extinction of species at local and global scales (Jetz *et al.,* 2007; Sala *et al.,* 2000; Thomas *et al.,* 2004;

Thuiller *et al.,* 2005). These drivers rarely change independently as the modification of one tends to impact the other, which may create a cascade effect that will ultimately effect the species distributions. The results of Chapter 5 show that in face of these environmental changes, species can adapt to the new conditions or, depending on their trait characteristics (e.g. pollinator wing size which is linked to dispersal ability), shift their ranges towards more suitable areas. Given the observed species geographic shifts, and their areal range changes within the study area, it is imperative to investigate how this may impact the protection status of these species as well as if, how and to what extent the ecosystem functions (i.e. pollination of wild plants) and services (i.e. pollination of crops) they provide may have been disrupted in the past or are likely to be disrupted in the future.

Studies on the effects that climate change can have on biodiversity are highly relevant given the predictions of changing temperature and precipitation patterns, as well as increases in extreme weather events, that are occurring around the world (Kirtman *et al.,* 2013). In this thesis I show that although land use conditions are often highlighted as some of the most important drivers of species occurrences, climatic drivers are also highly important determinants of range limits for species. In Chapter 4, in a study carried out for three pollinator groups in the Netherlands, I specifically show that the importance of climatic drivers for determining species range limits, especially those related to temperature, has significantly increased during recent decades now reaching that of land use. The results suggest that for the Netherlands the influence of these climatic drivers will continue increasing and will probably surpass the importance of land use impacts on species distribution, especially given that land use related drivers have mostly stabilized during these last decades (Bouma *et al.,* 1998; Knol *et al.,* 2004). These results are most likely transferable to other highly industrialized countries in temperate regions. However, a more in depth research in tropical regions, where strong land use changes are still ongoing, is still needed to investigate the applicability of our results to these regions.

One of the main challenges when investigating biodiversity responses to past climatic and land use changes is the lack of historical data on species occurrences and environmental conditions. Given this lack of data most studies apply a space-for-time substitution approach. In this set-up a series of landscapes differing in climatic and land use conditions are analysed as representatives of the modifications that could have occurred in a single landscape across time (e.g. Brosi *et al.,* 2008; Uehara-prado *et al.,* 2007). This may not always be fully representative of the responses to changes, as the original state of the landscape could also be guiding the responses of the remaining biodiversity (Kuussaari *et al.,* 2009). In Chapter 6 I ask if recent landscape modifications (partially) drive current species distributions and whether historical landscape conditions are also responsible for the distribution patterns we see at present. I show that for most of the pollinator groups I analysed, the historical landscape state (i.e. before changes occurred) significantly constrains subsequent species responses to landscape changes. This means that many of the species distribution patterns that we see at present may actually be constrained by past landscape characteristics, pointing out to a possible extinction debt (delayed loss of biodiversity after habitat loss and/or fragmentation events) (Tilman *et al.*, 1994), but also to possible “colonization debts” (as it may take time for species to colonize newly suitable areas). While my study provides new insights into this issue, more research is needed to disentangle what the time lags are for the effects of past landscape characteristics on current species distribution patterns, and what underlying ecological/evolutionary mechanisms cause this delayed time-effect.

The finding of this thesis and other recent studies have shown that both climate and land use characteristics define biodiversity distributions locally and globally (Newbold *et al.,* 2015; Wu *et al.,* 2011). However, the relative importance of each of these drivers for setting species range limits may, however, not be equal and constant over time. In Chapter 4, by analysing the importance that different land use characteristics have for setting species range limits, I show that habitat composition, fragmentation and spillover potential have constantly been major drivers of pollinator species distributions over the last half century in the Netherlands. Especially habitat composition, which I analyse as the amount of each land use type in the landscape and the variety of the land use classes, has been a highly important driver over time; even more so than fragmentation and spillover potential.

I have shown that land use is a major driver of species distributions and that although both past and present landscape characteristics are important, for the Netherlands, the historical land use characteristics have constrained the present biodiversity of pollinators even more than the landscape changes (Chapter 6). Still, as shown in Chapter 5, the way in which different pollinator groups respond to these changes (also to climatic changes) in terms of range modifications and geographical shifts greatly depend on their functional traits and the pollinator group identity (Chapter 5).

Implications for conservation and concluding remarks

Biodiversity conservation actions are increasingly based on analysis made with tools such as SDMs (Franklin, 2010; Guisan *et al.,* 2013). The results of this thesis show that the selection of the methodological details when fitting SDMs should not be done haphazardly, as the outputs of different methods may render diverse and sometimes even contrasting results. As shown in Chapter 2, no single algorithm will be best under all circumstances. I therefore suggest selecting the preferable modeling tool for the aim (e.g. determining the range of spatially restricted species, environmental variables profiling) and data characteristics (e.g. number and spatial distribution of species presence records) in a given study via a calibration-evaluation procedure. Chapter 2 provides a template for such a calibration-evaluation procedure.

Biodiversity conservation actions tend to focus on single groups that may represent the effects that climatic and land use changes have on general species within bigger biodiversity groups (Fleishman *et al.,* 2000; Ozaki *et al.,* 2006), e.g butterflies are often used to represent insect biodiversity. Based on these groups, conservation actions are then proposed. This approach has been recently challenged by studies that favour a multi-group approach for biodiversity conservation (Gerlach *et al.,* 2013; Maes & Dyck, 2005). The reason is that different (pollinator) groups are often impacted by different drivers (climate or land use) or by the same driver in a different manner or intensity. The results obtained in this thesis show that, although the pollinator groups present synergies in their responses to climatic and land use impacts, their responses cannot be generalized (see for example chapters 4 to 6). Given the diversity of responses observed between pollinator groups, I suggest that multi-group approaches that account for the different responses of biodiversity to these drivers of change should be considered when planning future conservation actions. The findings of this thesis further emphasize the limited value of one-size-fits-all type of biodiversity conservation measures and suggest that including historical and present climatic and land use information when planning future biodiversity conservation programmes is of critical importance.

The findings of this thesis suggest future challenges as in the field of biodiversity conservation and applied ecology. The inclusion of multi-species responses to climatic and land use changes and of historical climatic and land use information in future conservation plans are definitely two with high importance. Moreover, including multi-species interaction information in the modelling framework is a challenge that deserves much attention given that species distributions and persistence clearly depend on them. This is of main concern as most research for biodiversity conservation purposes is carried out with multiple species which makes this process more complex than when modelling only few species. Lastly, the coupling of new technologies as remote sensing techniques, e.g. LiDAR (light detection and ranging) and (hyper)spectral data, with the modelling of species distributions should be more deeply explored as new research suggest this could be highly advantageous for the field of conservation biology and in our case for investigating more in depth and at high spatial resolution how the landscape context, e.g landscape structure, defines species range limits at high spatial resolution.

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8

Summary / Samenvatting

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Photo: *J. C. Biesmeijer*

Summary

The discovery of the patterns and processes that define the distribution of biodiversity around the world has greatly excited ecologists and conservation biologist along the last century. This continues being an important topic of research for academics and the general public, as having this knowledge not only improves biodiversity conservation actions but also generates economic wealth. Answering the where, how and why of biodiversity distributions is exciting and also challenging. For the purpose of answering these questions different tools and methodologies have been developed. Species distribution models (SDMs), also called ecological niche models (ENM) or habitat suitability models (HSM), are an example of these tools. SDMs are mathematical algorithms that can identify suitable conditions for the existence of a given species given its environmental preferences. Moreover, these algorithms can elucidate the importance that different environmental correlates have for defining the species range limits. SDMs can also be applied for investigating if and to what extent different closely related taxa occupy similar or equivalent ecological niches, which renders insights into the between species ecological relationships. Most studies applying these tools (e.g. SDMs) for the protection of biodiversity given anthropogenic and natural global environmental changes focus on future impacts, neglecting the effects of historical environmental changes on biodiversity. However, looking to how biodiversity has responded to historic-to-present environmental modifications can renders insights as how it may respond to future changes in these conditions.

In Chapter 1 of this thesis I give a general introduction to two of the main drivers of biodiversity change, climate and land-use changes, and to some of the main tools used for investigating their impacts on biodiversity (e.g. SDMs). In Chapter 2 I investigate which are the most commonly used species distribution modelling techniques and which of them generate(s) the most robust distribution projections. The results show that in deed some of them as an ensemble of model predictions and machine learning techniques, (i.e. MaxEnt), often render high model performance independently of the number of species record locations and their spatial distribution. Moreover, there are also algorithms that are most consistent in the prediction of the

importance that environmental variables have for setting species range limits. Given the results obtained I concluded that there is not an always best performing algorithm over all others, but that however, some of them tend to offer more robust predictions across species and data characteristics (e.g. number of records and their spatial distribution). I suggest that accounting for the data characteristics (e.g. number and distribution of presence records) should be a first step when selecting the modelling algorithms to use. In chapter 2 I give more insights into the protocol that can be followed when selecting and fitting the SDM for the specific purpose of the study.

Based on the results from Chapter 2 I selected the MaxEnt algorithm and further tested its performance when modelling species from the genus *Pinus* in Central and North America (Chapter 3). I selected these locations as in comparison to the Netherlands they contain highly varied environmental and topographic conditions, and thus represent conditions that differ from those where the algorithm was tested in Chapter 2. In this analysis I specifically investigate how species distribution modelling techniques can be applied to extract the ecological niche space where species are distributed. I then compare the species' ecological niches to investigate the identity of closely related Mexican white pine taxa. I show that the ecological niches of the analysed taxa are similar, which corresponds to the fact that they belong to the same pines group (white pines) but are not equivalent, showing that they are in deed not the same species, something that is still under debated.

In Chapter 4 I model the distribution of three different pollinator groups, bees, butterflies and hoverflies, and investigate if the importance that environmental drivers have for setting the species range limits has changed over time. With this research I give an insight on the role that drivers related to climate, as temperature and precipitation, and those related to land use, as habitat composition, fragmentation and spillover, have played for setting current species distributions. I show that although in the past (~1950) land use drivers were significantly more important than climatic drivers for setting species range limits, in the present climatic drivers have gained equal importance to those of land use. Given the expected changes in climatic conditions in the near future and the fact that the major changes in land use conditions already occurred decades ago in the study area (as in other highly industrialised countries) it is expected that the importance of climatic drivers of species distributions may overpass that of land use.

In Chapter 5 using the same modelling technique and the same pollinator groups than in the preceding chapter I investigate the species areal range changes, latitudinal and longitudinal shifts as a response to changes in climatic and land use conditions since the 1950's. Furthermore, I analyse if and how different species functional traits related to climatic and land use conditions may explain the observed species geographic distribution shifts and areal range changes. I show that all pollinator groups have increases their distributional area during the last half century, and that all of them also presented shifts towards more northern areas. Latitudinal shifts differed between pollinator groups. I further show that information on species traits can help predict the areal range changes and latitudinal and longitudinal shifts related to climatic and land use changes. The traits involved in the different spatial distribution changes may vary between pollinator groups and in some cases they can respond in opposite direction (e.g. see traits involved in longitudinal shifts for bees and butterflies). The fact that all groups showed shifts towards northern latitudes underlines the role that climatic changes may have in setting species range limits. This raises concerns about further impacts of changes in climatic conditions on the distribution of biodiversity given the projected increases in temperature and in extreme weather events in the near future.

Lastly, in Chapter 6 with land use change data and species richness change data since the year 1900 I investigate the role that landscape composition, fragmentation and spillover have had for defining species richness changes of bees, butterflies and hoverflies in the Netherlands. I ask if recent landscape modifications (partially) drive current species distributions and whether historical landscape conditions are also responsible for the distribution patterns we see at present. I show that the effects of landscape changes varied per pollinator group and that for the majority of the pollinators past landscape characteristics conditioned the more recent pollinator richness changes. Given the obtained results I concluded that the species distribution patterns that we see at present may actually be a result of past landscape characteristics and that more research is needed as to disentangle what the time lags are of the effects of past landscape conditions on current species distribution patterns.

Samenvatting

Weten hoe biodiversiteit verspreid is in de wereld en waarom is een belangrijk onderwerp in zowel de academische gemeenschap als bij het algemene publiek. Dit komt waarschijnlijk omdat deze kennis niet alleen bijdraagt aan het behouden van biodiversiteit, maar omdat het ook economische welvaart oplevert. Uitvinden hoe biodiversiteit is verdeeld en het bestuderen van de patronen in biodiversiteit op verschillende locaties houdt ecologen al jaren bezig. Een antwoord vinden op de waar, hoe en waarom van de verspreiding van biodiversiteit is spannend maar ook een echte uitdaging. Vanwege deze uitdaging zijn er verschillende methoden ontwikkeld om deze vragen ten minste gedeeltelijk te beantwoorden. Een voorbeeld van één van deze methoden is de wiskundige algoritmes die geschikte leefgebieden van een specifieke soort kan identificeren en ook kan aangeven hoe belangrijk de verschillende omgevingsfactoren zijn voor de verspreidingslimieten van de soort. Bovendien kunnen deze methoden ook identificeren of en in hoeverre verschillende nauw verwante taxa gebruik maken van dezelfde of vergelijkbare ecologische niches, wat inzicht geeft in de ecologische relaties tussen soorten. Een groot deel van de studies die onderzoekt hoe deze methoden/hulpmiddelen kunnen bijdragen in het beschermen van biodiversiteit voor antropogene en natuurlijke veranderingen in het globale milieu focussen zich op de toekomstige gevolgen, waarbij ze het verleden negeren. Bestuderen hoe biodiversiteit heeft gereageerd op veranderingen in het milieu in het verleden kan belangrijke inzichten geven in hoe het kan reageren op toekomstige veranderingen, zoals bijvoorbeeld veranderingen in het klimaat en landgebruik. In dit proefschrift in hoofdstuk 1 geef ik een algemene introductie in de belangrijkste factoren die veranderingen in biodiversiteit veroorzaken en de meest gebruikte methoden/hulpmiddelen om de gevolgen ervan te onderzoeken (bijvoorbeeld soorten distributie modellen). In hoofdstuk 2 onderzoek ik wat de meest gebruikte soort distributie modelleer technieken zijn en welke de meest naukeurig resultaten oplevert. Ik heb geconstateerd dat sommige als ensemble van model voorspellingen goede prestaties leveren, evenals machine learning technieken, zoals MaxEnt. Gebaseerd op deze resultaten heb ik het MaxEnt algoritme geselecteerd om zijn prestaties verder te testen tijdens het modelleren van soorten van het *Pinus* genus in Centraal en Noord

Amerika, gebieden met een hoge variëteit in milieu en topografische omstandigheden (Hoofdstuk 3). In deze analyse onderzoek ik hoe soort distributie modelleer technieken gebruikt kunnen worden om de verspreiding van verschillende soorten in de ecologische niche ruimte/het ecosysteem te extraheren. Daarna vergelijk ik de ecologische niches van de soorten om de identiteit van de nauw verwante Mexicaanse witte den taxa te onderzoeken. Ik toon aan dat de ecologische niches van de onderzochte taxa vergelijkbaar zijn, wat overeenkomt met het feit dat ze tot dezelfde den groep behoren, maar dat ze niet exact hetzelfde zijn, wat laat zien dat het inderdaad niet dezelfde soorten zijn, iets wat nog steeds onder discussie staat. In hoofdstuk 4 modelleer ik de verspreiding van drie verschillende bestuivergroepen, bijen, vlinders en zweefvliegen, en onderzoek ik of de belangrijkheid van de omgevingsfactoren die de verspreiding van soorten limiteren zijn veranderd in de loop van de tijd. Met dit onderzoek geef ik inzicht in de rol die factoren gerelateerd aan het klimaat, zoals temperatuur en neerslag, en die gerelateerd aan landgebruik, zoals habitat/leefgebied compositie, fragmentatie en spillover, hebben gespeeld voor de huidige soorten distributies. Ik laat zien dat hoewel in het verleden (~1950) landgebruikfactoren significant belangrijker waren dan klimaatfactoren als limiet voor soorten distributies, de klimaatfactoren tegenwoordig even belangrijk zijn als het landgebruik. Gezien de verwachtte veranderingen in het klimaat in de nabije toekomst en het feit dat de grote veranderingen in landgebruik decennia geleden al hebben plaatsgevonden in het onderzoeksgebied (net zoals in andere zeer geïndustrialiseerde landen), is het te verwachten dat de belangrijkheid van klimaatfactoren die van landgebruikfactoren gaat passeren. Ten slotte onderzoek ik in hoofdstuk 5 aan de hand van data over de veranderingen van landgebruik en soortenrijkdom data sinds 1900 de rollen die landschap compositie, fragmentatie en spillover hebben gehad bij het definiëren van de soortenrijkdom veranderingen van bijen, vlinders en zweefvliegen in Nederland. Ik heb gevonden dat voor de meerderheid van de bestuivers de landschap karakteristieken uit het verleden de meer recente bestuiver rijkdom veranderingen verklaren.

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J. Aguirre-Gutiérrez

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CV and list of publications

Jesús Aguirre Gutiérrez was born in Sahuayo Michoacan, Mexico. He lived and carried out his license degree (4.5 years) in biology with a special focus on conifer plants at the University of Guadalajara in Guadalajara Jalisco, Mexico, where he also obtained a scholarship from the Mexican government for students with high academic performance. During the license degree he studied for six months at the University of Sussex, in Brighton, UK as an exchange student and also carried out a six months internship at the Instuto de Tecnología Química e Biológica, University Nova de Lisboa about pines genetics and biotechnology. After finishing his degree he worked as coordinator of a nature conservation and educational project at the Indigenous Mission Bawinokachi, in the Tarahumara forest, Chihuahua, Mexico. Then, and after obtaining the HSP-NUFFIC scholarship from the Netherlands Organization for International Cooperation, he started his master degree in Ecology and Evolution -Tropical Ecology at the University of Amsterdam in the Institute for Biodiversity and Ecosystem Dynamics. He then obtained four years of funding for his PhD project from the Mexican National Council for Science and Technology (CONACyT) as well as from Naturalis Biodiversity Center in the Netherlands.

Publications in peer review journals:

Aguirre Gutierrez J./ Biesmeijer, J. C./ van Loon, E. E./ Reemer, M./ WallisDeVries, M. F./ Carvalheiro, L. G. (*2015*). Susceptibility of pollinators to ongoing landscape changes depends on landscape history. *Diversity and Distributions. In press*.

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Thesis co-authors and contribution to the thesis

Chapter 2

J. Aguirre-Gutiérrez, L. G. Carvalheiro and J. C. Biesmeijer conceived and designed the experiments. Performed the experiments: J. Aguirre-Gutierrez, L. G. Carvalheiro. Analyzed the data: J. Aguirre-Gutierrez, L. G. Carvalheiro and J. C. Biesmeijer. Contributed reagents/materials/analysis tools: C. Polce and M. Reemer. Wrote the paper: J. Aguirre-Gutiérrez. Contributed significantly to the manuscript revisions: L. G. Carvalheiro, J. C. Biesmeijer. C. Polce, N. Raes, E. van Loon, M. Reemer and J. C. Biesmeijer.

Chapter 3

J. Aguirre-Gutiérrez and H. Serna-Chavez. conceived the idea. J. Aguirre-Gutiérrez designed and carried out the analyses and together with H. Serna-Chavez and N. Raes interpreted the results. A.Villalobos-Arámbula and J. Pérez de la Rosa gathered the data, prepared it for the analyses and/or provided information to help with data interpretation. J. Aguirre-Gutiérrez drafted the text and all other authors provided corrections to manuscript drafts and discussed ideas within it.

Chapter 4

J. Aguirre-Gutiérrez, W. D. Kissling and L. G. Carvalheiro conceived the idea. J. Aguirre-Gutiérrez designed and carried out the analyses and together with W. D. Kissling and L. G. Carvalheiro interpreted the results. J. C. Biesmeijer, M. WallisDeVries and M. Reemer gathered the data, prepared it for the analyses and/or provided information to help with data interpretation. J. Aguirre-Gutiérrez drafted the text and all other authors provided corrections to manuscript drafts and discussed ideas within it.

Chapter 5

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Chapter 6

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