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Published in:
Journal of Biogeography

DOI:
[10.1111/jbi.12937](https://doi.org/10.1111/jbi.12937)

[Link to publication](#)

Citation for published version (APA):

Aguirre-Gutiérrez, J., Kissling, W. D., Biesmeijer, J. C., WallisDeVries, M. F., Reemer, M., & Carvalheiro, L. G. (2017). Historical changes in the importance of climate and land use as determinants of Dutch pollinator distributions. *Journal of Biogeography*, 44(3), 696-707. DOI: 10.1111/jbi.12937

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ORIGINAL
ARTICLE



Historical changes in the importance of climate and land use as determinants of Dutch pollinator distributions

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ABSTRACT

Aim Species distribution models are often used to project species distributions to different environmental conditions. However, most models do not consider whether the importance of abiotic factors may change over time. If they change, this has implications for the assessment of how abiotic changes affect species distributions. Here, we use spatially explicit historical data on species occurrences, climate and land use to test whether the importance of different climatic and land-use drivers as determinants of species distributions has remained constant over a period of > 60 years (1951–2014).

Location The Netherlands.

Methods Using species distribution models and a comprehensive country-wide dataset at 5 × 5 km resolution, we modelled the distribution of a total of 398 pollinator species (bees, butterflies and hoverflies) for three periods (1951–1970, 1971–1990 and 1998–2014). We then evaluated whether the importance of variables related to climate (precipitation, temperature) and land use (landscape composition and habitat fragmentation) in determining pollinator distributions has changed over time.

Results Variables related to landscape composition were highly important in determining pollinator distributions in all periods. Precipitation was generally less important than temperature, and habitat fragmentation less than landscape composition. Land-use variables remained equally important across time for all pollinator groups, except for bees where the importance of habitat fragmentation decreased significantly over time. Among climate variables, the importance of precipitation did not change across time for any pollinator group. However, the importance of temperature increased significantly in recent times for bees and hoverflies.

Main conclusions Determinants of species distributions can change in their importance over time when changes in the magnitude and range of environmental conditions occur. Given future temperature rises, our results imply that species distribution models calibrated with current climatic conditions may not adequately predict the future importance of environmental factors in driving species distributions.

Keywords

biodiversity change, climate change, ecological niche models, environmental variable importance, global warming, habitat fragmentation, habitat loss, species distribution models

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INTRODUCTION

Recent rapid changes in climatic conditions (e.g. temperature and precipitation; McCain & Colwell, 2011) have raised considerable concerns about their effect on biodiversity (e.g. Thomas *et al.*, 2004). For instance, changes in temperature (Dawson *et al.*, 2011) and the increase of extreme weather events (Hansen *et al.*, 2012) have led 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 & Lambin, 2011), habitat fragmentation (Krauss *et al.*, 2010) and land-use intensification (Tschardt *et al.*, 2005). Climate and land-use change are, therefore, considered to be 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 (Fox *et al.*, 2014).

Climate and land-use 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 major habitat changes in several industrialized countries were more intense before 1970 (Fuchs *et al.*, 2015). In regions that have experienced strong climate and land-use changes, the range and magnitudes of environmental variables have thus changed through time. If a given climate or land-use variable changes, the range and magnitude of this environmental variable might increase to values that are not equally suitable for a species. Consequently, the importance of such a variable in determining the distribution of species will also increase. However, if the range of values of an environmental variable (within the study region) is equally suitable or unsuitable to a species, the importance of this variable in determining the distribution of a species will be minimal. Therefore, the magnitude of the effect of an environmental variable in determining the distribution of a species depends on the range of values the environmental variable has within the study area, but also on the spatial scale (extent and grain size) of the dataset (Pearson & Dawson 2003). The different temporal and regional patterns of climate and land-use variables and their range of values may thus impose different effects on the distribution of biodiversity.

Several tools have been developed to investigate changes in climate and land-use conditions (see Klein Goldewijk *et al.*, 2011; Stocker *et al.*, 2013) and how these changes may impact the distribution of biodiversity (Elith & Leathwick, 2009). Species distribution models (SDMs; Thuiller, 2004) are often used to analyse the effects of climate and land use on biodiversity and to project species distributions under potential future global change scenarios. Generally, SDM projections into the future are based on present-day species responses to climatic and land-use drivers, which are then extrapolated across time using future climate and land-use scenarios. However, changes in the importance of drivers of species distributions across space and time are little explored. This is of potential concern for the extrapolation of SDMs to

areas where the range of values of the environmental variables differs to areas where the model was trained, e.g. in the case of expanding range margins under climate change (Eskildsen *et al.*, 2013). Recent studies suggest that the selection of predictors and the range of environmental conditions across different time periods and study regions is, therefore, of central importance for accurate predictions of SDMs (e.g. Randin *et al.*, 2006; Austin & Van Niel, 2011). Hence, it is crucial to evaluate how variability in global change drivers affects their importance in SDMs for driving species distributions. 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 for exploring the dynamics of such relationships and the validation of model results.

Here, we use a unique set of spatially explicit species occurrence records of several groups of flower visitors (bees, butterflies and hoverflies; hereafter referred to as 'pollinators') and environmental data from the Netherlands from 1951 to 2014 to investigate whether the importance of climate (temperature and precipitation) and land use (i.e. landscape composition and habitat fragmentation) as drivers of species distributions has changed over time. A pollinator's access to feeding and nesting resources greatly depends on landscape conditions (Winfree *et al.*, 2011). We, therefore, expect landscape composition and habitat fragmentation to be of high importance in determining species distributions. Moreover, although small-scale land-use changes are still taking place, most large-scale land-use changes in the Netherlands have occurred before the 1990s and land-use dynamics are now less accentuated (Harms *et al.*, 1987; European Environment Agency 2010). Hence, we expect that the importance of land-use factors has decreased or remained relatively constant over the considered time period. The recently recorded changes in precipitation regimes and temperature in our study area (Klein Tank, 2004; Ligtvoet *et al.*, 2013) might have led to changes in habitat suitability for Dutch pollinators. Specifically, we expect that climate has recently become more important in determining species distributions than in previous decades. Finally, as species functional traits that constrain their tolerance and responses to environmental changes vary between the different pollinator groups (Aguirre-Gutiérrez *et al.*, 2016), we expect that the importance of a given environmental variable for driving the distribution of species within the study region might differ between pollinator groups.

MATERIALS AND 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. The Netherlands has also experienced major changes in climate (KNMI, 2014) and land-use conditions (Knol *et al.*, 2004; Hazeu *et al.*, 2010) over the last century. All three aspects (biodiversity, climate and land use) are well documented with spatially explicit data across more than 50 years. Important increases in average temperature in the Netherlands have been recorded over the last century (*c.* 1.7°C; Ligtvoet *et al.*, 2013), with the most rapid warming taking place during the last 20 years (Klein Tank, 2004). This might strongly affect the distribution of pollinators. Important changes in the temporal distribution and amount of precipitation have also been observed, with the average annual winter precipitation increasing by *c.* 20% during the last century (Klein Tank, 2004; Ligtvoet *et al.*, 2013). In addition, after the Second World War (*i.e.* during 1950–1970), the Netherlands suffered rapid natural vegetation 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 & Sutherland, 2003). Given 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 importance of environmental conditions in determining species distributions has 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 (NDFD, www.ndff.nl). Experts from the EIS and the NDFD 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 at www.ndff.nl/validate.

All species occurrence records were compiled at a resolution of 5 × 5 km grid cells to accommodate the higher uncertainty in geographical coordinates of the older records relative to the higher location accuracy of the more recent records. To be able to include rare and narrowly distributed species (which are likely to be more strongly affected by changes in environmental conditions), we included species that were present in as few as ten 5 × 5 km grid cells and only those that were represented in each of the three time periods. Our selection criteria allowed us to analyse a total of 398 pollinator species, including 178 bee species, 52 butterfly species, and 168 species of hoverflies (Table S1 in Appendix S1 in Supporting Information). From a total of 1820 grid cells (5 × 5 km each) in the Netherlands, 914 had

records for bees in TP1, 894 for butterflies and 1094 for hoverflies. In TP2, bees were present in 972 grid cells, butterflies in 1484 and hoverflies in 1376. In TP3, bees were sampled in 1346 grid cells, butterflies in 1655 and hoverflies in 1592 (see Fig. S1 in Appendix S1 for the spatial distribution of the sampled grid cells across time).

Climatic data

We obtained climate data for the Netherlands on maximum and minimum values of temperature 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) and aggregated as an average for each of the three time periods. These data were used to calculate the 19 bioclimatic variables described in Hijmans *et al.* (2005). The bioclimatic variables represent annual trends in climatic conditions, seasonality and climate extremes. We only included variables with Pearson’s correlation coefficients ≤ |0.65| (Figs S2–S4 in Appendix S1), a threshold well below the one which is estimated to start distorting model predictions (Dormann *et al.*, 2013). The choice of which variable would be excluded from the analyses was done by taking into consideration which variables are known to determine most strongly the distribution of insects, *e.g.* those that capture extreme conditions during the year (see Table 1 for selected variables). These variables may have important impacts on the distribution and persistence of pollinators (*e.g.* Rasmont *et al.*, 2015).

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% to 98% (Knol *et al.*, 2004; Hazeu *et al.*, 2010). The years of the land-use maps represent the central points in time for each of the time periods for which the species data were obtained: 1960 (representing TP1, see above), 1980 (TP2) and 2008 (TP3). 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 and representative land-use types: agriculture, grassland, forest, moors/peat, sandy soils, swamps, urban and water. Based on these reclassified land-use maps, we calculated a total of 12 land-use metrics for each 5 × 5 km grid cell and for each time period (Table 1). These land-use metrics can be important in determining the distribution of pollinators because they represent limiting factors related to feeding and nesting resources or to

Table 1 Variables used in species distribution models of Dutch pollinator groups (bees, butterflies and hoverflies) and their grouping for subsequent analyses in the mixed-effects model. The variables were divided into four groups related to climate (temperature and precipitation) and land use (landscape composition and habitat fragmentation). The climatic variables were incorporated in the models as yearly averages across the study period.

Variable specifications		
Variable names	Climate or land-use variable input in mixed model as:	Units
<i>Climate variables</i>		
Annual precipitation	Precipitation	mm
Precipitation of driest month	Precipitation	mm
Precipitation of warmest quarter	Precipitation	mm
Mean diurnal range [mean of monthly (maximum temperature–minimum temperature)]	Temperature	°C
Mean temperature of wettest quarter	Temperature	°C
Mean temperature of driest quarter	Temperature	°C
Mean temperature of warmest quarter	Temperature	°C
<i>Land-use variables</i>		
% of each land-use class (agriculture, grassland, forest, moors/peat, sandy soils, swamps, urban and water)	Landscape composition	%
Number of land-use classes	Landscape composition	Count
Total edge density	Habitat fragmentation	m/ha
Average patch area of suitable habitat	Habitat fragmentation	ha

movement between suitable habitat types (see Aguirre-Gutiérrez *et al.*, 2015). The calculated metrics characterize two major aspects of landscape and habitat structure (Tschardtke *et al.*, 2012): landscape composition (nine metrics) and habitat fragmentation (two metrics) (see below).

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 composition and turnover of species assemblages (Tschardtke *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 land-use 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’. Sandy soils were classified as suitable because of the natural variation in floral resources that they offer. Agriculture was considered not suitable because in the Netherlands it mostly refers to highly intensified monocultures with high input of fertilizers and

Importance of drivers for pollinator distributions over time

pesticides (see Aguirre-Gutiérrez *et al.*, 2015) and temporally restricted flower resource availability. For total edge density, we calculated the density of edges between all land-use types in a grid cell.

All calculations of land-use metrics were carried out in R (v3.3.1; Development Core Team, <http://cran.r-project.org>) with the ‘SDMTools’ package (VanDerWal *et al.*, 2014).

Changes in climatic and land-use conditions over time

We quantified the changes in abiotic conditions (climate and land use) 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 of the 18 climatic and land-use variables (Table 1). After obtaining the change values, we used a Student’s *t*-test to investigate if significant changes in climate and land-use conditions between time periods 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 v.3.3.3e (Phillips *et al.*, 2006). MAXENT is a machine learning technique that has been extensively used for modelling large datasets of species in areas with varied sets of environmental conditions, rendering high model accuracy (Elith & Graham, 2009; Marshall *et al.*, 2015). We selected MAXENT after an in-depth comparison with other algorithms for a wide range of species with different sample sizes and spatial distributions of their recording locations in our study area (for details, see Aguirre-Gutiérrez *et al.*, 2013). This comparison showed that MAXENT was one of the best performing algorithms with high scores of various evaluation metrics. We fitted the species distribution models in MAXENT using only linear and quadratic feature types (i.e. transformations of variables; see Elith *et al.*, 2011) to avoid model overfitting (Merow *et al.*, 2013). More in-depth explanations of the MAXENT modelling and feature types can be found in Elith *et al.* (2011).

As species sampling collections are often geographically biased (e.g. Merow *et al.*, 2013), this can also generate bias in the selection of environmental gradients. We accounted for this by only extracting background information from those collection localities where species from the same pollinator group had been sampled (‘target group approach’, Mateo *et al.*, 2010). This has been shown to considerably increase model performance (Mateo *et al.*, 2010). Moreover, this approach allows to account for possible sampling and environmental selection biases because the modelled data contain the same collection bias as the data used for the background selection (Elith *et al.*, 2011). To account for the

variation obtained when creating model predictions with different sets of data, we computed SDMs for each species using 10 repetitions with a bootstrap approach where 80% of the data were used for training and 20% for model testing. We used the area under the curve (AUC) value of the receiver-operating characteristic to summarize model performance (Hanley & McNeil, 1982). AUC values are often correlated with other model performance measures such as the true skill statistic (TSS; Allouche *et al.*, 2006). However, AUC values are constrained by the fraction of the geographical area covered by a species and are often low for species with large sample sizes and increase when the number of sampling records decreases (Aguirre-Gutiérrez *et al.*, 2013; van Proosdij *et al.*, 2016). As different models are constructed with different sets of data, we obtained an ensemble model for each species to account for between-model variability and to avoid basing our model selection on AUC values only. This was done by averaging the suitability scores across the 10 model repetitions. We used this ensemble model in subsequent analyses.

To investigate the importance of environmental drivers in determining species distributions, we obtained three different evaluation metrics for each predictor variable: the 'permutation importance', 'percentage contribution' and the 'test gain' (Phillips, 2006). A preliminary analysis with the 'test gain' metric showed that its importance values were greatly dependent on the number of occurrence records per species. This was not the case for the two other evaluation metrics (permutation importance and percentage contribution). These two evaluation metrics have further been successfully applied in other studies (e.g. Gallardo & Aldridge, 2013; Quillfeldt *et al.*, 2013). We, therefore, excluded the test gain metric from further analysis. For the permutation importance, the values of the focal 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 a variable with high importance for the final model. For the percentage contribution, during each model iteration MAXENT identifies which environmental variables contribute to the fitted model 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 to obtain its final contribution. In the percentage contribution, the evaluation of the importance value of each variable depends on the specific path taken by the algorithm to obtain the optimal model. Hence, similar models may present different importance values for the same environmental variable.

For the final values of the two evaluation metrics (permutation importance and percentage contribution), we averaged the results of the 10 model repetitions. The obtained importance values were used to assess if and how the importance of drivers varied between the three analysed time periods for each of the three pollinator groups (see below).

Environmental drivers of pollinator distributions across time

We used a linear mixed-effects model with Gaussian error structure (Zuur *et al.*, 2009) to test whether the importance of environmental drivers (i.e. seven climate variables and 11 land-use variables; Table 1) in determining pollinator distributions differed among pollinator groups, time periods and type of environmental variable (temperature, climate, landscape composition and habitat fragmentation, Table 1). The averaged variable importance values (permutation importance, percentage contribution) across the four environmental variables groups outlined above were used as response variables and the group of environmental variables (precipitation, temperature, landscape composition and habitat fragmentation), the pollinator group (bee, butterfly and hoverfly) and the time period (TP1, TP2 and TP3; included as a factorial term) as well as their two- and three-way interactions as explanatory variables. We further used the species identity and the SDM model accuracy (AUC) as random factors in the mixed-effects model. We then tested for pairwise significant differences in environmental variable importance between pollinator groups, time periods and type of environmental variable by performing post hoc pairwise comparison tests (Tukey's HSD).

All analyses were performed using the importance values of both the permutation importance and the percentage contribution. However, given that the percentage contribution test depends on the particular path that MAXENT uses to obtain the optimal solution (Phillips, 2006) and the permutation importance tests depend only on the final model, we present the permutation importance results in the main text and the percentage contribution in the supplementary material.

The mixed-effects models were implemented using the 'lme4' package (Bates *et al.*, 2015) and the multiple comparison tests using the 'multcomp' package (Hothorn *et al.*, 2008) with the 'glht' function in the R platform (v3.3.1; <http://cran.r-project.org>).

RESULTS

Spatial distribution of pollinators

We obtained a total of 1780 species distribution models for bees, 520 for butterflies and 1680 for hoverflies per time period (i.e. 10 for each species) from which we constructed the final ensemble model for each species within each pollinator group (Table S1). The AUC values per pollinator group varied depending on the number of records available for each species. The average AUC scores for bees were 0.78, 0.76 and 0.75 for TP1, TP2 and TP3, respectively. For butterflies, the average AUC scores were 0.77, 0.75 and 0.74 and for hoverflies 0.75, 0.76 and 0.75 for TP1, TP2 and TP3, respectively. The modelled pollinator distributions showed strong shifts over time as a function of the climatic and land-use

conditions (Fig. 1). Some of the 5×5 km grid cells lost more than 30 pollinator species, whereas other grid cells gained more than 40 species. These dynamics showed substantial variation among pollinator groups, time periods and geographical location (Fig. 1).

Changes in climatic and land-use conditions over time

All climate and land-use variables showed significant changes between the first (1951–1970) and the last (1998–2014) time period (Fig. 2; Table S2 in Appendix S1). Changes in the frequency distributions of each variable are provided in Figs S5–S7 in Appendix S1. While average annual precipitation per 5×5 km grid cell increased between the first and last time periods (25 mm on average), average values of precipitation of driest month and precipitation of warmest quarter decreased (Fig. 2). All temperature-related variables showed increases between 0.2 °C (mean diurnal range) and 3.8 °C (mean temperature of driest quarter) (Fig. 2). For landscape composition, average cover of forest, swamps and urban classes increased, whereas the average coverage of agriculture, grasslands and moors/peat decreased (Fig. 2). For fragmentation variables, the average patch area of suitable habitats also

showed significant declines of up to 90 ha per 5×5 km grid cell (Table S2 in Appendix S1). The total amount of edges also increased significantly, and the number of land-use classes increased on average by 1.5 from the first to the last time period (Table S2 in Appendix S1).

Importance of climate and land use in determining pollinator distributions across time

Analyses based on ‘permutation importance’ values (see Table 2 for statistical details) and on the ‘percentage contribution’ values gave qualitatively similar results (Figs 3 and S8; Tables S3–S8 in Appendix S1). The most important exception was precipitation for which a slight decrease in importance over time was detected using the ‘percentage contribution’ for all three pollinator groups, while ‘permutation importance’ showed a more static pattern (Tables S6–S8 in Appendix S1). In all time periods, at least one climate-related variable was important and statistically significant in determining pollinator distributions (Fig. 3a–b; Table S3 in Appendix S1). Temperature (Fig. 3b) tended to have higher importance values than precipitation (Table S4 in Appendix S1). While the importance of temperature increased significantly between TP1 and TP3 for bees and hoverflies, the precipitation

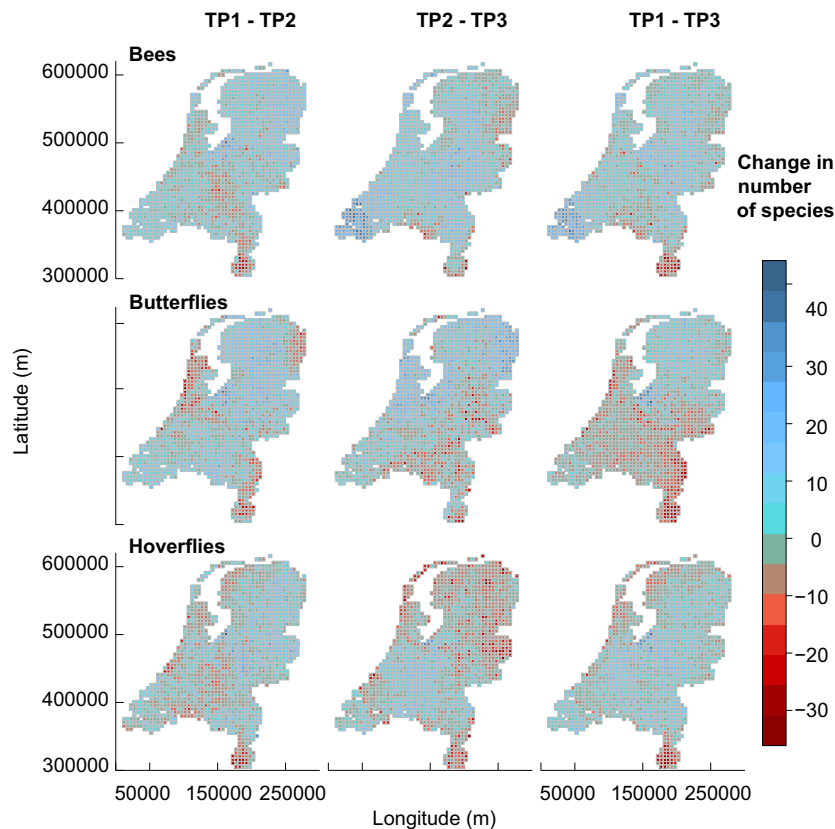


Figure 1 Maps of net changes in the number of species per pollinator group in 5×5 km grid cells between time periods (TP1–TP2: 1951–1970 vs. 1971–1990; TP2–TP3: 1971–1990 vs. 1998–2014; TP1–TP3: 1951–1970 vs. 1998–2014) across the Netherlands. The maps show the difference between the predicted number of species colonizing a grid cell and the number of species abandoning the same grid cell. Blue colours represent cells with more species colonizing. Red colours represent more species abandoning the grid cell.

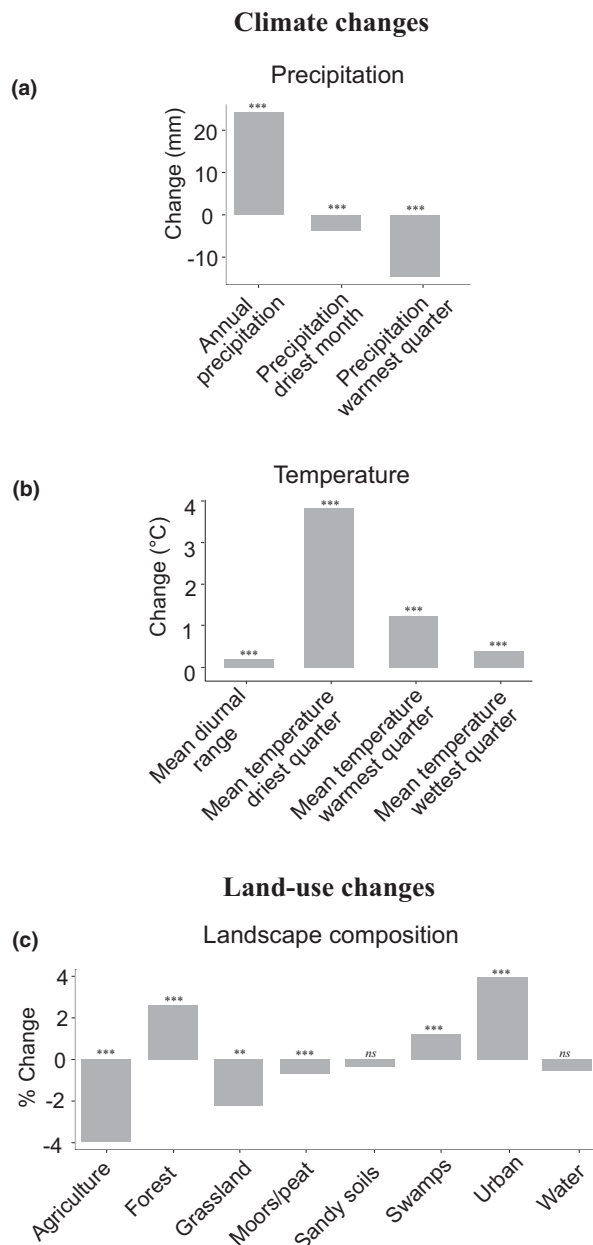


Figure 2 Average changes in climatic (a, b) and land-use (c) conditions per 5 × 5 km grid cell across the Netherlands between the first (TP1, 1951–1970) and the last (TP3, 1998–2014) time period. Changes were calculated as the post-period minus the pre-period value using Student’s *t*-tests. Significance levels: ****P* < 0.001; ***P* < 0.01; **P* < 0.05; ns: not significant. For statistical details, see the Supplementary material Appendix S1, Table S2. Details on changes in edge density, number of land-use classes and average patch area of suitable habitat can be found in the Supplementary material Appendix S1, Table S2.

importance did not significantly increase across time for any of the three pollinator groups (Fig. 4).

Land-use variables also had a statistically significant effect in determining pollinator distributions (Fig. 3c–d; Table S3 in Appendix S1). The importance of fragmentation

Table 2 Statistical details of the mixed-effects model analysing the environmental variable importance (‘permutation importance’) across pollinator groups and time periods in the Netherlands. Further statistical details of post hoc tests are found in Tables S3–S5. *EV*: Environmental Variables (climate: precipitation and temperature; land use: composition and fragmentation); *TP*: Time period (TP1: 1951–1970, TP2: 1971–1990, TP3: 1998–2014); *PG*: Pollinator group (bees, butterflies and hoverflies).

	Sum of squares	Mean sum of squares	df	<i>F</i>	<i>P</i>
<i>EV</i>	227.87	75.96	3	200.48	< 0.001
<i>TP</i>	0.64	0.32	2	0.85	0.43
<i>PG</i>	1.29	0.64	2	1.70	0.18
<i>EV:TP</i>	41.66	6.94	6	18.32	< 0.001
<i>EV:PG</i>	22.35	3.73	6	9.83	< 0.001
<i>TP:PG</i>	0.80	0.20	4	0.53	0.72
<i>EV:TP:PG</i>	14.59	1.22	12	3.21	< 0.001

significantly decreased from TP1 to TP3 for bees, but not for butterflies and hoverflies (Fig. 4). When comparing climate with land-use variables, overall, temperature and landscape composition showed the highest importance for species distributions across time, being stronger than the importance of precipitation and fragmentation (Fig. 3). Moreover, while in TP1 landscape composition was more important than temperature, this trend reverted and temperature became significantly more important than landscape composition in the last time period (TP3) for all three pollinator groups (Table S4 in Appendix S1).

DISCUSSION

Using spatially explicit historical data (1951–2014) of species occurrences, climate and land use, we investigated to what extent the importance of climate and land-use variables as determinants of Dutch pollinator distributions has changed over time. The observed shifts in the modelled species distributions across the last half-century for all three pollinator groups may be mainly the result of the observed changes in climate and land-use conditions (Fig. 1). The changes related to temperature and landscape composition emerged as particularly important (Fig. 2). Our results suggest that, over the studied time period, precipitation and habitat fragmentation variables tended to have a constantly high importance in determining pollinator distributions, but being lower in importance than temperature and landscape composition. Moreover, our results suggest that in recent decades, the importance of temperature has significantly increased and that it is currently more important than landscape composition in determining the distributions of all three pollinator groups.

Within temperate regions such as the Netherlands, the recent rapid changes in temperature and precipitation as well as increases in extreme weather events may have strong effects on population dynamics of pollinators (Rasmont *et al.*, 2015). Our results suggest that the range of values of

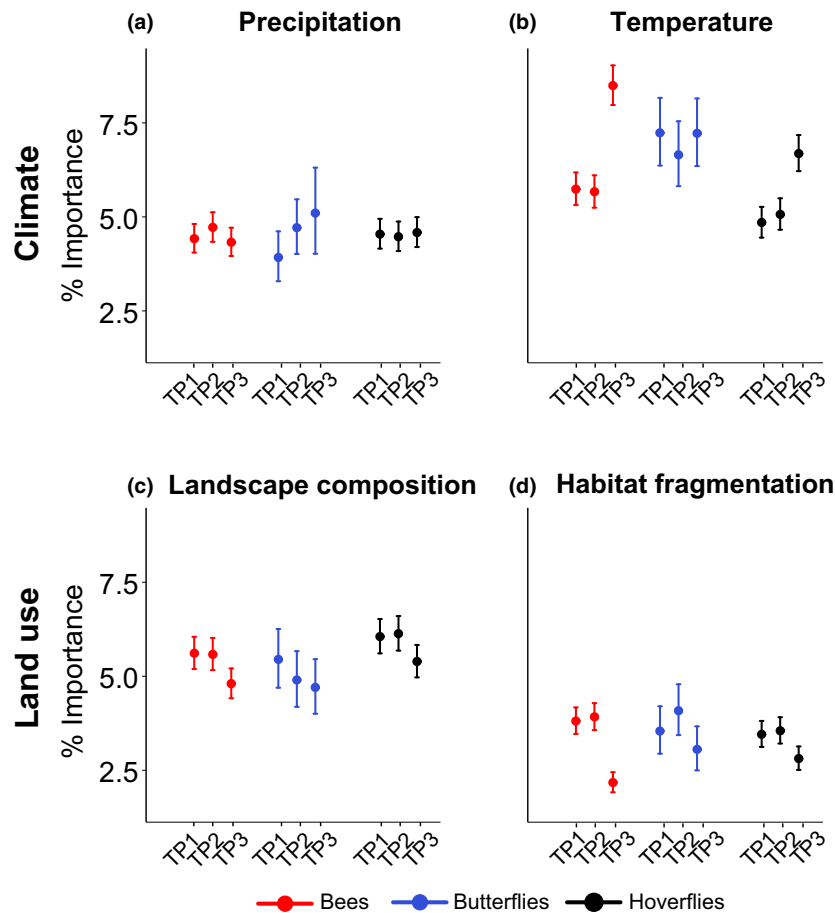


Figure 3 Average importance of climate (*a, b*) and land use (*c, d*) for species distributions of different pollinator groups (bees, butterflies and hoverflies) across time (periods: TP1, 1951–1970; TP2, 1971–1990; TP3, 1998–2014) using the ‘permutation importance’ metric from MAXENT. The permutation importance values (mean \pm 95% confidence intervals) represent the average percent increase in variable importance when the focal variable (one of the climate or land-use predictors) is included relative to the same variable being randomly permuted. The included environmental predictor variables were grouped into climate and land use as follows (compare Table 1): (a) precipitation (annual precipitation, precipitation of driest month, precipitation of warmest quarter); (b) temperature (mean diurnal range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter); (c) landscape composition (percentage of each of eight land-use classes, number of land-use classes); (d) habitat fragmentation (total edge density, average patch area of suitable habitat). For details of the mixed-effects model, see Supplementary material Appendix S1, Tables S3–S5.

the included temperature-related variables was similarly suitable between the earliest time periods for the pollinator groups analysed here. However, this has changed in recent decades where the importance of temperature-related variables for bee and hoverfly distributions has increased, becoming comparable in importance to those observed for butterflies. The lack of a significant change in the importance of temperature for butterflies could be explained by their already continuously high importance set by temperature and their wide within-group differences in habitat preferences and responses to climate impacts (e.g. Parmesan *et al.*, 1999; Heikkinen *et al.*, 2010). Meanwhile for some species, the changes in temperature conditions could have had an important impact on their distribution for other species such changes did not represent an important effect, buffering in this way the changes in the importance of temperature at the

group level (see Fig. 3 wider intervals for butterflies). In contrast, the within-group differences for bees and hoverflies seem to be less accentuated, showing less variation among species in the importance of temperature as a driver of their distribution. Previous studies have also reported spatial shifts in the distribution of these pollinator groups over the study area (e.g. Aguirre-Gutiérrez *et al.*, 2016). The fact that the importance of climate for butterflies has been consistently high across the last half-century may be a reflection of the high susceptibility of butterflies to even small changes in temperature-related conditions in contrast to the other pollinator groups here studied (Heikkinen *et al.*, 2010; Oliver *et al.*, 2015). Overall, the future importance of climate as a driver of the distribution of pollinator species may thus depend on the current climate limits of the study region and the pollinator group investigated.

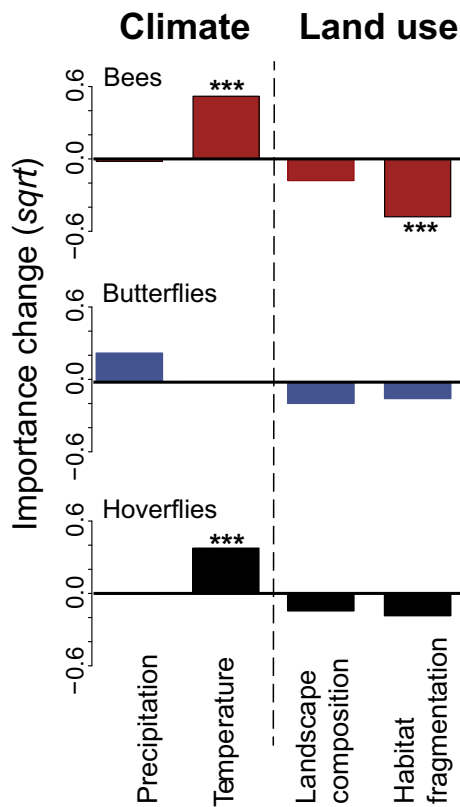


Figure 4 Results of mixed-effects model for changes in the importance of climate and land-use drivers for bee, butterfly and hoverfly distributions between the first (TP1, 1951–1970) and the last (TP3, 1998–2014) time period in the Netherlands. Average changes in the importance ('permutation importance') of climate variables are shown on the left and those of land-use variables on the right side of the dotted line. Climate variables include precipitation (annual precipitation, precipitation of driest month, precipitation of warmest quarter) and temperature (mean diurnal range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter), and land-use variables include landscape composition (percentage of each land-use class, number of land-use classes) and habitat fragmentation (total edge density, average patch area of suitable habitat). The change in importance is expressed as *square-root* transformed values based on the mixed-effects model results from Fig. 2. Significance level: *** $P < 0.001$. For statistical details, see Supplementary material Appendix S1, Tables S3–S5.

Like in other highly industrialized countries, the major land-use changes in the Netherlands have occurred in earlier time periods (*c.* 1950–1970), whereas they are less pronounced during the last half-century. In fact, we observed that although the average values of landscape composition have fluctuated over the period analysed, the range in these values did not change strongly (Fig. S6). Nevertheless, land use, particularly landscape composition, remains of high importance in determining species distributions. This may reflect the high importance of fine-scale habitat availability (here represented by landscape composition) for pollinators. Indeed, climatically suitable areas may not be occupied by

species if habitat conditions remain unsuitable (Oliver *et al.*, 2012). We found a decrease in the importance of habitat fragmentation (*i.e.* habitat patch area and edge density) for bees, and also to a lesser degree for butterflies and hoverflies (but small and not significant). This confirms our initial expectations of slightly lower impacts of land-use changes in the present time period (TP3) in comparison to initial periods (*e.g.* TP1 and TP2; Fig. 3c–d) given that most large-scale land-use changes have ceased decades ago in the Netherlands (Harms *et al.*, 1987; European Environment Agency 2010). As a consequence, the already existing restrictions for the accessibility of species to feeding and nesting resources in the surrounding landscape (*e.g.* Steffan-Dewenter, 2003) have been kept relatively constant with no major changes in the importance of fragmentation variables. Moreover, also the increase in importance of temperature, for bees and hoverflies, may hinder the already low possible impact of habitat fragmentation. We expect that in biodiversity-rich countries with expanding agriculture and economy and large areas becoming fragmented and changed in terms of their landscape composition (see Lambin & Meyfroidt, 2011), future impacts of land-use changes may be even more pronounced than in highly industrialized countries where major land-use changes have often ceased decades ago.

Overall, our results call for SDM applications that capture how the importance of environmental drivers for species distributions may change in different areas and over time. Moreover, these applications should try to capture specific meta-population processes such as dispersal limitation and species interactions. Such processes are not yet fully accounted for in current SDMs (Franklin, 2010; Martínez-Freiria *et al.*, 2016) and they could also influence the importance of environmental drivers in defining species distributions (Ehrlén & Morris, 2015). Accounting for these processes and for the possible changes in the importance of environmental drivers is essential given the predicted future changes in environmental conditions. This is essential because species may currently occupy unsuitable sites that were suitable in the past, representing a landscape suitability debt (Krauss *et al.*, 2010). However, species may also not yet fully occupy already suitable habitat areas due to a lack of dispersal (Schurr *et al.*, 2012). Thus, coupling SDMs with other more trait-based community-level and mechanistic approaches may be an appropriate solution for analysing future species responses to climate and land-use change (Pacifi *et al.*, 2015).

CONCLUSIONS

Predictions based on species distribution models strongly rely on the constancy of the relationship between species occurrences and environmental conditions. However, how the importance of environmental variables for species distributions changes over time has been little studied. Our historical analysis shows that temperature and landscape composition have been the most important drivers for pollinator

distributions across time. However, our study also reveals that the importance of temperature has strongly increased in recent time periods at least for two out of three pollinator taxa. This suggests that ongoing and future climate change could continue to increase in importance as a driver of species distributions. The (non-)stationarity of climate versus land-use drivers of species distributions requires further testing, e.g. with historical data for other taxa, other areas such as tropical and arctic regions, and at different spatial extents and grain sizes. This would help to deepen our understanding about the generality of our findings and its relevance to other taxonomic and functional groups and regions.

ACKNOWLEDGEMENTS

The authors thank Peter Linder, Richard Pearson, Şerban Procheş, Oliver Schweiger and two anonymous referees for their constructive comments that greatly improved the article. J.A.G. was funded by the Mexican National Council for Science and Technology (CONACyT, ref: 310005). L.G.C. and J.C.B. were funded by EU FP7 projects 'Status and Trends of European Pollinators' (244 090, www.STEP-project.net) and COST Action FA1305 SUPER-B (Sustainable Pollination in Europe), and L.G.C. was also funded by the EU FP7 project 'Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales' (www.scales-project.net). W.D.K. acknowledges a University of Amsterdam starting grant.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary tables (Tables S1–S8) and figures (Figs S1–S8).

BIOSKETCH

Jesús Aguirre Gutiérrez (<http://jesusaguirregutierrez.myreesites.net/>) is interested in the effects that environmental changes, such as climate and land-use modifications, have on the species distributions across time and space. He is also interested in the application of remote sensing techniques for biodiversity conservation. The team of authors is interested in how biodiversity is affected by past, present and future global change.

Author contributions: J.A.G, L.G.C and J.C.B. conceived and designed the analyses; J.A.G. performed the analyses and together with W.D.K. and L.G.C. interpreted the data. M.F.W. and M.R. gathered the data, prepared it for the analyses and/or provided information to help with data interpretation. J.A.G led the writing with significant input from W.D.K. and L.G.C. All other authors provided corrections to manuscript drafts and discussed ideas within it.

Editor: Şerban Procheş