Article

Projected decline in European bumblebee populations in the twenty-first century

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Habitat degradation and climate change are globally acting as pivotal drivers of wildlife collapse, with mounting evidence that this erosion of biodiversity will accelerate in the following decades[1–3]. Here, we quantify the past, present and future ecological suitability of Europe for bumblebees, a threatened group of pollinators ranked among the highest contributors to crop production value in the northern hemisphere[4–8]. We demonstrate coherent declines of bumblebee populations since 1900 over most of Europe and identify future large-scale range contractions and species extirpations under all future climate and land use change scenarios. Around 38–76% of studied European bumblebee species currently classified as 'Least Concern' are projected to undergo losses of at least 30% of ecologically suitable territory by 2061–2080 compared to 2000–2014. All scenarios highlight that parts of Scandinavia will become potential refugia for European bumblebees; it is however uncertain whether these areas will remain clear of additional anthropogenic stressors not accounted for in present models. Our results underline the critical role of global change mitigation policies as effective levers to protect bumblebees from manmade transformation of the biosphere.

The current degradation of habitats, fuelled by local stressors and largely amplified by global climatic drivers, constitutes an unmatched challenge in human history[1]. One of the most sudden consequences of this ecological upheaval is the abrupt collapse of insect populations, a pervasive phenomenon driven by an unprecedented combination of biotic and abiotic disruptions[2,9]. This continuing defaunation implies cross-lineage insect losses in both abundance and diversity[3,10], with considerable uncertainty remaining about how this situation will evolve in the near future[11]. Identifying regions most likely to experience drastic changes in their insect populations has now become pivotal for ensuring their effective conservation[12].

Insect pollinators constitute a prime case study to unravel the effects of combined environmental perturbations on species extirpation and recolonization. Growing concern about the impacts of pollinator decline on global ecosystem services has emerged in the past decades, especially because nearly 90% of all wild plants and most of the world's crops benefit from animal pollination[12–16]. Amidst these critical ecosystem service providers are bumblebees (*Bombus*), a genus of both wild and managed bees ranked among the highest contributors to crop production value in temperate and cold ecosystems of the northern hemisphere[7]. In the past decades, however, these predominantly cold-adapted pollinators have undergone sharp population reductions across continents[17–19], with national reports of local extinctions of around 20–25% of species[20,21] and a continental report documenting negative population trends for more than 45% of species[6]. In spite of these already severe findings, it remains unknown whether this decline has already reached its climax or if we are only at the dawn of a much more dramatic collapse in bumblebee populations.

Here, we analyse the past, present and future ecological suitability of the European continent for 46 bumblebee species on the basis of a set of harmonized climate, land use and human population data obtained through the Inter-Sectoral Impact Model Intercomparison Project Phase 2b (ISIMIP2b)[22,23] for the last century, the present period and for upcoming years to 2080. Our observational dataset comprises 401,046 unique georeferenced occurrence records of bumblebee presence split into 'past' (1901–1970 inclusively) and 'present-day' time periods (2000–2014 inclusively; Methods). To model the species–environment relationships between our bumblebee occurrence records and the set of ISIMIP2b variables, we train ecological niche models on georeferenced data corresponding to each period using a boosted regression tree (BRT) approach[24]. The resulting predictive probability is here interpreted as a measure of ecological suitability given local environmental conditions and varies between 0 (unsuitable environmental conditions) and 1 (highly suitable environmental conditions). In addition to the computation of commonly used area under the receiver operating characteristic curve (AUC) metric, we assessed the predictive performance of our ecological niche models by computing a prevalence-pseudoabsence-calibrated Sørensen's index (SI_{ppc}; Methods; Extended Data Fig. 1 and Extended Data Table 1). Using the same index, we then evaluated the predictive performance of our models by assessing the ability of ecological niche models trained on past occurrence and environmental data to predict present-day distributions when projected on present-day environmental data, as well as the ability of ecological niche models trained on present-day occurrence and environmental data to predict past distributions when projected on past environmental data (Methods; Extended Data Table 2).

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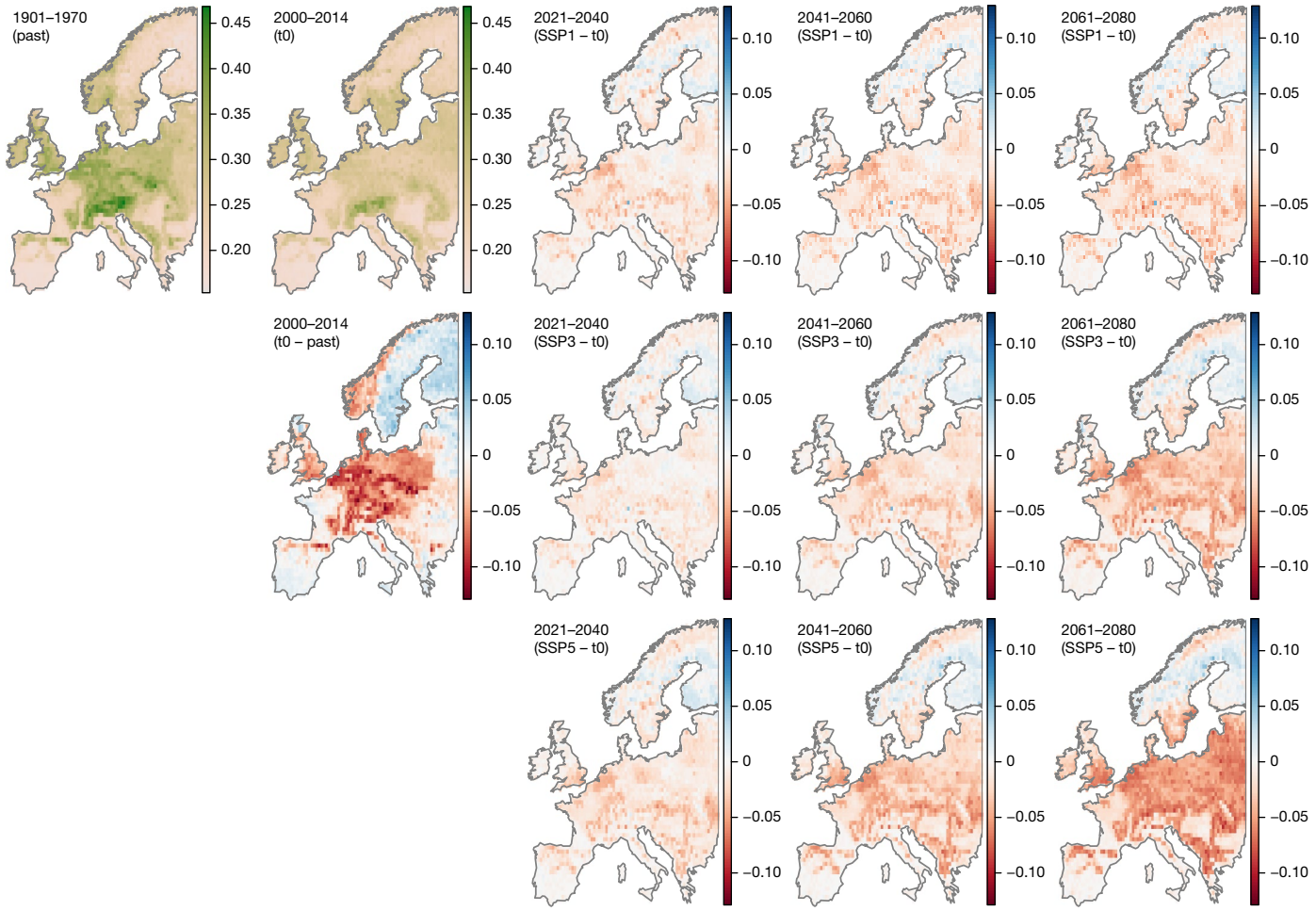

Fig. 1 | Changes in ecological suitability for 46 European bumblebee species based on an observational dataset of 401,046 unique georeferenced occurrence records. We here report the ESI defined as the local mean ecological suitability averaged over species (and thus ranging from 0 to 1). We report ESI estimates for the past and present-day (t0, 2000–2014) projections, as well as the differences between past (1901–1970), present (t0) and future (2021–2040, 2041–2060 and 2061–2080) projections. Colour bar gradients in the 'past' and 't0' maps (top left corner) reflect the averaged ecological suitability across all studied species. In all other maps, colour bar gradients reflect the change in averaged ecological suitability for the same species (blue for increased ecological suitability and red for decreased ecological suitability). Models are based on harmonized climate, land use and human population data obtained through ISIMIP2b.

In addition to training and mapping BRT models with the past and present-day occurrence data and environmental conditions, models trained on present-day data are further used to project the changes in ecological suitability maps in the next decades. For this purpose, we use environmental layers projected for three time windows (2021–2040, 2041–2060 and 2061–2080) according to three climate change scenarios, that is the representative concentration pathways (RCPs) corresponding to three distinct shared socioeconomic pathways (SSPs): SSP 1-2.6, SSP 3-6.0 and SSP 5-8.5 (+2.6, +6.0 and +8.5 W m^{-2} of radiative forcing by 2100 relative to pre-industrial values, corresponding to low, medium-high and high greenhouse gas emissions, respectively). We used three different global change trajectories instead of a single one to account for uncertainty surrounding future global changes, which are contingent on societal decisions.

Recent decades were marked by a notable decrease in ecological suitability mostly concentrated in central Europe (Fig. 1). Although our ecological suitability index (ESI, here defined as the local mean ecological suitability averaged over species) only decreased by 4.5% on average, it dropped up to 33.1% locally. In addition, we find a continental-scale drop in bumblebee species richness below 55° N (as measured by a species richness index defined in the Methods; Extended Data Fig. 2). These large-scale drops in both local ecological suitability and species richness depict an unambiguous reduction in Europe's ecological suitability for the present bumblebee fauna. Some of the countries identified by our analyses as especially impacted by this decline (for example, Belgium, Germany, northern France and the Netherlands) encompass areas for which significant reductions and local extinctions in certain bumblebee species have been repeatedly and consistently documented in the past decades (see ref. 5 for occurrence maps and Table 12 of ref. 20 for a list of useful references).

For each examined species, we also investigate the environmental factors mostly responsible for the projected trends in ecological suitability by calculating an environmental value difference (EVD) metric, defined as the difference between the averaged predictor value in 2061–2080 under the SSP 3-6.0 trajectory and that at present-day. As the suitability of the continent is expected to vary over time following global changes, we compute in parallel a value of ecological suitability difference (ESD), defined as the difference between the ecological suitability averaged over the study area at present-day and in 2061–2080 under the same SSP 3-6.0 trajectory. We find a negative correlation between our index of ESD and increases in local values of several environmental factors such as temperature, precipitation and fraction of land devoted to pastures or croplands (Fig. 2), in line with previously suspected causes of reductions of bumblebee populations[17,18].

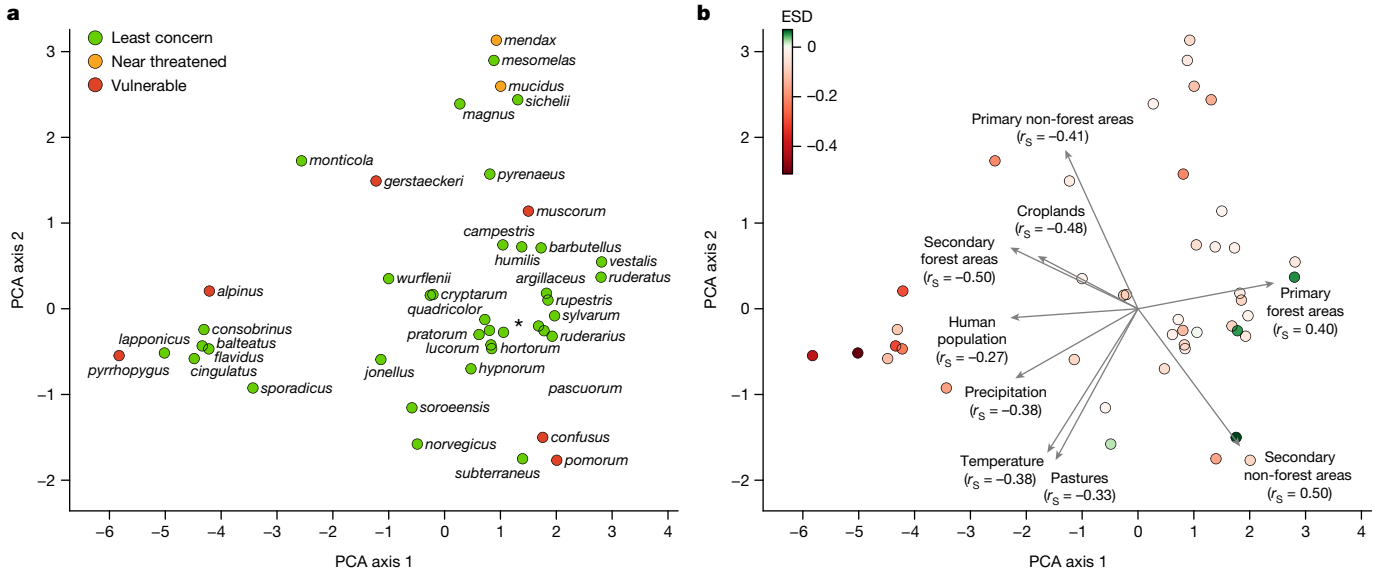

Fig. 2 | Analysis of the loss of areas ecologically suitable for bumblebee species. a,**b**, Both **a** and **b** report the PCA based on the different EVDs computed for each species. For a specific environmental factor, the EVD is here computed as the difference between the averaged value of the environmental factor at the present time and in 2061–2080 under the SSP 3-6.0 trajectory. The EVD values are species-specific because, for a given species, we only considered the grid cells for which the ecological suitability is estimated to be higher than the median value of the threshold maximizing SI_{ppc} for the ecological niche models trained on present-day occurrence and environmental data (Extended Data Table 1; Methods). **a**, PCA with species dots coloured according to their current IUCN conservation status (green for 'Least Concern', orange for 'Near Threatened' and red for 'Vulnerable'). * refers to a subset of species for which the name is not reported owing to a lack of space (*B. bohemicus*, *B. lapidarius*, *B. sylvestris* and *B. terrestris*). **b**, PCA with species dots coloured according to their ESD value (see the colour bar), which is computed as the difference between the ecological suitability averaged over the selected grid cells (see above) at the present time and in the projection for 2061–2080 under the SSP 3-6.0 trajectory. In addition, we also report the Spearman correlation coefficient (r_S) value between ESD and EVD values. Specific epithets only are shown in the figure; genus *Bombus*.

The estimated ecological suitability between the past and present-day has dropped more abruptly for some species than others (for example, for the declining *B. pomorum* and *B. veteranus*), whereas a subset of other species is showing an increased ecological suitability of the continent in the present times compared to the past (for example, for the already expanding *B. hypnorum* and *B. terrestris*). These trends are also consistent with previous empirical observations of bumblebee population trends across the continent, with a large fraction of species shown to suffer from global changes and a more restricted subset benefitting from the same alterations in climatic and land use conditions[25].

We further compare our results with the current conservation assessments for the IUCN Red List of Threatened Species by the International Union for Conservation of Nature (IUCN), based on IUCN Red List assessments undertaken over the period 2012–2014 for the European Red List of Bees[6] to evaluate whether the latter system—based on past and present observation data and experts' opinions—succeeds at estimating the fate of bumblebees in the following decades. We find that the current IUCN risk assessments of the examined bumblebee species are not reflective of their species-specific projected population trends (Kruskal–Wallis test, $P = 0.76$; Methods), with several species presently listed as 'Least Concern'[6] projected to show acute decreases in the spatial extent of their ecological niche on the basis of all trajectories of global change. We find no obvious clustering of species sharing similar IUCN status based on their EVDs for each examined environmental factor (Fig. 2b), suggesting that a complex array of bioclimatic alterations explain the current extinction risk of bumblebees. A clearer clustering, however, appears based on the overall distribution of species across Europe, with species now presenting the largest ranges sharing more similar EVDs. Most importantly, most species with negative loadings on the first principal component (Fig. 2) are Arctic/Arcto-alpine bumblebees, a phylogenetically diverse group of *Bombus* species restricted to the coldest areas of the continent[26]. These especially heat-sensitive species[27] have already raised concern because of climate-attributed uphill shifts in the high altitudes of southern Europe[28], as well as their rarefaction in the Arctic[5].

As the IUCN assessment guidelines allow to consider projections of census data into the future for refining risk assessments[29], we compute the ratio between the number of ecologically suitable grid cells in 2061–2080 and in present-day conditions, for each of the trajectories considered in the study (Extended Data Table 3; Methods). A grid cell is considered as ecologically suitable if it is associated with an ecological suitability value higher than the optimized SI_{ppc} threshold value obtained for the considered species (Extended Data Table 1; Methods). Amongst the bumblebee species examined here, 38–76% of species (depending on the SSP trajectory) listed as 'Least Concern' by the IUCN now are expected to undergo losses of at least 30% of suitable areas by 2061–2080 (Extended Data Table 3). Given that a projected loss of 30% of probability of occurrence can make species fall into a threatened category following the IUCN criterion A3 (which applies within the next 10 years or three generations, whichever is longer), our most severe scenario suggests that a longer-term vision on the same criterion (in the next 40–60 years) would make more than 75% of the species considered 'threatened', regardless of their present status. Most distinctively, a set of aforementioned Arctic or Arcto-alpine species, including *B. alpinus, B. flavidus* and *B. pyrrhopygus*, could be at the verge of extinction in Europe, with an expected loss of at least 90% of ecologically suitable territory in the same period. Significant losses (up to about 65–70% under the SSP 5-8.5 trajectory) of ecologically suitable cells are also expected for 'Least Concern' species associated with montane habitats such as *B. monticola* and *B. pyrenaeus*. Overall, the mismatch between the IUCN conservation statuses and the projected patterns of decline suggests that we might only be at the outset of a much stronger ecological crisis, with the present IUCN statuses underestimating the magnitude of this forthcoming erosion

of diversity. Overall, Europe below 60° N is expected to become largely unsuitable for the persistence of numerous bumblebee species, should human activities continue unabated.

As the global biodiversity patterns are significantly reshaped by the compounding effects of land use and climate changes[30], predicting the fate of given species under future environmental changes has become central for conservation planning[31]. Although under all our analysed scenarios (Fig. 1 and Extended Data Fig. 2) geographically restricted areas of high latitude (Scandinavia) appear as ecologically suitable refugia for European bumblebees, their potential for acting as such will rely on an intrinsic potential for species to disperse, colonize and successfully maintain viable populations across these territories[32]. Integrating species-specific knowledge about dispersal distances would substantially improve estimates of potential range changes and their implications for conservation management but the dispersal ability of the overwhelming majority of wild bumblebee species is unknown. Preliminary evidence suggests that mass-migration exists in bumblebees, with reports documenting specimens crossing large water bodies and possibly migrating hundreds of kilometres[33]. The introduced buff-tailed bumblebee *B. terrestris* was, for instance, shown to have rapidly widened its spatial footprint in South America[34]. However, the latter species was shown to be a physiological and ecological outlier in comparison to other bumblebees[25,35] and the very few proposals about the dispersal ability of these other species suggest much smaller dispersal capacities[4]. A previous large-scale investigation of both European and North American bumblebee species demonstrated their failure to track climate warming along their northern range limits following the climate warming of the past decades, although suffering losses at their southern limits[19]. The same study noted, however, that European bumblebees with southern geographical ranges could retreat to higher elevations, a trend also recently observed in the Pyrenees[36].

It remains uncertain whether the identified refugia in Scandinavia will stay cleared of additional, co-occurring anthropogenic stressors that are not recognized in current models. It is unclear if synergistic pressures including the development of infrastructures (for example, tourism and transport), pesticide use, pollution (for example, nitrogen and heavy metals), the spread of exotic plants, invasion of managed species and subsequent pathogen spillover (all known to severely impact pollinator populations[37,38]) will further worsen in the future in these areas. Despite an already appalling aspect, our projections are likely to be conservative in light of the non-consideration of the future disruptions of species–species interactions (for example, plant–pollinator, mutualisms, predator–prey, hybridization and competition). Similarly, the lack of consideration of extreme weather events, known to severely impact insect populations (for example, through direct death[27], indirectly by impairing cognition[39] or reducing fertility[40]), may lead to local extirpations sooner than expected by our simulations. Conversely, the potential for local adaptation and subsequent population persistence in the face of global changes can never be excluded[41,42]. Sufficient genetic variation in fitness-related traits (for example, associated with physiological limits or phenological timing) could, for instance, increase the likelihood of local adaptation to altered climatic conditions[41]. Overall, it remains uncertain whether the regions identified as refugia here will act as such, or (by contrast) will act as sinks for the species that would be able to shift their distributions towards these ecologically 'safe' areas.

The originality of the present study lies in the combination of (1) ecological niche modelling for community-level mapping using both climate and land use change scenarios at a continental scale, (2) the implementation of original metrics to quantify and visualize change in ecological suitability, (3) the use of the latter metrics to highlight potential refugia for these pollinators and (4) the use of the same metrics to address the current IUCN risk assessement with a longer-term vision in the twenty-first century. Further use of our modelling approaches could give valuable insights into the fate of other threatened invertebrates amidst the challenges posed by impending global changes. However, long-term and large-scale observation datasets verified by expert taxonomists remain rare commodities, even for other ecologically critical decomposers, soil engineers, nutrient recyclers, seed dispersers and other highly informative bioindicators. Irrespective of the metrics used, risks to these organisms are expected to increase with rises in temperatures[11] and conversion of natural areas to agricultural land[2]. Reducing their exposure to the combined pressure of human stressors has therefore become urgent for properly shaping conservation and restoration plans for natural habitats[14]. Mitigation strategies aiming to protect habitats across species' dispersal corridors, accompanied with landscape management providing microrefugia in areas in which losses are more concentrated, could significantly contribute to buffering the impacts of anthropic disturbances on wildlife. Further works accounting for the effects of finer-scale variation in climate on land use will also help improve our understanding of how species will respond to global changes. The subsequent conservation measures will then have to be applied hand in hand with strict global policies aiming to mitigate the human footprint on such vital ecosystem providers, incorporating strengthened regulations on the greenhouse gas emissions and landscape management at national and continental scales.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06471-0.

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Methods

Studied species, study area and datasets of occurrence records

We focused on bumblebees (Apidae, genus *Bombus*), for which long-term observation data, literature on biogeography and life history are available at the European spatial scale[5]. The European bumblebee fauna received particularly sustained attention in the fields of taxonomy and biogeography over the past decades[4,26,43–48], making the knowledge about species boundaries and distribution ranges extremely precise compared to other continents. We considered all previously cited up-to-date taxonomic revisions of the genus *Bombus*. This step is crucial given that cryptic species can present differentiated ecoclimatic requirements[49]. This led us (1) to remove the occurrence data of the cryptic *B. konradini* from *B. monticola* in the Central Apennines and (2) to separate the Corsican endemics *B. renardi* and *B. xanthopus* from their respective mainland sister taxa *B. lucorum* and *B. terrestris*. Unlike ref. 50, we also did include in our analysis multiple representative taxa belonging to the subgenus *Alpinobombus*, a group of especially cold-adapted bumblebee species now undergoing sharp declines as a result of their northern geographic range or distributions in high altitudes[5].

Spatially referenced occurrence records were retrieved from ref. 5 and are available at http://www.atlashymenoptera.net/page.aspx?id=169. This large-scale dataset consists of geographically referenced occurrence data accumulated from published literature, as well as from bumblebee collections deposited in universities and museums. These data were checked by expert entomologists to ensure their reliability and remove any record that could not be reconciled with comparisons of range maps published in the most up-to-date IUCN Red List Reports (http://www.iucnredlist.org/, accessed October 2022). Only records including both georeferencing data and collection/observation date were retained.

In total, we retained 46 species which had at least 30 unique occurrence records in both studied periods. We ensured that every bumblebee subgenus occurring in our study area is represented in this set of species, following the latest subgeneric classification of ref. 51. All species retained for the analysis appeared sampled within their actual European range on the basis of the most updated understanding of their biogeography (more precisely discussed in ref. 5). Duplicate records were removed to reflect species presence rather than species density and to further decrease potential sampling biases. The final dataset contained a total of 401,046 unique occurrence records used species-specifically for the ecological niche modelling analyses. These data were split into past (1901–1970 inclusively, with 125,283 unique records; Extended Data Fig. 3) and present-day time periods (2000–2014 inclusively, with 275,763 unique records; Extended Data Fig. 4). The rationale for selecting these time periods is driven by the fact that, starting from the 1970s, Europe underwent profound land use changes following the agricultural intensification associated with the Mansholt Plan. The subsequent reshaping of habitats has resulted in the loss of numerous floral resources once supporting bumblebee populations, leading to drastic shifts in their communities[5,52–54]. The second time period unfolds at the dawn of the twenty-first century, subsequent to the aforementioned landscape transformations that exerted profound changes on European bumblebee communities. These two time periods are also analogous to those selected by ref. 50 in their recent work on bumblebee decline across Europe and North America, facilitating comparability between both studies. Finally, the comparatively lower quantity of data available for the twentieth century implies that the latter period extends over a longer time span than the former. This necessary compromise offers the possibility to capture species' distribution in both periods as accurately as possible with the data available.

Training and projecting ecological niche models

We performed all ecological niche modelling analyses using the BRT approach implemented in the R package 'dismo'[24]. BRT is a machine-learning approach that can be used to generate a collection of sequentially fitted regression trees optimizing the predictive probability of occurrence given local environmental conditions[55], a predictive probability that is here interpreted as a measure of ecological suitability, which varies between 0 (unsuitable environmental conditions) and 1 (highly suitable environmental conditions). One of the interests of the BRT approach lies in its ability to model complex nonlinear relationships between the response and various predictor variables[24].

We run the BRT analysis using both verified occurrence data and pseudoabsence data, the latter being randomly sampled from the background of the study area[55,56]. To limit the impact of heterogeneous observational/collection efforts and avoid artificially treating undersampled areas as ecologically unsuitable, we only sampled pseudoabsence points in background grid cells in which we have at least one other *Bombus* species occurrence record in our overall dataset[57]. As it requires only a single occurrence record to consider the presence of a considered species in a grid cell, we randomly conserved a single occurrence record per grid cell. We applied the same filtering step for the pseudoabsences but further discarded pseudoabsence points falling in grid cells with at least one occurrence record[49]. For each of the 46 bumblebee species, we trained two distinct BRT models: one based on past and one based on present-day occurrence data, using temporal mean environmental layers computed for the corresponding period.

We used a spatial rather than a standard cross-validation procedure to select the optimal number of trees in each BRT model. A standard cross-validation procedure may lead to an overestimation of the ability of the BRT model to make a reliable estimation because spatial data are usually autocorrelated[58]. Thus, we used a spatial cross-validation procedure, based on the blocks generation proposed by ref. 59, by using a function from the 'blockCV' R package—see also the work of ref. 56 for the application of a similar approach. All BRT analyses were run and averaged over ten cross-validated replicates, with a tree complexity set at five, an initial number of trees set at ten, a learning rate of 0.005, a tolerance parameter set to 0.001, a step size of five and considering five spatial folds. We first evaluated the inferences using the area under the receiver operating characteristic (ROC) curve, also simply referred to as AUC. Mean AUC values obtained for each species are all reported in the GitHub repository of the present study and ranged from 0.66 (*B. humilis*) to 0.96 (*B. pyrrhopygus*) when based on presence occurrence data, as well as from 0.65 (*B. pascuorum*) to 0.95 (*B. lapponicus*) when based on past occurrence data. However, the use of the AUC metric alone has been repeatedly criticized in previous works because of its dependence on prevalence (the proportion of recorded sites where a given species is present)[60–62], we further assessed the predictive performance of our past and present-day ecological niche models by computing SI_{ppc} defined as follows[63,64]:

$$SI_{ppc} = (2 \times TP)/(2 \times TP + x \times FP_{pa} + FN)$$

where

$$x = (P/A) \times ((1 - prev_{sp})/prev_{sp})$$

and

$$prev_{sp} = P/(P + A)$$

with TP corresponding to the number of true positives, FP_{pa} to the number of false positives associated with sampled pseudoabsence points, FN to the number of false negatives, P to the number of presence points and A to the number of pseudoabsence points. This index has its lower limit at 0 and its upper limit at 1 (interpreted as a maximal predictive performance). Because the computation of this index

requires binary presence–absence data but ecological niche models instead return ecological suitability values ranging from 0 to 1, we performed an optimization procedure similar to one adopted by ref. 65 by varying the threshold values in the range [0, 1] with a 0.01 step increment and eventually selecting the threshold value maximizing the SI_{ppc}. We computed a SI_{ppc} for each of the ten independent ecological niche models trained for each species and for each period and reported the resulting median as well as minimum and maximum values (Extended Data Table 1). As detailed in Extended Data Table 1, all SI_{ppc} values are higher than 0.50 (greater than 0.55) and on average equal to 0.73 when considering all ecological niche models (trained either on past or present-day data). For each species and for each ecological niche model trained on past or present-day data, we also report the evolution of the SI_{ppc} according to the ecological suitability threshold value ranging from 0 to 1 (Extended Data Fig. 1).

We further computed SI_{ppc} values to assess the ability of ecological niche models trained on past occurrence and environmental data to predict present-day distributions when projected on present-day environmental data, as well as the ability of ecological niche models trained on present-day occurrence and environmental data to predict past distributions when projected on past environmental data (Extended Data Table 2). When comparing the median estimates obtained for each species, we observe a median SI_{ppc} decrease of 0.19 (95% confidence interval (CI) = [−0.03, 0.44]) when evaluating ecological niche models trained on past data and then projected on present-day data and only a median decrease of 0.09 (95% CI = [−0.09, 0.31]) when evaluating models trained on present data and then projected on past data. Because ecological niche models trained on present-day data were used to project the ecological suitability of bumblebee species based on future environmental conditions, the latter result is of importance as it assesses the performance of those models to predict relevant ecological suitability maps when projected on alternative environmental conditions.

As stated in the main text, we trained two distinct BRT models per species: one based on past (1901–1974) and one based on present-day (2000–2014, also referred to as t0 in the figures) occurrence data, using temporal mean environmental layers computed for the corresponding period of the time (see below). BRT models trained on past and present-day occurrence data were then, respectively, projected on past and present environmental conditions to get the corresponding ecological suitability maps and BRT models trained on present-day data were further used to project the evolution of ecological suitability maps in the near future. For these future projections, we used climate and land use projections at three time windows (2021–2040, 2041–2060 and 2061–2080) according to three climate scenarios, that is RCP 2.6, 6.0 and 8.5 corresponding to three SSPs: low (RCP 2.6-SSP 1), medium-high (RCP 6.0-SSP 3) and high (RCP 8.5-SSP 5) CO_2 emissions. We used three different global change trajectories instead of a single one to account for uncertainty about future global changes, which in turn depends on societal choices.

BRT models were based on the following environmental factors: climate, land use and human population data available through the ISIMIP2b[22]. The climate information consists of daily gridded near-surface air temperature and surface precipitation fields derived from the four bias-adjusted[66] global climate models (GCMs: GFDL-ESM2M (ref. 67), HadGEM2-ES(ref. 68), IPSL-CM5A-LR (ref. 69) and MIROC5 (ref. 70)) participating in the fifth phase of the Coupled Model Intercomparison Project Phase 5 (CMIP5). All information was temporally averaged over each analysis time window. The four GCMs were chosen on the basis of forcing data availability and representativeness of the full CMIP5 ensemble[66]. The GCM output is bias-adjusted[22,66] to better capture the statistical distribution of observational weather data while preserving simulated trends. We considered simulations conducted under historical climate forcings and RCP 2.6, 6.0 and 8.5. In addition, we considered observation-based gridded temperature and precipitation from the concatenated products GSWP3 and EWEMBI[22] for assessing the current (2000–2014) and past (1901–1974) conditions. For land-cover data we used v.2 of the Land Use Harmonization (LUH2) providing historical and projected land-cover states under a range of SSPs and from which we considered SSP 1-2.6, 4-6.0 and 5-8.5. Finally, we retrieved gridded population projections under SSP 2-2.6 (ref. 71). For each combination of product (GCM, GSWP3-EWEMBI, LUH2 and gridded population), scenario (historical, RCP and SSP) and analysis window (1901–1974, 2000–2014, 2021–2040, 2041–2060 and 2061–2080), we computed the grid-cell temporal mean. All land use data were harmonized by the LUH2 group to smoothly connect the historical reconstructions with the future projections into a single format, whereas the population and climate data were harmonized by the ISIMIP data team into a common spatial resolution and data format for use in impact modelling.

To assess how each environmental factor contributed to the different BRT models, we computed their relative importance (RI) in those models and their response curves showing how ecological suitability varies with one specific factor. RI values were obtained by evaluating the number of times a specific environmental factor was selected for splitting a tree, weighted by the squared improvement to the model as a result of each split, averaged over all trees[24]. For each environmental factor, the median RI value and 95% CI computed from all models either trained on past or present data are reported in Extended Data Table 4 (and species-specific RI values in both kinds of models are all reported in the GitHub repository of the present study). Although some differences can be noticed (for example, for the 'pastures and rangeland' environmental factor, with a median RI of 10.9 for the models trained on past data against a median RI of 17.7 for models trained on present-day data), both sets of median RI values still present highly similar trends as environmental factors follow almost exactly the same order when sorted by median RI value. Response curves for each tested environmental and climatic variable were obtained by computing the ecological suitability variation associated with one specific variable, whereas all others were kept constant at their mean value (see Extended Data Fig. 5 for the response curves obtained for the BRT models trained on present-day datasets).

Comparing past, present and future ecological suitability maps

To perform overall comparisons of past, present and future ecological suitability maps, we defined two distinct metrics computed for each pixel of the grid encompassing the study area: (1) the species richness index (SRI) defined as the local number of species associated with an ecological suitability higher than the median threshold value retrieved from the optimization step of the SI_{ppc} computed for each of ten ecological niche models trained on present-day data, hereafter referred to as the optimized SI_{ppc} threshold and (2) the ESI defined as the local mean ecological suitability averaged over species (ranging from 0 to 1).

To explore the potential impact associated with the projected evolution of particular environmental factors, we performed a principal component analysis (PCA) based on the EVDs computed for each species. In the resulting PCA, each point corresponds to a specific species whose position along the two first axes reported in Fig. 2 is defined by the different EVDs computed for that species and for each considered environmental variable. For a specific environmental factor, the EVD was computed as the difference between the averaged value of the environmental factor at the present time and in 2061–2080 under the SSP 3-6.0 trajectory. The EVD values were species-specific because, for a given species, we only considered the grid cells for which the ecological suitability is estimated to be higher than its optimized SI_{ppc} threshold value. We performed the PCA using the 'dudi.pca' function implemented in the R package 'ade4' and displayed the scatterplot of species dots obtained when reporting the two first axes of the resulting

PCA, along with the eigenvectors corresponding to the different environmental factors. Species dots were first coloured according to a metric of ESD, defined as the difference between the ecological suitability averaged over selected grids at present-day and in 2061–2080 under the same SSP 3-6.0 trajectory. As for the computation of the EVD metric, we only considered the grid cells for which the ecological suitability is estimated to be higher than its optimized SI_{ppc} threshold value. This first PCA visualization allowed an assessment of the link between EVDs and the gain/loss of ecologically suitable areas. We also reported Spearman correlation coefficients computed between EVD and ESD values (Fig. 2b).

In a second graph, species dots of the same PCA were coloured according to the IUCN red list categories ('Least Concern', 'Vulnerable' and 'Near Threatened'), which allowed a visual assessment of the association between EVDs and the current conservation status of each species (Fig. 2a). In addition to the visualization through the PCA, we also performed a Kruskal–Wallis test to assess if some ESD variability among species could be significantly associated with their present IUCN status.

Finally, we also computed an ecological suitability ratio (ESR) metric defined as the ratio between the number of grid cells ecologically suitable in 2061–2080 under each trajectory considered in the study (SSP 1-2.6, 3-6.5 and 5-8.5) and at present-day (Extended Data Table 3). We again defined a grid cell as ecologically suitable if associated with an ecological suitability value higher than the optimized SI_{ppc} threshold value obtained for the considered species. For the different analyses described above, the EVD, ESD and ESR metrics were all averaged over the estimates obtained for the four climate models considered in the present study.

Acknowledging uncertainties in species distribution models

In the realm of scientific research, every model is inherently a representation based on the available data and any future prediction naturally carries limitations in terms of interpretation. Here, we addressed the uncertainties pertaining to the fate of the studied European bumblebee species by two means.

First, we selected three scenarios of climate forcing based on three distinct trajectories to avoid potential pitfalls of relying solely on a single trajectory. The ecological response of our species is expected to partly depend on the climate trajectories and implied radiative forcing at the end of the century but the magnitude of this forcing is still unknown as it will depend on societal choices. By using several RCPs corresponding to three potential societal evolutions, we can provide a range (and not a single estimate) of ecological responses that include 'best-case' and 'worst-case' scenarios. Depending on the trajectory considered, up to 76% of the studied species now considered as 'Least Concern' (37 of 46) could lose 30% of suitable habitat based on our ESR metric.

Quantifying the predictive performance of our models when projected onto time periods for which occurrence data are available was a second way to acknowledge the uncertainties associated with our study (Extended Data Table 2). As detailed above, we only measure a median SI_{ppc} decrease of 0.09 (95% CI = [−0.09, 0.31]) when evaluating models trained on present data and then projected on past data. This decrease, however, illustrates the additional uncertainty that can be expected when projecting our present-day ecological niche models on environmental conditions of other time periods and that projections of our models on future environmental conditions should then be interpreted with caution.

Overall, the objective of this work is to assess continental-scale, rather than fine-scale, changes in ecological suitability for bumblebees given several scenarios of global change. The results of this study should therefore be seen as a large-scale warning of what could be expected in the absence of drastic societal efforts to reduce human imprint on the global climates and ecosystems.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Bombus occurrence data are available on Atlas Hymenoptera: http://www.atlashymenoptera.net/page.aspx?id=169). All ISIMIP2b data used are publicly available on https://www.isimip.org/protocol/2b/.

Code availability

R scripts related to the ecological niche modelling and projections are all available at https://github.com/sdellicour/projections_bombus.

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Competing interests The authors declare no competing interests.

Additional information

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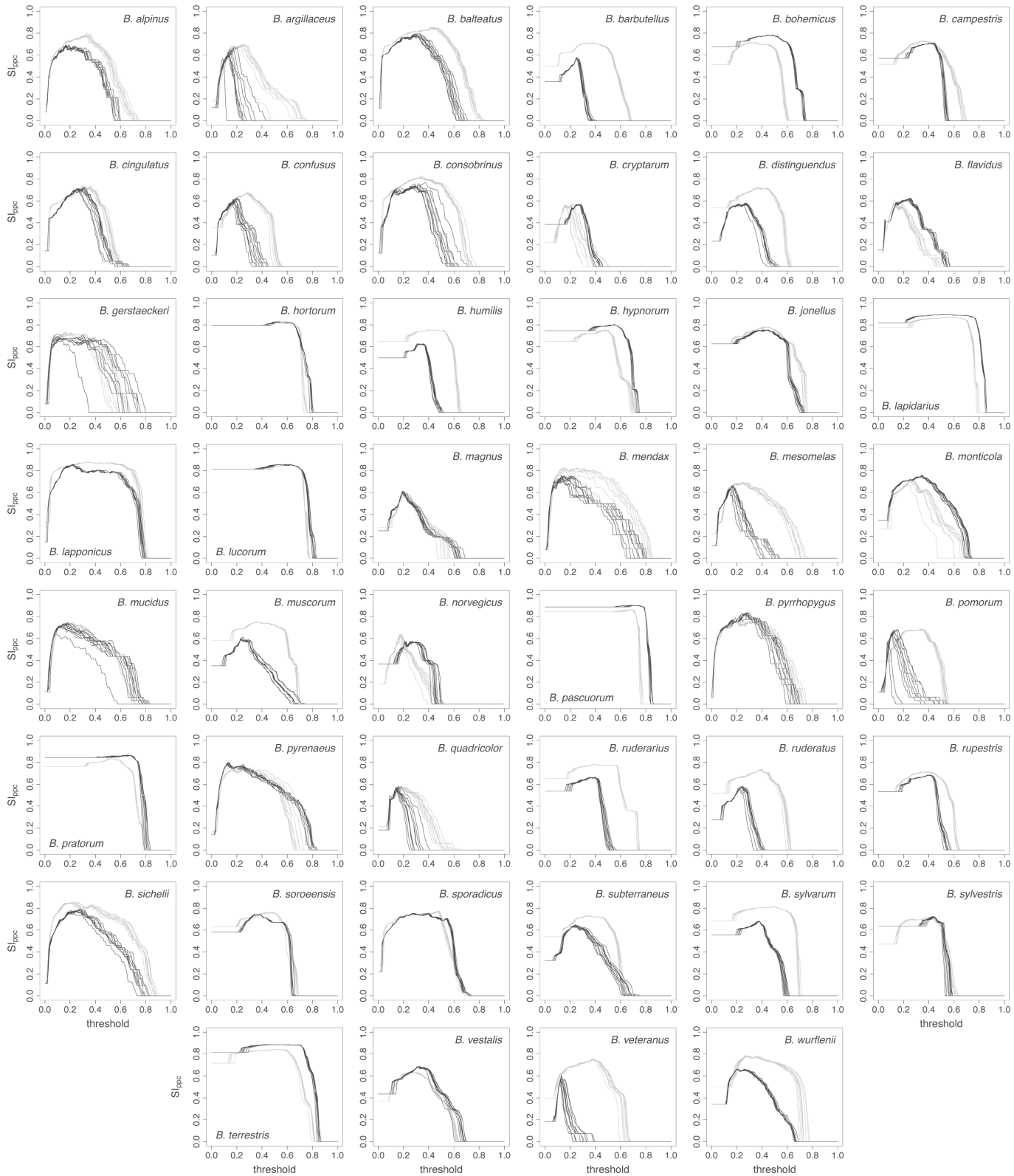
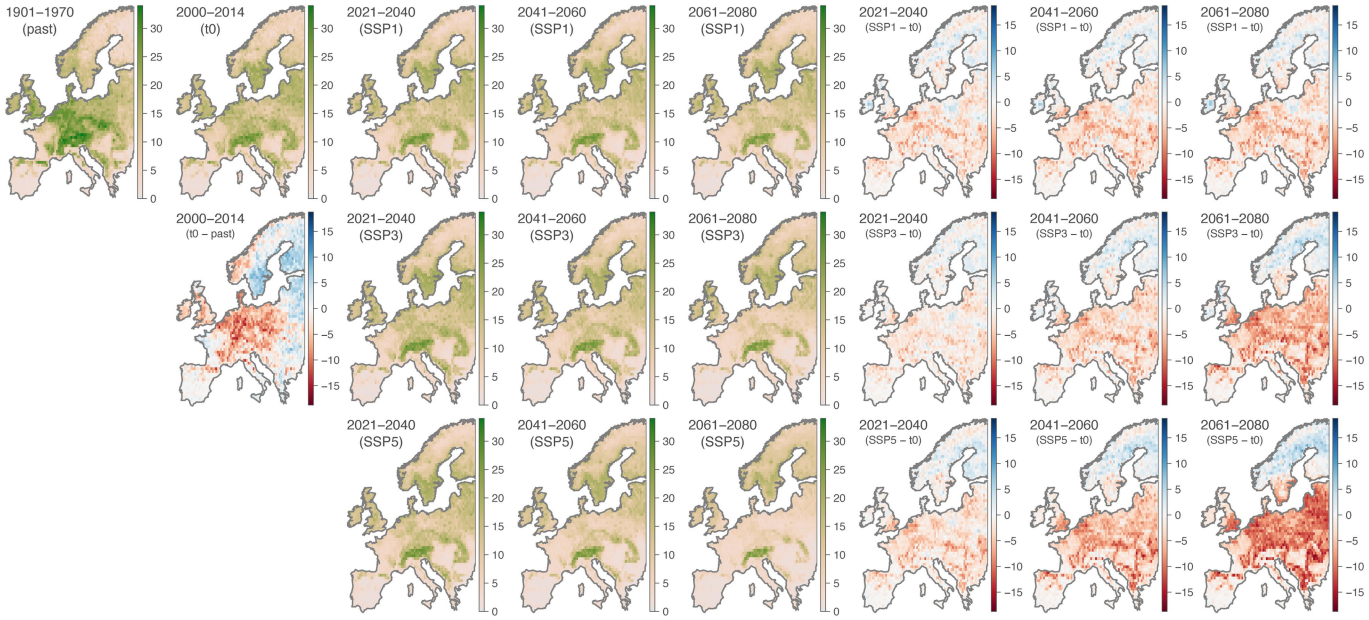


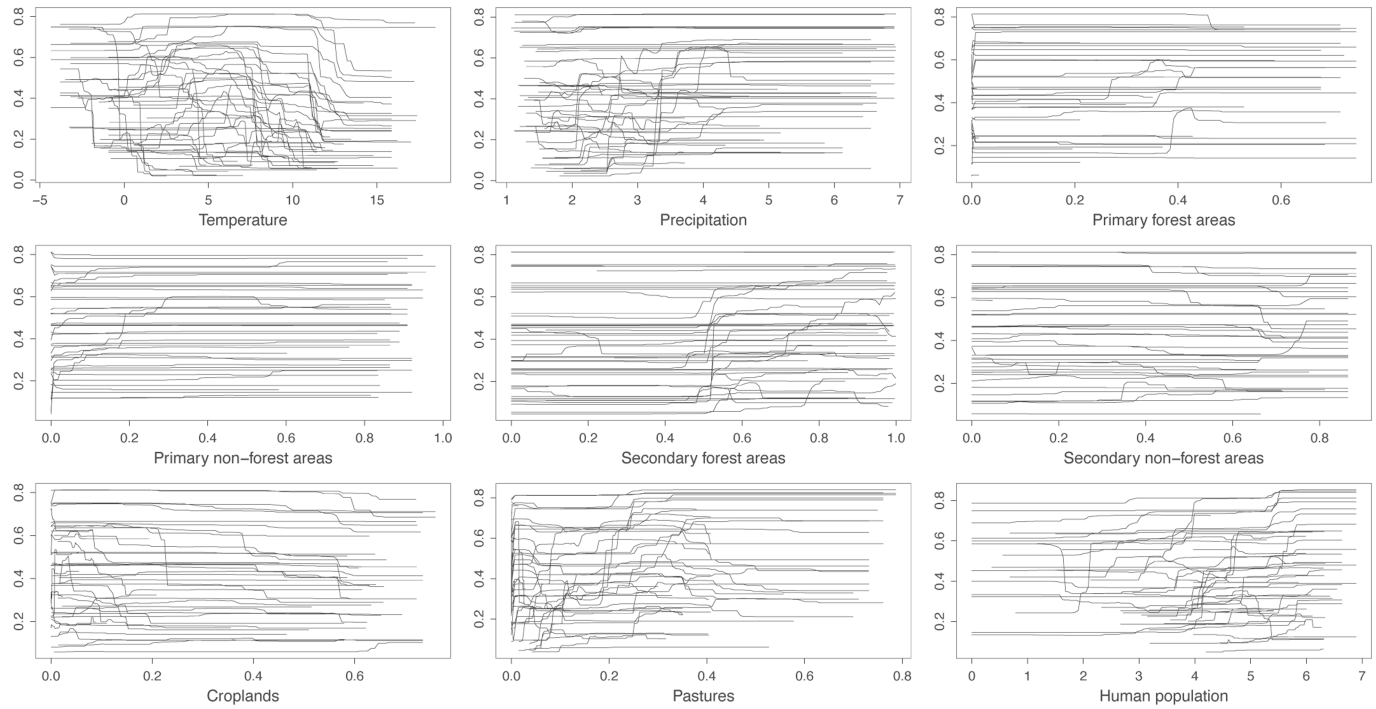
Extended Data Fig. 1 | Assessment of the predictive performance of species-specific ecological niche models trained on past (1901–1970) and present-day (2000–2014) occurrence and environmental data. Specifically, we computed the prevalence-pseudoabsence-calibrated Sørensen index (SI_{ppc}) while performing an optimization of the ecological suitability threshold in the range [0, 1] with a 0.01 step increment. This threshold value was used to generate binary versions of the ecological suitability maps necessary for the computation of this index and we eventually selected the threshold value maximizing the SI_{ppc} (see Extended Data Table 1 for the optimized SI_{ppc} values and associated threshold). We here report the evolution of the SI_{ppc} according to the considered ecological suitability threshold value. We report this relationship for each species and for each ecological niche model trained on past (light grey curves) and present-day (dark grey curves) data.



Extended Data Fig. 2 | Evolution of the ecological suitability map of European bumblebees as measured by the species richness index (SRI). The SRI is here defined as the local number of species associated with an ecological suitability higher than the median threshold value retrieved from the optimization step of the prevalence-pseudoabsence-calibrated Sørensen index (SI_{ppc}) computed for each of ten ecological niche models trained on present-day data (see the Methods for further detail). We here report the SRI estimates for the past, present ('t0') and future projections, as well as the differences between past, present ('t0') and future projections.

Extended Data Fig. 3 | Occurrence data available for the 46 selected European bumblebee species for the first time period (1901–1974). Duplicate records were removed to reflect species presence rather than species density and to further decrease potential sampling biases. All species distributions are represented by at least 30 unique data records. A total of 125,283 unique records were retained for this time period.

Extended Data Fig. 4 | Occurrence data available for the 46 selected European bumblebee species for the second time period (2000–2014). Duplicate records were removed to reflect species presence rather than species density and to further decrease potential sampling biases. All species distributions are represented by at least 30 unique data records. A total of 275,763 unique records were retained for this time period.



Extended Data Fig. 5 | Response curves associated with the different environmental variables included in the ecological niche models. Each curve was retrieved from a boosted regression tree (BRT) model trained for a distinct species on present-day (2000–2014) occurrence data.

Extended Data Table 1 | Assessment of the predictive performance of species-specific ecological niche models trained on past (1901–1970) and present-day (2000–2014) occurrence and environmental data

	1901-1970 ecological niche models		2000-2014 ecological niche models	
Species	SI_{ppc}	Optimised thres.	SI_{ppc}	Optimised thres.
B. alpinus	0.78 [0.77-0.80]	0.32 [0.31-0.36]	0.69 [0.67-0.70]	0.17 [0.15-0.19]
B. argillaceus	0.69 [0.64-0.70]	0.24 [0.17-0.25]	0.63 [0.57-0.68]	0.14 [0.09-0.18]
B. balteatus	0.85 [0.85-0.86]	0.42 [0.41-0.46]	0.78 [0.77-0.80]	0.29 [0.27-0.33]
B. barbutellus	0.71 [0.71-0.71]	0.32 [0.31-0.38]	0.57 [0.56-0.58]	0.25 [0.25-0.26]
B. bohemicus	0.72 [0.71-0.72]	0.30 [0.30-0.34]	0.78 [0.78-0.78]	0.46 [0.44-0.48]
B. campestris	0.73 [0.73-0.73]	0.34 [0.34-0.37]	0.71 [0.71-0.71]	0.44 [0.42-0.44]
B. cingulatus	0.73 [0.73-0.74]	0.30 [0.29-0.36]	0.71 [0.70-0.72]	0.28 [0.23-0.32]
B. confusus	0.67 [0.66-0.68]	0.28 [0.28-0.29]	0.61 [0.58-0.63]	0.18 [0.16-0.21]
B. consobrinus	0.81 [0.81-0.82]	0.34 [0.33-0.35]	0.73 [0.72-0.77]	0.29 [0.25-0.37]
B. cryptarum	0.56 [0.54-0.57]	0.17 [0.15-0.22]	0.57 [0.56-0.57]	0.27 [0.25-0.29]
B. distinguendus	0.72 [0.71-0.72]	0.37 [0.36-0.39]	0.57 [0.57-0.58]	0.27 [0.25-0.28]
B. flavidus	0.58 [0.57-0.61]	0.12 [0.12-0.14]	0.62 [0.61-0.62]	0.24 [0.23-0.26]
B. gerstaeckeri	0.72 [0.71-0.74]	0.17 [0.14-0.20]	0.68 [0.66-0.71]	0.11 [0.08-0.25]
B. hortorum	0.83 [0.83-0.83]	0.59 [0.57-0.59]	0.83 [0.83-0.83]	0.52 [0.51-0.53]
B. humilis	0.75 [0.75-0.75]	0.41 [0.39-0.42]	0.63 [0.62-0.63]	0.34 [0.31-0.36]
B. hypnorum	0.75 [0.75-0.75]	0.48 [0.47-0.50]	0.80 [0.80-0.80]	0.55 [0.53-0.55]
B. jonellus	0.78 [0.78-0.78]	0.42 [0.41-0.45]	0.75 [0.75-0.76]	0.44 [0.41-0.45]
B. lapidarius	0.87 [0.87-0.87]	0.54 [0.53-0.59]	0.90 [0.89-0.90]	0.54 [0.52-0.55]
B. lapponicus	0.88 [0.88-0.88]	0.34 [0.33-0.35]	0.85 [0.85-0.86]	0.22 [0.21-0.23]
B. lucorum	0.85 [0.85-0.85]	0.58 [0.58-0.60]	0.86 [0.85-0.86]	0.54 [0.53-0.59]
B. magnus	0.58 [0.58-0.59]	0.22 [0.21-0.23]	0.60 [0.59-0.61]	0.19 [0.19-0.20]
B. mendax	0.81 [0.76-0.83]	0.16 [0.12-0.25]	0.74 [0.73-0.76]	0.14 [0.11-0.21]
B. mesomelas	0.69 [0.68-0.70]	0.24 [0.19-0.25]	0.65 [0.63-0.66]	0.16 [0.13-0.17]
B. monticola	0.71 [0.68-0.72]	0.25 [0.23-0.28]	0.75 [0.74-0.76]	0.35 [0.33-0.35]
B. mucidus	0.73 [0.73-0.75]	0.18 [0.16-0.23]	0.73 [0.64-0.75]	0.16 [0.09-0.21]
B. muscorum	0.75 [0.75-0.75]	0.37 [0.37-0.38]	0.59 [0.59-0.61]	0.24 [0.23-0.25]
B. norvegicus	0.63 [0.62-0.64]	0.17 [0.16-0.18]	0.57 [0.56-0.58]	0.22 [0.21-0.31]
B. pascuorum	0.86 [0.86-0.86]	0.69 [0.66-0.70]	0.90 [0.90-0.90]	0.69 [0.67-0.72]
B. pyrrhopygus	0.77 [0.76-0.78]	0.18 [0.15-0.32]	0.83 [0.81-0.84]	0.26 [0.23-0.30]
B. pomorum	0.68 [0.67-0.69]	0.33 [0.32-0.34]	0.66 [0.57-0.68]	0.12 [0.07-0.15]
B. pratorum	0.83 [0.83-0.84]	0.51 [0.51-0.52]	0.87 [0.86-0.87]	0.66 [0.65-0.68]
B. pyrenaeus	0.74 [0.73-0.75]	0.28 [0.16-0.30]	0.80 [0.78-0.80]	0.13 [0.12-0.14]
B. quadricolor	0.57 [0.57-0.58]	0.17 [0.17-0.21]	0.57 [0.56-0.58]	0.15 [0.14-0.18]
B. ruderarius	0.78 [0.78-0.78]	0.40 [0.39-0.40]	0.66 [0.66-0.67]	0.40 [0.36-0.40]
B. ruderatus	0.73 [0.73-0.74]	0.39 [0.38-0.40]	0.57 [0.55-0.58]	0.24 [0.21-0.25]
B. rupestris	0.72 [0.71-0.72]	0.35 [0.35-0.41]	0.68 [0.68-0.69]	0.40 [0.39-0.41]
B. sichelii	0.85 [0.84-0.86]	0.21 [0.19-0.22]	0.78 [0.75-0.79]	0.24 [0.21-0.30]
B. soroeensis	0.76 [0.76-0.76]	0.48 [0.47-0.49]	0.74 [0.74-0.75]	0.38 [0.34-0.39]
B. sporadicus	0.77 [0.77-0.78]	0.48 [0.47-0.48]	0.75 [0.75-0.76]	0.29 [0.27-0.40]
B. subterraneus	0.73 [0.73-0.73]	0.35 [0.33-0.35]	0.64 [0.63-0.65]	0.24 [0.22-0.25]
B. sylvarum	0.81 [0.81-0.82]	0.49 [0.49-0.50]	0.68 [0.68-0.68]	0.38 [0.37-0.38]
B. sylvestris	0.71 [0.71-0.72]	0.40 [0.39-0.44]	0.72 [0.72-0.73]	0.44 [0.43-0.45]
B. terrestris	0.84 [0.84-0.84]	0.52 [0.48-0.56]	0.89 [0.89-0.89]	0.45 [0.44-0.50]
B. vestalis	0.63 [0.63-0.64]	0.27 [0.27-0.31]	0.69 [0.68-0.69]	0.31 [0.31-0.33]
B. veteranus	0.76 [0.75-0.76]	0.38 [0.37-0.39]	0.56 [0.53-0.61]	0.12 [0.12-0.13]
B. wurflenii	0.78 [0.78-0.79]	0.28 [0.27-0.29]	0.66 [0.66-0.67]	0.21 [0.20-0.26]

We computed the prevalence-pseudoabsence-calibrated Sørensen index (SI_{ppc}) while performing an optimization of the ecological suitability threshold ('thres.') in the range [0, 1] with a 0.01 step increment. This threshold value was used to generate binary versions of the ecological suitability maps necessary for the computation of this index and we selected the threshold value maximizing the SI_{ppc}. We computed a SI_{ppc} for each of the ten independent ecological niche models trained for each species and for each period and here report the resulting median [as well as minimum and maximum] values (see also Extended Data Fig. 1 for the evolution of SI_{ppc} values according to the considered threshold values).

Extended Data Table 2 | Assessment of the predictive performance of ecological niche models to predict present and past ecological suitability maps

	1901-1970 ecological niche models		2000-2014 ecological niche models	
Species	SI_{ppc}	Optimised thres.	SI_{ppc}	Optimised thres.
B. alpinus	0.48 [0.48-0.49]	0.14 [0.14-0.15]	0.54 [0.53-0.55]	0.08 [0.08-0.09]
B. argillaceus	0.36 [0.33-0.36]	0.13 [0.12-0.25]	0.42 [0.40-0.43]	0.11 [0.08-0.12]
B. balteatus	0.58 [0.56-0.59]	0.05 [0.05-0.06]	0.66 [0.66-0.67]	0.26 [0.21-0.28]
B. barbutellus	0.43 [0.43-0.43]	0.13 [0.13-0.17]	0.62 [0.62-0.62]	0.20 [0.19-0.21]
B. bohemicus	0.74 [0.74-0.74]	0.16 [0.16-0.17]	0.60 [0.60-0.60]	0.46 [0.46-0.51]
B. campestris	0.62 [0.61-0.62]	0.16 [0.15-0.27]	0.62 [0.62-0.62]	0.38 [0.29-0.40]
B. cingulatus	0.45 [0.45-0.46]	0.05 [0.05-0.19]	0.57 [0.57-0.57]	0.13 [0.12-0.13]
B. confusus	0.21 [0.21-0.22]	0.21 [0.21-0.22]	0.43 [0.42-0.48]	0.05 [0.04-0.05]
B. consobrinus	0.52 [0.52-0.52]	0.41 [0.37-0.43]	0.65 [0.65-0.67]	0.13 [0.11-0.15]
B. cryptarum	0.39 [0.39-0.40]	0.09 [0.00-0.10]	0.30 [0.29-0.30]	0.26 [0.23-0.27]
B. distinguendus	0.34 [0.34-0.34]	0.40 [0.27-0.42]	0.66 [0.66-0.67]	0.10 [0.09-0.10]
B. flavidus	0.38 [0.37-0.38]	0.08 [0.07-0.08]	0.30 [0.30-0.31]	0.06 [0.05-0.06]
B. gerstaeckeri	0.50 [0.48-0.51]	0.11 [0.07-0.11]	0.48 [0.47-0.48]	0.15 [0.07-0.17]
B. hortorum	0.81 [0.81-0.81]	0.50 [0.48-0.52]	0.80 [0.80-0.81]	0.46 [0.45-0.49]
B. humilis	0.58 [0.58-0.58]	0.38 [0.38-0.39]	0.73 [0.73-0.73]	0.30 [0.30-0.30]
B. hypnorum	0.77 [0.77-0.78]	0.28 [0.27-0.29]	0.72 [0.71-0.72]	0.55 [0.53-0.55]
B. jonellus	0.69 [0.68-0.69]	0.29 [0.20-0.30]	0.71 [0.71-0.71]	0.37 [0.36-0.38]
B. lapidarius	0.88 [0.88-0.88]	0.58 [0.56-0.59]	0.85 [0.85-0.85]	0.51 [0.50-0.53]
B. lapponicus	0.61 [0.61-0.61]	0.14 [0.13-0.14]	0.79 [0.79-0.80]	0.08 [0.08-0.09]
B. lucorum	0.82 [0.82-0.82]	0.50 [0.49-0.52]	0.83 [0.83-0.83]	0.50 [0.50-0.53]
B. magnus	0.44 [0.43-0.44]	0.22 [0.20-0.23]	0.45 [0.44-0.46]	0.17 [0.17-0.19]
B. mendax	0.56 [0.49-0.56]	0.24 [0.11-0.27]	0.61 [0.57-0.64]	0.05 [0.04-0.06]
B. mesomelas	0.48 [0.48-0.49]	0.29 [0.23-0.38]	0.53 [0.46-0.54]	0.05 [0.05-0.06]
B. monticola	0.61 [0.60-0.61]	0.15 [0.12-0.15]	0.54 [0.54-0.55]	0.36 [0.33-0.37]
B. mucidus	0.55 [0.55-0.56]	0.21 [0.18-0.22]	0.55 [0.53-0.57]	0.08 [0.07-0.09]
B. muscorum	0.48 [0.48-0.48]	0.36 [0.34-0.36]	0.68 [0.68-0.68]	0.12 [0.11-0.14]
B. norvegicus	0.38 [0.38-0.38]	0.07 [0.06-0.08]	0.24 [0.23-0.25]	0.19 [0.18-0.21]
B. pascuorum	0.89 [0.89-0.89]	0.61 [0.59-0.66]	0.85 [0.84-0.85]	0.64 [0.58-0.70]
B. pyrrhopygus	0.52 [0.50-0.53]	0.09 [0.09-0.10]	0.58 [0.58-0.59]	0.26 [0.22-0.27]
B. pomorum	0.26 [0.25-0.27]	0.36 [0.36-0.37]	0.54 [0.53-0.55]	0.06 [0.06-0.07]
B. pratorum	0.86 [0.85-0.86]	0.34 [0.33-0.35]	0.79 [0.79-0.79]	0.62 [0.60-0.67]
B. pyrenaeus	0.60 [0.59-0.61]	0.31 [0.29-0.33]	0.69 [0.68-0.70]	0.13 [0.12-0.14]
B. quadricolor	0.24 [0.23-0.24]	0.11 [0.09-0.15]	0.33 [0.32-0.34]	0.12 [0.11-0.12]
B. ruderarius	0.63 [0.63-0.63]	0.30 [0.30-0.31]	0.75 [0.75-0.75]	0.31 [0.29-0.32]
B. ruderatus	0.41 [0.41-0.42]	0.43 [0.38-0.44]	0.64 [0.64-0.65]	0.10 [0.08-0.11]
B. rupestris	0.60 [0.60-0.60]	0.21 [0.21-0.22]	0.64 [0.64-0.64]	0.28 [0.26-0.29]
B. sichelii	0.55 [0.52-0.55]	0.18 [0.17-0.41]	0.58 [0.58-0.59]	0.07 [0.06-0.07]
B. soroeensis	0.67 [0.66-0.67]	0.45 [0.44-0.45]	0.69 [0.69-0.69]	0.26 [0.26-0.27]
B. sporadicus	0.64 [0.64-0.64]	0.39 [0.38-0.40]	0.64 [0.64-0.64]	0.11 [0.10-0.11]
B. subterraneus	0.49 [0.49-0.50]	0.36 [0.36-0.39]	0.65 [0.64-0.66]	0.14 [0.13-0.16]
B. sylvarum	0.63 [0.63-0.64]	0.35 [0.34-0.36]	0.76 [0.76-0.77]	0.31 [0.30-0.32]
B. sylvestris	0.66 [0.65-0.66]	0.16 [0.15-0.18]	0.62 [0.62-0.63]	0.46 [0.46-0.47]
B. terrestris	0.87 [0.87-0.87]	0.22 [0.21-0.25]	0.81 [0.81-0.82]	0.61 [0.60-0.64]
B. vestalis	0.58 [0.58-0.59]	0.16 [0.16-0.18]	0.54 [0.53-0.54]	0.30 [0.26-0.32]
B. veteranus	0.32 [0.31-0.33]	0.30 [0.25-0.32]	0.59 [0.56-0.60]	0.10 [0.10-0.10]
B. wurflenii	0.53 [0.52-0.53]	0.32 [0.28-0.37]	0.67 [0.67-0.68]	0.16 [0.15-0.17]

We assessed (i) the performance of ecological niche models trained on past (1901–1970) occurrence and environmental data to predict present-day (2000–2014) distribution of occurrence records given present-day environmental conditions and (ii) the performance of ecological niche models trained on present-day occurrence and environmental data to predict past distribution of occurrence records given past environmental conditions. Specifically, we computed a pseudoabsence-calibrated Sørensen index (SI_{ppc}) for each of the ten independent ecological niche models trained for each species and report the resulting median [as well as minimum and maximum] values. Each SI_{ppc} was computed while performing an optimization of the ecological suitability threshold ('thres.') in the range [0, 1] with a 0.01 step increment. This threshold value was used to generate binary versions of the ecological suitability maps necessary for the computation of this index and we selected the threshold value maximizing the SI_{ppc}.

Extended Data Table 3 | Projection of the ecological suitability change between the present time and 2061–2080

Species	IUCN status	SSP1-2.6	SSP3-6.0	SSP5-8.5
B. alpinus	vulnerable	0.38 [0.18-0.60]	0.11 [0.04-0.19]	0.08 [0.03-0.20]
B. argillaceus	least concern	0.50 [0.45-0.57]	0.53 [0.46-0.63]	0.52 [0.48-0.60]
B. balteatus	least concern	0.55 [0.45-0.64]	0.37 [0.22-0.48]	0.31 [0.23-0.47]
B. barbutellus	least concern	0.61 [0.52-0.73]	0.56 [0.33-0.77]	0.30 [0.15-0.64]
B. bohemicus	least concern	0.68 [0.59-0.84]	0.65 [0.46-0.85]	0.45 [0.33-0.71]
B. campestris	least concern	0.81 [0.71-0.94]	0.59 [0.40-0.78]	0.40 [0.26-0.69]
B. cingulatus	least concern	0.51 [0.42-0.56]	0.59 [0.35-0.71]	0.27 [0.01-0.51]
B. confusus	vulnerable	1.18 [0.95-1.41]	1.10 [0.56-1.68]	0.41 [0.05-1.23]
B. consobrinus	least concern	0.79 [0.70-0.94]	0.52 [0.32-0.82]	0.40 [0.13-0.80]
B. cryptarum	least concern	0.32 [0.26-0.45]	0.25 [0.21-0.30]	0.26 [0.24-0.31]
B. distinguendus	vulnerable	0.35 [0.23-0.51]	0.05 [0.00-0.13]	0.02 [0.00-0.07]
B. flavidus	least concern	0.38 [0.16-0.52]	0.17 [0.03-0.32]	0.08 [0.01-0.25]
B. gerstaeckeri	vulnerable	0.96 [0.80-1.26]	0.86 [0.64-1.14]	0.58 [0.36-0.80]
B. hortorum	least concern	0.93 [0.88-0.99]	0.87 [0.72-0.96]	0.69 [0.54-0.90]
B. humilis	least concern	0.79 [0.72-0.91]	0.69 [0.46-0.87]	0.45 [0.26-0.77]
B. hypnorum	least concern	0.96 [0.88-1.08]	0.73 [0.57-0.90]	0.55 [0.45-0.76]
B. jonellus	least concern	0.83 [0.81-0.89]	0.73 [0.68-0.79]	0.68 [0.60-0.80]
B. lapidarius	least concern	0.94 [0.89-1.00]	0.85 [0.67-0.96]	0.65 [0.45-0.89]
B. lapponicus	least concern	0.45 [0.16-0.71]	0.19 [0.04-0.35]	0.10 [0.01-0.31]
B. lucorum	least concern	0.90 [0.83-1.00]	0.77 [0.59-0.96]	0.58 [0.45-0.85]
B. magnus	least concern	0.71 [0.64-0.76]	0.76 [0.71-0.84]	0.97 [0.92-1.04]
B. mendax	near threatened	0.66 [0.62-0.73]	0.75 [0.65-0.83]	0.70 [0.62-0.83]
B. mesomelas	least concern	0.96 [0.86-1.10]	0.72 [0.63-0.81]	0.64 [0.53-0.76]
B. monticola	least concern	0.56 [0.39-0.70]	0.40 [0.29-0.55]	0.34 [0.23-0.55]
B. mucidus	near threatened	0.66 [0.61-0.72]	0.65 [0.59-0.72]	0.61 [0.52-0.80]
B. muscorum	vulnerable	1.04 [1.00-1.08]	0.87 [0.70-0.99]	0.77 [0.68-0.93]
B. norvegicus	least concern	1.05 [0.94-1.18]	0.89 [0.83-0.99]	0.83 [0.81-0.84]
B. pascuorum	least concern	1.00 [0.97-1.03]	0.99 [0.98-1.01]	0.95 [0.92-0.98]
B. pyrrhopygus	vulnerable	0.32 [0.07-0.52]	0.07 [0.00-0.18]	0.04 [0.00-0.13]
B. pomorum	vulnerable	0.12 [0.05-0.19]	0.16 [0.03-0.44]	0.06 [0.01-0.19]
B. pratorum	least concern	0.96 [0.91-1.01]	0.89 [0.75-0.98]	0.71 [0.55-0.93]
B. pyrenaeus	least concern	0.52 [0.41-0.67]	0.44 [0.30-0.60]	0.28 [0.17-0.42]
B. quadricolor	least concern	0.30 [0.25-0.40]	0.19 [0.10-0.30]	0.11 [0.03-0.25]
B. ruderarius	least concern	0.84 [0.75-0.99]	0.60 [0.36-0.86]	0.34 [0.18-0.71]
B. ruderatus	least concern	1.13 [0.93-1.26]	1.47 [1.07-2.00]	2.16 [1.35-2.47]
B. rupestris	least concern	0.80 [0.69-0.97]	0.56 [0.30-0.84]	0.29 [0.14-0.62]
B. sichelii	least concern	0.71 [0.67-0.74]	0.56 [0.48-0.63]	0.60 [0.51-0.68]
B. soroeensis	least concern	0.88 [0.76-1.00]	0.80 [0.68-0.89]	0.70 [0.62-0.81]
B. sporadicus	least concern	0.92 [0.78-1.00]	0.67 [0.43-0.90]	0.37 [0.07-0.76]
B. subterraneus	least concern	0.63 [0.54-0.76]	0.40 [0.24-0.63]	0.21 [0.08-0.47]
B. sylvarum	least concern	0.99 [0.94-1.07]	0.87 [0.68-1.02]	0.60 [0.47-0.84]
B. sylvestris	least concern	1.04 [0.93-1.15]	0.89 [0.66-1.04]	0.72 [0.49-0.95]
B. terrestris	least concern	1.04 [1.02-1.06]	1.09 [1.07-1.11]	1.13 [1.08-1.19]
B. vestalis	least concern	0.54 [0.52-0.56]	0.68 [0.55-0.77]	0.63 [0.53-0.78]
B. veteranus	least concern	0.68 [0.62-0.85]	0.29 [0.20-0.41]	0.19 [0.16-0.26]
B. wurflenii	least concern	1.01 [0.80-1.32]	0.93 [0.64-1.26]	0.76 [0.47-1.10]

We here report an ecological suitability ratio (ESR) metric defined as the ratio between the number of grid cells ecologically suitable in 2061–2080 under each trajectory considered in the study (SSP1-2.6, SSP3-6.5 and SSP5-8.5) and at present-day. Because the threshold value above which a grid cell is considered as ecologically suitable remains arbitrary, we considered for each species the threshold value optimizing the prevalence-pseudoabsence-calibrated Sørensen index (SI_{ppc}) for the ecological niche models trained on present-day data, i.e. the respective median SI_{ppc} value reported in Extended Data Table 1 for the '2000–2014 ecological niche models'. ESR values were averaged over the estimates obtained for the four climate models considered and the present study and we also report under brackets the minimum and maximum ESR values obtained with those different models.

Extended Data Table 4 | Relative importance (RI) of the different environmental factors in the ecological niche models either trained on past (1901–1970) or present-day (2000–2014) occurrence and environmental data

Environmental factor	RI 1901-1970	RI 2000-2014
Air temperature	29.1 [9.4-61.2]	34.2 [8.2-76.3]
Precipitation	8.8 [1.1-48.8]	5.1 [0.5-25.2]
Forested primary land	5.2 [0.2-60.0]	2.0 [0.2-17.9]
Non-forested primary land	1.4 [0.0-12.1]	1.1 [0.0-16]
Forested secondary land	1.6 [0.1-18.1]	2.3 [0.0-19.4]
Non-forested secondary land	1.5 [0.0-27.0]	1.0 [0.0-10.1]
Croplands (all categories)	4.2 [1.1-23]	4.8 [0.7-14.3]
Pastures and rangeland	10.9 [1.3-31.9]	17.7 [3.3-44.8]
Human population (log_{10})	8.3 [0.9-56.4]	10.0 [2.3-45.7]

For each environmental factor, we report the median values as well as the 95% credible intervals based on the values obtained for all species.

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☐	☒ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We used bumblebee (Hymenoptera: Anthophila: Bombus) occurrence records that are available on the Atlas Hymenoptera website (http://www.atlashymenoptera.net/page.aspx?id=169), and all ISIMIP2b data used is publicly available on https://data.isimip.org/.
Data analysis	R scripts related to the ecological niche modelling and projections are all available at https://github.com/sdellicour/projections_bombus.

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Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

R scripts related to the ecological niche modelling and projections are all available at https://github.com/sdellicour/projections_bombus. Bombus occurrence data are available on the Atlas Hymenoptera website (http://www.atlashymenoptera.net/page.aspx?id=169). All ISIMIP2b data used is publicly available on https://data.isimip.org/.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	Not applicable to this study.
Population characteristics	Not applicable to this study.
Recruitment	Not applicable to this study.
Ethics oversight	Not applicable to this study.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We quantify the past, present and future ecological suitability of Europe for bumblebees, a threatened group of pollinators ranked among the highest contributors to crop production value in the northern hemisphere. We demonstrate coherent declines of bumblebee populations since 1900 over most of the European continent and identify future large-scale range contractions and species extirpations under all future climatic and land-use scenarios. 38–76% of European bumblebee species currently classified in non-threatened categories are projected to undergo losses of at least 30% of ecologically suitable territory by 2061-2080 compared to 2000-2014. All scenarios highlight that parts of Scandinavia will become potential refugia for European bumblebees, but it remains uncertain whether these areas will remain clear of additional anthropogenic stressors not considered in current models. Our results underline the critical role of climate change mitigation policies as effective levers to protect bumblebees from man-made transformation of the biosphere.
Research sample	Spatially-referenced occurrence records were used with the addition of new original data held in the database hosted at the University of Mons, available at http://www.atlashymenoptera.net/page.aspx?id=169. This large-scale dataset consists of geographically referenced occurrence data accumulated from published literature, as well as from bumblebee collections deposited in universities and museums. All these data were checked by expert entomologists to ensure their reliability and remove any record that could not be reconciled with comparisons of range maps published in the most up-to-date IUCN Red List Reports (http://www.iucnredlist.org/, accessed October 2022). Only records including both georeferencing and data information were retained.
Sampling strategy	We retained 46 bumblebee species. The final dataset contained a total of 401,046 unique occurrence records used species-specifically for the ecological niche modelling analyses.
Data collection	The referenced occurrence data was accumulated from published literature, as well as from bumblebee collections deposited in European universities and museums. Databasing was performed in the database Data Fauna Flora of the Laboratory of Zoology of the University of Mons.
Timing and spatial scale	Databasing of universities and museum collections started in 1989 by one of the authors (PR) and stopped in 2021.
Data exclusions	Only records including both georeferencing and data information were retained. We retained 46 species which had at least 30 unique occurrence records in both studied periods for ensuring the highest quality of our models.
Reproducibility	R scripts related to the ecological niche modelling and projections are all available at https://github.com/sdellicour/projections_bombus, which makes the study fully replicable. In addition, all Bombus occurrence data are available on the Atlas Hymenoptera website (http://www.atlashymenoptera.net/page.aspx?id=169) and can directly be imported in the R console. All ISIMIP2b data used is publicly available on https://data.isimip.org/.
Randomization	Not applicable to the study, as no groups needed to be formed as part of our modelling analyses.
Blinding	Not applicable to the study, as no blinding is needed for modelling analyses.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging