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Declines in European bumblebee habitat suitability attributable to climate change

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Climate change is increasingly implicated in the decline of insect pollinator populations, which provide critical ecosystem services. Isolating its contribution from other co-occurring environmental stresses remains challenging yet crucial for informing conservation strategies and mitigating biodiversity losses. Here we compare predictions of ecologically suitable areas for European bumblebee species from 1901 to 2019 under factual and counterfactual scenarios to evaluate whether climate change has led to a loss of suitable habitat. Community-level ecological suitability was reduced by climate change across Europe by 5% on average and up to 19% locally, with pronounced declines in southern and lowland central regions. By contrast, in the Alpine and Boreal regions, habitat suitability gains at higher altitudes partially offset losses at lower latitudes and altitudes, resulting in minimal net changes. Our results demonstrate that climate change is reshaping the ecologically suitable areas for these key pollinators and represents a pervasive pressure on European wildlife.

Global biodiversity loss is occurring at an unprecedented pace, with over one-fifth of all assessed plant and animal species now threatened by extinction[1]. This crisis stems from multiple, often interacting anthropogenic drivers, including habitat loss, overexploitation, pollution, invasive species and climate change[2]. As human pressure on ecosystems is set to continue, climate change is expected to become a dominant driver of biodiversity loss[3–6]. Since the beginning of the twentieth century, global mean surface temperatures have increased by over 1.2 °C (ref. 7) and are projected to rise by between 1.5 °C and 4.0 °C by 2100, depending on future greenhouse gas emission scenarios[8]. Beyond global warming, climate change alters precipitation regimes and increases both the intensity and frequency of extreme weather events such as floods, droughts, wildfires and heat waves[8–11]. These changes are reshaping biological communities by altering species distribution, abundance and diversity, raising global concerns about ecosystem resilience and human well-being[12,13]. Insects, critical providers of many ecosystem services, such as pest control and pollination[14], are expected to be rapidly impacted by climate change, given the sensitive thermal physiology and short life cycle of many species[15]. Regional studies have highlighted alarming rates of decline, with a decrease of flying insect biomass of 76% over 27 years in Germany's protected areas[16]. At a broader scale, authors have suggested that up to 40% of insect species could become extinct within the coming decades[17]. The decline of insect pollinator populations stands out given that almost 90% of wild plants and ~70% of major world-cultivated crops rely on animal pollination[18,19]. Yet, despite increasing research on the impact of climate change on wildlife, few studies have formally attributed observed biodiversity declines to climate change or quantified its contribution relative to other drivers.

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To address this issue, the Intergovernmental Panel on Climate Change presented an 'impact attribution' framework, enabling the separation of the impact of climate change from other concomitant drivers[20]. This approach compares the state of a natural, human, or managed system in the current climate with a counterfactual simulation representing a world without any long-term change in the climate, without disentangling the role of its underlying drivers[20,21]. Building on this framework, we aim to investigate to what extent climate change could have contributed to the population decline of European bumblebees (Apidae: *Bombus*). Bumblebees are a key group of pollinators in temperate and cold ecosystems, and a model group of invertebrates with long-term, reliable occurrence data available at a continental level[22–24]. In recent decades, widespread declines in bumblebee populations were documented across Europe, highlighting the urgency to evaluate the extent to which climate change has contributed to these trends[25–28]. Moreover, as predominantly cold-adapted species, bumblebees are particularly vulnerable to warming, positioning them as sentinel species to assess the impact of climate change on insect communities[23,29,30]. Using an ecological niche modelling approach, we here aim to compare historical climate and counterfactual scenarios to evaluate changes in areas ecologically suitable for European bumblebee species attributable to climate change, and assess how these effects vary among species and biogeographic regions.

Results

Species-specific ecological niche models were trained using a machine learning approach—boosted regression trees (BRT)—for 47 *Bombus* species based on georeferenced records across Europe for 2000–2019 (Supplementary Fig. 1). Environmental predictors included climatic, land-use and human population data at a resolution of 0.5 decimal degrees (Extended Data Fig. 1), all averaged over the same period of time, and retrieved from four historical climate reanalysis datasets (GSWP3-W5E5, 20CRv3, 20CRv3-ERA5 and 20CRv3-W5E5) available through the Inter-Sectoral Impact Model Intercomparison Project phase 3a (ISIMIP3a). The model output is an ecological suitability value ranging from 0 to 1, representing the degree to which local environmental conditions are favourable for the occurrence of a target species. Our model performance is high across species and reanalysis datasets, as indicated by both area under the receiver operating characteristic curve (AUC) and prevalence-pseudoabsence-calibrated Sørensen's index (SI_{ppc}) values (Extended Data Fig. 2; see the Methods for further details). Given that GSWP3-W5E5 serves as the ISIMIP3a reference dataset and W5E5 corresponds over land to ERA5 bias-adjusted using gridded station observations[31], we focused our analysis on the latter while treating the remaining datasets as robustness checks of our results. Models were projected to successive 20-year periods spanning from 1901 to 2019, under both factual and counterfactual scenarios. By subtracting the modelled ecological suitability values of the factual climate scenario from those of the counterfactual scenario, we obtain ecological suitability differences that reflect changes solely attributable to climate change.

To estimate the average change in ecological suitability at the community level, we estimated the evolution through time of the ecological suitability index (ESI) defined as the mean ecological suitability estimated across species at each grid cell. This metric declined by −5.2% on average across Europe between 1901–1919 and 2000–2019 owing to historical climate change, with local decreases (that is, decreases at the grid cell level) reaching −18.8% based on the GSWP3-W5E5 reanalysis dataset. This decrease was not linear in time and became especially marked after the 1980s (Fig. 1). Our results for other reanalysis datasets showed comparable magnitudes of ESI changes and spatial patterns. Across these datasets, the ESI decline attributable to climate change averaged between −4.1% and −6.2% and reached −14.7% to −17.8% locally (Extended Data Figs. 3–5). We also tested an alternative metric, the species richness index (SRI, defined as the number of species at each grid cell whose predicted ecological suitability exceeds the median SI_{ppc} threshold), and found spatiotemporal patterns consistent with those of the ESI (Supplementary Figs. 2–5).

To examine spatial heterogeneity beyond a continental perspective, we aggregated averaged changes in ecological suitability within European biogeographic regions (Extended Data Fig. 6), focusing on the Alpine, Atlantic, Boreal, Continental, Mediterranean and Pannonian regions as defined by the European Environment Agency[32]. This biogeographical aggregation revealed spatial heterogeneity in the impact of climate change on the European areas ecologically suitable for these bumblebee species. The Pannonian region experienced the steepest ESI decline related to climate change, decreasing on average by −16.3% under the GSWP3-W5E5 reanalysis dataset. ESI losses were also observed in the Atlantic (−6.2%), Continental (−7.8%) and Mediterranean (−9.5%) regions. By contrast, negligible ESI changes occurred in Boreal (~0.0%) and Alpine (+0.4%) regions, reflecting opposite local responses, with gains in some parts of Scandinavia and higher-altitude areas (for example, the Alps) offset by losses at lower-latitude or lower-altitude Alpine regions (for example, the Pyrenees or the Dinaric Alps; Fig. 1).

Species-specific responses to historical climate change varied widely, with average gains in ecological suitability ranging from +47.6% (*Bombus semenoviellus*) to −28.1% (*Bombus monticola*). Out of the 47 analysed species, 55% ($n = 26$) experienced a loss of ecological suitability related to climate change, while 45% ($n = 21$) showed an average gain. These proportions are consistent across reanalysis datasets (49–62% of species experiencing an ecological suitability loss), although the magnitude of species-specific change varies. Arctic or arcto-alpine species (for example, *B. alpinus*, *B. balteatus* and *B. lapponicus*) experienced a clear decrease in ecological suitability related to climate change. However, some high-elevation species exhibited increases in ecological suitability (for example, *B. mesomelas* and *B. mucidus*), while others showed inconsistent trends, with gains or losses depending on the considered reanalysis dataset (for example, *B. pyrenaeus* and *B. gerstaeckeri*). Several lowland species also underwent similar loss of ecological suitability related to climate change (for example, *B. jonellus*, *B. lucorum* and *B. pratorum*). By contrast, some species exhibited range-wide increases in ecological suitability under climate change (for example, *B. argillaceus* and *B. ruderatus*). For several other species (for example, *B. hypnorum* and *B. lapidarius*), the averaged gain of ecological suitability masked spatial heterogeneity with gains in northern or high-elevation areas but reductions elsewhere within their ranges (all species-specific projections under both scenarios are available in the GitHub repository of the present study; see also Extended Data Table 1 for the average changes in ecological suitability related to climate change for each species and reanalysis dataset).

We further assessed whether historical climate conditions improved the ability of species-specific ecological niche models to predict bumblebee occurrences compared with counterfactual scenarios. For each species, period and reanalysis dataset, we calculated differences in Boyce index (BI) between both scenarios and statistically assessed these differences. A significantly positive BI difference indicates better predictive performance for occurrence data in historical reanalysis datasets (see the Supplementary Information for further details). We found that BI differences increased over time (Supplementary Fig. 6), with an increasing proportion of species with significantly positive BI differences towards recent decades. By 2000–2019, 66% of species ($n = 31$ out of 47) showed significantly positive BI differences under the GSWP3-W5E5 reanalysis dataset (Supplementary Table 1), consistent with the signal observed for the ESI metric (Fig. 1). Although the magnitude of this effect varied among reanalysis datasets, a tendency of improved model performance under the historical climate change scenario was observed across datasets, suggesting an increasing influence of climate change in explaining the current distribution of European bumblebees.

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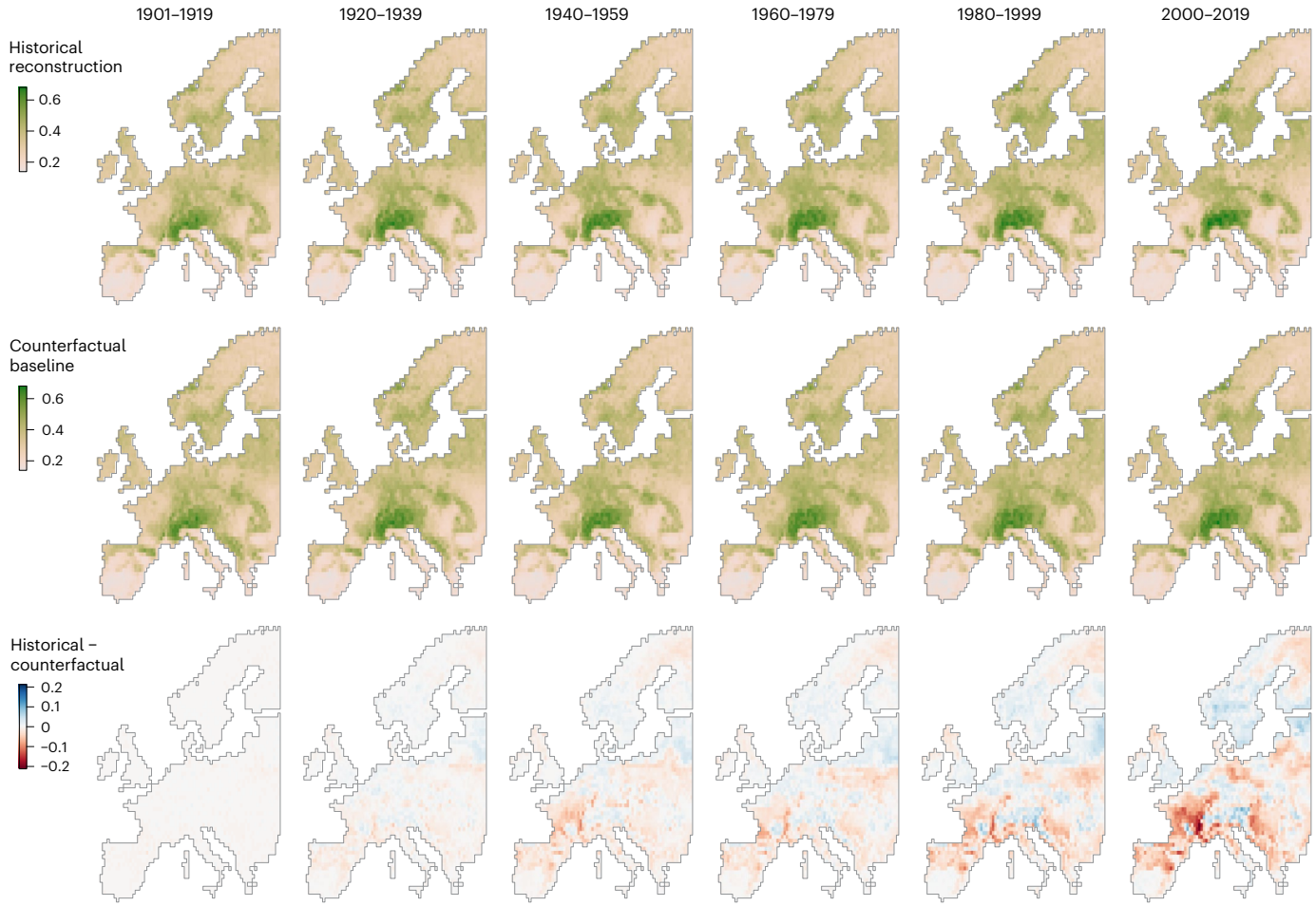

Fig. 1 | Evaluating the isolated impact of climate change on the European areas ecologically suitable for 47 bumblebee species. We report, for each period, the difference between bumblebee ecological suitability estimates based on (1) the reconstructions of the historical climate (top) and (2) a counterfactual baseline (middle). Bottom: maps reporting the difference, for each time period, between the two, that is, between the estimates based on the reconstructions of the historical climate and the counterfactual baseline. We focus on the ESI, defined as the local mean ecological suitability averaged over species (ranging from 0 to 1). The computation of the ESI metric was based on species-specific ecological suitability maps, which were obtained by averaging over the estimates of ten independent BRT models trained on present-day data retrieved from the ISIMIP3a reanalysis dataset GSWP3-W5E5. See Extended Data Figs. 3–5 for the corresponding results based on the three other ISIMIP3a reanalysis datasets—20CRv3, 20CRv3-ERA5 and 20CRv3-W5E5—considered in the present study. Basemap data from ISIMIP[69] under a Creative Commons license CC BY 4.0.

Discussion

Over the past few decades, Europe has experienced substantial warming[33], resulting in pronounced ecological consequences across multiple taxa. Here we provide a quantitative analysis assessing the contribution of climate change over the last century to the decline in areas ecologically suitable for European bumblebees. On average, climate change has contributed to making Europe less favourable to bumblebee species, with a marked decline in ecological suitability at the continental scale and even greater declines at the local scale. Furthermore, removing the climate change signal reduces the model predictive performances for the majority of the considered species, as indicated by BI estimates. These results highlight that climate change has already reshaped the present-day distribution of European bumblebees relative to a no-climate change baseline, and has contributed to a net contraction of ecological suitability areas at the continental scale. These findings are consistent with previous evidence linking climate change to declines and range contractions in North American bumblebee species, suggesting that the impacts of climate change may converge across continents[34,35].

Analysis by biogeographic regions revealed spatially uneven impacts of climate change on the European areas ecologically suitable for bumblebees, with stronger declines in more southern and central biogeographic regions, areas recognized as climate change hotspots[36,37]. The steepest decline observed in the Pannonian region aligns with evidence of declining abundance of bumblebee and other temperate-adapted insect species in the context of warming and drying trends in Central Europe[38,39]. Similarly, the Mediterranean and Continental regions experienced a decline in ecological suitability, consistent with increasing temperatures, more frequent droughts and heat extremes[37] known to negatively affect bumblebee populations[40]. The Atlantic region exhibits comparatively smaller declines in ecological suitability than the previously mentioned biogeoregions, although negative trends appear in our results. This smaller decrease may reflect the more moderate warming trends experienced there relative to southern and continental Europe[41], possibly due to its oceanic climate and the cooling influence of the North Atlantic warming hole[42]. Nevertheless, this biogeographic region is among the best studied in Europe, and previous studies report national decline of pollinators, primarily driven by historical agricultural changes[43,44]. Our results suggest that, in addition to these pressures, climate change has probably further reduced the ecological suitability of bumblebees in this region.

By contrast, Alpine and Boreal regions experienced no net change in ecological suitability when aggregated at the community level. This apparent stability does not indicate an absence of climate change influences, but results from spatially heterogeneous changes in the ESI, with increases in some areas (especially at the highest elevations and parts of Scandinavia) offset by decreases elsewhere. Ecological suitability gains at the community level in these biogeographic regions are consistent with previous empirical and model-based studies reporting losses at southern species' range margins and shifts towards higher-altitude areas[34,45,46]. However, our results also indicate ecological suitability losses in the Boreal and Alpine regions, especially in mountain ranges located at lower latitudes and elevations. This suggests that only part of these cooler and mountainous habitats are becoming more suitable under climate change, rather than a community-wide possibility for expansion across northern and mountain areas. Indeed, although some bumblebee species have shifted northwards and uphill in response to climate change, their northern and upper altitudinal range limits have not expanded accordingly, resulting in an overall range contraction[34,45,46]. Moreover, even when such poleward shifts occur, species may fail to track the pace of warming, accumulating a 'climatic debt' as observed in European birds and butterflies[47]. Thus, while some areas appear increasingly suitable under climate change, such ESI gains do not necessarily imply actual occupancy, as these newly suitable areas may be geographically unreachable and colonization depends on species' dispersal abilities.

Beyond these spatial considerations, a temporal signal emerged, with stronger ESI loss and greater BI divergence after the 1980s. This period also coincides with reported upward altitudinal shifts of several bumblebee species in southern European mountains[45,48] and a stronger rate of global warming in recent decades, linked to atmospheric circulation changes and decreasing aerosol emissions[8,49,50]. Yet, as warming continues, future projections under land-use and climate change scenarios point to further, more widespread losses of suitable habitat across Europe by the end of the century[23,30]. Using ecological niche models projected on future environmental conditions expected under distinct shared socioeconomic pathways, Ghisbain and colleagues[23] estimated that, under a high greenhouse gas emission scenario, up to 76% of investigated 'Least Concern' European bumblebee species may experience losses of ecologically suitable habitat of over 30% by the end of the century. In addition, several cold-adapted species may be extirpated in Europe over the same period of time[23]. Together, these findings reveal that the ecological impact of climate change on bumblebees is already underway and likely to intensify in the coming decades.

At the species level, responses to historical climate change are not uniform, and species restricted to the coldest areas emerged as particularly vulnerable to climate change. This follows previous evidence of high heat sensitivity in these species under simulated heatwaves[29,51]. Moreover, critical thermal limits estimated for three North American bumblebee species revealed that high-altitude species had lower heat tolerance than low-altitude ones[52]. Although Alpine and Boreal regions show no net change at the community level, strong declines in ecological suitability for montane and arctic/arcto-alpine species suggest a possibility of species turnover rather than stability in community composition. Montane species that do not show a consistent decline in ecological suitability, or even show an increase, inhabit South European mountains and may respond differently to warming trends, for example, through greater heat resistance (in *B. mesomelas*)[29]. Conversely, 38–51% of species (from 18 to 24 out of 47 species, depending on the reanalysis dataset) showed an average increase in ecological suitability under climate change. While some only exhibited marginal gains, others appear to have benefited from climate change. For example, *B. semenoviellus* has expanded westwards from the Russian taiga into central Europe[24,53], in line with increasing ecological suitability over these areas reported in our models. Similarly, *B. terrestris* and *B. lapidarius* are spreading to Fennoscandia[54] while *B. hypnorum* has been rapidly spreading in the British Isles[55]. Yet, such expansions may conceal areas of contraction as suggested by declining ecological suitability attributed to climate change at these species' southern range margins. Favourable microclimatic conditions or non-climatic factors, such as land-use changes and urbanization, may also facilitate range expansions and local persistence, even in the case of less favourable climatic conditions[56–58]. However, these same non-climatic factors may also conceal and counteract gains from increasing ecological suitability. For instance, both *B. pomorum* and *B. confusus* have undergone local extirpations, reportedly driven by the widespread loss of leguminous crops due to agricultural intensification[26–28], despite an increase in ecological suitability related to climate change in our results. This highlights the need to consider multiple interacting stressors when evaluating global bumblebee population health[25,59]. Nevertheless, we find that climate-related losses remain a major driver shaping bumblebee populations across Europe. Despite regional or species-level gains, ecological suitability losses that can be attributed to climate change exceed gains, both spatially and across species, potentially explaining part of the continental decline of the European bumblebee fauna.

While these results represent valuable insight into the climatic drivers of the decline of European areas ecologically suitable for bumblebees, they should be interpreted in light of several methodological limitations. First, we assess changes in habitat suitability rather than abundance or species diversity, and our results should not be interpreted as direct measures of either. Second, while our analytical framework isolates the impact of climate change, it does not capture its indirect and cascading effects. For example, climate change can alter the availability and phenology of floral resources and the spatiotemporal overlap between pollinators and their host plants[60–62]. Such indirect effects have been shown to drive bumblebee abundance more strongly than direct climatic effects[63]. Likewise, climate change can interact with other drivers, potentially exacerbating their impacts by, for example, increasing pesticide use and toxicity[64,65] or the impact of land-cover changes[66] or altering disease dynamics[67]. As these disruptions are not accounted for, our estimated climatic impact may differ from real-world outcomes. Yet, incorporating indirect impacts and interacting drivers remains challenging in the context of ecological niche modelling, given that data are scarce. Moreover, our approach is constrained by the environmental variables available within the ISIMIP framework for model training. Third, we focused on species for which sufficient data were available, excluding those with geographically restricted distributions. Given the potentially narrow environmental niche and small population size of these species, their responses to ongoing climate change may differ from those reported here and warrant dedicated investigation. We have also excluded species occurring marginally in Europe, as the study area (that is, Europe west of the 29° E meridian) does not cover the relevant portion of their range needed to accurately model their ecological niche. Finally, for several modelled species, the study area covers only part of their range. However, restricting the analysis to continental Europe offers sufficient sampling coverage, which reduces sampling bias, whereas extending beyond this area would rely on scarce occurrence data and may lead to higher model uncertainties and overfitting.

Our impact attribution analysis[20] links changes in ecologically suitable areas of European bumblebees to climate change. Because the counterfactual scenarios are based on detrended data[21], we do not disentangle the role of different drivers of climate change, that is, anthropogenic or naturally driven. The attribution to anthropogenic climate change is therefore indirect, based on the assumption that the dominant driver of trends removed from climate variables is predominantly human-driven. This is justified for many temperature-driven climate variables, including temperature means and extremes, given the established human influence on warming and related thermodynamic changes[8,68]. By comparing historical and counterfactual

scenarios, we highlight that climate change can directly be related to the decline of suitable areas for bumblebees across Europe. Furthermore, declining suitability has been intensifying since the 1980s, probably linked to faster warming rates across Europe, with expected increased impacts in the future. These findings provide evidence that climate change is already changing the ecologically suitable areas of insects, highlighting its pervasive impact on ecosystems. This approach provides a framework to quantify responses of organisms to warming trends and to identify areas and species most at risk. Addressing climate-driven declines will require both ambitious greenhouse gas emissions reduction policies and appropriate habitat management to buffer climate change impacts.

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/s41558-026-02734-6.

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Methods

Data acquisition and curation of bumblebee occurrence records

Occurrence records were retrieved from the dataset compiled by Sentil and colleagues[70,71], which aggregates georeferenced records at the European scale from published literature, open-source databases, universities, museums and privately held collections. These records were carefully curated by taxonomic experts to remove any erroneous or doubtful entries, ensuring that species distributions are consistent with the most comprehensive and up-to-date knowledge of bumblebee distribution and taxonomy in Europe[24]. The European study area was restricted to the region west of the 29° E meridian, as this extent encompasses regions for which sufficient monitoring data were available for bumblebee species, thus reducing the risk of unreliable ecological niche model training due to heterogeneous collection efforts. From this dataset, we retained only species with a minimum of 30 unique occurrences (that is, occurrence in 30 distinct grid cells, following ref. 23), between 2000 and 2019. This temporal coverage encompasses reliable and spatially extensive occurrence data available for European bumblebees, and corresponds to the time window used for ecological niche models training. We further discarded the following species: (1) *Bombus cullumanus*, *B. haematurus*, *B. laesus* and *B. schrencki*, as their distribution in Europe is poorly representative of their global distribution; (2) the parasitic *B. inexspectatus*, due to its highly restricted distribution, which is, in addition, thought to be strictly associated with that of its host (*B. ruderarius*); (3) *B. magnus*, because of important sampling bias due to its morphological appearance that is cryptic with several closely related species; and (4) *B. xanthopus*, due to its insular endemism (Corsica and Tuscan archipelago)[24]. We strictly excluded insular species to prevent training ecological niche models on distributions that may be constrained due to major physical barriers (that is, large sea areas). The absence of these species from continental regions may therefore reflect physical isolation rather than a lack of suitable environmental conditions. In total, the final dataset includes 829,448 occurrences from 47 species (see Supplementary Fig. 1 for the maps of species-specific occurrence records), out of the 1,728,495 occurrences from 67 species that were present before filtering, which were used for species-specific ecological niche model training.

The environmental predictors used to train the ecological niche models were retrieved from ISIMIP3a, which provides gridded climatic, land-use, and human population data (Extended Data Fig. 1) across four observed historical reanalysis datasets (GSWP3-W5E5, 20CRv3, 20CRv3-ERA5 and 20CRv3-W5E5; see, for example, the study of Erazo and colleagues[72] for a presentation of these reanalysis datasets). Among the four available historical reanalysis datasets, we focus on GSWP3-W5E5, as it is a bias-adjusted version of ERA5 that aims to provide an improved representation of historical climate and is the reference dataset in ISIMIP3a[69]. The other three datasets (20CRv3, 20CRv3-ERA5 and 20CRv3-W5E5) are also considered in a comparative framework to assess the robustness of our results across the choice of reanalysis dataset. Climatic data included near-surface air temperature, relative humidity and precipitation, all averaged by season and over the 2000–2019 period. Winter includes December–February, spring March–May, summer June–August and autumn September–November. These climatic predictors represent primary abiotic constraints on the physiology (and therefore distribution) of bumblebees, while seasonal average climatic data, instead of annual averages, were used to represent seasonal variation across bumblebee life-cycle stages. Six land-use variables were retrieved from the second version of the Land Use Harmonization project (LUH2), namely primary and secondary forested areas, primary and secondary non-forested areas, pastures and rangeland, as well as croplands[73]. These variables were used to represent different degrees of semi-natural or intensively managed landscapes, which differ in the availability of floral resources and nesting opportunities for the studied species.

Training and evaluating ecological niche models

Ecological niche models were trained using a BRT algorithm implemented in the R package 'dismo'[74]. BRT is a machine learning approach that sequentially fits multiple regression trees to the training dataset, which optimizes the predictive probability of occurrence in relation to local environmental variables[75]. The BRT output is interpreted here as a continuous measure of local ecological suitability, ranging from 0 to 1, the upper limit representing highly favourable ecological conditions for the target species. We used a BRT approach because it can model nonlinear relationships between the response variable and environmental predictors, as well as handle interactions between variables. Moreover, this approach can be applied without prior data transformation or outlier filtering[75]. All model training was conducted on grid cells with a resolution of 0.5 decimal degrees (30 arcmin). The BRT analyses were run separately for each of the 47 species using a Bernoulli approach, which requires both presence and absence data. We automatically categorized all grid cells containing at least one observation of the target species as presence locations (presence cells). To avoid artificially representing oversampled areas as ecologically suitable areas, one occurrence record per grid cell was randomly retained[76]. Because true absence data are unavailable for bumblebees, we generated pseudo-absences by randomly sampling grid cells within a 'background' area. This background area is defined as the study area grid cells that include one or more *Bombus* occurrences, excluding presence cells previously defined as such for the target species. The number of generated pseudo-absences was, each time, equal to the number of presence cells for the target species (1:1 ratio). Sampling pseudo-absences in a defined background area representing confirmed *Bombus* occurrences increases the probability of sampling in areas where a minimum of sampling effort was carried out, reducing the risk of misclassifying unsampled areas as true absences[77]. For several species (n = 7/47), the number of background grid cells was too limited to meet the 1:1 ratio; in these cases, the remaining pseudo-absences were sampled from the rest of the study area. Because BRT is sensitive to the random generation of pseudo-absences, ten independent BRT models per species were run, each using a different random set of pseudo-absences.

To account for the spatial autocorrelation of occurrence data and avoid model overfitting, we used a spatial cross-validation approach instead of standard cross-validation, which is known to be sensitive to this issue[78]. Specifically, we spatially divided training and test sets using the block-based spatial cross-validation method implemented in the 'blockCV' R package[79]. We then ran the BRT analyses with the following parameters: a tree complexity of 5, 10 initial trees, a learning rate of 0.005, a step size of 5, and 5 cross-validation folds. To assess model performance, the AUC was computed for each of the ten independent specific analyses. Although AUC is still a widely used statistic in ecological niche modelling, several authors have pointed out its limitations, including dependencies on prevalences[80,81]. To address these concerns, we followed the approach of previous studies[23,72] and additionally evaluated model performances using a prevalence-pseudoabsence-calibrated Sørensen's index (SI_{ppc}). This alternative metric also ranges from 0 to 1, with higher values indicating good predictive performance. As ecological niche model outputs provide a continuous range of ecological suitability values, whereas this metric requires binary presence-absence data, we implemented an optimization procedure involving a stepwise increase of the threshold value by 0.01 across the [0, 1] ecological suitability range, selecting the threshold that maximized the SI_{ppc} value[82]. The evolution of the species-specific SI_{ppc} values along the ecological suitability threshold range, along with their averaged maximum value over ten replicates (and corresponding threshold in parentheses), is reported in Extended Data Fig. 2 for each of the ten BRT replicate analyses conducted for each species.

Projecting and comparing ecological niche models

While model training is based on recent *Bombus* occurrence records (2000–2019) and environmental variables averaged over the same period, we projected each species-specific BRT model over six successive time slices of 20 years, ranging from 1901 to 2019, and under two climatic scenarios based on: (1) factual climatic data and (2) a counterfactual baseline. The factual datasets represent observed historical climatic conditions, while counterfactual projections represent a version of the observed historical climate data in which any long-term climate trends correlated with global mean temperature change have been removed by detrending the factual data using the ATTRICI method[21]. This detrending procedure preserves the rank structure of the variable while, to the first order, removing the effects of climate change. Because the differences obtained between both kinds of projections are, by definition, solely due to climate change, the comparisons allow us to attribute changes in areas ecologically suitable for European bumblebees to climate change trends, without explicitly disentangling the role of its drivers, such as anthropogenic emissions of greenhouse gases and aerosols or long-term trends from natural drivers and natural variability[20,21]. To compare model projections between scenarios and across all species, we used two metrics, computed for each grid cell[23]: (1) the ESI, defined as the mean ecological suitability value averaged across species at each grid cell (that is, suitability values were first averaged for each grid cell across the ten BRT replicates for each species and then averaged across species), with values ranging from 0 to 1, and (2) the SRI, defined as the number of species at each grid cell whose predicted ecological suitability is higher than the median SI_{ppc} threshold derived from the ten ecological niche models trained on present-day data. While the ESI metric can be used to evaluate changes in the ecological suitability averaged across species, the SRI thus allows the estimation of changes in potential species richness, as estimated by ecological niche modelling analyses and projections. Our attribution framework allows us to isolate the effect of climate change on how it has modified the areas ecologically suitable for European bumblebee species and not the actual occurrence of European bumblebee populations.

To capture spatial heterogeneity in climate change impacts across the continent, we evaluated changes in ecological suitability attributable to climate change across European biogeographic regions (Extended Data Fig. 6). Biogeographic regions represent areas with similar biotic characteristics and shared climatic and ecological conditions. We focused on six regions substantially occurring in our study area, that is, Alpine, Atlantic, Boreal, Continental, Mediterranean and Pannonian regions, using the biogeographic region boundaries as delimited in the shapefile provided by the European Environment Agency[32]. The Alpine region comprises mountainous areas characterized by cold climates and strong altitudinal gradients; the Atlantic region includes northwestern Europe characterized by oceanic climate and mild temperatures; the Boreal region encompasses northern Europe characterized by cool climate and long winters; the Continental region covers Central and Eastern Europe with pronounced seasonal variability; the Mediterranean region corresponds to southern Europe characterized by warm, dry summers; and the Pannonian region consists of the lowland region of the Carpathian basin with a continental climate.

We also compared changes in model performance between the historical and counterfactual scenarios through time, using the BI, a presence-only predictive performance metric[83,84]. For each species, period and reanalysis dataset, we calculated the mean BI differences between both scenarios, with positive values indicating higher model performance under historical climate conditions. Statistical significance of BI differences was assessed using Wilcoxon–Mann–Whitney tests with a Benjamini–Hochberg correction for multiple testing (see the Supplementary Information for further details).

Reporting summary

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

Data availability

All datasets used in this study are freely and openly available. European bumblebee occurrences were initially retrieved from Sentil and colleagues[70,71]. This dataset was curated as described in the Methods, and the final curated version generated for this study is available via Zenodo at https://doi.org/10.5281/zenodo.21620753 (ref. 85). All ISIMIP3a data used in this study can be retrieved from the ISIMIP platform (https://data.isimip.org/).

Code availability

R scripts related to the ecological niche modelling are all available via GitHub at https://github.com/BastienDT/counterclim_bombus and via Zenodo at https://doi.org/10.5281/zenodo.21620753 (ref. 85). This GitHub repository also gathers the CSV files reporting the predictive performance metrics of species-specific ecological niche models, such as the AUC and SI_{ppc}, as well as the maps displaying the evolution of areas ecologically suitable estimated for both the reconstructions of the historical climate and a counterfactual baseline.

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Author contributions

B.D.T., K.S., D.E., G.G. and S.D.: conceptualization and methodology. B.D.T., G.G. and S.D.: formal analyses, validation. B.D.T., G.G. and D.M.: occurrence data collection and curation. R.P., F.M. and W.T.: climate data preparation. B.D.T., G.G. and S.D.: original draft writing and editing. G.G. and S.D.: equally contributed to the supervision of the study. All authors contributed to data interpretation and critically revised and approved the final paper.

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Competing interests

The authors declare no competing interests.

Additional information

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Extended Data Table 1 | Relative average loss in ecological suitability related to climate change reported for each species and reanalysis dataset

	GSWP3-W5E5	20CRv3	20CRv3-ERA5	20CRv3-W5E5
Bombus alpinus	13.14	18.11	18.01	16.85
Bombus argillaceus	−34.35	−5.93	−9.72	−7.28
Bombus balteatus	11.35	11.22	12.22	11.37
Bombus barbutellus	3.34	−0.4	1.3	3.09
Bombus bohemicus	4.41	2.85	−0.02	3.71
Bombus campestris	0.92	−7.07	−6.02	−1.93
Bombus cingulatus	12.1	11.44	13.27	11.7
Bombus confusus	−9.45	−2.91	−5.23	−4.55
Bombus consobrinus	8.56	10.93	11.5	11.94
Bombus cryptarum	14.87	8.58	10.97	11.49
Bombus distinguendus	−5.7	−2.34	−2.49	−4.37
Bombus flavidus	10.12	16.66	15.33	15.08
Bombus gerstaeckeri	−15.38	−7.27	0.06	2.17
Bombus hortorum	11.52	3.09	8.36	8.99
Bombus humilis	−7.67	−6.62	−9.58	−9.17
Bombus hyperboreus	7.01	10.57	9.86	9.66
Bombus hypnorum	9.69	6.54	9.29	9.38
Bombus jonellus	22.31	14.6	18.64	20.09
Bombus lapidarius	9.46	1.65	4.34	5.69
Bombus lapponicus	11.48	12.55	13.2	12.21
Bombus lucorum	16.68	8.83	12.33	13.35
Bombus mastrucatus	1.96	8.57	17.74	17.34
Bombus mendax	−29.87	−12.54	−9.7	−4.89
Bombus mesomelas	−37.55	−5.03	−9.62	−9.23
Bombus monticola	28.13	22.95	27.86	26.72
Bombus mucidus	−26.86	−2.41	1.39	1.87
Bombus muscorum	−3.74	−8.19	−10.2	−5.93
Bombus norvegicus	−5.71	−0.19	−2.03	1.29
Bombus pascuorum	7.26	3.51	4.97	6.71
Bombus pomorum	−21.5	−4	−9.87	−8.91
Bombus pratorum	11.24	5.35	9.64	9.26
Bombus pyrenaeus	−5.28	−0.96	7.08	9.17
Bombus pyrrhopygus	8.92	13.2	11.89	12.07
Bombus quadricolor	9.14	5.61	6.14	11.73
Bombus ruderarius	−3.44	−10.67	−8.8	−3.64
Bombus ruderatus	−19.65	−17.54	−13.49	−12.99
Bombus rupestris	−2.22	−8.9	−7.58	−3.06
Bombus semenoviellus	−47.55	−50.64	−53.97	−49.99
Bombus sichelii	−22.49	−7.31	−3.03	−2.07
Bombus soroeensis	5.46	4.66	−0.2	5.12
Bombus sporadicus	12.04	11.77	13.03	11.03
Bombus subterraneus	−4.92	−4.21	−7.54	−4.43
Bombus sylvarum	−12.07	−9.32	−13.78	−9.18
Bombus sylvestris	4.65	0.39	−2.1	1.69
Bombus terrestris	1.66	−4.62	−2.24	0.06
Bombus vestalis	−8	−11.44	−8.75	−6.56
Bombus veteranus	−13.93	−12.28	−20.24	−16.47

Relative average loss in ecological suitability related to climate change reported for each species and reanalysis dataset. Specifically, we report the average difference between present-time (2000-2019) ecological suitability values based on a counterfactual baseline and historical climate. Negative values thus indicate an increase in mean ecological suitability under the historical climate relative to the counterfactual baseline, while positive values indicate a decrease in mean ecological suitability.

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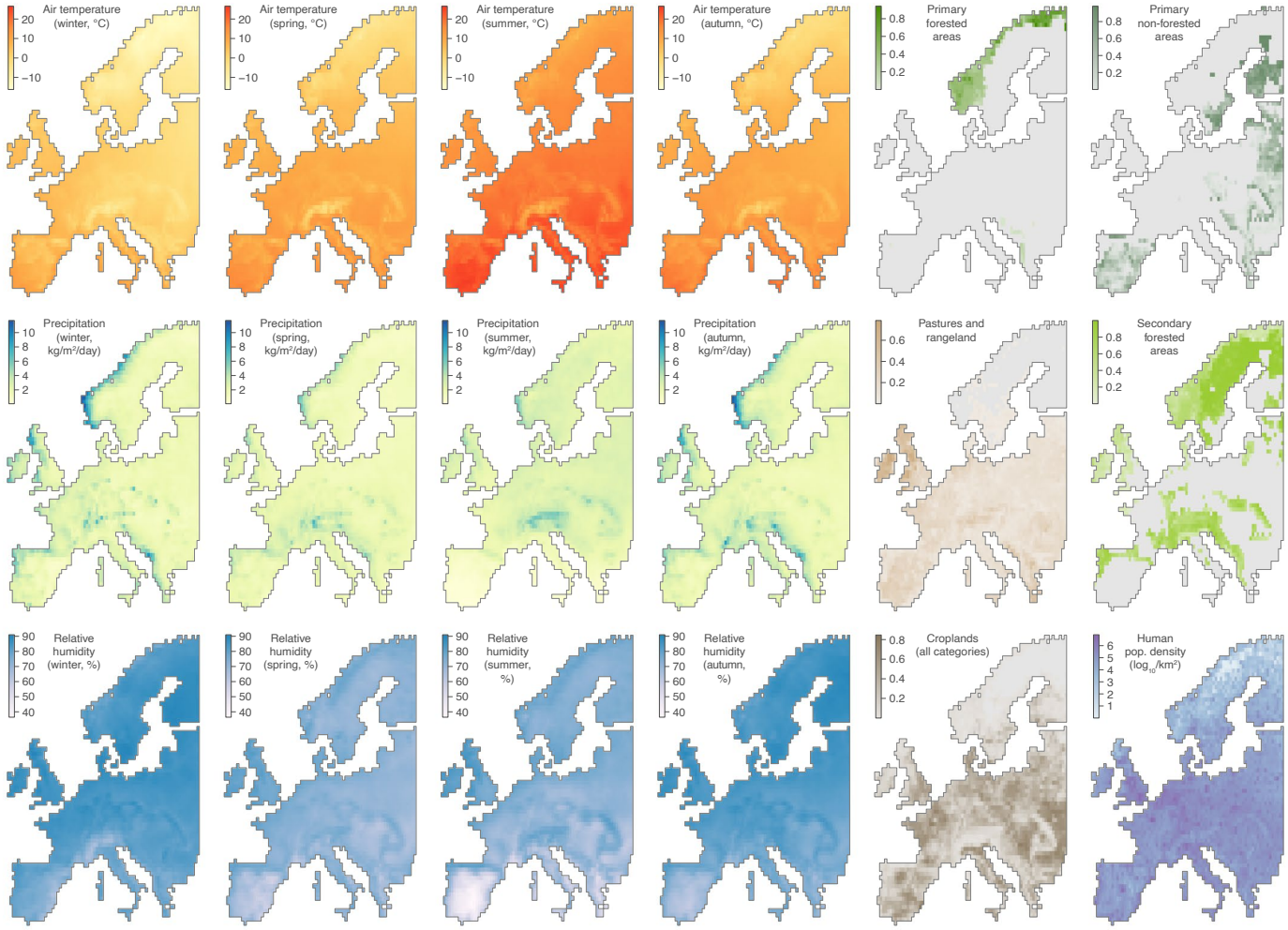

Extended Data Fig. 1 | Environmental factors included in the ecological niche modelling analyses of bumblebee species in Europe. We display the environmental values extracted from the ISIMIP3a reanalysis dataset GSWP3-W5E5 for 2000-2019. Basemap data from ISIMIP[69] under a Creative Commons license CC BY 4.0.

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Extended Data Fig. 2 | Assessment of the predictive performance of species-specific ecological niche models based on the computation of the prevalence-pseudoabsence-calibrated Sørensen's index (SI_{ppc}). Specifically, we computed the 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 maximising the SI_{ppc}. The maximised SI_{ppc} value averaged across ten replicate boosted regression trees (BRT) analyses is reported within each species-specific graph (along with the corresponding averaged threshold value in parentheses). The results reported here are based on ecological niche models trained with the GSWP3-W5E5 reanalysis dataset, but similar results are obtained when considering the models trained on the three alternative reanalysis datasets considered in the study.

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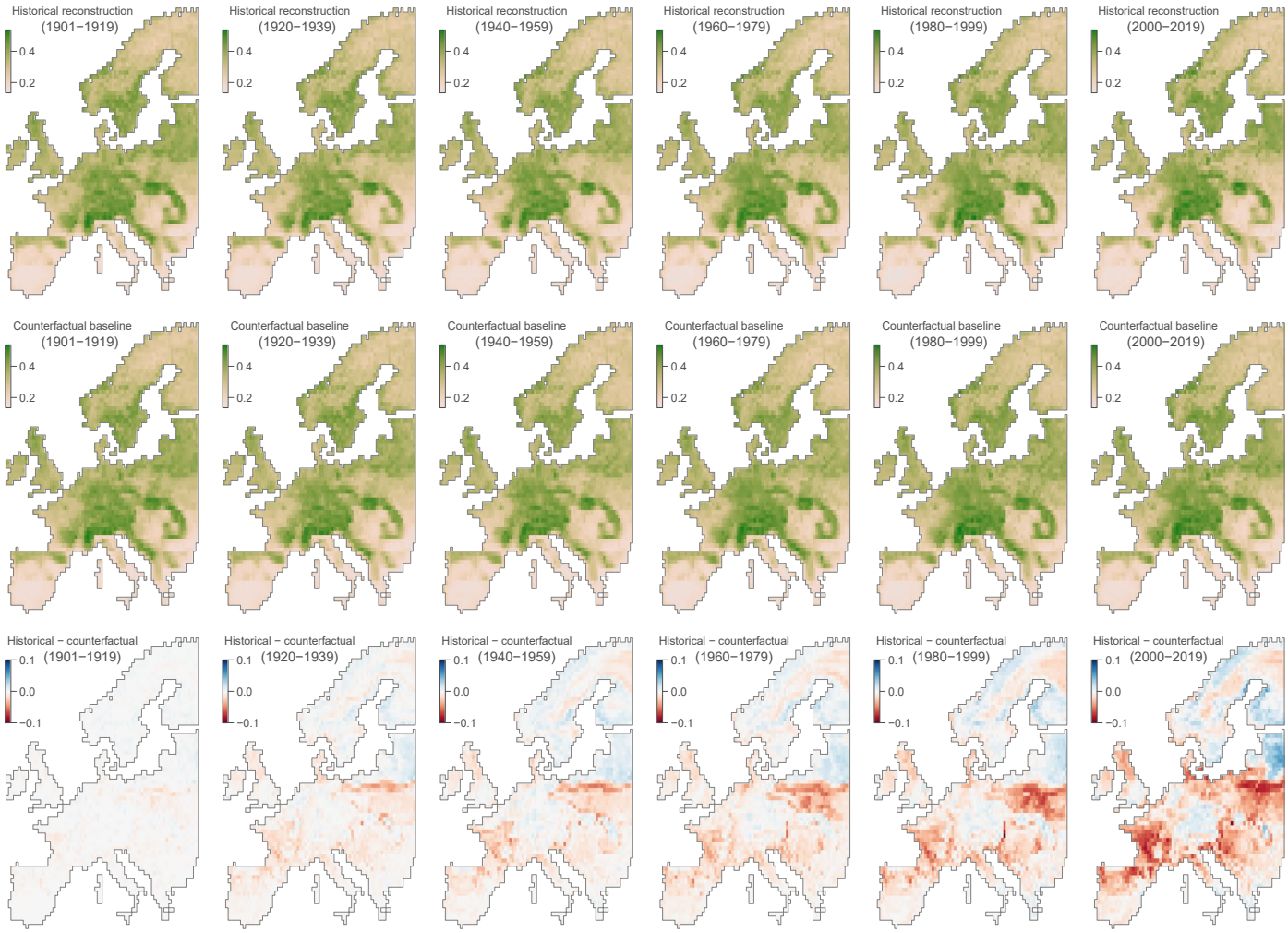

Extended Data Fig. 3 | Investigating the changes in ecological suitability for bumblebees in regard to climate change over the last century in Europe, as estimated with the ecological suitability index for the results based on the ISIMIP3a reanalysis dataset 20CRv3. For each successive time period and each scenario (historical or counterfactual), we report a map of the ecological suitability index (ESI), defined as the local mean ecological suitability averaged over species (and thus ranging from 0 to 1). The first and second rows of maps report local ESI estimates based on the reconstructions of the historical climate and a counterfactual baseline, respectively, and the third row of maps reports the difference, for each time period, between the two, that is, between the estimates based on the reconstructions of the historical climate and a counterfactual baseline. Basemap data from ISIMIP[69] under a Creative Commons license CC BY 4.0.

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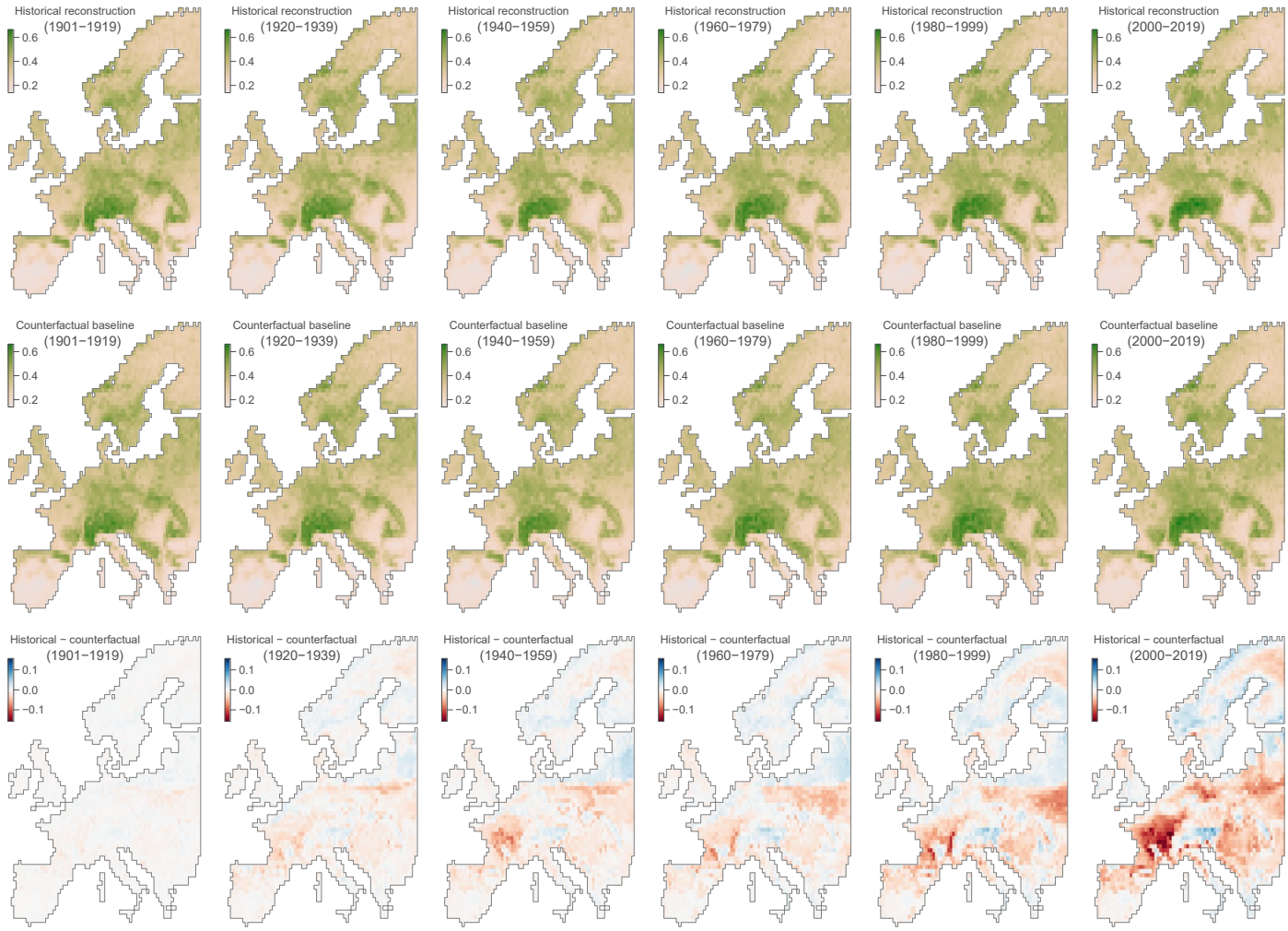

Extended Data Fig. 4 | Investigating the changes in ecological suitability for bumblebees in regard to climate change over the last century in Europe, as estimated with the ecological suitability index for the results based on the ISIMIP3a reanalysis dataset 20CRv3-ERA5. For each successive time period and each scenario (historical or counterfactual), we report a map of the ecological suitability index (ESI), defined as the local mean ecological suitability averaged over species (and thus ranging from 0 to 1). The first and second rows of maps report local ESI estimates based on the reconstructions of the historical climate and a counterfactual baseline, respectively, and the third row of maps reports the difference, for each time period, between the two, that is, between the estimates based on the reconstructions of the historical climate and a counterfactual baseline. Basemap data from ISIMIP[69] under a Creative Commons license CC BY 4.0.

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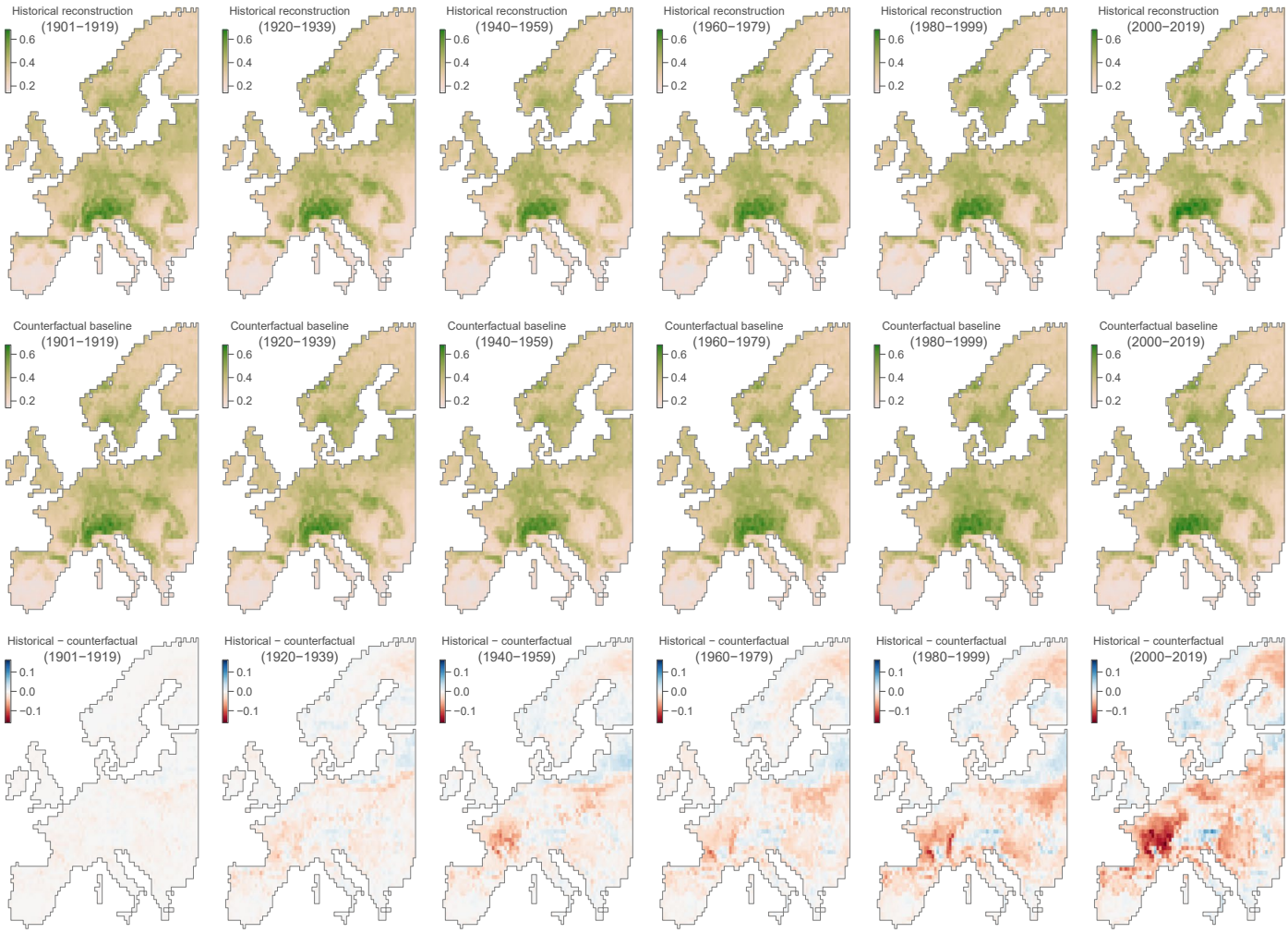
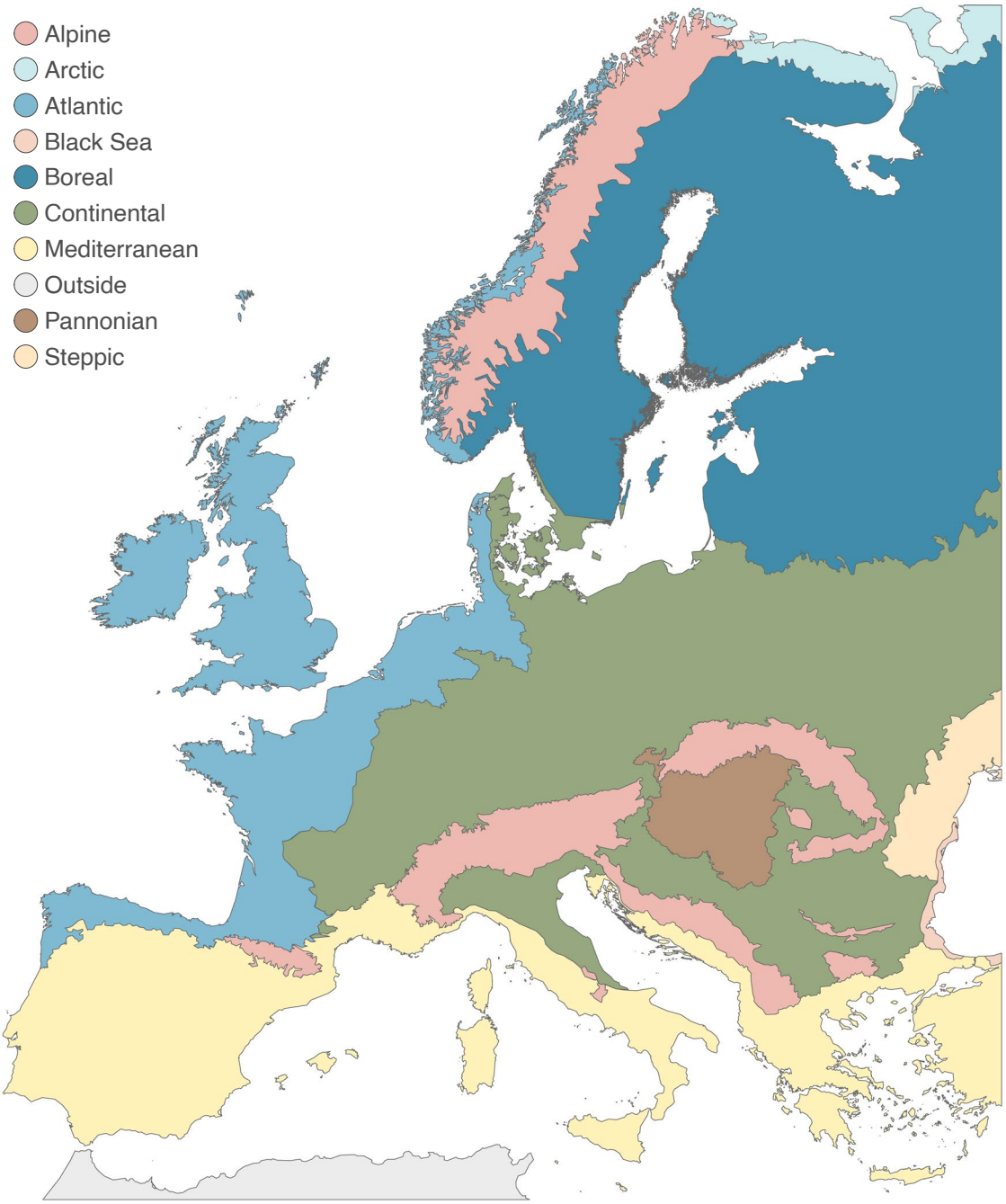


Extended Data Fig. 5 | Investigating the changes in ecological suitability for bumblebees in regard to climate change over the last century in Europe, as estimated with the ecological suitability index for the results based on the ISIMIP3a reanalysis dataset 20CRv3-W5E5. For each successive time period and each scenario (historical or counterfactual), we report a map of the ecological suitability index (ESI), defined as the local mean ecological suitability averaged over species (and thus ranging from 0 to 1). The first and second rows of maps report local ESI estimates based on the reconstructions of the historical climate and a counterfactual baseline, respectively, and the third row of maps reports the difference, for each time period, between the two, that is, between the estimates based on the reconstructions of the historical climate and a counterfactual baseline. Basemap data from ISIMIP[69] under a Creative Commons license CC BY 4.0.

https://doi.org/10.1038/s41558-026-02734-6



Extended Data Fig. 6 | Map of the biogeographic regions in Europe. These biogeographic regions correspond to the official delineations used in the Habitats Directive (92/43/EEC) and for the EMERALD Network set up under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; source: https://www.eea.europa.eu/en/analysis/maps-and-charts). Basemap data from EEA[32] under a Creative Commons license CC BY 4.0.

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Reporting Summary

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

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☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	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	No software was used for data collection.
Data analysis	For the ecological niche modelling we used the boosted regression tree (BRT) algorithm implemented in the R package "dismo" (version 1.3-16). To account for spatial autocorrelation, we implemented a spatial cross-validation procedure based on the blocks generation described by Valavi and colleagues and implemented in the R package "blockCV" (version 3.1-4; Valavi et al. 2019). All analyses were performed using R (R Statistical Software version 4.5.2 R Foundation for Statistical Computing, https://www.r-project.org/). R scripts related to the ecological niche modelling are all available at https://github.com/BastienDT/counterclim_bombus, and archived in Zenodo at https://doi.org/10.5281/ZENODO.21620753.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

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

All datasets used in this study are freely and openly available. European bumblebee occurrences were initially retrieved from Sentil et al. 2026 (https://doi.org/10.5281/ZENODO.17107215). This dataset was curated as described in the main text, and the final curated version generated for this study is available via Zenodo (https://doi.org/10.5281/ZENODO.21620753). All ISIMIP3a data used in this study can be retrieved from the ISIMIP platform (https://data.isimip.org/).

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	N/A
Reporting on race, ethnicity, or other socially relevant groupings	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

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

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Ecological, evolutionary & environmental sciences study design

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

Study description	Species-specific ecological niche models were trained using a machine learning approach – boosted regression trees (BRT) – for 47 Bombus species based on georeferenced records across Europe spanning over two decades of entomological observation data (2000-2019). Environmental predictors included gridded climatic, land-use, and human population data, all averaged over the same period of time and retrieved from four historical climate reanalysis datasets (GSWP3-W5E5, 20CRv3, 20CRv3-ERA5, and 20CRv3-W5E5) available through the Inter-Sectoral Impact Model Intercomparison Project phase 3a (ISIMIP3a). The model output was an ecological suitability value ranging from 0 to 1, representing the degree to which local environmental conditions are favourable for the occurrence of a target species. Ecological niche models were then projected to successive 20-year periods spanning from 1901 to 2019, under both a factual and a counterfactual scenario; the latter corresponding to climatic conditions where long-term climatic trends were removed. By subtracting the modelled ecological suitability values of the factual climate scenario from the values of the counterfactual scenario, we obtain suitability differences that reflect a gain or a loss solely attributable to climate change.
Research sample	Bombus species occurrence records were retrieved from the dataset compiled by Sentil et al. (2026), which aggregates georeferenced records at the European scale from published literature, open-source databases, universities, museums, and privately held collections. These records were carefully curated by taxonomic experts to remove any erroneous or doubtful entries, ensuring that species distributions are consistent with the most comprehensive and up-to-date knowledge of bumblebee distribution and taxonomy in Europe.
Sampling strategy	We retained only Bombus species with a minimum of 30 unique occurrences (i.e. occurrence in 30 distinct grid cells) between 2000 and 2019 within the European study area.
Data collection	As detailed above, Bombus species occurrence records were retrieved from the dataset compiled by Sentil et al. (2026); and we retrieved climate, land-use, and population data from the Inter-Sectoral Impact Model Intercomparison Project phase 3a (ISIMIP3a) database.

Timing and spatial scale	We used geo-referenced Bombus species occurrence records across the European continent (restricted to the region west of the 29° E meridian) for the period 2000-2019, as well as climatic, land-use, and human population data for the corresponding years.
Data exclusions	We retained only Bombus species with a minimum of 30 unique occurrences (i.e. occurrence in 30 distinct grid cells) between 2000 and 2019 within the European study area. We further discarded the following species: (i) Bombus cullumanus, B. haematurus, B. laesus, and B. schrencki, as their distribution in Europe is poorly representative of their global distribution; (ii) the parasitic B. inexspectatus, due to its distribution being associated with that of its host (B. ruderarius), and thus not reflecting independent ecological requirements; (iii) B. magnus, because of significant sampling bias due to its morphological appearance that is cryptic with several closely-related species; and (iv) B. xanthopus, due to its insular endemism (Corsica and Tuscan archipelago). We excluded strictly insular species to prevent training ecological niche models on distributions that may be constrained due to major physical barriers (i.e. large sea areas). The absence of these species from continental regions may therefore reflect physical isolation rather than a lack of suitable environmental conditions.
Reproducibility	R scripts related to the ecological niche modelling and projections are all available at https://github.com/BastienDT/counterclim_bombus, and archived via Zenodo at https://doi.org/10.5281/ZENODO.21620753, which makes the study fully replicable. All raw Bombus occurrence data are available from Sentil et al. (2026). Curated occurrence data used in this study are available through the above-mentioned GitHub repository and the associated Zenodo archive. All ISIMIP3a data used in this study can be retrieved from the ISIMIP platform (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
☒	☐ Plants

Methods

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

Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A