

PRIMARY RESEARCH ARTICLE

Large variability in response to projected climate and land-use changes among European bumblebee species

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Abstract

Bumblebees (*Bombus* spp.) are among the most important wild pollinators, but many species have suffered from range declines. Land-use change, agricultural intensification, and the associated loss of habitat have been identified as drivers of the observed dynamics, amplifying pressures from a changing climate. However, these drivers are still underrepresented in continental-scale species distribution modeling. Here, we project the potential distribution of 47 European bumblebee species in 2050 and 2080 from existing European-scale distribution maps, based on a set of climate and land-use futures simulated through a regional integrated assessment model and consistent with the RCP-SSP scenario framework. We compare projections including (1) dynamic climate and constant land use (CLIM); (2) constant climate and dynamic land use (LU); and (3) dynamic climate and dynamic land use (COMB) to disentangle the effects of land use and climate change on future habitat suitability, providing the first rigorous continental-scale assessment of linked climate-land-use futures for bumblebees. We find that direct climate impacts, although variable across species, dominate responses for most species, especially under high-end climate change scenarios (up to 99% range loss). Land-use impacts are highly variable across species and scenarios, ranging from severe losses (up to 75% loss) to considerable gains (up to 68% gain) of suitable habitat extent. Rare species thereby tend to be disproportionately affected by both climate and land-use change. COMB projections reveal that land use may amplify, attenuate, or offset changes to suitable habitat extent expected from climate impact depending on species and scenario. Especially in low-end climate change scenarios, land use has the potential to become a game changer in determining the direction and magnitude of range changes, indicating substantial potential for targeted conservation management.

KEYWORDS

integrated assessment, MaxEnt, pollinators, RCP, species distribution modeling, SSP

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1 | INTRODUCTION

The global food system greatly benefits from insect pollination that provides an estimated economic value between €9.7 bn (Vallecillo et al., 2019) and ~€14 bn in the European Union (Potts et al., 2015) and ~€153 bn globally (Gallai et al., 2009). While the area of insect-pollinated crops is on the rise (Aizen et al., 2008), a decline of wild pollinator abundance and diversity has been observed across scales (Goulson et al., 2008; Potts et al., 2010; Powney et al., 2019), driven by agricultural intensification (Goulson et al., 2015; Grab et al., 2019; Newbold et al., 2015; Potts et al., 2016; Woodcock et al., 2017) and a changing climate (Kerr et al., 2015; Soroye et al., 2020). Yield losses due to pollinator decline have been observed (Deguines et al., 2014; Garibaldi et al., 2011), thus threatening future food supply (Potts et al., 2016) and the quality of human diet, as the crops concerned provide high shares of proteins, vitamins, and minerals (Eilers et al., 2011; Klatt et al., 2014).

Bumblebees (*Bombus* spp.) are among the most important wild pollinators in temperate regions due to their relatively high abundance and coevolved pollinator associations with many native plant species and their generalist life-history strategy (Goulson et al., 2008). Moreover, bumblebees are able to pollinate at relatively low temperatures and in bad weather conditions, thus being more efficient than managed honey bees (Goulson, 2010). Their ability to 'buzz-pollinate' makes them the most important pollinators for certain flowering crops (e.g., tomatoes) that rely on this form of insect pollination (De Luca & Vallejo-Marín, 2013). However, bumblebees are sensitive toward several environmental changes, such as the loss of floral resources and increased pesticide usage associated with agricultural intensification (Carvell et al., 2006; Rundlöf et al., 2015), resulting in declining populations across spatial scales. Potts et al. (2015) report declining population trends for roughly half of the 68 European bumblebee species (with 20 species remaining stable and only nine species increasing); a finding repeated for more than half of the 23 species present in the United Kingdom (with seven species increasing) (Comont & Dickinson, 2020). Similar trends can be observed in North and South America (Bartomeus et al., 2013; Cameron et al., 2011; Krechmer & Marchioro, 2020). Concerns have been raised that such trends will continue or even amplify in the future with ongoing climate and land-use change (Marshall et al., 2018; Rasmont et al., 2015; Sirois-Delisle & Kerr, 2018). An improved understanding of how individual environmental pressures, and particularly the interactions among them, affect bumblebee populations and bumblebee habitat is essential to develop conservation strategies that counteract declines in bumblebee distribution.

A rich body of literature exists demonstrating the impacts of a changing climate on bumblebee populations and ecological traits across geographic regions (e.g., Casey et al., 2015; Gérard et al., 2020; Kerr et al., 2015; Marshall, Perdijk, et al., 2020). On the European scale, Rasmont et al. (2015) showed a decrease in climatically suitable areas for 49–55 European bumblebee species in 2100, depending on the climate scenario considered. Similarly, Sirois-Delisle and Kerr (2018), who assessed potential range changes

of 31 North American bumblebee species under four representative concentration pathway (RCP) climate scenarios, identified range losses for 15–30 species depending on climate scenario and assumptions about dispersal ability. Recently, Soroye et al. (2020) identified a higher risk of local extinction rates for North American and European bumblebees, if climate conditions exceed historically observed ranges. However, continental-scale studies often do not account for the effects of land-use change (e.g., agricultural intensification, urbanization, or expansion of cropland and grazing land) on bumblebee habitat. When included, it is only through ad hoc scenarios and with little thematic detail (Marshall et al., 2018; Soroye et al., 2020). As a result, important drivers of the future distribution of bumblebee populations and associated pollination services are underrepresented in current assessments.

The knowledge regarding the impacts of land-use change and agricultural management on bumblebee ecology and habitat (e.g., fewer nests sites in intensive agricultural landscapes or reduced colony growth and queen production due to pesticide application) is well established from the plot- to landscape scale (e.g., Aguirre-Gutiérrez et al., 2015; Goulson et al., 2010; Senapathi et al., 2015; Whitehorn et al., 2012). However, the effects of these drivers on large-scale bumblebee distributions and their interaction with climate change are less understood. Land-use change, where included, was found to have non-significant (Kerr et al., 2015) or minor negative effects (Soroye et al., 2020) as a driver of shifts in historical distribution patterns at continental scale and is to date hardly accounted for in projections of future distribution at the continental scale (Rasmont et al., 2015; Sirois-Delisle & Kerr, 2018). Marshall et al. (2018) were the first to include dynamic land-use changes in European-scale, predictive bumblebee distribution modeling, finding significant changes in range dynamics upon accounting for land-use variables in their models. Yet, the land-use changes they considered were limited, and had relatively low importance compared to climate change impacts; a finding they attributed partly to the difficulty of capturing land-use and land-management changes at a level of detail relevant for bumblebee ecology (Marshall, Beckers, et al., 2020).

Partly due to such methodological limitations, there have been no attempts yet to quantify potential future changes of bumblebee habitat area in a framework where different levels of climate change and various plausible land-use futures are combined to a coherent set of linked climate–land-use scenarios. Moreover, there has been little focus on the variability among individual species' responses to these interacting environmental pressures. However, an improved understanding of how individual species react to different levels of environmental change is crucial to identify locations that require more detailed analyses on the interactions between land use and bumblebees and to design targeted land-management policies that support as many species as possible under a changing climate. Here, we thus combine land-use change projections for Europe from a regional integrated assessment platform running a full set of socioeconomic and climate scenarios (the IMPRESSIONS Integrated Assessment Platform (IAP2); Harrison et al., 2019) with established species distribution models (SDMs) for 47 European bumblebee

species developed by Polce et al. (2018). We do so in order to (1) quantify changes in bumblebee habitat suitability due to isolated climate and land-use change effects at the individual species level and (2) assess the impact of different land-use change futures on bumblebee habitat suitability under different levels of projected climate change. We specifically focus on the heterogeneous impact across bumblebee species to evaluate at which levels of climate change and for which species the choice of land use has the potential to become a game changer in a changing climate.

2 | MATERIALS AND METHODS

2.1 | Overview

We combined established knowledge on the distribution of 47 European bumblebee species (Table S1) with projections of climate and land-use change to quantify the species-specific response to a set of climate and land-use scenarios at the European scale (Figure 1). Baseline bumblebee distributions were based on SDMs at 10×10 km spatial resolution (Polce et al., 2018) and adjusted to be consistent with land-use data from the projections. Future climate and land-use data were taken from CMIP5 climate model simulations (Taylor et al., 2012) and the IAP2 (Harrison et al., 2019), respectively. Various levels of climate and land-use change were considered through the scenario framework of the Intergovernmental Panel on Climate Change, combining representative concentration pathways (RCPs) with shared socioeconomic pathways (SSPs) (O'Neill et al., 2017; van Vuuren et al., 2011), with socioeconomic developments adjusted to the European context (Kok et al., 2019). We applied the SDMs to the time periods representative for the years 2050 and

2080 to obtain estimates of the future distributions of the 47 bumblebee species. We established an expert-based mapping between the Coordination of Information on the Environment (CORINE) land cover and the IAP2 land-use classes to represent major changes in European land management in the SDMs. All extrapolations were repeated for a series of modeling experiments where climate predictors (CLIM), land-use predictors (LU), or both (COMB) were allowed to dynamically change. The details of the individual steps in the analysis are described in the following sections.

2.2 | Baseline bumblebee distribution

The potential distribution of 47 bumblebee species (Table S1) and SDM model coefficients were made available by Polce et al. (2018). The distribution maps indicate for each species (1) the probability of occurrence and (2) presence/absence at a spatial resolution of 10×10 km, based on a maximum entropy (MaxEnt) modeling approach (Phillips et al., 2006) that establishes a functional relationship between species occurrence and 22 environmental predictor variables (Tables 2 and 3). Species occurrence data for the years 1991–2012 underlying the MaxEnt models originate from the Atlas Hymenoptera (Rasmont & Francis, 2018) and consisted of validated presence-only bumblebee records, gathered from different data donors in Europe (see Rasmont et al., 2015 and Supplementary Material 7 in Polce et al., 2018 for further details), collated during the 'Status and trends of European pollinators' project (Potts et al., 2015). The environmental predictors were based on CORINE land cover for the year 2006 for land-related variables (Bossard et al., 2000), 'E-OBS' gridded meteorological data for bioclimatic variables (Cornes et al., 2018), and

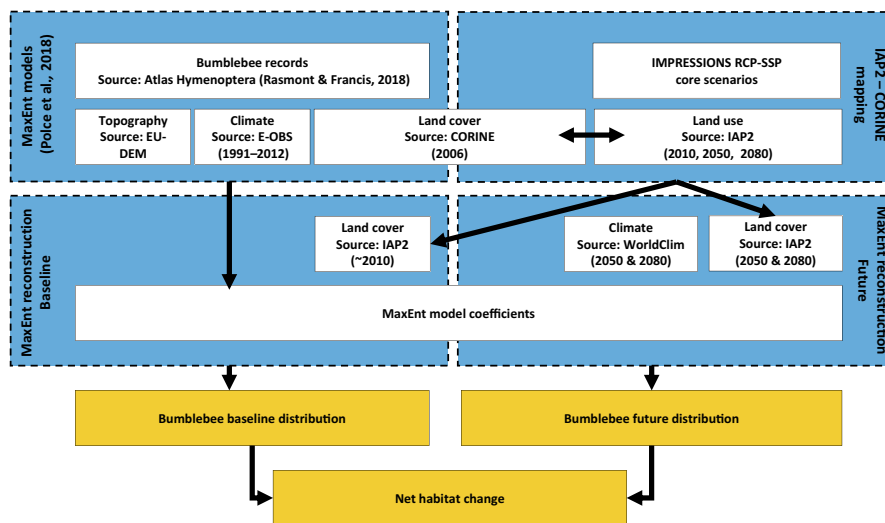


FIGURE 1 Overview of the analysis. MaxEnt models from Polce et al. (2018) are adjusted through the exchange of land-related predictor variables based on IAP2 land use and projected to 2050 and 2080 under various combinations of climate (WorldClim v1.4 RCP scenarios) and land-use change (IMPRESSIONS RCP-SSP core scenarios; Table 1). Net habitat changes per species are calculated as the difference between suitable habitat area in the future maps and suitable habitat area in the baseline map (based on mapped IAP2 land use for around 2010 and climate 1991–2012). All net habitat changes are expressed as percentage of the baseline habitat extent to provide a comparable measure across species

TABLE 1 Broad storyline and overview of major land-use trajectories in the Integrated Assessment Platform (IAP2) core scenarios used in this study. The numbers depict the magnitude of change in land-use areas as percentage of the baseline areas representing the year 2010. For a comprehensive description of the scenarios and IAP2 outputs, please see Harrison et al. (2019), Kok et al. (2019), and Nowak et al. (2018)

Storyline		Agriculture		Pasture		Forest		Non-Forest		Urban	
		2050	2080	2050	2080	2050	2080	2050	2080	2050	2080
SSP1	RCP2.6	+23	+39	+40	+60	-51	-72	-7	-20	+77	+107
Europe of sustainable development, characterized by political stability, low level of inequality, resource-saving lifestyles, and a successful transition toward renewable energy. Moderate economic growth and CO ₂ neutrality by 2050.	RCP4.5	+9	+20	+6	+13	-24	-40	+1	-2	+77	+107
SSP3	RCP4.5	+21	+29	-46	-71	-2	+5	+12	+16	+22	+13
Highly unequal Europe characterized by political instability, resource-intensive lifestyles, severe ecosystem failures, and substantial increases in energy and food prices. Low economic growth and high carbon intensity.	RCP8.5	+8	+15	-56	-80	+14	-17	+14	+65	+22	+13
SSP4	RCP2.6	-22	-53	-68	-85	+53	+91	+5	+2	+57	+72
Europe with increasing concentration of power in a small business and political elite. Characterized by growing inequalities and shift toward green technologies, driven by economic crisis and climate change impacts. High economic growth.	RCP4.5	-33	-60	-71	-86	+61	+79	+8	+26	+57	+72
SSP5	RCP8.5	-26	-42	-57	-79	+22	+8	+30	+77	+98	+132
Europe of rapid technological progress and economic growth that is almost fully based on further exploitation of fossil fuels due to a lack of environmental concern. Very energy-intensive lifestyle and severe environmental degradation.											

the 'EU-DEM' for topography (EEA, 2017). Details of the modeling process are described in Polce et al. (2018). To establish a consistent baseline for the extrapolations that were based on IAP2 land-use projections, we adjusted the baseline distribution maps using the IAP2-simulated baseline land-use areas (approximating the year 2010; Figure 1; Table 2). This simulated baseline is used in the IAP2 as a coherent outcome of varied input data, and used here as a consistent starting point from which scenario outcomes develop; a consistency that would not be possible with other (observational) baseline land-cover data. The same methodology as for retrieving the extrapolations was applied (details in the following sections), including the preprocessing of IAP2 outputs, the

mapping between CORINE and IAP2 legends, and the reconstruction of the MaxEnt models from the model coefficients. The exchange of land-use predictor variables resulted in some deviations compared to the original distribution maps (Figure S1).

2.3 | Climate and land-use data

The extrapolations of the SDMs were based on two major data sources (Tables 2 and 3). Land-cover variables (i.e., fractions of CORINE classes; Table 2) were obtained for a range of scenarios (Table 1) from the IAP2 for the time slices 2050 (2041–2070) and

TABLE 2 Overview of land-related environmental predictors to model the distribution of bumblebees and mapping between CORINE and IAP2 legends. 'Original data source' refers to data used in Polce et al. (2018). 'Baseline data source' refers to data used to derive baseline bumblebee distributions consistent with IAP2 data

Major land-use class	Mapping rule(s)	Predictor (Acronym)	CORINE classes included	Original data source	Baseline data source (future data source, if different)
Water	Constant from CORINE 511 & 512	Inland waters (IWB)	511, 512	CORINE 2006 Accounting Layer (version 18.5, Mar. 2017) ^a	IAP2 2010 mapped to CORINE legend (IAP2 2050 and 2080 under seven different scenarios mapped to CORINE legend)
Wetlands	Direct from IAP2 'Inland marshes' & 'Salt marshes'	Inland wetlands (IW) Salt marshes (BW)	411, 412 421		
Artificial	Proportional. IAP2 'Urban' scaled by respective CORINE classes	Discontinuous urban fabric (DUF)	112		
Forest	Proportional. Sum of IAP2 'Managed forest' & 'Unmanaged forest' scaled by respective CORINE classes	Green urban areas (GUS) Broad-leaved forest (BF) Coniferous forest (CF)	141, 142 311 312		
Agriculture	Complex (1) If IAP2 'Arable crops' < IAP2 'Intensively farmed', all 'Arable crops' map to CORINE 'Arable land'. Remaining agricultural areas proportionally distributed across respective CORINE classes (2) If IAP2 'Arable crops' >= IAP2 'Intensively farmed', all 'Intensively farmed' maps to CORINE 'Arable land'. Remaining agricultural classes are set to zero	Mixed forest (MF) Arable land (AL) Permanent crops (PC) Agriculture with natural vegetation (AGNV) Heterogeneous agricultural areas (HAG)	313 211, 212, 213 221, 222, 223 243 241, 242, 244		
Pasture	Direct from IAP2 'Intensively grass' & 'Extensively grass'	Pastures (PA)	231		
Natural vegetation	Proportional. Sum of IAP2 'Very extensively grass' & 'Unmanaged land' scaled by respective CORINE classes	Natural grasslands (NG) Scrub vegetation associations (SMH) Sparsely vegetated areas, including beaches and dunes (BDSV)	321 322, 323, 324 331, 333		
—	—	Average distance from natural and semi-natural areas (SND_KM)	—		CORINE 2006 Accounting Layer (version 18.5, Mar. 2017) ^a

Note: The mapping between CORINE and IAP2 is done at 10 km spatial resolution. The predictor 'SND_KM' cannot be derived from the mapped data at this spatial resolution and is kept constant at baseline level for the future time period.

^aThe CORINE 2006 Accounting Layer was produced by the European Environmental Agency (EEA) through a harmonization method, allowing the use of the CORINE land-cover data series to detect changes over time (<https://sdi.eea.europa.eu/catalogue/srv/eng/catalogue/search#/search?from=1&to=30>). Version 18.5 used in Polce et al. (2018) is now superseded by version 20.

Predictor (Acronym)	Original data source	Baseline data source	Future data source
Temperature seasonality (Tseas)	E-OBS	E-OBS	WorldClim v1.4
Maximum temperature of warmest month (Tmax)			from MPI-ESM for RCP2.6 and HadGEM for RCP4.5 and RCP8.5
Mean temperature of wettest quarter (Tmean)			
Precipitation seasonality (Pseas)			
Mode of elevations in 10km grid (elmode)	EU-DEM	EU-DEM	EU-DEM

TABLE 3 Bioclimatic and topography predictor variables to model the distribution of bumblebees. 'Original' and 'Baseline' data sources according to Table 2

2080 (2071–2100) by mapping the fractions of IAP2 land-use output to CORINE classes as indicated in Table 2 and described in the following section. The IAP2 is an interactive web-based platform that integrates a series of interlinked meta-models representing urban development, water resources, flooding, forests and agriculture, and biodiversity to assess climate change impacts, vulnerability, and adaptation (Harrison et al., 2016, 2019). The IAP has been applied and evaluated in a large number of studies including sensitivity and uncertainty analyses (e.g., Brown et al., 2015; Fronzek et al., 2019; Harrison et al., 2015, 2016, 2019; Holman et al., 2017; Kebede et al., 2015). A full model description and the online model itself are available at http://www.impressions-project.eu/show/IAP2_14855. Land use is modeled on a 10 arcmin grid across Europe and the allocation is based on both biophysical conditions (e.g., soil type, climate suitability) and socioeconomic aspects (e.g., prices, support rules, costs), resulting in multiple land uses proportionally for each cell (Holman

& Harrison, 2012). We used the core scenarios of the IMPRESSIONS project (Kok et al., 2015; Table 1), which represent a set of socioeconomic and climatic developments and associated land-use futures in Europe under the RCP-SSP scenario framework. The Eur-SSPs used in these scenarios are regional versions of the global SSPs adjusted to the European context (Kok et al., 2019) and are run in combination with different RCPs representing various levels of climate impact. Climate data within IAP2 simulations were based on the MPI-ESM-LR/REMO (RCP2.6) and HadGEM2-ES/RCA4 (RCP4.5; RCP8.5) regional climate models (Harrison et al., 2019; Kok et al., 2018). Climate effects on land use, for example through spatially explicit changes in crop yields, flooding, and other aspects of suitability, are included in the IAP2 projections (Harrison et al., 2019). However, this must not be confused with direct climate impact on bumblebee habitat suitability included in the SDMs by the bioclimatic variables (Table 4). The native spatial resolution of the IAP2 at

TABLE 4 Overview of modeling experiments and scenarios. For a summary of the major climate and land-use trends in the scenarios, see Supporting Information S3, Figures S3 and S4

Modeling experiment	Scenario	Land use	Climate (direct)	Climate (indirect)
CLIM	CLIM-RCP2.6	Constant at 2010 conditions	Dynamic, WorldClim v1.4, MPI-ESM	—
	CLIM-RCP4.5		Dynamic, WorldClim v1.4, HadGEM	
	CLIM-RCP8.5		Dynamic, WorldClim v1.4, HadGEM	
LU	LU-RCP2.6-SSP1	Dynamic, IAP2 mapped to CORINE	Constant at 2010 conditions	Dynamic, MPI-ESM-LR/REMO
	LU-RCP2.6-SSP4			
	LU-RCP4.5-SSP1			Dynamic, HadGEM2-ES/RCA4
	LU-RCP4.5-SSP3			
	LU-RCP4.5-SSP4			
	LU-RCP8.5-SSP3			Dynamic, HadGEM2-ES/RCA4
COMB	COMB-RCP2.6-SSP1	Dynamic, IAP2 mapped to CORINE	Dynamic, WorldClim v1.4, MPI-ESM	Dynamic, MPI-ESM-LR/REMO
	COMB-RCP2.6-SSP4			
	COMB-RCP4.5-SSP1			Dynamic, HadGEM2-ES/RCA4
	COMB-RCP4.5-SSP3			
	COMB-RCP4.5-SSP4			
	COMB-RCP8.5-SSP3			Dynamic, HadGEM2-ES/RCA4
	COMB-RCP8.5-SSP5		Dynamic, WorldClim v1.4, HadGEM	Dynamic, HadGEM2-ES/RCA4

the European extent is 10 arcmin (WGS84; EPSG:4326). To obtain land uses for the 10 × 10 km grid, we overlaid polygons projected to WGS84 with the IAP2 maps and aggregated the IAP2 land uses weighted by the 10 arcmin cell contribution to these polygons. In this way, we aimed to minimize distortions in the spatial configuration of land-use fractions from the IAP2 in the 10 × 10 km grid.

The bioclimatic variables 'temperature seasonality (Tseas)', 'maximum temperature of the warmest month (Tmax)', 'mean temperature of the wettest quarter (Tmean)', and 'precipitation seasonality (Pseas)' were obtained from WorldClim v1.4 for the time slices 2050 (2041–2060) and 2070 (2061–2080). WorldClim v1.4 based on CMIP5 (Taylor et al., 2012) instead of the more recent WorldClim v2.1 based on CMIP6 (Eyring et al., 2016) was used to be consistent with the climate impact on land use in the IAP2 scenarios. Projections were taken from the MPI-ESM (RCP2.6) and HadGEM (RCP4.5; RCP8.5) models, respectively, as these were used in the IAP2 scenarios. All climate data were downloaded from www.worldclim.org at 10 arcmin spatial resolution (WGS84; EPSG:4326) and projected to 10 × 10 km grids in Lambert azimuthal equal area projection (EPSG:3035) using bilinear interpolation.

2.4 | Mapping between IAP2 land use and CORINE land cover

CORINE land-cover classes as listed in Table 2 have been used as predictor variables in the SDMs by Polce et al. (2018). As land-cover projections based on the CORINE legend do not exist, we use projections from the IAP2 and map these onto the CORINE legend (Table 2). The IAP2 integrates a set of meta-models to represent the land-use sector (Holman & Harrison, 2012) and provides, among others, output for the classes 'Intensively farmed', 'Intensively grass', 'Extensively grass', 'Very extensively grass', 'Managed forest', 'Unmanaged forest', 'Unmanaged land', and 'Urban' that add up to 100% of the grid cell area. Additionally, the class 'Arable crops' provides information about the crop types within the agricultural areas. In the absence of a direct mapping between the IAP2 and CORINE legends, we developed an expert-based approach that distributes the fractions of major IAP2 land-use classes across the CORINE land-cover classes on a cell-by-cell basis. First, we grouped both legends into the major categories 'Agriculture', 'Artificial', 'Forest', 'Natural vegetation', 'Pasture', 'Wetlands', and 'Water'. Within these major classes, land-use fractions from the IAP2 were allocated to CORINE land-cover fractions either directly (if one or more IAP2 classes correspond to one CORINE class; 'Wetlands' and 'Pastures'), proportionally to the distribution of CORINE classes in 2006 (if one or more IAP2 classes correspond to more than one CORINE class; 'Artificial', 'Natural vegetation', and 'Pastures'), or following particular rules (if additional information was available from the IAP2; 'Agriculture'). Water courses/bodies were assumed to be constant over time. The major objective of the mapping was to represent land-use changes projected by the IAP2 compared to the baseline under different scenarios (Table 4) as closely as possible in the CORINE classes relevant for the SDMs. In this way, we created new maps of CORINE fractions based on the IAP2

land-use distribution for the baseline, 2050, and 2080 under each scenario. Given the lack of knowledge about possible future changes to the spatial configuration of CORINE land cover within a 10 km × 10 km grid cell, we kept the CORINE proportions constant over time. For example, if the IAP2 indicates an increase in forest area, the additional forest area was distributed across CORINE forest classes proportional to their distribution in the CORINE 2006 map. While some CORINE classes can be directly derived from the IAP2 classes (e.g., forests), others are more difficult to represent (e.g., CORINE class 'Heterogeneous agricultural areas'). Such classes represent a mixture of land cover/use, which is impossible to map from the IAP2 classes without additional information on the spatial configuration within grid cells. In consequence, the quality of the mapping differs across categories (Figure S2). However, all our analysis is based on the relative changes from the mapped CORINE land cover at around 2010 to the mapped CORINE land cover in the projections and thus we present a consistent set of modeling experiments.

2.5 | Reconstruction of SDMs and modeling experiments

The SDMs developed in Polce et al. (2018) were reconstructed from the model coefficients for each of the 47 bumblebee species for both the baseline period and a set of modeling experiments in 2050 and 2080. The MaxEnt models establish a functional relationship between the predictor variables (Tables 2 and 3) and the probability of occurrence (Phillips et al., 2006), based on a combination of forward and reverse 'hinge' features. 'Hinge' features represent base functions of piecewise linear splines (Phillips & Dudík, 2008), that is, for a given environmental predictor the model response is 0 below the hinge value and linearly increases to 1 at the maximum value of the predictor variable (forward hinge) or the model response is 1 at the minimum value of the predictor and linearly decreases to the hinge value, after which it is 0 (reverse hinge). The model coefficients were provided in 'lambda files', which allowed us to reconstruct the probability distribution of species occurrence (Wilson, 2009).

First, an adjusted baseline distribution for each bumblebee species was created by exchanging the original CORINE fractions by the land-cover fractions mapped from the IAP2. Subsequently, the SDMs were applied to the years 2050 and 2080 based on the climate and land-use data as described above (Tables 2 and 3). All projections were carried out three times with (1) dynamic climate and constant land use (CLIM), resulting in three maps per species and year (CLIM-RCP2.6, CLIM-RCP4.5, and CLIM-RCP8.5); (2) constant climate and dynamic land use (LU), resulting in seven maps per species and year (LU-RCP2.6-SSP1, LU-RCP2.6-SSP4, LU-RCP4.5-SSP1, LU-RCP4.5-SSP3, LU-RCP4.5-SSP4, LU-RCP8.5-SSP3, and LU-RCP8.5-SSP5); and (3) dynamic climate and dynamic land use (COMB), resulting in another seven maps per species and year (COMB-RCP2.6-SSP1, COMB-RCP2.6-SSP4, COMB-RCP4.5-SSP1, COMB-RCP4.5-SSP3, COMB-RCP4.5-SSP4, COMB-RCP8.5-SSP3, and COMB-RCP8.5-SSP5). By this experimental setup, we distinguished between the isolated climate (CLIM) and land-use (LU) effects on future suitable bumblebee habitat area, as well as their combined impacts (COMB).

2.6 | Assessment of land-use and climate impacts

To assess the impacts of land-use and climate change on the distribution of bumblebees, we calculated 'net habitat changes' from the difference of gains and losses of suitable habitat area in 2050 and 2080 compared to the baseline. We assume, following Polce et al. (2018), every grid cell in a distribution map with a probability of occurrence greater than the minimum training presence in the respective MaxEnt model as potential suitable habitat for a species. Gains and losses are then calculated from the difference between the number of grid cells indicating suitable habitat in the future (2050 or 2080) and the number of grid cells indicating suitable habitat in the baseline maps. In consequence, we focus on changes in potential habitat area and do not assess changes of habitat quality within grid cells. Due to a large range in the baseline habitat extent (Table S1), net habitat changes are expressed as percentage of the baseline habitat extent to provide a comparable measure across species.

3 | RESULTS

3.1 | Climate impact on bumblebee habitat suitability

Suitable bumblebee habitat on average decreases for all levels of climate change and both time periods (Figure 2a). The average change in habitat extent across the 47 species amounts to -1.44% , -25.43% , and -41.90% for CLIM-RCP2.6, CLIM-RCP4.5, and CLIM-RCP8.5

in 2080, respectively. For both CLIM-RCP2.6 and CLIM-RCP4.5, changes in habitat extent tend to happen mainly until 2050, while for RCP8.5 the average habitat loss becomes more severe toward the end of the century. The results show considerable variation in the individual species' response across climate scenarios: while for CLIM-RCP2.6 net losses in 2080 hardly exceed 20%, CLIM-RCP4.5 and CLIM-RCP8.5 lead to net losses greater than 90% for several species. Similarly, species that are projected to gain habitat tend to show greater variation under CLIM-RCP8.5 than under CLIM-RCP4.5 and CLIM-RCP2.6.

For a majority of the 47 species, climate change impacts result in net habitat losses in 2080 (Figure 3a-i). However, four species gain habitat across all RCPs (*B. mesomelas*, *B. muscorum*, *B. schrencki*, and *B. subterraneus*), three in two RCPs (*B. argillaceus* for CLIM-RCP4.5 and CLIM-RCP8.5; *B. magnus* and *B. terrestris* for CLIM-RCP2.6 and CLIM-RCP4.5), and another 11 in CLIM-RCP2.6. Climate impacts on potential habitat extent become increasingly negative under higher levels of climate change for most species (41 out of 47), resulting in larger habitat losses, smaller habitat gains, or a switch from habitat gain to habitat loss between scenarios (Table S2). However, some species have their largest habitat extent across the three climate scenarios in CLIM-RCP4.5 (*B. schrencki*, *B. mesomelas*, *B. subterraneus*, and *B. muscorum*) or CLIM-RCP8.5 (*B. argillaceus*). *B. pomorum* is the only species which shows the largest habitat loss in CLIM-RCP4.5. There is a tendency of higher absolute habitat losses (darker colors in Figure 3a-i) for species with medium to large baseline extents, particularly in CLIM-RCP4.5 and CLIM-RCP8.5. On a relative scale (Figure 3b-i),

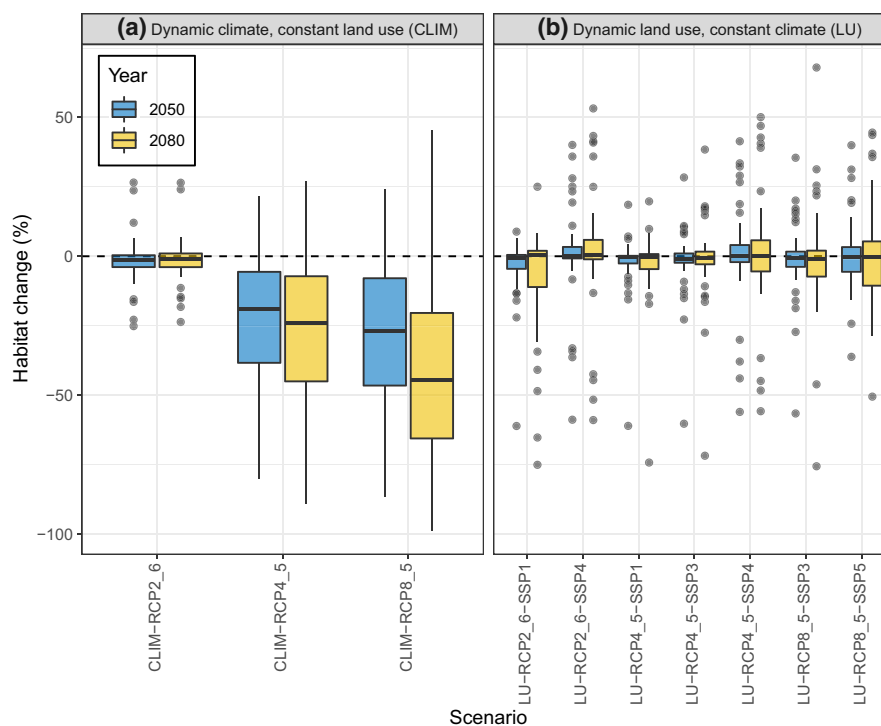


FIGURE 2 Net changes of suitable habitat area for 47 European bumblebee species in response to various levels of climate change (a) and different land-use futures (b)

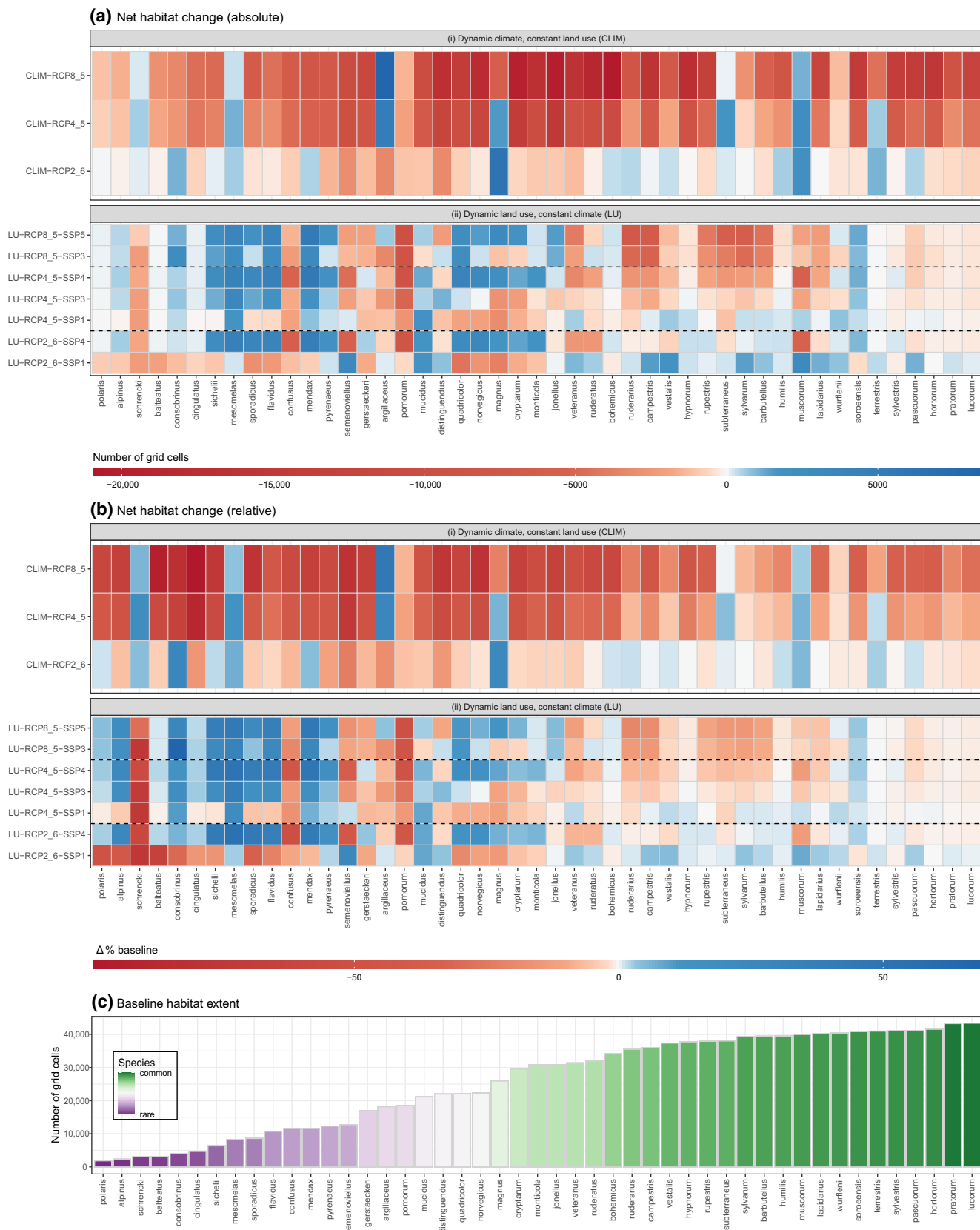


FIGURE 3 Species-specific net changes of suitable habitat extent in 2080 compared to the baseline (~2010) for the CLIM (i) and LU (ii) modeling experiments (a)/(b) and baseline suitable habitat extent (c). Suitable habitat extent is expressed as the number of presence grid cells in (a) and (c), while (b) shows changes as percent difference compared to the baseline suitable habitat extent. Species are ordered along increasing habitat extent in the baseline maps ('rare to common') in all panels. See Figure S5 for results of 2050

it is the rare species that lose larger percentages of their baseline habitat extent.

3.2 | Land-use impact on bumblebee habitat suitability

The extrapolations for the LU modeling experiments (i.e., direct climate effects constant at baseline conditions) generally result in smaller impacts on bumblebee habitat extent compared to the CLIM modeling experiment. Average changes in habitat area in 2080 range from -7.55% in LU-RCP2.6-SSP1 to $+1.90\%$ for LU-RCP2.6-SSP4. A common feature across all LU extrapolations is a large variation in the individual species response and many species identified as 'outliers' in the boxplots (Figure 2b), indicating a large spread in land-use impacts on individual species. In the LU modeling experiments, climate change impacts on land use are considered through the IAP2 scenarios (see Section 2), leading to different outcomes under the same SSP storyline. The SSPs, however, show a consistent land-use impact on bumblebee habitat area across the climate scenarios: combinations with SSP1 cause the largest average habitat losses (-2.45% for LU-RCP4.5-SSP1 in 2050 up to -7.55% for LU-RCP2.6-SSP1 in 2080), while combinations with SSP4 lead to small habitat gains ($+0.82\%$ up to $+1.90\%$ for LU-RCP2.6-SSP4 in 2050 and 2080, respectively).

Land-use change tends to have little effect on common species, while the habitat response is highly variable both in direction and intensity of change for species with low to medium current suitable habitat extent (Figure 3a-ii). Most species (44 out of 47) show a positive response to land-use change in at least one of the scenarios (Table S2). Rare species tend to benefit from land-use changes following the SSP3, SSP4, and SSP5 storylines, while SSP1, which is dominated by agricultural intensification and loss of forest, induces severe habitat losses (up to -75% in 2080). In contrast, common species show habitat increases mostly in scenarios associated with SSP1 land-use changes and habitat losses in SSP3-, SSP4-, and SSP5-related scenarios, indicating a higher adaptive capacity to agriculturally dominated landscapes.

3.3 | Comparison of isolated land-use and climate effects

In Figure 4, the maximum extent of habitat changes observed in 2080 across the three scenarios in the CLIM modeling experiment and the seven scenarios in the LU modeling experiment per species are plotted against each other. While the magnitude of potential net habitat changes is larger for most species in the CLIM modeling experiment (data points below the 1:1 line), land-use effects can be as large as climate effects or even larger for individual species. Climate effects tend to be dominant for species with larger habitat extent in the baseline maps (common species), while land-use effects are of the same order of magnitude for species with smaller habitat extent

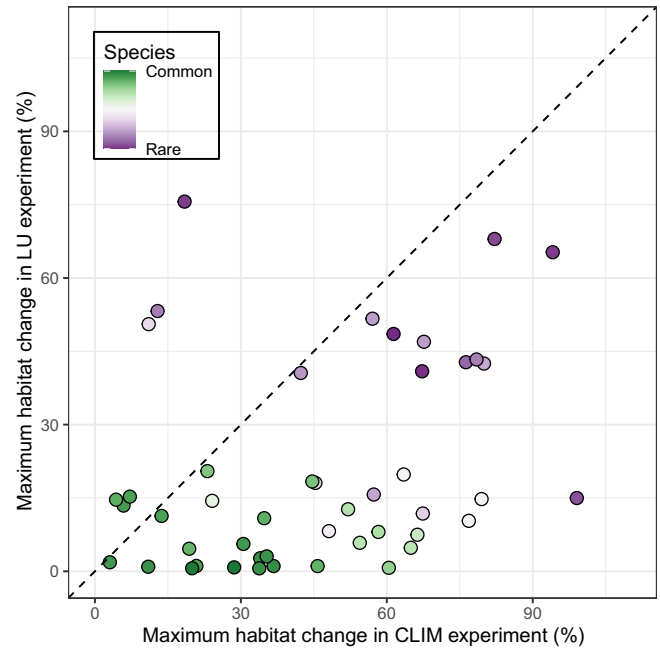


FIGURE 4 Relation between the maximum change in habitat extent in the CLIM scenarios ($n = 3$) and LU scenarios ($n = 7$) in 2080. The maximum change in habitat extent (can be both net gain and loss) is considered as a measure of the potential magnitude of isolated climate or land-use impact across the scenarios, respectively. Each dot represents a bumblebee species. The color gradient is based on the habitat extent in the baseline maps (~ 2010), indicating the rareness/commonness of a species (Table S1). CLIM, dynamic climate and constant land use; LU, constant climate and dynamic land use

in the baseline maps (rare species). Despite the magnitude of habitat changes, the direction of isolated CLIM and LU effects show considerable variation across scenarios and species (Figure 3b). For example, *B. schrencki* shows habitat gains across all climate scenarios, but suffers from habitat losses due to land-use change across land-use scenarios. In contrast, other species (e.g., *B. consobrinus*, *B. sichellii*) experience habitat losses in the CLIM-RCP4.5 and CLIM-RCP8.5 scenarios, but habitat gains in all land-use scenarios but LU-RCP2.6-SSP1. In consequence, the effect of including dynamic land use in the extrapolations may amplify, attenuate, or offset changes to suitable habitat area expected from climate impacts.

3.4 | Land-use modulation within climate scenarios

Given a certain level of climate change (RCP2.6, RCP4.5, or RCP8.5), including dynamic land-use change (COMB modeling experiment) has varying impacts on the species' response across land-use scenarios (Table 5). In a world consistent with RCP2.6 climate in 2080, land use following the SSP1 storyline results in an average additional habitat change of -7.50% , which is largely driven by large losses of individual species (Table S4). In contrast, SSP4 land-use changes

TABLE 5 Average difference of net habitat change response between COMB and CLIM modeling experiments (=land-use modulation) for all species ('Total') and subgroups of species (Q1–Q4) which were grouped based on the quartiles ('Q') of baseline suitable habitat extent

	RCP2.6				RCP4.5				RCP8.5					
	SSP1		SSP4		SSP1		SSP3		SSP4		SSP3		SSP5	
	2050	2080	2050	2080	2050	2080	2050	2080	2050	2080	2050	2080	2050	2080
Q1	-12.48	-31.21	+7.49	+11.37	-6.68	-8.41	-3.33	-1.70	2.36	+4.53	-2.19	-3.31	4.20	+4.48
Q2	-3.25	-1.57	-2.06	-0.75	-3.57	-3.81	-4.63	-4.00	-0.38	0.64	-3.48	-4.80	-0.67	-1.01
Q3	+0.38	+2.35	-0.88	-1.66	-1.33	-0.93	-2.03	-2.43	-2.63	-4.92	-2.76	-5.47	-4.15	-7.34
Q4	+0.46	+1.15	-0.55	-0.83	-0.32	-0.32	-1.44	-1.99	-2.47	-3.23	-2.54	-5.37	-2.01	-3.01
Total	-3.81	-7.50	+1.03	+2.09	-3.03	-3.43	-2.89	-2.54	-0.74	-0.69	-2.75	-4.72	-0.63	-1.69

almost offset average habitat losses from climate change (+2.09%). In the COMB-RCP2.6-SSP1 scenario 22 species lose additional habitat compared to the respective CLIM-RCP2.6 scenario, while 25 species gain habitat. In COMB-RCP2.6-SSP4 19 species lose habitat, while 28 gain habitat; but, more importantly, it is different species that are affected in the one or other direction. SSP1 land use leads to strong additional habitat losses for rare species (-31.21% for the lower quartile) while common species tend to benefit (+2.35% and +1.15% for the third and upper quartiles). SSP4 land use, in contrast, attenuates habitat losses for rare species (+11.37% for the lower quartile) and common species experience additional losses (-1.66% for third and -0.83% for the upper quartile). For 35 out of 47 species, the choice of land-use scenario has an opposite effect on the net change to suitable habitat area (i.e., habitat loss in one land-use scenario contrasts with habitat gain in the other) and for 24 species it has the potential to change the sign of the combined signal compared to the CLIM modeling experiment (Figure 5; Table S2).

Differences between land-use scenarios do also exist in RCP4.5 and RCP8.5 worlds in 2080, although the importance of land-use decreases with higher levels of climate change. The average modulating effect of including dynamic land use is -3.43%, -2.54%, and -0.69% for SSP1, SSP3, and SSP4 in a RCP4.5 climate, and -4.72% and -1.69% for SSP3 and SSP5 in a RCP8.5 climate. For all land-use scenarios, the majority of species experiences additional habitat losses, with COMB-RCP4.5-SSP4 and COMB-RCP8.5-SSP5 representing the scenarios with the largest number of species still likely to gain from land use (20 and 22, respectively). Rare species benefit most from SSP4 in a RCP4.5 climate, and SSP5 land use tends to be more beneficial than SSP3 land use in a RCP8.5 world (Table 5). However, land-use impacts and interactions between land use and climate are—in contrast to RCP2.6—more important than isolated climate impacts for only a few species (Tables S3 and S4).

4 | DISCUSSION

In this study, we extrapolate the potential distribution of 47 European bumblebee species to 2050 and 2080, considering various levels of climate and land-use change, consistent with the RCP-SSP scenario

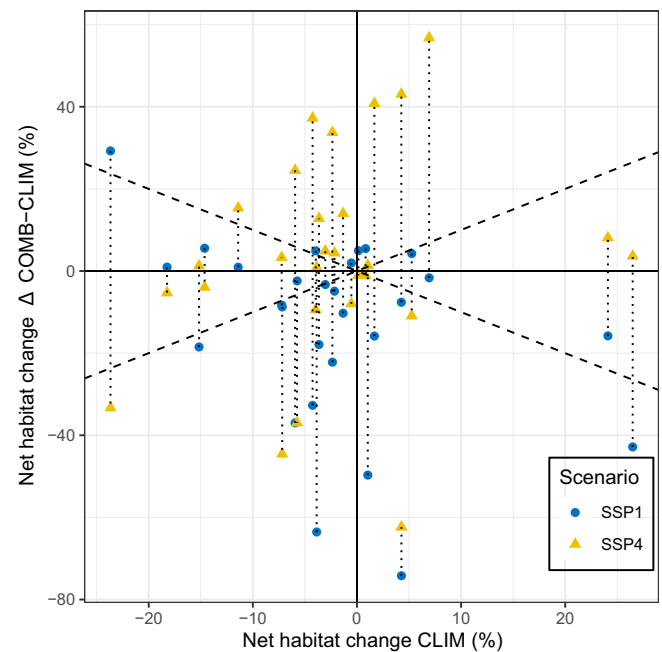


FIGURE 5 Modulation of net habitat response in 2080 in a RCP2.6 climate when dynamic land use is included in the COMB modeling experiment. Species with small effects (<5%) in both land-use scenarios are excluded. CLIM, dynamic climate and constant land use; COMB, dynamic climate and dynamic land use

framework. By contrasting projections with dynamic climate or land use (while keeping the other constant at baseline conditions), we isolate changes to the potential future habitat suitability due to climate and land use, at the species level. An additional modeling experiment with both dynamic climate and dynamic land use allows us to assess the modulating effect of including land use in the SDMs within a given climate. To our knowledge, this is the first implementation of the RCP-SSP scenario framework in bumblebee distribution modeling at the European scale and, hence, it is the first assessment of species dynamics across an established, representative range of potential futures. While we use bumblebees as a target species here, our methodology is also applicable to other taxa.

4.1 | Isolated climate and land-use impact on bumblebee habitat suitability

We find substantial changes to potential bumblebee habitat extent in Europe due to climate change (CLIM modeling experiment; land-use constant) that gradually increase with the severity of climate change. This finding is generally consistent with previous work from Rasmont et al. (2015), who assessed future climatic niches and associated climatic risk for bumblebees under a SRES-based scenario framework. However, our results indicate substantially smaller habitat losses for most species and net habitat gains for a few species in at least one of the RCP scenarios, which is most probably related to differences in methodology and scenarios. For example, Rasmont et al. (2015) use a coarser spatial resolution (50 × 50 km), do not include land-related variables in their SDMs, and use different thresholds (maximization of 'true skill statistic' compared to MaxEnt 'minimum training presence') to derive binary presence/absence maps, all of which have been shown to affect the magnitude of projected habitat changes (Escalante et al., 2013; Marshall, Beckers, et al., 2020). Moreover, the SRES-based scenarios used by Rasmont et al. (2015) are difficult to compare with the RCP-SSP scenarios and for the low-end RCP2.6 scenario there is no 'equivalent' in the SRES framework (van Vuuren & Carter, 2014). Sirois-Delisle and Kerr (2018), who projected potential shifts in the distribution of 31 North American bumblebee species under four RCP scenarios, report similar patterns in the habitat response than found in our CLIM simulation: they show, for example, particularly larger changes of habitat extent in RCP4.5 and RCP8.5 compared to RCP2.6, amplifications of both habitat gains and losses for individual species in higher-level climate scenarios, and the inversion of habitat changes toward the end of the century in RCP2.6 compared to further amplification in RCP4.5 and RCP8.5. The results are indeed not fully comparable to our study due to differences among species and environmental conditions, but North American and European species have been previously shown to respond similarly to climate change (Kerr et al., 2015; Soroye et al., 2020).

Isolated land-use impacts on bumblebee habitat suitability (=LU modeling experiment) can reach similar magnitude than isolated climate impacts (=CLIM modeling experiment; Figure 4), although overall changes in habitat extent due to climate change are larger. Relatively small land-use effects in large-scale assessments and at coarse spatial resolutions have been reported before (e.g., Kerr et al., 2015; Luoto et al., 2007; Marshall et al., 2018). However, the small effects might be to some extent an artifact of the coarse thematic resolution of land-use categories in current assessments that are not able to sufficiently characterize bumblebee habitat (Marshall, Beckers, et al., 2020), as well as of limited land-use change scenarios that do not explore a representative range of future conditions. Nonetheless, we find a large variability of responses to land-use changes across individual species (from up to >65% gain to <-75% loss), reflecting the variation in habitat requirements and ecological traits across bumblebee species (Cariveau & Winfree, 2015; Winfree

et al., 2011). Different land-use storylines result in heterogeneous habitat change responses across species, with SSP1- and SSP4-related scenarios revealing the most contrasting patterns between rare and common species (see Figure 3). While the SSP1 storyline results in widespread expansion of arable land and pasture, both are contracting in the SSP4 scenario. The rare species, which tend to be habitat specialists, may be disproportionately threatened by this strong expansion of agricultural land in SSP1 scenarios (Cariveau & Winfree, 2015; Persson et al., 2015; Rasmont et al., 2015), while common species may better adapt or even benefit from additional resources in agricultural landscapes (Westphal et al., 2003). On the other hand, SSP4 scenarios seem to be beneficial for rare species due to higher availability of semi-natural land while common species might be not able to further expand their existing habitat due to abandoned agricultural land turning to forests in these scenarios, which is not considered a preferred bumblebee habitat (Winfree et al., 2011). While the SSPs represent narrative storylines rather than predictive pathways (O'Neill et al., 2017), previous uncertainty analysis suggests that, in the context of the IAP model used here, SSPs 3 and 4 may produce land-use outcomes reasonably central within overall scenario uncertainty (Brown et al., 2015). This does not necessarily make these outcomes more likely, but suggests that they could be representative of a range of scenario conditions.

4.2 | Game changer land use in a RCP2.6 world?

The COMB simulation (=dynamic climate and land use) suggests that the choice of the land-use scenario becomes particularly important under low-level climate impacts, that is, the RCP2.6 scenario. A majority of the species show substantial discrepancies in response to the two land-use scenarios in a RCP2.6 world, with some species losing >50% of their climatically suitable habitat under one scenario (see Figure 5). In consequence, some of the land-use change impacts on bumblebees seem currently obscured by a focus on climate change and high-end climate scenarios in existing assessments (Titeux et al., 2016). Yet, the way we shape our landscapes in future may turn climatically suitable bumblebee habitat into unsuitable habitat. Similarly, land management strategies targeted at bumblebee conservation may turn locations considered unsuitable under current conditions into suitable habitat in future. How the land-use storyline (SSP1 and SSP4) affects the extent of climatically suitable habitat depends on the ecology of individual species, implying trade-offs between species that may have spatially overlapping habitat. Careful balancing of species requirement is thus needed when developing land-based conservation strategies.

We do not explicitly assess interactions between land-use and climate impacts here nor the impacts on individual stages of the bumblebee life cycle, but both might be less detrimental in a RCP2.6 than in a RCP4.5 or RCP8.5 climate (González-Varo et al., 2013). For example, low-end climate change may make fewer areas in the

North or at higher altitudes suitable for growing crops (Ceglár et al., 2019), thus leaving larger semi-natural areas supporting bumblebee survival. Similarly, if pressure from a changing climate is lower, key stages in the bumblebee life cycle such as hibernation or the founding of new nests may be affected differently (Iserbyt & Rasmont, 2012), allowing some species to survive in less suitable conditions than indicated in our results. On the other hand, the world is arguably not following emission pathways consistent with a RCP2.6 climate at the moment (Hausfather & Peters, 2020) and the effects of including dynamic land use are either small or reinforcing of habitat losses in RCP4.5 and RCP8.5. While our results suggest that land use is important to manage, climate mitigation is relatively more important for future bumblebee distribution.

4.3 | Potential caveats and further research

In our analysis, we link established knowledge on bumblebee distribution (Polce et al., 2018) with land-use projections from the IAP2 (Harrison et al., 2019) based on a mapping between IAP2 and CORINE legends. Uncertainties in this approach remain primarily regarding (1) the quality of mapping between IAP2 and CORINE legends and (2) the relation of CORINE classes to bumblebee habitat. CORINE classes such as 'Heterogeneous agricultural areas' or 'Agricultural land with natural vegetation', by definition include a mixture of agriculture and natural vegetation that cannot be spatially resolved from IAP2 classes. Moreover, as IAP2 outputs are not necessarily consistent with CORINE land cover (Holman et al., 2015), spatial mismatches are unavoidable (Figure S2) and evaluation of the IAP2 land-use projections based on more recent CORINE maps is not possible. We approach these issues by proportionally mapping broad IAP2 land-use classes to the spatial pattern of the CORINE baseline map and assessing changes in comparison to this mapped baseline only. While this approach provides an internally consistent assessment of land-use impact on bumblebee habitat suitability, we advise against using our results as absolute effects, for example, to derive recommendations for conservation management. Instead, the results emphasize the heterogeneous response of individual species to a set of combined climate and land-use changes that requires further attention in future research.

The CORINE predictor variables feeding into our SDMs include little information about land-use intensity (e.g., crop diversification or fertilizer and pesticide application) and landscape configuration (e.g., the availability of floral resources or semi-natural habitat patches within agricultural landscapes). Similarly, the representation of bumblebee habitat with broad land-use/land-cover classes may be overly simplistic at a spatial resolution of 10 × 10 km. Both simplifications have been shown to be important for bumblebee population dynamics and distribution (e.g., Luoto et al., 2007; Marshall, Beckers, et al., 2020). In consequence, a more detailed description of bumblebee habitat would affect some of the results of our analysis. For example, scenarios following the SSP1 storyline lead to a strong increase in agricultural land which translates to severe losses

of suitable habitat for several species, while scenarios following the SSP4 storyline are characterized by the abandonment of agricultural land leading to smaller losses or habitat gains (Harrison et al., 2019; Kok et al., 2019). However, these results may be biased to some extent as in a more sustainable world (=SSP1) agricultural systems may substantially differ from the ones in SSP4 in terms of land-use intensity (Kok et al., 2019; Mitter et al., 2020), resulting in different habitat qualities provided by agricultural landscapes (Persson et al., 2015). Including such effects, however, would require a more mechanistic representation of key ecological processes, which, in turn, rely on far higher-resolution data and modeling than currently available to overcome the limitations of SDM approaches (Singer et al., 2016). A key element for a better understanding of the distribution of bumblebee species as a function of land use and climate is set by the EU pollinators' initiative (European Commission, 2018). Action 1 of this initiative, a European pollinator monitoring scheme is proposed (Potts et al., 2021) based on more than 2000 sites where insects, including bumblebee species, will be systematically monitored. It will provide a valuable source of data to test the assumptions and predictions made in this study. Nevertheless, our analysis provides insights into the modulating effects of land use for bumblebee habitat suitability, especially in a world with limited climate change, where a wise management of land can become a game changer in the conservation of key pollinator species.

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DISCLAIMER

The views expressed in the article are personal and do not necessarily reflect an official position of the European Commission.

DATA AVAILABILITY STATEMENT

Land-use and bumblebee projections are made available at <https://doi.org/10.5281/zenodo.4557528>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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