



SAFEGUARD

**Pan-European maps of current and future
risks for pollinator assemblages and
landscape-level impacts on community
assembly processes under global change**

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Safeguard
Safeguarding European wild pollinators



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Summary

This deliverable reports projected impacts of climate change on European wild bee diversity using Species Distribution Models (SDMs) fitted for 1,086 species, and a complementary mechanistic model of intraspecific floral resource competition in eusocial bees. SDMs were calibrated under current conditions (1980-2015) and projected across six scenario–period combinations (SSP1-2.6, SSP2-4.5, SSP5-8.5 for 2050 and 2090) under three dispersal assumptions (limited, intermediate, unlimited), yielding 18 scenario–dispersal combinations in total.

At large European scales and under the worst-case scenario (SSP5-8.5, 2090, intermediate dispersal), average change in predicted suitability (stacked across all potentially occurring species) across Europe was generally decreasing on average across Europe. Cold-adapted eusocial species (*Bombus*) lost suitability in 97.1% of the grid cells (10 km), while thermophilic generalists (*Anthophora*, *Xylocopa*, *Amegilla*) gained in 97.1% of the cells. This pattern is best characterised as a functional reorganisation rather than a uniform decline, where the composition of the European bee community is projected to shift, rather than to shrink. Functional trait clustering outperformed taxonomy in predicting these trajectories. The Megachilidae family alone contains the strongest projected group of winners (*Megachile*, mean suitability change: +2.0) but also a group of consistent losers (*Chelostoma* and *Heriades*, mean change: -1.6), confirming that genus- or family-level generalisations about pollinator vulnerability can be inadequate.

Our results highlight increasing polarisation of bee diversity across Europe under global change. The current Mediterranean hotspot retreats and fragments under warming, while northern Europe transitions from coldspots toward a zone of relatively suitable conditions. However, dispersal capacity governs whether newly suitable northern habitats translate into biodiversity gains. While under limited dispersal the mean suitability change between the worst-case scenario and current conditions reaches -18.8, under unlimited dispersal it reaches +0.6.

At the landscape scale, the mechanistic consequences of intraspecific floral resource competition for bee colony dynamics and pollination services in heterogeneous agricultural landscapes were investigated using an established model combining optimal foraging and population dynamics, extended to incorporate floral resource depletion and realistic colony dynamics. Intraspecific competition was found to occur late in the season, forcing bees to forage underutilised sites at the limits of their foraging range. The resulting reduction in energy acquisition limits colony peak size and delays its timing, while paradoxically contributing to a more stable and efficacious pollination service. Recently developed dispersal functions to investigate source-sink dynamics demonstrated that source sites have a disproportionate influence on pollination services, directly via foraging and indirectly via maintenance of nest sites in the matrix via dispersal, and that losses of source habitats have a greater proportional impact on pollinators with long-distance dispersal. A simplified version of the model accounting for density-dependent population regulation will be made publicly available via GitHub as a SAFEGUARD product.

List of abbreviations

EU	European Union
SDM	Species Distribution Models
SSP	Shared Socioeconomic Pathways
CMIP6	Coupled Model Intercomparison Project Phase 6
LUC	Land Use Cover

1. Future scenarios

This section presents environmental suitability projections for European wild bees under future climate and land use change scenarios, thereby combining species distribution models with functional trait analysis across a range of future scenarios, time horizons, and dispersal assumptions.

1.1 Methods

1.1.1 Data curating

1.1.1.1 Wild bee occurrence data

As part of D1.1, occurrence data with precise spatial records of pollinators was compiled, comprising a total of 52 bio-geographical databases of European wild bees from both restricted (shared under ad hoc agreement) and public sources. However, publication requirements for certain databases required clustering spatial records into geographic grid cells, which resulted in a uniform simplification at 10 km x 10 km applied across the entire dataset. We filtered all wild bee observations recorded from 1980 to 2015 to allow meaningful comparisons with our extensive large-scale environmental dataset for current conditions and future predictions.

1.1.1.2 Climatic Data

Climatic variables were derived from monthly gridded observation of minimum temperature (Tmin), maximum temperature (Tmax), and precipitation for the years 1980-2015, representing current conditions from the WorldClim database. We then derived four biologically relevant bioclimatic variables: Annual Mean Temperature, Temperature Seasonality, Annual Precipitation, and Precipitation Seasonality. All variables were aggregated across the full temporal window, representing the average climatic conditions during that period.

For future climatic conditions, we collected data from WorldClim v2.1 at 2.5 arc-minute resolution, representing 20-year averages centered on **2050** (i.e. 2041-2060) and **2090** (2081-2100). We also implemented three Shared Socioeconomic Pathways based on CMIP6 models:

- **SSP1-2.6:** strong mitigation with an increase of 1.5-2 Degree C warming.
- **SSP2-4.5:** moderate action or “Middle of the Road” with an increase of 3 Degree C warming.
- **SSP5-8.5:** fossil fuel-intensive development with an increase of 4-5 degree C warming.

In this report, we only used a single CMIP6 General Circulation Model (HadGeM3-GC31-LL). For each combination of scenario (SSP x Time Horizon), we extracted the same bioclimatic variables as described for current conditions.

1.1.1.3 Land cover variables

Land cover data were derived from the LUCAS historical land use and land cover change dataset for Europe (Hoffmann et al. 2021). For the current conditions (1980-2015), annual land cover layers were processed and temporally averaged across all years within each period. Five land cover classes relevant to bee habitat were extracted: bee-friendly habitat (by merging the following LUC: grasslands, heath, wetland margins, and shrublands), coniferous forest, arable cropland, and urban and bare surfaces.

For future projections, land cover data were obtained from LUCAS future land use and land cover change for Europe (Hoffmann et al. 2021b). To ensure consistency between climatic and land cover variables, the same time periods (2050 and 2090) and SSP scenarios were selected. Future land cover projections are therefore scenario-specific, with SSP1-2.6, SSP2-4.5, and SSP5-8.5 land cover trajectories matched to their corresponding climatic projections.

1.1.1.4 Soil variables

Soil composition such as percentage of clay, sand and silt, were derived from the LUCAS topsoil survey (Ballabio et al., 2016). While these variables were considered as constant for the future projections, they influence nesting availability and are highly relevant to ground-nesting bee species. Therefore, these variables were kept in all analyses.

All data were reprojected to the ETRS89 Lambert Azimuthal Equal-Area projection (EPSG:3035) and aggregated to the 10 km x 10 km EEA reference grid. Using hierarchical clustering, we assessed multicollinearity of all variables across all current and future scenarios. We then retained the following environmental variables:

- Annual Mean Temperature
- Annual Precipitation
- Proportion of bee-friendly habitat
- Proportion of arable land
- Proportion of clay
- Proportion of silt
- Proportion of sand

1.1.2 Species distribution modelling (SDM)

1.1.2.1 Creating the SDMs using MaxENT

SDMs were fitted for each bee species using MaxEnt (Phillips et al. 2017) at a 10 km spatial resolution. Prior to modelling, occurrence records and all environmental raster layers were masked to exclude Belarus, Ukraine, Iceland, and Moldova, due to insufficient occurrence data in these regions. Only species with a minimum of ten unique spatially distinct

occurrence records at this resolution and within the current calibration period (1980-2015) were retained for model calibration, yielding 1,136 candidate species.

First, an alpha hull was computed for each species from all cleaned occurrence records using the concaveman algorithm (concavity = 2) (Merow et al. 2013). A species-specific sigma was computed from the median nearest-neighbour distance among occurrence points scaled by a factor of two, constrained to a minimum of 20 km and a maximum of 150 km, in order to reflect plausible connected metapopulations. Background points were sampled within a buffer of twice the sigma around the hull, constraining pseudo-absence space to the ecologically accessible region.

To account for uneven sampling effort across data sources and Europe, we summed up the total number of occurrence records per 10 km grid cell, log-transformed and rescaled to a 0-1 range using min-max normalization, and used it as a probability weight during background point sampling (Phillips et al. 2009; Fourcade et al. 2014). While the hull extent correction described earlier constrained spatial scope, the sampling effort correction corrected for heterogeneity within that scope.

For species with 30 or more occurrence records, a data-driven environmental filtering procedure was applied using the `occfilt_env` function in `flexsdm` (Velazco et al. 2022), tested across bin values of 2 to 10. The optimal bin was selected by minimising mean Moran's I across the three primary environmental predictors, subject to a minimum retention threshold of 30% of original records (using the `occfilt_select` function). If fewer than 10 records remained after filtering, we kept the unfiltered dataset instead. For species with fewer than 30 records, environmental filtering was skipped entirely, as constrained background sampling within the hull provides sufficient implicit bias correction at small sample sizes and information loss from thinning outweighs any gain (Ten Caten & Dallas 2023).

Model predictive performance was evaluated using the continuous Boyce index (Boyce et al. 2002), which measures the correlation between predicted suitability and observed presence frequency across the suitability gradient. This metric is specifically suited to presence-only data. Models with a Boyce index below 0.5 were excluded from all analyses, removing 50 species from the candidate pool and resulting in 1,086 species. In addition, spatial block cross-validation was performed using five folds assigned via `blockCV` (Valavi et al. 2019) with over 100 iterations of random block selection. Mean and standard deviation of cross-validated AUC were recorded for each species.

1.1.2.2 Spatial envelope

Raw MaxEnt outputs were then post-processed using a spatial envelope framework (Thuiller, unpublished). The framework first constructs a smoothed spatial envelope by applying a Gaussian decay function from the alpha hull boundary using the species-specific sigma. Then, a kernel density surface is estimated independently within Louvain-detected occurrence communities using the median nearest-neighbour distance within each community as the kernel density estimate bandwidth, which we clamped between 10 km and 500 km. We then applied the Permanence of Ratios correction, scaling raw suitability by the species' realised spatial envelope and suppressing suitability in areas that are climatically suitable but currently inaccessible (Elith et al. 2011).

1.1.2.3 Future scenarios

SDM suitability outputs were projected onto each of six SSP, as well as year combinations (SSP1-2.6 x 2050, SSP1-2.6 x 2090, SSP2-4.5 x 2050, SSP2-4.5 x 2090, SSP5-8.5 x 2050, SSP5-8.5 x 2090), and using three dispersal scenarios representing the range of biologically plausible range shift outcomes.

Limited dispersal: Species are assumed unable to colonise newly suitable areas outside their current range boundary regardless of connectivity, defined by the spatial envelope calculated for the current conditions. This scenario represents a very limited range expansion capacity.

Intermediate dispersal: Species-specific annual range shift rates were estimated empirically from occurrence records (D1.1) spanning 1960-2020 using a decadal quantile regression approach. Records were assigned to 10-year periods and spatially clustered using DBSCAN (epsilon = 300 km, minimum points = 30) to identify geographically coherent sub or metapopulations. Northern range edges were calculated using quantile regression of decimal latitude on decade midpoint at the 90th percentile (northern edge) (Chen et al. 2011). Slope estimates in degrees latitude per year were then converted to km per year. Species failing quality criteria (enough number of occurrence points or decades for the quantile regression) were assigned cluster-mean shift rates derived from their functional trait cluster (see below for functional trait cluster analysis). Empirically derived shift rates were then applied northward for 2050 and 2090 to define accessible areas under each future scenario.

Unlimited dispersal: Raw MaxEnt suitability projections with no spatial constraint during current and future projections were applied. This overly optimistic dispersal scenario assumes unlimited dispersal of wild bees, irrespective of their geographical starting point. For example, a wild bee species only observed in the south of Spain could reach the north of Norway by 2050 under this dispersal scenario.

While all three dispersal scenarios quantify the sensitivity of projected outcomes to species dispersal capacity, the intermediate scenario is considered the most biologically realistic estimate for most species.

1.1.2.4 Functional Trait Clustering

To identify functional groups with coherent responses to climate change independent of taxonomic identity, species were clustered based on functional trait data using Partitioning Around Medoids (PAM) based on Gower distance, which allows mixed variable types (continuous, ordinal, binary) and missing trait values. Trait information for all wild bees was extracted at the species level from the literature and based on expert taxonomist knowledge (provided by the University of Mons).

Five functional traits related to morphology, biology, ecology, behaviour/behavior and spatial distribution were selected comprising 17 trait categories (Table 1). For the mean intertegular distance (ITD), we only retained trait information for females of non-social and workers of social bees. For nest area, we aggregated the detailed nest area requirements into three major groups: below ground, above ground and both.

Table 1: List of functional and categorical traits selected

Functional trait	Trait categories	Description
ITD	(one continuous variable)	Mean inter-tegular distance of females or workers in mm
Sociality	Solitary, parasocial, facultive inquiline, eusocial, cleptoparasite	Degree of sociality
Voltinism	Univoltine, bivoltine, multivoltine	Number of generation a species displays within a year
Nesting area	Belowground, above ground, both	Area where bees species build their nests
Lecty	Oligolectic, polylectic, cleptoparasitic	Foraging behaviour
Species Temperature Index	(one continuous variable)	Mean temperature of a species' distribution area

1.1.3 Spatial Analyses

1.1.3.1 Stacking suitability

Predicted stacked suitability maps were generated by summing individual species suitability scores across all 1,086 species for each scenario and dispersal combination. We applied this stacking approach at three levels of taxonomic and functional aggregation. First, we stacked all species suitability maps to estimate overall wild bee suitability across Europe. Then we generated genus-level and functional trait cluster subsets. In this report, we will only focus on the following genera: *Bombus*, *Andrena*, *Megachile* and *Colletes*. Similarly, we only discuss the results of a few functional clusters, which will be defined in the results section below.

The resulted stacked suitability values do not represent species richness in the traditional sense. Each grid cell receives a value reflecting the sum of predicted environmental suitability scores across all species considered (overall, genus-level, trait cluster), where higher values indicate that more species find this particular cell highly suitable. A high stacked suitability score is thus a grid cell where conditions are favourable for a large number of species, whereas a low score indicates that only few species might find these conditions favourable.

1.1.3.2 Hotspot and coldspot detection

Spatial hotspots and coldspots of bee suitability were assessed using the Getis-Ord G_i^* statistic, which identifies statistically significant local clustering of high (hotspots) and low (coldspots) suitability values relative to the European mean. G_i^* was computed for each period, scenario, dispersal combination, and taxonomic/clustering grouping. Significance thresholds of 99% confidence (z -score > 2.58 or < -2.58) were applied to identify hotspot and coldspot grid cells. The spatial neighbourhood was defined using a fixed distance band of 20 km. Changes in hotspot extent between periods were quantified as the absolute and proportional change in the number of significant hotspot or coldspot cells.

It is important to note that a hotspot identified under future conditions does not necessarily indicate an improvement in absolute suitability compared to current conditions. A hotspot simply means that a given cell is significantly more suitable than the European average for that specific time period and scenario. If overall suitability declines across Europe but declines less severely in a particular region, that region may emerge as a hotspot in 2090 relative to the degraded European baseline, even though fewer species find it suitable in

absolute terms compared to current conditions. Hotspots and coldspots are therefore not absolute gains or losses across the scenarios.

1.2 Results

1.2.1 Current distribution of European wild bee suitability and spatial clustering

Summed suitability across all 1,086 European wild bee species revealed a pronounced south-north gradient in the current distribution of bee diversity across the continent (Figure 1). Mean summed suitability across all valid European grid cells was 117.0, with peak values reaching 367.0 in the most suitable cells. The Mediterranean basin consistently supported the highest suitability values, with particularly elevated concentrations across the Iberian Peninsula, southern France, and the Italian and Balkan peninsulas. Suitability declined progressively northward, with Scandinavia and the British Isles carrying the lowest values across the continent.

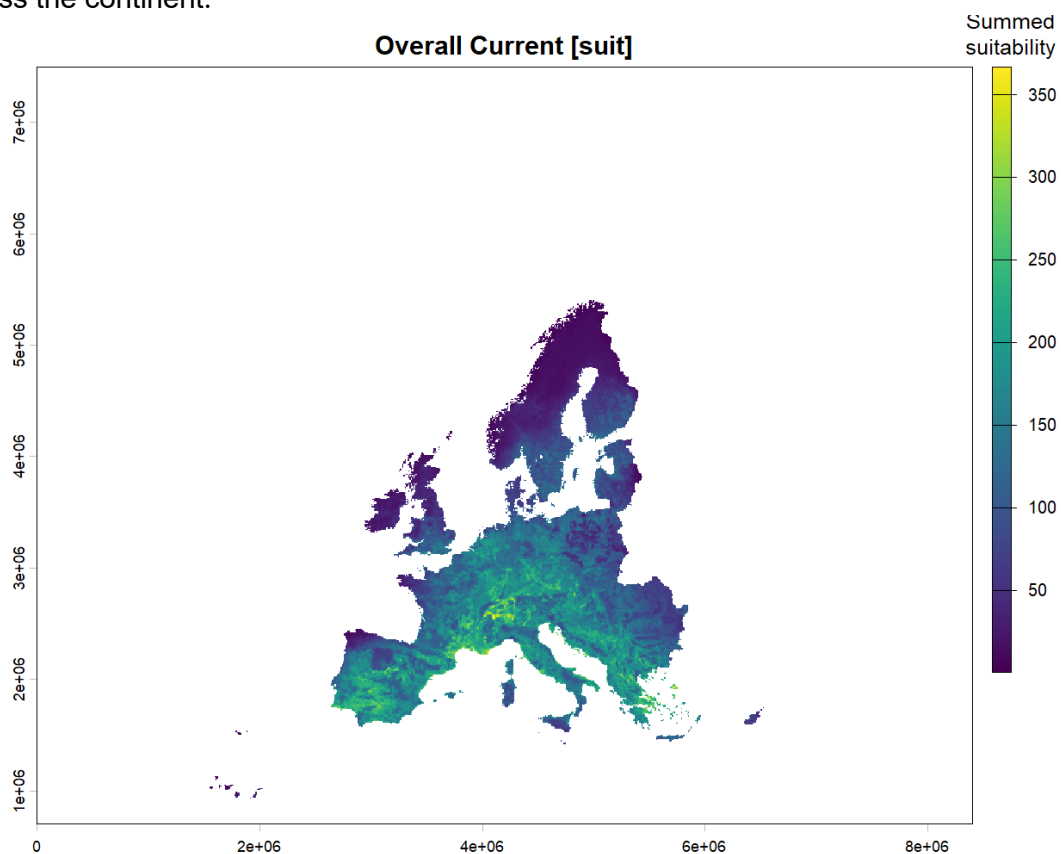


Figure 1: Stacked habitat suitability for wild bees across Europe under current conditions.

Getis-Ord spatial analysis identified hotspot zones at the 99% confidence level encompassing 11,365 cells across the Mediterranean arc, with an additional 2,949 cells classified as hotspot at the 95% level (Figure 2). Corresponding coldspots dominated the northern periphery, with 11,032 cells classified as coldspot at 99% confidence and a further 2,724 at 95%. Northern-central Europe, spanning much of Germany and Poland, occupied a spatially intermediate zone of largely non-significant values between these two poles, punctuated by discrete 99% hotspot patches across the Netherlands, the Rhine region, Austria, and extending further east into the Czech Republic, Slovakia, and Hungary. The

near-symmetry between hotspot and coldspot cell counts underlines the bipolar continental structure of current European bee diversity, with the Mediterranean basin and northern Europe representing opposing extremes of a single continental gradient.

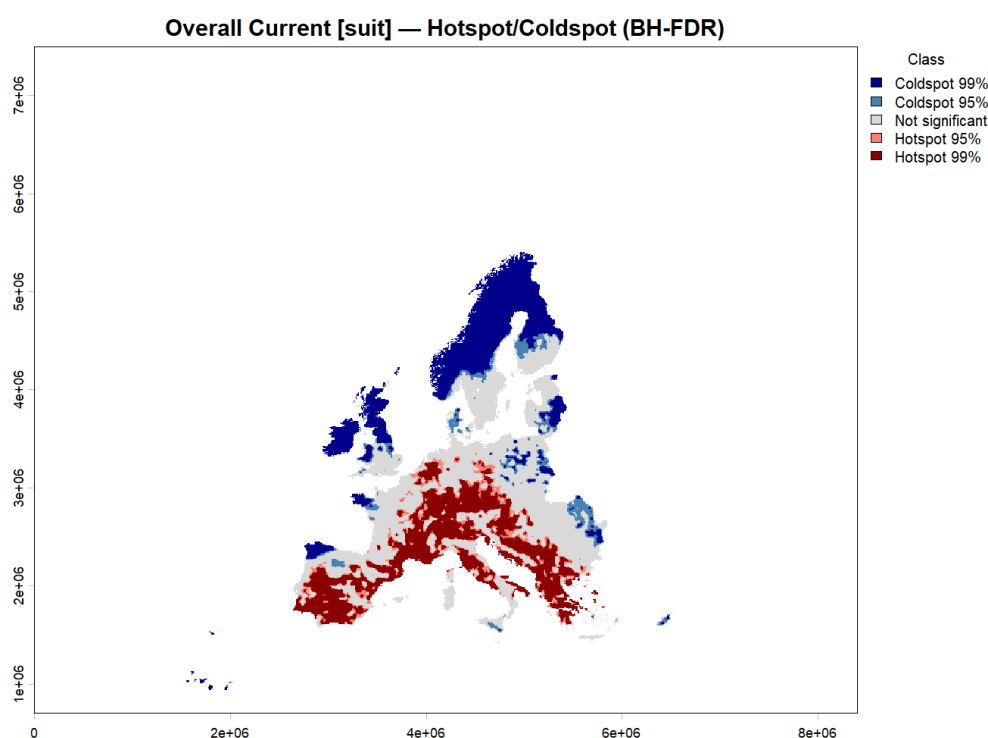


Figure 2: Spatial hotspots and coldspots of wild bee diversity across Europe under current conditions.

1.2.2 Future scenarios showing spatial polarisation of hotspots

Under all three emissions scenarios and across both time horizons, projected suitability declined relative to current conditions under the most realistic intermediate dispersal scenario, with the magnitude of change increasing with emission severity (SSP scenarios) and time horizon (Figure 3).

Under SSP1-2.6 by 2050, mean suitability change was -9.8 with 65.3% of cells losing, moderating to -2.0 and 46.0% by 2090 as partial northward redistribution offset southern losses. Under SSP2-4.5 the pattern intensified (2050: -10.6, 65.0% losing; 2090: -3.0, 45.3% losing). The most severe trajectory, SSP5-8.5, projected a mean change of -12.3 by 2050 with 64.7% of cells losing, and -2.9 with 48.5% losing by 2090. The apparent improvement from 2050 to 2090 reflects cumulative northward colonisation under intermediate dispersal rather than any improvement in climate conditions. For instance, under limited dispersal, where no such colonisation occurs, the 2090 trajectory is marginally worse than 2050 across

all three SSPs (Figure 4).

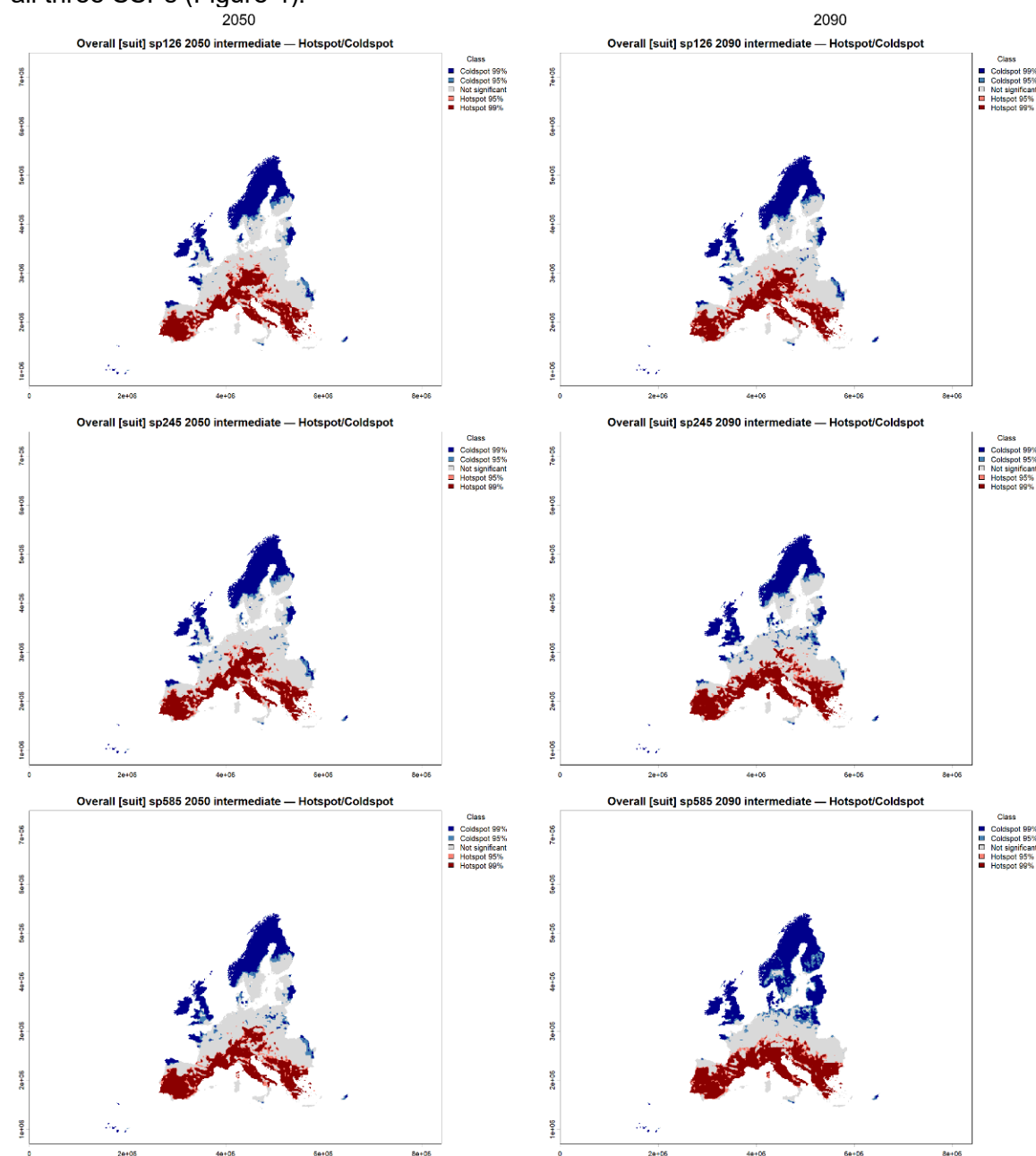


Figure 3: Spatial hotspots of wild bee diversity across Europe under future climate scenarios.

Under the scenario SSP5-8.5 2090, hotspot cell count increased to 13,438 while coldspot cells reached 14,424, both being above the current conditions' values of 11,365 and 11,032 respectively. However, this does not reflect improvement. Indeed, hotspots and coldspots are defined relative to the European mean for that period. Suitability collapses across southern Europe while partially redistributing northward, increasing the contrast between zones and increasing spatial polarisation, where the northern coldspot expands and consolidates while the Mediterranean hotspot retreats and fragments. This results in a structural reorganisation of the current north-south gradient rather than a proportional decline across the continent.

1.2.3 Dispersal capacity and future scenarios

The magnitude and geography of projected suitability can vary substantially across dispersal assumptions, revealing high sensitivity of outcomes based on species dispersal capacity. Here, we look at the projected changes in overall suitability of wild bees between the worst-case scenario (SSP5-8.5) and current conditions, by comparing how dispersal capacity may impact those changes (Figure 4).

Under limited dispersal, which assumes species are unable to travel beyond their current ranges, mean suitability change across Europe was -18.8, with 73.9% of cells experiencing net loss and only 26.1% gaining. Under intermediate dispersal, reflecting biologically plausible range shifts, mean change was -2.9 with losses and gains near parity at 48.5% and 51.5% respectively. Under unlimited dispersal, which assumes no constraint on range expansion into newly suitable habitats, the mean was near-neutral at +0.6, with 44.0% of cells losing and 56.0% gaining.

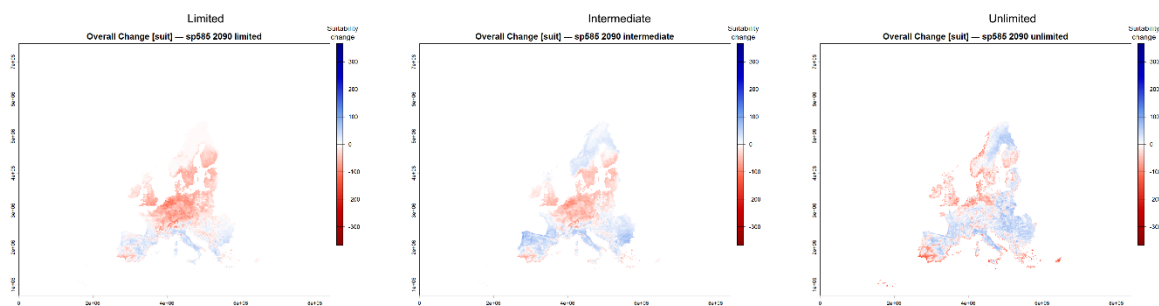


Figure 4: Projected changes in suitability between SSP5-8.5 2090 and current conditions, under different dispersal scenarios.

The direction of change was consistent across all three assumptions. However, while southern Europe lost overall suitability under every scenario and dispersal rate, its magnitude and the extent of northern gain varied considerably. Under limited dispersal the northern domain showed neither gain nor loss because species were unable to colonise newly suitable habitats regardless of their availability. Under intermediate and unlimited dispersal, newly suitable northern cells demonstrated gains that partially offset southern losses at the European scale. The prime examples being the Macaronesian islands and Cyprus, which show little changes under limited and intermediate dispersal in contrast to the unlimited dispersal scenario.

1.2.4 Genus level changes in projected suitability change

Here, we focus on projected suitability changes between SSP5-8.5 2090 and current conditions, with intermediate dispersal, for four focal genera: *Bombus*, *Andrena*, *Megachile*, and *Colletes*.

As the projected suitability changes differed substantially among the genera, revealing sharply divergent trajectories, it also reflected contrasting ecological profiles. *Bombus* showed the most severe geographically widespread decline, with mean suitability change of -7.3 and losses recorded in 97.4% of European cells (Figure 5a). The near-total absence of gain anywhere across the continent confirms *Bombus* as the most exposed genus in the European fauna, reflecting the cold-adapted thermal physiology of this genus. Gain was recorded in only 2.6% of cells, confined to the northernmost periphery of the modelled range.

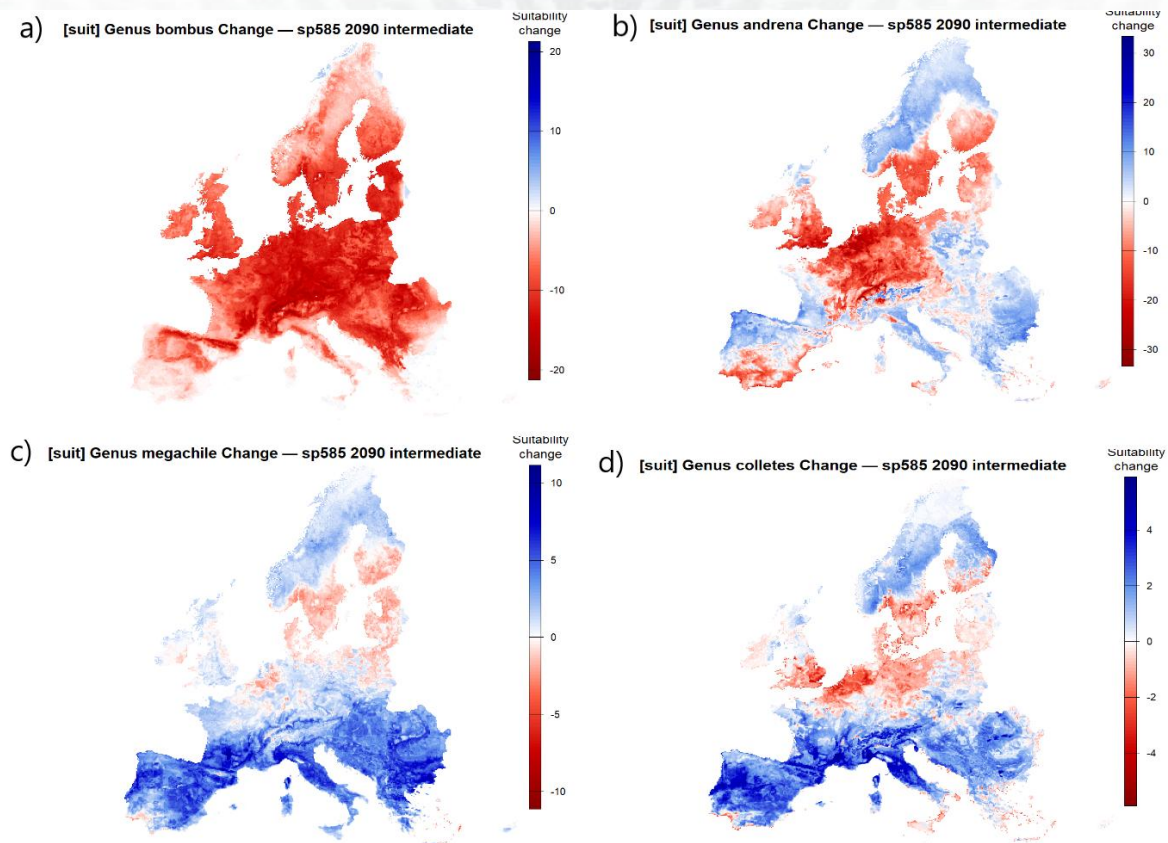


Figure 5: Habitat suitability change between the future scenario SSP5-8.5 2090 and current conditions for the genera a) *Bombus*, b) *Andrena*, c) *Megachile* and d) *Colletes*, all under intermediate dispersal.

Even under unlimited dispersal assumptions, *Bombus* showed no noticeable gain, confirming that its decline is driven by direct thermal unsuitability rather than dispersal limitation (Figure 6).

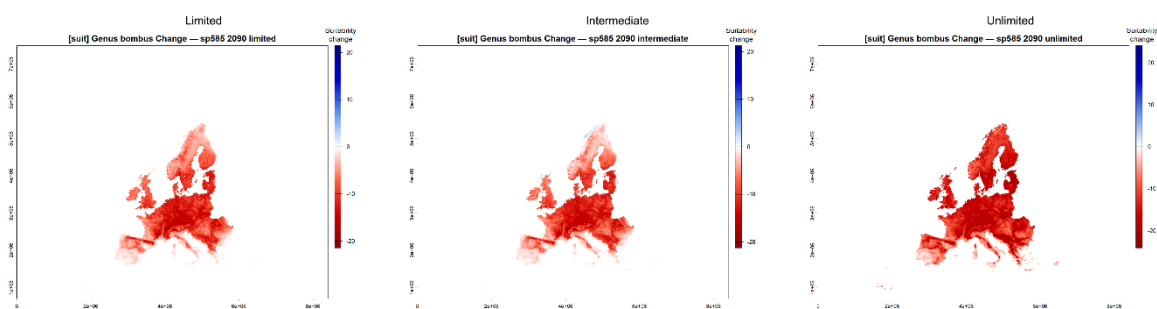


Figure 6: Habitat suitability change between SSP5-8.5 2090 and current conditions for the genus *Bombus*, across all three dispersal scenarios.

Andrena showed overall intermediate losses, with a mean change of -1.8 and near-equal proportions of losing (51.0%) and gaining (49.0%) cells (Figure 5b). This resulted in a structured pattern of Mediterranean loss and central-to-northern European gain, reflecting the ecological heterogeneity of this large and taxonomically diverse genus.

Megachile was the clearest winner among the focal genera, with mean change of +2.0 and gains in 79.8% of cells. As thermophilic, largely polylectic, cavity-nesting genus, *Megachile* is projected to capitalise on northward expansion of thermally suitable habitats under intermediate dipsersal (Figure 5c).

Finally, *Colletes* showed a positive mean change of +0.8, with gains in 70.3% of cells (Figure 5d). Yet, the genus-level suitability change map also revealed a spatially incoherent pattern, with strong gains in the south and strong losses in the Netherlands, Denmark, north of Germany and Poland, highlighting a more nuanced picture than simply labeling clear winners.

1.2.5 Functional cluster analysis

The functional clustering of our 1,086 species produced 21 clusters, four of which were recovered as genus-dominated clusters. For instance, clusters 11 (all *Bombus* and one *Seladonia*), 9 (mostly *Andrena*), 19 (mostly *Nomada*), and 17 (all *Megachile*), all validated the clustering approach by recovering ecologically coherent taxonomic groups from trait data alone. The remaining clusters were cross-taxonomic, assembling species from multiple genera and families around shared functional traits.

Among the genus-dominated clusters, cluster 11 (*Bombus*) showed the most severe projected decline, with mean suitability change of -6.9 and losses in 97.1% of cells, consistent with the *Bombus* genus-level results reported in 1.3.4 (Figure 5 and Figure 7). Hotspot cell count contracted from 11,115 under current conditions to 7,869 under this scenario, representing a 29.2% reduction in the spatial extent of statistically significant suitability concentration. Cluster 9 (*Andrena*) showed moderate loss with mean change of -3.5 and losses in 62.6% of cells (Figure 7). Cluster 17 (*Megachile*) however showed a mean change of +2.0 and gains in 79.8% of cells, while hotspot cell count increased from 9,040 to 12,185, resulting in a 34.8% expansion (Figure 7). Cluster 19 (*Nomada*) showed near-neutral aggregate response with mean change of +0.4 and near-equal proportions of losing (45.0%) and gaining (55.0%) cells, reflecting their identity as cleptoparasites and their likely larger dependence on host species trajectories (Figure 7).

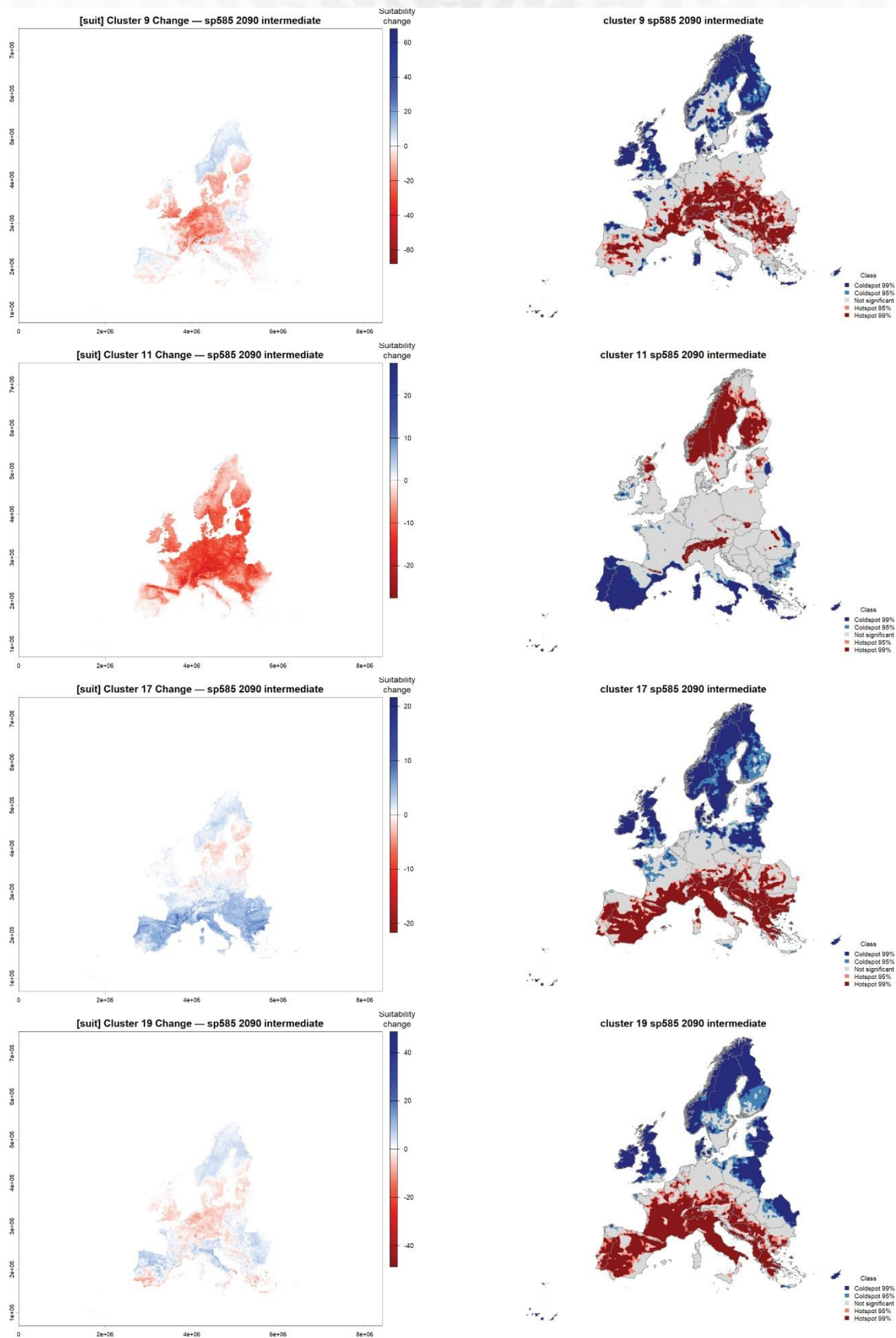


Figure 7: Habitat suitability changes between the future scenario SPP5-8.5 2090 and current conditions for the clusters 9, 11, 17, and 19, all under intermediate dispersal. Hotspot and coldspot for the scenario SPP5-8.5 2090 are also shown for each cluster.

Vulnerability and resilience patterns were not phylogenetically structured, with functionally coherent clusters spanning multiple genera and families (Figure 8). Cluster 10, comprised of *Chelostoma*, *Macropis*, *Melitta*, *Panurgus*, *Dufourea*, *Rophites*, *Heriades*, *Panurginus*, and others across multiple families, emerged as a robust cross-taxonomic loser, with losses in 74.1% of cells and mean change of -1.6. These small oligolectic specialists suggest that ecological specialisation may constitute an independent climate vulnerability beyond the obvious thermal constraints driving *Bombus* decline. Cluster 4, comprising *Anthophora*, *Amegilla*, *Xylocopa*, *Habropoda*, *Rhodanthidium*, *Dasypoda*, and others across Apidae, Megachilidae, and Melittidae, emerged as the strongest cross-taxonomic winner with gains in 97.1% of cells, mean change of +3.3, and hotspot expansion from 7,187 to 10,955 cells. Cluster 5, representing small-bodied cavity-nesting thermophiles including mostly *Ceratina* and a diverse assemblage of Mediterranean specialists, gained in 81.6% of cells with mean change of +1.0.

The near-perfect symmetry between cluster 11 (*Bombus*, 97.1% losing) and cluster 4 (thermophilic large-bodied generalists, 97.1% gaining) is perhaps the starkest result of this analysis. Cold-adapted social bees and thermophilic generalists sit at opposing ends of a climate vulnerability gradient, and their near-identical proportions moving in opposite directions reflect a functional replacement rather than a net loss. Crucially, clusters 10 and 4 show that this gradient extends well beyond the *Bombus*-*Megachile* contrast, cutting across taxonomy and including species from multiple genera around shared functional traits of vulnerability and resilience.

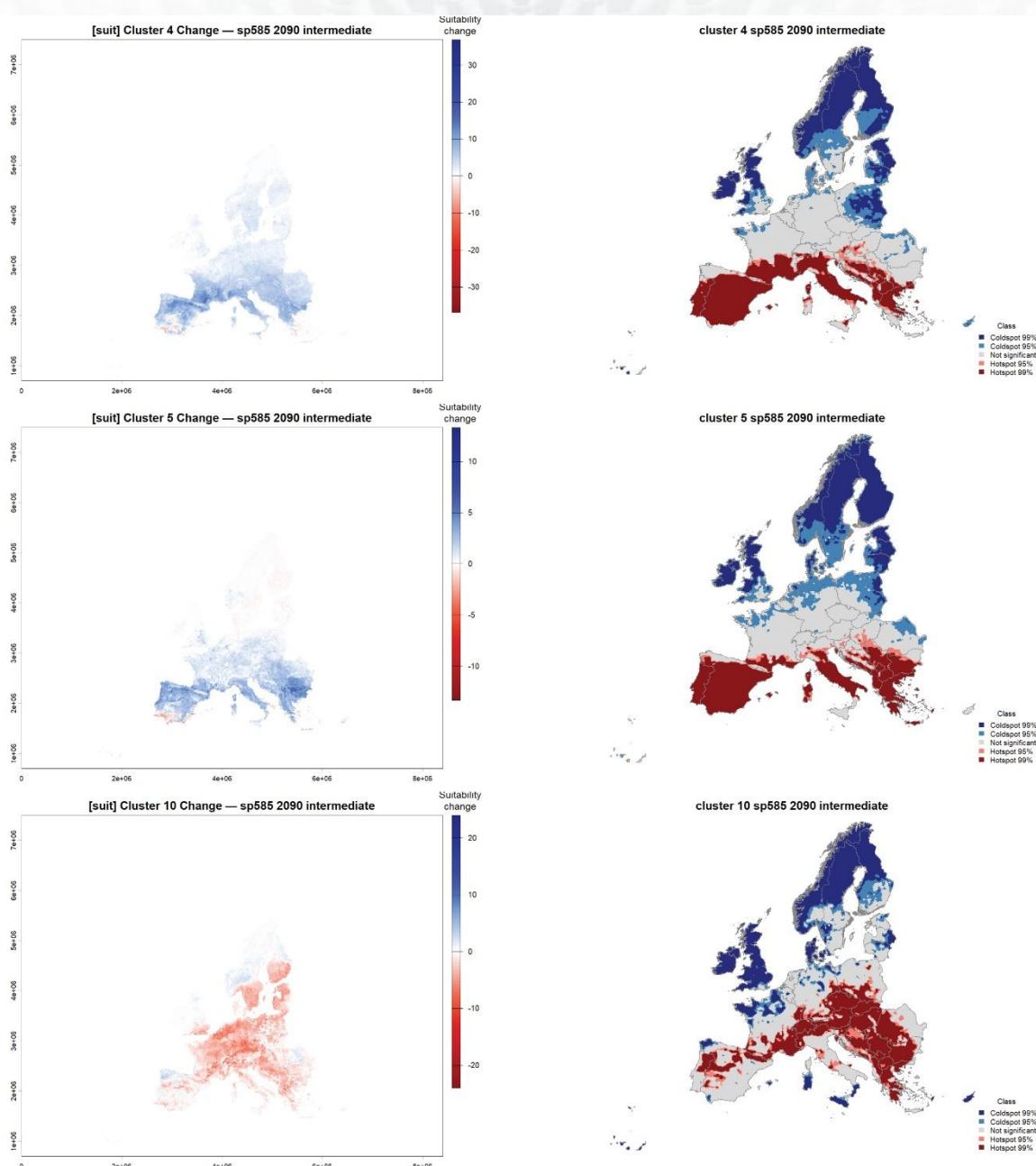


Figure 8: Habitat suitability changes between the future scenario SPP5-8.5 2090 and current conditions for the clusters 4,5, and 10, all under intermediate dispersal. Hotspot and coldspot for the scenario SPP5-8.5 2090 are also shown for each cluster.

1.3 Discussion

1.3.1 A functional reorganisation of wild bees

Our results show that projected climate change impacts on European wild bee diversity are better characterised as a functional reorganisation than a uniform taxonomic decline. Under the worst-case scenario and intermediate dispersal, the overall mean suitability change was only -2.9, yet it revealed opposing trajectories of similar magnitude. Cold-adapted, socially complex, and specialist species drive the collapse of the Mediterranean hotspots, while

thermophilic generalists drive the emergence of a northern concentration zone. While these opposing trends partially cancel at the European scale, their ecological significance is far greater than what the stacked suitability of all wild bees suggests.

This distinction indeed matters, because a uniform decline would suggest that European bee diversity is contracting toward a smaller version of its current composition. On the other hand, a functional reorganisation means the composition itself is changing: the bees of 2090 may well be functionally different from today. The cold-adapted eusocial *Bombus* group and the specialist assemblages of cluster 10 are exactly the groups projected to lose most range. Their roles as pollinators of boreal and alpine plant communities, as well as specialised to oligolectic plant hosts, will unlikely be replaced by the thermophilic generalists projected to expand into newly suitable habitats.

1.3.2 Taxonomy as an insufficient predictor of climate vulnerability

The functional clustering approach revealed that taxonomic identity is a relatively poor predictor of climate trajectory, consistent with the broader finding that life history traits outperform phylogeny in predicting extinction risk across taxa (Cardillo et al., 2005; Pearson et al., 2014). The *Colletes* case illustrates this at the genus level. Initially suggested a climate winner, the genus also contained a net-losing cluster. This aligns with the conservation literature that coarse taxonomic surrogates are not sufficient proxies for functional vulnerability, particularly within species and ecologically diverse genera.

More revealing, however, is where taxonomy and functional traits do align. The clustering independently recovered genus-dominated clusters for *Bombus*, *Andrena*, *Megachile*, and *Nomada* from trait data alone, suggesting that where ecological coherence is phylogenetically conserved, the functional approach naturally recovers taxonomic structure. *Megachilidae* illustrates well where traits and taxonomic diverge. The same family encompasses the strongest projected winners (cluster 17, *Megachile*, +2.0, 79.8% gaining) and some of the most consistent losers (cluster 10, *Chelostoma* and *Heriades*, -1.6, 74.1% losing). Dietary specialisation, body size, and thermal niche appear to be more reliable predictors of climate trajectory than taxonomy alone, and genus- or family-level generalisations about pollinator vulnerability should be treated with considerable caution.

1.3.3 Dispersal capacity as a determinant of reorganisation severity

Southern suitability loss was severe under all three dispersal assumptions, confirming that Mediterranean decline is driven by global change rather than dispersal capacity. Even under unlimited dispersal, where species can potentially move all over Europe, southern losses still persisted.

What dispersal determines is whether newly suitable northern habitats translate into biodiversity gain, and while it does not under limited dispersal, it partially does under intermediate and unlimited dispersal. However, it is never enough to offset southern losses at the continental scale. This distinction is particularly relevant for cold-adapted species such as *Bombus*, where gains were extremely minimal even under unlimited dispersal, suggesting that newly suitable habitats remain negligible for this group regardless of how far they can travel, and that their decline is mainly a thermal constraint rather than a dispersal problem.

1.3.4 Hotspot dynamics and the spatial inversion of bee diversity

The increase in overall hotspot cell counts from 11,365 under current conditions to 13,438 under SSP5-8.5 2090 does not reflect more suitable areas for bees, but rather reflects the opposite. When suitability declines broadly across Europe, the areas that hold up relatively well become increasingly distinct from the degraded surrounding landscape, which is what drives stronger clustering, not an absolute improvement in conditions. The hotspot expansion signals a contraction of suitable habitats into fewer, more distinct refugia rather than any genuine gain. As a result, wild bees are not spreading but concentrating into the areas that remain relatively tolerable as the surrounding habitats deteriorate.

At the functional level, this concentration is driven by trait syndromes. The contraction of the Cluster 11's hotspot extent reflects the collapse of cold-adapted social bee concentrations across the Mediterranean zones, whereas the expansion of cluster 4 and 17 hotspots reflects thermophilic generalists consolidating in the north. The net increase in hotspot cells is therefore not a recovery signal, instead the areas that remain highly suitable in 2090 are simply occupied by a functionally different community than the hotspots of today.

1.3.5 Limitations and perspectives

While our SDM framework captures environmental suitability, it does not incorporate biotic interactions or their mismatches, e.g. between bees and host plants. The functional clustering is also limited by trait data completeness across our 1,086 species.

That being said, the direction of functional reorganisation was consistent across all 18 scenario-dispersal combinations regardless of SSP scenarios or dispersal assumptions. European wild bee diversity under climate change is heading toward functional replacement in addition to proportional decline. This trajectory will have consequences for plant-pollinator community structure that go well beyond what species-level richness metrics typically capture.

2. Consequences of intraspecific competition for floral resources in heterogeneous landscapes for bees

The mechanistic consequences of floral resource competition for bee colony dynamics and pollination services in heterogeneous agricultural landscapes have since been published by Walters et al. (2024).

"Agricultural intensification is widely recognised as a primary driver of pollinator loss, but the success of land-management actions designed to remediate its impact is often mixed. Payments to farmers to increase habitat connectivity or the availability of floral and nesting resources may only result in short-term gains or even unintended consequences. The reasons may lie in changes to interaction networks or competition intensity that remain poorly understood. Models of pollination service typically implicitly assume pollinator population dynamics are regulated by nest-site availability, even though empirical evidence suggests nest-site occupancy is likely at least in part dependent on floral resource availability. To investigate the consequences of competition for floral resources in coarse-grained agricultural landscapes we extended an established model for bees combining optimal foraging and population dynamics, to include new functions for floral resource

depletion and realistic colony dynamics. We find that intra-specific competition occurs late in the season forcing bees to forage underutilised sites situated further towards their foraging range limits. A lower rate of energy acquisition ultimately limits the size of the colony peak and delays its timing. Consequently, competition for floral resources can limit population size and distribution while at the same time contributing to a more stable and efficacious pollination service. Although competition was not found to be important in nest-site establishment success, the effect of a hunger gap early in the season on nest-site occupancy indirectly influences competition later in the season leading to complex outcomes."

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3. Modelling bee population dynamics and pollination services in agricultural landscapes

In the first part of SAFEGUARD, ULUND developed and improved mechanistic models translating land-use change and agricultural management to predictions on population densities and pollination capacity, including key functions such as including explicit foraging functions allowing dynamic landscape use, improved colony dynamics allowing accounting for phenological variation in food availability and food depletion to allow explicitly accounting for population regulation. We have now shown the utility of this model in accounting for large-scale source-sink dynamics, which is planned as a manuscript (Figure 9). However, the published version of the model does not allow for large-scale predictions due to computational demands, so we have been working with a simplified model that still is able to account for density-dependent population regulation by forage availability; this model will be published on GitHub for free use as a SAFEGUARD product.

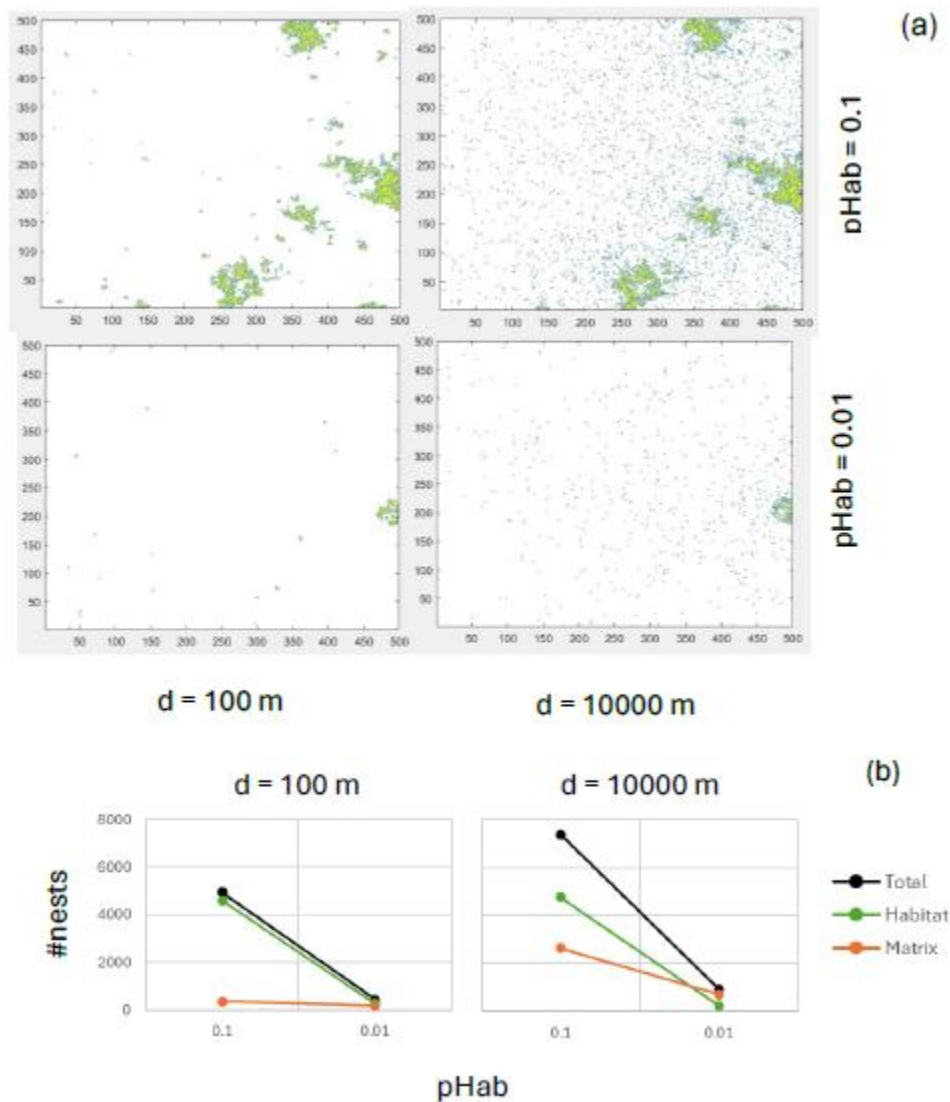


Figure 9: Example model output from recently developed dispersal functions to investigate source-sink dynamics. We simulated the effects of passive dispersal on nest-site occupancy in simulated landscapes (using the midpoint displacement fractal algorithm). These landscapes can vary in the amount of semi-natural habitat ($pHab$), its aggregation (H , Hurst parameter), and area in matrix suitable for nesting (pN matrix). These functions have been integrated into Walters et al. (2024) to investigate correlations between local visitation rates and pollinator abundance at different spatial scales. Initial findings reveal source sites have a disproportionate influence on pollination services, directly via foraging and indirectly via maintenance of nest sites in the matrix via dispersal (sink areas). (a) Nest sites in relation to amount of source habitat and the dispersal distance of generic bumblebee species with different dispersal distances. (b) The consequences of habitat loss for bumblebee abundance across the landscape, separately for the whole landscape, the source habitat and the agricultural matrix ($H=0.25$, $pN_{matrix} = 0.05$). Note that loss of source habitat has a greater proportional impact on those pollinators with long-distance dispersal. These findings have important implications for defining *threshold amounts of habitat* in intensively managed landscapes for different species, both in respect to population viability and the maintenance of ecosystem services.

4. References

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