



SAFEGUARD

Synthesis report on cross-scale impacts of multiple pressures on pollinators

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**Safeguard
Safeguarding European wild pollinators**



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List of abbreviations

AIC	Akaike information criterion
EEA	European Environment Agency
EU	European Union
ITD	Inter-tegular distance
GLMM	Generalized linear mixed models
NA	Missing values
RLQ	R-mode linked to Q-mode analysis
TERENO	Terrestrial Environmental Harz/Central German Lowland Observatory
VIF	Variance Inflation Factor

Summary

The recent decline in pollinator populations, with their significant ecological and economic importance, has prompted global attention, leading to concerted national and international efforts to address these declines. While numerous pressures, including climate change, land cover, land-use intensity, and vegetation phenology, have been recognized, existing studies often focus on individual pressure groups and spatial scales, leaving a gap in understanding the combined impacts across multiple scales.

Our study aims to bridge this gap by investigating the direct and indirect effects of these factors on pollinator species richness across Europe at various spatial scales, using wild bee distributional data collected as part of D1.1 and data of species traits as part of D1.2. We found significant associations between species richness and climate, land cover, land use intensity, and vegetation. Species richness generally increased with higher mean annual temperatures, but responses varied among wild pollinator taxonomic groups and spatial scales, suggesting high context dependency. Positive relationships between bee-friendly habitats and wild bee species richness highlighted the importance of habitat quality and resource availability for pollinators. Agricultural intensification and high nature value farmlands showed mixed effects on pollinator richness, with responses differing across taxonomic groups. A multi-trait approach highlighted climatic conditions and land cover as major filters of functional wild bee community composition, emphasizing the importance of considering

species-specific responses to environmental pressures, particularly within the context of climate change.

We also identified strong impacts of extreme heat and drought events on local wild bee populations, leading to severe declines in the majority of species and even to local extinctions for some. The severity of such an extreme event depended on species traits, initial population stability and the landscape context. Our results also show options for land use-based mitigation which should aim at (i) increasing population stability; (ii) increasing the amount of woody features such as hedgerows and mass flowering crops locally; and (iii) increase the proportion of semi-natural habitat at the landscape scale to buffer negative effects of heat and drought waves.

Overall, our results support calls for tailored conservation strategies for bees, focusing on habitat restoration, sustainable farming practices, climate change adaptation, and urban green space enhancement to support pollinator diversity. To achieve this, a strong legislative framework (such as the currently suggested Nature Restoration Law of the European Commission) is urgently needed.

1. Objectives

- (i) Assess how large-scale environmental variables such as climate, land cover, land-use intensity, and vegetation phenology influence species richness of wild bees at multiple scales and to quantify and disentangle the relative importance of these pressures across Europe.
- (ii) Analyse the impact of functional traits on wild bee community assembly processes and how environmental pressures can shape pollinator communities.
- (iii) Identify context-specific responses of wild bee populations to extreme weather events.

2. Methods

2.1. Pollinator distribution data

As part of Task D1.1, distributional information with precise spatial records of pollinators was compiled. A total of 52 bio-geographical databases of European wild bees were collected from both restricted (shared under ad hoc agreement) and public sources. However, publication requirements for certain databases, such as those from Greece and The Netherlands, required clustering spatial records into geographic grid cells, which resulted in a uniform simplification at 10 km x 10 km² applied across the entire dataset. To mitigate potential observer and sampling bias inherent in the data collected from the various sources, we established minimum observation thresholds for each grid cell at different spatial scales (10 km x 10 km, 25 km x 25 km, and 50 km x 50 km) to enhance the reliability and representativeness of our dataset. Specifically, we required a minimum of 150 observations per grid cell at the 10 km x 10 km scale, 250 observations per grid cell at the 25 km x 25 km scale, and 350 observations per grid cell at the 50 km x 50 km scale. This filtering process helped minimize the impact of sparse or unevenly distributed data points, thereby improving the validity of our analyses. Similarly, we filtered all wild bee observations recorded from 1980 to the present to allow meaningful comparisons with our extensive large-scale environmental dataset.

We measured species richness for all wild bees and for each of the primary wild taxonomic groups outlined in D1.1. Within the Apidae group, we made the distinction between taxa from the *Bombus* genus and the remaining taxa of the Apidae group, resulting in a total of six “taxonomic groups”: Apidae (excluding *Bombus*), all *Bombus*, Megachilidae, Halictidae, Andrenidae, and Melittidae.

2.2. Wild bee trait data

Trait information for all wild bees was extracted at the species level from the literature and based on expert taxonomist knowledge (University of Mons).

Five functional traits related to morphology, biology, ecology, behaviour 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

2.3. Large-scale environmental variables

To assess the impact of a pan-European set of pressures on the community composition of wild bees, we gathered information on pressures from high-resolution data derived from various sources covering (i) climate, (ii) land cover, (iii) land-use intensity, and (iv) vegetation phenology at three spatial scales: 10 km x 10 km, 25 km x 25 km and 50 km x 50 km (Table 2).

At each spatial scale, large-scale environmental variables were aggregated within the corresponding grid cell size by calculating the mean values of the continuous variables and proportions of the categorical variables at the chosen temporal resolution. The data was then reprojected to the desired common projection ETRS89-extended / LAEA Europe, using the “sf”, “terra”, “raster” and “exactextractr” packages (Fig. 1).

Table 2: Overview of the large-scale environmental variables gathered, with their respective spatial and temporal resolution

Dataset	Spatial resolution	Temporal resolution	Source
Bioclimatic variables	~ 1km	1970-2000	WorldClim
Soil surface moisture	0.1 x 0.1 degree	1991 – 2022	Copernicus
Corine Land Cover	100 x 100 meters	2018	Copernicus
Nitrogen input to agro-ecosystems	1 x1 km	2010	EEA
High Nature Value Farmland	100 x100 m	2012	EEA
Length of the growing season	500 x 500 m	2000 - 2015	EEA

2.3.1. Climate

We collected long-term bioclimatic variables (30-year averages from 1970-2000; spatial resolution of 30 arc sec, ~1km) related to annual trends (i.e., mean annual temperature and annual precipitation sum) and seasonality (i.e., annual range in temperature and precipitation) from the WorldClim database (Fick and Hijmans 2017).

Additionally, we obtained data on soil surface moisture (0-7cm depth) from ERA5-Land (via Copernicus), with records from 1991 to 2022 and a temporal and spatial resolution of 1 hour and 0.1 x 0.1 degrees.

2.3.2. Land cover

Corine Land Cover data was extracted from Copernicus for the year 2018, providing land use information at a resolution of 100 m x 100 m. While consisting of 44 distinct land use categories, the data underwent a reclassification process to create three aggregated land cover types relevant to wild bees.

First, areas primarily designated for agricultural activities, such as crop cultivation and farming, were reclassified as arable land. This category includes non-irrigated and permanently irrigated arable land, vineyards, as well as annual and permanent crops and other land principally occupied by agriculture.

Second, we reclassified land use areas suitable for supporting bee populations and promoting pollinator diversity as bee-friendly habitat. This category mostly encompasses natural and semi-natural habitats known to provide suitable foraging and nesting sites for wild bees, including natural grasslands, moors and heathland, sclerophyllous vegetation, transitional woodland-shrub and sparsely vegetated areas. Additionally, it includes broad-leaved and mixed forests, green urban areas, fruit tree plantations, pastures, and olive groves.

Finally, we grouped under the urban category all developed areas characterized by human-made structures, infrastructure, and built environments. This classification includes cities,

towns, residential areas, industrial zones, and other urbanized landscapes dominated by buildings and paved surfaces.

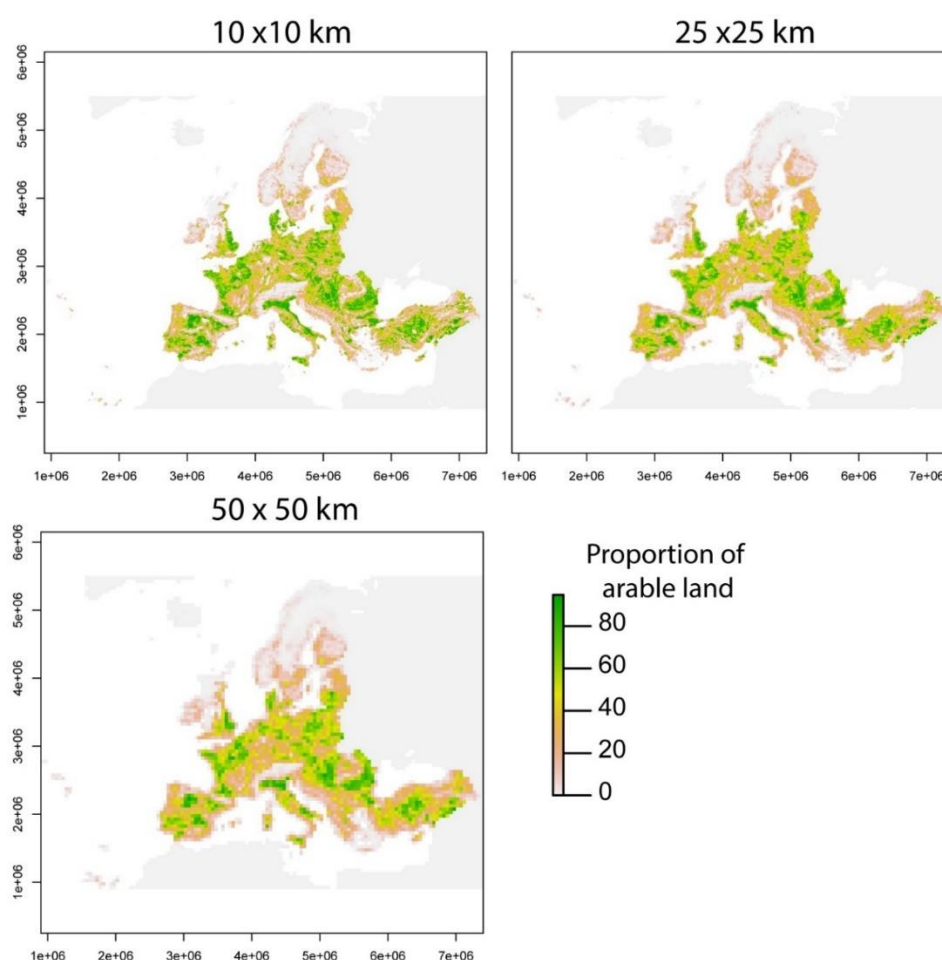


Figure 1: A comparison between the proportions of arable land aggregated at different spatial scales: 10 km x 10 km, 25 km x 25 km and 50 km x 50 km grid cells.

2.3.3. Land-use intensity

We selected two indicators of land-use intensity: a) the amount of nitrogen input to agro-ecosystems and b) the proportion of high-value nature farms, both extracted from the European Environment Agency (EEA).

Information on total nitrogen input to agricultural soils was only accessible for the year 2010, measured in kg/ha/year at a resolution of 1 km.

High nature value farmlands (100 m resolution) included semi-natural pastures, meadows, and orchards, along with peripheral semi-natural features like large hedges. More importantly, these areas represent low-input farming systems as opposed to intensive agricultural farming systems, and were not correlated with bee-friendly habitats as described in 2.3.2.

2.3.4. Vegetation phenology

To address vegetation phenology, we collected information representing trends in the season length of land surface vegetation growth, which were derived from remote sensing time series of vegetation indices. The indicator uses the Plant Phenology Index (PPI), and was based on

time series ranging from the years 2000 to 2015. These datasets were sourced from the European Environment Agency (EEA) at a resolution of 500 m.

2.4. Statistical analyses

2.4.1. Cross-scale impact of stressors on pollinator composition

All analyses were performed in the R software (ver. 4.3.3) (R Core Team 2024).

To assess the relative importance of large-scale environmental variables on overall wild bee species richness across multiple scales, we performed generalized linear mixed effects models (GLMMs), using the “glm.nb” from the “MASS” R-package (Bates et al. 2015). Prior to the analyses, multicollinearity among independent variables was assessed using the variance inflation factor (VIF), calculated with the “vif” function from the “car” package (Fox and Weisberg 2019). Species richness of all wild bees was used as a response variable; however, due to the testing across multiple spatial scales, the presence of correlated variables was detected at various spatial resolutions. At the scale of 10 km x 10 km, the final explanatory variables included in the models were annual mean temperature, annual precipitation, precipitation seasonality, temperature seasonality, soil surface moisture, proportion of arable land, bee-friendly habitat and urban areas, nitrogen input (log-transformed), and length of the growing season. At the scale of 25 km x 25 km, soil surface moisture was excluded. At the scale of 50 km x 50 km, soil surface moisture and the proportion of urban areas were excluded. To assess potential context-dependency of the impact of arable land on wild bee richness, an interaction effect between annual mean temperature and arable land was included in all models. GLMMs were fitted with a negative binomial error distribution, following validation and model assumptions (Zuur, Ieno, and Elphick 2010). The relative importance of all explanatory variables was determined using a multi-model inference approach. First, we used the ‘dredge’ function from the R-package ‘MuMIN’ (Bartoń 2009) to select all combinations of best models based on the lowest Akaike information criterion (AIC) with $\Delta AIC_c < 2$. The relative importance of each predictor from the best models was then quantified using the “varImp” function from the “caret” package (Kuhn 2008). Models were developed for all wild bees and separately for the main wild taxonomic groups described in 2.1.

2.4.2. Relationships between pollinator traits and environmental variables

The relationships between pollinator traits and large-scale environmental variables were analysed using a combination of RLQ (Dolédéc et al. 1996) and fourth-corner analyses (Legendre, Galzin, and Harmelin-Vivien 1997). It allows for the simultaneous analysis of three tables: an environmental table (named R), a species traits table (named Q), and a species presence-absence table (named L) that is used as the link between Q and R. Due to missing values, we had to focus on the following environmental variables: Annual mean temperature, annual precipitation, precipitation seasonality, temperature seasonality, and the proportions of bee friendly habitats, arable land, urban areas and high nature value farmlands, data aggregated at the 10 km x 10 km spatial scale, and the following species traits: ITD, sociality, voltinism, nest area requirement, lecty, and species temperature index. We then performed a principal component analysis (PCA) on the environmental table and the trait table by considering species and site weights derived from the correspondence analysis species scores. We assessed the overall significance of the relationship between wild bee traits and large-scale environmental variables via a Monte-Carlo test (999 random permutations) and clustered the species into groups using the Calinski-Harabasz stopping criterion to identify the

optimal number of clusters based on Euclidian distances between species along the first two RLQ axes and Ward's hierarchical clustering. Following the RLQ analysis, we performed a fourth-corner analysis by testing the correlation between each wild bee trait and each environmental variable, using Pearson r correlation coefficients. We used the library *vegan* (Oksanen et al. 2007) for the cluster analysis, and the library *ade4* (Dray and Dufour 2007) for the RLQ and fourth-corner analyses.

2.5. Population response to extreme weather events

2.5.1. Population trends, species traits, and environmental data

Wild bee populations have been monitored within the Terrestrial Environmental Harz/Central German Lowland Observatory (TERENO; Zacharias et al. 2011) at six agricultural landscapes of 4 km x 4 km. The landscapes are located in Saxony-Anhalt, Central Germany, and represent typical agricultural landscapes within this region. Within each landscape, we monitored 16 local wild bee communities (in total 69 communities) with standardised pan traps annually from 2010 to 2021 (still ongoing; Frenzel et al. 2016). Traps were emptied biweekly and operational for six weeks in spring to early summer and six weeks in late summer. Collected specimens were identified to species level by experts. During these observation years, in 2018 a severe heat and drought wave was affecting the entire ecosystem (Fig. 2).

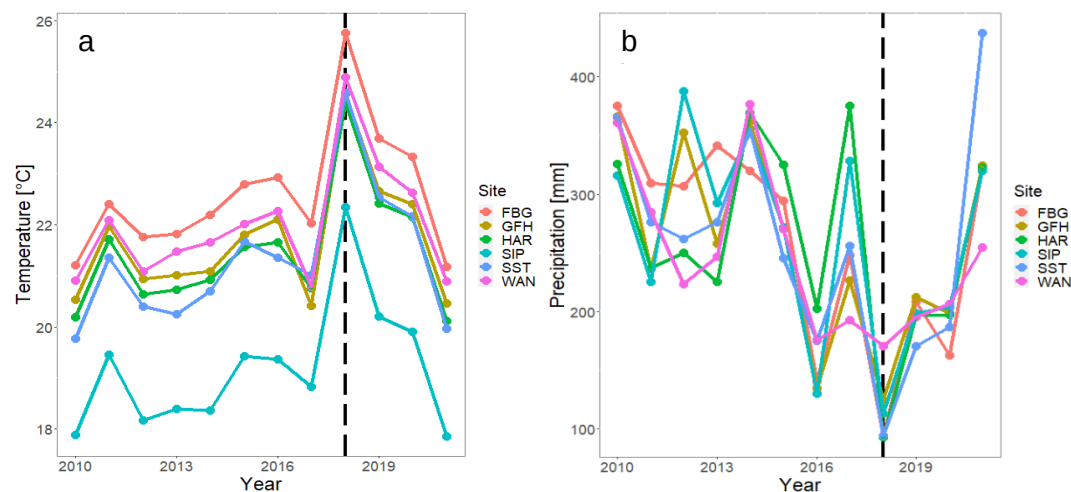


Figure 2: Temperature (a) and precipitation patterns during the period of wild bee monitoring in agricultural landscapes. Weather data were calculated as mean daily maximum temperatures and precipitation sum across the observation period covering the flight activity of the majority of species (April to August). The dashed vertical line indicates the year of an extreme weather event (2018). Data have been obtained from the closest weather stations of the German Weather Service.

To assess potential context-dependency of population-specific responses to this extreme weather event, we used species traits and landscape characteristics at the local and landscape scale. We selected the following species traits: (i) ITD as a reliable measure of body size and a highly relevant trait related to multiple ecological processes, in particular to temperature performance (Gérard et al. 2018); (ii) species temperature index (STI) and (iii) species continentality index, which have been shown to define responses to changing climates (Devictor et al. 2012); and (iv) nest location, which has been classified into above- and below-ground, since a potential buffer mechanism for below-ground nesters has been assumed. We calculated the following landscape metrics from digitised habitat maps at the local scale within

a radius of 200 m of the respective pan trap: percentage of (i) semi-natural habitat; and (ii) woody features; (iii) area of mass flowering crops (mainly oilseed rape); (iv) Shannon diversity of different crop types; and at the landscape scale: percentage of (v) semi-natural habitats; and (vi) woody features.

2.5.2. Statistical analyses

To assess the impact of the extreme weather event, we split the data set into a period before the event (period0; 2010 to 2017) and a period of and after the event (period1; 2018 to 2021) to cover direct effects in 2018 as well as potential legacy effects thereafter. To minimise a potential 'visitor effect', we restricted the data set to species occurring in at least 10 locations and with at least four years of local occurrence, leading to a final data set covering 63 wild bee species and 1453 populations at the local scale (pan traps) and 568 (meta-)populations at the landscape scale (4 km x 4 km landscapes).

We measured the change in population size from one period to the other by a population-specific change index defined as the mean abundance during period0 (before the event) divided by the sum of the mean abundances in period0 and period1 (during and after the event). This index ranges between zero and one, with 0.5 indicating no change, 1 indicating total loss of the population, and values approaching 0 indicating strong increases in population size. In addition to the impacts of species traits and landscape characteristics, we also included internal population dynamics in the subsequent analyses, since the level of temporal stability of a population can have a considerable impact on its response to additional pressures. As a measure of temporal population stability, we calculated the respective coefficient of variance during period0 for each population. Since in particular effects of the landscape context and population stability can be scale-dependent, e.g. in the context of meta-population dynamics, we conducted analyses at two spatial scales, the local population scale (pan traps) and the landscape scale (4 km x 4 km landscapes).

We used linear mixed effects models to explain population-specific differences in the change index by population stability before the extreme event, species traits and landscape characteristics at two spatial scales. Impacts of potential multi-collinearity were excluded, verified with the variance inflation factor. For analyses at the local population scale, we included proportions of semi-natural habitat and woody feature at both (local and landscape) scales, while for analyses at the landscape scale local scale landscape characteristics were excluded. To identify potential synergistic or antagonistic effects, in particular between population stability, species traits and landscape characteristics, we included the interactions of population stability, ITD and species temperature index respectively with proportions of semi-natural habitat and woody features, and area of mass flowering crops at local scale for local scale analyses. For analyses at the landscape scale, interactions were tested for proportions of semi-natural habitat and woody features at the landscapes scale. To control for pseudo replication and to consider potential effects of phylogenetically related species, we used two crossed random effects for local scale analyses: landscape and species nested in genus. For analyses at the landscape scale, only species nested in genus was considered as a random effect. Models were simplified with a stepwise backwards approach based on p-values for conservative hypothesis testing. To quantify the relative importance of the explanatory variables, we calculated semi-partial R^2 s following the Nakagawa and Schielzeth approach (Nakagawa, Johnson, and Schielzeth 2017).

3. Results

3.1. Cross-scale impact of stressors on pollinator composition

After applying a threshold for a minimum number of observations per grid cell, our dataset consisted of 3284 grid cells at the 10 km x 10 km spatial scale, compared to the initial 4148 available grid cells. At spatial scales of 25 km x 25 km and 50 km x 50 km, there were 2323 and 1365 grid cells, respectively. Similarly, the threshold affected the total number of bee species included in the analyses, resulting in 1602 species at the 10 km x 10 km scale, 1734 species at the 25 km x 25 km scale, and 1806 species at the 50 km x 50 km scale.

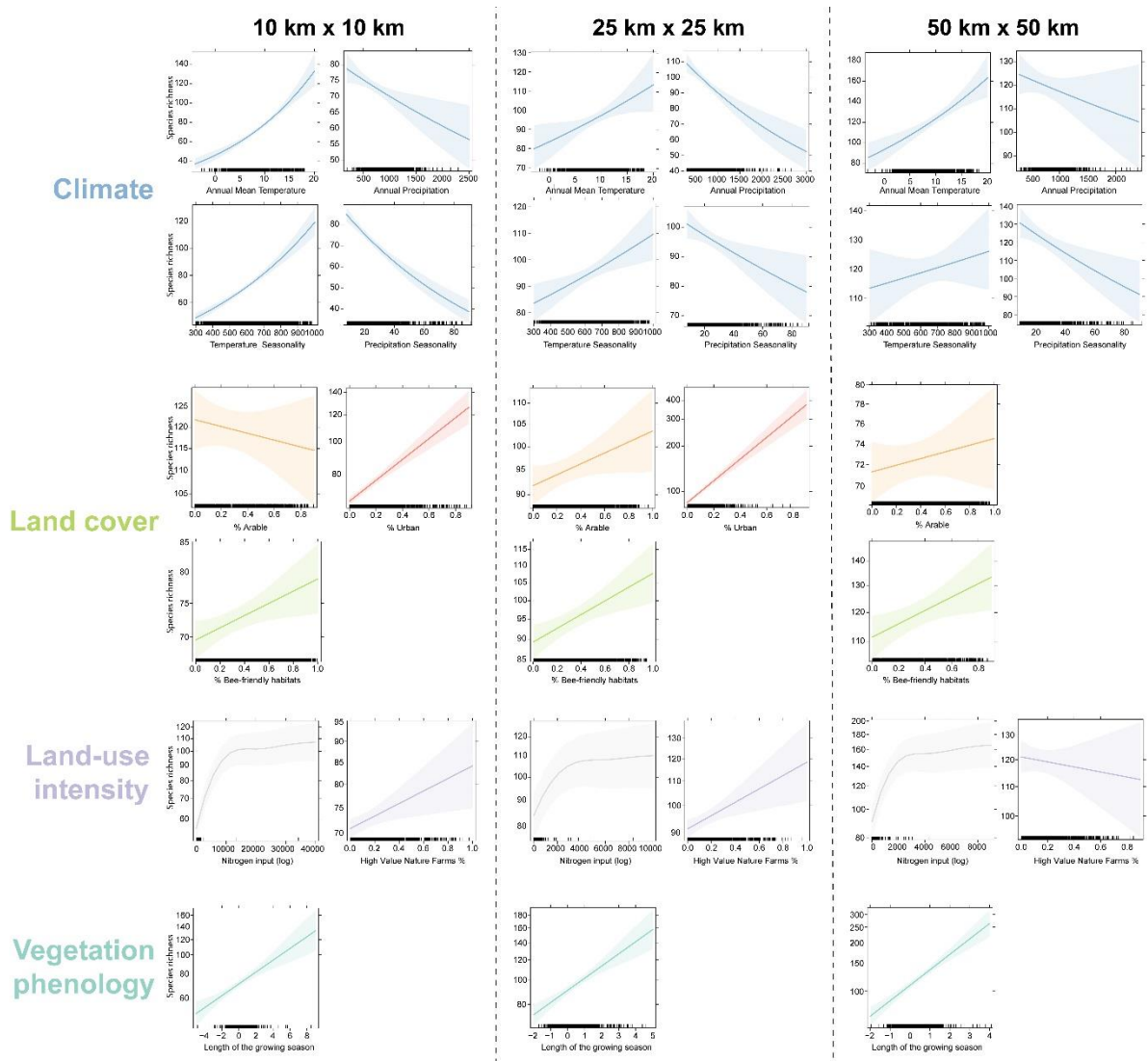


Figure 3: GLMMs representing relationships between species richness of all pollinators at the scales of 10 km x 10 km, 25 km x 25 km and 50 km x 50 km.

3.1.1. Climate

The overall species richness of all wild bees was positively correlated with both annual mean temperature and temperature seasonality, and responded negatively to annual precipitation and precipitation seasonality consistently across all spatial scales (Table 3, Fig.3). Analysing the richness of various taxonomic groups separately revealed nuanced responses to climatic conditions. Annual mean temperature showed a consistent negative impact on the richness of bumble bees across all scales. In contrast, it was in general positive for all other groups, with the exception of Megachilidae, Halictidae, and Melittidae at the 25 km scale and Halictidae at the 10 km scale, where its impact was negative. The effects of temperature seasonality on bee species richness varied across spatial scales and taxonomic groups with the only consistent responses of *Bombus* (negative), Halictidae (negative), and Megachilidae (positive; Table 3).

Responses of species richness to annual precipitation were mostly taxon-specific but consistent across all scales, with negative correlations observed for the species richness of Apidae, Megachilidae, Halictidae, and Melittidae, while *Bombus* and Andrenidae richness responded positively. Responses to soil surface moisture reflected that of annual precipitation. Similarly, most taxonomic groups exhibited negative responses to precipitation seasonality across all scales, except for Megachilidae and Halictidae richness, which displayed positive correlations at the 25 km x 25 km scale (Table 3).

3.1.2. Land cover

The proportion of bee-friendly habitats, arable land, and urban area had a consistent positive effect on overall wild bee species richness across all spatial scales, with the exception of a negative impact of arable land at the 10 km scale (Table 3, Fig. 3).

Similar to climatic conditions, the richness of taxonomic groups in relation to the proportion of land cover exhibited taxon-specific and scale-dependent patterns (Table 3). The only consistent pattern was found for the impact of bee-friendly habitat on Andrenidae (positive) and Melittidae (negative); the impact of arable land on *Bombus* (positive), and Megachilidae and Halictidae (both negative). In contrast, the proportion of urban areas was positively associated with species richness across all taxonomic groups and at all spatial scales (Table 3).

Table 3: Summary of the positive (“+”) and negative (“–”) effects of large-scale environmental variables on the different taxonomic groups at each spatial scale.

	Annual Mean Temperature			Annual Precipitation			Temperature Seasonality			Precipitation Seasonality			Soil surface moisture			Bee-friendly habitat %			Arable land %			Urban %			Nitrogen input			High Nature Value Farmlands			Length of growing season		
Scale (km)	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50	10x10	25x25	50x50
All wild bees	+	+	+	-	-	-	+	+	+	-	-	-	-			+	+	+	-	+	+	+	+		+	+	+	+	+	-	+	+	+
Apidae	+	+	+	-	-	-	+	-	-	-	-	-	-			+	+	+	-	-	-	+	+		+	+	+	+	+	+	+	+	+
Bombus	-	-	-	+	+	+	-	-	-	-	-	-	+			+	-	+	+	+	+	+	+		-	+	+	-	-	-	-	-	+
Megachilidae	+	-	+	-	-	-	+	+	+	-	+	-	-			-	-	+	-	-	-	+	+		+	+	+	+	+	+	+	+	+
Halictidae	+	-	-	-	-	-	-	-	-	-	+	+	-			+	-	-	-	-	-	+	+		+	+	+	-	-	-	+	+	+
Andrenidae	+	+	+	+	+	+	+	-	+	-	-	-	-			+	+	+	-	+	+	+	+		+	+	+	+	+	-	+	+	+
Melittidae	+	-	+	-	-	-	+	+	-	-	-	-	+			-	-	-	+	-	+	+	+		+	+	+	+	+	-	-	-	-

Positive effects of arable land were surprising, but analyses of interaction effects revealed its dependency on temperature (Fig. 4). For overall species richness of all wild bees, the impact of arable land was positive only under cooler conditions, while it turned into a negative impact under warmer conditions. This effect was most pronounced at the 50 km scale, while it flipped at the 25 km and 10 km scales (Fig. 4).

For the separate taxonomic groups, the interaction effect was similar to that observed for all wild bees at the 50 km scale in most of the cases. The impact of arable land was positive under cool conditions at all spatial scales (Andrenidae, *Bombus*, Melittidae), and negative under warm conditions across all spatial scales (Megachilidae, Melittidae) (Fig. S15).

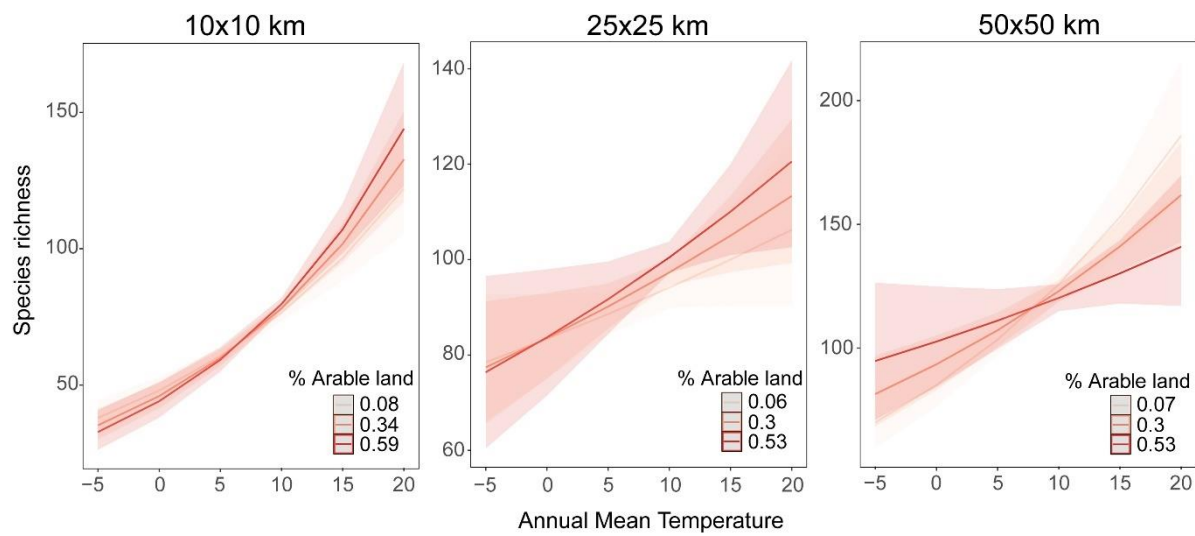


Figure 4: Interaction effects of annual mean temperature and proportion of arable land on overall species richness of all wild bees at the scales of 10 km x 10 km, 25 km x 25 km and 50 km x 50 km.

3.1.3. Land use intensity

In contrast to our expectations, nitrogen input in agro-ecosystems was positively correlated with both overall species richness of all wild bees and species richness of all taxonomic groups across all spatial scales (Table 3, Fig. 3). Bumble bee richness was the only one observed to decrease with increasing nitrogen input, but this trend was evident solely at the 10 km x 10 km scale.

At finer scales, the presence of high nature value farmlands showed a positive association with overall species richness of all wild bees. However, at the broadest scale, this relationship became negative. The same pattern was observed for the species richness of the taxonomic groups Andrenidae and Melittidae. The number of species of Apidae and Megachilidae showed a positive correlation with high nature value farmland across all spatial scales. In contrast, bumble bees and Halictidae richness responded negatively to high nature value farmland across all spatial scales (Table 3).

3.1.4. Vegetation phenology

In general, the length of the growing season positively influenced bee species richness. Across all scales, overall species richness of all wild bees increased with the duration of the growing season. This trend was similarly observed for the species richness of the taxonomic groups

Apidae, Megachilidae, Halictidae, and Andrenidae. However, bumble bee and Melittidae richness showed a negative correlation with longer growing season across all spatial scales, except for a positive relationship between bumble bee richness and growing season length at the broadest scale (50 km x 50 km; Table 3).

3.1.5. Relative importance of explanatory variables

While all explanatory variables were found to significantly influence species richness across all scales, their relative importance differed greatly among taxonomic groups and spatial scales (Fig. 5).

For overall wild bee species richness, climatic variables were consistently among the most important factors across all spatial scales, but the importance changed among different climatic variables, in particular with measures of seasonality being more important at the finest spatial scale (10 km; Fig. 5). Of the land cover variables, proportion of urban areas emerged as one of the most influential variables explaining species richness at finer spatial scales. Bee-friendly habitats were of lower importance at the 10 km scale, but gained importance at larger spatial scales. Most importantly, bee-friendly habitats were consistently of more importance than arable land. In terms of land-use intensity, the impact of Nitrogen input was strong at the 50 km scale, moderate at the 10 km scale, but of minor importance at the 25 km scale. The importance of high nature value farmlands was either of equal importance as bee-friendly habitats (10 km scale), or of lesser importance (25 km and 50 km scale).

Moreover, the relative importance of our large-scale environmental variables also greatly varied among taxonomic groups (Fig. S16). For Andrenidae, land cover and vegetation phenology were identified as the most important variables, whereas climatic conditions appeared to have the least impact on explaining species richness. Land-use intensity variables demonstrated moderate importance for Andrenidae richness. Temperature variables and the proportion of urban areas were found to best explain the richness of Apidae, Halictidae, and *Bombus*. Land-use intensity and vegetation phenology measures exhibited moderate to high importance for these groups. For the Megachilidae and Melittidae taxonomic groups, the proportion of arable land emerged as one of the least important variables. However, urban areas and land-use intensity were among the more influential ones. Finally, vegetation phenology played a considerable role for Megachilidae but held less importance for Melittidae (Fig. S16).

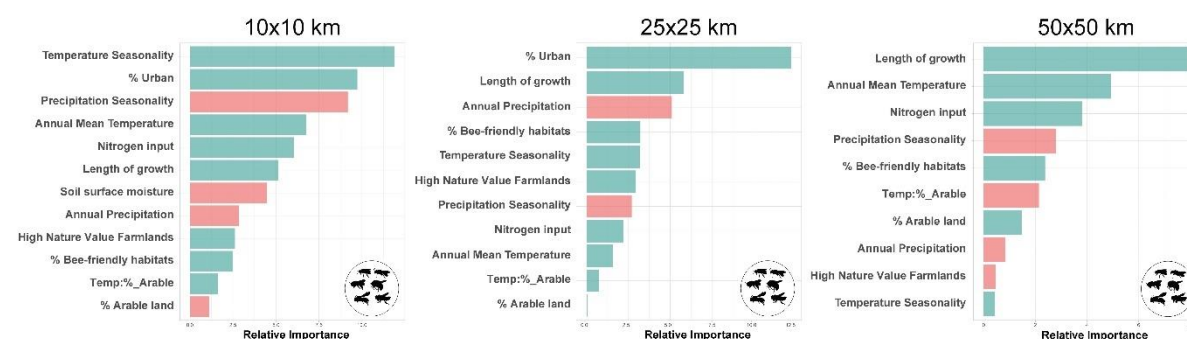


Figure 5: Relative importance of large-scale environmental variables explaining overall wild bee species richness at the scales of 10 km x 10 km, 25 km x 25 km and 50 km x 50 km. Pink cells, negative associations; turquoise cells, positive associations.

3.2. Relationships between pollinator traits and environmental variables

The first RLQ axis, explaining 76 % of the total variation, represented a gradient of annual mean temperature and precipitation seasonality from left to right, and a gradient of annual precipitation from right to left (Fig. 6a). The second axis, explaining 15.2% of variation, showed an ecological gradient dominated by the proportion of bee-friendly habitats and temperature seasonality. The relationship between wild bee traits and large-scale environmental variables was globally significant (p -values < 0.001).

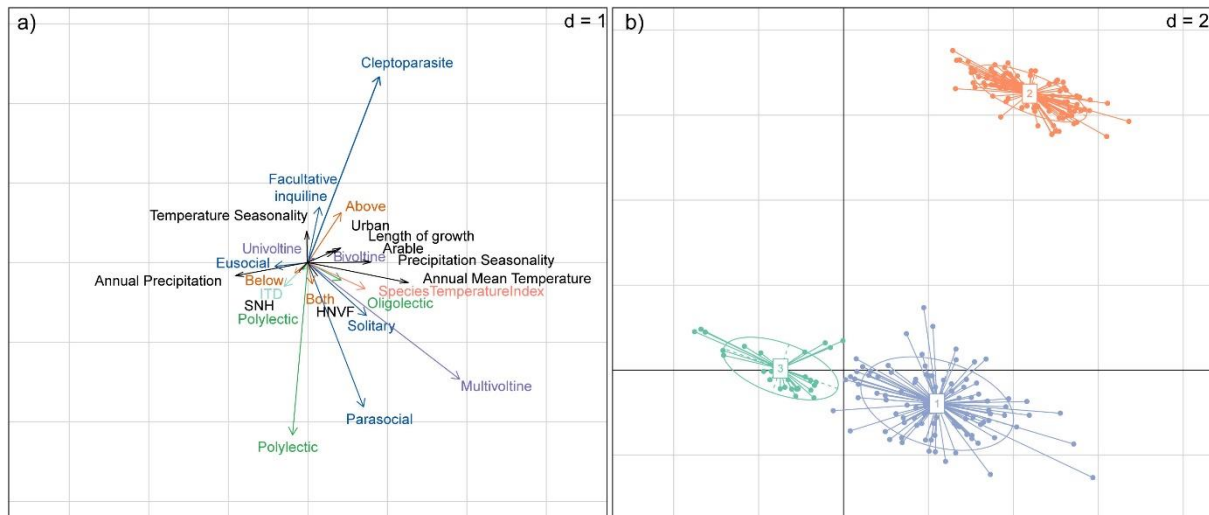


Figure 6: RLQ plot showing a) the decomposition of co-correlations between environmental variables and wild bee traits, constrained by the presence of wild bees. Arrows represent the size and direction of environmental variables and traits; b) scores for wild bee species in the RLQ analysis. Three cluster groups were identified from cluster analysis along the first two RLQ axes, as indicated by different colours.

Three clusters of common traits were identified based on the mean position of each species on both RLQ axes (Fig. 6b) by examining the traits that were shared among species filtered by different environmental variables. The first cluster primarily comprised solitary bees (i.e. non-*Bombus* bees), irrespective of their nesting requirements or foraging behaviour (Fig. 7). This cluster was highly heterogeneous and did not appear to prefer any specific habitat types. Wild bees belonging to cluster 2 were characterized as small bees who build their nests above ground, and were greatly represented by the genera *Nomada* and *Coelioxys*. This cluster predominantly consisted of cleptoparasitic bees and was commonly found in regions characterized by high annual mean temperatures and a substantial proportion of urban or arable land (Figure 7). Cluster 3 consisted exclusively of bumble bees that demonstrated high sensitivity to temperature variations. These bumble bees showed a preference for habitats characterized by high annual precipitation and low annual mean temperatures (Fig. 7).

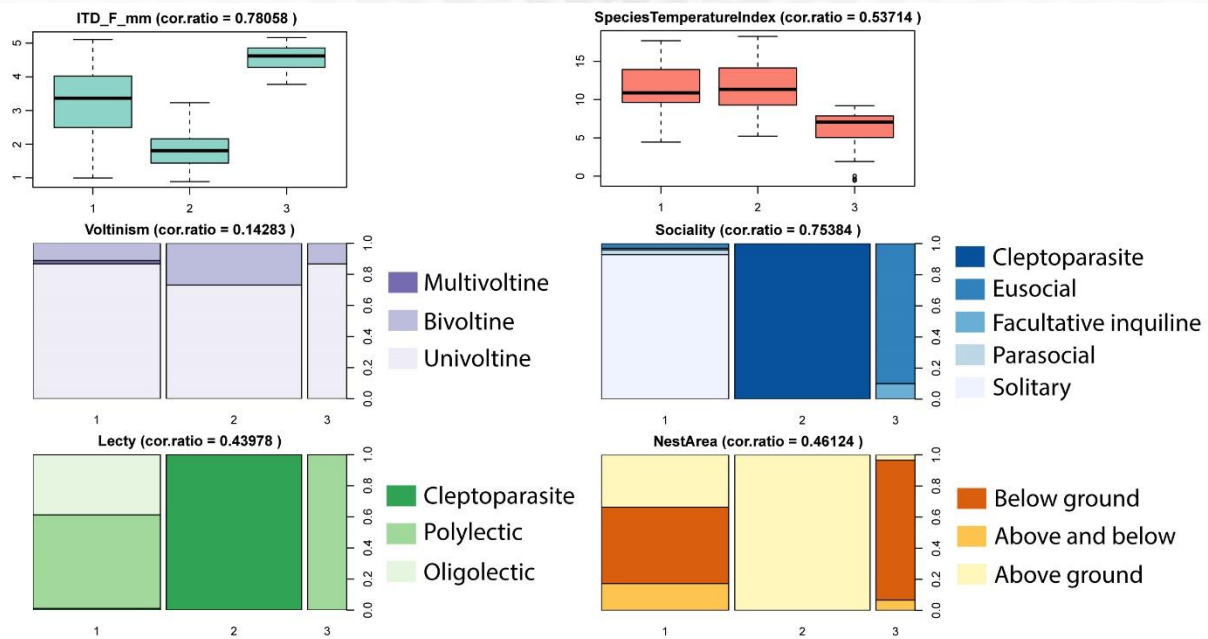


Figure 7: Wild bee traits shared by the three identified clustered groups (1,2,3) associated with large-scale environmental variables based on the mean proportion of each species on both RLQ axes. The width of the bars represents the relative abundance of each cluster group and its relative proportions of each cluster assigned to each different traits are represented by the height of the bar for each functional trait.

The fourth-corner analysis detected few significant relationships between wild bee traits and large-scale environmental variables (Fig. 8). Most of the identified significant relationships were observed between climatic variables and functional traits associated with social behaviour and ITD. For instance, higher annual mean temperature negatively influenced eusocial bees, such as bumble bees, while positively affecting solitary bees. Annual precipitation was positively correlated with ITD, and although it had a positive effect on eusocial bees, it had a negative impact on solitary bees and cleptoparasites. Cleptoparasites showed a positive correlation with precipitation seasonality and length of the growing season, whether expressed through social behaviour or feeding habits. Precipitation seasonality also had a positive relationship with polylectic bees. Moreover, the length of the growing season was negatively associated with ITD. Finally, the species temperature index was negatively influenced by annual precipitation, but positively correlated with annual mean temperature, precipitation seasonality, length of the growing season and the proportion of arable land.

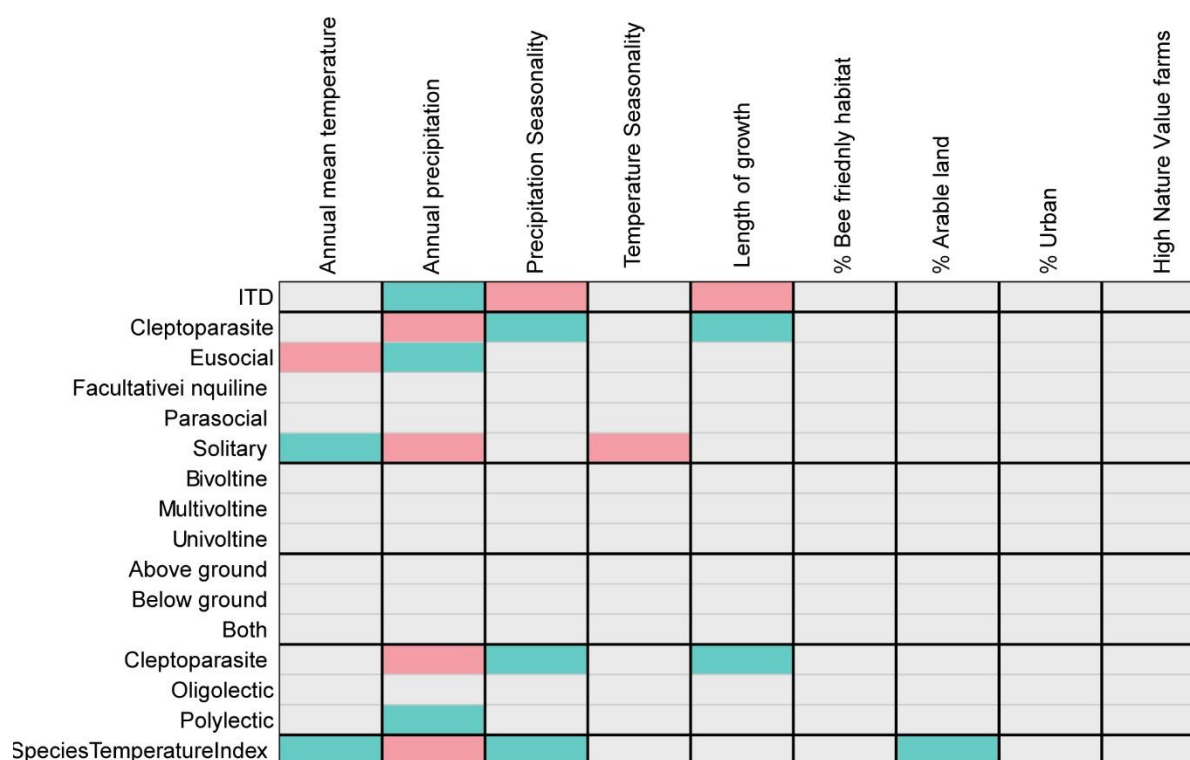


Figure 8: Relationships between traits and environmental variables resulting from the fourth-corner analysis. Pink cells, positive associations; turquoise cells, negative associations (p-adjusted < 0.05).

3.3. Population response to extreme weather events

Compared to average population sizes before the extreme event in 2018 (2010 to 2017; period0), 73% of the species declined in the period during or after the event (period1), but with variation across landscapes and locations (Fig. 9). Furthermore, on average 5% of local populations went extinct, i.e. they have not been observed within the four years of period1 (2018 to 2021) but this also varied across landscapes and locations (Fig. 9). However, no species got extinct across all landscapes. Population change in reaction to extreme weather conditions also varied across taxonomic groups (Fig. 10). Species from the genera *Andrena*, *Bombus*, and *Nomada* were consistently suffering from the extreme weather conditions, while population sizes of *Osmia* species increased. Parts of the species from the genera *Hylaeus* and *Lasioglossum* decreased while others increased.

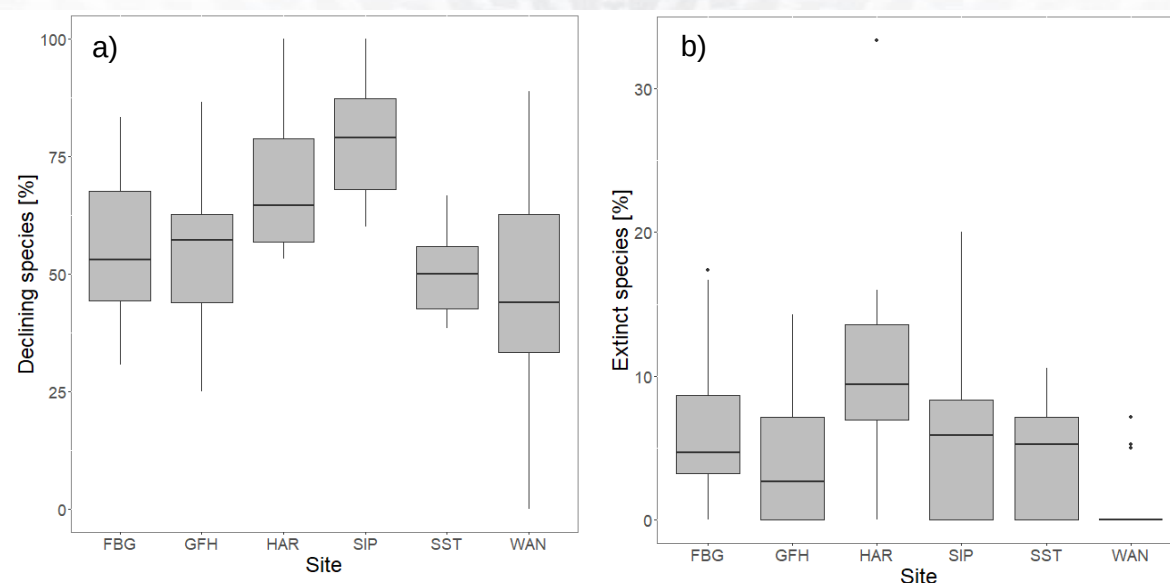


Figure 9: Proportions of declining (a) and locally extinct species (b) in response to an extreme heat and drought event.

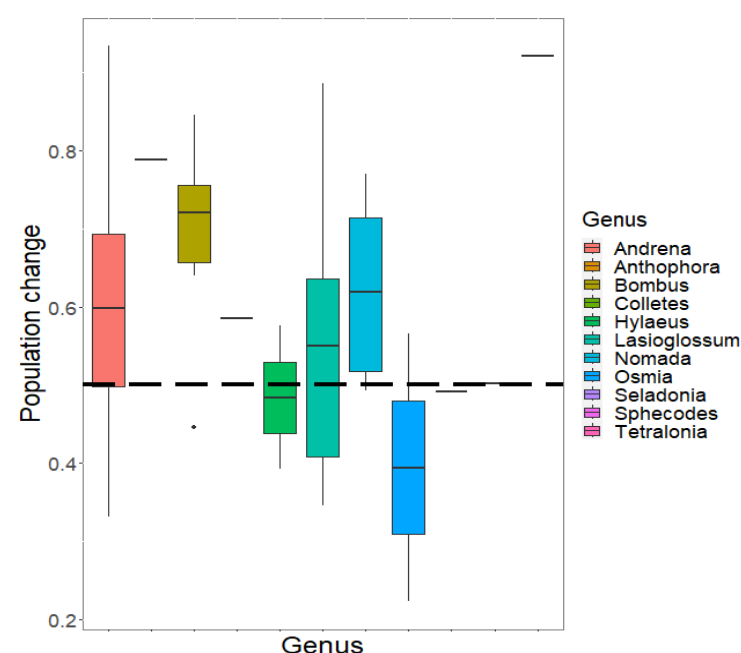


Figure 10: Average population change per species within a genus in response to an extreme heat and drought event. Horizontal dashed line at 0.5 indicates no change, higher values of the index indicate decreasing population sizes (reaching total loss at 1), and lower values than 0.5 indicate population gains.

For models relating population change to measures of population stability, species traits and landscape characteristics at the local scale, model performance was somewhat limited (marginal $R^2 = 0.08$, conditional $R^2 = 0.40$). However, we found significant effects of all three groups of explanatory variables on changes in population size as response to the extreme weather event. Species traits (ITD and STI) were most important, followed by population stability, while landscape characteristics had a minor impact (Fig. 11). However, ITD and STI showed interaction effects with landscape metrics. Population declines increased with

increasing ITD, particularly when local proportions of woody features were low. However, this effect was considerably buffered by an increasing amount of local proportions of woody features (Fig. 12a). Populations of species with low values of STI (i.e. cooler temperature niches) declined drastically, while warm-adapted species (high values of STI) even increased. This effect was modified by the local area of mass flowering crops where at locations with large areas of mass flowering crops warm-adapted species benefitted more from the extreme event, while cold-adapted species suffered more compared to areas with low amount of mass flowering crops (Fig. 12b). As expected, populations with initially low stability in period0 (i.e. CV in abundance in period0) declined more than initially more stable populations (Fig. 13).

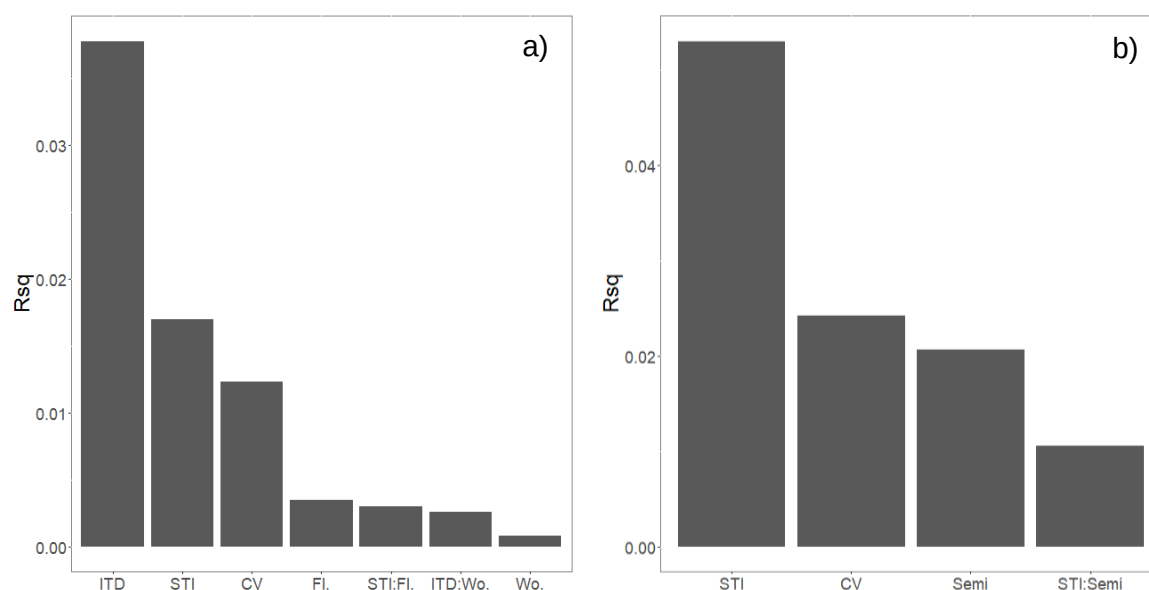


Figure 11: Relative importance of population stability, species traits, and landscape characteristics on population responses to an extreme weather event at the local (a) and landscape scale (b). Rsq , semi-partial R^2 ; ITD, intertegular distance; STI, species temperature index; CV, population stability (measures as coefficient of variation in population size before the extreme event); FI., area of mass flowering crops, Wo., local woody features; Semi, local proportion of semi-natural habitat.

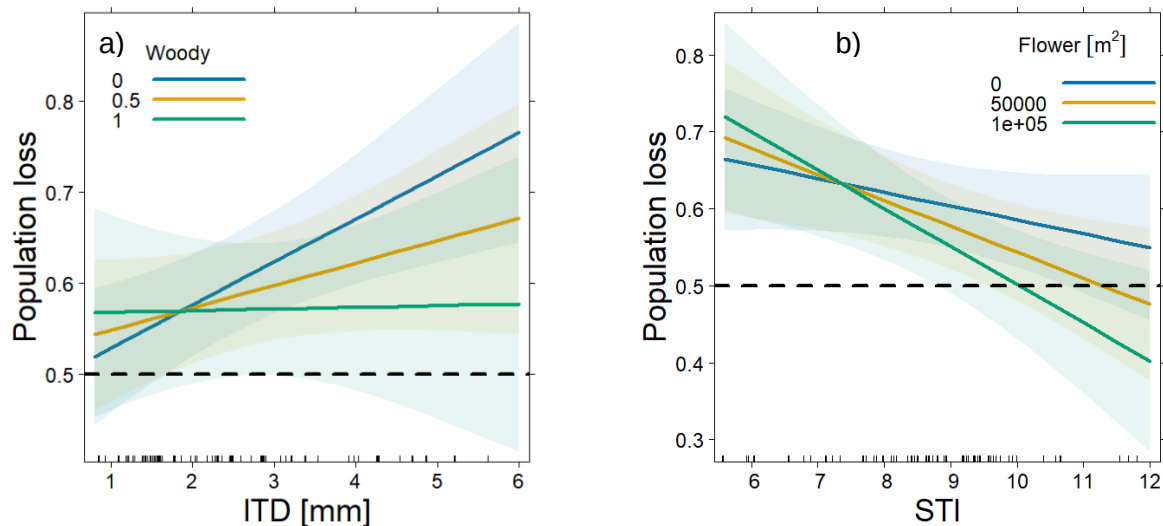


Figure 12: Interactive effects of ITD and woody features (a) and STI and mass flowering crops (b) on local population change in response to an extreme weather. Horizontal dashed line at 0.5 indicates no change, higher values of the index indicate decreasing population sizes (reaching total loss at 1), and lower values than 0.5 indicate population gains. ITD, intertegular distance; STI, species temperature index; Woody, proportion of local woody features; Flower, local area of mass flowering crops.

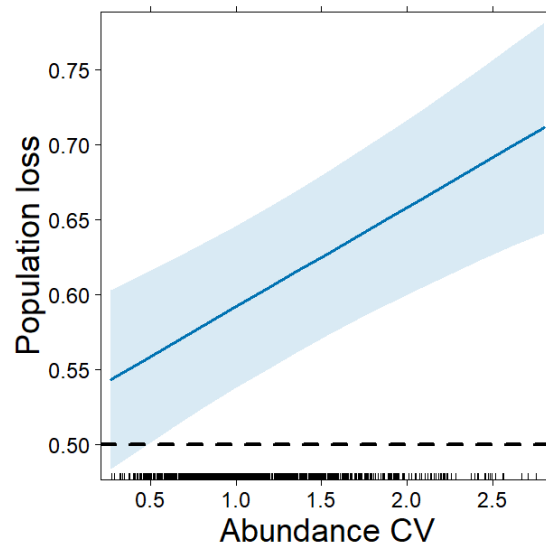


Figure 13: Effect of population stability on local population change in response to an extreme weather event. Horizontal dashed line at 0.5 indicates no change, higher values of the index indicate decreasing population sizes (reaching total loss at 1), and lower values than 0.5 indicate population gains. Abundance CV, population stability (measures as coefficient of variation in population size before the extreme event).

At the landscape scale, model performance was slightly better than at the local population scale (conditional $R^2 = 0.11$; marginal $R^2 = 0.55$). We also found significant effects of all three groups of explanatory variables on changes in population size as response to the extreme

weather event in the same order of importance as for the local scale analyses (Fig. 11b). STI was the most important determinant of change (ITD was not relevant at this scale), followed by population stability. At this scale, landscape properties, represented by proportion of semi-natural habitat, had a higher impact compared to the local level analysis (Fig. 11b) and interacted with STI. In particular, high proportions of semi-natural habitat at the landscape scale buffered the negative relationship between STI and population declines, i.e. at high levels of semi-natural habitat, cold-adapted species declined less but warm-adapted species also benefitted less from the extreme event compared to conditions of low proportions of semi-natural habitat (Fig. 14a). The impact of population stability at the landscape scale was comparable to that at the local population scale, i.e. initially less stable populations declined more than initially stable populations (Fig. 14b).

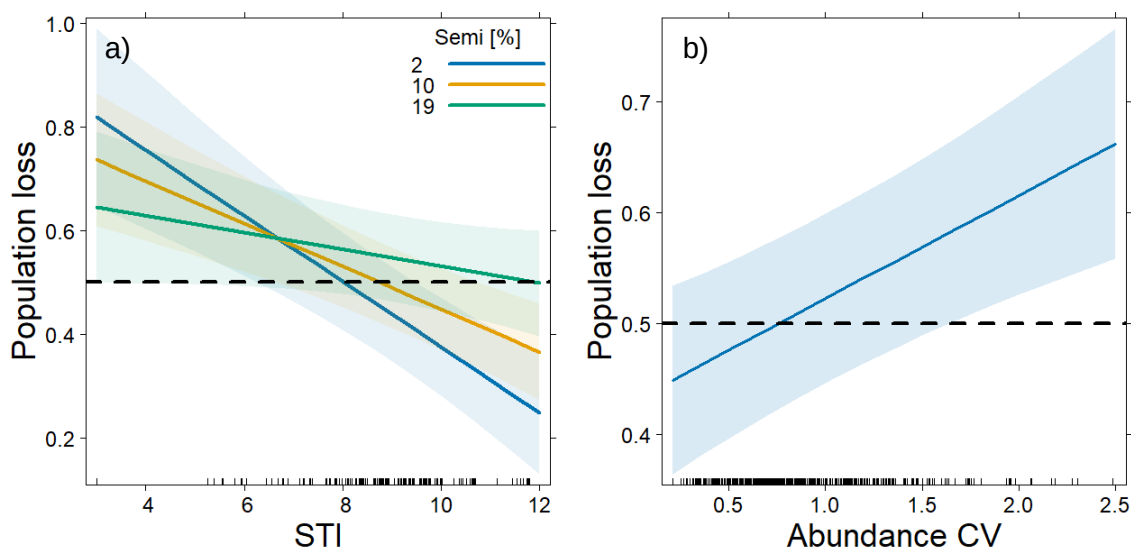


Figure 14: Interactive effect of species temperature index and proportion of semi-natural habitat (a) and main effect of population stability (b) on population change at the landscape scale in response to an extreme weather event. Horizontal dashed line at 0.5 indicates no change, higher values of the index indicate decreasing population sizes (reaching total loss at 1), and lower values than 0.5 indicate population gains. STI, species temperature index; Semi, proportion of semi-natural habitat at the landscape level; Abundance CV, population stability (measures as coefficient of variation in population size before the extreme event).

4. Discussion

Our results showed that all selected large-scale environmental variables were major drivers of pollinator distribution across Europe. Although these effects were mostly consistent across spatial scales when considering species richness of all wild bees altogether, we found these effects to be highly context dependent varying among taxonomic groups and spatial scales.

4.1. Climate

Higher mean annual temperatures were associated with increased species richness among all wild bees and several taxonomic groups, suggesting that warmer climates like those in Spain or Italy may support a greater diversity of wild bee species compared to colder regions

such as Sweden. However, not all taxonomic groups responded positively to high temperatures. Specifically, bumble bee richness declined with elevated temperatures, while it increased with annual precipitation, contrasting with the overall trend where most taxonomic groups and overall species richness decreased with increased precipitation. The varying responses of taxonomic groups to climatic conditions likely represents the phylogenetic origin of the taxa, e.g. with bumble bee being cold-adapted with respective morphological (large body size, super-dense fur-like hairs) and physiological (endothermy) adaptations. Also, differing responses to precipitation levels may stem from morphological differences in body size among taxa (Lawson and Rands, 2019), or indirectly mediated through available floral resources. In addition, dry conditions may lead to reduced pollinator richness due to critical water availability for floral resources and nesting sites. Temperature and precipitation seasonality also emerged as significant factors shaping pollinator species richness, with responses varying among taxonomic groups and spatial scales. Given the taxon-specific responses observed across multiple spatial scales to climatic variables, a thorough comprehension of the relationships between wild bees and climate conditions becomes imperative amidst the ongoing climate change.

4.2. Land cover

The positive relationship between the proportion of bee-friendly habitats in the landscape and overall pollinator species richness highlights the importance of habitat quality and availability in supporting diverse pollinator communities. Bee-friendly habitats, characterized by a diverse array of flowering plants and suitable nesting sites, can provide essential resources for wild bees, promoting their diversity across various spatial scales (Rundlöf, Nilsson, and Smith 2008; Marini et al. 2012; Martínez-Núñez et al. 2022). However, certain taxonomic groups exhibited more nuanced responses to the availability of bee-friendly habitats. For example, while Megachilidae richness decreased with the availability of bee-friendly habitat at finer scales, it showed an increase of species richness at broader scales, suggesting potential scale-dependent effects of habitat availability or variation depending on the insects' seasonal activity and requirements (Maurer et al. 2022).

While arable land positively influenced wild bee richness, notably in cooler climates where it can provide vital foraging resources such as mass flowering crops favoured by bumble bees, its impact diminished under warmer temperatures. Pesticide severity and resource saturation may lead to increased competition among wild bee species, while nesting site availability may further modulate this relationship. The escalation of negative impacts under warmer conditions may be aggravated by intensified agricultural practices, increased habitat fragmentation and reduced floral diversity (Leclère et al. 2020).

Finally, the positive relationship between urban areas and pollinator richness emphasized the crucial role of urban green spaces and gardens as essential habitats for supporting pollinator diversity within human-modified landscapes, potentially acting as a hotspot for bees (Theodorou et al. 2020).

4.3. Land-use intensity

Contrary to our expectations, the positive correlation between nitrogen input in agro-ecosystems and overall species richness of all wild bees suggests that nitrogen fertilization may have complex effects on pollinator communities. While nitrogen input is typically associated with more intensified agricultural practices, its positive relationship with pollinator

species richness across all spatial scales suggests that other factors may be at play. One possible explanation is that nitrogen-rich habitats support a greater abundance of floral resources, attracting a diverse array of wild bees. Another explanation might be a potential sampling bias toward high sampling intensities in central Europe that coincided with high nitrogen input, which has not been entirely removed by our selection criteria. Furthermore, conservation areas are notably underrepresented in our dataset, mostly due to the predominant focus of pollinator projects on agricultural landscapes and, more recently, urban habitats.

Similarly, the presence of high nature value farmlands showed a nuanced relationship with pollinator species richness across spatial scales. While high nature value farmlands showed a positive association with the overall species richness of all wild bees at finer scales, this relationship became negative at the broadest scale, suggesting that the benefits of high nature value farmlands for pollinator diversity may be context-dependent. However, the negative response of bumble bees and halictid richness to high nature value farmland highlights the need for targeted conservation efforts to address the specific ecological requirements of these taxonomic groups, if deemed necessary. Our results emphasize the potential benefits of prioritizing bee-friendly habitat over high nature value farmland in restoration efforts aimed at safeguarding wild bees. This is especially relevant for decision-makers seeking to maximize the positive impact of their restoration projects on pollinator communities.

Our results indicated when it comes to restoration efforts aimed at enhancing pollinator diversity, investing in bee-friendly habitat appears to yield more significant benefits compared to high nature value farmland (HNVF). This insight provides valuable guidance for decision-makers and conservation practitioners seeking to maximize the impact of their restoration initiatives on pollinator communities.

4.4. Vegetation phenology

The positive impact of longer growing season on bee species richness suggests that extended vegetation periods may provide wild bees greater opportunities for foraging, ultimately supporting more diverse pollinator communities. This shows the importance of temporal availability of floral resources in shaping the distribution and potentially co-occurrence of wild bee species. For instance, longer vegetation periods may provide more options for temporal niche partitioning for more species, while in short vegetation periods foraging niches might strongly overlap for many species potentially leading to competitive exclusion. This also highlights the potential consequences of climate-driven changes in growing season length on pollinator populations. However, the decline of bumble bee and Melittidae richness with prolonged growing seasons across all spatial scales suggests potential constraints or trade-offs. Bumble bees and Melittidae may be adapted to shorter growing seasons.

4.5. Trait-environment relationships

The multi-traits approach revealed the importance of climatic conditions and land cover as filters of the functional trait composition of wild bees. Solitary bees with high heterogeneity in nesting requirements and foraging behaviours highlighted the adaptability of solitary species to a wide range of habitats. In contrast, small cleptoparasitic bees were associated with warmer climates and intensive land use, highlighting the vulnerability of specialized species to habitat degradation and environmental change. Bumble bees showed a significant sensitivity to temperature variations and precipitation patterns, reflecting the importance of

climatic factors in shaping the distribution and abundance of key pollinator taxa and the particular threat of climate change to cold-adapted species. The observed correlations between climatic variables and functional traits associated with social behaviour, reproductive strategies, and resource utilization showed the importance of considering taxon-specific responses to climate variability in predicting the impacts of climate change on wild bee communities.

4.6. Population response to extreme weather events

Our results show that extreme heat and drought events can have severe impacts on pollinator populations leading to drastic declines in abundance, and, due to local extinctions (at least for the four years of observation after the event) and trait-specific responses, also to changes in taxonomic and functional community composition. The most important factors defining population responses to such extreme events were species traits with an expected impact of the species temperature index (STI) with strong declines of cold-adapted species and less, neutral or positive responses of warm-adapted species and increasing declines with increasing body size. In addition, less stable populations with already high inter-annual abundance fluctuations were increasingly threatened by this event. Finally, landscape characteristics beneficial for wild bees buffered the negative effects of extreme weather conditions but these buffering effects were stronger at the landscape scale than at the local population scale.

The impact of STI was as expected since cold-adapted species are likely to suffer from increased temperatures. However, species usually have some compensatory mechanisms to overcome a certain level of hostile conditions, such as adjusting foraging behaviour or fanning behaviour in bumble bees to cool down the nest. However, our results indicate that these compensatory mechanisms have their limits, particularly under extreme weather conditions.

Our results indicate that large wild bees suffered more from heat and drought waves than smaller species. Explanations might be linked to thermoregulation, particularly to lower heat stress tolerance (Martinet et al. 2021) or increased energetic costs of thermoregulation (e.g. fanning behaviour) of larger bees (Rasmont and Iserbyt 2012). Such effects might be also reflected by STI. However, our results were independent of STI, and, since we used species nested within genus as random effect, also independent of taxonomic groups, e.g. an overly strong impact of bumble bees. An alternative reason might be indirect effects caused by food shortage due to drought via reduced quantity or quality of floral resources of which larger wild bees need more in total for their larval growth than smaller wild bees.

Inter-annual population fluctuations are driven by internal population dynamics but can be increased by environmental pressures in general, potentially driving populations towards their carrying capacity on the one hand or towards particularly low population sizes on the other hand. At both ends the population will be particularly sensitive to additional pressure such as an extreme weather event, resulting in the observed increased population declines of populations with an already low level of stability, i.e. high level of inter-annual fluctuation.

Our results further indicate that the expected increasing severity and frequency of heat waves under different climate change scenarios (IPPC 2021) will pose a serious threat to pollinator communities. Reductions or even local extinctions of species will not only be of concern from a conservation point of view but may also affect entire ecosystems and the provision of pollination services to wild and crop plants driven by drastically reduced overall abundances

and shifts in taxonomic and functional community composition. However, our results also show options for land-based mitigation. Respective actions should aim at (i) increasing population stability, e.g. by reducing other pressures such as food shortage or pesticides; (ii) increasing the amount of woody features such as hedgerows and mass flowering crops locally; and (iii) increase the proportion of semi-natural habitat at the landscape scale to buffer negative effects of heat and drought waves. To archive this, a strong legislative framework (such as the currently suggested Nature Restoration Law of the European Commission) is urgently needed.

Conclusion

Our study presents novel insights into how large-scale environmental pressures shape wild bee communities at multiple spatial scales across Europe. This holds particular significance in the context of climate change, which will have direct or indirect repercussions on both wild bees and plant communities in the forthcoming decades. The diverse responses observed among taxonomic groups highlight the need to account for taxon-specific sensitivities to environmental pressures. Such considerations can facilitate the prediction and mitigation of climate change and habitat loss effects on pollinator diversity and ecosystem functioning. Tailored conservation strategies are now more crucial than ever for safeguarding pollinator populations in the face of global change, and require an understanding of the various ecological requirements of different pollinator taxa and their spatial distribution.

Moreover, our findings emphasize the importance of examining pollinator communities across multiple spatial scales. Doing so can reveal nuanced patterns of species-environment relationships that might not be discernible at broader or finer resolutions. Our local and landscape scale analyses, for instance, helped to identify land-based mitigation and restoration options to buffer adverse effects of a large-scale driver of climate change.

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6. Supplementary information

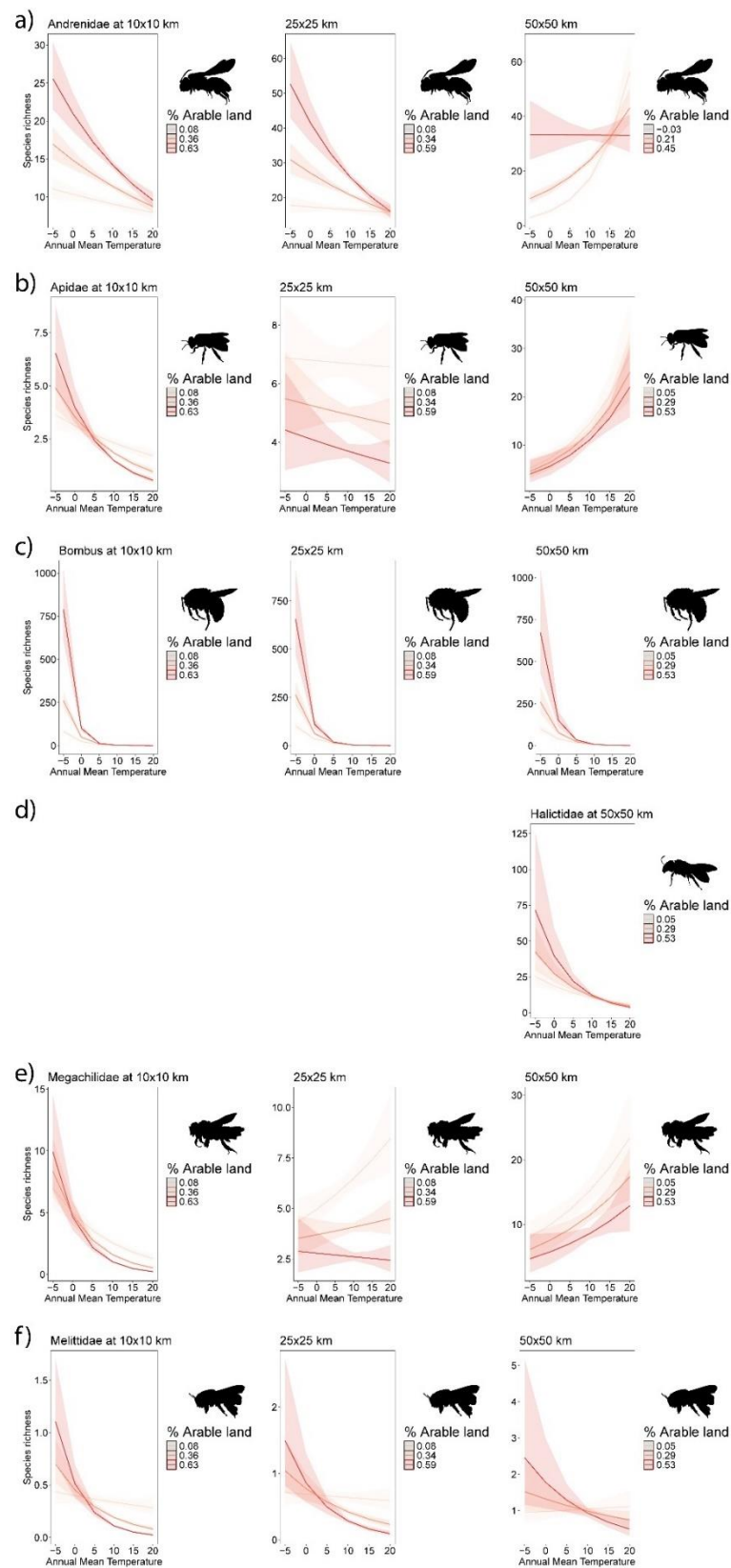


Figure 15: Interactions effects between Mean Annual Temperature and Arable land on species richness of taxonomic groups. a) Andrenidae; b) Apidae; c) *Bombus*; d) Halictidae; e) Megachilidae; f) Melittidae

