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# Potential for climate change driven spatial mismatches between apple crops and their wild bee pollinators at a continental scale

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## ABSTRACT

Visitation by wild bee species alongside managed pollinators is necessary to ensure consistent yields and fruit quality in apple fields. Wild bee species are vulnerable to several environmental changes. Climate change is expected to lead to broad-scale changes to wild bee distributions that will impact the service they provide as crop pollinators. We modelled selected wild bee species known to be important for apple production in Europe and we quantified the shifts in distribution range for these key apple-pollinating bee species (KABS) under three climate change scenarios (RCP 2.6, 4.5 and 8.5) for 2041–2060 and 2061–2080. We compared species distribution maps (after the expected range changes) to the distribution of areas with suitable habitat for apple orchards and with national apple production statistics to estimate potential pollination service at the landscape scale. Overall, KABS are widespread species found across Europe and while most species have projected range contractions, these contractions are limited (~10% loss). Only under the worst-case climate change scenario (RCP8.5) do we project range contractions over 50% and only under RCP8.5 is the average loss of overlap between suitable apple conditions and KABS likely to decrease by over 10%. However, range contractions at the southern limit of many species' ranges mean that the potential impact of climate change on apple pollination is not evenly shared between apple producing countries; France and Italy for example are projected to have high range loss of KABS and loss in potential pollination service. Climate change is not the only threat to apple pollination and future pollination deficits will also depend on local orchard intensification and ecological infrastructure. Key changes to intensive, commercial apple orchards towards a more agroecological approach are needed to maintain a diverse wild bee community and apple production in areas that may become climatically unsuitable in the future.

## 1. Introduction

Insect pollination is a key agro-ecosystem service (Klein et al., 2007) and one which is increasing over the long-term, as the global area dedicated to pollinator-dependent crops has increased by over 300%

since 1961 (Aizen et al., 2019). Apple (*Malus domestica* Borkh., 1803) is globally one of the most economically important crops, worth a reported US\$45 billion in 2019 (FAO, 2019). Apple production relies on insect pollinators as apple flowers are, in general, self-incompatible (Pardo & Borges, 2020). The absence of efficient pollination can lead to a

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pollination deficit, whereby fruit production requiring cross-pollination is limited because of insufficient receipt of pollen (Vaissière et al., 2011). For apples, the presence and extent of pollination deficits because of suboptimal pollination varies between regions and even between orchards within regions, ranging from severe deficits all the way to over-pollination (Garratt et al., 2021). Apple production is often (over-)reliant on honey bees, but numerous wild bee species are also partially responsible for their pollination (Hutchinson et al., 2021; Kleijn et al., 2016; Russo et al., 2015; Allen-Perkins et al., 2022; Weekers et al., 2022a). In Europe an overreliance on a single pollinator, in this case the western honey bee, is unlikely to be a resilient, long-term strategy (Potts et al., 2010; but see Prendergast et al., 2021). Increased diversity of wild bee pollinators, both taxonomic and functional, is beneficial for crop production (Garibaldi et al., 2013; Roquer-Beni et al., 2022; Weekers et al., 2022b), improving apple yield and quality (Garratt et al., 2014; Woodcock et al., 2019). In addition to such benefits, the local availability of a diverse community of wild bee pollinators also increases crop stability (Garibaldi et al., 2011; Senapathi et al., 2021), likely offering a safeguard when other managed pollinators are limited (Osterman et al., 2021).

In well-studied areas with long-term data, a wide taxonomic range of wild bees have been shown to be declining (Bartomeus et al., 2013a; Biesmeijer et al., 2006; Carvalheiro et al., 2013; Nieto et al., 2014; Potts et al., 2016; Powney et al., 2019), because of several intertwined causes (Potts et al., 2010; Vanbergen and The Insect Pollinators Initiative, 2013). One driver of decline expected to increase in severity over the coming decades is climate change (Potts et al., 2016). Increasing temperatures, changes to precipitation and increased occurrence of extreme weather events are expected to affect the spatial distribution of biodiversity (Bellard et al., 2012) and to drive species to higher elevations and latitudes (Lenoir & Svenning, 2015; Parmesan & Yohe, 2003). Current evidence suggests that future climate and land use changes will affect bumblebee distributions (Marshall et al., 2018; Prestele et al., 2021; Rasmont et al., 2015) and that their capacity to shift their distribution with the climate is limited (Kerr et al., 2015). While in certain regions, some bumblebee species have been shown to shift to higher elevations in line with changes in local climates (Marshall et al., 2020; Ormosa et al., 2017; Pyke et al., 2016), the response of bumblebees to environmental conditions and changes at a broad scale is likely to be highly species specific (Ghisbain et al., 2020; Marshall et al., 2021; Maebe et al., 2021a). This is also likely the case for non-bumblebee wild bees.

Alongside changes in biodiversity, present-day and future climate changes are expected to fundamentally alter agricultural practices by shifting suitable conditions, altering the availability of inputs and water regimes, changing disease and pest dynamics and changing the yields and quality of products, among many others (Myers et al., 2017). Concurrently, climate change will impact the distribution and diversity of wild species (Araújo & Rahbek, 2006). The intersection of these two phenomena can lead to substantial impacts on crop pollination, since it can disrupt spatial and temporal overlap between crops and their pollinators (Potts et al., 2016; Settele et al., 2016; Schweiger et al., 2008).

Assessing changes in crop and pollinator distributions and the potential for pollination deficits because of climate change is a key goal in understanding the potential impacts of pollinator loss (Vanbergen and The Insect Pollinators Initiative, 2013). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) assessment report on pollinators, pollination and food production cites climate change driven disruptions of apple pollination as an ‘established but incomplete’ fact (Potts et al., 2016), as, until now, only national level assessments have been conducted. These previous studies project significant mismatches between fruit trees and their pollinators in the UK (Polce et al., 2014), for a variety of crops and crop pollinators across Brazil (Giannini et al., 2017, 2020) and for key tomato producing regions of the US (Carrasco et al., 2020). Here, we assess the potential for future mismatches between apple crops and their wild bee pollinators at a continental scale (Europe). We use a species distribution modeling

approach (Elith & Leathwick, 2009) to project suitable habitat conditions for apple pollinating wild bee species and European apple orchards in 2060 and 2080 under three climate change scenarios (IPCC, 2014). We use the resulting projections to determine whether there will be spatial mismatches between apple crops and their pollinators under projected climate change in Europe. We additionally link the results to apple production statistics in Europe to determine countries most at risk and discuss other factors which are likely to interact with climate to determine the availability of wild bee pollinators for apple crops in Europe in the future.

## 2. Methods

### 2.1. Study area

The study area included the known distribution area of all European bees registered in our database, the extent ranging from approximately 17 W to 35E and 20S to 72 N. This extent included northwestern Africa (Morocco) and western Asia in order to cover the full distribution of the species. This allowed us to estimate the full climatic niche range of species as completely as possible and avoid truncation effects (Thuiller, 2004). The extent for the projections of habitat suitability was smaller and defined as the European Union (EU) and all other countries included within the geographical bounds of the EU (Fig. S1). Species occurrences and environmental data were aggregated into 25 x25km cells within the study area.

### 2.2. Species data

We selected key apple-pollinating bee species (KABS) using two methodologies. Using the CliPS (Climate change and its effect on Pollination Services) study conducted in 2019 across 88 commercial apple orchards in fifteen European countries (Belgium, Bosnia and Herzegovina, Czech Republic, Estonia, France, Germany, Ireland, Italy, Latvia, Netherlands, Norway, Serbia, Slovenia, Spain and the United Kingdom) (see Table S1, Leclercq et al. (2022) and Leclercq et al., (2023), for site information and the methodology behind their selection). Any species that was found within the top 5% of species visiting the apple blossoms in two or more sites was classified as a KABS. We did not include species for (i) which the literature indicated would not have Rosaceae as part of their diet (Wood & Roberts, 2017), or (ii) which are managed within the orchards or (iii) parasitic species which do not collect pollen. Therefore, *Andrena ferrugineicrus* Dours, 1872, *Andrena humilis* Imhoff, 1832, *Apis mellifera* Linnaeus, 1758, *Bombus terrestris/Bombus lucorum* agg., *Osmia bicornis* (Linnaeus, 1758), *O. cornuta* (Latreille, 1805) and *Nomada fabriciana* (Linnaeus, 1767), were removed for the following analyses. *Osmia cornuta*, while often an abundant native pollinator in Southern parts of Europe, was excluded because its potential to be managed makes it complicated to exclude the human impact on its future distribution and because the available distribution data in its Southern European range was poor in comparison to other species. For more details on the CliPS methodology, see (Prendergast et al. 2021; Leclercq et al. 2022; Weekers et al., 2022a, 2022b). We also expanded on this selection of species using relevant literature to identify other species as KABS besides those observed in the CliPS study (Hutchinson et al., 2021; Kleijn et al., 2016). In total, we selected 33 KABS (Table S2).

The occurrence records for these 34 KABS were in the most part compiled from data collated as part of EU FP7 project STEP (Potts et al., 2011), and the full dataset is aggregated and available on the Atlas Hymenoptera webpage ([atlashymenoptera.net](http://atlashymenoptera.net)). The database was supplemented with occurrences from (i) the Bees, Wasps & Ants Recording Society (BWARS; <https://www.bwars.com/>) program for the United Kingdom; (ii) the National Biodiversity Data Centre program for Ireland (NBDC; <https://biodiversityireland.ie/>) and (iii) for *Colletes cunicularius* (Linnaeus, 1761) alone, the *Colletes* spp. databases collated and managed by Dr. M. Kuhlmann. Due to an ongoing lack of taxonomic

clarity in the literature, some species occurrence records were aggregated together; these include *Andrena scotica* Perkins, 1916, and *A. carantonica* Perez, 1902, (hereafter *A. scotica*) (Wood et al., 2022). We selected only occurrence records collected since 1980 to match the 'present' period as defined by the climate data. Some of the *Andrena* data is obtained from Klaus Warncke's manuscript conserved at the Oberösterreichisches Landesmuseum, and includes collections from before 1980; however, these data are necessary to demarcate the southern limits of many *Andrena* species and were therefore retained. To limit the spatial sampling bias towards northern and western countries in European bee records, we first randomly sampled/thinned adjacent occurrence records (within 25 km) for each species using the 'thin' function from the spThin package, v0.2.0 (Aiello-Lammens et al., 2015). A random starting occurrence was selected, and adjacent cells were removed iteratively. This was repeated five times and we selected the repetition that maximized the number of occurrence records. The final dataset was reduced to a single point per species per grid cell to equalize the weight of each cell where species were present.

### 2.3. Apple data

The apple data used consisted of occurrence records of apple orchards and national level statistics of apple production. The occurrence records of apple orchards in Europe were sourced from Land Use/Cover Area frame Survey (LUCAS), a survey providing statistics on land use and land cover across the whole of the EU (EUROSTAT, 2021). The survey data of apple orchards from 2009, 2012, 2015, and 2018 were used to model the habitat suitability of apple orchards at the European scale. National level statistics on apple yield (t/ha), and apple production (tonnes) were extracted for 2019 from the Food and Agricultural Organization of the United Nations (FAO, 2019) for all countries in the projected study area (Table S3).

### 2.4. Climate data

Climate data was sourced from CHELSA (Climatologies at high resolution for the earth's land surface areas) climate dataset at 30 arc seconds resolution (Karger et al., 2017). We started with 19 bioclim variables, as well as the minimum, mean and maximum temperatures per month, and mean precipitation per month for the period 1980–2010. Using the monthly values, we calculated the 18 Environmental Rasters for Ecological Modeling (ENVIREM) variables, which include climatic and topographic variables specifically designed for spatial modeling (Title & Bemmels, 2018). Before beginning modeling we trimmed the list of 37 climate variables (19 bioclimes, 18 ENVIREM) to only those that had been shown to be ecologically relevant when modeling wild bee diversity. We followed the findings of Orr et al. (2021) and selected 18 variables relevant for wild bees (see Table S4 for full details and justification), from which we would later conduct species specific model selection. Future climate projections of each of these 18 variables were also sourced from CHELSA (Karger et al., 2017). We extracted modeled projections (General Circulation Models [GCMs]) for 2041–60 and 2061–2080 for three climate change scenarios, RCP 2.6, 4.5 and 8.5 (IPCC, 2014). To account for variability and uncertainty in CMIP5 models, for each variable we took the average of the following 8 GCMs; ACCESS1-0, CESM1-BGC, CESM1-CAM5, GFDL-ESM2G, GISS-E2-H, HadGEM2-AO, IPSL-CM5A-MR and MPI-ESM-MR. We used GCMeval to select these 8 GCMs. They accurately represented the present European climate and were uncorrelated (Parding et al., 2020).

### 2.5. Land use and soil data

Due to the extent of the model training area and the availability of accurate future projections of land use change at the global scale, we chose to use land use variables that remain static in the future projections. Land use data was sourced from the 2015 Copernicus Global

Land Cover at 100 m × 100 m resolution (Buchhorn et al., 2020). We selected shrubland, herbaceous vegetation, cropland, urban, open forest and closed forest as relevant land use habitats for modeling wild bee species. We aggregated each of these variables to percentage cover within 25 × 25 km grid cells. Soil data was obtained from the global soil regions classification from the USDA Natural Resources Conservation Service Soils (USDA, 2005). We used the percentage cover of each 'soil region' that was found in at least 3% of gridcells as the input variables. Eight soil regions were included, alfisols, aridisols, entisols, gelisols, histosols, inceptisols, mollisols, and spodosols.

### 2.6. Species & apple distribution modeling

We modeled the distribution for each KABS using Maximum Entropy (MaxEnt) (Phillips et al., 2006). We chose to use MaxEnt because it has previously performed well for wild bees (Marshall et al., 2015) and other flying insects (Aguirre-Gutiérrez et al., 2013) for a variety of evaluation measures and is robust against overfitting (Aguirre-Gutiérrez et al., 2013; Phillips et al., 2006). We used target-group sampling to select our background grid cells (Mateo et al., 2010). We specified that the background samples could only be selected from grid cells where at least two other wild bee species have been recorded since 1980 and that had been sampled in at least three separate years. The background cells were thinned using the same methodology as for the KABS occurrence records.

Firstly, we conducted variable selection of the 24 climate and land use variables (Table S4), for each species, by running multiple series of ten MaxEnt models per species. After each set of ten models, the variables that contributed less than 1% to the best model (lowest AICc) were removed and where two variables were correlated with a Pearson's  $r > 0.7$  then the variable contributing less was removed. These steps of ten models were repeated until all variables contributed  $> 1\%$  and no variables were highly correlated ( $r > 0.7$ ) (Jueterbock et al., 2016). These selected variables were then used to run MaxEnt models with multiple parameter options using the 'ENMevaluate' function from the 'EMNeval' package, v2.0.0 (Kass et al., 2021). For species with less than 100 records, we ran models with both linear and quadratic features and for species with  $> 100$  records, more complex hinge features were also included, these models were run in combination with regularization multipliers from one to five. We determined model performance using a spatially independent cross-validation where species were grouped into two, three, or five spatially distinct clusters based on their coordinates. Species with fewer than 20 records were clustered into two spatial blocks, with fewer than 50 in three blocks, and those with  $> 50$  records into five blocks. The average of different performance metrics was taken for each block for each EMNeval model run.

The best model from each run was selected as the model which met three criteria. (i) The 10% training omission rate, which indicates the number of the occurrences in the training dataset incorrectly projected to be unsuitable above a 10% threshold. (ii) Area under the curve (AUC) of the receiver operating characteristic (Fielding & Bell, 1997), which measures a model's capacity to correctly distinguish between presences and the background samples (Jiménez-Valverde, 2012). And (iii) sample size, corrected Akaike information criteria (AICc) (Akaike, 1998; Burnham & Anderson, 2003) which, for SDMs, assesses model fit while also selecting for appropriate complexity (Warren & Seifert, 2011). The following criteria were applied sequentially: (i) the lowest average test omission rate (rounded to two decimals); (ii) the highest average AUC value (rounded to two decimal places); and, if there were still ties between models, (iii) the lowest AICc.

For each 'best model', its AUC value was compared to average AUC values from 100 null models (randomized occurrence points) with the same model parameters and blocking structure as the original 'best model' (Raes & ter Steege, 2007). Models were only used for future analyses when the average AUC value was higher than a one-sided 95% confidence interval of the null distribution of average AUC values. This

indicates that the KABS had specific niche requirements that were captured by the predictors. The contribution of a variable to the model was measured as the percentage increase in gain as the predictors are added to the model (Phillips et al., 2006). Each best model was used to project onto the present and three future scenarios (RCPS 2.6, 4.5, 8.5) for the periods 2041–2060 and 2061–2080. Each projection was then converted into a binary presence/absence map using the largest threshold that would leave out a maximum of 10% of the occurrence records. This method is robust to problems assessing true absences in presence only modeling (Merow et al., 2013) and is also stricter and less affected by extreme localities (Radosavljevic & Anderson, 2014). The preceding modeling protocol, from the first variable selection process to the binary map creation, was repeated ten times for each species to allow us to account for model variability and uncertainty.

The models of apple orchard distribution followed a similar protocol as above. Yet, as replacement of natural and urban areas by crop land is unlikely to happen at large extent in the study region, we limited the predictions of suitable habitat to only climate variables and additionally added in soil classes. The projected distributions of apple orchard habitat suitability were then constrained to areas known to be agricultural habitats to produce two separate distribution maps (i) all areas designated as agriculture and (ii) areas known to be fruit crops, in the present. For full model details see Appendix A for an ODM description of all parameters (Zurell et al., 2020).

## 2.7. Post-Modeling analysis

Change in the spatial extent of species distributions was measured by comparing binary map outputs *per* species, *per* scenario, and *per* period. Species distributional range change was a percentage measured as distribution gain minus loss. Percentage loss and gain were measured as the total number of cells lost or gained between the present and future projections divided by the number of cells occupied in the present. Range gain was determined for three different dispersal scenarios: (i) no dispersal, resulting in no range gain, (ii) full dispersal, including all range change, and (iii) intermediate dispersal, limited to a 250 km buffer for 2060 and 500 km buffer for 2080. The actual dispersal capacity for most species is unknown, and it is unclear to what extent the data available can be generalized to remaining species, therefore the goal was not to provide an accurate dispersal limit for all species but to provide a middle point for comparison between no dispersal and full dispersal. Change in the spatial extent of species distributions was calculated using the 'Biomod2' package in R, v3.4.6 (Thuiller et al., 2020). Species richness maps were made using consensus maps for each species based on all model runs better than a null distribution.

Spatial overlap with apple orchards was measured using the model outputs *per* species and for apple orchards. We tested two hypotheses of the distribution of apple orchard habitat suitability in time; (i) apple orchard habitat suitability was constrained by the distribution of agriculture within the 25 km grids (minimum 10% agriculture within the grid cells) as measured from CORINE Land Cover data from 2009 to 2018 (Büttner, 2014), and (ii) apple orchard habitat suitability was constrained by the distribution of fruit trees within the 25 km grids (presence/absence) as measured from CORINE Land Cover data from 2009 – 2018. Apple orchard distribution maps were based on 100% consensus of all runs better than a random null distribution. For each of the apple distribution hypotheses we compared overlap (%) between habitat suitability for each species for each of the three dispersal hypotheses by intersecting the binary projection maps. We then compared how overlap changed over time *per* scenario and for each species to determine the potential and extent of future spatial mismatches.

To test whether changes in broad-scale habitat suitability will impact apple production in Europe, we compared production and yield statistics at the national level to changes in species richness and projected range change. We visualized these comparisons with bivariate maps, using the 'biscale' package, v0.2.0 (Prener et al., 2020) and following a simplified

example of Carrasco et al. (2020). We further compared these measures by using a linear model to test if areas of high production and or yield are more likely to be experiencing declines in KABS. All modeling and post-modeling analyses were conducted in R, v4.0.2 (R Core Team, 2020).

## 3. Results

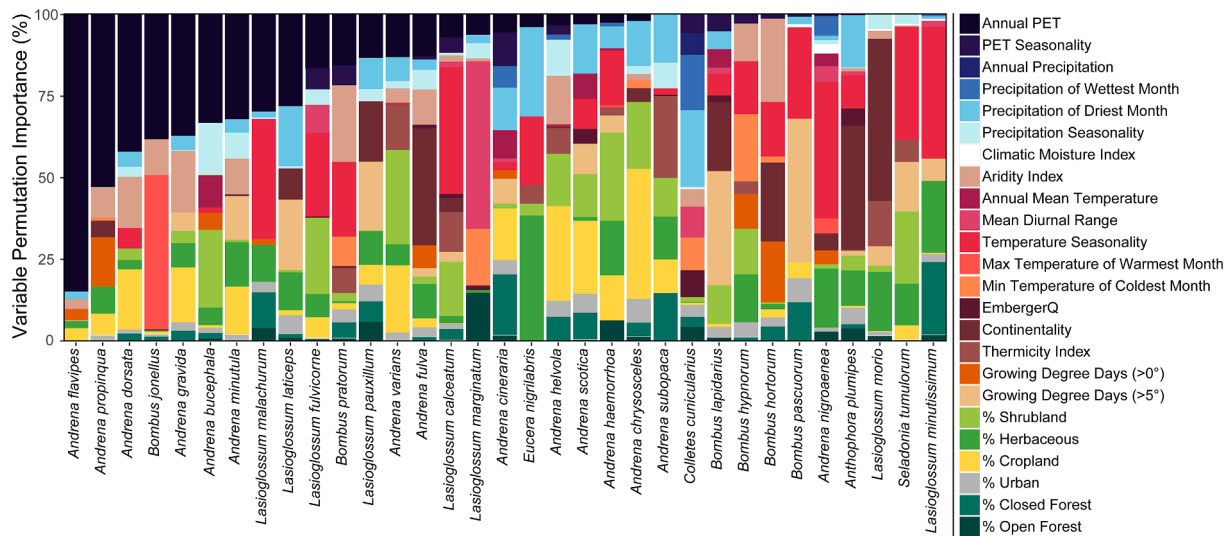
### 3.1. Model performance and variable contribution

The average AUC value per model across the spatial blocks, that were determined to be better than a random null model, ranged from 0.52 to 0.95 with a mean of  $0.70 \pm 0.08$ . All species had model runs better than the 95% confidence interval of a null distribution, except *A. nitida* (Müller, 1776), which was excluded from further analyses. Of the 33 species in the final analysis, 24 had all ten model runs better than random. Only two species had fewer than five runs, both with three, *A. dorsata* (Kirby, 1802), and *L. laticeps* (Schenck, 1869). All 24 variables were selected in at least three model runs (Fig. 1). On average the variable with the greatest permutation importance across all species was annual potential evapotranspiration (24.9), followed by maximum temperature of warmest month (20.2) and number of growing degree days ( $>5^{\circ}\text{C}$ ) (19.1). The most important land use variable on average was the percentage cover of herbaceous vegetation (9.1), although this was the 13th most important variable overall. Climate variables (mean of 11.8) were significantly more important overall than land use (6.1) variables (95% CI = 3.6 and 7.8,  $t = 5.3$ ,  $df = 451.58$ ,  $p = \text{less than } 0.0001$ ; Fig. 1). See Appendix C for records and spatial blocking for all species and Appendix D for response curves for all species and variables.

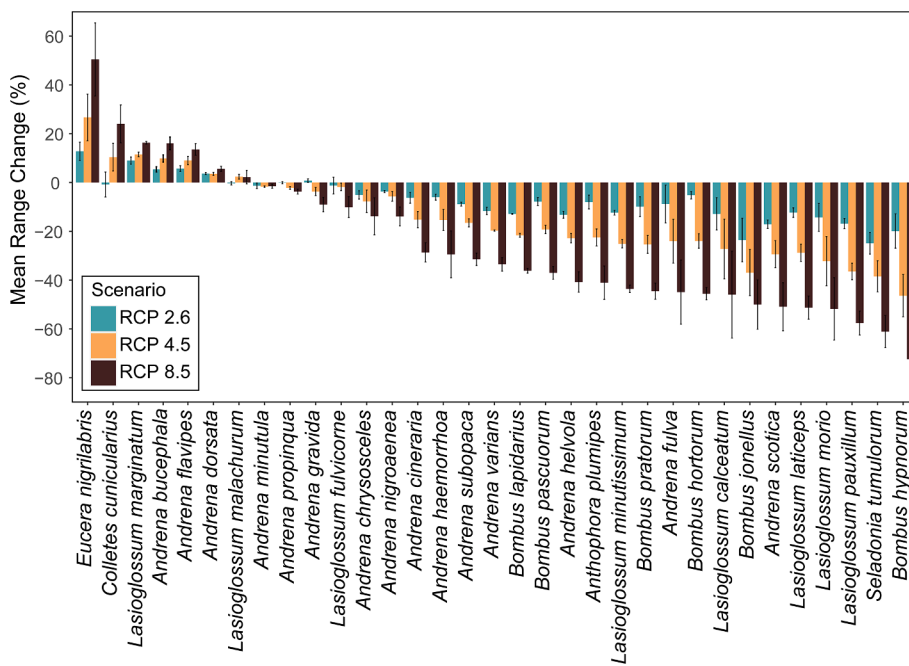
### 3.2. Overall projected range changes for key apple pollinating species

Under the intermediate dispersal hypothesis, we observed an overall mean difference of paired estimates with the full dispersal hypothesis of 0.2% ( $p\text{-value} = 1$ ). This value is ecologically irrelevant and therefore, we focus our results on the full dispersal hypothesis (Fig. S2). Overall, under the three climate change scenarios, the 33 KABS are projected to experience average range reductions of (i)  $8.2\% \pm 11.3$  in 2060 and  $7.3\% \pm 9.5$  in 2080 under RCP2.6, (ii)  $12.3\% \pm 15.3$  in 2060 and  $-14.8\% \pm 18.6$  in 2080 under RCP 4.5, and (iii)  $16.3\% \pm 20.4$  in 2060 and  $24.9\% \pm 30.5$  in 2080 under RCP 8.5 (Fig. 2). A one-way ANOVA and *post-hoc* test indicated that the three scenarios were significantly different from each other based on average projected range change ( $df = 2$ ,  $f = 40.4$ ,  $p$  less than 0.0001). The majority of these range changes are driven by the loss of suitable environmental conditions,  $76\% \pm 35\%$  of the total range change on average.

Seven species are predicted to lose more than half of their range by 2080 but only under RCP 8.5; *B. hypnorum* (Linnaeus, 1758), ( $72.4\% \pm 12.3$ ) and *Seladonia tumulorum* (Linnaeus, 1758), ( $61.1\% \pm 6.6$ ) are the two species with the most severe predicted range losses. The same two species are mostly affected under RCP 4.5, and under RCP 2.6 it is *S. tumulorum* and *B. jonellus* (Kirby, 1802), (Fig. 2). Conversely, only five species are expected to increase in range across all three scenarios, namely *A. bucephala* Stephens, 1846, *A. dorsata*, *A. flavipes* Panzer, 1799, *Eucera nigrilabris* Lepeletier, 1841, and *L. marginatum* (Brullé, 1832). Only *E. nigrilabris* is projected to increase  $>25\%$  under both RCP4.5 ( $26.7\% \pm 9.59$ ) and RCP8.5 ( $50.4\% \pm 15.0$ ). Species richness in the present and all scenarios peak at 23 species (Fig. 3). However, if we take ten species as a proxy for a diverse community of KABS, then the number of  $25 \times 25$  km cells with at least ten species (4500 in the present) decreases by 16% (RCP2.6), 32% (RCP4.5) and 55% (RCP8.5) by 2080 (Fig. 3). Increases in diversity were almost completely absent from the projections with only a few cells in Northern Europe showing an increase of up to five species.



**Fig. 1.** Proportional variable permutation importance for all species. Proportional contribution of selected variables per species for every run (n = 10) better than a 95% quantile of a 100 null model distribution. Permutation importance is calculated as the decrease in predictive performance when a variable is removed from the model. Species are ordered by descending order of the, overall, most important variable Annual PET. ‘PET’ stands for potential evapotranspiration, a measure of the ability of the atmosphere to remove water.



**Fig. 2.** Overall species range change in 2080 under three climate change scenarios. Range change is a combination of grid cells lost and gained between the present period and 2080. Error bars show the uncertainty in the predictions across all models better than a random null distribution. A one-way ANOVA and *post-hoc* test indicated that the three scenarios were significantly different from each other based on average projected range change (df = 2, f = 49.5, p less than 0.0001). Results shown are under the full dispersal hypothesis with no spatial limitations to range change in the future.

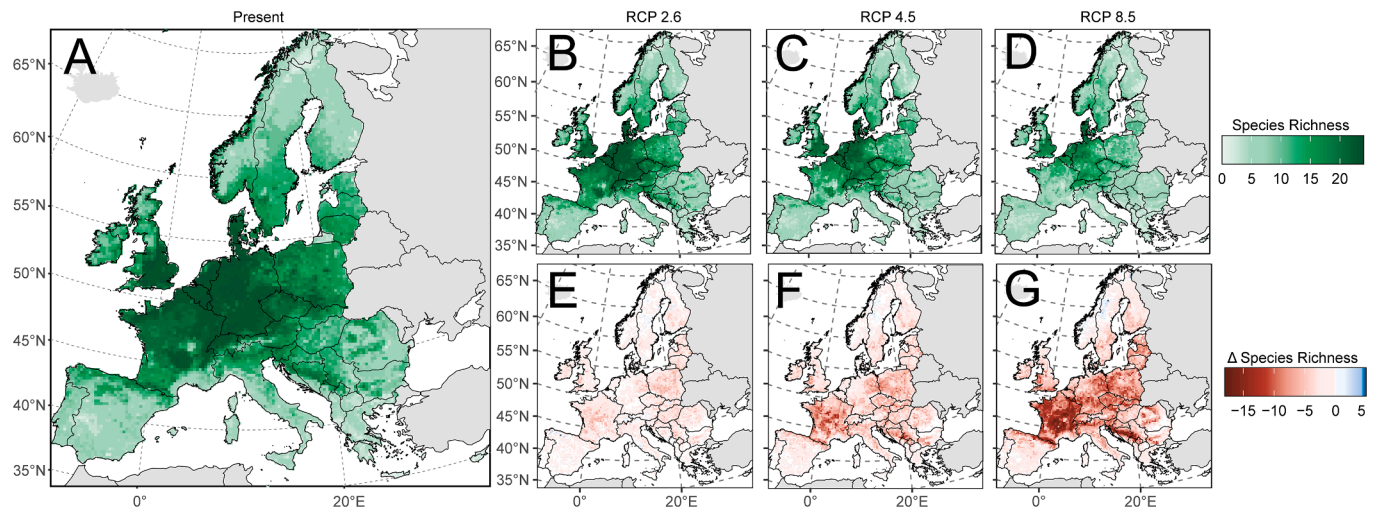
**3.3. Spatial mismatch with apple orchards**

We identified consistent decreases in overlap between KABS and apple orchards only under the worst-case scenario of climate change (RCP8.5). Across all species, the mean overlap with apple orchard habitat suitability is presently 73% ±12 and is projected to decrease down to 70% ±14 (RCP2.6), 67% ±16 (RCP4.5), and 60% ±20 (RCP8.5). Only a single species, *B. jonellus*, decreased by >10% of its overlap range under RCP2.6, and this increased to five species under RCP 4.5 and 17 species under RCP8.5 (Fig. 4). For all three scenarios, we found a clear positive statistical relationship (p less than 0.001) between loss of overlap by 2080 and overlap in the present day. In other words, species with less overlap in the present were projected to lose more absolute overlap in the future. When we limited apple orchards to only

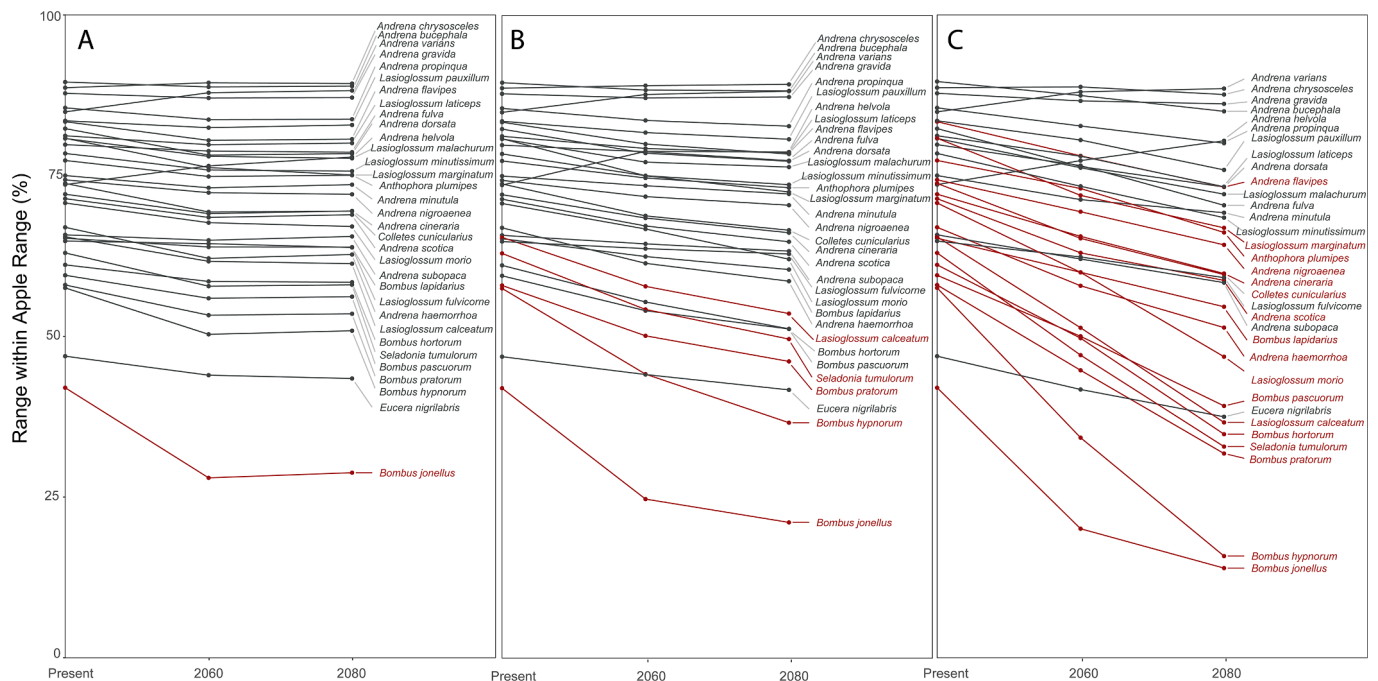
areas where apples are currently expected to grow, we observed the overall percentage overlap decreases although the trends *per* species remain the same (Fig. S3).

**3.4. National level patterns**

According to FAO statistics (FAO, 2019), Poland, Italy, and France produce the most apples in tonnes in Europe. When measuring yield (tonnes per hectare), Switzerland, Belgium, and the Netherlands make up the top three (none of which are in the top ten of production in tonnes); Italy (4th) and France (6th) are still in the top ten. When we combined this information with range change projections of KABS, we clearly observed that certain regions will suffer more (Fig. 5; RCP8.5 2080; for other scenarios see Figs S4 & S5). France is predicted to lose on



**Fig. 3.** Species richness changes of key apple pollinating species under three climate scenarios in 2080. (A) projected species richness in the present. (B-D) species richness projections under three climate change scenarios (RCP2.6, 4.5 and 8.5). (E-G) change in species richness ( $\Delta$ ) projections under three climate change scenarios (RCP2.6, 4.5 and 8.5). All maps are based on a conservation 10% consensus between binary prediction maps. Map projections are in EPSG:3035.



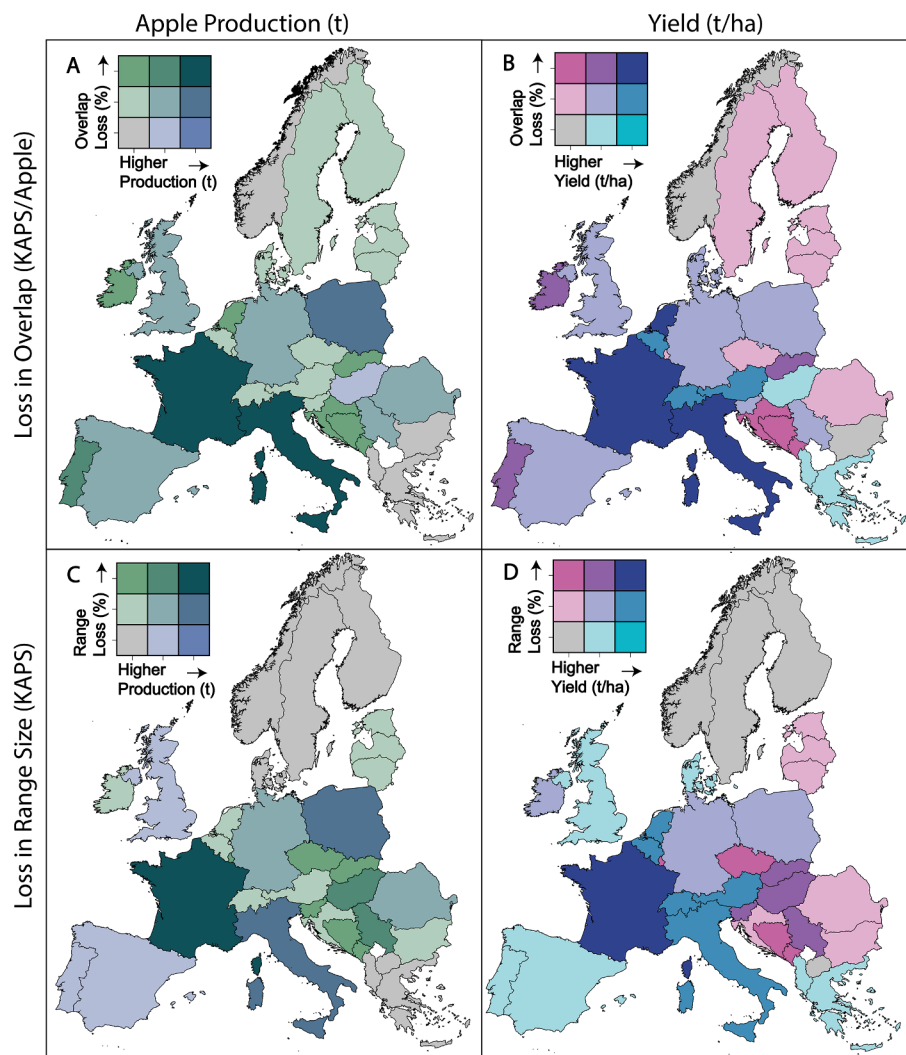
**Fig. 4.** Change in overlap between suitable habitat for apple orchards and suitable habitat for key apple pollinating species in the present, 2060 and 2080. Apple habitat suitability is based on a consensus binary prediction of all 10 runs. (A) RCP2.6 (B) RCP4.5 (C) RCP8.5. Species colored in red are those predicted to lose more than an absolute 10% of range overlap. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

average 36% of the distributional range of each species, although this is highly variable (SD = 27%), the average range overlap between KABS and the habitat suitability of apple orchards is also expected to decrease by 48% (Fig. 5). Italy is not projected to experience great loss of species richness ( $18\% \pm 14$ ) but will experience the greatest average loss of overlap of 54%. Of the high yielding countries, Belgium is also projected to be at risk with average range losses per species of  $30\% \pm 29$  but a projected loss of average range-overlap of only 18% (Fig. 5). The projected risks to Switzerland and the Netherlands are also potentially worrisome, with highly variable predicted range losses of  $21\% \pm 23$  and  $20\% \pm 26$  and the loss of range overlap with apple crops projected at 18% and 43% (Fig. 5). The loss of range and overlap of KABS was not only high in areas with important apple production, and there was not a

statistically clear relationship between the distribution change metrics and the apple production at the country level. We cannot reject the null hypothesis that countries which produce a greater absolute quantity of apples are not at a greater risk of losing KABS ( $p > 0.1$ ).

#### 4. Discussion

In this study, we show that under projected climate change scenarios we expect an increased spatial mismatch between wild bees that pollinate apple crops and the area most suitable for cultivating apple crops. However, the spatial mismatch is dependent on the severity of the projected climate change and in all scenarios, it is unlikely to lead to a complete absence of wild pollinators. Furthermore, the projected



**Fig. 5.** Bivariate plots of per country changes in wild bee distributions and apple production statistics. (A) Average percentage loss of overlap with apple orchard habitat suitability per species under RCP8.5 in 2080 vs. national apple production in tonnes (t). (B) Average percentage loss of overlap with apple orchard habitat suitability per species under RCP8.5 in 2080 vs. national apple yield in tonnes per hectare (t/ha). (C) Average percentage loss of range per species under RCP8.5 in 2080 vs. national apple production in tonnes (t). (D) Average percentage loss of range per species under RCP8.5 in 2080 vs. national apple yield in tonnes per hectare (t/ha). Average overlap loss percentage per country ranges from an increase of 8% to a decrease of 54%. Average range loss percentage per country ranges from -4% to -49%. Average production in tonnes per country ranges from 1,490 t to 3,080,600 t. Average yield in tonnes per hectare per country ranges from 30.2 t/ha to 507.8 t/ha. Map projections are in EPSG:3035. The bivariate classes were made using Fisher breaks. In Fig. 5A and 1B North Macedonia has been removed as it represents an outlier (>4 standard deviations from the mean) because of a large increase in overlap of 57%.

mismatches and range losses are not equally distributed across Europe and certain countries with high apple production are at greater risk.

We classified 33 species of wild bees as key apple pollinating species, which is only a tiny subset of the ~ 2050 species which represent the full diversity of wild bees in Europe (Nieto et al., 2014; Rasmont et al., 2017). This finding is supported by Kleijn et al. (2016) which found that only a small number of common species make up the majority of crop visiting species. While our study focuses specifically on bees, which are likely the most common pollinators of apple crops, it is worth noting that other insects, such as Syrphidae and some Coleoptera, may also be important pollinators for apples (Rader et al., 2016; Roquer-Beni et al., 2021). All of the KABS are common species, and none are at risk according to the European red list; all species are listed as “Least Concern”, except for seven *Andrena* spp., which are data deficient (Nieto et al., 2014). Furthermore, in general, the KABS are broadly spread across Europe and therefore we did not project large range contractions; if we treat RCP 4.5 as a “business as usual” scenario, then there is little risk that any of the KABS will lose >50% of their range. This is similar to results from Giannini et al. (2020) who found that potential crop pollinating wild bees with restricted or medium range sizes were projected to be more severely affected by climate change than widespread species. There was a longer tail of species that were found to be visiting apple orchards across Europe that did not meet the KABS classification (Weekers et al., 2022b). Additionally, southern Europe was comparatively less well sampled than western, central and northern Europe,

meaning that some KABS may have been overlooked. Given that the number of wild bee species necessary for successful crop pollination increases with area (Winfrey et al., 2018), it is possible that species not included in this model may have future range expansions and become important apple pollinators. This indicates that maintaining high bee diversity, even for species that do not currently provide pollination services, is a resilient strategy in the long term (Garibaldi et al., 2013).

Overall, our results suggest that continental extinctions of important apple pollinators are highly unlikely, however some species may experience severe range contractions (>50% range contractions) under RCP 8.5, and this will lead to depleted communities of KABS at the southern limit of apple production in Central Europe. Conversely, the models do not predict range increases into Scandinavia. Apple production is currently limited in Scandinavia in comparison to more southern countries (FAO, 2019), this is not projected to change with our modeling approach, unless there are significant land use changes not accounted for in our model. This failure to shift the northern limit in conjunction with the southern limit has already been shown to be the case for bumblebees (Kerr et al., 2015). These limited northern shifts may be driven by our choice of static land use variables, which means that we assume that land use is not shifting with climate change. While including dynamic land use change can have a significant effect on certain species’ future distribution ranges, the differences do not seem to change the overall patterns of range contractions or expansions and are expected to be more accurate than climate-only models (Marshall et al., 2018;



Thuiller et al., 2004). Here, we prioritized minimizing range truncation over having dynamic land use change variables. The absence of a temporal aspect to the land use included in the model could explain why we see an overall greater importance of climate variables, and may, in part, explain why we saw no significant effect of limiting the dispersal capabilities of species. Relevant changes to land use in the North of Europe may provide more suitable habitat for wild bees in the future (Marshall et al., 2018; Prestele et al., 2021). Although, for a robust modelling approach, high thematic resolution land use change scenarios would be needed for the whole range of the species (Marshall et al., 2021).

In terms of spatial mismatches under RCP2.6 and 4.5, we project that climate change will not bring about significant spatial mismatches in the time periods considered, and that the proportion of shared habitat suitability between KABS and apple orchards will not vary by >10% for most species. This gap increases under RCP 8.5, but full spatial mismatches are never projected and the species with the greatest overlap in the present maintain a significant overlap under all scenarios in 2080. Our results for the UK, a country in the top 10 of apple producers for both yield and total production where we expect a minimal impact of KABS range contractions and spatial mismatch, are in marked contrast with a previous report by Polce et al. (2014) who projected a clear geographical mismatch between apple pollinating wild bees and apple orchards in 2050. One explanation for this discrepancy is due to the truncation of the climate niche of the different species, none of the species that pollinate apples in the UK are endemic to the UK (Niето et al., 2014) and most of the apple varieties grown in the UK are also grown widely on the continent. Many of the species in our study have very large ranges and avoiding the impacts of truncation of the climate niche at the boundaries of Europe was important. Therefore, we included species' full distribution ranges into southern Morocco and towards the Ural Mountain range in the East in the training dataset. Truncation at national borders can lead to an underestimation of the temperature and rainfall extremes that these species can occur in and project more extreme impacts of climate change (El-Gabbas & Dormann, 2018; Sánchez-Fernández et al., 2011; Thuiller, 2004). The significant assumptions of this approach is that phenotypic plasticity in terms of the climate niche is consistent in populations in different areas, or that populations will be able to disperse with their niche. Without these assumptions the future contractions may be more severe than projected here (Valladares et al., 2014). Conversely, it may be possible that the climate range underestimates the plasticity of the species and future habitat predicted as unsuitable may actually be within the scope of adaptation (Maebe et al., 2021a). Only species-specific testing of these wild bee species' climatic limits will reveal this possibility (see e.g. Martinet et al., 2015; Maebe et al., 2021b).

The absence of plastic and adaptive responses to climate change may in part explain the limited range expansions we predict for KABS. Another explanation may be due to the classification of the present-day habitat suitability. The habitat suitability of the species is defined only by its relationship to climate and land use and may lead to broader projections of the present-day extent for many species. We can see from our models that areas of northern UK and coastal Scandinavia have higher predicted species richness in the present than are seen from occurrence records alone. Therefore, if a species' northern range is already projected to occur in these areas, even if the species is not currently observed there, then future range expansion predictions will be limited. We observe a clear example of this with the species *Lasiosglossum malachurum* (Kirby, 1802), and *L. pauxillum* (Schenck, 1853). They are both obligately eusocial bees (Smith and Weller, 1989) that are currently limited in their expansion by the length of the season in order to complete their social life cycle. In the UK, during the 1990–2010 period their range expanded substantially towards the north (Else and Edwards, 2018). Therefore, we would hypothesize that this range expansion would continue in the future into the north as seasons become longer. However, our models do not project this expansion because the northern areas of the UK are already classified as suitable habitat in the

present. It is therefore likely that the limiting factor is not the abiotic conditions but the lifecycle of the species which is not accounted for in our models. It is also worth noting that we do not include climatic variables that explicitly account for season length. The impact of these model limitations on our results is that we may be underestimating range expansion and potentially over-estimating range contraction. Detailed information on demography, behavior, dispersal, physiology as well as abiotic conditions would greatly improve both our present day and future range projections (Urban et al., 2016). While our focus here is on the presence of overlapping suitable conditions between bees and apple crops, it is important to note that warming conditions can affect bee development (Kierat et al., 2017), which may lead to weaker populations (Maebe et al., 2021a). As a result, climate change may have a negative impact on pollination services due to lower abundance of KABS resulting from population declines.

In terms of apple production, the value of wild pollinators lies in their contribution to improving fruit set, yield and crop economic value (Garibaldi et al., 2013; Garratt et al., 2014; Pérez-Méndez et al., 2020). Our results suggest that certain European countries are more at risk from climate change than others: wild pollinator declines will have a much greater impact on crop production in areas where these crops are economically important (Giannini et al., 2017). For example, yield and production of apples are highest in certain western European countries, including France, Italy, Netherlands, Germany, Belgium, and Switzerland. In contrast to the findings of Carrasco et al. (2020) for tomato pollination in the USA, we did not find that range contractions and loss of overlap were more likely in areas with high apple production. Indeed, the range losses and potential spatial mismatches are not evenly distributed across the top apple producing countries in terms of both yield and total production, with France, Belgium, Poland and Italy being at a greater risk. Although not all major apple-producing countries were considered in the calculation of KABS, it is anticipated that the KABS for countries like Poland and Switzerland would be similar to those of the surrounding sampled countries. Pollinator conservation initiatives in Belgium and France are under development (Schatz et al., 2021), and apple is a well-studied crop in terms of crop pollinators, making it a good candidate for targeted wild pollinator conservation. However, at the broadest scale, consistent actions at the governmental level to limit greenhouse gas emissions and restricting climate conditions to those seen in RCP2.6 will have the greatest benefit to maintaining agricultural pollination services (IPCC, 2014). In that sense, the problem of pollinator loss due to climate change is a global problem and concerns biodiversity loss in general (Cardinale et al., 2012).

Whilst climate change will act at the global scale changing species distributions (Parmesan & Yohe, 2003), the actual occurrence of a diverse community of wild pollinators at the orchard level is dependent on many other factors (Potts et al., 2016). These include the surrounding local landscape (Feon et al., 2010; Kammerer et al., 2016), the soil conditions (Carvalho et al., 2021), atmospheric pollution (Rollin et al., 2022; Ryalls et al., 2022), the dominance of honey bees (Weekers et al., 2022a), neighboring agricultural crops (Osterman et al., 2021); local intensification (Deguines et al., 2014) and management decisions (Roquer-Beni et al., 2021). It is possible that species from northern Africa (for example, carpenter bees; Ghisbain et al. 2021) may also move to Europe and mitigate the loss of European populations. Furthermore, even more complex and uncertain is the extent to which range contractions and spatial mismatches could lead to pollinator deficits. Pollinator deficits in apple crops appear to be dependent on spatial context, management and crop variety (Garratt et al., 2021). Finally, the spatial mismatches as presented here are not the only potential impact of climate change on crop pollination. Climate change has the potential to strongly disrupt plant-pollinator networks (Memmott et al., 2007). Certain European wild bee species already show shifts to becoming active early in the year (Duchenne et al., 2020) and if this is true for the KABS, and apple flowering does not shift similarly, then phenological mismatches are also possible. The evidence for disruptive asynchrony in

apple-pollinator relationships is relatively scarce in the literature at the moment, with apple crops in the USA and Romania showing similar trends in earlier flowering (Chitu & Paltineanu, 2020; Wolfe et al., 2005) and communities of wild bees in New York (USA) showing strong synchronicity with apple blooming times (Bartomeus et al., 2013b). In the UK, Wyver et al., (2023) also found evidence that both Bramley apple flowering and peak pollinator flight periods had advanced alongside warming spring temperatures. Therefore, we believe the greater risk of climate change for crop production is potential spatial mismatches as projected here. These forecasts of climate change impacts on pollinators can help to inform present day conservation efforts through a greater understanding of the key areas at risk (Giannini et al., 2015). We show that the additive effect of climate change on species occurrence has the potential to impact the availability of key wild pollinators to a globally important crop, and that this is not geographically equal.

Our results suggest that future climate niches of orchards and wild bee pollinators may become spatially distinct, therefore threatening pollination services. By and large, commercial and intensive apple production systems are designed as perennial monocrops with an almost obligate dependence upon external inputs such as water, fertilizers and synthetic pesticides. Diverse and robust pollinator communities may be able to be maintained in agricultural habitats that become climatically unsuitable, if specific approaches to mitigate and adapt to the impacts of intensive agriculture and climate change are made (Potts et al., 2016). Ecological intensification within and around orchards, through agroforestry practices (Alam et al., 2014), maintaining natural and semi-natural habitat in the surroundings (Marini et al., 2012; Ricketts et al., 2008), and limiting agricultural inputs (Park et al., 2015) increases landscape heterogeneity and connectivity and can ensure suitable habitats for many species and not only, highly mobile, wide-spread, generalists (Potts et al., 2016). Furthermore, diversified and extensive orchards also tend to provide a better spread of the flowering season, allowing a longer interaction with diverse communities of pollinators (Heller et al., 2019). In the case of strawberries for example, their sharing of pollinators with apple trees and a delayed timing of their blooming period drive higher yields than when they are cultivated on their own or when their flowering period is not adjusted (Grab et al., 2017). The effectiveness of these measures, much like the impacts themselves, is likely to vary significantly between regions and will depend on an area's current vulnerability and development status (Potts et al., 2016). However, adaptations at the local orchard scale will be required to maintain pollinator diversity and the service this provides, and in turn limit the impacts of expected climate changes.

#### CRediT authorship contribution statement

**Leon Marshall:** Conceptualization, Methodology, Formal analysis, Investigation, Investigation, Writing – original draft, Writing – review & editing. **Nicolas Leclercq:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing. **Timothy Weekers:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Insafe El Abdouni:** Methodology, Formal analysis, Data curation, Investigation, Writing – review & editing. **Luísa G. Carvalho:** Methodology, Data curation, Writing – review & editing. **Michael Kuhlmann:** Data curation, Writing – review & editing. **Denis Michez:** Conceptualization, Data curation, Writing – review & editing, Funding acquisition. **Pierre Rasmont:** Data curation, Writing – review & editing. **Stuart P.M. Roberts:** Data curation, Writing – review & editing. **Guy Smagghe:** Conceptualization, Writing – review & editing, Funding acquisition. **Peter Vandamme:** Conceptualization, Writing – review & editing, Funding acquisition. **Thomas Wood:** Methodology, Validation, Investigation, Writing – review & editing. **Nicolas J. Vereecken:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data and code are available from Zenodo: <https://doi.org/10.5281/zenodo.8318932>.

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#### Appendix A–D. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloenvcha.2023.102742>.

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