A hierarchical framework for mapping pollination ecosystem service potential at the local scale

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A B S T R A C T

Wild bees play a major role in the cultivation of crops for human use, in the reproduction of many wild plants and are a key component of biodiversity. Mainly due to human activities, wild bees, like other insects, face a rapid decline in Europe. Understanding species distribution can help to design efficient conservation measures. Species distribution can also be used to estimate pollination ecosystem service potential, which can benefit the production of crops relying on pollination and the reproduction of wild plant communities. The presence of pollinators depends on a combination of environmental and biotic factors, each playing a determining role at different spatial scales. We therefore developed a model composed as a hierarchical framework for environmental predictors: climatic data and Land Use/Land Cover (LULC) variables at the European scale and species-specific habitat information at the local scale. The model combines the advantages of two different existing approaches: pollinator species distribution predictions based on their environmental requirements and knowledge on bee species life-history traits and habitats. This paper presents the predicted distribution of twenty-five wild bee species of the *Andrena* genus in an agricultural region in Northern Germany. We used oilseed rape pollinators as a case study and compared the potential pollination services to the potential demand in the Case Study Area. The developed framework allows to determine the capacity of landscapes to support pollination ecosystem services from wild bees at the local scale, which can support the identification of vulnerable areas and the design of local scale measures for habitat improvement and for conservation. The hierarchical approach leaves potential for further adaptations in order to improve the prediction of wild bee species dynamics and factors influencing their spatial distribution.

1. Introduction

Pollination is a key ecosystem service, vital to both wild plants and cultivated crops (Klein et al., 2007). Gallai et al. (2009) estimated that 10% of the total economic value of food production in Europe depends upon insect pollination. There is growing evidence that wild bees play a significant role in crop pollination (Javorek et al., 2002; Greenleaf and Kremen 2006a; Klein et al., 2007; Bommarco et al., 2012; Garibaldi et al., 2013), and that the pollination service delivered by wild pollinators cannot entirely be substituted by honeybees (Brittain et al., 2013; Garibaldi et al., 2013). An increasing number of insect pollinators are in decline or threatened, mainly because of anthropogenic stressors such as

environmental pollution, land use change and agricultural intensification but also climate change (Winfree et al., 2009; Potts et al., 2010; Cameron et al., 2011; Ollerton et al., 2014; Nieto et al., 2014). This decline of pollinating species will not only have an impact on agricultural productivity and resilience (IPBES 2016), it can also lead to a parallel decline of wild plant species (Biesmeijer et al., 2006), as globally estimated 85% of flowering plants (78% in temperate zones) are adapted to animal pollination (Ollerton et al., 2011), mainly to bees (Potts et al., 2010). Therefore ongoing declines in pollinator diversity may result in community cascade effects, i.e., the subsequent loss of other species that directly or indirectly rely upon extinct or declining species (Chapin et al., 1997). This in turn can have an impact on wild food, fibre and

medicine supplies, as well as decrease the cultural and aesthetic values of a landscape (IPBES 2016).

In light of these observations, there are increasing calls and efforts to conserve wild pollinator species and their habitats (IPBES 2016). An effective biodiversity conservation policy should provide a clear guidance to planning authorities on how to develop targeted species-specific conservation options for organisms that contribute to pollination services at relevant scales (Kremen et al., 2007). To this end, there is a need for better spatial assessments of pollination. Understanding spatial patterns of pollinators is also crucial for estimating their availability to pollinate cultivated crops and wild plants (Kremen et al., 2004), to facilitate monitoring and inform on the habitats and vulnerability of local pollinators (Kremen et al., 2007; Kremen and Chaplin-Kramer 2007).

Up to now, the main approaches for building pollinator ecosystem service maps are by using InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) (Sharp et al., 2016) and ESTIMAP (Ecosystem Service Mapping Tool) (Zulian et al., 2013). InVEST and ESTIMAP models are primarily based on expert judgements on the presence and preferences of pollinators (essentially nesting places and floral feeding resources). The main issues with expert-based knowledge are that this knowledge may strongly depend on their selections, experience and expertise (Polce et al., 2018; Lonsdorf et al., 2009), and therefore can be biased towards specific species or species groups. Fewer studies are based on Species Distribution Models (SDMs) and actual species records (Polce et al., 2013; Polce et al., 2018; Nogué et al., 2016). SDMs rely on the correlation between environmental variables and geo-localized species records to determine the environmental variables that drive species presence and delineate potential species distribution (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Araújo and Guisan 2006). Contrary to SDMs, InVEST and ESTIMAP models do not allow to dynamically consider different environmental conditions (Lonsdorf et al., 2009; Zulian et al., 2013). When mapping pollination ecosystem service potential at national or sub-national scales, bioclimatic conditions can largely vary and be a major determinant of bee species occurrence. Conversely, existing pollination models based on SDMs are at relatively coarse resolution, constrained by occurrence data and environmental variables typically available at coarse spatial resolution. Especially in highly fragmented landscapes, this resolution may fail to cover important habitats such as hedgerows, small pastures and forests, and therefore obtain biased pollinator distribution maps. Thus, to improve our ability to predict pollinator diversity and the associated pollination ecosystem service, one possibility could be to combine the advantages of the two different approaches: species distribution predictions through SDMs and knowledge on bee species life-history traits and habitat requirements as implemented in InVEST and ESTIMAP frameworks.

The aim of this study is to develop a high-resolution pollinator species model to predict spatial patterns of pollination ecosystem services potential from wild bees at the local scale. Hereby we assume that pollinator species richness and landscape suitability are good proxies of pollination service potential. This is a common assumption in existing pollination models (Kremen et al., 2007; Lonsdorf et al., 2009; Zulian et al., 2013) and is supported by the fact that pollination quantity, quality and stability tend to increase in landscapes with a diverse pollinator community (Klein et al., 2007; Albrecht et al., 2012; Dainese et al., 2019). The model is used as a tool to provide clear guidance for potential users such as planning authorities on how to optimize conservation measures for wild bee conservation and to inform on how management decisions can affect pollination ecosystem services and therefore pollination-dependant crop productivity. We apply the model in an agriculture-dominated case study area in northern Germany to test this approach at the local scale and its applicability for landscape management, using selected bee species as an example. The approach also allowed us to assess how and which environmental variables affect wild bee species distribution, as well as the role of life-history traits on their spatial distribution.

2. Materials and methods

2.1. Case study area (CSA)

The CSA is located in the region of the Bornhöved Lake District in the federal state of Schleswig-Holstein in Northern Germany (Fig. 1). The extent of the area is approximately 140 km^2. Agroecosystems dominate the landscape in a catchment area of five glacially formed and consecutively connected lakes. The CSA shows a suit of habitats with a high proportion of hedges and wall hedges that are characteristic in the province, shaping a highly diverse and fragmented landscape (see Fig. 1 and Fränzle et al. 2008). Only small settlements, following a north-south alignment, are located in the CSA.

2.2. Datasets

2.2.1. Bees

We selected species from the genus *Andrena*, also called mining bees, as they represent a highly various group including small bees to ones larger than honey bees, species that differ in seasonality or soil preference as well as specialists (oligolectic) and generalist (polylectic) species. This genus of bees is therefore a good representative of a broad range of bee species. From the *Andrena* genus, we selected species that were identified in the region and documented in the federal red list (van der Smissen 2001). This step accounts for historical and current dispersal limitations and helps to determine which species in the global source pool could have dispersed to the CSA (Guisan et al., 2017). The selected *Andrena* species are listed amongst the most important pollinators for crops in Europe, particularly of oilseed rape flowers and apple trees (Klein et al., 2007; Kleijn et al., 2015), or wild flowers (Westrich 2018). Plant families visited by each species are listed in Table 1 in the supplementary material. We obtained 125,681 presence-only records of twenty-six wild bees from the Global Biodiversity Information Facility[1] (GBIF). Occurrence records retrieved from GBIF were cleaned using the "CoordinateCleaner v.2.0–14″ package (Zizka et al., 2019). Occurrences with sea coordinates, zero coordinates or without geographic coordinate, country mismatches, country centroids, outlier coordinates and coordinates assigned to biodiversity institutions were excluded. We also removed data older than 1950 as old records are more likely to be unreliable (Maldonado et al., 2015), data records with unprecise coordinates and duplicates. We also checked for taxonomic errors, including spelling mistakes and synonyms. To reduce model overfitting derived from spatial autocorrelation and overdominance of specific regions due to sampling bias, we then thinned the records using the package "spThin v.0.2.0″ (Aiello-Lammens et al., 2015).

We only selected species that had more than 50 GBIF occurrence records, as this is a key criterion for SDM modelling quality (Guisan et al., 2017). After geographic and taxonomic cleaning, only 10,928 records of twenty-five wild bee species were retained for modelling (Table 1 in the supplementary material).

2.2.2. Environmental variables

We used bioclimatic and Land Use/Land Cover (LULC) data as environmental predictors (see Table 2 in the supplementary material for a complete list of the environmental variables). We first selected the main drivers of species ranges based on knowledge about mechanistic relationship between environmental variables and physiology of the targeted species. We further reduced the number of variables as too many variables increase the risk of overfitting and collinearity issues between the variables (Dormann et al., 2013; Guisan et al., 2017). Collinearity refers to the non-independence of predictor variables and
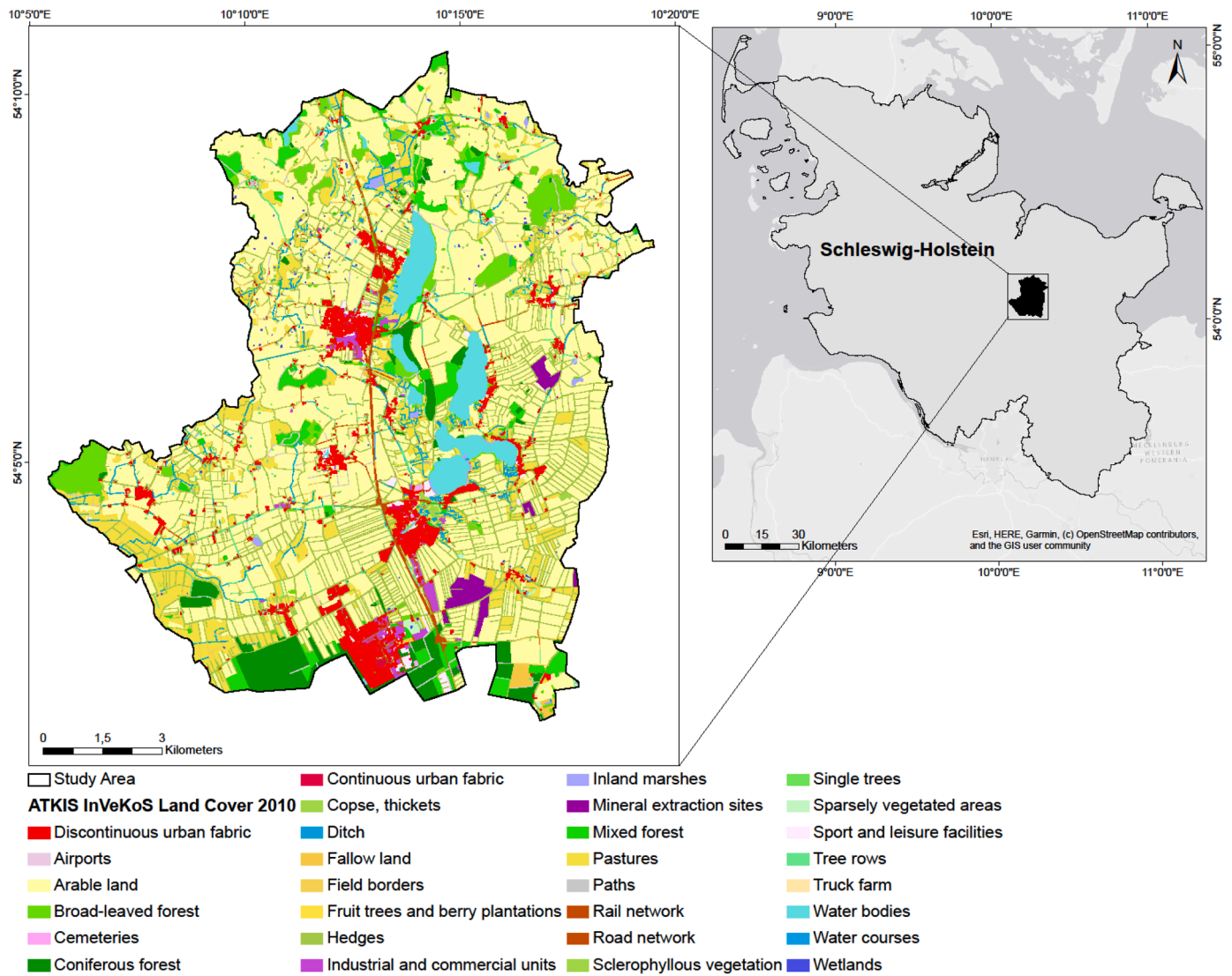
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[1] https://www.gbif.org/

Fig. 1. Location of the study area in Northern Germany (on the right) and distribution of Land Use / Land Cover classes (AKTIS/InVeKoS (2010)) in the case study area (on the left).

can be a problem for parameter estimation as it inflates the variance of regression parameters and potentially leads to the wrong identification of relevant predictors. Therefore, reducing the number of environmental variables maximizes the performance of SDMs and the accuracy of the predictions (Araujo and Guisan 2006). A Principal Component Analysis (PCA) was used to visualize the correlation between variables, to identify the main environmental gradients in the study area and to investigate the distribution of species in the environmental space (Guisan et al., 2017). We conducted our PCA using the "ade4 v.1.7–16″ package from R (Dray and Dufour 2007). We also analysed correlations between environmental variables with a Pearson analysis for all bioclimatic and LULC variables. Only the most relevant uncorrelated variables, i.e. with a Pearson's correlation coefficient below 0.7, were finally selected (Dormann et al., 2013).

The bioclimatic variables were first selected based on their impact on diurnal foraging activity of bees, nesting success and plants availability. During active months, low temperatures and high precipitation values reduce the number of foraging days and consequently potentially decrease bee fitness (Westrich 2018). High precipitation values probably impact the nesting success for ground nesters (Bystriakova et al., 2018). Extreme temperature and precipitation also indirectly affect bees by impacting the bloom of plants and therefore resource availability (Nieto

et al., 2014). Climatic data were retrieved from WorldClim[2] on a 30 second resolution raster grids (~1 km^2 at the equator) from WorldClim 2.0 (Fick and Hijmans 2017). From the 19 available climatic variables, we first selected the variables expected to be the most causal for the species distribution: Bio_02 (Mean Diurnal Range), Bio_5 (Max Temperature of Warmest Month), Bio_6 (Min Temperature of Coldest Month), Bio_7 (Temperature Annual Range, Bio_5 - Bio_6), Bio_8 (Mean Temperature of Wettest Quarter), Bio_10 (Mean Temperature of Warmest Quarter), Bio_11 (Mean Temperature of Coldest Quarter), Bio_14 (Precipitation of Driest Month), Bio_16 (Precipitation of Wettest Quarter), Bio_18 (Precipitation of Warmest Quarter) and Bio_19 (Precipitation of Coldest Quarter). The results of the PCA indicated that from the nine pre-selected bioclimatic variables, eight were strongly correlated (Bio_5, Bio_6, Bio_10 and Bio_11, Bio_14 and Bio_18 as well as Bio_19 and Bio_16) and one (Bio_8) did not significantly contribute to the overall environmental variation (see Fig. 1 in the supplementary material). We selected Bio_19, Bio_11, Bio_2, Bio_7 and Bio_14 for the modelling, as they are good variables for discriminating between bee species and the rest of the environment.

In temperate zones, wild bee species distribution are influenced by the proportion of heathland, woodland, grassland and urban areas coverages at the landscape scale (Senapathi et al., 2015). As major threats to wild bees in Europe, agricultural intensification and expansion, pollution and urban sprawl will generally have a negatively impact wild bee species distribution (Nieto et al., 2014). For this study, LULC data was derived from the CORINE (Coordination of Information on the Environment) Land Cover 2018 dataset[3], with a 100 m resolution. This dataset is produced by the European Environmental Agency (EEA) and is composed of 44 different LULC classes belonging to the five main land cover categories artificial surfaces, agricultural, forest, semi-natural areas, wetlands or water bodies. We used the hierarchical level 3 from CORINE and first aggregated the data in 1 km * 1 km grid cells, representing the percentage cover of each LULC per 1 km * 1 km grid. This was a necessary first step to generate a clean data structure for modelling (all predictors having the same resolution). The resolution of the predicted results is the same as the one of the environmental variables (1 km * 1 km). We first selected 15 LULC classes based on their ecological relevance: Continuous urban fabric, discontinuous urban fabric, road and rail networks and associated land, non-irrigated arable land, pastures, complex cultivation patterns, broad-leaved forest, coniferous forest, mixed forest, natural grasslands, moors and heathland, transitional woodland-shrub, sparsely vegetated areas, water courses and water bodies. We run the complete model a first time to select the most important variables for the select wild bee species distribution. This led to the selection of the following LULC variables: discontinuous urban fabric, non-irrigated arable land, pastures, coniferous forest, sparsely vegetated areas, water courses and water bodies. The selected LULC variables are neither correlated within each other nor with the selected bioclimatic variables (see Pearson correlation coefficients in Table 3 in supplementary material).

In total, five bioclimatic variables and seven LULC classes were selected for modelling the potential distribution of the twenty-five bee species.

2.2.3. Habitat filter variables

We used the ATKIS (version 2012, Authoritative Topographic and Cartographic Information System), the official topographic information system for Germany and the InVeKoS (version 2010, Integrated Administration and Control System) datasets to build our species-specific habitat filters. The ATKIS dataset is originally mapped at a scale of 1:25.000 and describes 182 object classes that belong to artificial surfaces, traffic, vegetated areas (mainly agricultural, forest and natural areas), water bodies and relief (such as dams, cliffs, dunes). The InVeKoS dataset was used to obtain landscape elements such as hedgerows and tree rows for the CSA. For both datasets, the spatial resolution depends on the feature classes and has a MMU between 0.1 and 1 hectare (Bach et al., 2006). The ATKIS/InVeKoS datasets was used to map bee species habitat as described by Westrich (2018). To our knowledge, it is the most appropriate way to map bee species habitat at a high thematical and spatial resolution in our CSA. Though the latest generation of satellite products may allow to map LULC at a high resolution and to describe the presence of landscape elements at European scale, this data is not available yet. We created a habitat filter for each of the twenty-five selected bee species, by keeping only the LULC classes described as potential habitats (Table 4 in the supplementary material).

2.3. Model calibration and evaluation

2.3.1. Conceptual model

We aimed at developing a species-centred approach based on the Ecosystem Services Providers (ESP) concept, i.e., species, functional groups, species communities, or habitats that produce ecosystem

services (Kremen et al., 2007). In our model, the ESP are wild bees that provide pollination ecosystem services. The conceptual framework (Fig. 2) is inspired by the Ecological Production Function framework from Kremen et al. (2007). Key elements for species geographical distribution depend on the spatial scale of the influencing factors (Pearson and Dawson 2003; Thuiller 2004; Milbau et al., 2009; Hortal et al., 2010). At the global scale, species occurrence is governed by bioclimatic and land cover variables (Fig. 2a) (Hegland et al., 2009). For bee species, distribution drivers at the global scale are not yet well understood (Bystriakova et al., 2018), while local determinants are relatively well known and mainly depend on the presence of nesting places and floral resources at the local scale, which define the habitat of a species (Fig. 2b) (Westrich 2018). The analysis of the role of different environmental drivers at their operating scales is required to appropriately predict wild bee occurrences at the local scale. We therefore use a hierarchical framework that builds on the work of Milbau et al. (2009): environmental drivers operating at large scales are used to predict species distribution using SDMs, and the outputs are combined with a species-specific habitat suitability filter to refine the suitability maps at the local scale. The pollination efficiency of each species depends on life-history traits, such as morphology and behaviour (Willcox et al., 2017). One important trait for the pollination of crops is the foraging range (Fig. 2c), because it determines the distance over which pollen can be transported and if crop fields or target plants are reachable for the different species. The pollination potential is defined as the sum of each predicted species probability of presence combined with foraging distances. The pollination ecosystem service potential on crop fields was restricted to the probability of presence of crop pollinators on potential pollination-dependant fields (Fig. 2d).

2.3.2. Species distribution model

Species distribution modelling was carried out with the "biomod2 v.3.4.6″ library (Thuiller et al., 2016) implemented in R (Version 4.0.3) (R Core Team 2017). All maps were created using ArcGIS (Version 10.6.1).

Occurrence data from GBIF are typically presence-only data, with no recorded absence data, whereas the algorithms used for modelling need presence-absence points, so pseudo-absence points were generated with the following approach: several sets of pseudo-absence data were generated to prevent sampling bias and to be able to test the effect of each pseudo-absence selection on the predictive ability of the model. Following Phillips et al. (2009), we restricted the selection of the background points in a 10 km buffered convex hull around the GBIF *Andrena* records to reflect species sampling bias. One thousand pseudo-absence data points were sampled randomly from the background region and we repeated the random selection ten times to build a ten-fold internal cross-validation of the models (Phillips et al., 2009; Barbet-Massin et al., 2012).

We chose to combine different algorithms with ensemble modelling as no statistical tools will *per se* perform better than any other (Elith and Leathwick 2009; Aguirre-Gutiérrez et al., 2013; Araújo et al., 2019) and as predictions based on an ensemble of several algorithms are often more robust than predictions derived from a single model (Araújo and New 2007; Araújo et al., 2019). For each bee species model, we used three different algorithms: Generalized Linear Model (GLM), a flexible regression model allowing to handle non-normally distributed response variables, Flexible Discriminant Analysis (FDA), a flexible classification approach derived from Linear Discriminant Analysis methods and Random Forest, a bagging approach. To train the SDMs and test their predictive performances, we used a cross-validation with a random subset of 70% of the points to calibrate the model for every single species, while the remaining 30% of the points were used for validation. Each single model was run on the training data and evaluated on the test data using performance evaluation metrics. This process was repeated four times with different partitioning of the original dataset into a training and a test set. Cross-validation was used to decrease bias in the
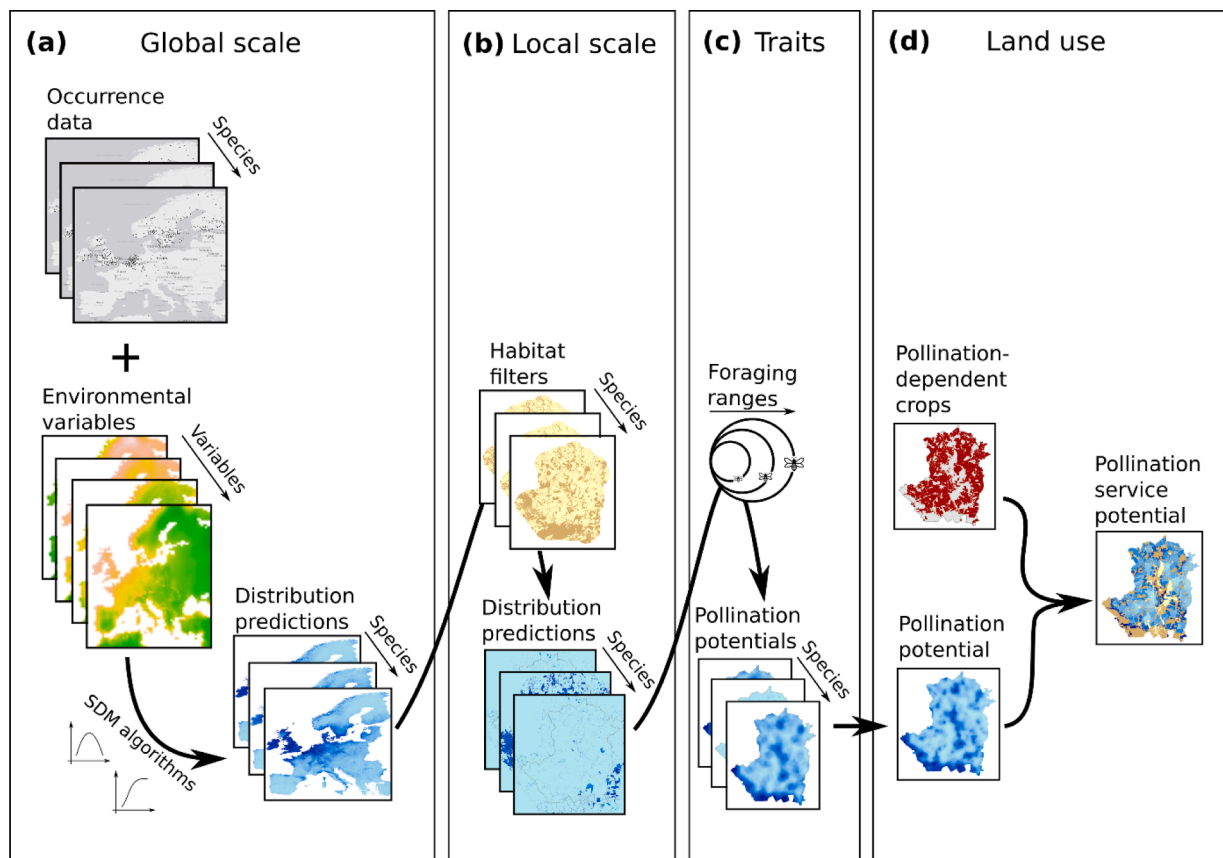
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[3] https://land.copernicus.eu/pan-european/corine-land-cover/clc2018

Fig. 2. Flow chart representing the different steps of the hierarchical modelling approach to predict pollination potential at the local scale.

predictive performance of the measuring models (Pearce and Ferrier 2000).

We used different performance evaluation metrics: Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot, True Skills Statistics (TSS) and the continuous Boyce index (CBI). AUC is a threshold-independent model evaluation indicator (Franklin 2010), which continuously discriminates between suitable and unsuitable habitats, independently of prevalence of target species (Elith and Burgman 2002). It plots the commission error against omission error and ranges between 0.5 and 1, where 1 represents a perfect discrimination between presence and absence, and 0.5 represents a random fit. TSS is a threshold-dependant measure of model accuracy and, contrary to AUC, is based on binary predictions of predicted suitability/unsuitability for each species (Allouche et al., 2006). It ranges from -1 to +1, with +1 indicating perfect agreement between predictions and observations, and 0 or less indicating an agreement no better than a random classification (Zhang et al., 2015). This metric is negatively related to species prevalence (Allouche et al., 2006). Contrary to AUC and TSS, CBI does not require absence data and is therefore considered as more appropriate when working with presence-only data. The metric measures how observed presences are distributed across the gradient of predicted presences and how this differs from a random distribution. It also varies from -1 to +1, where positive values indicate a good agreement between predictions and the distribution of presences in the evaluation dataset, values close to zero indicate predictions not different from a random distribution and negative values indicate incorrect models (Hirzel et al., 2006).

One of the main challenges in modelling pollination potential is that each pollinator species has its specific potential geographical range and habitat needs, so each species needs to be modelled independently. For each bee species, a total of 120 models was built (using three algorithms, four cross-validations to sample test and training data and ten pseudo-

absences samplings). Only models with a TSS greater or equal to 0.6 were kept to build the final ensemble (Landis and Koch 1977). Ensemble predictions were calculated as weighted averages of single-model predictions, with weights assigned to each modelling technique using the TSS (Allouche et al., 2006).

To ensure transparency and reproducibility of our SDMs, we included an Overview, Data, Model, Assessment, and Prediction (ODMAP) protocol from Zurell et al. (2020) in the supplementary material.

2.3.3. Habitat filter

The next step was to combine the SDM ensemble models with the corresponding habitat filters for each modelled bee species into a unique predicted distribution (or environmental suitability) map for the CSA (Fig. 2b). To do so, for each species and each grid cell of the CSA, we multiplied the species distribution prediction and the binary habitat filter values. The resulting maps represent the suitability of the area to support the different bee species, according to its environmental conditions and the presence of potential habitats for each species.

2.3.4. Foraging range

As bees are central place foragers, their foraging ranges determine their capacity to pollinate and to potentially increase the yield of adjacent crop fields. The foraging ranges of the species were added to the model to determine the final pollination potential map (Fig. 2c). Foraging distances are species-specific and are a function of the intertegular distance (i.e., the distance between the wing-attachment points on either side of the thorax) (Greenleaf et al., 2007). Kendall et al. (2019) implemented the "pollimetry v.1.0.1″ library, which allows to calculate foraging distances based on intertegular measurements of bees and provide the resulting database intertegular measurements of 4035 bee specimens. We used this package in R to estimate the average

foraging range of the twenty-five selected bee species. When no data were found, we used the average of all foraging ranges over the *Andrena* genus. Foraging range values are presented in Table 5 in the supplementary material. Using the "raster v3.4–5″ package (Hijmans et al., 2013), we then implemented a circular moving window, with a focal corresponding to the average foraging distance of each bee species. For each grid cell of the CSA, the pollination potentials were computed based on the foraging ranges and the suitability of the area to support the different bee species.

2.3.5. Relative pollination potential

The total pollination potential of the CSA was calculated as the sum of the pollination potential of each species, determined in the previous step. We made the assumption that local species communities are made of species with the same environmental requirements and we neglected macroecological controls on community assembly such as competition and synergies between species (Guisan and Rahbek 2011). We chose to work with occurrence probability maps and not with binary presence/absence maps, as Calabrese et al. (2014) and D'Amen et al. (2015) showed that the addition of predictions of occurrence probabilities from individual SDMs is preferable to setting arbitrary thresholds to obtain binary predictions and then combining those into a stacked-SDM, as this tend to be biased and overpredict of species richness.

The resulting map represents the relative pollination potential of the area, i.e. the potential of the area to sustain pollination from the selected *Andrena* species.

2.3.6. Comparison with independent field data

In the CSA, flower visiting insects were collected using one yellow pan trap in 12 rapeseed fields between May 4th to June 6th 2018. Traps were set up at one border of each field, close to a near-natural habitat (such as hedgerows or forests), with their tops approximately even with the surrounding oilseed rape flowers. The traps were filled with diluted detergent solution and emptied weekly. All bees were identified to species level. The trap locations were selected to cover the landscape diversity in the CSA: from locations surrounded by a landscape with a high proportion of near-natural habitats to locations with a low proportion of near-natural habitats.

We used linear regression to assess whether the pollination model outputs reflect the pollinator community abundance and species richness collected in the field. We compared the abundance and richness of oilseed rape pollinators from the *Andrena* genus from the collected data with the predicted pollination potential. We also compared *Andrena* species richness from the collected data with the predicted richness of *Andrena* species obtained with the model (the sum of all the predicted suitability using the SDMs and the habitat filters, Fig. 2b in the workflow). For this comparison, we calculated the mean predicted species richness for all pixels within a radius of 200, 300 and 500 m radius of trap locations.

3. Results

3.1. Model evaluation

The evaluation scores of all ensemble models were high to very high (ROC between 0.892 and 0.978, TSS between 0.623 and 0.887 and CBI between 0.965 and 1), which means that the predictive accuracies of the models were good to very good. An overview of all these performances measures can be found in Table 7 in the supplementary material.

The importance of each predictor for each species model varied with the tested algorithms and modelled species. Bioclimatic variables indicated a higher percentage of the data variances than LULC variables. Bio_2 (Mean Diurnal Range), Bio_11 (Mean Temperature of Coldest Quarter) and Bio_7 (Temperature Annual Range) appear to be generally the most important variables, followed by Bio_19 (Precipitation of Coldest Quarter) and Bio_14 (Precipitation of Driest Month). LULC

variables have a more minor importance for the models and generally only few categories are relevant for each species. Discontinuous urban fabric is overall the most important LULC variable, followed by non-irrigated arable land and sparsely vegetated areas (Table 6 in the supplementary material).

3.2. Species distribution models

Figs. 3 and 4 illustrate the different results for two species (*Andrena barbilabris* and *Andrena carantonica*). The predicted presence of each species is determined through a SDM at the European scale (Figs. 3 and 4 (B)) based on occurrence data (Figs. 3 and 4(A)). Even at the local scale of the CSA, we obtained different distribution predictions for each species. For instance, the model predicted that overall, the area is slightly more suitable for *A. carantonica* than for *A. barbilabris* (Figs. 3 and 4(C)). Habitat filtering was done with a buffer of 2 km around the CSA to account for foraging distances and the possibility that bees can nest outside and forage inside the CSA (Figs. 3 and 4(D)). The differences in the final predicted presence of species were also due to habitat preferences of each species: For instance, *A. carantonica* has a wider range of potential habitats and a broader distribution over the CSA than *A. barbilabris*. *A. carantonica* has a wider foraging range than *A. barbilabris* (700 m compared to 200 m), which also explains the differences in species respective pollination potential in the final maps (Figs. 3 and 4(E)).

3.3. Potential pollination map for the CSA

The model predicted the CSA as suitable for all the target species. The predicted pollination service potential (sum of the pollination potential of all target wild bee species) scores from 0 (none of the modelled species is potentially present) to 15 (highest predicted scores when adding the pollination service potential of the twenty-five wild bee species) for each grid cell (see Fig. 2 in the supplementary material). Areas where none of the species is potentially present have no potential pollination ecosystem service performed by the selected and modelled species, whereas a high predicted landscape suitability and wild bee species richness increase the pollination service potential of the area.

Fig. 5 compares the predicted spatial patterns of oilseed rape pollinators and the potential pollination ecosystem service demand for oilseed rape (the main pollination-dependant crop in the CSA), estimated with the ATKIS/InVeKoS "arable land" LULC class. The location of rapeseed fields generally changes annually, as a result of crop rotation, changing market prices and changes in political schemes and subsidies. The demand for pollination ecosystem services will therefore change annually and can potentially occur on all arable fields. This is why we did not directly map rapeseed fields and assumed that it could potentially grow on every arable field. For this analysis, we restricted the pool of modelled wild bee species to oilseed rape flowers visitors (as documented in Table 1 in the supplementary material). Our model predicted that most of the fields have a low pollination potential and the mean pollination potential value on arable fields was 1.5. The model predicted low mean pollination ecosystem service potentials particularly the North-Eastern part of the CSA (e.g. in Fig. 5(C)). Fields with relatively high mean pollination ecosystem service potentials are more evenly distributed over the CSA.

3.4. Comparison with independent field data

Yellow pan traps captured 801 individual bees from 42 different species. From the collected wild bees, 681 were from the genus *Andrena*, from 19 different species. Form the genus *Andrena*, 576 individuals were known oilseed rape flower visitors, from 9 different species. Abundance and richness of oilseed rape visitors from the genus *Andrena* increased with the predicted pollination service potential ($r = 0.28$, d.f. $= 10$, $p = 0.07$) and ($r = 0.29$, d.f. $= 10$, $p = 0.07$), however not significantly (Fig. 6(a) and (b)). Oilseed rape visitor richness increased with the mean
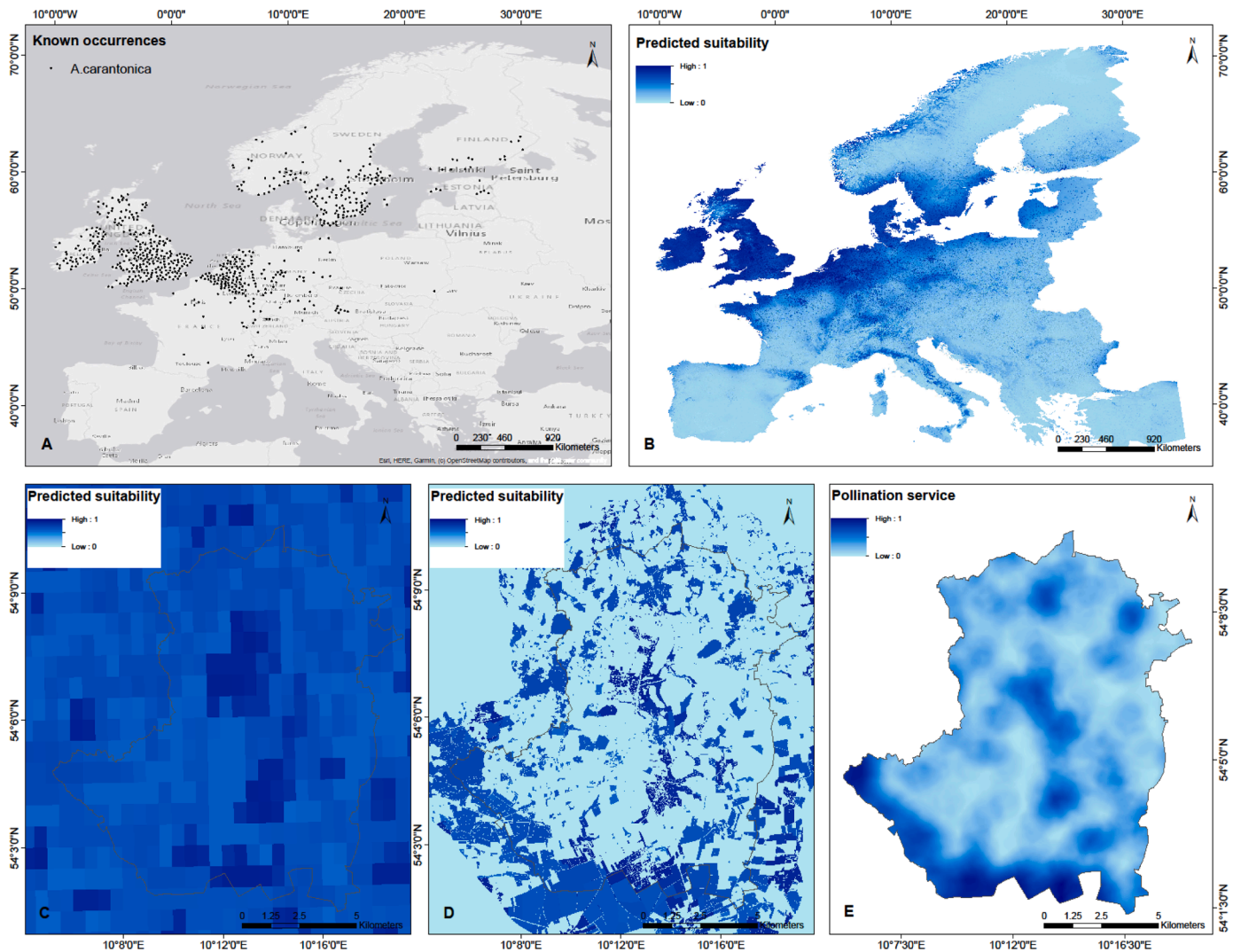
Fig. 3. Examples of species distribution model outputs for A. carantonica. (A): Occurrence points, retrieved from the GBIF database and cleaned, (B): predicted probability of presence at the European level (ensemble model of the best performing algorithms), (C): Zoom of the predicted probability of presence covering the CSA, (D): predicted probability of presence on potential habitats (SDM results X habitat filter; including buffer around the CSA), (E): predicted pollination ecosystem service potential by A. carantonica in the CSA.

predicted pollinator richness within a radius of 500 m ($r = 0.28$, d.f. $= 10$, $p = 0.07$, not shown here), 300 m ($r = 0.38$, d.f. $= 10$, $p = 0.03$) and 200 m ($r = 0.48$, d.f. $= 10$, $p = 0.01$) (Fig. 6(c) and (d)).

4. Discussion

We have predicted the current potential occurrence of twenty-five selected bee species at the local scale in order to estimate the potential pollination ecosystem service supply for pollination-dependant crops and wild plants. The aim was to develop a model based on peer-reviewed knowledge rather than on expert-judgement, adapted to the region of interest and its bioclimatic conditions and with consideration to the availability of foraging resources and nesting places, for which a fine resolution is needed. One further novelty of the developed method is that it combines environmental drivers at larger and local spatial scales and thereby goes beyond existing pollination models, which typically focus on one scale, despite the importance of integrating environmental drivers at multiple geographical scales (Milbau et al., 2009; Mateo et al., 2019b).

4.1. Modelling pollination service potential

SDMs results highlighted the role of bioclimatic factors in bee species occurrence at continental to local scales, as previously illustrated by Polce et al., (2013); Nogué et al., (2016); Polce et al., (2018) and Bystriakova et al., (2018). This is indicated by the predicted suitability maps (Figs. 3b & 4b): SDMs predicted that the suitability for *A. carantonica* and *A. barbilabris* is highly variable across Europe countries and we also obtained different predictions at the local scale (Figs. 3c & 4c). As the ESTIMAP and InVEST models only express the relative suitability for pollinators in terms of availability of floral resources and nesting sites (Lonsdorf et al., 2009; Zulian et al., 2013), they neglect the variability of bee species distributions due to bioclimatic factors. To our knowledge, no study has yet assessed these models in regard to the use or non-use bioclimatic factors. Furthermore, SDMs provide an effective alternative to local expert opinion on species potential occurrence (Gastón et al., 2014) and can be used to discriminate present from absent species in a given location. In addition, as the modelling framework allows to assess the relative importance of environmental variables on different species, it can be also used to analyse the impact of climate and land cover changes on wild bee species and future pollination service potential.
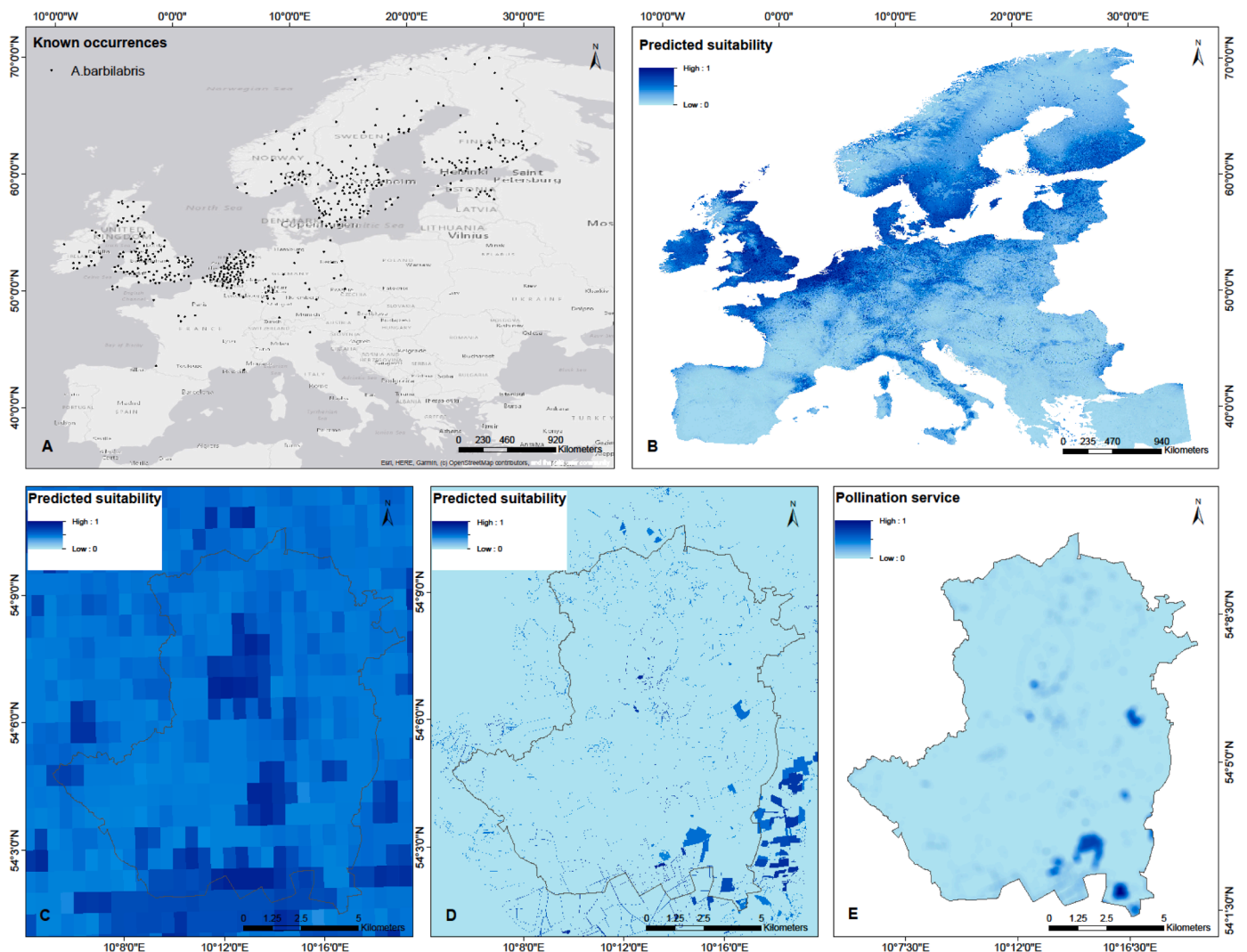
Fig. 4. Species distribution model outputs for A. barbilabris. (A): Occurrence points, retrieved from the GBIF database and cleaned, (B): predicted probability of presence at the European level (ensemble model of the best performing algorithms), (C): Zoom of the predicted probability of presence covering the CSA, (D): predicted probability of presence on potential habitats (SDM results X habitat filter; including buffer around the CSA), (E): predicted pollination ecosystem service potential by A. barbilabris in the CSA.

As they do not account for natural and semi-natural areas, previous pollination (or wild bee species distribution) models based on SDMs also probably overpredict the distribution of bee species at the local scale (Polce et al., 2013; Nogué et al., 2016; Polce et al., 2018; Bystriakova et al., 2018). These models may therefore significantly overpredict the pollination potential and minimize areas where pollination demand exceeds pollination service potential, as only specific areas in croplands provide suitable habitats for wild bee species (mainly natural and semi-natural habitats) (Westrich 2018). This is particularly problematic when pollination-dependant crops are isolated from natural and semi-natural habitats (Ricketts et al., 2008; Garibaldi et al., 2011). The importance of the presence of natural and semi-natural areas at small spatial scales within agricultural landscapes for wild pollinator species has been described in many studies (Gathmann and Tscharntke 2002; Zurbuchen et al., 2010; Ricketts et al., 2008; Kennedy et al., 2013) and is also supported by our results. This is indicated by the differences between the predicted suitability and pollination potential maps (Figs. 3 & 4): our results of SDMs predict that the whole CSA is highly suitable for *A. carantonica* and *A. barbilabris*, whereas their final suitable areas are much more restricted when accounting for habitat availability. This is consistent with Fournier et al., (2017) and Hattab et al., (2014), which also found that adding species-specific habitat filters greatly refined

habitat suitability for terrestrial and marine species. As it integrates information on drivers operating across different scales, our multi-scale approach should provide more accurate predictions and a better understanding of processes underlying species distribution compared to single-scale models (Pearson et al., 2004; Mateo et al., 2019b; Mateo et al., 2019a; Bellamy et al., 2020; Fournier et al., 2017).

Despite the low number of sampling sites and the restricted sampling period during the mass-flowering of oilseed rape, our model correlated fairly well with the data observed in the field. The model was able to predict a significant proportion of the variation in oilseed rape pollinator richness from independent data. Oilseed rape pollinator richness and abundance from the collected data were also correlated with the predicted pollination service potential, however with no significance. This analysis can be considered as a first approach to evaluating the model results, but not yet a validation of our model due to the small number of sampling sites and the absence of replication.

4.2. Limitations and uncertainties of the study

The presented approach comes with several modelling limitations. First, the performance of each SDM is constrained by the quantity and quality of the GBIF occurrence data. In principle, the performance of
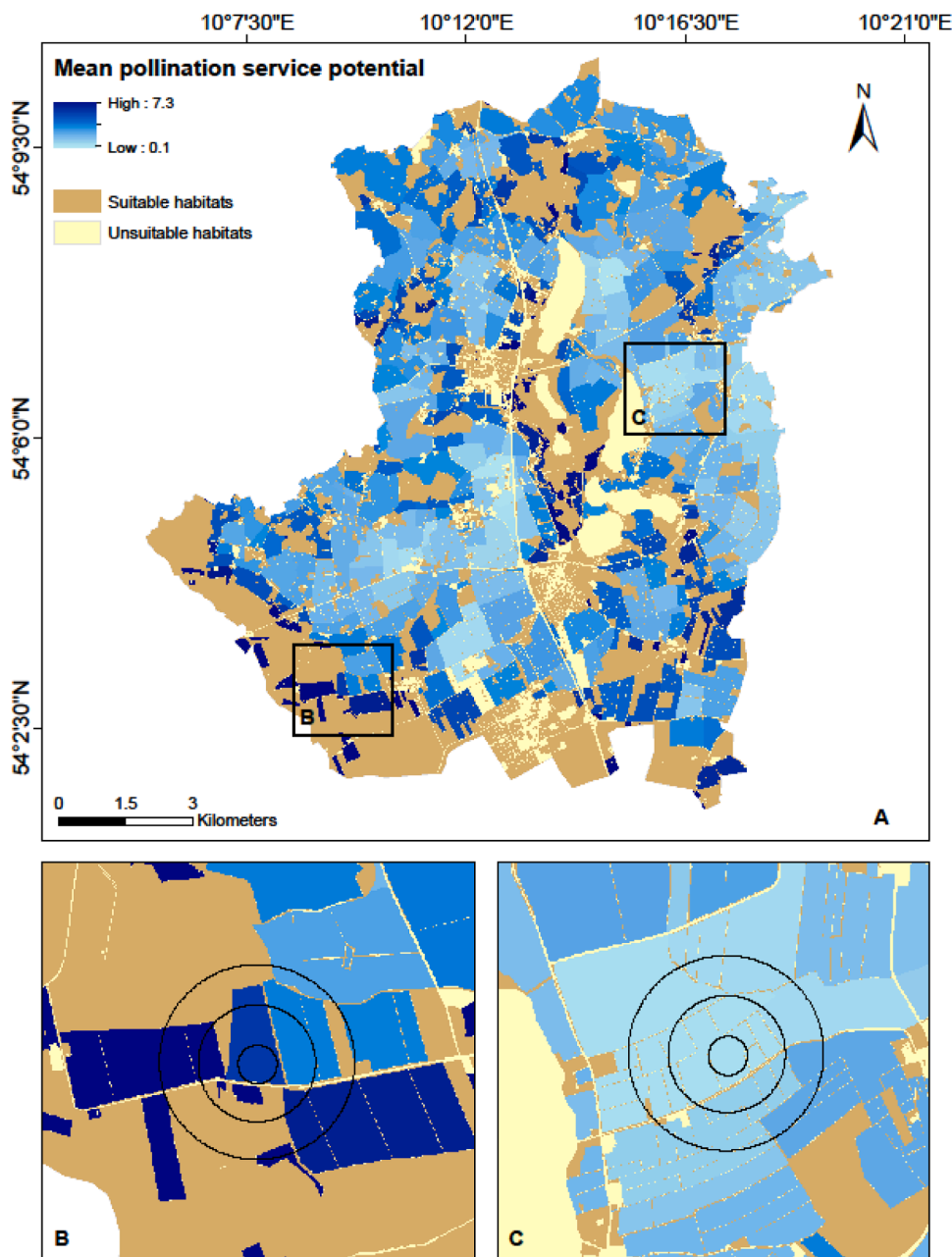
Fig. 5. Predicted mean pollination potential on arable lands (A) and zoom over two contrasting pollination service potential results (B and C). Brown areas represent potential suitable habitats for the different bee species. Light yellow areas represent unsuitable habitats other than arable lands. Arable lands are marked with a gradient from light to dark blue, depending on the predicted mean pollination service potential for each parcel of the CSA (the mean is calculated over each parcel). In (B), the landscape has a larger proportion of potential habitats such as grasslands and forests, whereas in (C), the landscape is largely dominated by arable lands. In (C), the mean pollination potentials tend to be lower than in (B) (values between 0.9 and 6.2 in (B); 0.2 and 4.2 in (C)). The circles represent the principal foraging ranges of the selected bee species (100, 300 and 500 m radius), so the principal distances around fields within which the presence of habitats for pollinators can increase pollination ecosystem service supply.

each SDM can be improved by including more species occurrence data. For the selected bee species, GBIF occurrence data are particularly biased towards higher occurrences in Northern European countries including Great Britain, Sweden, Belgium and Germany, which may make the outputs of the SDMs less reliable for regions with very different bioclimatic conditions such as Southern European countries. This is however less problematic in the studied CSA, located in Northern Germany.

Second, our model might overpredict single species occurrences because there is no limit on the number of species that can occupy a given area, i.e. the carrying capacity of ecosystems is not considered in SDM approaches (Graham and Hijmans 2006; Thuiller et al., 2015). This is particularly the case when interactions between species (competition, parasitism, mutualism, predator-prey) strongly influence species co-occurrences and can exclude species from a community. For instance, honeybees have been reported to negatively impact the presence of wild bees because of their density and their outstanding foraging capacity

(Thomson 2004; Hudewenz and Klein 2013), although this is debatable (Greenleaf and Kremen 2006b; Westrich 2018). One way to account for biotic interactions in SDMs is to test models' residual for evidence of species interaction using Joint Species Distribution Models (jSDMs) (Pollock et al., 2014). Using jSDMs instead of SDMs may increase the explanatory power when modelling pollinator communities. However, when restricted to relatively few species, the present model should not lead to an overprediction of the local pollination potential.

Our habitat filter is based on the work from Westrich (2018), which gathered knowledge on wild bees in Germany based on more than 3000 scientific publications. As habitat preference of wild bee species may be different in other countries, the habitat filter should be adapted to local characteristics when using the model in other regions of the world.

We found that two precipitation variables and three temperature-related variables were the most important for predicting the potential distribution of bee species over Europe: Precipitation of the Coldest Quarter and of the Driest Month, Temperature Annual Range, Mean
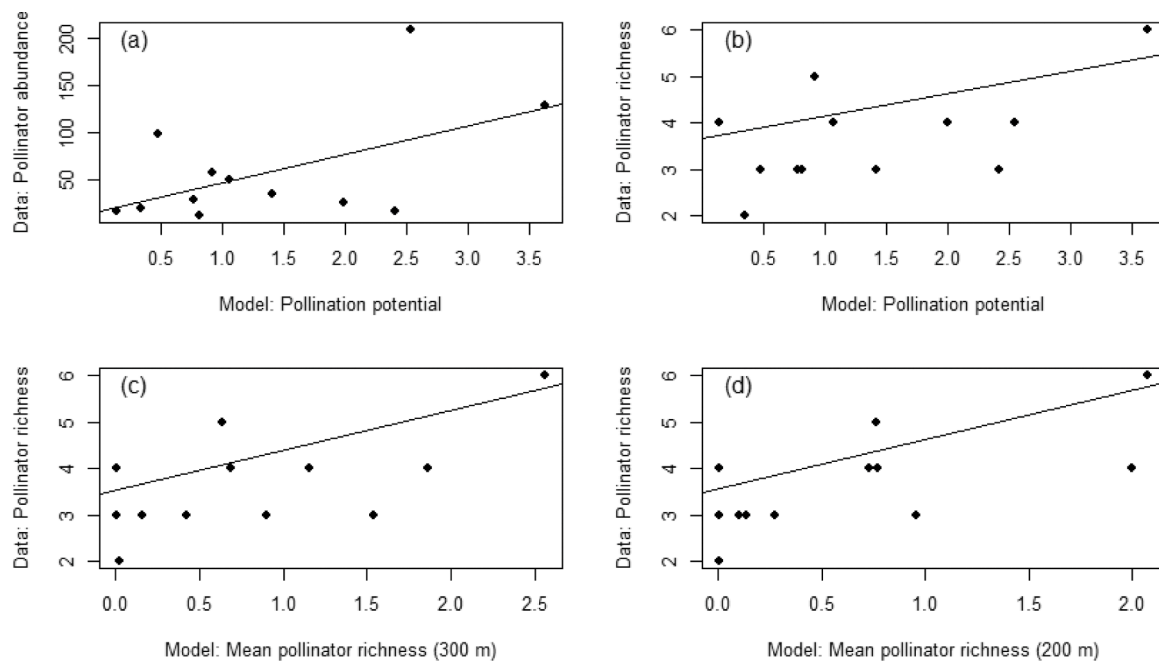
Fig. 6. Linear regressions with one independent dataset from the CSA: between oilseed rape pollinator abundance and the predicted pollination potential (a), between oilseed rape pollinator richness and the predicted pollination potential (b), between oilseed rape pollinator richness and the mean predicted oilseed rape pollinator richness for a radius of 300 m (c) and 200 m (d) around the pan trap locations.

Temperature of Coldest Quarter and Mean Diurnal Range. These variables all have a direct or indirect ecological implication that can be explained. Precipitation and temperature extremes affect nesting suitability, foraging behaviour and resource availability. Low temperature and high precipitation values might have a higher impact on the presence of bees during their active season (principally spring and early summer), by directly reducing their foraging capacity. Instead of using bioclimatic variables from WorldClim, SDM predictions might be improved by using temperature and precipitation values restricted to each respective bee-active season. We found that LULC variables have a much lower impact on species distribution, except discontinuous urban fabric, non-irrigated arable land and sparsely vegetated areas for some species and depending on the algorithm. These results on the relative importance of environmental data for predicting bee species distribution are comparable to Polce et al., (2013) but not Bystriakova et al., (2018) nor Polce et al., (2018). This may be due to the selected bee species, as the latter two studies were calibrated with Bumblebee species or bees of the subfamily Colletinae, whereas the study from Polce et al., (2013) was calibrated with species from different genera, including some *Andrena* species. Besides, Polce et al., (2013) found that the use of pesticides plays a significant role in bee distribution. As there is growing evidence that pesticides inputs can have a considerable negative impact on wild bee species (Brittain et al., 2010; Whitehorn et al., 2012), this variable should be used when available to refine the different SDMs.

Effective pollination depends on the pollination effectiveness or performance of each species, which in turn depends on a broad range of factors, e.g. pollinator morphology and behaviour, flower visitation rates, pollen deposition but also plant health (Willcox et al., 2017). There is growing evidence that not all species are equally important for the pollination of a given crop (Kleijn et al., 2015; Winfree et al., 2015) or wild plant species (Gorenflo et al., 2017). Empirical data linking yield gain specifically to one pollinator taxon are however still scarce (but see Rader et al., (2009) and Jauker et al., (2011)), so we did not include information about pollination efficiency of each wild bee species in our model. Furthermore, there are a wide range of community-level factors that may influence pollination efficiency, such as species interactions and niche complementarity (Willcox et al., 2017). Instead, we assumed

that the pollination ecosystem service potential of an area increases with the likelihood of the presence of bees and bee species richness, which is supported by Klein et al., (2009), Garibaldi et al., (2011) and Woodcock et al., (2019). Accounting for functional diversity and specifically choosing bee species with a high functional divergence (characterised by non-overlapping traits) could however greatly improve the informative value of pollination models and allows to ultimately link crop pollination service potential to service provision and contribution to crop yield, seed quality and eventually economic return (Woodcock et al., 2019; Gagic et al., 2015). Building on Woodcock et al., (2019), the framework could be further improved by adding an extra step converting species probability of presence into a functional divergence index (i. e., a composite index derived from species effect traits that play an important role for the pollination of the considered crops), whenever this data is available. To do this, the function divergence index from Woodcock et al., (2019) or a similar composite of traits influencing species pollination efficiency could be included in step (c) (Fig. 2) of the framework, along with the foraging range, a trait which is already accounted for in the model. Similarly, including information about temporal dynamics, particularly about bee flight seasons can further increase the robustness of the model predictions. This could be done by adding flighting season filters (similar to the habitat filters) between step (b) and (c) (Fig. 2) of the framework and running the model for each month of the crop flowering season to estimate the monthly pollination service potential throughout the entire crop flowering season. This will allow to assess whether the entire crop flowering time is covered by a high pollination potential or if there is a temporal mismatch between ES demand and potential.

Lastly, the presented pollination potential maps are based on solely one genus (*Andrena*) and twenty-five species, whereas around 300 species have been observed in the region – of which only 110 species are not threatened by extinction nor are already extinct (van der Smissen 2001). As we selected species from the genus *Andrena* and only species that are soil-nesting and solitary, the results certainly do not represent each single bee species occurring in the region. For a better wild bee species richness assessment, other genera should be included in the model. For instance, above-ground nesting bees and species with different degrees

of sociality are not represented in our model. Including bees with these characteristics could have an impact on the resulting pollination potential maps, if sociality and nesting requirements play a major role in species distribution. The selected bees are nevertheless suitable for pollination potential modelling, as they represent a highly variable group due to their varied size, seasonality, soil preference for nesting and foraging behaviour and as the vast majority of wild bees are soil-nesting and solitary (Westrich 2018).

4.3. Applications

The pollination potential maps in the studied CSA can help to assess the needs for practical conservation measures to promote insect pollinators in agri-environmental schemes. Spatially explicit maps of the pollination potential in comparison to maps of pollination demand will allow the identification of areas where pollination service is deficient. The resulting maps can support land management recommendations such as where to prioritize habitat conservation measures in agricultural landscapes to sustain biodiversity, ecosystem functions and services that support crop production. One advantage of the developed model is the combination of SDMs and species-specific habitat filters. This can help to develop relevant habitats for species, for which large-scale factors such as climatic parameters are also suitable. For example, in Fig. 4 (C), the dark blue zones indicate a high suitability for *A. barbilabris*. However, as there are only few potential habitats for this species at these spots, the species cannot colonize a large part of these suitable areas. These areas could thus be potential targets for *A. barbilabris* conservation measures, such as the inclusion of fallow in the crop-rotation pattern. Conservation measures such as hedgerows, field margins and flower strips have been shown to have a positive and significant effect on wild bee abundance and diversity (M'Gonigle et al., 2015), particularly for bumblebees (Pywell et al., 2005; Carvell et al., 2011; Pywell et al., 2012). This demonstrates the importance of these habitats at the small scale for pollinator community conservation. Furthermore, Pywell et al., (2012) highlighted the importance of using ecological knowledge of targeted species when designing conservation measures and showed that species-specific measures are much more efficient and sustain a higher species richness than generalized conventional conservation measures.

As climatic factors have a significant effect on the distribution of bees, climate change will certainly affect bee distribution in the future and disrupt plant–pollinator interactions (Memmott et al., 2007; Biesmeijer et al., 2006). Our results show that the consideration of climatic factors (and therefore climate change) is essential when developing conservation measures for the long term, for pollinator biodiversity and to preserve plant-pollinator interactions.

5. Conclusions

To our knowledge, this is the first work that developed a framework that predicts geographical patterns of pollinators based on SDM and multi-scale environmental drivers to predict pollination ecosystem service potential at the local scale. The results of the different models show that the framework can be adapted for a local scale assessment. This approach allowed us to predict the pollination potential from mining bee species and to identify areas with high or low pollination ecosystem services potential. The comparison with independent samples showed good agreement between the model outcomes and species occurrence data collected in the field. The developed model can support land-use decisions but also help to identify conservation measures and areas for prioritizing species conservation planning. This method is transferable to other European regions and other countries in the World, provided that they have enough species occurrence data. It can also be used to investigate the effect of climate and land-use changes on pollinators' distribution and pollination potential and help to implement mitigation measures for vulnerable areas and species.

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