CRANFIELD UNIVERSITY
&
CZECH UNIVERSITY OF LIFE SCIENCE

MSc. Environmental Data Science
&
MSc. Nature Conservation

Academic Year 2017 - 2018

Title: Assessing the effect of the landscape context on European bees

Author: Juan Gallego-Zamorano

Supervisors in UK: Dr Ron Corstanje & Prof Andy Purvis (NHM)
Supervisor in CZ: Prof Miroslav Šálek

December 2017

This thesis is submitted in partial fulfilment of the requirements for the degrees of MSc. Environmental Data Science and MSc. Nature Conservation

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Environmental Sciences

DIPLOMA THESIS ASSIGNMENT

Juan Gallego Zamorano

Nature Conservation

Thesis title

Assessing the effect of the landscape context on European bees

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Objectives of thesis

The aim of the study is to evaluate how the landscape context, such as the heterogeneity of the land cover, the connectivity or the accessibility of flowers, affects the abundance of bees species across Europe.

Methodology

Using a combination of one of the most comprehensive global biodiversity databases, PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems), and a set of models which estimate the floral resource and connectivity, I calculated three landscape measurements: habitat heterogeneity (Simpon's Diversity), accessible floral resources, and functional connectivity, in 2km buffers around 1766 sites across Europe where total abundance of bees and land use intensity was assigned. Then mixed models were used for analysing the effects of the different variables.

The proposed extent of the thesis

20-50 pp

Keywords

Ecosystem services; Landscape ecology; Connectivity; Habitat heterogeneity; Pollination

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Recommended information sources

Boscolo D, Tokumoto PM, Ferreira PA, et al (2017) Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. Perspect Ecol Conserv 15:18–24.

Hudson LN, Newbold T, Contu S, et al (2017) The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. Ecol Evol 7:145–188

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, Massachusetts, USA

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Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218.

Expected date of thesis defence

2017/18 SS – FES

The Diploma Thesis Supervisor

prof. Dr. Mgr. Miroslav Šálek

Supervising department

Department of Ecology

Advisor of thesis

doc. Mgr. Jiří Reif, PhD

Electronic approval: 1. 12. 2017

doc. Ing. Jiří Vojar, Ph.D.

Head of department

Electronic approval: 4. 12. 2017

prof. RNDr. Vladimír Bejček, CSc.

Dean

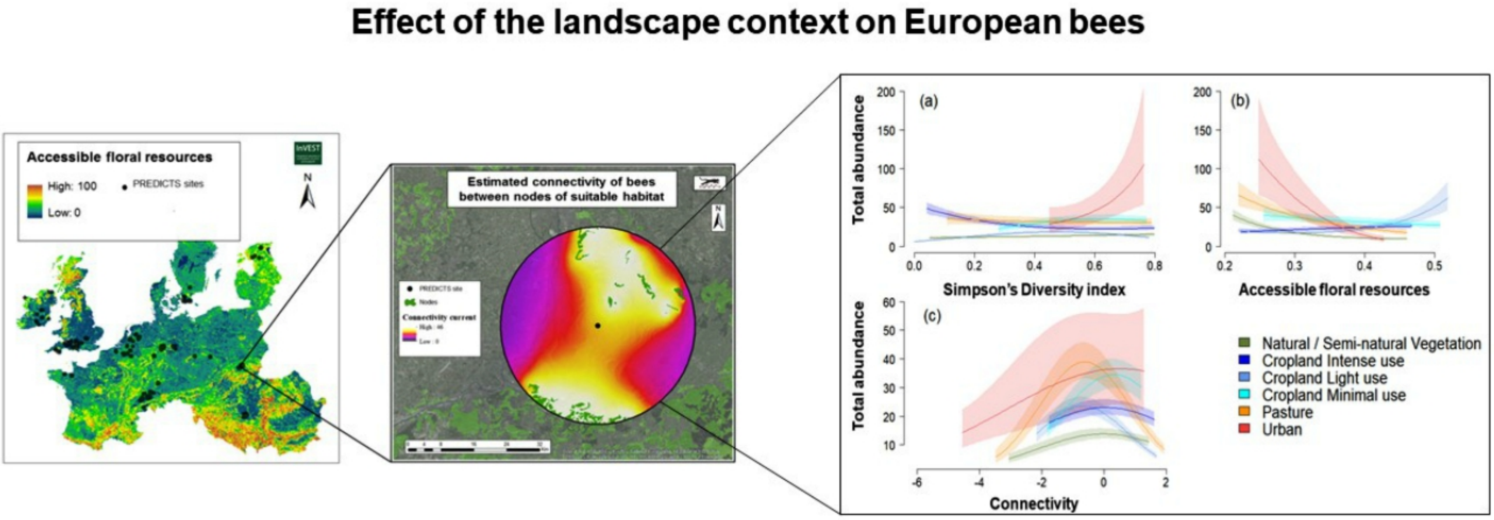
Prague on 04. 12. 2017

Declaration

I hereby declare that I am the sole author of the thesis entitled: "Assessing the effect of the landscape context on European bees". I duly marked out all quotations. The used literature and sources are stated in the attached list of references.

Juan Gallego-Zamorano

GRAPHICAL ABSTRACT



ABSTRACT

Bees are considered one of the most valuable biological groups providing beneficial ecosystem services, such pollination. Land-use changes and intensification have lead to bee habitat fragmentation, impeding their movement and thus the accessibility to flowers (food). However, habitat heterogeneity seems to provide a positive response in the abundance and richness of bee populations. Functional connectivity estimates the movement of bees providing insights into how the landscape context affects their abundance. However, the inclusion of landscape context variables is scarce in global biodiversity models. Here I show that the surrounding landscape is one of the most important factors affecting the total-local abundance of bees across Europe. Using a combination of PREDICTS (one of the most comprehensive global biodiversity databases) and a set of models which predict floral resource and connectivity, I calculated three landscape measurements, habitat heterogeneity (Simpon's Diversity), accessible floral resources, and functional connectivity, in 2km buffers around 1766 sites across Europe where total abundance of bees and land use intensity was assigned, then mixed models were used for analysing the effects of the different variables. The interaction between land use intensity and the accessible floral resources was the most significant variable, particularly having a positive effect on the abundance of bees in croplands. In contrast to other studies that show the importance of habitat heterogeneity in croplands (Boscolo et al. 2017) here, there was only a positive effect in urban areas. Moreover, intermediate levels of connectivity enhanced the abundance in general. These results demonstrate the importance of the landscape configuration for the abundance of pollinators, especially the accessibility of floral resources in all kind of land uses. Large scale studies implementing different landscape variables to study pollinator abundance are rare, this research reveals the importance of improving floral spaces and connectivity to improve the ecosystem services that pollinators provide.

Keywords: Ecosystem services; Landscape ecology; Connectivity; Habitat heterogeneity; Pollination

Number of words in the Abstract: 300 (8 keywords)

Number of words in the main body of the paper: 6125

ACKNOWLEDGEMENTS

I would like to thank Ron Corstanje for understand my requirements of moving to the NHM, supervising me, and lead me during the analysis process. Also thanks to Andy Purvis for accepted me in their marvellous group, he is just an amazing supervisor. Adriana de Palma, Isabel Fenton and Samantha Hill for their guidance and help during the process. Last, I would like to thank my parents (Ana and Eduardo), my brother (Dani) and my “blue lycaenid” (Cristina) for their emotional and unconditional support during this months, without you would not be possible.

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PREDICTS	Projecting Responses of Ecological Diversity In Changing Terrestrial Systems
LC	Land cover
LU	Land use
SIDI	Simpson’s Diversity Index
ITD	Inter-tegular distance
GLMM	Generalized Linear Mixed Models
ML	Maximum Likelihood
REML	Restricted Maximum Likelihood
df	Degrees of freedom
SE	Standard error

TITLE: Assessing the effect of the landscape context on European bees

Authors: Juan Gallego Zamorano[1], Ron Corstanje[1], Samantha L. L. Hill[2, 3], Andy Purvis[2, 4], Adriana De Palma[2, 4]

Affiliations:

[1]Cranfield Soil and Agrifood Institute, Cranfield University, Cranfield, Bedfordshire MK43 0AL, United Kingdom

[2]Department of Life Sciences, Natural History Museum, London, U.K

[3]United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, U.K

[4]Department of Life Sciences, Imperial College London, Ascot, UK

Name of corresponding author: Juan Gallego Zamorano

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Bees are considered one of the most valuable biological groups providing beneficial ecosystem services, such pollination. Land-use changes and intensification have lead to bee habitat fragmentation, impeding their movement and thus the accessibility to flowers (food). However, habitat heterogeneity seems to provide a positive response in the abundance and richness of bee populations. Functional connectivity estimates the movement of bees providing insights into how the landscape context affects their abundance. However, the inclusion of landscape context variables is scarce in global biodiversity models. Here I show that the surrounding landscape is one of the most important factors affecting the total-local abundance of bees across Europe. Using a combination of PREDICTS (one of the most comprehensive global biodiversity databases) and a set of models which predict floral resource and connectivity, I calculated three landscape measurements, habitat heterogeneity (Simpon's Diversity), accessible floral resources, and functional connectivity, in 2km buffers around 1766 sites across Europe where total abundance of bees and land use intensity was assigned, then mixed models were used for analysing the effects of the different variables. The interaction between land use intensity and the accessible floral resources was the most significant variable, particularly having a positive effect on the abundance of bees in croplands. In contrast to other studies that show the importance of habitat heterogeneity in croplands (Boscolo et al. 2017) here, there was only a positive effect in urban areas. Moreover, intermediate levels of connectivity enhanced the abundance in general. These results demonstrate the importance of the landscape configuration for the abundance of pollinators, especially the accessibility of floral resources in all kind of land uses. Large scale studies implementing different landscape variables to study pollinator abundance are rare, this research reveals the importance of improving floral spaces and connectivity to improve the ecosystem services that pollinators provide.

Keywords: Ecosystem services; Landscape ecology; Connectivity; Habitat heterogeneity; Pollination

1 INTRODUCTION

1.1 Bees and their conservation

Human well-being is dependent on the functions that nature provides, and their ecosystem services (Daily 1997). Mobile organisms provide ecosystem services, such as pest control, seed dispersal, or pollination, thanks to their movement between patches of habitat (Lundberg and Moberg 2003). Among these services, pollination is considered one of the most important and valued ones (Klein et al. 2007; Aizen et al. 2009; Potts et al. 2010) because it is essential for food production. However, in the last few decades, many studies have shown a severe decline of pollinators around the world (Potts et al. 2010) due essentially to land-use change and the increase of land-use intensity (Goulson et al. 2010; De Palma et al. 2016).

It is important to recognise, that other species (e.g. hoverflies) are often underestimated as pollinators (Jauker et al. 2009; Potts et al. 2010). But within pollinators, wild bees play a key role in enhancing ecosystem services (Klein et al. 2007; Garibaldi et al. 2013; Bartomeus et al. 2014).

Recently, Boscolo et al. 2017 have shown that the heterogeneity and the connectivity of the landscape influence positively the bee’s abundance and richness in farmlands of São Paulo, Brazil. Although, the study of these effects at a large-scale is scarce (Viana et al. 2012)

1.2 Global Models

In order to assess the current and future impacts of human pressures on biodiversity (and pollinators), it is important not only to make local studies but also to investigate these processes in a national and global scale (Alkemade et al. 2009; Newbold et al. 2015). The use of meta-analysis gives the possibility of joining local studies and therefore understand general trends (Alkemade et al. 2009; Newbold et al. 2015) Although in order to be able to identify global trends, it is necessary to have an extensive and representative database (Hudson et al. 2017) not only a mix of studies. Given that, the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (from now on PREDICTS) project, has developed an extensive database of site-level assemblages in different land uses with the help of more than 500 authors (Hudson et al. 2017). Using this database, global models were created to explain and predict the effects of human pressures on local biodiversity (Newbold et al. 2015). In terms of pollinators data, the PREDICTS database (Hudson et al. 2017), it has been used before for studies of pollinators in Europe (De Palma et al. 2015, 2016).

While these global models provide a general view of how biodiversity change when land use change, they extrapolate the result for each sampled point to the rest of the landscape without considering the landscape context and/or configuration as drivers. Because PREDICTS counts with extensive information on biodiversity from many different regions, it will be useful in the understanding of how the landscape context affects the bees diversity in a large-scale and not only in a local-scale as small studies do. In addition, the implementation of different landscape measurements as new explanatory variables, could improve the power of the models, and therefore our knowledge about the general tendencies of biodiversity.

1.3 Connectivity analysis

From a conservation point of view, connectivity facilitates the movement of organisms and thus the genetic interchange between populations, which is critical for the viability and persistence of species (Crooks and Sanjayan 2006; Frankham et al. 2010). In this sense, conservation corridors can improve landscape connectivity because they assist the movement of animals between patches of the landscape (Gilbert-Norton et al. 2010). For this reason, the study of the landscape configuration and the landscape connectivity has been a hot topic in conservation biology in the last few decades (Fahrig et al. 2011; Viana et al. 2012).

Saura and Torne in 2009, divided the definition of landscape connectivity into two terms: “Structural connectivity” and “Functional connectivity”. Structural connectivity is based on the landscape view, using the graph theory (Bunn et al. 2000; Urban and Keitt 2001), which understands the landscape as a network of nodes (patches) and vertices (links between patches) (Figure 1) (Bunn et al. 2000; Fortin et al. 2012).

When land use intensity increases, different habitats can be destroyed or fragmented, and the links between them can be interrupted. Which leads to a decrease in connectivity between patches and thus between populations (Crooks and Sanjayan 2006). This has been proven to have a negative impact on abundance and richness of pollinators (Krewenka et al. 2011).

Structural connectivity studies the spatial organization of the physical structures, involving the description of different metrics like the distance between different patches, the diversity of patches, the size of them, or the least-cost path (Saura and Rubio 2010). So in essence, the configuration of the different elements in the landscape (Bunn et al. 2000) that can affect the movement of bees (Krewenka et al. 2011; Boscolo et al. 2017).

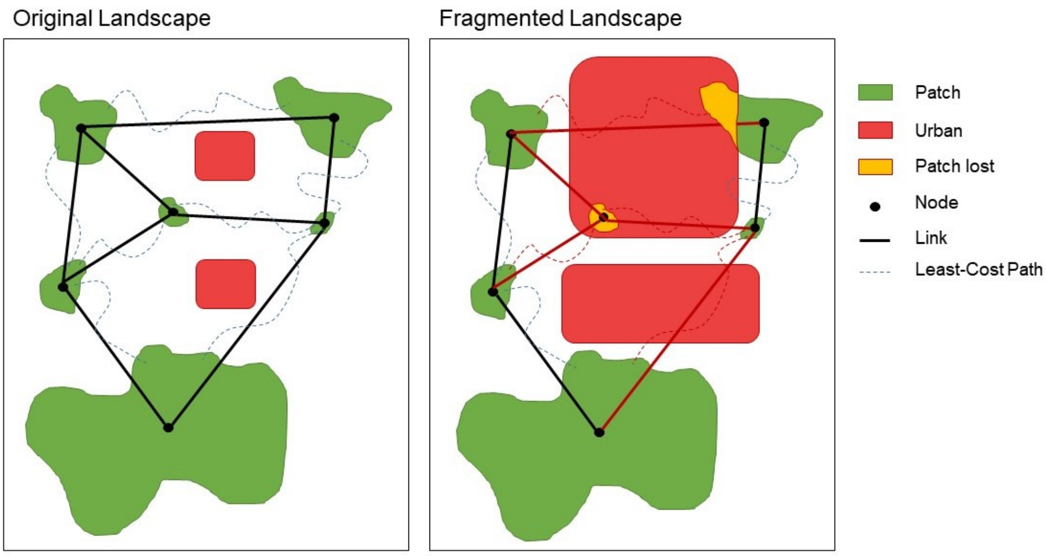


Figure 1 Graph theory

The graph theory represents the landscape as a network of nodes (patches) and vertices (links between patches). The actual movement of species can be represented as least-cost path. Graph metrics can characterise the contribution of each patch to the overall connectivity of the landscape. When a landscape becomes more fragmented the connectivity between patches decrease as well as the overall connectivity of the landscape.

The landscape configuration is an important factor in the understanding of how animals use the habitat, but the description of a suitable patch does not mean that animals will be there or move through it always (LaPoint et al. 2013). Abundance and richness of bees seem to have a positive response to the habitat heterogeneity (Rundlöf et al. 2015; Moreira et al. 2015; Boscolo et al. 2017) which is normally measured by patch diversity indexes, like Shannon's or Simpson's diversity index (McGarigal et al. 2012).

In the study of landscape effects on bees, it is important to not only focus on one landscape measurement, but to include different landscape measurements (Viana et al. 2012). Within this context, functional connectivity is species-specific but also landscape-specific (McRae et al. 2008) and therefore returns the behavioural response of a species to their specific perspective of the landscape, which provides a better knowledge of the behaviour of the species and their use of the landscape.

The circuit theory understands the landscape as conductive surfaces, where high resistances are assigned to features that obstruct the movement, e.g. barriers, and low resistances to suitable paths or permeable features, e.g. forests (McRae et al. 2008). In addition, it is connected with the random walk theory and it has the capacity of evaluating the contribution of multiple pathways simultaneously. Since each resistance value, is based on the capacity of movement of the selected species through the different features of the landscape, the circuit theory is optimal to understand the functional connectivity and how the landscape configuration affects the movement of animals (McRae et al. 2008).

1.4 Aim and hypothesis

The aim of this study is to assess the effect of landscape configuration and connectivity on European wild bees using the PREDICTS database.

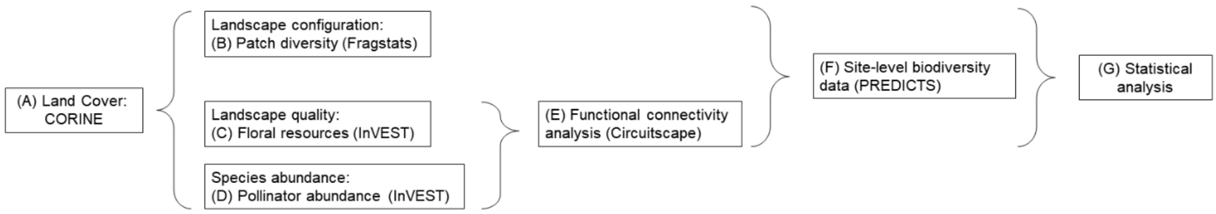
The first hypothesis of my work is that a) the heterogeneity of the landscape may correlate positively with the abundance of bees in the temperate zone of Europe. In addition to the effect of heterogeneity, the abundance of suitable habitats are expected to have a positive impact in bees populations, therefore b) the abundance of flower areas may show a positive effect on the abundance of bees. And as explained, connectivity is key in the well-being of wild populations, thus the last hypothesis is that c) the abundance of bees may be higher when there is better connectivity between source populations.

2 MATERIAL AND METHODS

The underlying process for the analysis of this study is described in Figure 2. A more detailed explanation of each step is explained below in sub-sections. The aim of this study is to understand how landscape configuration and connectivity affects the local abundance of bees in Europe. Assessing landscape configuration and connectivity at spatial scales relevant for bee species requires land use data at a high spatial resolution; I therefore, used the finest pan-European land cover raster available (A, Corine, 100m resolution). I characterised the landscape configuration in a 2 km buffer around local-biodiversity sites based on the mean foraging distance of bees (Westphal et al. 2006), with a measurement of the diversity of the landscape (B) using the software Fragstats (McGarigal et al. 2012), which will help to answer the first hypothesis. Because a spatial estimate of the habitat quality was needed, I used the Invest model of crop pollination (Lonsdorf et al. 2009; Sharp et al. 2016) as this effectively describes food and nesting availability (C, second hypothesis) and estimates the potential species abundance (D) for whole Europe. With the results of (C) and (D) I obtained the necessary inputs (node layer and resistance raster layer) for the connectivity analysis in Circuitscape software (E) (Shah and McRae 2008) which provides the base for answer the last hypothesis. Together (B), (C), and (E) were merged with site-level biodiversity data from PREDICTS (F) (Hudson et al. 2017), to analyse statistically their effect on bee biodiversity (G) being able to response all the hypothesis of this study.

Figure 2 Flow chart

A) Is the land cover raster (Corine) used as a base to characterise the landscape. B) Analyse the landscape configuration with the software Fragstats, which provides a measurement of patch diversity; C) and D) are results from the crop pollination model from InVEST giving information about the landscape quality and the potential pollinator abundance in the landscape. E) With the previous steps, the necessary inputs are obtained for calculating the functional connectivity for the bees with Circuitscapes software. F) The previous results (B, C and E) are merged with site-level biodiversity data from the PREDICTS database for, G) Statistical analysis of the effect of the landscape configuration and the connectivity on local bee abundance.



2.1 Material

2.1.1 Land cover raster: CORINE

The base map for the characterization of the connectivity of the landscape for bees was the CORINE land cover data from the year 2006 (Figure 2, A).This is the most current pan-European land cover map based on remote sensing data, is derived using Landsat TM and ETM+ imagery and visual interpretation (Bossard et al. 2000). Weather conditions are essential for bees, thus to ensure the spatial correlation of the weather and the flowering, I subset CORINE for the regions with Temperate-forest biome defined by the WWF (Olson et al. 2001). ArcGIS® software by Esri was used for all the spatial analysis. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license.

2.1.2 Biodiversity database: PREDICTS

The PREDICTS project is a collation of biodiversity data from 540 scientific papers, it was developed to better understand the impact of land use change on biodiversity. The PREDICTS database is one of the most extensive and representative biodiversity databases available, with a total of 31,248 sites from 97 countries and 47,044 species (Purvis et al. 2017; Hudson et al. 2017). Because PREDICTS has been used before for analysis of European bees (De Palma et al. 2015, 2016). It was used as a biodiversity data source for the purpose of this study (Figure 2, F).

For each of the sites in the database, a predominating land cover (LC) and the land-use intensity (UI) was assigned based on the information provided by the authors of the papers, or the description of the studies areas in the manuscripts (Hudson et al. 2017). The land-use classes include: Primary forest, Primary non-forest, Secondary mature vegetation, Secondary intermediate vegetation, Secondary young vegetation, Secondary vegetation (indeterminate age), Cropland, Plantation Forest, Pasture, Urban). Land-use intensity can have an impact on biodiversity, but because it is hard to obtain such information, land use intensity was assigned using a coarse three-point scoring system: Minimal use, Light use or Intense use (Hudson et al. 2017).

For this research, LC and UI of the sites were combined into a new variable called Land-use-intensity (LUI). Due to low sample sizes, the LUI categories were collapsed in six levels:

- Natural / Semi-natural Vegetation (resultant from Primary and Secondary vegetation), Cropland Intense use, Cropland Light use, Cropland Minimal use, Pasture, Urban. The detailed definition of each level used in this study is in Appendix A,Table 3.

The PREDICTS database was then queried for biodiversity records where sites in the temperate-forest region in Europe were sampled for bees (i.e., sampled species belonged to one of the following families of bees according to the Tree of Life (Maddison et al. 2007): Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae, Stenotritidae, Meganomiidae, Dasypodaidae).

2.2 Methods

2.2.1 Bee's mobility

Bee's mobility is correlated with the distance (in millimetres) between the two insertion points of the wings (inter-tegular distance, ITD). The ITD is high-correlated with the species mobility (Greenleaf et al. 2007), therefore many studies use the ITD as an indicator of the species foraging distance. The maximum foraging distance for solitary bees does not exceed the 1500m (Zurbuchen et al. 2010). In the PREDICTS database, bumblebees are the species with highest ITD (De Palma et al. 2015), and although they can move up to ~10km (Goulson and Stout 2001) their mean foraging distance is typically ~2.5 km (Westphal et al. 2006). Bees preferably forage at the most rewarding source available at the shortest distance from the colony (Gathmann and Tscharntke 2002; Wolf and Moritz F.A. 2008).

For these reasons, I created a 2km buffer around the PREDICTS sites that captures the mean foraging distance for all the species and provides a reasonable landscape window to analyse. But because some individuals can cover long distances (Goulson and Stout 2001) I created a bigger buffer of 15 km to capture better the variability of the probability of connectivity for the connectivity analysis with Circuitscape.

2.2.2 Landscape configuration: FRAGSTATS

In this particular study, I am interested in the fragmentation and diversity of the landscape (how heterogeneous is a certain landscape). For that reason, I selected the landscape metric of FRAGSTATS (McGarigal et al. 2012) that gives information about how the different patches (types of land cover) configure the landscape: Simpson's Diversity Index (SIDI). Diversity indexes depend on 2 components, richness and evenness. Richness in terms of landscape configuration, which refers to the number of patch types present in the landscape, while evenness refers to the area among patch types. SIDI is less sensitive to the influence of patch richness than other indices (e.g. Shannon's diversity index) and therefore gives more weight on the common patch types (McGarigal et al. 2012) and is less influenced by rare types. A complete definition and the equation of the metric can be found in Appendix B.

2.2.3 Landscape quality: InVEST

The InVEST pollination model version 3.3.3 (Sharp et al. 2016) uses estimates of the availability of floral resources and nest sites within wild bees flight ranges, to calculate an index of “potential pollinator abundance” (PA). This index describes where pollinators are active in the landscape. Another relevant, intermediate result from InVEST model is the “accessible floral resources” (ACF), which takes into account the foraging activity of the selected species and the floral availability in the different land covers. The full description of the model, the inputs and results are described Appendix C.

Three inputs are required to run the model:

- Land cover map: in this case, I used Corine as LC base map.
- Table of biophysical LC attributes: containing information on the nesting availability and floral resources for each LC class (Table 4), described with relative indices from 0 to 1. Here, I used values from Zulian et al. 2013, to implement them in the new version of InVEST.
- Species information table: with information (Table 5) of the modelled species (nesting suitability substrate, the season of foraging activity, and the mean distance that the species travel to forage flowers). Here I created a model bee species that can nest in cavities and on the ground, and with a mean forage distance of 2 km based on the literature (Westphal et al. 2006) in order to be standardized with the previously selected buffer.

2.2.4 Functional connectivity: Circuitscape

Circuitscape implements circuit theory to model connectivity of populations in heterogeneous landscapes (Shah and McRae 2008). It is a widely used tool for the study of functional connectivity (McRae et al. 2008; Pelletier et al. 2014). Because it describes the landscape as conductive surfaces and requires two main inputs: a layer of nodes, and a resistance raster. Then it calculates the connectivity between all pairs of nodes, using the resistance raster as landscape. Each cell has a resistance value that contemplates the degree to which the cell facilitates or impedes the movement of individuals (higher values, means higher resistance to movement)

Here I considered as nodes the values above the mean of the PA from InVEST, which means a high activity of bees in those places. As resistance raster the ACF because the movement of bees is highly dependent on the amount of flowers, and its accessibility (Hatfield and LeBuhn 2007; Rundlöf et al. 2008). I used the justified 15 km buffer for running the analysis, and then the 2 km buffer to extract the mean value of the current flow between nodes as an indicator of the probability of connectivity of populations (here after, as connectivity).

2.2.5 Statistical analysis

2.2.5.1 Model selection

For each PREDICTS site, the total abundance of species was calculated as the sum of abundances of all taxa at a site, regardless of how abundance was measured, using the R package "yarg" version 0.1-8 (The PREDICTS team 2014a). In order to normalise residuals and equalise variance, total abundance was ln+ 1 transformed. I then merged the results of the previous analysis: Simpson's diversity index, accessible floral resources, and the connectivity analysis; with information of local-abundance from PREDICTS into a single matrix.

Generalized linear mixed effects models (GLMM) were used to take care of the nested structure of the PREDICTS database, and the variability of sampling methods of the different authors (Zuur et al. 2009). In addition, the resultant model will provide information about how the landscape heterogeneity (SIDI, hypothesis A), the accessible floral resources (suitable areas, hypothesis B), and the connectivity (hypothesis C) affects the total abundance of bees in the PREDICTS sites.

Several candidate models were run to explain the total abundance of bees by the LUI, the Simpson's diversity index, the accessible floral resources, and the connectivity, alone as fixed effects, and the study site and the study site block as random effects. Moreover, the interaction between LUI and the different landscape context measures was added as explanatory variables, as well as the interaction between different landscape context measurements, full model (Eq. 1).

Eq. 1 Full model equation

Full model equation, the response variable is the site-level total abundance of bees; the fixed-effects are the LUI, the landscape context variables, and the interactions between them; the random effects are the study sites (SS) and the blocks in the study sites (SSB).

$$\overbrace{\text{Total abundance}}^{\text{Response variable}} \sim \overbrace{\text{LUI} + \text{Connectivity} + \text{Simpson} + \text{ACF} + \text{LUI:Connectivity} + \text{LUI:Simpson} + \text{LUI:ACF} + \text{Connectivity:ACF}}^{\text{Fixed-effects: Explanatory variables and interactions}} + \overbrace{(1|\text{SS}) + (1|\text{SSB})}^{\text{Random effects}}$$

The best model was selected using a stepwise selection from the ranking of candidate models based on the Akaike information criterion (AIC). This method selects the best fitting model, taking into account the minimum number of parameters (Zuur et al. 2009). To compare models with different fixed-effects structures, I used the Maximum Likelihood (ML) (Zuur et al. 2009). Once I identified the best fixed-effects structure, I used the Restricted Maximum Likelihood (REML) to calculate the estimates of the best model, because this represents an unbiased estimation of the variation among random effect since it corrects the degrees of freedom (Zuur et al. 2009). All the analysis were conducted with the software R version 3.3.1 (R Core Team 2016) using the lmer function from the “lme4” package (Bates et al. 2014) which is embedded in the “roquefort” package version 0.1-2 (The PREDICTS team 2014b).

In addition, the marginal r-squared (which explains the variability of the residuals by the structure of the random effects) and conditional r-squared (which only use the fixed-effects) were used to check the power of the model. Because the hierarchical nature of the PREDICTS database, normally the majority of the variation is explained by the marginal r-squared (high values) and therefore the power of the model is given by the random effects.

2.2.5.2 Model validation

The assumptions of normality and homogeneity were tested using the diagnostics plots. For normality I used a Q-Q plot, the plots show non-normality if there is any deviation from the observed residuals quantiles from the model and the expected quantiles from a theoretical normal distribution (Zuur et al. 2009). The histogram of the residuals also provides information about normality, it should show a normal distribution shape. To check the homogeneity, the standardised residuals vs the fitted values were plotted. Any observable pattern in the dispersion of the residuals over fitted values will represent the violation of homogeneity (Zuur et al. 2009).

Additionally, the collinearity between the explanatory variables was checked. Collinearity could inflate the estimated SE. It was checked using the Pearson correlation between the continuous variables (values above 0.7 indicates collinearity) and the GVIF between continuous and categorical variables (corvif function, Zuur et al. 2009). GVIF is the generalized variance inflation factor. GVIF scaled by the degrees of freedom provides an indication of how much this is likely to happen, values below 3 indicates no collinearity. See the Appendix D, D.3, for further details.

3 RESULTS

3.1 Final dataset

The final dataset used for this analysis includes information from 28 articles (references described in Appendix E), 50 studies, 19 known species from 5 genera, and 1766 sites in 11 countries across Europe (Figure 3). All LUI levels had at least 100 sites, except for urban areas, which were scarce in the dataset with only 20. The summary statistics for the different landscape context parameters are described in Table 1.

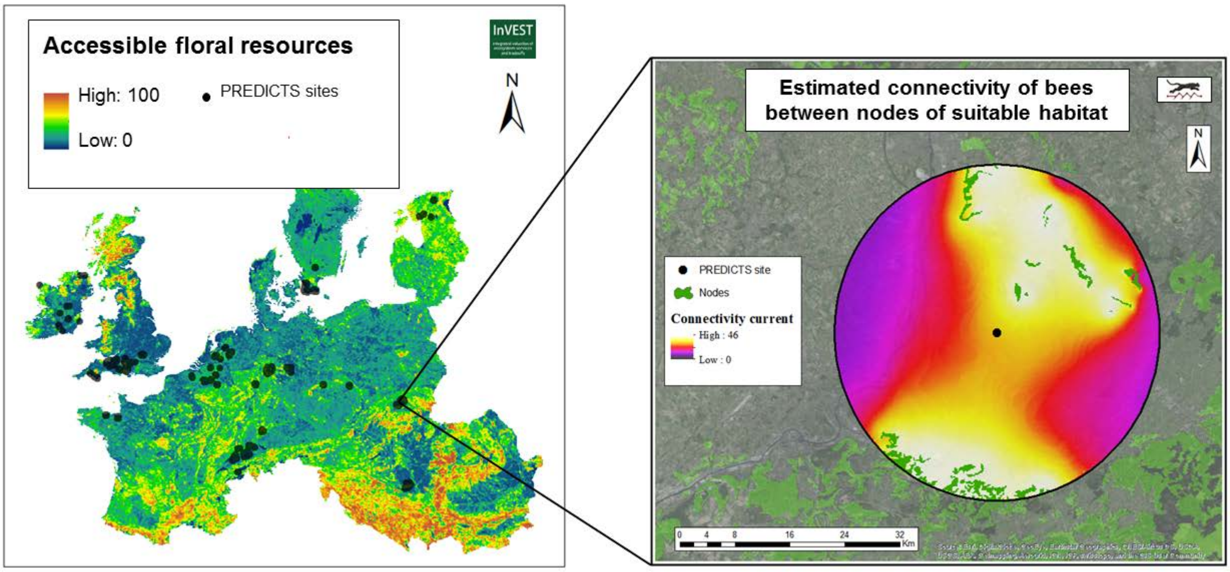


Figure 3 PREDICTS sites, ACF and estimated connectivity

A total of 1766 sites from PREDICTS are plotted against the accessible floral resources, an intermediate output from the InVEST crop pollination model. Connectivity is expressed as the cumulative current flow between all pairs of nodes.

Table 1 Summary statistics of landscape measurements

The min, max and mean of the different landscape context measurements extracted from the 2km buffer surrounding the PREDICTS sites. In addition, the accessible floral resources in Europe is presented.

	Min	Max	Mean
Total abundance	0	1000	40
SIDI	0	0.84	0.5
ACF	20.8 %	56.9 %	34.2 %
ACF in Europe	0 %	100 %	39.9 %
Connectivity	0	7.5	1.8

3.2 GLMM results

The whole ranking of candidate models can be found in Appendix D, D.1. The best candidate model (with an AIC of 4913 and 49 df, the 2nd best model had an AIC of 4983 with 45 df) was the full model (Equation 1) where the impact of LUI on bee abundance was significantly influenced by each of the landscape-level variables (Table 2). Although the Land Use Intensity and ACF were significant on their own, they are meaningless in this analysis because their interaction with LUI was also significant. The interaction between LUI and ACF was the most significant variable explaining the total abundance of bees (Figure 4, b); the interactions between LUI and Simpson's diversity index (Figure 4, a); LUI and Connectivity (Figure 4, c); and ACF with Connectivity, were also significant. The conditional r squared (which express the contribution of only the fixed effects) was 0.1 and the marginal (together, fixed and random effects) was 0.73. The full model with its estimates is in Appendix D, D.2; there was no collinearity of the co-variables and no issues of normality or homogeneity (Appendix D, D.3).

Table 2 ANOVA type II table for the best candidate model

Results of the best-ranked model. Total abundance of bees was the response variable. LUI is Land Use Intensity, ACF is Accessible Floral resources, Connectivity is the estimated functional connectivity, and Simpson's Diversity index is the measurement of habitat-patch diversity. All of the measurements are the mean value extracted from the 2 km buffer around the 1766 PREDICTS sites. Df are the degrees of freedom. Significance is showing with asterisks.

Explanatory variables	**Chisq**	**Df**	**P-value**	
LUI	84.40	5	0.00	***
ACF	9.75	2	0.01	**
Connectivity	1.24	2	0.54	
Simpson's diversity index	1.12	2	0.57	
LUI : ACF	47.91	10	0.00	***
LUI : Simpson	31.88	10	0.00	***
LUI : Connectivity	21.79	10	0.02	*
ACF : Connectivity	36.47	4	0.00	***

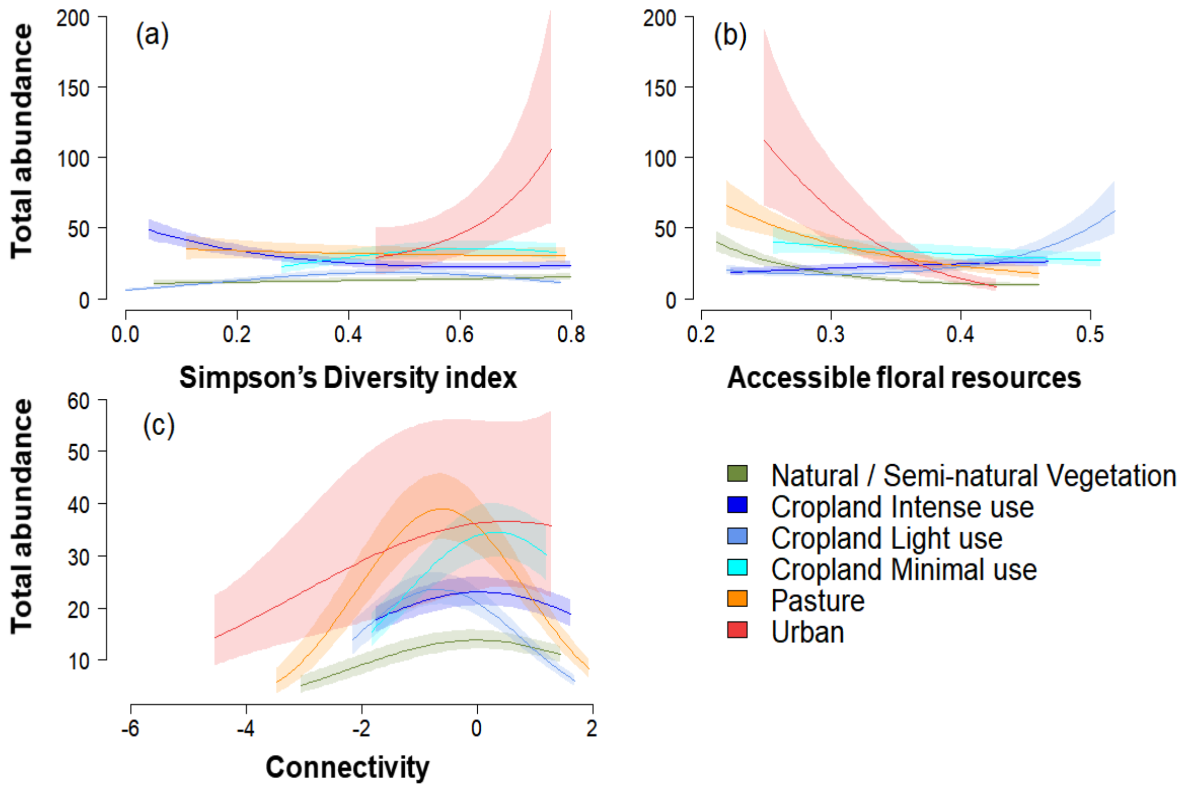


Figure 4 Response of local total abundance of bees to landscape context variables

Modelled significant effects of Simpson's Diversity index, Accessible Floral Resources and Connectivity interacting with Land Use Intensity, on the predicted total local abundance of bees. Holding other variables at their median level. Shaded polygons are shown as ± 0.5 x SE of the mean for clarity. Connectivity is log-transformed for clarity. a) Where the landscape had high levels of patch diversity (SIDI), urban areas tended to shelter greater site-level total bee abundance. b) As accessible floral resources increase, the total abundance of bees in Natural / Semi-natural Vegetation, Pasture and Urban sites decrease; a less pronounced decrease can be observed in Cropland Intense Use. On the other hand, there is an increase in the total abundance of bees in lightly and intensively-used cropland as ACF increases. c) Intermediate levels of connectivity increase the total abundance of bee species in all the different land uses, with a pronounced peak in pastures.

4 DISCUSSION

Biodiversity models rarely consider the impacts of land-use change at both local and landscape scales (Viana et al. 2012; Marshall et al. 2017). Statistical models that analyse the bee abundance in relation to landscape changes have the possibility to inform and improve conservation plans. The landscape measurements have been demonstrated to have an impact on pollinators (Rundlöf et al. 2008; Kennedy et al. 2013; Boscolo et al. 2017) and different taxa perceive the landscape differently (Jauker et al. 2009). Because bees are one of the key pollinators (Klein et al. 2007; Garibaldi et al. 2013), here I presented a novel approach to understanding the abundance of bees by the integration of the landscape context using three different landscape aspects: landscape heterogeneity/configuration (e.g. Simpson’s diversity of the patches in the landscape), accessible floral resources (surrounding suitable areas within foraging distances) and the functional connectivity of the landscape for bees. Separately, the different aspects have been confirmed as drivers of abundance of bees (Kennedy et al. 2013; Boscolo et al. 2017), and although Kennedy and colleagues analysed 39 crops systems globally, in general, there is a lack of large-scale studies that includes different landscape measurements (Viana et al. 2012).

4.1 Landscape configuration

The first hypothesis of this study postulated that higher landscape heterogeneity should correlate with higher total (site-level) abundance of bees. However, whereas other studies (Rundlöf et al. 2008; Moreira et al. 2015; Boscolo et al. 2017) showed that landscape heterogeneity has an important effect on bee abundance and richness in agricultural lands, here the most marked effect was in urban areas (Figure 4, a). This suggests that when the surrounding landscape in urban areas is more diverse, the abundance of bees is better maintained (Bates et al. 2011). Therefore, higher levels of urbanization (more spread urban areas) have a clear negative effect on pollinators across Europe (Bates et al. 2011) because it could reduce the heterogeneity of the landscape, thus reducing local diversity in urban areas. These inferences were based on few data compared to other land uses, more data from urban areas are needed to better understand the impact of high levels of urbanization on bees (Hernandez et al. 2009).

4.2 Landscape quality

The second hypothesis proposed that site-level abundance of bees would be higher where the landscape had higher levels of accessible floral resources. The results, however, show that these effects vary significantly with land use: in fact, the interaction of ACF and LUI was the most significant driver of the local total abundance of bees. The total abundance of bees decreases with increasing accessible floral resources in places such urban areas, pastures, and natural/semi-natural vegetation (e.g. woodland). These land uses can support food (e.g. exotic plants can extend the flowering season) and nesting (e.g. cavity-nesting bee species have higher abundances in urban compared to suburban) (Hernandez et al. 2009). Because the sampling is normally done during foraging behaviours, these results may suggest that bees have preferences for flowers outside these land uses. In consequence, if the degree of accessible floral resources increases in the surroundings of urban, pastures or natural/semi-natural vegetation, it appears that the bees will follow the flowers (Wolf and Moritz F.A. 2008) resulting in a decrease in the abundance of bees in those sites. In contrast, in lightly- and intensively-used croplands, the total abundance of bees increases when the landscape contains high levels of accessible floral resources (Figure 4, b). Croplands with minimal intense use showed a slight decrease of total abundance but not very significant. Several studies (Rundlöf et al. 2008; Power and Stout 2011; Samnegård et al. 2011) have shown the importance of enhancing the habitat quality around farmland areas. The results presented here show that this pattern is maintained for higher intensity croplands, not only for a specific study area but in average for 11 countries across Europe. This reveals the importance of improving conservation plans in farmland areas, in order to increase and maintain the floral resources near and in between the croplands and therefore increase the pollination services in areas where this ecosystem service has been declined (Rundlöf et al. 2008).

4.3 Functional connectivity

The last hypothesis asserted that sites that are well connected to a source population will have a higher local total abundance of bees. While the results reveal that connectivity was a significant predictor of local bee abundance, conversely to the hypothesis, the total abundance of bees was low when connectivity was too low or too high, creating the observable bell-shapes in all the land uses (Figure 4, c). The accessible floral resources was used to assign the resistance values for the functional connectivity analysis, therefore this functional connectivity is not only showing the permeability of the different landscape features to the movement of bees, but it also reflects the landscape quality. They did not show correlation between them (Appendix D) so this may suggest the significant effect of their interaction (Table 2) but due to its difficult interpretation, is not discussed or infer. It is possible that when connectivity is low (thus the cost of moving is high) generalist species may become the predominant species and therefore the only able to survive, which is consistent with the results and the discussion of Boscolo et al. 2017. Moreover, when the connectivity is high, there are more possibilities for pollinators of reaching suitable places for nesting or feeding; the low local abundances may, therefore, be driven by pollinator dilution, as more individuals move into the surrounding landscape. The more potential sources of food and nesting, the more disperse will be the bee community and therefore, we are not able to capture precisely where the bees are (Viana et al. 2012). For a complete understanding of where the bees go when the connectivity is high, a mark/recapture analysis should be carried out on a local scale to look at the population and metapopulation level.

4.4 Conclusion

This research reveals the importance of enhancing floral resources in the surrounding landscape. Conservation plans should focus not only on one landscape measure but should use the knowledge from different studies (or studies that used different measures) in order to improve the state of pollinators across Europe and therefore improve the ecosystem services. Of all the landscape measurements analysed in here, the accessibility to floral resources appeared to be the most important one. Particularly in urban areas, the implementation of more floral resources and green spaces will create a more diverse landscape inside and outside the urban areas, which will benefit the abundance of pollinators in cities and their surroundings (Bates et al. 2011; De Palma et al. 2016). Moreover, the improvement of floral resources in the surroundings of croplands will help the pollination services (Samnegård et al. 2011; Bates et al. 2011).

In conclusion, bees respond to the landscape context in different ways in different land uses. However, there is a need of increasing studies that combines different bee species, in different landscapes, with different configurations, and in different parts of the world, to be able to extrapolate this results to other regions. Studies of how different aspects of the landscape affect the local abundance of bees are scarce (Viana et al. 2012). This analysis recalls the importance of integrating different landscape measurements from many regions to better understand the general patterns of pollinators.

4.5 Limitations and further development

There are a few limitations in this study to keep in mind. This approach will be difficult to use in other regions as the data in PREDICTS for bees are globally biased, most data are from Western Europe and North America, and the bumblebees species are overrepresented, however, it is proven that the responses of the biodiversity vary across regions (De Palma et al. 2016). The data used here is mainly from the temperate forest biome, whereas I would expect there to be different responses in other biomes such as the Mediterranean (southern regions) or the Taiga and Tundra (northern regions). In addition, the data available from urban areas is low and should be increased to better capture the tendencies in this areas. Nonetheless, the mean accessible floral resources in the sample sites (34.2%) was not statistically different from the mean in Europe (39.9%), which may suggest that for the temperate region PREDICTS has a good representation of the accessible floral resources.

Further developments of this research could use more detailed land cover data for characterising landscape context; for instance, the use of remote sensing data may provide finer scale information on the different land covers. In addition, analysis of suitable areas and connectivity for specific species should be carried out to observe the responses of the different species to different pressures in more detail. These developments could help to improve the robustness of analysis such as the one presented here.

ACKNOWLEDGEMENTS

I would like to thank Ron Corstanje for understand my requirements of moving to the NHM, supervising me, and lead me during the analysis process. Also thanks to Andy Purvis for accepted me in their marvellous group, he is just an amazing supervisor. Adriana de Palma, Isabel Fenton and Samantha Hill for their guidance and help during the process. Last, I would like to thank my parents (Ana and Eduardo), my brother (Dani) and my “blue lycaenid” (Cristina) for their emotional and unconditional support during this months, without you would not be possible.

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APPENDICES

Appendix A PREDICTS

This appendix shows the definition of the different land use classes used in this study and derived from the definition of the PREDICTS project (Purvis et al. 2017).

A.1 Land Use and Land Use Intensity classes

Table 3 Land Use classes and land use intensities

Land Use classes and Land Use intensities used for this study and from the PREDICTS database (Hudson et al. 2017).

Predominant Land Use	Definition	Minimal Use	Light Use	Intense Use
Natural / Semi-natural Vegetation	Result from the collapse of the PREDICTS classes Primary vegetation and Secondary vegetation (Hudson et al. 2017). Primary vegetation is considered native vegetation that is not known to have ever been changed, destroyed, by human actions or by extreme natural events that do not belong to the ecosystem dynamics. Secondary vegetation is where the original vegetation was completely destroyed, and now the ecosystem is recovering its initial state.			

Cropland	Land occupied by herbaceous crops. If it is abandoned, it becomes Secondary vegetation	Low-intensity farms, with mixed crops, crop rotation. Without pesticide use, fertilizers, ploughing, irrigation, and machinery.	Medium intensity farming, there is an increase in the use of pesticides, fertilizers, annual ploughing…etc	High-intensity monoculture farming, showing large fields, annual ploughing, inorganic fertilizers, irrigation, machinery and without crop rotation
Pasture	Land where livestock is known to be grazed regularly or permanently			
Urban	Human-dominated lands where the Primary vegetation has been removed, is typically covered by buildings.			

Appendix B FRAGSTATS metric

This appendix defines the Simpson's diversity index used in this research as an index of the heterogeneity of the landscape. It was calculated with the software FRAGSTATS (McGarigal et al. 2012) for each 2 km buffer around the PREDICTS sites.

B.1 Simpson's Diversity Index (SIDI)

"Simpson's Diversity Index is equals to 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared. SIDI = 0 when the landscape contains only 1 patch (i.e., no diversity). SIDI approaches 1 as the number of different patch types (i.e., patch richness, PR) increases and the proportional distribution of area among patch types become more equitable" (McGarigal et al. 2012).

Pi = proportion of the landscape occupied by patch type (class) i.

$$\boldsymbol{SIDI = 1 - \sum_{i=1}^{m} P_i^2} \qquad \textbf{Eq. A- 1}$$

Appendix C InVEST model

This appendix describes the various equations used in the InVEST model for the calculation of the accessible floral resources and the potential pollinator abundance. The complete model and further information can be found in http://www.naturalcapitalproject.org/

C.1 List of variables

- xx - a pixel coordinate.
- XX - set of all pixels in the landcover map.
- ss - bee species.
- nn - nesting type (ground, cavity).
- NN - set of all nesting types.
- jj - season (fall, spring, etc).
- JJ - set of all seasons (ex: {fall, spring}).
- αsαs - mean foraging distance for species s.
- ns(s,n)ns(s,n) - nesting suitability preference for species ss in nesting type nn.
- HN(x,s)HN(x,s) - habitat nesting suitability at pixel xx for species ss [0.0, 1.0].
- N(l,n)N(l,n) - the nesting substrate index for landcover type ll for substrate type nn in the range [0.0,1.0][0.0,1.0].
- RA(l,j)RA(l,j) - index of relative abundance of floral resources on landcover type ll during season jj. [0.0,1.0][0.0,1.0]
- fa(s,j)fa(s,j) - relative foraging activity for species ss during season jj.
- FR(x,s)FR(x,s) - accessible floral resources index at pixel xx for species ss.
- D(x,x′)D(x,x′) - euclidean distance between the centroid of pixel xx and x′x′.
- PS(x,s)PS(x,s) - pollinator supply index at pixel xx for species ss.
- PA(x,s,j)PA(x,s,j) - pollinator abundance at pixel ss for species ss.

C.2 Pollinator supply

$$PS(x,s) = FR(x,s)HN(x,s)sa(s) \quad \textbf{Eq. A- 2}$$

C.3 Accessible floral resources

$$\boldsymbol{FR(x,s)} = \frac{\sum_{x' \in X} \mathbf{exp}(-\boldsymbol{D(x,x')/\alpha_s}) \sum_{j \in J} \boldsymbol{RA(l(x'),j)fa(s,j)}}{\sum_{x' \in X} \boldsymbol{exp(-D(x,x')/\alpha_s)}} \quad \textbf{Eq. A- 3}$$

C.4 Habitat nesting suitability

$$HN(x,s) = \max_{n \in N}[N(l(x),n)ns(s,n)] \quad \textbf{Eq. A- 4}$$

C.5 Pollinator abundance index

$$PA(x,s,j) = \left(\frac{RA\ (l(x),j)fa(s,j)}{FR(x,s)}\right) \frac{\sum_{x' \in X} PS(x',s)\exp(-D(x,x')/\alpha_s)}{\exp(-D(x,x')/\alpha_s)} \quad \textbf{Eq. A- 5}$$

C.6 Inputs information

Table 4 Biophysical attributes for the Corine land cover classes

Table that contains information about the nesting availability and the floral resources for each Corine land cover class. This table is one of the necessary inputs for the InVEST crop pollination model.

Corine class name	LC-code	Nesting cavity availability index	Nesting ground availability index	Floral resources all-year index
Continuous urban fabric	1	0.1	0.1	0.05
Discontinuous urban fabric	2	0.3	0.3	0.3
Industrial or commercial units	3	0.1	0.1	0.05
Road and rail networks and associated land	4	0.3	0.3	0.25
Port areas	5	0.3	0.3	0
Airports	6	0.3	0.3	0.1
Mineral extraction sites	7	0.3	0.3	0.05
Dump sites	8	0.05	0.05	0
Construction sites	9	0.1	0.1	0
Green urban areas	10	0.3	0.3	0.25
Sport and leisure facilities	11	0.3	0.3	0.05
Non-irrigated arable land	12	0.2	0.2	0.2

Permanently irrigated land	13	0.2	0.2	0.05
Rice fields	14	0.2	0.2	0.05
Vineyards	15	0.4	0.4	0.6
Fruit trees and berry plantations	16	0.4	0.4	0.9
Olive groves	17	0.4	0.4	0.2
Pastures	18	0.3	0.3	0.2
Annual crops associated with permanent crops	19	0.4	0.4	0.5
Complex cultivation patterns	20	0.4	0.4	0.4
Land principally occupied by agriculture, with significant areas of natural vegetation	21	0.7	0.7	0.75
Agro-forestry areas	22	1	1	0.5
Broad-leaved forest	23	0.8	0.8	0.9
Coniferous forest	24	0.8	0.8	0.3
Mixed forest	25	0.8	0.8	0.6
Natural grasslands	26	0.8	0.8	1
Moors and heathland	27	0.9	0.9	1
Sclerophyllous vegetation	28	0.9	0.9	0.75
Transitional woodland-shrub	29	1	1	0.85
Beaches, dunes, sands	30	0.3	0.3	0.1
Bare rocks	31	0	0	0
Sparsely vegetated areas	32	0.7	0.7	0.35
Burnt areas	33	0.3	0.3	0.2
Glaciers and perpetual snow	34	0	0	0
Inland marshes	35	0.3	0.3	0.75
Peat bogs	36	0.3	0.3	0.5
Salt marshes	37	0.3	0.3	0.55
Salines	38	0	0	0
Intertidal flats	39	0	0	0
Water courses	40	0	0	0
Water bodies	41	0	0	0
Coastal lagoons	42	0.2	0.2	0
Estuaries	43	0	0	0
Sea and ocean	44	0	0	0

Table 5 Bee species information

Information about the studies species, their ability of nesting in ground or cavities, their foraging activity period and their foraging range (Alpha)

Species	Nesting suitability cavity index	Nesting suitability ground index	Foraging activity spring index	Foraging activity summer index	Alpha
Bombus sp.	1	1	0.8	1	2000

Appendix D GLMM’s

This appendix contains the process for the selection of the best-candidate model for the explanation of the total abundance in the PREDICTS sites, as well as the whole summary of estimates and the validation of the best-candidate model.

D.1 Candidates models

Table 6 Ranking of all candidate models

Ranking of the best candidates for the final model with the random structure of Study Site and Study Site Block. The best-ranked model with an AIC of 4913 was the most complicated one with interactions between LUI and all the variables and also the interaction of ACF and Connectivity, and 49 degrees of freedom (df)

Explanatory variables	df	AIC
LUI	9	5206.43
ACF	21	5119.83
Connectivity	21	5142.74
Simpson	21	5141.69
Only variables (no LUI)	18	5178.80
Without interactions	45	4983.87
With interactions (between LUI and variables)	49	4913.01

D.2 Best candidate estimates

Table 7 Full summary of the best candidate model

A complete summary of the best candidate model, it shows the estimates of each parameter that is included in the fixed effects for the explanation of the local-total abundance of bees. Each component is compared to the intercept (baseline) of Natural / Semi-natural Vegetation.

Response variable: Total abundance of bees	**Estimate**	**SE**	**df**	**t-value**	**p-value**	
(Intercept) Natural / Semi natural Vegetation	2.66	0.22	67.42	11.83	0.00	***
Cropland Intense use	0.55	0.16	1196.12	3.53	0.00	***
Cropland Light use	0.13	0.18	1337.35	0.75	0.45	
Cropland Minimal use	0.58	0.22	1487.76	2.57	0.01	*
Pasture	0.68	0.19	1523.39	3.60	0.00	***
Urban	0.88	1.08	1433.94	0.82	0.41	
poly(ACF, 2)1	-14.21	4.66	1654.13	-3.05	0.00	**
poly(ACF, 2)2	10.15	3.81	1682.84	2.67	0.01	**
poly(Connectivity, 2)1	3.51	6.20	1196.09	0.57	0.57	
poly(Connectivity, 2)2	-1.31	3.62	1489.05	-0.36	0.72	
poly(Simpson, 2)1	3.68	3.31	1696.38	1.11	0.27	
poly(Simpson, 2)2	0.05	2.86	1684.40	0.02	0.98	
Cropland Intense use:poly(ACF, 2)1	20.58	5.46	1653.53	3.77	0.00	***
Cropland Light use:poly(ACF, 2)1	25.94	6.75	1671.30	3.84	0.00	***
Cropland Minimal use:poly(ACF, 2)1	10.81	10.12	1688.42	1.07	0.29	

Pasture:poly(ACF, 2)1	-0.84	8.75	1594.65	-0.10	0.92	
Urban:poly(ACF, 2)1	-33.07	35.28	1413.62	-0.94	0.35	
Cropland Intense use:poly(ACF, 2)2	-6.94	4.73	1580.79	-1.47	0.14	
Cropland Light use:poly(ACF, 2)2	1.10	5.33	1593.64	0.21	0.84	
Cropland Minimal use:poly(ACF, 2)2	-5.76	8.10	1672.56	-0.71	0.48	
Pasture:poly(ACF, 2)2	-4.27	7.25	1584.27	-0.59	0.56	
Urban:poly(ACF, 2)2	-12.93	36.20	1507.44	-0.36	0.72	
Cropland Intense use:poly(Connectivity, 2)1	-0.35	6.42	1354.58	-0.05	0.96	
Cropland Light use:poly(Connectivity, 2)1	-11.20	7.01	1405.66	-1.60	0.11	
Cropland Minimal use:poly(Connectivity, 2)1	7.52	8.38	826.68	0.90	0.37	
Pasture:poly(Connectivity, 2)1	-9.47	6.94	1671.86	-1.36	0.17	
Urban:poly(Connectivity, 2)1	-0.36	19.61	1521.23	-0.02	0.99	
Cropland Intense use:poly(Connectivity, 2)2	1.98	4.84	1154.66	0.41	0.68	
Cropland Light use:poly(Connectivity, 2)2	-10.46	5.70	1252.32	-1.83	0.07	.
Cropland Minimal use:poly(Connectivity, 2)2	-5.31	11.11	700.57	-0.48	0.63	
Pasture:poly(Connectivity, 2)2	-10.11	4.05	1666.65	-2.50	0.01	*
Urban:poly(Connectivity, 2)2	5.37	9.33	1601.53	0.58	0.57	
Cropland Intense use:poly(Simpson, 2)1	-10.29	3.95	1683.61	-2.60	0.01	**
Cropland Light use:poly(Simpson, 2)1	-1.85	4.64	1688.10	-0.40	0.69	
Cropland Minimal use:poly(Simpson, 2)1	6.92	10.13	1659.04	0.68	0.49	
Pasture:poly(Simpson, 2)1	-5.41	6.42	1654.55	-0.84	0.40	
Urban:poly(Simpson, 2)1	12.19	61.72	1459.46	0.20	0.84	
Cropland Intense use:poly(Simpson, 2)2	4.05	3.37	1687.87	1.20	0.23	
Cropland Light use:poly(Simpson, 2)2	-9.46	3.87	1689.30	-2.45	0.01	**

Cropland Minimal use:poly(Simpson, 2)2	-6.92	8.46	1658.37	-0.82	0.41	
Pasture:poly(Simpson, 2)2	0.41	5.21	1535.88	0.08	0.94	
Urban:poly(Simpson, 2)2	12.53	47.29	1456.78	0.27	0.79	
poly(ACF, 2)1:poly(Connectivity, 2)1	-412.52	93.25	722.98	-4.42	0.00	***
poly(ACF, 2)2:poly(Connectivity, 2)1	51.06	77.79	1151.44	0.66	0.51	
poly(ACF, 2)1:poly(Connectivity, 2)2	-6.93	107.17	916.31	-0.06	0.95	
poly(ACF, 2)2:poly(Connectivity, 2)2	331.36	77.67	1336.52	4.27	0.00	***

D.3 Model validation

Section describing the validation of the best-ranked model. Diagnostic plots (Figure 5), Pearson correlation between the explanatory continuous variables (Table 7), and the variance inflation factor (Table 8), were used to validate the model.

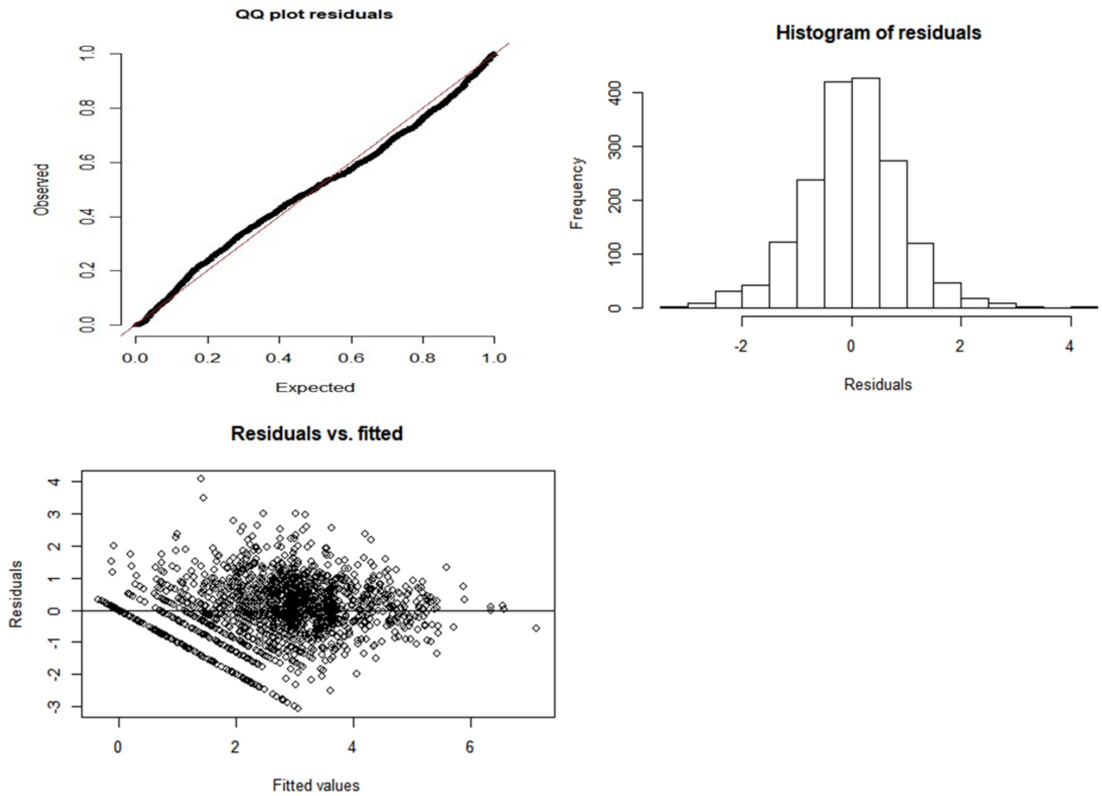

Figure 5 Diagnostic plots

Diagnostic plots for the best-ranked model. The Q-Q plot shows a small deviation from the theoretical normal line. The residuals show a normal distribution. And there is no clear pattern in the representation of the residuals vs fitted values. So this reveals that there is no violation of the assumptions of normality and homogeneity.

Table 8 Pearson correlation between explanatory continuous variables

Table showing the Pearson correlation between the continuous variables used to explain the total abundance of bees in the models. Typically, values above 0.7 are considered an indicator of collinearity between variables (Zuur et al. 2009).

Pearson correlation	ACF	Simpson	Connectivity
ACF	1.00	0.55	0.35
Simpson	0.55	1.00	0.10
Connectivity	0.35	0.10	1.00

Table 9 Variance inflation factors for each explanatory variable

Variance inflation factors (corvif function, Zuur et al. 2009) for the dataset used to model the effect of the landscape context on total abundance of bees. GVIF is the generalized variance inflation factor. Collinearity between the explanatory variables can cause an inflation of the SE, GVIF scaled by the degrees of freedom provides an indication of how much this is likely to happen, values above 3 indicates a medium degree of collinearity between variables.

Explanatory variable	GVIF	Df	$GVIF^{0.5Df}$
LUI	1.17	5	1.02
ACF	1.79	1	1.34
Simpson	1.49	1	1.22
Connectivity	1.20	1	1.10

Appendix E PREDICTS data sources

This is the list of references that provided data for the PREDICTS database and were used in this study as a source of information on biodiversity of bees.

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