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Crop diversity in the landscape boosts pollinators and yield of pollinator dependent crops across the world.

Tuanjit Sritongchuay[a,b,c,*], Michael Beckmann[a,d], Bo Dalsgaard[e], Alexandra-Maria Klein[b,f], Angela Lausch[a,g,h], Anders Nielsen[i], Julia Osterman[b,j,k], Peter Selsam[l], Kanuengnit Wayo[m,n], Ralf Seppelt[a,h,o,p]

[a] Department Computational Landscape Ecology, UFZ – Helmholtz Centre for Environmental Research, Permoserstr. 15, Leipzig 04318, Germany
[b] Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Stefan-Meier-Strasse 76, Freiburg 79104, Germany
[c] Department of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences, Postboks 5003 NMBU, Ås 1432, Norway
[d] Chair of Environmental Planning, Brandenburg University of Technology Cottbus-Senftenberg, Erich-Weinert-Str. 1, Cottbus 03046, Germany
[e] Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, Øster Farimagsgade 5, bygning 7, Copenhagen Ø 1353, Denmark
[f] Centre for Environmental and Climate Science, Lund University, Sölvegatan 37, Lund 22362, Sweden
[g] Institute for Geoinformation and Surveying, Department of Architecture, Facility Management and Geoinformation, Bauhausstraße 8, Dessau 06846, Germany
[h] Institute of Geoscience & Geography, Martin-Luther-University Halle-Wittenberg, Von-Seckendorff-Platz 4, Halle 06120, Germany
[i] Norwegian Institute of Bioeconomy Research (NIBIO), P.O. Box 115, NO-1431 Ås, Norway
[j] Department of Biological and Environmental Sciences, University of Gothenburg, Medicinaregatan 7 B, Gothenburg 41390, Sweden
[k] Gothenburg Global Biodiversity Centre, University of Gothenburg, Medicinaregatan 7 B, Gothenburg 41390, Sweden
[l] Department Monitoring and Exploration Technology, UFZ –Helmholtz Centre for Environmental Research, Permoserstr. 15, Leipzig 04318, Germany
[m] Futuristic Science Research Center, School of Science, Walailak University, Nakhon Si Thammarat 80160, Thailand
[n] Research Center for Theoretical Simulation and Applied Research in Bioscience and Sensing, Walailak University, Nakhon Si Thammarat 80160, Thailand
[o] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, 04103 Leipzig, Germany
[p] Luxembourg Centre for Socio-Environmental Systems (LCSES) University of Luxembourg 7 Av. des Hauts-Fourneaux 4362 Esch-Belval Esch-sur-Alzette, Luxembourg

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ABSTRACT

There is a global concern about the decline of wild pollinators and the ecosystem services they provide. Although land-use change is a major threat to biodiversity, it is still poorly understood how land-use heterogeneity (or land-use structure) impacts pollinator communities and entomophilous crop production. Based on a literature review, we performed a meta-analysis to (1) assess how landscape structure, both composition and configuration, affects pollinator species richness and abundance, and (2) examine the impact of landscape structure on the production of key entomophilous crops. We extracted information on pollinator communities and crop production from 101 studies with a total of 920 site replicates distributed widely across the globe. To obtain landscape structure (total area of all crops, crop diversity, and landscape Shannon's Diversity Index) information, we sourced data from the database Map-SPAM as well as satellite images. We found that pollinator species richness increased with the number of crop species in the surrounding area. Pollinator abundance increased with the number of different crops but decreased with increasing agricultural area in the surrounding landscape. Crop production of several crops was associated with landscape heterogeneity. Notably, fruit set increased with an increasing number of crop species in neighbouring fields and decreased with increasing agricultural area, that is, when nature is substituted with agriculture in the surrounding landscape. We also found positive correlations between edge density of an area and pollinator species richness and entomophilous crop production suggesting that edge density can be used as a landscape structure indicator to assess pollinator diversity. The effects of landscape structure were more pronounced in crops with high pollinator dependence, showing stronger relationships with both pollinator diversity and crop production. These findings highlight the importance of maintaining landscape heterogeneity through crop diversity and natural habitats to support pollinators and their services, though unmeasured factors such as intensification or local management may also play a role.

* Corresponding author at: Department of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences, Postboks 5003 NMBU, Ås 1432, Norway.
E-mail address: t.sritongchuay@gmail.com (T. Sritongchuay).

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1. Introduction

Land-use change is the most detrimental anthropogenic driver of biodiversity loss (Dicks et al., 2021; Newbold et al., 2020; Potts et al., 2010). Furthermore, land-use change e.g. changes in landscape structure and homogenization, can disrupt interactions between species before they disappear from the ecosystem or landscape (Felipe-Lucia et al., 2020; Habel et al., 2023). Consequently, the disruption of interactions can act as an "early warning signal" that can be observed before biodiversity loss occurs or can be detected (Doncaster et al., 2016). For instance, there is a growing concern about a global pollinator crisis: fewer and fewer pollinating insects are observed ((Lowe et al., 2021; Zattara and Aizen, 2021), which can lead to secondary plant extinctions and decrease in crop production due to insufficient pollination services (Garibaldi et al., 2015; Seppelt et al., 2020; Tamburini et al., 2019). Moreover, insufficient pollination, due to declines in important pollinator populations, is responsible for nutritional insecurity in many parts of the world and puts large burdens of disease on the human population in many countries due to lack of healthy food (Smith et al., 2022).

Landscape structure such as spatial arrangement and organization of different elements is decisive for pollinator habitat suitability (Martin et al., 2019). Landscape composition is characterized by the amounts of different landscape elements, whereas landscape configuration focuses on their spatial arrangement (Fahrig et al., 2011; Marja et al., 2022; Valente et al., 2023). Enhancing crop diversity, which is defined as reducing field size, increasing the richness and spatial evenness of crops grown in a landscape, and incorporating temporal diversification through more complex crop rotations, has been proposed as a strategy to reverse the negative effects of homogeneous agricultural landscapes without taking land out of crop production (Fahrig et al., 2011; Tamburini et al., 2020; Tscharntke, 2021). Diverse crop systems provide a more heterogeneous matrix of food resources and habitats for nesting and movements for pollinators and biodiversity in general (Magrach et al., 2023). Consequently, increased crop diversity, as a measure of landscape heterogeneity, may support higher pollinator diversity and densities, particularly in insect-pollinated crops (Aguilera et al., 2020; Kennedy et al., 2013; Priyadarshana et al., 2024; Sirami et al., 2019). Similarly, it has been suggested that increasing the farmland configurational heterogeneity, for example by reducing field size, may also promote biodiversity in agricultural landscapes (Garibaldi et al., 2023; Hass et al., 2018; Martin et al., 2019; Sirami et al., 2019).

Previous studies have shown that at the regional scale, declines in pollinator abundance and species richness have been recorded in Western Europe and North America, while there is a striking lack of studies addressing the trends and drivers of pollinator loss in tropical ecosystems (Breeze et al., 2016). A decline in pollinator abundance can limit crop production at both continental and global scales (Garibaldi et al., 2016, 2009; Moreaux et al., 2022; Reilly et al., 2024; Siopa et al., 2023). However, the consequences of these changes for crop production depend on the degree to which crops rely on animal pollination. In crops with high pollinator dependence, variation in pollinator communities driven by landscape context can have a pronounced effect on yield. By contrast, crops with low pollinator dependence may be less sensitive, as yields can often be maintained through self-pollination or wind pollination, even if pollinator communities are diminished (Adamidis et al., 2019). Small field sizes and high crop richness at the landscape scale resulted in high yield values across crops in Spain (Magrach et al., 2023). However, the only study that investigated the impacts of landscape crop diversity on pollination, found no effect of crop diversity on seed-set of phytometer plants (Hass et al., 2018). Yet, it has not been tested whether decreasing field size results in more pollinators and crop production. Although it has been suggested that an increase in landscape crop diversity supports higher biodiversity (Raderschall et al., 2021), there is still a lack of knowledge on how increased landscape crop diversity benefits pollinator densities, pollination and production of entomophilous crops at the global scale.

Therefore, there is a need to improve our understanding of how landscape composition and/or configuration affect pollination services and crop production. Our main aim is to investigate whether increasing crop diversity in agricultural areas can be an effective approach to supporting pollinators and pollination services. Knowledge of the relationship between crop and pollinator diversity would greatly benefit from a synthesis of multiple studies across species, regions, study designs, and land cover. This study identifies studies on pollinator abundance or richness and crop production via a systematic literature review and assesses the relationship between different aspects of landscape structure on pollinator diversity, pollinator abundance, and pollination services. We use indices of landscape structure, both composition (i.e. crop species richness, Shannon's Diversity Index, and total area of all crops) and configuration (i.e., homogenous zone area, neighbour frequency, edge density, and boundary diversity) as predictors to test the following hypotheses: (1) Pollinator richness and abundance are higher at sites surrounded by a higher landscape composition and configuration (2) Production of key crops will be higher at sites with higher landscape composition and configuration.

2. Materials and methods

2.1. Literature search and screening protocol

To obtain data on the relationship between pollinator diversity and entomophilous crop production we conducted a systematic review of the literature on crop production published in research articles worldwide. The review was structured using the four stages of the PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analysis) guidelines: identification, screening, eligibility, and inclusion of case studies (Moher et al., 2009). We performed a Web of Science search of the Science Citation Index Expanded (SCI-EXPANDED) on 5th October 2022 using the criteria '*(("pollinator" AND ("richness" OR "diversity" OR "abundance")) OR* "pollinat*" *OR "pollinat* network*") AND ("crop" AND "yield")*' in all fields. This gave a total of 287 results.

In the identification and screening phase, we selected studies that appeared to be suitable for analysis based on their titles and abstracts, without conducting a more detailed assessment. In the eligibility phase, the selected studies were checked for eligibility on the basis of: (1) they included data on pollinator (defined here as a pollinator visitor) diversity and/or community-level pollination networks. For instance, the studies focusing on only hoverfly or only one leafcutter bee species were excluded; and (2) a measurement of crop production in response to pollination treatments in different unit measures (i.e., a measure of fruit set of pollination treatments, berry weight, number of fruits, and kg per hectare, among others).

Finally, we included studies identified as potentially relevant (123 studies) with, apparently, complete and accurate datasets, and the authors were contacted to obtain the raw data (see Fig. S1). For each case study, we incorporated the following information at each study site: pollinator abundance; species richness; at least one variable to describe crop production. We were able to obtain complete and accurate datasets from 101 studies.

2.2. Extraction of pollinator richness, abundance and production measure

The data on pollinator abundance and richness were extracted from 101 studies (see Fig. 1A and B for the global distribution of the studies). Sampling techniques (pan traps, sweep nets, transects, focal observations), duration, frequency, sampled field sites, and targeted pollinator species were noted. We recognize that species richness and abundance are generally positively correlated. However, as our meta-analysis relies on published summary data from a wide range of studies with heterogeneous methods and without access to species-level raw data, rarefaction was not feasible. To investigate the impact of pollinator diversity and landscape structure on crop production, data were collected in different units of measure (i.e., a measure of fruit set of pollination treatments, berry weight, number of fruits, and kg per hectare, among others). The degree of pollinator dependence of each crop type was classified as low or high according to Klein et al. (2007) and Aizen et al. (2008). The low dependence category included crops in which either fruit or seed number or weight decreases < 40 % in the absence of pollinators, in this study strawberry and oilseed rape, and sunflower whereas the high dependence category included crops in which either seed or fruit number or weight decreases > 40 %, here apple, blueberry, cherry, and coffee.

2.3. Land-use diversity characterization

To identify possible effects of landscape composition and configuration on pollinator communities and crop production, we conducted two complementary types of landscape characterization using data from both Map-SPAM 2010 (Yu et al., 2020) and Landsat (Wulder at al., 2019).

First, landscape composition was assessed using Map-SPAM, which provided the data of land use such as crop types. The physical area of 42 crops was obtained from Map-SPAM 2010 (Yu et al., 2020) for year 2010. This measure represents the total area of land covered by each crop species, with a resolution of 5 arc minutes (about 81 square kilometres at the equator). Ground truthing was not conducted in this study. However, in Map-SPAM, the regional-level quantitative validations were done when third-party independent crop maps were available. Among the limited third-party independent spatial crop distribution data, the Cropland Data Layer (CDL; https://nassgeodata.gmu.edu/CropScape/, last access: 11 December 2020) is a crop-specific land cover dataset created for the continental United States using moderate-resolution satellite imagery and extensive agricultural ground truth, which has been applied to validate the SPAM2010 product at the regional scale by correlating the grid-level crop area. The results indicated a high degree of accuracy in the SPAM2010 estimates, with correlation coefficients (R^2) ranging from 0.53 to 0.78 which suggest that SPAM2010 effectively captures regional crop distributions (Yu et al., 2020). Sixteen studies conducted in the United States benefited from the quantitative validations. Three types of landscape structure: Shannon's Diversity Index (SHDI) calculated for crop types; crop species richness (number of crop types); and total area of all crops were calculated from the Map-SPAM 2010 dataset. Crop species richness, Shannon's Diversity Index (SHDI), and total area of all crops were chosen as key indicators of landscape composition because they describe the types, diversity, and abundance of elements within a landscape. All landscape structure types were calculated in four nearby grid cells (about 400 square kilometres at the equator) for each studied field site (Fig. 1C). The SHDI metric quantifies the diversity of landscape fragments and is equal to 0 when there is only one crop type in the landscape and increase with the amount of different fragment crop types or the proportional fragment distribution of distinct crops. The SHDI has been shown to be an appropriate indicator to assess landscape texture (heterogeneity), and is positively related to biodiversity (Griffith et al., 2000).

Second, landscape configuration was characterized using Landsat satellite imagery from the Landsat 5 through 9. Landsat data has long term temporal records allowing us to retrieve the data as close as possible to the time of data collection. The segmentation from Landsat data achieves a much higher spatial resolution. We used Landsat data (Wulder et al., 2019) with a spatial resolution of 30 × 30 m provided by the USGS – RS (remote sensing) data portal (https://earthexplorer.usgs.gov/). Two criteria had to be fulfilled by Landsat datasets to be useful for our analysis:

1) data had to be retrieved as close as possible to the time of the data collection of the individual studies included in the meta-analysis (2011–2022);
2) to ensure statistical confidence in inferring landscape structure from RS data, all Landsat datasets with less than 25 % cloud cover were loaded, and then images with clouds within 5 km radius of the field site of each meta-study sites discarded.

In most cases, three data sets per summer season (May to October) could be analysed. This captures the main growing season in much of the northern hemisphere which covers more than 70 % of field sites. This window may not fully represent early-season crops (e.g., oilseed rape, winter cereals) or crop calendars in the southern hemisphere. The algorithms for deriving landscape configuration from RS data provided the indicators 1) homogenous zone area; 2) relation (hereafter called neighbour frequency); 3) edge density; 4) boundary diversity (see Table 1, see also ESIS-documentation and tool (Selsam et al., 2024, 2023)). These metrics were chosen as they provide information about the spatial arrangement, relationships, and complexity of different elements within a landscape.

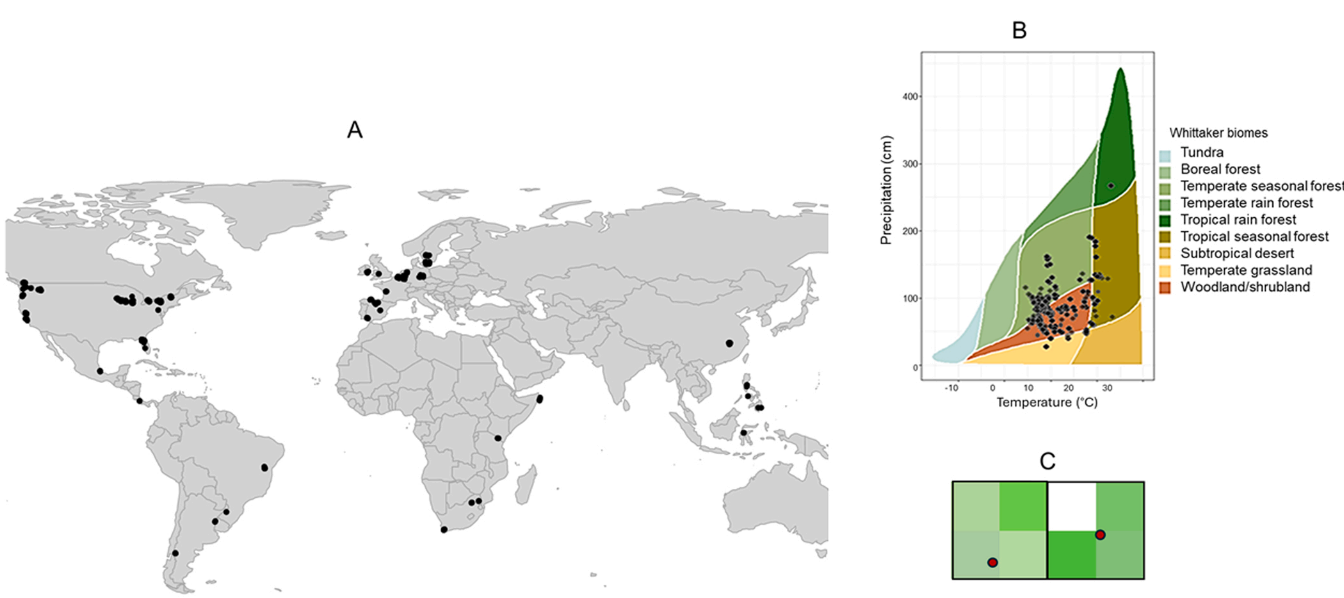

Fig. 1. Locations of sites included in the meta-analysis. (A) Sites that were extracted from 101 studies. (B) Illustrates the distribution of sites and cases across climate zones in a Whittaker plot classified base on temperature and precipitation. (C) Example of the four nearby grid cells (ca. 400 km² each) for each studied field site.

For each field site, we first defined segment of a surrounding landscape by combining four adjacent grid cells (totaling approximately 400 km^2). Segments are contiguous areas of the image with largely identical spectral pixel characteristics analogous to the OBIA (Object Based Image Analysis) concept (Blaschke, 2010). An area of 400 square kilometres was evaluated for each measuring point. These segments averaged about 3 ha in area (≈30 pixels each), yielding roughly 15,000 segments per 400 km^2 landscape. The boundaries follow the maximum spectral pixel contrasts in the image. This process depends only on the spectral image features and a parameter for the average size of the zones (Fig. 2). An iterative "watershed" process (Vincent and Soille, 1991) was used to generate these zones. Each step combines the most locally spectrally similar pixels under a common ID. A threshold prevents extreme combinations. The threshold is the mean contrast of all pixels in the image. The first principal component of all normalized brightness differences ((a-b)/(a+b), where a and b are brightness value from two spectral bands of the same pixel, is used as "contrast". Normalisation promotes differentiation in dark areas of the image. The principal component enhances the effect of contrasts that occur in only one spectral channel.

We used pairwise meta-analysis to estimate pooled effects from low and high levels of landscape characteristics to account for potential non-linear or threshold ecological responses, and to reduce the influence of outliers and heterogeneity in crop production data. We first categorized the land-use classes based on the frequency distribution of each landscape characteristic by calculating the median. We defined two broad classes of land-use diversity: “low” if the landscape characteristic value was lower than the median, and “high” if the landscape characteristic value was higher than the median. The distribution plots of all landscape characteristics were provided in Fig. S3.

2.4. Statistical analyses

All analyses were conducted in R version 4.1.2 using the package metafor version 3.0–2 (Viechtbauer and Viechtbauer, 2015). In our initial analysis, we evaluated both continuous and categorical representations of the landscape variables. The effect may not change smoothly across the full range but instead shows a threshold or step-change. In some study cases, there were a very limited number of study sites. In addition, crop production responses contained several influential outliers. Together, these factors reduced the robustness of models using continuous predictors, which did not reveal consistent or statistically significant trends. Given these limitations, we proceeded with categorical representations of landscape variables in the main analyses. The methodology and results of the continuous-variable analyses are provided in Appendix 2. Because studies reported crop production using different units (fruit set, berry weight, fruit counts, yield per hectare, etc.), we standardized all measures by calculating comparable effect sizes to enable meta-analytic synthesis. We used Hedges’ g, an unbiased, weighted standardized mean difference (denoted as d), as the effect size metric in our meta-analysis, calculated using the escalc function in metafor. The d values are reported, as these correspond directly to the values provided by escalc. Effect sizes were calculated for each comparison (low vs high of landscape variables) in the dataset. We initially composed a correlation matrix to identify correlations between all landscape indices from remote sensing and Map-SPAM using Pearson’s correlation tests (Fig. S4). We used multilevel meta-analytical models with study ID and Whittaker biome as a random effect to calculate the grand mean effect as well as the means (calculated using the “rma.mv” function in metafor). Using study ID as a random effect accounts for the non-independence of multiple observations within the same study. Restricted maximum likelihood approach (REML) was used to estimate the parameters of the meta-analysis models. To determine the effect of pollinator dependency, we used t-tests to compare effect size between low and high pollinator dependency. Spatial autocorrelation was checked by using Moran’s I (Gittleman and Kot, 1990) with the

Table 1
Landscape structure indicators derived from Map-SPAM and Landsat time series.

Indicator	Description	Formula
Shannon’s Diversity Index (SHDI)	Landscape diversity indices, combining evaluations of both richness and evenness. Interpretation: The larger SHDI index, the more diverse the landscape.	$1-\sum_{i=1}^{N} p_i \ln(p_i)$ N: the number of land cover types (crop type) p_i: the area of the ith crop type
Crop species richness	The number of land cover types (crop species types)	N: the number of land cover types (crop species types)
Total area of all crops	Total area covered by crops	$\sum p_i$ pi: the area of the ith crop type
Homogeneous zone area	Logarithm of the largest area of a homogeneous zone in the Landsat image, i.e., a field. Interpretation: The larger the area of a homogeneous zone, the less diverse the landscape.	$ln(A)$ A: area of zone
Relation (Neighbour frequency)	The ratio of the perimeter p of a homogeneous zone and the number of its neighbours n. Interpretation: The more neighbours a homogeneous zone has, the smaller is the value. The smaller the value, the more diverse the landscape.	p / n p: perimeter n: number of neighbours
Edge density	Ratio of perimeter p and area A of a homogeneous zone. Interpretation: Small, thin or finger-shaped zones have large values of edge density, compact, circular zones have small values. Thus, edge density integrates size and shape of a homogeneous zone. Edge density is a shape indicator that describes local landscape diversity.	p / A p: perimeter A: area of zone
Boundary diversity	Diversity returns the multispectral distance from a given location to all neighbouring zones. For each neighbouring zone, the distance is scaled by the length of the common boundary. Each multispectral distance is calculated as the first principal component of all differences between equal bands of the two zones. The diversity of the zone of interest is the mean of all contributions. Interpretation: Diversity depends on the spectral difference and on the shape of the zones. Long boundaries with low differences will have the same effect as short boundaries with large differences.	$\sum_{i=1}^{n} p_{0,i}\sqrt{(v_0-v_i)^2}$ v_0: Spectral values zone of interest v_i: spectral values neighbouring zones $p_{0,i}$: common edge between zone of interest 0 and neighbouring zone i n: number of neighbours

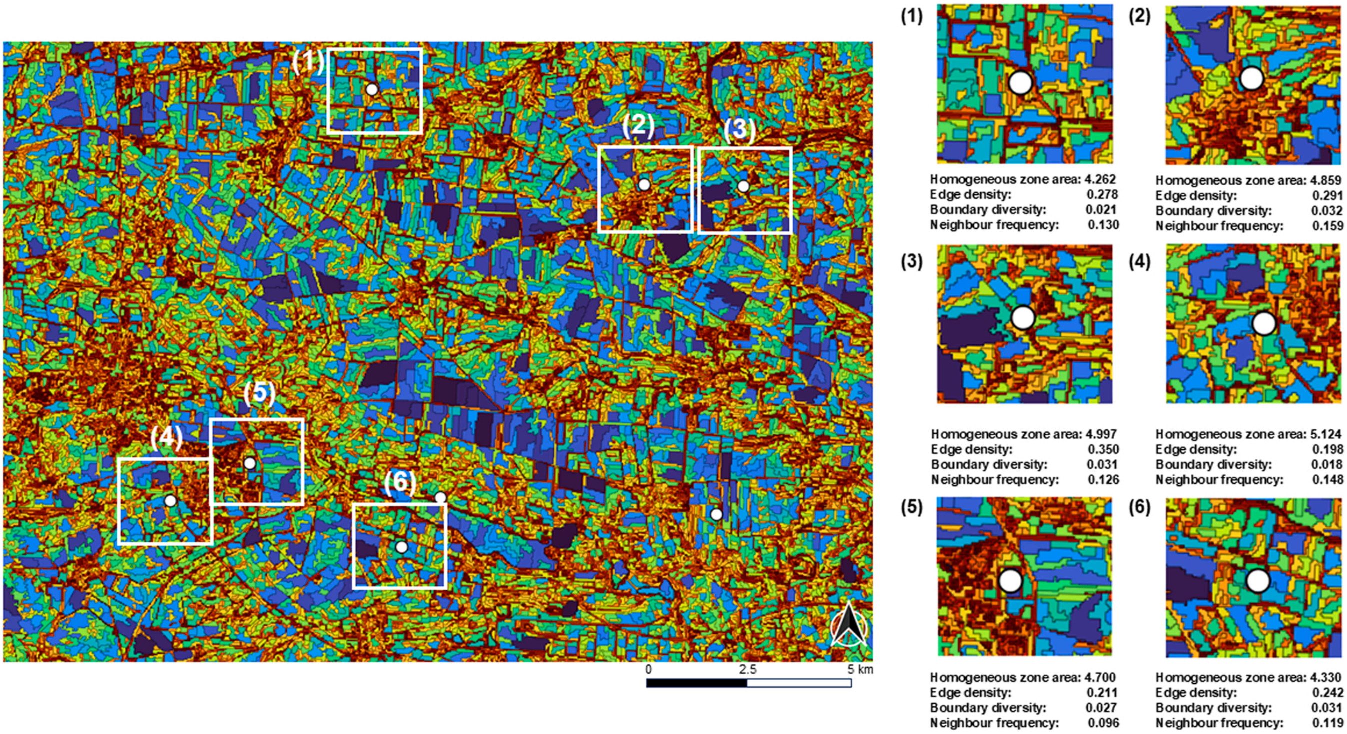

Fig. 2. Representation of the shape indicator for the French meta-study, as well as study examples and their further indicators for the region (1–6), including: 1) homogeneous zone area (logarithm of the largest area of a homogeneous zone); 2) edge density (ratio of perimeter and area of a homogeneous zone); 3) boundary diversity (diversity returns the multispectral distance from a given location to all neighbouring zones); 4) neighbor frequency (the ratio of the perimeter of a homogeneous zone and the number of its neighbours.

"ape" package (Paradis and Schliep, 2019), and no significant spatial autocorrelation was found (P > 0.05 in all models).

3. Results

From 101 studies (total 920 individual site replications), more than 70 percent of studies (72 studies) were conducted in North America and Europe. We found less than 20 percent of studies (19 studies) from Africa or Asia (Fig. 1). Overall, pollinator species richness positively correlated with crop species richness (d = 0.47, 95 % CI = 0.11–0.82; Fig. 3) and landscape Shannon's Diversity (d = 0.27, 95 % CI = 0.08–0.45; Fig. 3). Pollinator species richness did not show correlations with total area of crops (Fig. 3). Pollinator abundance positively related with crop species richness (d = 0.42, 95 % CI = 0.18–0.66; Fig. 3). In contrast, pollinator abundance negatively correlated with total area of all crop species (d = −0.32, 95 % CI = −0.62 to −0.02; Fig. 3). Pollinator abundance did not show correlations with landscape Shannon's Diversity (Fig. 3). Crop production positively related to both landscape Shannon's Diversity (d = 0.46, 95 % CI = 0.11–0.77; Fig. 3), and crop species richness (d = 0.30, 95 % CI = 0.01–0.58; Fig. 3). In contrast, crop production negatively related to total area of all crop species (d = −0.91, 95 % CI = −1.21 to −0.61; Fig. 3).

Regarding the indicators from remote sensing, pollinator species richness showed a positive relation to edge density (d = 0.49, 95 % CI = 0.20–0.76; Fig. 3) but negative relation to homogenous zone area (d = −0.31, 95 % CI = −0.54 to −0.02; Fig. 3). The effect of edge density on pollinator species richness was higher in crops with high pollinator dependence (P < 0.05; Fig. 4). Pollinator species richness showed a positive correlation with edge density in crops with high pollinator dependence (d = 0.45, 95 % CI = 0.10–0.83; Fig. 4) while the correlation was not significant in crops with low pollinator dependence (Fig. 4). Pollinator abundance showed negative relation to neighbour frequency (d = −0.51, 95 % CI = −0.70 to −0.33; Fig. 3) and edge density (d = −0.27, 95 % CI = −0.54 to −0.01; Fig. 3). The effect of neighbour frequency on pollinator abundance was higher in crops with high pollinator dependence (P < 0.05; Fig. 4). Pollinator abundance showed a negative correlation with neighbour in crops with high pollinator dependence (d = −1.03, 95 % CI = −1.43 to −0.66; Fig. 4) while the correlation was not significant in crops with low pollinator dependence (d = −0.09, 95 % CI = −1.04–0.86; Fig. 4). Crop production showed a positive relation to edge density (d = 0.44, 95 % CI = 0.15–0.71; Fig. 3) but negative relation to homogenous zone area (d = −0.41, 95 % CI = −0.63 to −0.18; Fig. 3). The effect of homogenous zone area on crop production was significantly different between high and low pollinator-dependent crops (P < 0.05; Fig. 4). Homogenous zone area showed a negative correlation with crop production in crops with high pollinator dependence (d = −0.66, 95 % CI = −0.99 to −0.3; Fig. 4) while the correlation was not statistically significant in crops with low pollinator dependence (Fig. 4). Crop production did not show correlations with neither neighbor frequency nor boundary diversity.

4. Discussion

We found that, at a global scale, landscape structure, both composition and configuration, increased pollinator species richness and abundance, and crop production. Especially smaller agricultural fields with high edge density and small homogeneous zone areas were associated with more pollinator richness and higher crop production. This supports the hypothesis that crop diversification is an important measure to support pollinator communities and associated crop production. Although our results demonstrate the agricultural benefits crop diversification could have, the extent to which farmers adopt these practices is limited (Duru et al., 2015).

Landscape composition such as crop species richness, total crop area, and landscape diversity, was strongly associated with crop pollinators (both abundance and species richness) and crop production. Species richness and abundance are generally positively correlated, suggesting that they are not fully independent. Although analyzed separately to

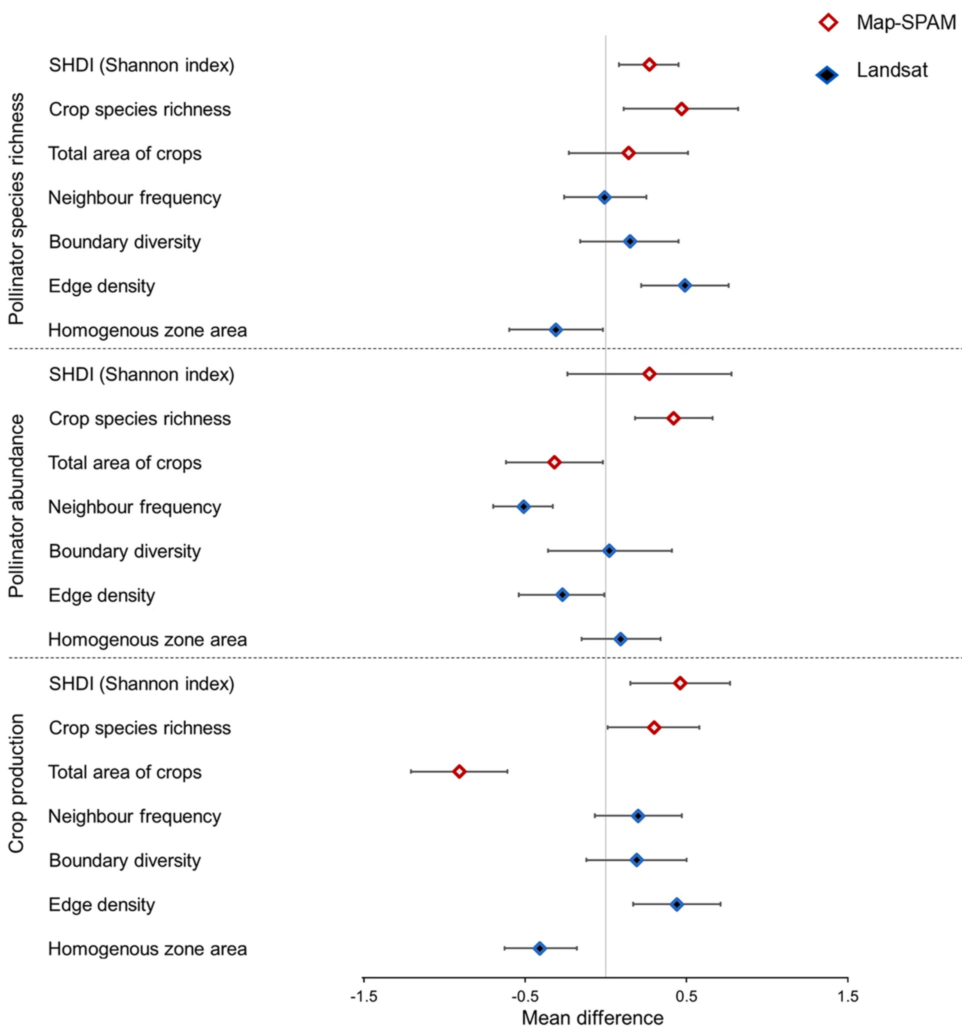

Fig. 3. Hedges' g values ± 95 % confidence intervals for effects of landscape variables on pollinator species richness, pollinator abundance, and crop production. The landscape variables included: 1) Shannon's Diversity Index (landscape diversity indices, combining evaluations of both richness, and evenness); 2) Crop species richness (the number of crop types); 3) Total area of all crops (total area covered by crops); 4) Neighbour frequency (the ratio of the perimeter of a homogeneous zone, and the number of its neighbours); 5) Boundary diversity (diversity returns the multispectral distance from a given location to all neighbouring zones); 6) Edge density (ratio of perimeter and area of a homogeneous zone); 7) Homogeneous zone area (logarithm of the largest area of a homogeneous zone in the Landsat image).

investigate potentially distinct patterns, their interrelationship should be taken into account when interpreting the findings. The positive correlation between number of crop types and pollinator richness and abundance is congruent with other observations showing that wild bee densities increase with larger numbers of crop types (Hass et al., 2018). Our findings are consistent with previous meta-analyses that report positive correlations between animal species richness and crop diversity, which are related to plant species richness (Kral-O'Brien et al., 2021). This may imply that more heterogeneous landscapes, with higher number of crop species (average of 10 crop types within 5 km radius), can support more abundant and diverse pollinator communities and might be able to yield higher crop production. However, some studies showed that the pollinator communities are unaffected (Fahrig et al., 2015) by a larger number of crop species and instead respond positively to landscape configuration (i.e., smaller mean field sizes (Magrach et al., 2023)). Total crop area was negatively associated with pollinator abundance and crop production. This pattern might be due to a possible reduction in natural and semi-natural areas in landscapes with high total crop area. Previous studies have shown that biodiversity in crop fields is more dependent on the presence of semi-natural field boundary habitats such as semi-natural grassland which are important for many pollinator groups including wild bees and honey bees (Dicks et al., 2021; Raderschall, 2021; Eeraerts, 2023; Johansen et al., 2019; Ricketts et al., 2008). We found that increasing crop species richness and landscape diversity is positively associated with higher pollinator richness, pollinator abundance, and importantly crop production at a global scale. This aligns with the well-established role of pollinators in supporting seed and fruit development in many crops, such as apples (Osterman et al., 2021). We also assessed the direct relationship between pollinator abundance/diversity and crop yield; however, these results were not statistically significant (Fig. S7). Nevertheless, we acknowledge that these landscape patterns may reflect broader processes such as agricultural intensification, which can involve additional factors such as pesticide use, loss of semi-natural habitats, and field expansion. Thus, while landscape composition appears to be a key correlation of both pollinator communities and crop production, it may serve as a proxy for more complex underlying drivers.

Landscape configuration is considered a key factor influencing the structure of pollinator communities (Martin et al., 2019). For this study, four spatial arrangements (homogenous zone area, boundary diversity, edge density, and neighbour frequency) were tested. We found that edge density which is a shape indicator describing local landscape diversity and the amount of homogeneous zone areas have impacts on pollinator communities and pollinator-dependent crop production. Higher edge

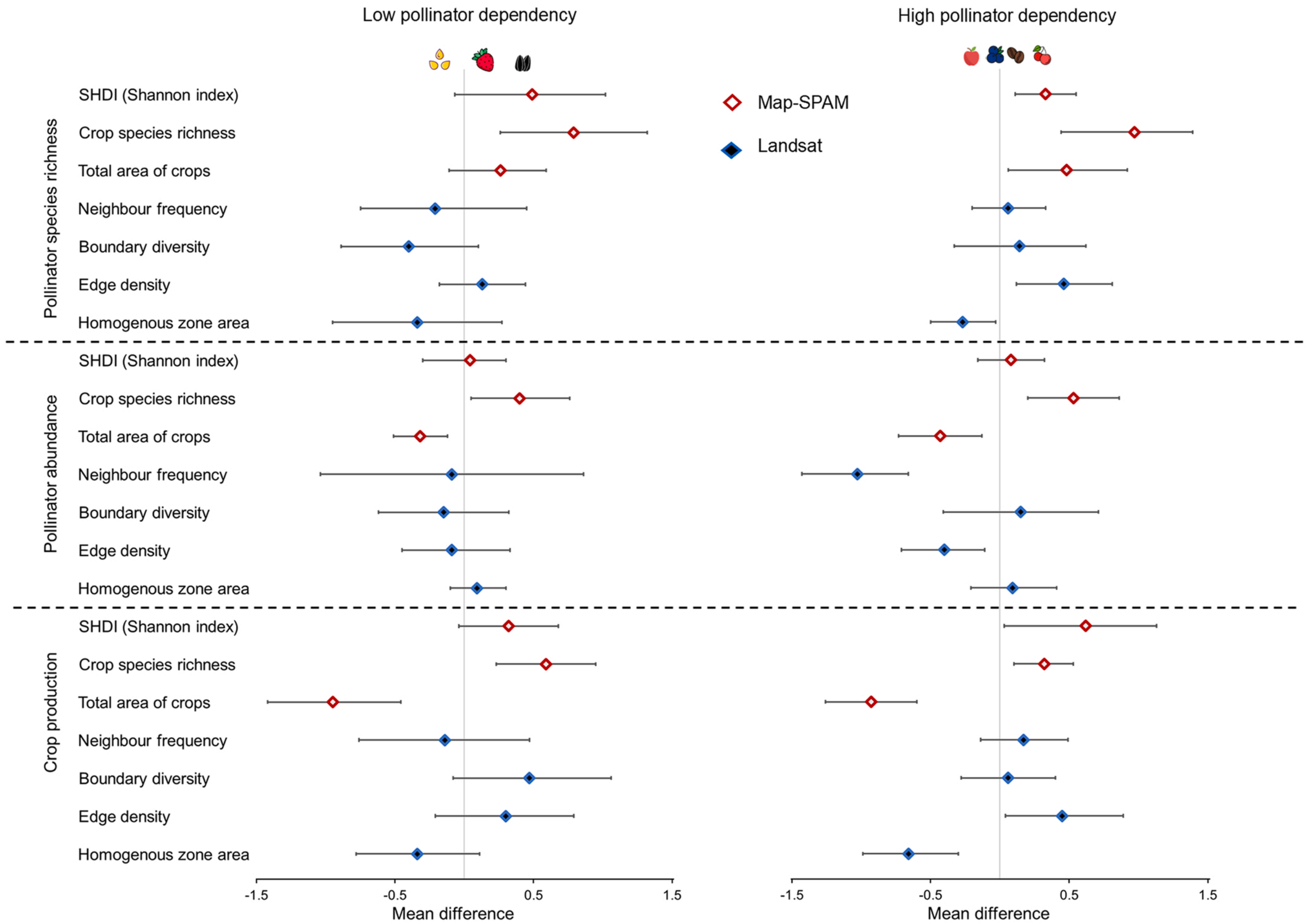

Fig. 4. Hedges' g values ± 95 % confidence intervals for effects of landscape variables on pollinator species richness, pollinator abundance and crop production in low and high pollinator-dependent crops. The low dependence category includes strawberry, and oilseed rape whereas the high dependence category includes apple, blueberry, cherry, coffee, and sunflower.

density (small, thin or finger-shaped zones) provides higher pollinator species richness and crop production. Conversely, crop production was higher in sites with less homogeneous areas. These results are consistent with our hypotheses, namely that species in landscapes with small crop fields benefit from easy access to field boundary habitats (Merckx et al., 2009). In addition, larger fields with low edge density tend to be managed more intensively, with more frequent tillage and more frequent use of fertilizes and pesticides (Hammond et al., 2006; Larsen and Noack, 2021) leading to lower pollinator abundance and potentially lower crop production. Previous studies have shown that crop diversity may enhance crop production of non-entomophilous crop (wheat and barley) driven by soil properties and pest control (Duflot et al., 2022). However, we found that the magnitude of both the effect of local crop diversity and the amount of homogeneous area on pollination services varies with the degree of pollinator dependence of the focal crop. For instance, while neighbour frequency and homogenous zone area showed no effect on the production of crops with low pollinator dependency, it negatively affected pollinator abundance and production of crop production with a high pollinator dependency. Over the last decades there has been an increase in pollinator dependance in global agriculture and therefore a parallel increase in agricultural diversification and more diversified agricultural landscapes can be means to make food production more pollinator-friendly while at the same time producing more food (Aizen et al., 2019).

In this global synthesis, we show that high crop diversity is beneficial for pollinators and crop production, possible through higher pollination services provisioning. In addition to crop diversification including field size reduction, surrounding areas with small, thin or finger-shape edge habitats could mitigate pollinator decline. We have shown that the edge density can serve as a useful proxy of habitat heterogeneity which is associated with pollinator diversity in agricultural landscapes. Our findings have important implications for conserving pollination services in agricultural landscapes and can contribute to better landscape design directives. Carefully designed agricultural landscapes may thus affect the productivity of many crops, affecting farmers' economy, food security and ultimately human well-being. The local scale attributes, such as shape diversity and the area of homogeneous zones, clearly influence pollinator communities and crop production. The expansion of monoculture crops beyond the field scale, resulting in large areas of homogeneous landscapes in many parts of the world, has serious ecological implications for the conservation of biodiversity and the sustainability of ecosystem services in agroecosystems (Garibaldi et al., 2021). Practices such as growing mass-flowering crops in large area may lead to a dilution of pollinator foraging density and therefore a reduction in pollen deposition in crops. Although we did not find the pollinator dilution effect in this study (Fig. S6), we suggest the future study should explicitly assess how mass-flowering crop area interacts with surrounding landscape structure such as semi-natural habitat availability to influence pollinator richness, abundance, and pollen deposition at larger scales. The smallholder-dominated landscapes often produce and maintain landscape complexity with high levels of agricultural and wild diversity (Lesiv et al., 2019). Yet these farmers and their mixed farming systems, with critical contributions to regional and global food and nutrition security (Duru et al., 2015), are often put under pressure by socio-economic drivers and are being replaced by conventional, high-input large-scale monocultures. Hence, it is necessary to enhance and value farms and landscapes' multifunctionality and actively manage these for production, biodiversity, human well-being, and overall ecosystem resilience (Tscharntke, 2021). While our analyses highlight the role of landscape structure in supporting pollinators and crop production, we acknowledge that other unmeasured factors, such as agricultural intensification, pesticide use, or soil management, may also influence these patterns. Recognizing these additional pressures emphasizes the importance of the land-sharing approach, which integrates biodiversity conservation into agricultural landscapes (Phalan et al., 2011; Tscharntke et al., 2012). Future studies incorporating detailed management data would help clarify these effects. In addition, national and international efforts must be better aligned to repurpose incentives and policies supporting sustainable agriculture.

CRediT authorship contribution statement

Alexandra-Maria Klein: Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Bo Dalsgaard:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Anders Nielsen:** Writing – original draft, Methodology, Conceptualization. **Angela Lausch:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Ralf Seppelt:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Michael Beckmann:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Tuanjit Sritongchuay:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Peter Selsam:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Julia Osterman:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Kanuengnit Wayo:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109943.

Data availability

Data will be made available on request.

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