Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis

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AUTHOR CONTRIBUTIONS

T.S.P. conceived the idea, conducted the literature search, analysed the data, and wrote the first draft. B.A.W. helped with the statistics. E.A.M., C.S., E.G., C.M.-N., M.-B.L., C.A.R., L.B., A.O. and T.T. provided the necessary datasets. E.A.M., C.S., B.A.W., E.G., C.M.-N., M.-B.L., T.T., and E.M.S. edited the first draft, and all the authors worked on subsequent drafts, and gave final approval for publication.

DATA AVAILABILITY

All the data and R codes for the statistics are accessible to editors and reviewers via the Digital Repository of Nanyang Technological University (DR-NTU), at https://researchdata.ntu.edu.sg/privateurl.xhtml?token=bdb1218d-a8ee-49c5-8ac8-94aee8438a67. These data and source codes will be made publicly available upon the acceptance of the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

Biodiversity benefits from spatial heterogeneity in agricultural landscapes: A meta-analysis

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ABSTRACT

Agricultural intensification, while vital for global food production, is one of the main drivers of the widespread decline in biodiversity and associated ecosystem services. Increasing spatial heterogeneity through crop and landscape heterogeneity has been suggested to provide benefits for biodiversity in agricultural landscapes, mitigating these losses. These spatial effects can be partitioned broadly into those affecting compositional (diversity of land cover types) and configurational heterogeneity (arrangement of land cover types) for both crop and non-crop semi-natural habitats. Reported effects of these heterogeneity components on biodiversity have been mixed and are often context-dependent, reflecting unique properties of the systems, focal taxonomic groups and functional characteristics. To address this ambiguity, we synthesise current evidence using meta-analytic models across 122 studies covering 6,397 fields in Asia, Europe, North and South America. We demonstrate overall positive effects of crop and landscape compositional and configurational heterogeneity on alpha-level biodiversity (total abundance, species richness or diversity) for plants, invertebrates, vertebrates, pollinators, and pest predator species. Overall, our results suggest that both compositional and configurational heterogeneity are important drivers of agroecosystem biodiversity, but their effects vary across different taxa (invertebrates vs. vertebrates) and functional groups (pollinators vs. predators). We also find that the positive effects of these heterogeneity components are consistent for invertebrates and vertebrates, in both tropical/sub-tropical and temperate agroecosystems, annual and perennial cropping systems, and local and landscape scales. While these results reiterate the importance of semi-natural habitats for native biodiversity in agroecosystems, we show that in-field agricultural management that promotes cover type diversity can also be valuable for agroecosystem biodiversity. This may be achieved by incorporating diverse crops, diversified crop rotations through regenerative agricultural practices, and increasing connectivity between cover types

through smaller fields, increasing the overall length of field margins/edges. While this has the potential to be a win-win for biodiversity and farmers, increased heterogeneity may have practical constraints (e.g., small field sizes) that may not be compatible with some management systems. However, we demonstrate that small structural shifts in compositional and configurational heterogeneity compatible with commercial farming systems may have significant value for native biodiversity.

INTRODUCTION

The intensification of agriculture has resulted in significant losses of biodiversity and associated ecosystem services (Sánchez-Bayo & Wyckhuys 2019; Zabel *et al.* 2019). This has occurred at a time when there is an urgent need to increase agricultural production to meet rising global food demands (Ray *et al.* 2013), causing additional challenges to biodiversity and the essential ecosystem services it underpins (Tilman *et al.* 2011; Díaz *et al.* 2019). The loss of ecosystem services provided by components of biodiversity (e.g., pollination, pest control, and nutrient cycling) has been shown to negatively impact yield and increase production cost (Altieri 1999; Zhang *et al.* 2007; Power 2010; Isbell *et al.* 2017; Dainese *et al.* 2019). Supporting biodiversity mediated ecosystem services may therefore have economic benefits for farmers, as well as being compatible with many government initiatives aimed at reducing the impacts of intensive agriculture, such as integrated pest management and regenerative farming approaches (Scherr & McNeely 2008; Piñeiro *et al.* 2020; Sietz *et al.* 2022). To achieve these kinds of biodiversity-friendly management policies will require innovative system-level approaches to conserving biodiversity in agroecosystems that consider not just surrounding semi-natural areas, but also the crops that make up the majority of landcover in these systems (Vasseur et al. 2013; Fahrig *et al.* 2011; Tscharntke *et al.* 2021).

Various strategies have been proposed to support biodiversity and the ecosystem services it provides in agricultural landscapes (see Perfecto & Vandermeer 2008; Pe'er *et al.* 2014; Duru *et al.* 2015; Perfecto *et al.* 2019). One of the most common strategies involves creating new natural or semi-natural habitats, which can have direct or indirect impacts by increasing landscape complexity (Gonthier *et al.* 2014; Holland *et al.* 2017; Estrada-Carmona *et al.* 2022). Yet due to real or perceived losses of cropped areas, yield and profitability, this approach may be met with resistance from farmers where subsidies are not provided (Bowman & Zilberman 2013; Rosa-Schleich *et al.* 2019). Therefore, there has been increasing emphasis on field-level crop diversification, supported through agroforestry, crop rotation, polyculture, and intercropping, which have been increasingly shown to have positive effects on biodiversity (Lichtenberg *et al.* 2017; Tamburini *et al.* 2020; Beillouin *et al.* 2021). However, the viability of these field-level practices are often highly crop specific, while their economic attractiveness and feasibility can be limited, especially for smallholders (Bowman & Zilberman 2013).

Developing new approaches to manage already existing crop and non-crop areas could offer a practical and appealing approach for farmers to contribute to biodiversity conservation (Scherr & McNeely 2008; Perfecto *et al.* 2019). Promoting spatial heterogeneity through diversity and connectivity between crop and non-crop cover types within the landscape (i.e., landscape heterogeneity) is one such approach (Fahrig *et al.* 2011). Recent studies have also increasingly focused on heterogeneity of the crop mosaic itself, while keeping the amount of non-cropped areas constant (Fahrig *et al.* 2015; Sirami *et al.* 2019; Priyadarshana *et al.* 2021). This has enabled consideration of whether promoting crop diversity and connectivity between crop fields (i.e., crop heterogeneity) could itself support increased agroecosystem biodiversity (Fahrig *et al.* 2015; Hass *et al.* 2018; Sirami *et al.* 2019; Alignier *et al.* 2020; Priyadarshana *et al.* 2021).

Spatial heterogeneity can be partitioned into two components (Fahrig *et al.* 2011): 1) the diversity of land cover types (or crops) in a given landscape, i.e., compositional heterogeneity; and 2) the arrangement of land cover types (or crops) in a given landscape, i.e., configurational heterogeneity. Although likely to be correlated (Pasher *et al.* 2013), these two components affect ecological processes independently (Fahrig *et al.* 2011). Empirical studies have shown contrasting and mixed effects of these components depending on the study taxa, their functional traits, and the spatial scales at which the landscape components are measured (Martin *et al.* 2016; Hass *et al.* 2018; Reynolds *et al.* 2018; Raderschall *et al.* 2021). In addition, other system properties such as crop identity and intensive farming techniques (e.g., application of agrochemicals, or tilling) may also affect biodiversity responses to these heterogeneity components (Hass *et al.* 2018; Martin *et al.* 2020). As a result, no consensus is currently available on the overall strength and direction of the effects of these heterogeneity components on biodiversity in agricultural landscapes (see Estrada-Carmona *et al.* 2022). There is a growing interest in grassroots social movements embracing agroecology and diversified farming systems (Rosset & Martínez-Torres 2012; Hart *et al.* 2016). However, in the absence of a consensus on the consequences of landscape-scale effects within this context, there may be many missed opportunities for agricultural public policies that aim to improve biodiversity conservation while maintaining food security and improving farmers' well-being globally.

In this study, we address this knowledge gap by assessing whether crop and landscape heterogeneity promote overall field-level (i.e., alpha-level) biodiversity across agricultural landscapes. We used a meta-analytic modelling approach considering a range of spatial scales (0.1km to 4km radius around sampled sites) that includes data across Asia, Europe, and North and South America. We assessed biodiversity responses to landscape compositional heterogeneity (number of correlations, K = 1,263 and studies, N = 80), landscape configurational heterogeneity (K = 1,164 and N = 69), crop configurational heterogeneity (K = 463 and N = 27), and crop compositional heterogeneity (K = 313 and N = 34). Using these data, we specifically test the following questions and hypotheses to understand the generality of crop/landscape heterogeneity effects on agroecosystem biodiversity:

(Q1). Do crop and landscape heterogeneity within agricultural landscapes have overall

positive effects on agroecosystem biodiversity?

Previous studies have predicted that crop and landscape compositional heterogeneity may provide complementary resources, while crop and landscape configurational heterogeneity could enhance inter-field connectivity, thereby positively impacting agroecosystem biodiversity (Dunning *et al.* 1992; Fahrig *et al.* 2011; Batáry *et al.* 2020). However, mixed results in previous studies impede the establishment of a general consensus regarding the effects of these heterogeneity components on biodiversity (see above). We addressed this issue by quantifying the average effects of crop and landscape heterogeneity on the total abundance, species richness, and species diversity of invertebrates (arthropods), vertebrates, animals (both vertebrates and invertebrates), and plants, as well as several functionally important groups within agroecosystems – invertebrate pollinators, predators (including parasitoids) and agricultural pests. In line with the above hypotheses, we expected overall biodiversity, excluding pests, would be positively influenced by the crop and landscape heterogeneity components across multiple spatial scales.

(Q2). Does the relative strength of crop heterogeneity effects, compared to landscape heterogeneity effects, vary for different taxa?

Promoting crop and landscape heterogeneity components requires distinct management practices, due to their respective effects on biodiversity (see above). We therefore tested whether certain heterogeneity components have more impact on biodiversity compared to others. Such comparisons between these components, however, have been limited in previous studies (Batáry *et al.* 2020). We expected that different taxa would respond differently to each heterogeneity component. Specifically, we hypothesised that highly mobile taxa with larger body sizes, such as vertebrates (and including birds), would have a greater dependency on both crop and non-crop resources due to their ability to utilise complex resource parcels across wider spatial scales (Redlich *et al.* 2018b; Li *et al.* 2020; Pustkowiak et al. 2021; Martínez-Núñez *et al.* 2023). They would thus more strongly benefit from landscape heterogeneity than from crop heterogeneity. Conversely, less mobile taxa with smaller body sizes, such as invertebrates and invertebrate pollinators, would benefit from diverse cover types within their home ranges (Hass *et al.* 2018; Priyadarshana *et al.* 2021; Cano *et al.* 2022; Maurer *et al.* 2022). As such, both crop and landscape heterogeneity would have comparatively similar effects on them. Also, increased configurational heterogeneity would benefit invertebrate pollinators and predators by offering more semi-natural habitats along longer field margins/edges (Fahrig *et al.* 2015; Hass *et al.* 2018; Priyadarshana *et al.* 2021; Maurer *et al.* 2022). However, for plants unable to evade disturbances within crop fields, we hypothesised that they would derive greater benefits from landscape heterogeneity. Finally, we hypothesised that agricultural pests would benefit from monocultures and so would respond negatively to increased crop heterogeneity (Baillod *et al.* 2017; Almdal & Costamagna 2023; Priyadarshana *et al.* 2023).

(Q3). Do biodiversity responses to increased crop and landscape heterogeneity within agricultural landscapes remain consistent across different climatic regions and different cropping systems?

Previous studies on biodiversity responses to increased crop and landscape heterogeneity have mostly concentrated on temperate annual crop agroecosystems in Europe and North America (Priyadarshana *et al.* 2021; Tscharntke *et al.* 2021). The global generality of crop and landscape heterogeneity to support agroecosystem biodiversity is therefore unclear. To address this, we estimated and compared the differences in biodiversity responses to crop and landscape heterogeneity for different climatic regions (i.e., tropical/subtropical vs. temperate agroecosystems) and cropping systems (i.e., annual vs. perennial crops). We expected crop and landscape heterogeneity to support biodiversity in both annual and perennial crop systems, as well as in both tropical/subtropical and temperate agroecosystems. We note that data on management techniques for these studies were highly variable, and in some instances, lacking, meaning we could not estimate how such factors alter biodiversity responses to crop and landscape heterogeneity.

(Q4). Are biodiversity responses to increased crop and landscape heterogeneity scale dependent?

As many taxa in agroecosystems depend on resources available at different spatial scales (Gonthier *et al.* 2014), we expected that biodiversity would be positively influenced by crop and landscape heterogeneity at both local-level (i.e., < 0.5km radius area) and landscape-level (i.e., ≥ 0.5km, and < 1km; ≥ 1km radius area) scales. However, due to the differences in mobility between vertebrates and invertebrates (see *Q2* above), we predicted that vertebrates would strongly respond to landscape-scale heterogeneity, while invertebrates would respond to both local and landscape-scale heterogeneity.

MATERIALS AND METHODS

Literature search

We systematically searched for studies in 'Web of Science' (apps.webofknowledge.com/) and 'Scopus' (www.scopus.com/). All available papers published up to March 2023 were screened by article titles in the English language using the following search strings: TS=("landscape heterogeneity" OR "landscape diversity" OR "landscape complexity" OR "crop heterogeneity" OR "crop diversity" OR "farmland heterogeneity" OR "farmland diversity" OR "compositional heterogeneity" OR "configurational heterogeneity") AND TS=("diversity" OR "biodiversity" OR "richness" OR "evenness" OR "abundance"). After removing duplicates from these two datasets, we retrieved 647 studies in total. We then screened the abstracts and data availability statements and found 122 studies that met the inclusion criteria listed below. The literature search procedure is summarized in a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram (see Figure S1).

Inclusion criteria

We applied the following inclusion criteria: 1) Crop heterogeneity should be measured based on individual crop types only, whereas landscape heterogeneity components should be measured using both crop (often broad crop categories such as perennial, and annual crops) and non-crop land cover types (e.g., natural, semi-natural, and water); 2) Crop or landscape compositional heterogeneity should be measured using the Shannon diversity of land cover types as $H' = -\sum_{i=1}^{n} pi \ln pi$ (Shannon 1948), or Simpson diversity index of land cover types as $D' = 1/\sum_{i=1}^{n} pi^2$ (Simpson 1949), where p_i is the proportion of land cover type i in the area (Fahrig *et al.* 2011). In both cases, these were either available from the studies or post hoc calculated from raw data. These diversity indices of land cover types effectively combine the number of cover types (cover type richness) and cover type evenness (the proportion of each of the cover types) in the landscape, and have been widely used in previous crop/landscape heterogeneity studies (e.g., Fahrig *et al.* 2015, for crops, and Redlich *et al.* 2018b, for both crops and landscape); 3) Crop or landscape configurational heterogeneity should be measured using the edge density, field margin length, or mean size of land cover types (e.g., Martin *et al.* 2019, for landscape, and Sirami *et al.* 2019, for crops); 4) Compositional heterogeneity components should not be strongly correlated with configurational heterogeneity components within each study at a particular spatial scale (i.e., Pearson's $r \leq 0.6$, Table S1). This ensures each heterogeneity component provides unique and independent information; 5) To reduce bias within included studies, we also stipulated that biodiversity should be measured in crop fields, using field-level (i.e., alpha-level) data on species richness, species diversity (i.e., Shannon diversity), or total abundance (i.e., total abundance across all species).

Data compilation

From the selected primary studies, we compiled biodiversity data at the field-level and corresponding crop and landscape heterogeneity components at various spatial scales from radii of 0.1km to 4km around sampled sites (see Table S1). We also extracted the mean cultivated land area and semi-natural area as a percentage from the total land area across study sites for a particular spatial scale. We extracted effect size measures provided in each study when they matched our requirements described below; otherwise, we calculated the effect sizes from study data (see below). Studied taxa in each study were categorised into invertebrates, vertebrates, and plants. In addition, invertebrates and vertebrates were combined into a single group as animals, as well as further categorised into respective taxonomic orders and functional groups based on the definitions provided in the original studies (Table 1). If a taxon provides ecosystem services in two functional groups, it was included in both corresponding categories (e.g., wasps as both pollinators and pest predators) (Table S1). Study systems were categorised based on the climatic region (i.e., tropical/subtropical or temperate agroecosystems), and the dominant cropping system across the sampled sites for a particular study (i.e., annual or perennial crops). Following the data availability statement, the study data was sourced from the data repositories (e.g., 'Dryad', datadryad.org/; 'Figshare', figshare.com/) or directly from the papers' Supplementary Information. When data were not publicly available, we asked the corresponding author(s) to share their data.

Our dataset covered 6,397 fields across 60 major agricultural production regions in 24 countries across Asia, Europe, and North and South America (Table S1). These landscapes consisted of 75% ± 14% (standard deviation, SD) cultivated lands and 11% ± 8% (SD) semi-natural areas on average, indicating that they were predominantly agricultural lands. The final dataset contained data on more than 200 families of invertebrates, vertebrates, and plants, including animals belonging to four functional groups (i.e., agricultural pests, agricultural pest predators, pollinators, and decomposers; however, we did not analyse decomposers due to inadequate sample size; see Table 1). In total, this dataset included and analysed 1,263 and 1,164 biodiversity responses to landscape compositional and configurational heterogeneity respectively, and 463 and 313 biodiversity responses to crop configurational and compositional heterogeneity respectively.

Effect size calculation

Since the relationships between biodiversity and crop/landscape heterogeneity were correlative, we calculated effect sizes as the Pearson's correlation coefficients (r) between each component of crop/landscape heterogeneity and biodiversity (i.e., total abundance, species richness, and species diversity). These effect sizes were then transformed using Fisher's z with a variance of 1/(N−3) (N = the number of fields sampled within each study) in order to stabilise the variances and normalize the distributions (Koricheva *et al.*, 2013; Schmid *et al.* 2020). These effect sizes were calculated separately for each taxonomic and functional group at each spatial scale across all the studies (Table S1).

Statistical analyses

The global model structure

Most of the studies included in our dataset had more than one effect size within a particular study due the computation of different compositional and configurational heterogeneity components across multiple spatial scales per taxon (see Table S1). Different studies also used different land-cover maps to compute each heterogeneity component. These maps utilised land-use classifications that define biological and agronomical (in the case of crops) habitat classifications relevant to the study regions (see Table S1). Consistent global land-use maps that have been sufficiently spatially resolved while being temporally associated with the specific studies are lacking, particularly outside of Europe and North America. As such, the use of a single mapping system to compute these heterogeneity components was not possible for the spatial scales considered in our study. Therefore, these within-study and between-study variances in the observed effect sizes should be accounted for in the meta-analytic models that estimate the average effect size due to a common intervention (i.e., increased spatial heterogeneity) (Koricheva *et al.*, 2013; Schmid *et al.* 2020). To achieve this, we gave an identifier for each study (StudyID) and each effect size (EffectSizeID) and added them into the models as random variables. StudyID accounted for any between-study variances and EffectSizeID accounted for any within-study variances (Koricheva *et al.*, 2013; Schmid *et al.* 2020). The general structure of the global model was,

'Fisher's z ~ Moderators, V, random = ~1 | (StudyID / EffectSizeID)',

where Fisher's z is the transformed Pearson's correlation coefficient between crop/landscape heterogeneity components and biodiversity metrics, and V is the sampling error variance.

Moderator analyses for research questions

To address our research questions and hypotheses (see *Q1–Q4* in the Introduction), we ran several models by including different moderators into the above global model structure.

(Q1). Do crop and landscape heterogeneity within agricultural landscapes have overall positive effects on agroecosystem biodiversity?

The effects of heterogeneity type on biodiversity

Firstly, we estimated the average effects of overall spatial heterogeneity in the landscape on biodiversity by running models considering all crop and landscape heterogeneity components together (i.e., without any moderators). These models averaged across all the effect sizes while accounting for both within-study and between-study variances. We then ran models adding the heterogeneity type (i.e., spatial compositional heterogeneity vs. spatial configurational heterogeneity) as a moderator to separately estimate the average effects of each heterogeneity type (see Table 2). In these models, the effects of both crop and landscape heterogeneity components on biodiversity were averaged together.

The effects of land-use type on biodiversity

To then investigate the effects of land-use type (i.e., crop heterogeneity vs. landscape heterogeneity) on biodiversity, we ran models with the land-use type as a moderator (see Table 2). In these models, the land-use type was averaged across the corresponding heterogeneity types, i.e., compositional and configurational heterogeneity.

The effects of individual heterogeneity components on biodiversity

Finally, we ran models with the heterogeneity component as a moderator to separate out the effects of each heterogeneity component, i.e., crop compositional heterogeneity, crop configurational heterogeneity, landscape compositional heterogeneity, and landscape configurational heterogeneity (see Table 2).

We ran these models separately for the different taxonomic groups (invertebrates, vertebrates, animals [vertebrates and invertebrates together], and plants) and functional groups (pollinators, predators, and pests). In each case, we considered the response for each biodiversity metric separately (see Table S2). We excluded agricultural pests from the invertebrate and vertebrate groups to focus our analyses on the beneficial biodiversity components within each group. To investigate the effects of crop and landscape heterogeneity on biodiversity at lower-level taxonomic groups, we also ran separate models for the five most data-abundant taxonomic orders (i.e., Araneae, Coleoptera, Diptera, Hymenoptera, Lepidoptera) in our dataset, as well as for birds.

(Q2). Does the relative strength of crop heterogeneity effects, compared to landscape heterogeneity effects, vary for different taxa?

To determine whether particular heterogeneity components have a stronger influence on biodiversity than others, we compared the estimated average effects on biodiversity for each level of the moderators in the above models using comparison tests. When the moderator included only two levels (see Table 2), they were directly compared using likelihood ratio tests. However, when the moderator had more than two levels (see Table 2), we compared each level by applying the 'Benjamini–Hochberg' procedure to control for errors associated with multiple testing (Benjamini & Hochberg 1995).

(Q3 & Q4). Do biodiversity responses to increased crop and landscape heterogeneity within agricultural landscapes remain consistent across different climatic regions, different cropping systems, and different spatial scales?

To assess whether crop and landscape heterogeneity components have varying impacts on biodiversity across different climatic regions (i.e., tropical/subtropical vs. temperate agroecosystems), different cropping systems (i.e., annual vs. perennial crops), and different spatial scales (i.e., one local-level: < 0.5km, and two landscape-levels: 0.5km, and < 1km; ≥

1km), we ran separate models including each of these three components as moderators (see Table 2), and compared each level in them following the same procedure described for *Q2*. We ran separate models in order to avoid any dependencies between each level of the moderators (Schmid *et al.* 2020). Due to data limitations (N ≤ 5), we only estimated the average effects of the overall spatial heterogeneity (i.e., crop and landscape heterogeneity components together) in the landscape across different climatic regions, and different cropping systems on animal biodiversity (vertebrates and invertebrates together). However, we estimated the effect of overall spatial heterogeneity, and the effect of each heterogeneity type (i.e., compositional and configurational heterogeneity) separately across different spatial scales in the landscape on all taxonomic and functional groups.

We built all the above models (see Table S2, for a summary of the fitted models) using the 'rma.mv' function with Restricted Maximum Likelihood (REML) estimation in the 'metafor' package (Viechtbauer 2010) in the R statistical environment (www.r-project.org/; R version 4.2.2). We then used these models as 'working models' and applied the 'cluster-robust inference' method (or 'robust variance estimation') to account for any dependencies in the effect sizes (e.g., correlative heterogeneity components across different spatial scales, or studies conducted by the same investigator or laboratory) to avoid potential overestimation (Hedges *et al.* 2010; Pustejovsky & Tipton 2022). We report strong effects as those that do not contain zero within the 90% Confidence Intervals (CIs). Results derived from less than five studies (~ 2% of the dataset) were not considered to be robust and so are not discussed.

Sensitivity analyses

Testing for publication bias and model over-parameterization

We checked for publication bias by fitting a meta-analytic model with standard errors (SEs) of the observed effect sizes as a continuous moderator variable (Table 2) and examined the relationship between observed effect sizes and SEs (Nakagawa *et al.* 2022). No significant relationship between observed effect sizes and SEs was observed (Table S3), identifying no publication bias in our dataset. A visual inspection of a 'funnel plot' also suggested the absence of a publication bias (Figure S2). Over-parameterization was assessed using visual inspection of peaks within the 'profile likelihood plots', and it was not problematic for any analyses with only single peaks at the respective parameter estimates (Viechtbauer 2010).

Testing for influential and outlier studies

To check for influential studies, we aggregated all effect sizes belonging to the same study into a single combined effect size. We then fitted a random effects model with the 'DerSimonian-Laird' estimator, using the 'rma' function in the 'metafor' package (Viechtbauer 2010). Using 'Baujat plot' (Baujat *et al.* 2002), we confirmed that the influence of each study on the overall estimate was below 0.055, suggesting that there were no overly influential studies in our dataset (Figure S3) (Schmid *et al.* 2020). We also created a 'Gosh plot' (Olkin *et al.* 2012), to look for outliers among the studies. These analyses suggested all studies were intermixed (Figure S4), and there were no outliers (Viechtbauer 2010). Cook's distances extracted from this model further confirmed there were no outlier studies (Cook's distances < 0.2; Figure S5) (Schmid *et al.* 2020).

Testing for potential confounding effects

The estimated average effects of spatial heterogeneity on biodiversity through our models may be influenced by the amount of cropped and semi-natural areas within the landscape, leading to potential confounding effects. To assess the potential confounding effects of these variables on the estimated average effects of spatial heterogeneity on biodiversity, we conducted separate analyses treating them as continuous moderator variables (Table 2).

However, no significant effects were observed (Table S4), indicating that the estimated average effects of crop/landscape heterogeneity components on biodiversity by our models were not distorted by the quantity of crop or semi-natural area. Instead, the primary drivers were found to be the heterogeneity of crop and non-crop areas present within the landscapes.

RESULTS

(Q1). Do crop and landscape heterogeneity within agricultural landscapes have overall positive effects on agroecosystem biodiversity?

The effects of heterogeneity type on biodiversity

For the invertebrates, vertebrates, and pollinators, overall spatial heterogeneity (i.e., the average effects of all the crop and landscape heterogeneity components) increased the alpha biodiversity metrics of total abundance, species richness and diversity. This was also the case for predator species richness and diversity, and plant species richness. However, spatial heterogeneity did not have any significant influence on the total abundance of predators, pests or plants (Figures 1–6; Tables S5–S10). The effect of spatial compositional heterogeneity (i.e., the average effects of both crop and landscape compositional heterogeneity components) increased the species richness and diversity of invertebrates, vertebrates, pollinators, and predators, as well as the species richness of plants. Furthermore, it significantly increased the total of abundance of vertebrates and pollinators. However, the total abundance of invertebrates, plants, predators and pests were not significantly affected by spatial compositional heterogeneity (Figures 1–6; Tables S5–S10). The effect of spatial configurational heterogeneity (i.e., the average effects of both crop and landscape configurational heterogeneity components) increased the species richness and diversity of invertebrates, pollinators, and predators, as well as the species richness of vertebrates and plants. Furthermore, it increased the total abundance of vertebrates and pollinators. However, no significant effects of spatial configurational heterogeneity were observed on the total abundance of invertebrates, plants, predators or pests (Figures 1–6; Tables S5–S10).

The effects of land-use type on biodiversity

The effect of crop heterogeneity (i.e., the average effects of both crop compositional and configurational heterogeneity) increased all three biodiversity metrics (total abundance, species richness or diversity) for invertebrates, vertebrates, and pollinators, as well as the diversity of predators. However, it did not have any significant effects on the three biodiversity metrics of plants, or on the total abundance of pests (Figures 1–6; Tables S5–S10). The effect of landscape heterogeneity (i.e., the average effects of both landscape compositional and configurational heterogeneity) increased the total abundance of vertebrates and pollinators, as well as the species richness of invertebrates, vertebrates, pollinators, predators, and plants. It also increased the diversity of invertebrates, pollinators, and predators. Moreover, landscape heterogeneity increased the total abundance of pests, which was mainly driven by the landscape compositional heterogeneity component (see below) (Figures 1–6; Tables S5–S10).

The effects of individual heterogeneity components on biodiversity

The effect of crop configurational heterogeneity increased both the total abundance and species richness of invertebrates and pollinators. Furthermore, it increased the diversity of invertebrates, pollinators, and predators, while having no significant effects on vertebrates, plants, and pests (Figures 1–6; Tables S5–S10). The effect of landscape configurational heterogeneity increased the total abundance of vertebrates and pollinators, as well as the species richness of invertebrates, vertebrates, pollinators, and predators. This component also increased the diversity of invertebrates, pollinators, and predators, but no significant effect was observed on pest total abundance and plant species richness (Figures 1–6; Tables S5–S10). The effect of crop compositional heterogeneity increased the total abundance of pollinators and vertebrates, as well as the species richness and diversity of invertebrates and pollinators. However, it did not have any significant effects on predators, plants, or pests (Figures 1–6; Tables S5–S10). The effect of landscape compositional heterogeneity increased the total abundance of pollinators and pests, as well as the species richness of invertebrates, vertebrates, pollinators, and predators. It also increased the diversity of invertebrates, pollinators, and predators, but had no significant effects on the species richness of plants (Figures 1–6; Tables S5–S10).

The effect of spatial heterogeneity components on taxonomic orders

The majority of invertebrate taxonomic orders (i.e., Araneae, Coleoptera, Diptera, Hymenoptera, and Lepidoptera) in our dataset, along with birds, showed significant positive responses to most of the spatial heterogeneity components considered in this study. These heterogeneity components had stronger positive effects on the species richness and diversity of these taxonomic orders than on their total abundance, except for Hymenoptera and birds, which showed stronger positive responses in terms of abundance (see Figures S6–S11; Tables S11–S16).

(Q2). Does the relative strength of crop heterogeneity effects, compared to landscape heterogeneity effects, vary for different taxa?

For invertebrates, all crop and landscape heterogeneity components were important, and none of the components showed significantly greater importance than the others (Table S17). In contrast, vertebrate (mainly birds) species richness was increased significantly more by landscape compositional and configurational heterogeneity, as compared to crop compositional or configurational heterogeneity (Tables S18 and S19).

Pollinators also benefited from all the heterogeneity components, with no single heterogeneity component demonstrating a significantly higher level of importance compared to the others (Table S20). However, both Hymenoptera richness and Diptera diversity were increased significantly more by crop configurational heterogeneity compared to crop compositional heterogeneity (Tables S21 and S22). Moreover, crop configurational heterogeneity was as important as landscape compositional or configurational heterogeneity for Hymenoptera richness (Table S21). In contrast, for Diptera diversity, both landscape compositional and configurational heterogeneity were more important than crop compositional heterogeneity (Table S22). The diversity of predators, including Coleoptera, were significantly benefited more by spatial compositional heterogeneity compared to spatial configurational heterogeneity (Tables S23 and S24). For the diversity of Araneae, landscape heterogeneity was more important than crop heterogeneity, which was mainly driven by the importance of landscape compositional heterogeneity (Table S25). For plants, pests, and Lepidoptera, we only had limited data, so these comparisons were restricted between certain heterogeneity components, and did not significantly differ (see Tables S26–28).

(Q3). Do biodiversity responses to increased crop and landscape heterogeneity within agricultural landscapes remain consistent across different climatic regions and different cropping systems?

We assessed how spatial heterogeneity influenced invertebrates and vertebrates by integrating them into a single group (i.e., animals). We found that spatial heterogeneity had strong positive effects on all three biodiversity metrics for animals (Figure S12; Table S29). Importantly, these positive effects remained consistent, and were not significantly different between tropical/subtropical and temperate agroecosystems (Figure 7; Tables S30 and S31), as well as between annual and perennial cropping systems (Figure 8; Tables S32 and S33). We could not estimate differences in the effects of spatial heterogeneity on more specific taxa across these climatic regions or cropping systems due to the limited availability of studies (see above).

(Q4). Are biodiversity responses to increased crop and landscape heterogeneity scale dependent?

We found that both spatial compositional and configurational heterogeneity, positively and significantly influenced all three biodiversity metrics of taxonomic and functional groups at both local-level and landscape-level scales (Tables S34–S38). In general, these effects did not show much of a difference between the local-levels and landscape levels (Tables S39–S43). However, for vertebrates, we found that overall spatial heterogeneity at landscape levels was more important than at the local levels (Tables S36).

4. DISCUSSION

This synthesis provides strong evidence that biodiversity in agricultural landscapes benefits from increased spatial heterogeneity, both within the overall landscape and specifically within the crop fields. At least one of the crop or landscape heterogeneity components (i.e., compositional or configurational heterogeneity) significantly increased the alpha-level biodiversity (total abundance, species richness or species diversity) of invertebrates, vertebrates, and plants, as well as the biodiversity of pollinators (invertebrates only) and taxa providing predatory natural pest control (both invertebrates and vertebrates). Our findings further emphasise the significance of crop and non-crop heterogeneity, at both the smaller local levels and larger landscape levels across the agricultural mosaic, in maintaining and supporting agroecosystem biodiversity. These positive effects were consistent in both tropical/subtropical and temperate agroecosystems, as well as in both annual and perennial cropping systems. This likely reflects complex system-level utilisation of crop and non-crop cover resources by different taxonomic and functional groups. For those taxa able to persist in agricultural landscapes, crop and landscape heterogeneity appears to provide crucial complementary resources (Dunning *et al.* 1992; Fahrig *et al.* 2011). Overall, these results suggest that increasing spatial heterogeneity through crop and landscape heterogeneity could be a useful strategy to support biodiversity across agroecosystems globally.

(Q1) Do crop and landscape heterogeneity within agricultural landscapes have overall positive effects on agroecosystem biodiversity?

Promoting spatial heterogeneity through both crop and non-crop elements within the agroecosystem maximises benefits for biodiversity

Overall spatial heterogeneity that incorporates compositional and configurational heterogeneity of both crop and non-crop land-use elements together consistently had strong positive effects on the majority of biodiversity metrics. This was typically greater than those of the heterogeneity components when considered individually. For example, we found limited effects of each individual compositional or configurational heterogeneity component on the total abundance of studied taxa. However, the overall spatial heterogeneity incorporating both crop and non-crop heterogeneity components showed positive effects on all three biodiversity metrics of most of the studied taxa (see below). This could be because promoting a single heterogeneity component alone may not be able compensate for the absence of key habitats that provide fundamental resources (e.g., breeding and nesting sites, foraging habitats, and dispersal routes) for population persistence within the agroecosystem (e.g., Kleijn & Verbeek 2000, for plants; Holzschuh *et al.* 2011 and Kleijn *et al.* 2015, for wild bees; Redlich *et al.* 2018b, for non-crop nesting birds). This suggests that the historical approach of supporting biodiversity in agroecosystems by increasing semi-natural cover, including intercropping and wildflower strips adjacent to crop fields (Albrecht *et al.* 2020; Huss *et al.* 2022), while ignoring cropped areas, represents only one part of the solution. Rather, supporting biodiversity in agroecosystems depends on maximising both the diversity of semi-natural and crop land cover resources through increased compositional and configurational heterogeneity (see below).

Our results suggest that spatial heterogeneity may lead to a more favourable outcome for many taxa in agroecosystems, as it provides increased resources and improved access to those resources, enhancing many levels of biodiversity. For example, predator taxa may utilise crops for hunting when pest populations are high, moving into perennial field margin habitats to forage as the crops senesce, and finally overwintering in hedgerows or woodlands (Sotherton 1984; Bianchi *et al.* 2006; Gallé *et al.* 2018). Similarly, pollinator taxa may continue to use low-quality crop habitats that act as sink habitats by the continuously replenishment of individuals from perennial field margins or other natural/semi-natural source habitats within heterogenous agroecosystems (Hass *et al.* 2018; Iles *et al.* 2018). Generalists with flexible resource utilisation strategies that likely dominate in agricultural systems after decades of intensive management may be the most likely to benefit from such increased heterogeneity (Tscharntke *et al.* 2005; Martin *et al.* 2019). Current shifts to intensive agricultural practises with large fields and reduced heterogeneity will impact species adapted to utilise resources across spatially heterogenous crop and semi-natural systems. Our results suggest that increased compositional and configuration heterogeneity can go some way to reverting or at least slowing down the negative effects of agricultural intensification and landscape simplification.

Crop and landscape compositional heterogeneity have positive effects on biodiversity

Higher crop or landscape compositional heterogeneity indicate not only greater variability between land cover (or crop) types but also the presence of diverse habitats within agricultural landscapes (Benton *et al.* 2003; Tews *et al.* 2004; Fahrig *et al.* 2011). The presence of a diverse array of habitats within the landscape creates a wide range of biotic and abiotic resources (Tews *et al.* 2004; Fahrig *et al.* 2011). This habitat diversity could play a crucial role in promoting biodiversity as many species rely on multiple resources offered by different land cover types throughout their life cycle, highlighting the importance of resource complementarity (Dunning *et al.* 1992; Tews *et al.* 2004; Fahrig *et al.* 2011; Mandelik *et al.* 2012; Tscharntke *et al.* 2012). Furthermore, the continuity of resources across diverse habitats at the landscape level, both spatially and temporally, has been shown to positively impact biodiversity (Fahrig *et al.* 2011; Schellhorn *et al.,* 2015). In addition, as compositional heterogeneity increases, the proportion of each cover type within the landscape decreases due to the greater number of cover types present (Martin *et al.* 2019; Sirami *et al.* 2019). This in turn could result in reduced dispersal among competing taxa sharing the same resources within a specific cover type, lowering competition and uncoupling patch dynamics across the metacommunity and promoting species coexistence and increasing biodiversity (Amarasekare 2008; Fahrig *et al.* 2011). Our results are consistent with these hypotheses, as the positive relationships between crop or landscape compositional heterogeneity and biodiversity (i.e., species richness or diversity) were consistent among invertebrate and vertebrate taxa. Furthermore, similar positive trends were found for invertebrates involved in pollination and for both invertebrates and vertebrates involved in natural pest control.

Crop and landscape configurational heterogeneity have positive effects on biodiversity

Higher landscape or crop configurational heterogeneity results in agricultural landscapes becoming comprised of smaller land parcels, with more edges/field margins (i.e., margins of a field, with or without a field border) and longer margins (Fahrig *et al.* 2011; Hass *et al.*

2018; Martin *et al.* 2019). Such landscape structures may facilitate animal movements, and increase landscape complementarity by increasing resource accessibility, in turn supporting higher biodiversity (Fahrig *et al.* 2011; Tscharntke *et al.* 2012; Hass *et al.* 2018). For example, higher crop and landscape configurational heterogeneity has been found to increase the area of transition zones that facilitate animal movements and thus resource accessibility (Marshall & Moonen 2002; Hass *et al.* 2018). Our results are consistent with these concepts as we observed positive effects of crop or landscape configurational heterogeneity on biodiversity (i.e., species richness or diversity) of all studied groups, except plants, pests, and Coleoptera. Indeed, field margins and edges, as well as semi-natural vegetation, support more biodiversity relative to managed crop fields (Marshall & Moonen 2002; Collins & Fahrig 2017; Jeanneret *et al.* 2021). Previous studies have found that field margins or edges could offer foraging resources and nesting sites for pollinators (e.g., Marshall & Moonen 2002; Rands & Whitney 2011; Hass *et al.* 2018, but see Kennedy *et al.* 2013) and predators (e.g., Marshall & Moonen 2002; Fahrig *et al.* 2015; Ramsden *et al.* 2015; Baillod *et al.* 2017). They could also act as a buffer, reducing pesticide drift and limiting the movement of fertilisers and other pollutants across the landscape, thereby offering benefits to agroecosystem biodiversity (Marshall & Moonen 2002). Our study confirms the importance of such features as both pollinators and predators were positively affected by crop and landscape configurational heterogeneity.

(Q2). Does the relative strength of crop heterogeneity effects, compared to landscape heterogeneity effects, vary for different taxa?

Crop and landscape heterogeneity have varying degrees of effects on different taxa

As we hypothesised, different heterogeneity components had overall positive but variable effects on the different taxa studied. One of the obvious differences was that vertebrates, including birds, benefited more from landscape heterogeneity compared to crop heterogeneity. This suggests that resources provided by crop habitats only may be inadequate to support these taxa (Vickery *et al.* 2009; Lee & Goodale 2018; Redlich *et al.* 2018b). These groups are usually highly mobile and have larger body sizes compared to invertebrate taxa, thus they may be able to exploit specific crop and other non-crop resources available at different spatial scales rather than solely depending on crop resources at a particular spatial scale (Marshall & Moonen 2002; Martin *et al.* 2016; Redlich *et al.* 2018b).

The differences between the effects of crop and landscape heterogeneity were not significant for invertebrates or for invertebrate pollinator communities. This suggests that these communities might compensate for the absence of specific non-crop habitats by capitalising on the greater resource availability and accessibility resulting from increased crop heterogeneity, i.e., the semi-natural habitats along the field margins/edges. Previous larger scale studies in agricultural landscapes have also indicated that invertebrate communities in agricultural landscapes, particularly pollinators, tend to be generalists relying on a wide range of resources for both feeding and nesting (Kleijn *et al.* 2015).

Interestingly, our taxonomic order level analysis suggested that Hymenoptera and Diptera communities significantly benefited from crop configurational heterogeneity more than crop compositional heterogeneity. As these groups were primarily comprised of flying pollinators, it could be that they exploit resources from various cover types within the landscape, and thus it is the connectivity between different fields that is more important to support their movement, rather than a particular cover type (Hass *et al.* 2018; Priyadarshana *et al.* 2021). In contrast, for Coleoptera and Araneae, our results indicated that the compositional heterogeneity component is more important than configurational heterogeneity. As these groups were generally comprised of predators with low mobility, they may benefit more from the amount of resources available within a particular cover type than the connectivity between the cover types (Kromp 1999; Martin *et al.* 2016; Boetzl *et al.* 2020;

Priyadarshana *et al.* 2021). Overall, these results reiterate the importance of both compositional and configurational heterogeneity to support multiple taxa in agricultural landscapes.

(Q3). Do biodiversity responses to increased crop and landscape heterogeneity within agricultural landscapes remain consistent across different climatic regions and different cropping systems?

Our results suggest that the positive effect of overall spatial heterogeneity (the average effects of compositional and configurational heterogeneity together) on all three biodiversity metrics for animals (invertebrates and vertebrates) did not significantly differ between different climatic regions (tropical/subtropical vs. temperate) and different cropping systems (annual vs. perennial). This suggests that increasing crop and landscape heterogeneity can be a strategy to support agroecosystem biodiversity globally, despite the differences in climatic regions and cropping systems.

(Q4). Are biodiversity responses to increased crop and landscape heterogeneity scale dependent?

We found that the positive effect of spatial heterogeneity occurs at all scales in agroecosystems, including the effects of both compositional and configurational heterogeneity, at both the smaller local-levels and the larger landscape-levels. It is likely that animals in agricultural systems exploit resources from crop fields at local-level scales, while they may use resources from other non-crop land cover types at landscape-level scales (Marshall & Moonen 2002; Gonthier *et al.* 2014; Martin *et al.* 2016). Indeed, agriculture practices are not limited to single farms, and they operate within larger landscapes that encompass various crop and non-crop land cover types. Different scales may be important to different taxa, as suggested in the comparison of vertebrate and invertebrate taxa's responses to spatial heterogeneity (see above); indeed, vertebrates were most greatly affected at landscape-scales. In addition, the land cover in agroecosystems changes over space and time, resulting in continually dynamic compositional and configurational heterogeneity across the landscape. Our results suggest that promoting crop and landscape heterogeneity at both local and landscape level is crucial to maximise resource complementarity and to support agroecosystem biodiversity (see also Altieri 1999; Mandelik *et al.* 2012; Gonthier *et al.* 2014).

Potential adverse effects of increasing compositional and configurational heterogeneity

As we hypothesised, crop heterogeneity showed a negative effect on pest abundance, but it was not statistically significant. In contrast, we found a significantly positive effect of landscape heterogeneity on pest abundance, which was primarily driven by landscape compositional heterogeneity. This suggests that while increased landscape heterogeneity provides benefits to various taxa, it may also provide co-benefits to agricultural pests by creating favourable land cover recourses (Tscharntke *et al.* 2016). However, our results also found positive effects of increased crop and landscape heterogeneity on predators (see above). Promoting the natural predators of these pests through increased crop and landscape heterogeneity may help to keep the pests under control (Baillod *et al.* 2017; Dominik *et al.* 2018; Redlich *et al.* 2018a; Martin *et al.* 2019).

We acknowledge that while our synthesis demonstrates overall positive effects of increased crop and landscape heterogeneity on biodiversity without publication bias, there are empirical studies that have reported negative biodiversity effects of some crop and landscape heterogeneity components (e.g., Martin *et al.* 2016, 2020; Hass *et al.* 2018; Reynolds *et al.* 2018). These negative effects have been primarily attributed to the decrease of certain habitat covers, especially with increased compositional heterogeneity (e.g., Hass *et al.* 2018), or the presence of crop types with particularly intensive management techniques (e.g., Hass *et al.* 2018, 2019; Reynolds *et al.* 2018; Martin *et al.* 2020). In some instances, these negative effects were found at particular spatial scales due to a lack of certain habitat(s) at that scale (e.g., Martin *et al.* 2016). These divergent findings should also be taken into account when considering the complex relationship between crop/landscape heterogeneity and biodiversity, which can vary for different crop and land-use types.

Study selection bias

Our dataset included many studies from temperate agroecosystems in the global North, with tropical/sub-tropical agroecosystems in the global South being represented by a limited number of studies (see Table S1). While there was no publication bias in our dataset (see above), data availability meant that agroecosystems from Africa and Australia regions were not represented. Nevertheless, we have shown that the positive effects of increased crop and landscape spatial heterogeneity on animal biodiversity are consistent across both temperate and tropical/sub-tropical agroecosystems. Moreover, these positive effects are consistent between annual and perennial cropping systems. While ideally a greater geographical range would have been desirable, the focus on broad taxonomic groups and simple biodiversity metrics (e.g., total abundance, species richness, and diversity) suggests that the reported responses to spatial heterogeneity are likely to be also meaningful outside of the current geographic scope of this analysis.

CONCLUSIONS AND POLICY IMPLICATIONS

Our meta-analysis provides the strongest evidence to date that increasing spatial heterogeneity through the diversity of crop and non-crop cover types benefits biodiversity in agricultural landscapes. These landscapes comprised mostly of cultivated lands with only small amounts of semi-natural areas, suggesting that even intensive farming systems have the potential to be managed in a way that provides significant benefits for biodiversity. In part this can be achieved by growing more crop types (e.g., diversified crop rotations, see Liang *et al.* 2023) in smaller fields and therefore increasing margins and edges. If non-crop cover types such as semi-natural or natural vegetation are unavailable or insufficiently abundant to support biodiversity, farmers can still increase spatial heterogeneity by increasing crop heterogeneity, although benefits for biodiversity will be limited compared to increased spatial heterogeneity through both crop and non-crop types simultaneously. Importantly, these benefits extend to aspects of biodiversity that provide important ecosystem services that support crop production, such as pollination and natural pest control. Therefore, policies that encourage farmers to increase crop and non-crop diversity could be a win-win for both farmers and biodiversity.

Trends towards farming systems that depend on diversified crop rotations with more crop types will increase heterogeneity on farms. We could not estimate the influence of management techniques on the effects of spatial heterogeneity on biodiversity due to high variability and limited data availability. However, as with any management technique, there are limits on the extent to which spatial heterogeneity can be practically implemented. While some degree of landscape-level structural changes within and outside of the crop mosaic are possible, fundamental changes in existing farm infrastructure are likely to have both social and economic constraints that require further subsidies or policy-based solutions. Policies must be tailored, as far as possible, through stakeholder engagement (e.g., farmers, landowners, government agencies, environmental organisations, and local communities) if there is to be long term success in managing crop and non-crop areas within the whole landscape (Sayer *et al.* 2013; Reed *et al.* 2016; Landis 2017). Win-win outcomes will likely also require consideration of both farmer-owned and non-farmer-owned areas.

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REFERENCES

Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., *et al.* (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecol. Lett.*, 23, 1488–1498.

Alignier, A., Solé-Senan, X.O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D., *et al.* (2020). Configurational crop heterogeneity increases within-field plant diversity. *J. Appl. Ecol.*, 57, 654–663.

Almdal, C.D. & Costamagna, A.C. (2023). Crop diversity and edge density benefit pest suppression through bottom-up and top-down processes, respectively. *Agric. Ecosyst. Environ.*, 349, 108447.

Altieri, M.A. (1999). The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.*, 74, 19–31.

Amarasekare, P. (2008). Spatial dynamics of foodwebs. *Annu. Rev. Ecol. Evol. Syst.*, 39, 479–500.

Baillod, A.B., Tscharntke, T., Clough, Y. & Batáry, P. (2017). Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *J. Appl. Ecol.*, 54, 1804–1813.

Batáry, P., Báldi, A., Ekroos, J., Gallé, R., Grass, I. & Tscharntke, T. (2020). Biologia futura: Landscape perspectives on farmland biodiversity conservation. *Biol. Futur.*, 71, 9–18.

Baujat, B., Mahé, C., Pignon, J.-P. & Hill, C. (2002). A graphical method for exploring heterogeneity in meta-analyses: Application to a meta-analysis of 65 trials. *Stat. Med.*, 21, 2641–2652.

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V. & Makowski, D. (2021). Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Glob. Chang. Biol.*, gcb.15747.

Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. R. Stat. Soc.*, 57, 289–300.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.

Bianchi, F.J.J.., Booij, C.J.. & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B Biol. Sci.*, 273, 1715–1727.

Boetzl, F.A., Schuele, M., Krauss, J. & Steffan-Dewenter, I. (2020). Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position. *J. Appl. Ecol.*, 57, 1482–1493.

Bowman, M.S. & Zilberman, D. (2013). Economic factors affecting diversified farming systems. *Ecol. Soc.*, 18, 33.

Cano, D., Martínez-Núñez, C., Pérez, A.J., Salido, T. & Rey, P.J. (2022). Small floral patches are resistant reservoirs of wild floral visitor insects and the pollination service in agricultural landscapes. *Biol. Conserv.*, 276, 109789.

Collins, S.J. & Fahrig, L. (2017). Responses of anurans to composition and configuration of agricultural landscapes. *Agric. Ecosyst. Environ.*, 239, 399–409.

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., *et al.* (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.*, 5, 1–14.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., *et al.* (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science.*, 366 (6471), eaax3100.

Dominik, C., Seppelt, R., Horgan, F.G., Settele, J. & Václavík, T. (2018). Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *J. Appl. Ecol.*, 55, 2461–2472.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169.

Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M.-A., Justes, E., *et al.* (2015). How to implement biodiversity-based agriculture to enhance ecosystem services: A review. *Agron. Sustain. Dev.*, 35, 1259–1281.

Estrada-Carmona, N., Sánchez, A.C., Remans, R. & Jones, S.K. (2022). Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proc. Natl. Acad. Sci.*, 119, 1–10.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., *et al.* (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.*, 14, 101–112.

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., *et al.* (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agric. Ecosyst. Environ.*, 200, 219–234.

Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., *et al.* (2018). Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landsc. Ecol.*, 33, 1435–1446.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., *et al.* (2014). Biodiversity conservation in agriculture requires a multi-scale approach. *Proc. R. Soc. B Biol. Sci.*, 281, 20141358.

Hart, A.K., McMichael, P., Milder, J.C. & Scherr, S.J. (2016). Multi-functional landscapes from the grassroots? The role of rural producer movements. *Agric. Human Values*, 33, 305–322.

Hass, A.L., Brachmann, L., Batáry, P., Clough, Y., Behling, H. & Tscharntke, T. (2019). Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. *J. Appl. Ecol.*, 56, 294–304.

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C., *et al.* (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc. R. Soc. B Biol. Sci.*, 285, 20172242.

Hedges, L. V., Tipton, E. & Johnson, M.C. (2010). Robust variance estimation in meta-regression with dependent effect size estimates. *Res. Synth. Methods*, 1, 39–65.

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., *et al.* (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agron. Sustain. Dev.*, 37, 31.

Holzschuh, A., Dormann, C.F., Tscharntke, T. & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B Biol. Sci.*, 278, 3444–3451.

Huss, C.P., Holmes, K.D. & Blubaugh, C.K. (2022). Benefits and risks of intercropping for crop resilience and pest management. *J. Econ. Entomol.*, 115, 1350–1362.

Iles, D.T., Williams, N.M. & Crone, E.E. (2018). Source-sink dynamics of bumblebees in rapidly changing landscapes. *J. Appl. Ecol.*, 55, 2802–2811.

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., *et al.* (2017). Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.*, 105, 871–879.

Jeanneret, P., Lüscher, G., Schneider, M.K., Pointereau, P., Arndorfer, M., Bailey, D., *et al.* (2021). An increase in food production in Europe could dramatically affect farmland biodiversity. *Commun. Earth Environ.*, 2, 183.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., *et al.* (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.*, 16, 584–599.

Kleijn, D. & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary vegetation. *J. Appl. Ecol.*, 37, 256–266.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., *et al.* (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.*, 6, 7414.

Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.*, 74, 187–228.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton, New Jersey.

Landis, D.A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic Appl. Ecol.*, 18, 1–12.

Lee, M.-B. & Goodale, E. (2018). Crop heterogeneity and non-crop vegetation can enhance avian diversity in a tropical agricultural landscape in southern China. *Agric. Ecosyst. Environ.*, 265, 254–263.

Li, D., Lee, M., Xiao, W., Tang, J. & Zhang, Z. (2020). Non-crop features and heterogeneity mediate overwintering bird diversity in agricultural landscapes of southwest China. *Ecol. Evol.*, 10, 5815–5828.

Liang, Z., Xu, Z., Cheng, J., Ma, B., Cong, W.-F., Zhang, C., *et al.* (2023). Designing diversified crop rotations to advance sustainability: A method and an application. *Sustain. Prod. Consum.*, 40, 532–544.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., *et al.* (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Chang. Biol.*, 23, 4946–4957.

Mandelik, Y., Winfree, R., Neeson, T. & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecol. Appl.*, 22, 1535–1546.

Marshall, E.J.. & Moonen, A.. (2002). Field margins in northern Europe: Their functions and interactions with agriculture. *Agric. Ecosyst. Environ.*, 89, 5–21.

Martin, A.E., Collins, S.J., Crowe, S., Girard, J., Naujokaitis-Lewis, I., Smith, A.C., *et al.* (2020). Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices. *Agric. Ecosyst. Environ.*, 288, 106698.

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., *et al.* (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.*, 22, 1083–1094.

Martin, E.A., Seo, B., Park, C.-R., Reineking, B. & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecol. Appl.*, 26, 448–462.

Martínez-Núñez, C., Martínez-Prentice, R. & García-Navas, V. (2023). Land-use diversity predicts regional bird taxonomic and functional richness worldwide. *Nat. Commun.*, 14, 1320.

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L. & Albrecht, M. (2022). Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *J. Appl. Ecol.*, 59, 2604–2615.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., *et al.* (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods Ecol. Evol.*, 13, 4–21.

Olkin, I., Dahabreh, I.J. & Trikalinos, T.A. (2012). GOSH - A graphical display of study heterogeneity. *Res. Synth. Methods*, 3, 214–223.

Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C. & Lindsay, K.E. (2013). Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landsc. Ecol.*, 28, 371–383.

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., *et al.* (2014). EU agricultural reform fails on biodiversity. *Science (80-.).*, 344, 1090–1092.

Perfecto, I. & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems. *Ann. N. Y. Acad. Sci.*, 1134, 173–200.

Perfecto, I., Vandermeer, J. & Wright, A. (2019). *Nature's matrix: Linking agriculture, biodiversity conservation and food sovereignty*. Second edition. Routledge, London, pp. (1–295).

Piñeiro, V., Arias, J., Dürr, J., Elverdin, P., Ibáñez, A.M., Kinengyere, A., *et al.* (2020). A scoping review on incentives for adoption of sustainable agricultural practices and their outcomes. *Nat. Sustain.*, 3, 809–820.

Power, A.G. (2010). Ecosystem services and agriculture: Tradeoffs and synergies. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 2959–2971.

Priyadarshana, T.S., Lee, M., Ascher, J.S., Qiu, L. & Goodale, E. (2021). Crop heterogeneity is positively associated with beneficial insect diversity in subtropical farmlands. *J. Appl. Ecol.*, 58, 2747–2759.

Priyadarshana, T.S., Lee, M., Slade, E.M. & Goodale, E. (2023). Local scale crop compositional heterogeneity suppresses the abundance of a major lepidopteran pest of cruciferous vegetables. *Basic Appl. Ecol.,* 69, 39–48.

Pustejovsky, J.E. & Tipton, E. (2022). Meta-analysis with Robust Variance Estimation: Expanding the range of working models. *Prev. Sci.*, 23, 425–438.

Pustkowiak, S., Kwieciński, Z., Lenda, M., Żmihorski, M., Rosin, Z.M., Tryjanowski, P., *et al.* (2021). Small things are important: The value of singular point elements for birds in agricultural landscapes. *Biol. Rev.*, 96, 1386–1403.

Raderschall, C.A., Bommarco, R., Lindström, S.A.M. & Lundin, O. (2021). Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agric. Ecosyst. Environ.*, 306, 107189.

Ramsden, M.W., Menéndez, R., Leather, S.R. & Wäckers, F. (2015). Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *Agric. Ecosyst. Environ.*, 199, 94–104.

Rands, S.A. & Whitney, H.M. (2011). Field margins, foraging distances and their impacts on nesting pollinator success. *PLoS One*, 6, e25971.

Ray, D.K., Mueller, N.D., West, P.C. & Foley, J.A. (2013). Yield trends are insufficient to double global crop production by 2050. *PLoS One*, 8, e66428.

Redlich, S., Martin, E.A. & Steffan-Dewenter, I. (2018a). Landscape-level crop diversity benefits biological pest control. *J. Appl. Ecol.*, 55, 2419–2428.

Redlich, S., Martin, E.A., Wende, B. & Steffan-Dewenter, I. (2018b). Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLoS One*, 13, e0200438.

Reed, J., Van Vianen, J., Deakin, E.L., Barlow, J. & Sunderland, T. (2016). Integrated landscape approaches to managing social and environmental issues in the tropics: Learning from the past to guide the future. *Glob. Chang. Biol.*, 22, 2540–2554.

Reynolds, C., Fletcher, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C., *et al.* (2018). Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: A multi-scale and multi-taxon investigation. *Landsc. Ecol.*, 33, 241–255.

Rosa-Schleich, J., Loos, J., Mußhoff, O. & Tscharntke, T. (2019). Ecological-economic trade-offs of Diversified Farming Systems – A review. *Ecol. Econ.*, 160, 251–263.

Rosset, P.M. & Martínez-Torres, M.E. (2012). Rural social movements and agroecology: Context, theory, and process. *Ecol. Soc.*, 17, art17.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.*, 232, 8–27.

Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J.-L., Sheil, D., Meijaard, E., *et al.* (2013). Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proc. Natl. Acad. Sci.*, 110, 8349–8356.

Schellhorn, N.A., Gagic, V. & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends Ecol. Evol.*, 30, 524–530.

Scherr, S.J. & McNeely, J.A. (2008). Biodiversity conservation and agricultural sustainability: Towards a new paradigm of 'ecoagriculture' landscapes. *Philos. Trans. R.*

Soc. B Biol. Sci., 363, 477–494.

Schmid, C.H., Stijnen, T. & White, I.R. (2020). *Handbook of meta-analysis*. First edition. CRC Press. Boca Raton.

Shannon, C.E. (1948). A mathematical theory of communication. *Bell Syst. Tech. J.*, 27, 379–423.

Sietz, D., Klimek, S. & Dauber, J. (2022). Tailored pathways toward revived farmland biodiversity can inspire agroecological action and policy to transform agriculture. *Commun. Earth Environ.*, 3, 211.

Simpson, E.H. (1949). Measurement of diversity. *Nature*, 163, 688–688.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., *et al.* (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.*, 116, 16442–16447.

Sotherton, N.W. (1984). The distribution and abundance of predatory arthropods overwintering on farmland. *Ann. Appl. Biol.*, 105, 423–429.

Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., van der Heijden, M.G.A., Liebman, M., *et al.* (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci. Adv.*, 6, eaba1715.

Tews, J., Brose, U., Grimm, V., Tielbo¨rger, K., Wichmann, M.C., Schwager, M., *et al.* (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *J. Biogeogr.*, 31, 79–92.

Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011). Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad. Sci.*, 108, 20260–20264.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C. & Batáry, P. (2021). Beyond organic farming – Harnessing biodiversity-friendly landscapes. *Trends Ecol. Evol.*, 36, 919–930.

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., et al.

(2016). When natural habitat fails to enhance biological pest control – Five hypotheses. *Biol. Conserv.*, 204, 449–458.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecol. Lett.*, 8, 857–874.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012). Landscape moderation of biodiversity patterns and processes - Eight hypotheses. *Biol. Rev.*, 87, 661–685.

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M. & Baudry, J. (2013). The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agric. Ecosyst. Environ.*, 166, 3–14.

Vickery, J.A., Feber, R.E. & Fuller, R.J. (2009). Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. *Agric. Ecosyst. Environ.*, 133, 1–13.

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.*, 36, 1–48.

Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W. & Václavík, T. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nat. Commun.*, 10, 1–10.

Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. & Swinton, S.M. (2007). Ecosystem services and dis-services to agriculture. *Ecol. Econ.*, 64, 253–260.

Table 1. Functional groups, taxa and their orders included in this meta-analysis. Taxa identified only to class levels are not listed. See Table S1, for more details. K = Number of correlations. N = Number of studies. NA = Not Available.

Functional group (K, N)	Taxonomic identity (K%)	Order
Pest predators (K = 1595; N = 75)	Carabid beetles (> 27%)	Coleoptera
	Spiders (25%)	Araneae
	Birds (> 16%)	NA
	Wasps (including Parasitoids, > 12%)	Hymenoptera
	Rove beetles (7.65%)	Coleoptera
	NA (> 2%)	Diptera
	Ladybugs (> 2%)	Coleoptera
	True bugs (> 2%)	Hemiptera
	Dragonflies/Damselflies (> 1%)	Odonata
	Bats (all are insectivorous, > 1%)	Chiroptera
	NA (> 1%)	NA
	Tachinid Flies (< 1%)	Diptera
	Ants (< 1%)	Hymenoptera
	Frogs (< 1%)	Anura
	Lacewings (< 1%)	Neuroptera
	Harvestmen (< 1%)	Opiliones
	Earwigs (< 1%)	Dermaptera
Pollinators (K = 1483; N = 55)	Bees (including Bumblebees, > 49%)	Hymenoptera
	Hoverflies (> 24%)	Diptera
	Wasps (> 12%)	Hymenoptera
	Butterflies (> 11%)	Lepidoptera
	Tachinid flies (< 1%)	Diptera
Primary producers (K = 116; N = 23)	Plants (mostly herbaceous species, 100%)	NA
Agricultural pests (K = 170; N = 25)	Aphid (> 48%)	Hemiptera
	Pollen beetles (> 24)	Coleoptera
	Small Rodents (i.e., Voles and Mice, > 12 %)	Rodentia
	Cereal Leaf Beetles (> 5%)	Coleoptera
	Plant Bugs (> 3%)	Hemiptera
	Moths (> 1%)	Lepidoptera
	Butterflies (> 1%)	Lepidoptera
	Weevils (> 1%)	Coleoptera
	Fruit Flies (> 1%)	Diptera
Decomposers (K = 39, N = 2)	Dung Beetles (> 92%)	Coleoptera
	Collembolans/Springtails (> 7%)	NA

Table 2. Moderator variables used in this meta-analysis. NA = Not Applicable.

Moderator variables	**Data type**	**Each level in moderator variables**
Heterogeneity type	Categorical	(i). Spatial compositional heterogeneity (i.e., crop and landscape compositional heterogeneity together) (ii). Spatial configurational heterogeneity (i.e., crop and landscape configurational heterogeneity together)
Land-use type	Categorical	(i). Crop heterogeneity (ii). Landscape heterogeneity
Heterogeneity component	Categorical	(i). Crop compositional heterogeneity (ii). Landscape compositional heterogeneity (iii). Crop configurational heterogeneity (iv). Landscape configurational heterogeneity
Climatic region	Categorical	(i). Tropical/subtropical agroecosystems (ii). Temperate agroecosystems
Cropping system	Categorical	(i). Annual crops (ii). Perennial crops
Spatial scale	Categorical	(i). Local-levels (i.e., < 0.5km radius area) (ii). Landscape-levels (i.e., ≥ 0.5km, and < 1 km; ≥ 1km radius area)
*Standard errors of the observed effect sizes	Continuous	NA
*Average cultivated lands area	Continuous	NA
*Average semi-natural area	Continuous	NA

* These moderator variables were used only for the sensitivity analyses.

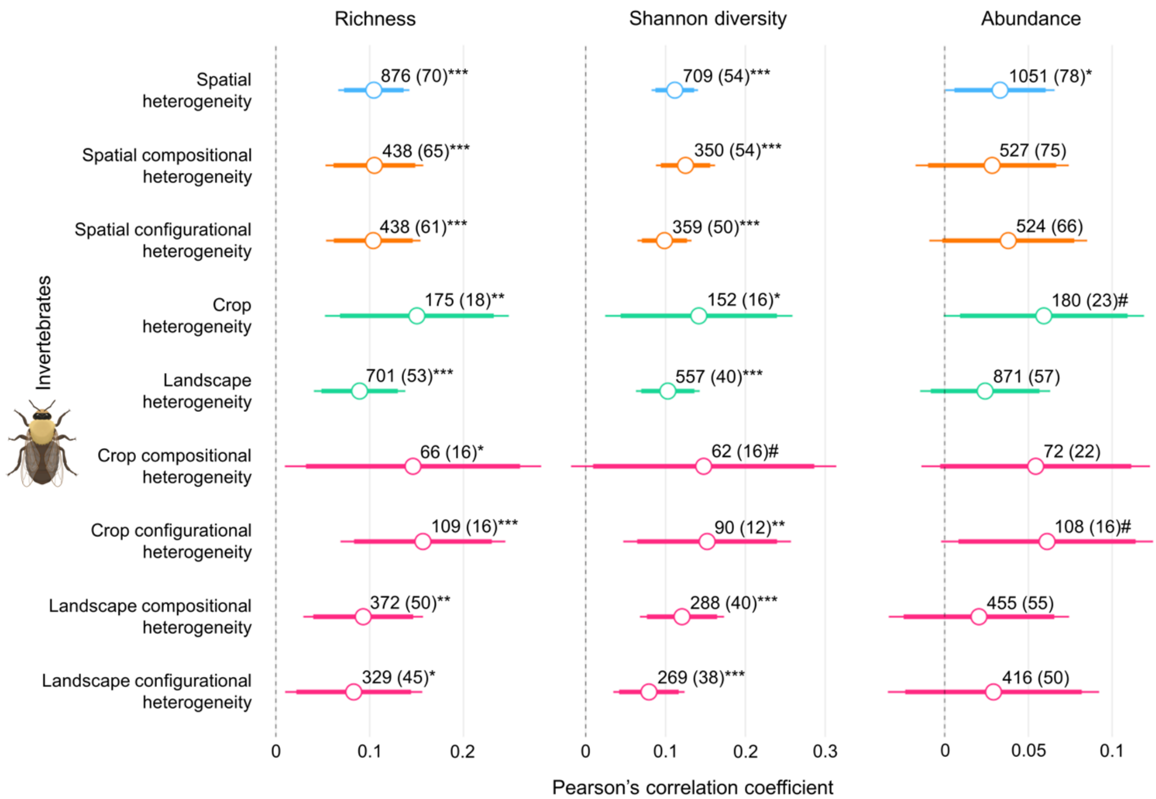

Figure 1. Estimated average Pearson's correlation coefficients among heterogeneity components and invertebrate/arthropod (no agricultural pests) biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). The number of correlations and studies (in brackets) included for each estimation are displayed beside the upper bound of the 95% CIs. Asterisks indicate level of the statistical significance (#*P*-value < 0.07, **P*-value < 0.05, ***P*-value < 0.01, ****P*-value < 0.001). The dashed line indicates the zero *X*-axis intercept. See Table S5, for detailed statistics.

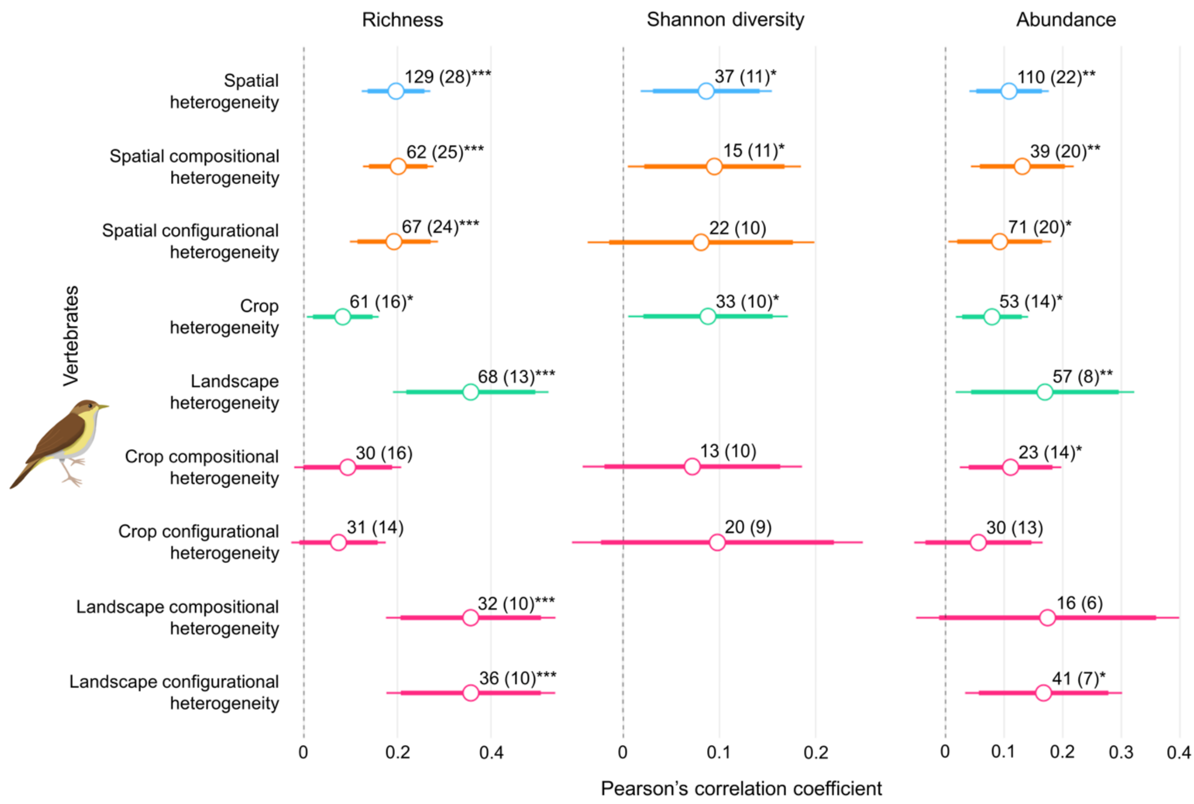

Figure 2. Estimated average Pearson's correlation coefficients among heterogeneity components and vertebrate (no agricultural pests) biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S6, for detailed statistics.

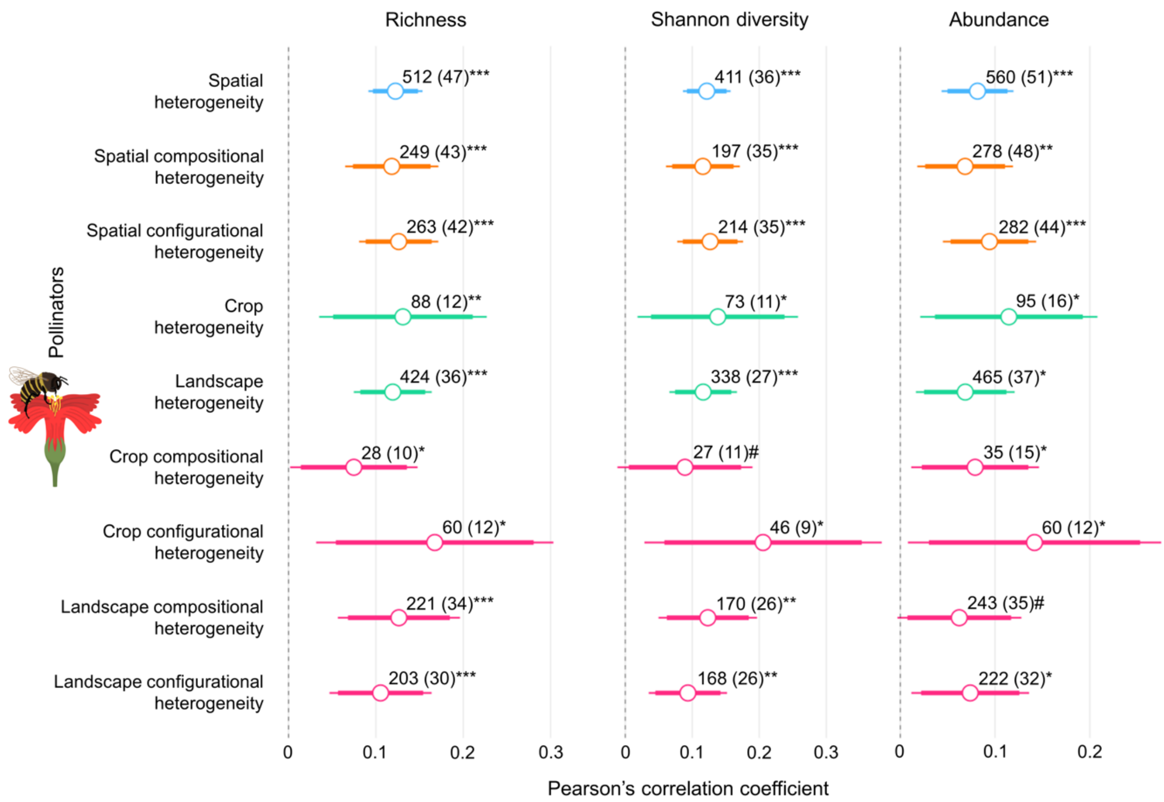

Figure 3. Estimated average Pearson’s correlation coefficients among heterogeneity components and pollinator biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S7, for detailed statistics.

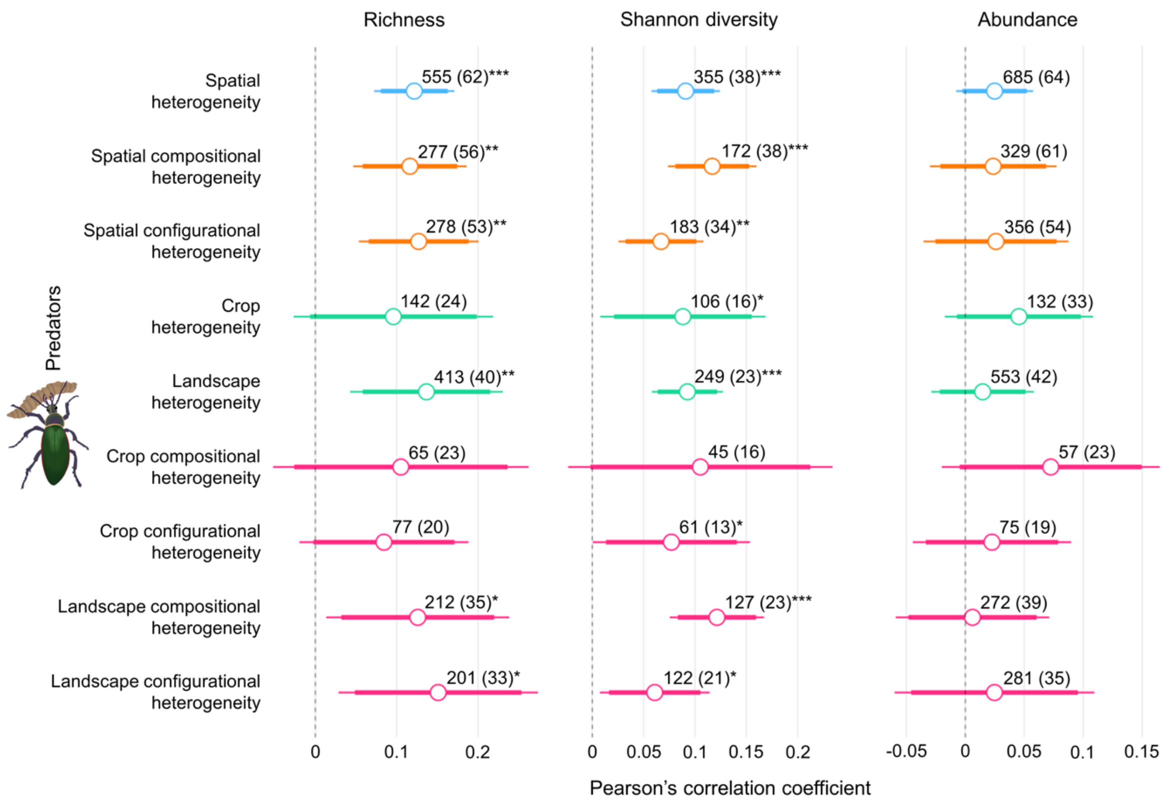

Figure 4. Estimated average Pearson's correlation coefficients among heterogeneity components and predator biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S8, for detailed statistics.

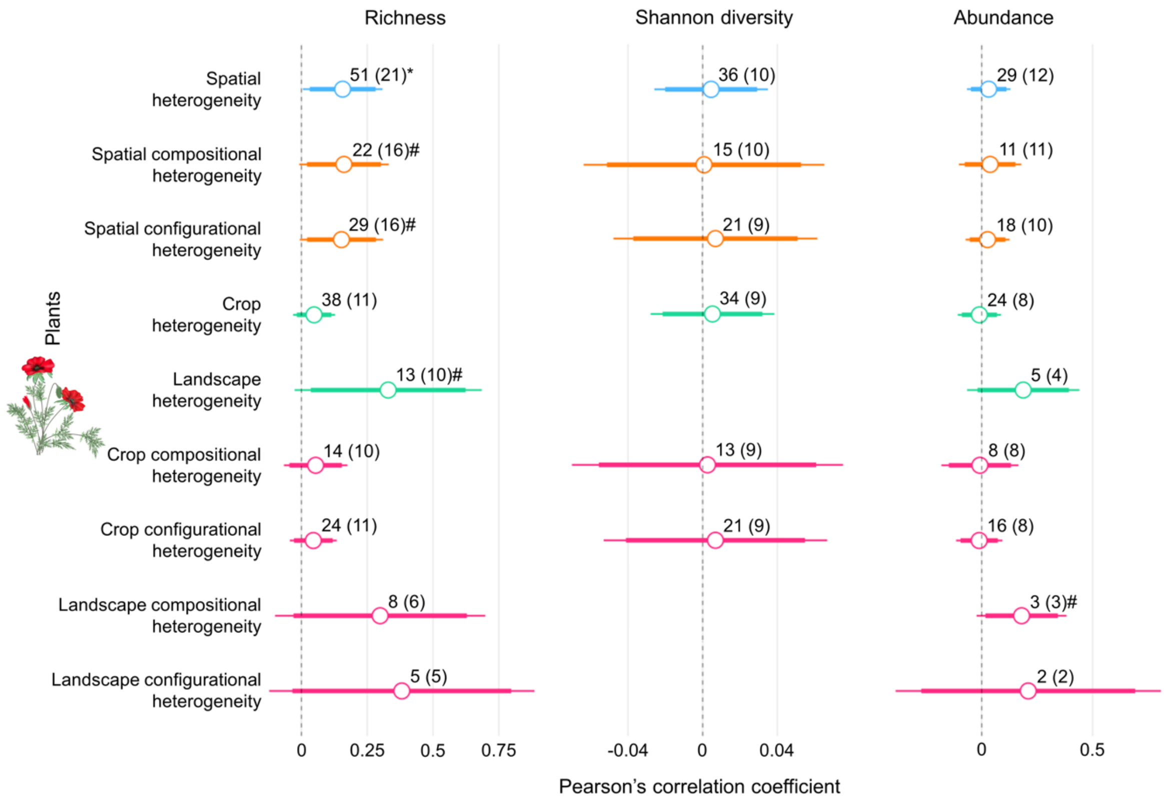

Figure 5. Estimated average Pearson's correlation coefficients among heterogeneity components and plant biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S9, for detailed statistics.

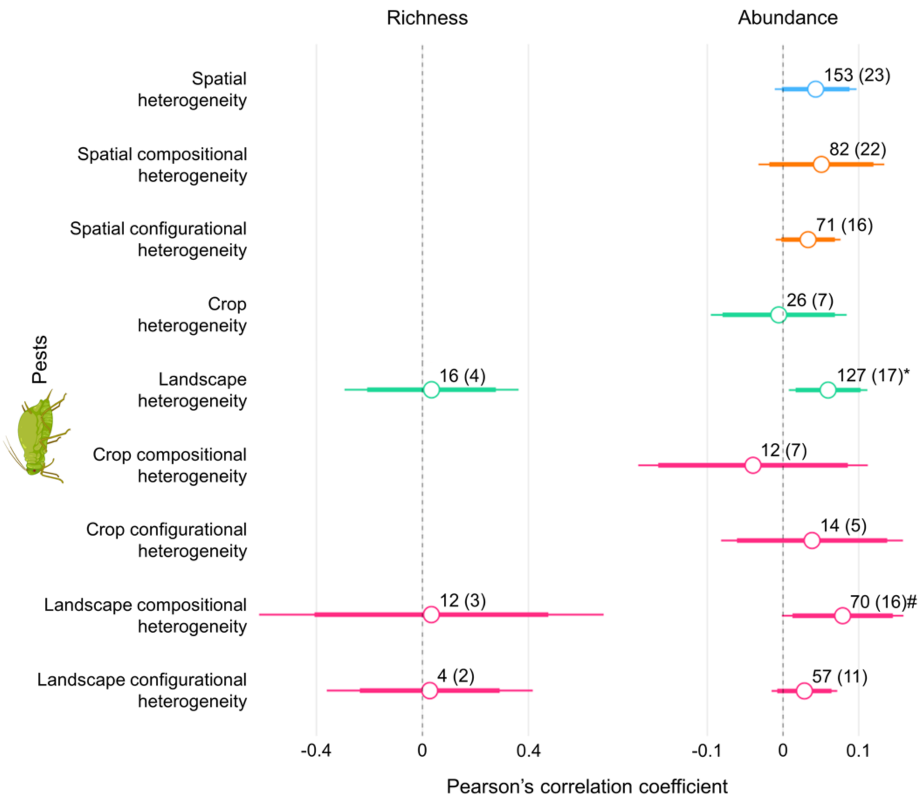

Figure 6. Estimated average Pearson's correlation coefficients among heterogeneity components and pest abundance (pest richness results were not interpreted due to the smaller number of studies, i.e., > 5), with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S10, for detailed statistics.

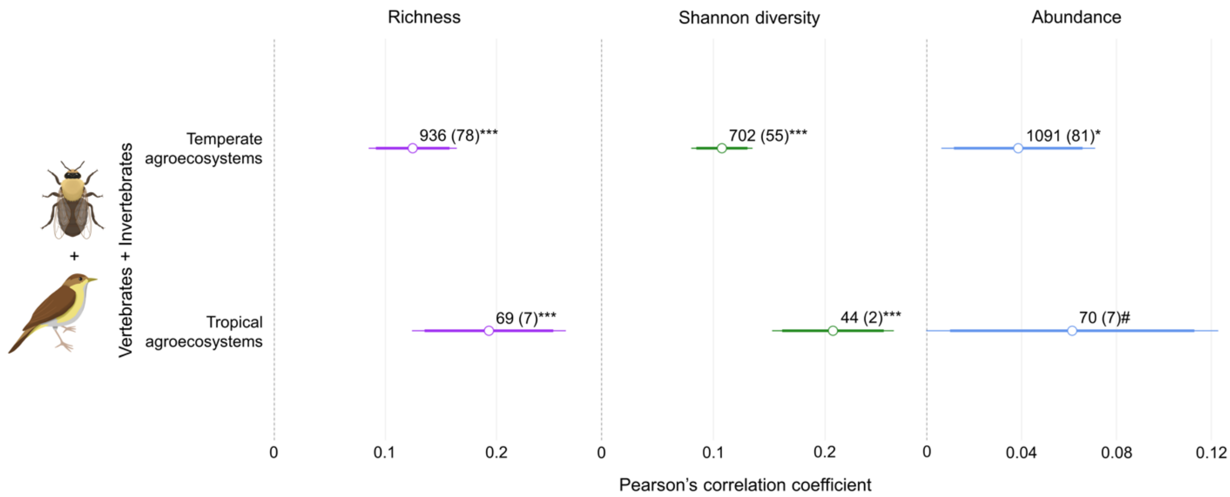

Figure 7. Estimated average Pearson's correlation coefficients among heterogeneity components and animal (vertebrates and invertebrates together) biodiversity in tropical and temperate agroecosystems, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 1. See Table S30, for detailed statistics.

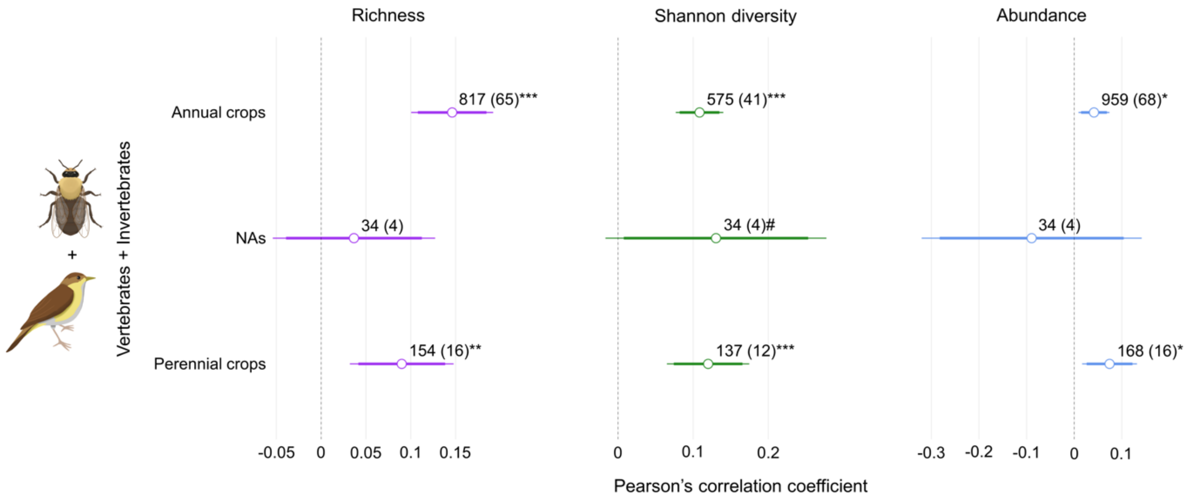

Figure 8. Estimated average Pearson's correlation coefficients among heterogeneity components and animal (vertebrates and invertebrates together) biodiversity in annual and perennial cropping systems. NAs = studies that could not be categorized into annual or perennial crops. Other details analogous to those in Figure 1. See Table S32, for detailed statistics.