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 files are publicly available in the Dryad Digital Repository, at https://doi.org/10.5061/dryad.dbrv15f7j (Priyadarshana *et al.* 2024). The source codes for the statistics are publicly available in the Zenodo Digital Repository, at https://doi.org/10.5281/zenodo.10799017. These data files and source codes are also accessible via the Digital Repository of Nanyang Technological University (DR-NTU), at https://doi.org/10.21979/N9/63PIP0, and the GitHub Digital Repository, at https://github.com/Tharaka18/spatial.heterogeneity.meta.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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

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ABSTRACT

Agricultural intensification increases food production but also drives widespread biodiversity decline. Increasing landscape heterogeneity has been suggested to increase biodiversity across habitats, while increasing crop heterogeneity may support biodiversity within agroecosystems. These spatial heterogeneity effects can be partitioned into compositional (land-cover type diversity) and configurational heterogeneity (land-cover type arrangement), measured either for the crop mosaic or across the landscape for both crops and semi-natural habitats. However, studies have reported mixed responses of biodiversity to increases in these heterogeneity components across taxa and contexts. Our meta-analysis covering 6,397 fields across 122 studies conducted in Asia, Europe, North and South America reveals consistently positive effects of crop and landscape heterogeneity, as well as compositional and configurational heterogeneity for plant, invertebrate, vertebrate, pollinator, and predator biodiversity. Vertebrates and plants benefit more from landscape heterogeneity, while invertebrates derive similar benefits from both crop and landscape heterogeneity. Pollinators benefit more from configurational heterogeneity, but predators favour compositional heterogeneity. These positive effects are consistent for invertebrates and vertebrates in both tropical/subtropical and temperate agroecosystems, and in annual and perennial cropping systems, and at small to large spatial scales. Our results suggest that promoting increased landscape heterogeneity by diversifying crops and semi-natural habitats, as suggested in the current UN Decade on Ecosystem Restoration, is key for restoring biodiversity in agricultural landscapes.

INTRODUCTION

Agricultural expansion and intensification have been the primary strategies for meeting rising global food demands (Tilman *et al.* 2011; Ray *et al.* 2013; Zabel *et al.* 2019), resulting in agriculture covering over 38% of the Earth's land surface (Ramankutty *et al.* 2008; Foley *et al.* 2011). This has led to significant losses in global biodiversity and ecosystem functioning (Newbold *et al.* 2015; Zabel *et al.* 2019; Wagner *et al.* 2021). Moreover, the loss of ecosystem services provided by biodiversity (e.g., pollination, pest control, and nutrient cycling) may also negatively impact yield and increase production costs (Altieri 1999; Losey & Vaughan 2006; Klein *et al.* 2007; Zhang *et al.* 2007; Power 2010; Isbell *et al.* 2017; Dainese *et al.* 2019). Hence, global agricultural policies have increasingly focused on farming strategies that provide co-benefits for both biodiversity and production (Pretty et al. 2018; Piñeiro *et al.* 2020; Sietz *et al.* 2022).

Biodiversity-friendly farming strategies often involve restoring semi-natural habitats to increase landscape complexity while targeting a reduction in farming intensity (Batáry *et al.* 2011; Gonthier *et al.* 2014; Tuck *et al.* 2014; Holland *et al.* 2017; Estrada-Carmona *et al.* 2022; Marja *et al.* 2022). These strategies can result in losses of cropped area, yield, and profitability, making farmers more likely to reject such strategies unless sufficient subsidies are provided (Bowman & Zilberman 2013; Rosa-Schleich *et al.* 2019; Priyadarshana 2021). Crop diversification at the field level, for instance through agroforestry, crop rotation, or intercropping, has been shown to provide positive effects on biodiversity (Lichtenberg *et al.* 2017; Tamburini *et al.* 2020; Beillouin *et al.* 2021). However, such practices are often highly crop specific, while their economic attractiveness and feasibility may be limited, especially for smallholders (Bowman & Zilberman 2013; Feliciano 2019).

Developing new approaches to manage existing crop and non-crop areas, without taking land out of production or changing practices, may be an appealing and practical approach for farmers to contribute to biodiversity conservation (Scherr & McNeely 2008; Perfecto *et al.* 2019; Tscharntke *et al.* 2021). Promoting spatial heterogeneity through habitat diversity and connectivity between crop and non-crop cover types within the landscape (i.e., landscape heterogeneity) has been suggested as a valuable approach (Fahrig *et al.* 2011). Recently, ecologists also have started testing whether increasing spatial heterogeneity of the crop mosaic itself, through increased crop diversity and connectivity between crop fields (i.e., crop heterogeneity), while keeping the area of non-cropped land constant, could increase biodiversity (Fahrig *et al.* 2015; Bertrand *et al.* 2016; Collins & Fahrig 2017; 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): (i) the diversity of land-cover types (or crops) in a given landscape, i.e., compositional heterogeneity; and (ii) the arrangement of land-cover types (or crops) in a given landscape, i.e., configurational heterogeneity (Figure 1a). Although likely to be correlated (Pasher *et al.* 2013), these two components affect ecological processes in different ways (Fahrig *et al.* 2011). Empirical studies have shown contrasting and mixed effects depending on the study taxa, their functional traits, and the spatial scales at which these components of heterogeneity are measured (Martin *et al.* 2016, 2020; Hass *et al.* 2018; Reynolds *et al.* 2018; Raderschall *et al.* 2021). In addition, factors such as crop identity and farming intensity levels (e.g., agrochemical inputs and tilling) may also affect biodiversity responses (Martin *et al.* 2016, 2020; Hass *et al.* 2018; Meyer *et al.* 2019). As a result, no consensus is currently available on the overall strength and direction of the effects of crop and landscape heterogeneity and their components (i.e., crop compositional heterogeneity, crop configurational heterogeneity, landscape compositional heterogeneity, and landscape configurational heterogeneity; Figure 1b) on biodiversity (see Estrada-Carmona *et al.* 2022).

We address this knowledge gap by assessing whether crop and landscape heterogeneity, and their compositional and configurational components, promote field-level biodiversity (i.e., abundance, species richness, and Shannon diversity). Using data from landscapes that are predominantly agricultural in Asia, Europe, and North and South America, we measured biodiversity responses to increased heterogeneity in landscape composition (number of correlations, K = 1,263; and studies, N = 80), landscape configuration (K = 1,164; N = 69), crop configuration (K = 463; N = 27), and crop composition (K = 313; N = 34). Meta-analytic models were then used to test the following questions and hypotheses:

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

Previous studies have predicted that crop and landscape compositional heterogeneity may each make available complementary resources to wildlife, while crop and landscape configurational heterogeneity may facilitate access to these resources, thereby positively impacting biodiversity (Dunning *et al.* 1992; Fahrig *et al.* 2011; Vasseur *et al.* 2013; Figure 1b). In line with these hypotheses, we predicted that beneficial biodiversity (i.e., excluding pests) would respond positively to an increase in both crop and landscape heterogeneity, as well as to an increase in both compositional and configurational heterogeneity (Figure 1c). We estimated the average effects of crop and landscape heterogeneity on the total abundance, species richness, and Shannon diversity of invertebrates, vertebrates, animals (both vertebrates and invertebrates), and plants, as well as for several functionally important groups (i.e., pollinators, predators and parasitoids, and pests).

(Q2). Does the relative strength of the effects of crop and landscape heterogeneity vary across taxa?

Previous studies have rarely compared the effects of crop and landscape heterogeneity or their compositional and configurational components on biodiversity (Batáry *et al.* 2020). We hypothesised that highly mobile large-bodied taxa, such as birds and other vertebrates, are able to use both crop and non-crop resources at large spatial scales (Monck-Whipp *et al.* 2018; Redlich *et al.* 2018; Li *et al.* 2020; Pustkowiak *et al.* 2021; Martínez-Núñez *et al.* 2023). We predicted they would benefit from landscape heterogeneity more than crop heterogeneity (Figure 1c). Conversely, less mobile small-bodied taxa, such as many invertebrates, may benefit from diverse cover types within their typically smaller home ranges (Zurbuchen *et al.* 2010; Hass *et al.* 2018; Priyadarshana *et al.* 2021; Cano *et al.* 2022; Maurer *et al.* 2022). Bees, spiders, and beetles, for example, generally have home ranges <0.5km^2 (Loreau & Nolf 1993; Zurbuchen *et al.* 2010; Seer *et al.* 2015), but large-bodied bees might exhibit larger foraging ranges (Greenleaf *et al.* 2007). As such, both crop and landscape heterogeneity would have comparatively similar effects on invertebrates (Figure 1c).

Plants are unable to evade disturbances within crop fields, therefore, we hypothesised that they would be primarily influenced by landscape heterogeneity, as it contains a larger extent of less-disturbed habitats hosting a larger source of seeds (Figure 1c). We also hypothesised that pests would benefit from monocultures and so respond negatively to increased crop heterogeneity (Baillod *et al.* 2017; Almdal & Costamagna 2023; Priyadarshana *et al.* 2023; Rakotomalala *et al.* 2023; Figure 1c). In addition, we hypothesised that pollinators and predators would benefit more from configurational heterogeneity as it may facilitate access to semi-natural habitats, i.e., along longer field margins (Fahrig *et al.* 2015; Hass *et al.* 2018; Sirami *et al.* 2019; Priyadarshana *et al.* 2021; Maurer *et al.* 2022).

(Q3). Does the relative strength of the effects of crop and landscape heterogeneity on biodiversity vary across different climatic regions and cropping systems?

Most large-scale assessments on biodiversity responses to crop and landscape heterogeneity have focused on temperate annual agroecosystems in Europe and North America (Tscharntke *et al.* 2021; Table S1). Nevertheless, several studies have been conducted in tropical/sub-tropical regions, as well as in perennial agroecosystems (see Table S1). 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 tropical/subtropical and temperate agroecosystems.

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

Wildlife in agricultural landscapes depends on resources available within different cover types and at various spatial scales (Gonthier *et al.* 2014). We predicted that biodiversity would respond positively to crop and landscape heterogeneity at various spatial scales (i.e., [i] <0.5km; [ii] ≥0.5km, but <1km; and [iii] ≥1km radius area) scales. However, differences in mobility between vertebrates and invertebrates (see *Q2*) suggest that vertebrates may respond strongly to heterogeneity measured at large spatial scale, while invertebrates may be affected by heterogeneity measured at small spatial scale.

MATERIAL AND METHODS

Literature search

We screened English Language papers published up to March 2023 from the 'Web of Science' (apps.webofknowledge.com/) and 'Scopus' (www.scopus.com/) using the search strings provided in the Supplementary Methods. After removing duplicates, we retrieved 647 studies in total. We then read the abstracts and data availability statements, and found 122 studies that met the inclusion criteria listed below. We have summarised this literature search in a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram (Moher *et al.* 2015; Figure S1).

Inclusion criteria

We applied the following inclusion criteria: (i) Crop heterogeneity should be measured based on individual crop types only, whereas landscape heterogeneity should be measured using both crop (often broad crop categories such as cereals, vegetables, and oilseeds) and non-crop land-cover types (e.g., natural/semi-natural vegetation and open water); (ii) 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 the 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). These were either available from the studies or post hoc calculated from raw data. These diversity indices effectively combine the number of cover types (cover type richness) and cover type evenness (proportion of each cover type) in the landscape, and have been widely used in previous studies (e.g., Fahrig *et al.* 2015, Redlich *et al.* 2018); (iii) 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; Sirami *et al.* 2019); (iv) Compositional heterogeneity components should not be strongly correlated with configurational heterogeneity components at a particular spatial scale (i.e., Pearson's r ≤0.6, Table S1). This ensured that the different heterogeneity components provided unique and independent information; (v) Biodiversity should be measured in crop fields, using field-level data on species richness, species diversity (i.e., Shannon diversity), or total abundance across all species.

Data compilation

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/natural area as a proportion of the total land area across study sites for a particular spatial scale. We extracted effect size measures and corresponding sampling sizes (N = the number of sampled fields) provided in each study when they matched our requirements described below; otherwise, we calculated the effect sizes and sampling sizes from study data (see below). Taxa in each study were categorised into taxonomic orders and functional groups, with a separate group for pests (Table 1), based on them being described as such in the original studies (Table S1). Where a taxon was considered to provide dual ecosystem services in the original study (e.g., wasps as pollinators and predators), it was included in both functional groups (Table 1). Taxa were also categorised into invertebrates, vertebrates, and plants. When using these groupings in analyses we excluded pest studies from the invertebrate and vertebrate groups to focus on the beneficial biodiversity components within each group. We also regrouped all animal taxa (excluding pests) into a larger category to address questions for which sample size was limited. Study systems were categorised based on the climatic region (i.e., tropical/subtropical or temperate agroecosystems) and the dominant cropping system of sites (i.e., annual or perennial crops).

To assess the effects of different kinds of heterogeneity in the agricultural landscapes on biodiversity, we categorised effect sizes into three main categories (Figure 1b): (i) spatial heterogeneity type (two levels: spatial compositional heterogeneity vs. spatial configurational heterogeneity); (ii) land-cover type (two levels: crop heterogeneity vs. landscape heterogeneity); and (iii) heterogeneity component (four levels: crop compositional heterogeneity, crop configurational heterogeneity, landscape compositional heterogeneity, and landscape configurational heterogeneity) (Table S2). To then assess biodiversity responses to these measures of heterogeneity in the landscapes at different spatial scales, we grouped effect sizes into three spatial scale categories that are commonly used in landscape ecology studies (Tables S1): (i) small (<0.5km radius area); (ii) intermediate (≥0.5km, but <1km radius area); and (iii) large (≥1km radius area) (Table S2), selecting these categories according to the range of scales available from the data sources. Data was sourced from data repositories (e.g., Dryad) following the data availability statement, directly from the papers' Supplementary Information, or requested from corresponding author(s).

Our dataset covered 6,397 fields across 60 major agricultural production regions of 24 countries across Asia, Europe, and North and South America (Table S1). These landscapes were predominantly cultivated lands (75% ± 14%, mean ± standard deviation), with low cover of semi-natural/natural vegetation (11% ± 8%). The remaining areas were represented by other anthropogenic land-cover types such as roads, buildings, or open water (13% ± 11%). This dataset contained more than 200 families of invertebrates, vertebrates, and plants, including animals belonging to four functional groups (i.e., pests, predators, pollinators, and decomposers; however, due to low sample sizes we did not analyse decomposers; Table 1). In total, we compiled 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

Given the relationships between biodiversity and crop/landscape heterogeneity were correlative, we calculated effect sizes as the Pearson's correlation coefficients (r) between each heterogeneity component (crop or landscape) and biodiversity (i.e., abundance, species richness, and Shannon diversity). These effect sizes were then transformed using Fisher's z with a sampling error variance (V) of 1/(N−3) (N = the number of fields sampled within an original dataset) to stabilise the variances and normalise the distributions (Borenstein 2009). These effect sizes were calculated separately for each taxonomic and functional group at each spatial scale across all the studies (Table S1).

Statistical analysis

Global model structure

The studies included in this analysis have computed crop or landscape heterogeneity components based on different land-cover maps, reflecting regional classification schemes (see Table S1). Consistent global land-cover 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, it was not possible to use a unique land-cover map to compute heterogeneity components and their effect sizes on biodiversity. At the same time, multiple effect sizes were derived from most of the studies for the computation of different heterogeneity components (composional vs.configurational, crop vs. landscape) across multiple spatial scales per taxon (see Table S1). Therefore, the true effect sizes from these measured/observed effect sizes varied due to both between study characteristics (i.e., between-study heterogeneity) and within-study specific random effects (i.e., within-study heterogeneity) (Raudenbush 2009). Meta-analytic models estimating the average true effect size resulting from a common intervention (i.e., increased spatial heterogeneity) must account for these variabilities/heterogeneities, which can be achieved by including random effects at both the study and the within-study effect size levels (Viechtbauer 2007; Raudenbush 2009). We therefore gave unique identifiers to each study (StudyID) and each effect size within each study (EffectSizeID), and included both in the models as random variables (see Tamburini *et al.* 2020). Taxa and measured heterogeneity component(s) for a particular study only contributed to the measured effect sizes in that study and did not cross between studies, resulting in EffectSizeID being nested within StudyID. 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 biodiversity metrics and crop/landscape heterogeneity components, and ‘V’ is the sampling error variance (see above).

Moderator analysis 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 (see Table S2).

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

(i) The effects of spatial heterogeneity type on biodiversity

Each crop and landscape heterogeneity component contributes to the overall spatial heterogeneity within the agroecosystem (Figure 1b). We first estimated the average effect of overall spatial heterogeneity in the landscape on biodiversity by running models without specifying any heterogeneity components as moderators (model 1 in Table S3). These models considered patterns across all the crop and landscape heterogeneity effect sizes to compute an average effect on biodiversity. We next ran models with only the spatial heterogeneity type (i.e., spatial compositional heterogeneity vs. spatial configurational heterogeneity) as a moderator to separate out the estimated average effect of compositional from configurational heterogeneity (model 2 in Table S3).

(ii) The effects of land-cover type on biodiversity

To investigate the effects of crop heterogeneity vs. landscape heterogeneity on biodiversity, we ran models including a moderator (i.e., land-cover type) that only specified each of these spatial components (model 3 in Table S3). In these models, the crop and landscape heterogeneity components were averaged across the corresponding heterogeneity types, i.e., compositional and configurational heterogeneity (Figure 1b).

(iii) The effects of heterogeneity components on biodiversity

To separate out the effects of the individual heterogeneity components, i.e., crop compositional heterogeneity, crop configurational heterogeneity, landscape compositional heterogeneity, and landscape configurational heterogeneity, we ran models including heterogeneity component as a moderator (Figure 1b; model 4 in Table S3).

These models were run separately for the different taxonomic (invertebrates, vertebrates, animals [vertebrates and invertebrates together], and plants) and functional (pollinators, predators, and pests) groups, considering the response for each biodiversity metric separately (Table S3). 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, and Lepidoptera) in our dataset, as well as for birds.

(Q2). Does the relative strength of the effects of crop and landscape heterogeneity vary across taxa?

To determine the relative importance of crop and landscape heterogeneity and their individual heterogeneity components on the taxa and functional groups, we conducted comparison tests on the estimated average effect for each level of the moderators in the above models (Table S3). Where moderators included two levels, they were directly compared using likelihood ratio tests. However, when the moderator had more than two levels, we compared each level by applying the 'Benjamini–Hochberg' procedure to control for errors associated with multiple testing (Benjamini & Hochberg 1995).

(Q3 & Q4). Does the relative strength of the effects of crop and landscape heterogeneity on biodiversity vary across different climatic regions, cropping systems, and spatial scales?

We assessed the effects of crop and landscape heterogeneity 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., [i] <0.5km; [ii] ≥0.5km, but <1km; and [iii] ≥1km). To do this, we ran separate models with each of these three factors as moderators (Table S2), and compared each level in them following the same procedure described for *Q2* (producing models 5–7 in Table S3). We ran separate models to avoid any dependencies between each level of the moderators (Viechtbauer 2007; Borenstein 2009). Due to data limitations, i.e., avoiding analyses when number of studies, N ≤ 5, we only estimated average effect of overall spatial heterogeneity (i.e., crop and landscape heterogeneity components together) in the landscape on animal biodiversity (vertebrates and invertebrates together) for different climatic regions and across different cropping systems. However, we estimated the average effect of overall spatial heterogeneity and the average effect of each heterogeneity type (i.e., compositional and configurational) across different spatial scales in the landscape for all taxonomic and functional groups.

We built the above models using the ‘rma.mv’ function with Restricted Maximum Likelihood (REML) estimation in the ‘metafor’ package (Viechtbauer 2010; Table S3) 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 only strong effects that did not contain zero within the 90% Confidence Intervals (CIs). Results derived from less than five studies (~ 2% of the dataset) were not considered robust and were excluded when making inferences.

Sensitivity analysis

We screened for model over-parameterisation, publication bias, influential studies, and outlier studies, and examined for confounding effects on our results that may be caused by the proportion of cropped, semi-natural, and other anthropogenic land-cover types (see Supplementary Methods). These tests found no issues (Figures S2–S5; Table S4) and confirmed that the primary drivers influencing our results were the heterogeneity of crop and non-crop habitats within the landscapes (Table S5).

RESULTS

Overall, increasing *spatial heterogeneity* (i.e., the average effects of all the components of crop and landscape heterogeneity) in the landscape increased all biodiversity metrics (total abundance, species richness, and Shannon diversity) for invertebrates, vertebrates, and pollinators. It also increased predator species richness and Shannon diversity, and plant species richness, but had no effects on the total abundance of plants, predators, or pests (Figures 2–7; Tables S6–S11).

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

(i) The effects of spatial heterogeneity type on biodiversity

Increasing *spatial compositional heterogeneity* (i.e., the average effect of both crop and landscape compositional heterogeneity) increased the species richness and Shannon diversity of invertebrates, vertebrates, pollinators (all insects), and predators, and the species richness of plants. It also increased the total abundance of vertebrates and pollinators. However, there were no significant effects on the total abundance of plants, invertebrates, predators, or pests (Figures 2–7; Tables S6–S11). Increasing *spatial configurational heterogeneity* (i.e., the average effect of both crop and landscape configurational heterogeneity) increased the species richness and Shannon diversity of invertebrates, pollinators, and predators, as well as the species richness of vertebrates and plants. Furthermore, it increased the abundance of vertebrates and pollinators, but had no significant effects on the total abundance of plants, invertebrates, predators, or pests (Figures 2–7; Tables S6–S11).

(ii) The effects of land-cover type on biodiversity

Increasing *crop heterogeneity* (i.e., the average effects of both crop compositional and configurational heterogeneity) increased the abundance, species richness, and Shannon diversity of invertebrates, vertebrates, and pollinators, along with predator Shannon diversity. However, there was no significant effect on any of the biodiversity metrics of plants, or on pest abundance (Figures 2–7; Tables S6–S11). Increasing *landscape heterogeneity* (i.e., the average effects of both landscape compositional and configurational heterogeneity) increased vertebrate and pollinator abundance, as well as the species richness of invertebrates, vertebrates, pollinators, predators, and plants. Moreover, it increased the Shannon diversity of invertebrates, pollinators, and predators, while also increasing pest abundance (Figures 2–7; Tables S6–S11).

(iii) The effects of heterogeneity components on biodiversity

Increasing *crop configurational heterogeneity* increased the abundance and species richness of invertebrates and pollinators. Furthermore, it increased the Shannon diversity of invertebrates, pollinators, and predators, while having no significant effects on vertebrates, plants, or pests (Figures 2–7; Tables S6–S11). Increasing *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 Shannon diversity of invertebrates, pollinators, and predators, but had no significant effect on pest abundance and plant species richness (Figures 2–7; Tables S6–S11). Increasing *crop compositional heterogeneity* increased the abundance of pollinators and vertebrates, as well as the species richness and Shannon diversity of invertebrates and pollinators. However, it had no significant effect on predators, plants, or pests (Figures 2–7; Tables S6–S11). Increasing *landscape compositional heterogeneity* increased the abundance of pollinators and pests, as well as the species richness of invertebrates, vertebrates, pollinators, and predators. It also increased the Shannon diversity of invertebrates, pollinators, and predators, but had no significant effect on the species richness of plants (Figures 2–7; Tables S6–S11).

Most invertebrate taxonomic orders in our dataset, i.e., Araneae, Coleoptera, Diptera, Hymenoptera, and Lepidoptera and birds, also responded positively to increases in both crop and landscape heterogeneity components. These components had more positive effects on the species richness and Shannon diversity of each taxonomic order than on their abundance, with the exception of Hymenoptera and birds, which showed stronger positive abundance responses (Figures S6–11; Tables S12–S17).

(Q2). Does the relative strength of the effects of crop and landscape heterogeneity vary across taxa?

For vertebrate richness (mainly birds), landscape heterogeneity was more important than crop heterogeneity (Tables S18–S19). In contrast, for the abundance, species richness, and Shannon diversity of invertebrates and pollinators, both crop and landscape heterogeneity were important without one being significantly more important than the other (Tables S20–S21). For plant species richness and pest abundance, only landscape heterogeneity had a significant positive effect, while crop heterogeneity had no effect (Tables S22–S23).

Regarding individual heterogeneity components, vertebrate species richness, including bird richness, showed significantly higher increases with increased landscape configurational heterogeneity compared to crop compositional heterogeneity (Tables S18–S19). Conversely, all biodiversity metrics for invertebrates and pollinators were positively influenced by all compositional and configurational heterogeneity components, with no significant differences (Tables S20–S21). Some pollinator groups, such as Hymenoptera richness and Diptera Shannon diversity showed significantly higher increases with increased crop configurational heterogeneity compared to crop compositional heterogeneity (Tables S24–S25). Moreover, crop configurational heterogeneity was as important as landscape compositional or configurational heterogeneity for Hymenoptera richness (Table S24). In contrast, both landscape compositional and configurational heterogeneity were more important than crop compositional heterogeneity for Diptera Shannon diversity (Table S25).

For predator Shannon diversity, including Coleoptera and Araneae, while compositional and configurational heterogeneity were important, they benefited significantly more from compositional heterogeneity (spatial or landscape) compared to configurational heterogeneity (Tables S27–S28). For plants, pests, and Lepidoptera, we only had limited data, so the comparisons between individual heterogeneity components were limited to certain heterogeneity components, which did not differ significantly (Tables S22–S23 & S29).

(Q3). Does the relative strength of the effects of crop and landscape heterogeneity on biodiversity vary across different climatic regions and cropping systems?

Increasing spatial heterogeneity (i.e., the average effects of all the components of crop and landscape heterogeneity) in the landscape had a strong positive effect on all studied biodiversity metrics for animals (i.e., invertebrates and vertebrates together) (Figure S12; Table S30). Importantly, these positive effects remained consistent, and were not significantly different between tropical/subtropical and temperate agroecosystems (Figures S13–S14; Tables S31–32), or between annual and perennial cropping systems (Figures S15–S16; Tables S33–34). These comparisons were not possible for other taxa or functional groups due to the limited availability of studies.

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

Increases in the overall spatial heterogeneity at all spatial scales significantly increased all studied biodiversity metrics for invertebrates, pollinators, and predators (Tables S35–S37). In contrast, for vertebrates, increasing spatial heterogeneity increased all biodiversity metrics only at intermediate or large spatial scales, i.e., ≥0.5km radius (Table S38). Increases in compositional and configurational heterogeneity at all spatial scales also increased most biodiversity metrics for invertebrates, vertebrates, pollinators, and predators (Tables S35–S38), although these positive effects differed little among each spatial scale (Tables S39–S42).

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. Increases in at least one of the crop or landscape heterogeneity components (i.e., compositional or configurational heterogeneity) significantly increased the field-level biodiversity (total abundance, species richness or Shannon diversity) of invertebrates, vertebrates, and plants, as well as the biodiversity of pollinators and taxa providing predatory natural pest control (both invertebrates and vertebrates). Our findings emphasise the value of enhancing crop and non-crop heterogeneity at all spatial scales to increase biodiversity in agricultural landscapes. These positive effects were consistent in both tropical/subtropical and temperate agroecosystems, as well as in both annual and perennial cropping systems. Although the presence of semi-natural cover is key to biodiversity conservation in agroecosystems (Duelli & Obrist 2003; Holland *et al.* 2017; Sirami *et al.* 2019), our sensitivity analysis confirmed that these results were not influenced by the proportion of semi-natural cover within the landscapes. Instead, our findings likely reflect complex system-level utilisation of crop and non-crop resources by different taxonomic and functional groups. For those taxa able to persist in agricultural landscapes, crop and landscape heterogeneity appears to make available crucial complementary resources (Dunning *et al.* 1992; Fahrig *et al.* 2011). Overall, our results suggest that increasing spatial heterogeneity through crop and landscape heterogeneity could be a useful strategy to support biodiversity across most agricultural landscapes around the world.

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

Overall spatial heterogeneity has a wide range of biodiversity benefits

Increasing overall spatial heterogeneity, which incorporates compositional and configurational heterogeneity for both crop and non-crop cover types, had strong positive effect on most biodiversity metrics. This was typically greater than those of the heterogeneity components (crop or landscape) when considered individually. For example, we found limited effects of each individual compositional or configurational heterogeneity component on the abundance of studied taxa. However, overall spatial heterogeneity incorporating both crop and non-crop heterogeneity components showed positive effects on all the biodiversity metrics, including the total abundance of most taxa. This could be because promoting a single heterogeneity component alone may not compensate for the absence of key habitats that provide fundamental resources (e.g., breeding sites, foraging habitats, and dispersal routes) required for population persistence (e.g., Kleijn & Verbeek 2000; Holzschuh *et al.* 2011; Kleijn *et al.* 2015; Redlich *et al.* 2018). This also suggests that supporting biodiversity in agroecosystems by increasing semi-natural cover, such as including wildflower strips adjacent to crop fields (Albrecht *et al.* 2020), represents only one part of the solution. Rather, supporting biodiversity in agroecosystems depends on maximising the diversity of both semi-natural and cropland cover resources through increased compositional and configurational heterogeneity. Shifts to intensive monocultures with large fields negatively impact species adapted to utilise resources across spatially heterogeneous systems, particularly specialist species (Tscharntke *et al.* 2005, 2012; Gámez-Virués *et al.* 2015; Martin *et al.* 2019; Hua *et al.* 2024). Our results, suggest that increased spatial heterogeneity in both crop and non-crop cover types can go some way to reverting or at least slowing down the negative effects of agricultural intensification on biodiversity.

Benefits to biodiversity can come from different heterogeneity components

Our results on the effects of different components of spatial heterogeneity on biodiversity contribute to a more mechanistic understanding of the factors influencing biodiversity in agricultural landscapes. Higher crop or landscape compositional heterogeneity increases the variability between land-cover (or crop) types by incorporating diverse habitat types into the landscape that often harbour different wildlife communities compared to monocultures of similar size (Benton *et al.* 2003; Tews *et al.* 2004; Fahrig *et al.* 2011; Tscharntke *et al.* 2012). The presence of such a diverse array of habitats creates a wider range of spatially separated biotic and abiotic resources within the landscape (Tews *et al.* 2004; Fahrig *et al.* 2011). This resource diversity could play a crucial role in promoting biodiversity as many species rely on multiple resources provided by several different habitats 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). Resource complementarity occurs when taxa need more than one (or at least two) non-substitutable resources that are spatially separated across landscapes (Dunning *et al.* 1992; Mandelik *et al.* 2012). For example, invertebrates often rely on spatially separated complimentary resources to complete their life cycles, e.g., nesting vs. nectar and pollen-providing sites for bees, host plants vs. nectar-providing flowering plants for butterflies, and host vs. food resources for parasitoids (Steffan-Dewenter & Tscharntke 1997; Landis *et al.* 2000; Requier *et al.* 2015; Antoine & Forrest 2021). Diverse crop and non-crop cover types can increase such resource complimentary habitats in the landscape (Benton *et al.* 2003; Fahrig *et al.* 2011; Vasseur *et al.* 2013; Sirami *et al.* 2019). Furthermore, diverse habitats are likely to ensure a continuity of resources across the landscapes, both spatially and temporally, and thereby positively impact biodiversity (Fahrig *et al.* 2011; Schellhorn *et al.,* 2015).

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; Priyadarshana *et al.* 2021). Such landscape structures may facilitate animal movements by increasing inter-field connectivity through increased transition zone areas, thereby reducing energy requirements for traveling between habitats, improving resource accessibility, and promoting biodiversity (Fahrig *et al.* 2011; Blitzer *et al.* 2012; Tscharntke *et al.* 2012; Hass *et al.* 2018). These field margins/edges are often comprised of semi-natural vegetation, which typically supports greater biodiversity relative to managed crop fields (Marshall & Moonen 2002; Collins & Fahrig 2017; Jeanneret *et al.* 2021). For example, field margins could offer foraging resources and undisturbed nesting sites for pollinators (e.g., Marshall & Moonen 2002; Woodcock *et al.* 2009, 2016; Rands & Whitney 2011; Kormann *et al.* 2016; Hass *et al.* 2018, but see Kennedy *et al.* 2013) and predators (e.g., Marshall & Moonen 2002; Woodcock *et al.* 2005, 2009, 2016; Holzschuh *et al.* 2009; Fahrig *et al.* 2015; Ramsden *et al.* 2015; Baillod *et al.* 2017).

Our results are consistent with hypotheses predicting positive effects of both compositional and configurational heterogeneity. We found consistent positive effects of crop and landscape compositional heterogeneity on species richness and diversity of invertebrates, vertebrates, pollinators, and predators. Similarly, our results showed positive effects of crop and landscape configurational heterogeneity on species richness and Shannon diversity for all the studied groups, except plants, pests, and beetles. Our study selection procedure ensured that the compositional and configurational heterogeneity components were not highly correlated ($r \leq 0.60$), suggesting their independent impact on biodiversity. Therefore, promoting both these heterogeneity components simultaneously could increase biodiversity benefits. Our results support this idea, as we found simultaneously increasing compositional and configurational heterogeneity in crop cover types (i.e., crop heterogeneity), or in both crop and non-crop cover types (i.e., landscape heterogeneity), consistently increased most biodiversity metrics for the studied taxa and functional groups.

(Q2). Does the relative strength of the effects of crop and landscape heterogeneity vary across taxa?

Vertebrates and plants benefit more from landscape heterogeneity than crop heterogeneity

As we hypothesised, increases in both crop and landscape heterogeneity had overall positive but variable effects on the different taxa. 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 insufficient to support vertebrate taxa (Vickery *et al.* 2009; Collins & Fahrig 2017; Lee & Goodale 2018; Monck-Whipp *et al.* 2018; Redlich *et al.* 2018). This group contained high-trophic level and larger-bodied taxa that are highly mobile and have larger home ranges (e.g., birds and bats) compared to many invertebrate taxa. Previous studies have shown that birds and bats in agricultural landscapes require varying vegetation structures such as native herbaceous plants, shrubs, woodlands, and large isolated trees, for foraging and breeding (Benton *et al.* 2003; Tscharntke *et al.* 2005; Manning *et al.* 2006; Mendes *et al.* 2017; Hunninck *et al.* 2022). As such, they are likely to exploit both crop and non-crop resources at intermediate to large spatial scales (Tscharntke *et al.* 2005, 2012; Martin *et al.* 2016; Mendes *et al.* 2017; Redlich *et al.* 2018).

For plants, our result show positive effects in response to increases in landscape heterogeneity only, which was not surprising since croplands do not include large tracts of undisturbed lands and plants are unable to move out of crop fields to avoid disturbances (e.g., herbicides or cultivation). Previous studies have found that some plant communities, such as herbaceous weeds, particularly non-native species, can live adjacent to crops and so would benefit from crop heterogeneity, especially from crop configurational heterogeneity (Roschewitz *et al.* 2005; Nagy *et al.* 2018; Zhou *et al.* 2018; but see Alignier *et al.* 2020). This hypothesis, however, was not supported by our results, suggesting that crop heterogeneity benefits might be insufficient to support a wide range of plant species; rather, many plant species need less-disturbed diverse semi-natural/natural cover types that landscape heterogeneity can provide.

Invertebrates derive similar benefits from both crop and landscape heterogeneity

In line with our hypothesis, the strengths of increasing crop heterogeneity and landscape heterogeneity were comparable for both invertebrates as a whole and for insect 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. Previous large-scale studies have also indicated that invertebrate communities, particularly pollinators, in agricultural landscapes, tend to be generalists relying on a wide range of resources for both feeding and nesting (Kleijn *et al.* 2015; Redhead *et al.* 2018). They may exploit resources for foraging and nesting by moving between crop fields and semi-natural habitats along field margins (Hass *et al.* 2018; Iles *et al.* 2018; Priyadarshana *et al.* 2021). However, these patterns may be different for specialist pollinators such as large-bodied bees with larger foraging ranges and bees that forage only on certain plant species

(Greenleaf *et al.* 2007; Antoine & Forrest 2021; Neira *et al.* 2024).

Pests also benefit from landscape heterogeneity

Contrary to our hypothesis, the decrease in monocultures through increased crop heterogeneity did not result in a significant negative effect on pest abundance. Instead, we found a 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 pests by offering favourable resources (Tscharntke *et al.* 2016). Alternatively, the results may suggest that natural enemy populations are insufficient or are mismatched spatially or temporally with economically significant pests in these landscapes (Tscharntke *et al.* 2016; Grab *et al.* 2018; Karp *et al.* 2018; Martínez-Núñez *et al.* 2021). Therefore, farmers may have to reconfigure the cover type mosaic by removing or reducing the area of the major pest source habitats, while incorporating more habitats that support their natural enemies (Bailey *et al.* 2009; Chaplin-Kramer *et al.* 2011; Gurr *et al.* 2016; Baillod *et al.* 2017; Dominik *et al.* 2018; Martin *et al.* 2019; Rakotomalala *et al.* 2023; Plata *et al.* 2024), although achieving this in practice is likely not realistic in most cases.

Pollinators could benefit more from configurational heterogeneity, while predators may benefit more from compositional heterogeneity

The positive effects of compositional and configurational heterogeneity on invertebrates did not significantly differ. However, our taxonomic order level analysis suggested that some pollinators, such as Hymenoptera and Diptera, benefited from configurational heterogeneity more than compositional heterogeneity in crop fields. As these groups are comprised of flying insect pollinators, they can exploit resources from various cover types within the landscape, and thus the connectivity between different fields may be more important to support their cross-habitat movements, rather than a particular cover type (Tscharntke *et al.* 2012; Hass *et al.* 2018; Priyadarshana *et al.* 2021). In contrast, for Coleoptera and Araneae, the compositional heterogeneity component was more important than configurational heterogeneity. As these groups are comprised of predators with low mobility, they may benefit from particular habitat types within the landscape (Kromp 1999; Aviron *et al.* 2005; Martin *et al.* 2016; Boetzl *et al.* 2020; Priyadarshana *et al.* 2021). For example, ground beetles and spiders may utilise certain crop fields for hunting when pest populations are high, and move into nearby field margins to forage as the crops senesce, highlighting the importance of temporal crop dynamics and semi-natural habitats (Sotherton 1984; Aviron *et al.* 2005; Bianchi *et al.* 2006; Gallé *et al.* 2018). This pattern, however, contrasts to that of highly mobile predators that move among distinct habitats at various spatial scales (Aviron *et al.* 2005; Tscharntke *et al.* 2012; Bertrand *et al.* 2016; see above).

(Q3). Does the relative strength of the effects of crop and landscape heterogeneity on biodiversity vary across different climatic regions and cropping systems?

Recent syntheses and meta-analyses have highlighted that the adverse effects of agricultural intensification on biodiversity could vary across different climatic regions/biomes and cropping systems/crop types (Batáry *et al.* 2020; Oakley & Bicknell 2022). This raises the question of whether a successful biodiversity-friendly farming initiative in one system will produce similar effects in other systems (Tscharntke *et al.* 2021). Interestingly, our results suggest that the positive effect of overall spatial heterogeneity (the average effects of crop and landscape heterogeneity together) on all the studied biodiversity metrics for animals (invertebrates and vertebrates) did not significantly differ between tropical/subtropical and temperate climatic regions, or between annual and perennial cropping systems. This suggests that increasing crop and landscape heterogeneity can be a strategy to support agroecosystem biodiversity in most parts of the world. However, although there was no publication bias in our dataset, it must be noted that our dataset lacked representation from African and Australian agroecosystems (Table S1). Nevertheless, the focus on broad taxonomic groups and fundamental biodiversity metrics (i.e., total abundance, species richness, and Shannon diversity) suggest that similar biodiversity responses to spatial heterogeneity are likely to be meaningful outside of our geographic scope.

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

Previous studies have hypothesised that different taxa may benefit from spatial heterogeneity at different spatial scales, based on their mobility and specific resource demands (Tscharntke *et al.* 2005, 2012; Martin *et al.* 2016). This hypothesis was supported by our results as vertebrate abundance, species richness and Shannon diversity increased significantly with increases in landscape scale heterogeneity at intermediate or large spatial scales (≥0.5km radius), while no such effect was observed at small spatial scale (<0.5km radius). This trend was consistent for both compositional and configurational heterogeneity components for vertebrates. Invertebrate taxa, however, benefited from spatial heterogeneity, including compositional and configurational heterogeneity, at all spatial scales. It is likely that both vertebrates and invertebrates exploit resources from crop small spatial scales, while they may use complementarity resources from other non-crop habitats at large spatial scale (Dunning *et al.* 1992; Marshall & Moonen 2002; Tscharntke *et al.* 2005, 2012; Gonthier *et al.* 2014; Martin *et al.* 2016). Therefore, promoting crop and landscape heterogeneity only at small spatial scale may not be enough to support some taxa; rather, the heterogeneity at smaller (often farmer-owned areas) to larger spatial scales (often non-farmer-owned areas) is crucial to maximise resource complementarity and to support agroecosystem biodiversity (Dunning *et al.* 1992; Altieri 1999; Mandelik *et al.* 2012; Gonthier *et al.* 2014).

CONCLUSIONS AND POLICY IMPLICATIONS

This meta-analysis provides the strongest evidence to date that increasing spatial heterogeneity through the diversity of crop and non-crop cover types in agricultural landscapes provides significant benefits to biodiversity. Importantly, the majority of the landscapes we considered in the analyses were dominated by cultivated lands, with limited semi-natural areas, suggesting that conventional farming systems have the potential to be managed in a way that provides significant benefits for biodiversity. Our results suggest that 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 (i.e., small fields and high crop diversity), although benefits for biodiversity will be limited compared to increased landscape-wide 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 crop production and biodiversity.

Like any management techniques, there are also 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 to regional conditions, as far as possible, through engagement with stakeholders (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). Ultimately, achieving win-win outcomes will likely require improvement of the heterogeneity of agricultural landscapes, considering both farmer-owned and non-farmer-owned areas.

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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**
Predators (K = 1595; N = 75)	Carabid beetles (27%)	Coleoptera
	Spiders (25%)	Araneae
	Birds (16%)	NA
	Wasps (including Parasitoids, 12%)	Hymenoptera
	Rove beetles (8%)	Coleoptera
	Ladybugs (2%)	Coleoptera
	True bugs (2%)	Hemiptera
	Dragonflies/Damselflies (1%)	Odonata
	Bats (all are insectivorous, 1%)	Chiroptera
	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 (49%)	Hymenoptera
	Hoverflies (24%)	Diptera
	Wasps (11%)	Hymenoptera
	Butterflies (11%)	Lepidoptera
	Tachinid flies (1%)	Diptera
Primary producers (K = 116; N = 23)	Plants (mostly herbaceous species, 100%)	NA
Pests (K = 170; N = 25)	Aphid (48%)	Hemiptera
	Pollen beetles (24%)	Coleoptera
	Small Rodents (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

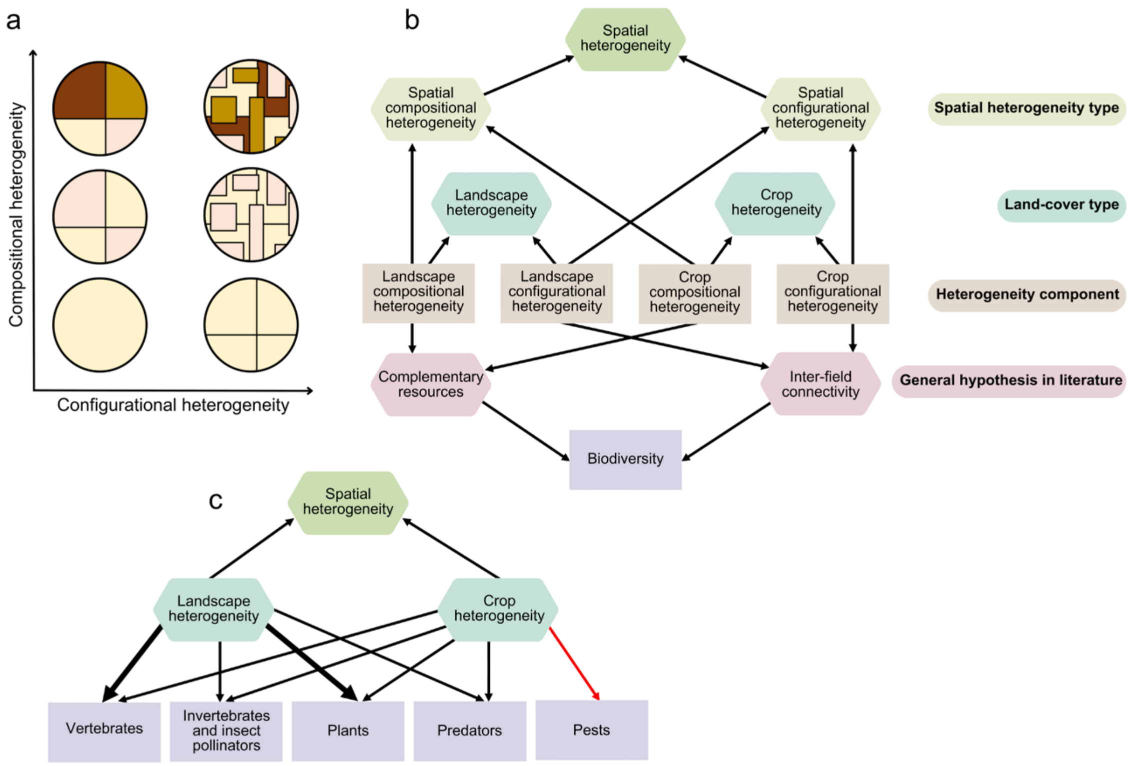

Figure 1. A graphical representation showing the key concepts of the study. **(a)** Difference between compositional and configuration heterogeneity components (adapted from Fahrig *et al.* 2011). Various cover types (crop and non-crop) are shown in different colours, with their margins/borders highlighted in black. Note that crop heterogeneity components are measured only based on crop types, while landscape heterogeneity components are measured based on both crop and non-crop cover types. **(b)** Conceptualised causal mechanisms. The conceptualised variables are presented in hexagonal shapes and the measured/observed variables are shown in rectangular shapes. **(c)** Tested hypotheses. Black arrows indicate positive effects, the red arrow suggests a negative effect, and the thicker arrows denote significantly stronger effects compared to other sources. Due to the complexity, hypotheses associated with individual compositional and configurational heterogeneity components are not shown in this figure. For more details, please see *Q1-Q4* in the Introduction.

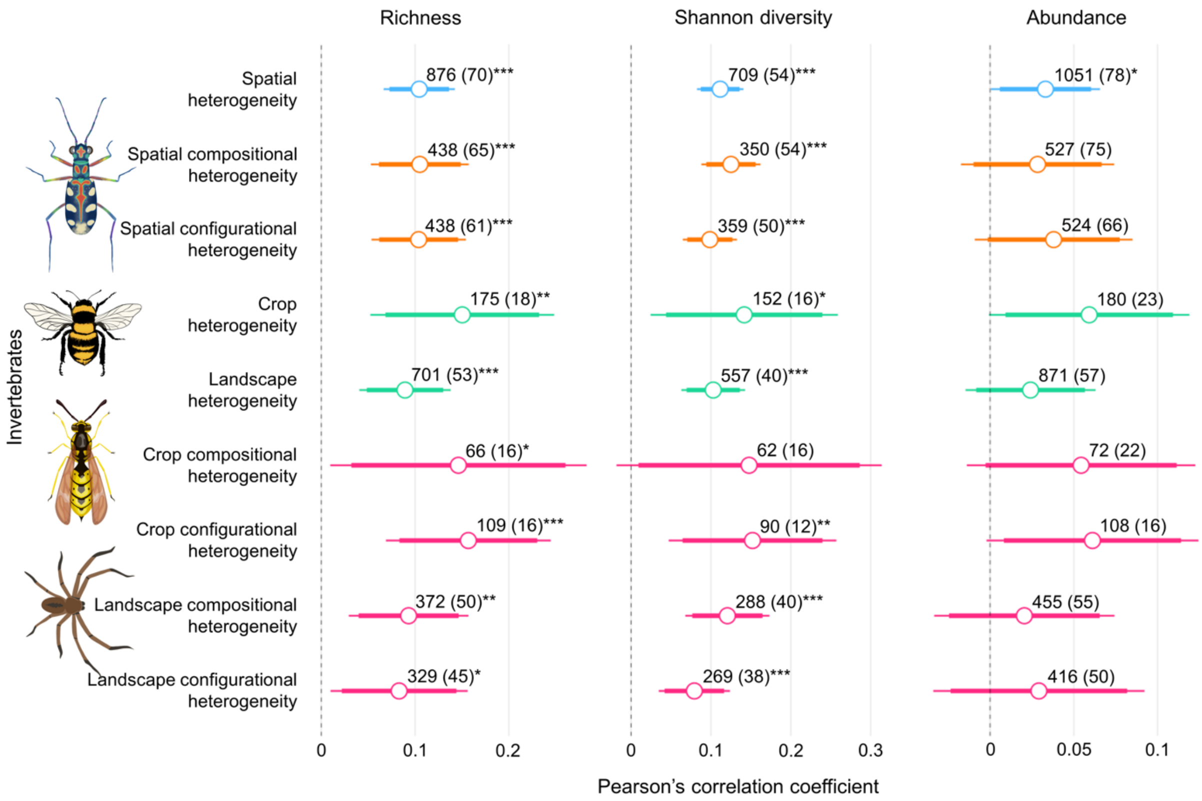

Figure 2. Estimated average Pearson's correlation coefficients among heterogeneity components and invertebrate, excluding pests, biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Different colours indicate how the data were subdivided for each corresponding model, i.e., blue for the model without a moderator, orange for the model with the 'Spatial heterogeneity type' as a moderator, green for the model with the 'Land-cover type' as a moderator, and pink for the model with the 'Heterogeneity component' as a moderator (see Table S3). The number of correlations and studies (in parentheses) included for each estimation are displayed beside the upper bound of the 95% CIs. Asterisks indicate level of the statistical significance (*P-value <0.05, **P-value <0.01, ***P-value <0.001). The dashed line indicates the zero X-axis intercept. See Table S6, for detailed statistics.

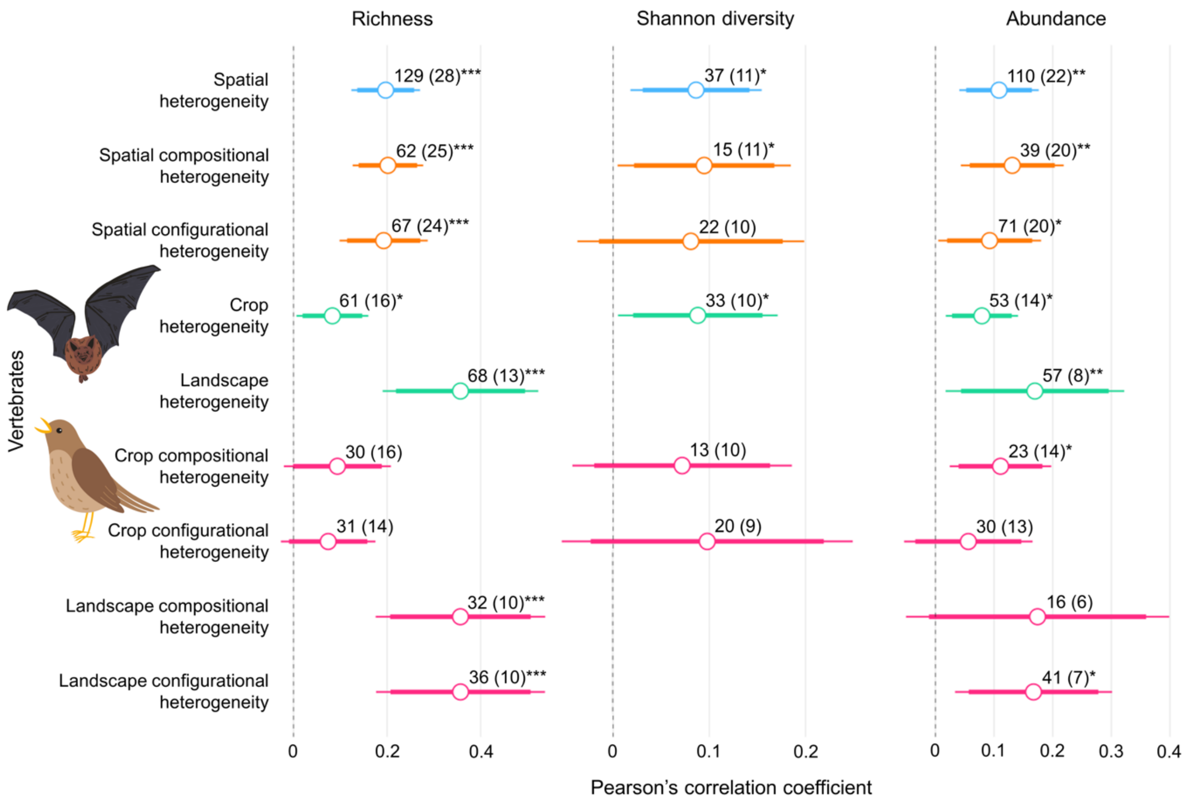

Figure 3. Estimated average Pearson's correlation coefficients among heterogeneity components and vertebrate, excluding pests, biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 2. See Table S7, for detailed statistics.

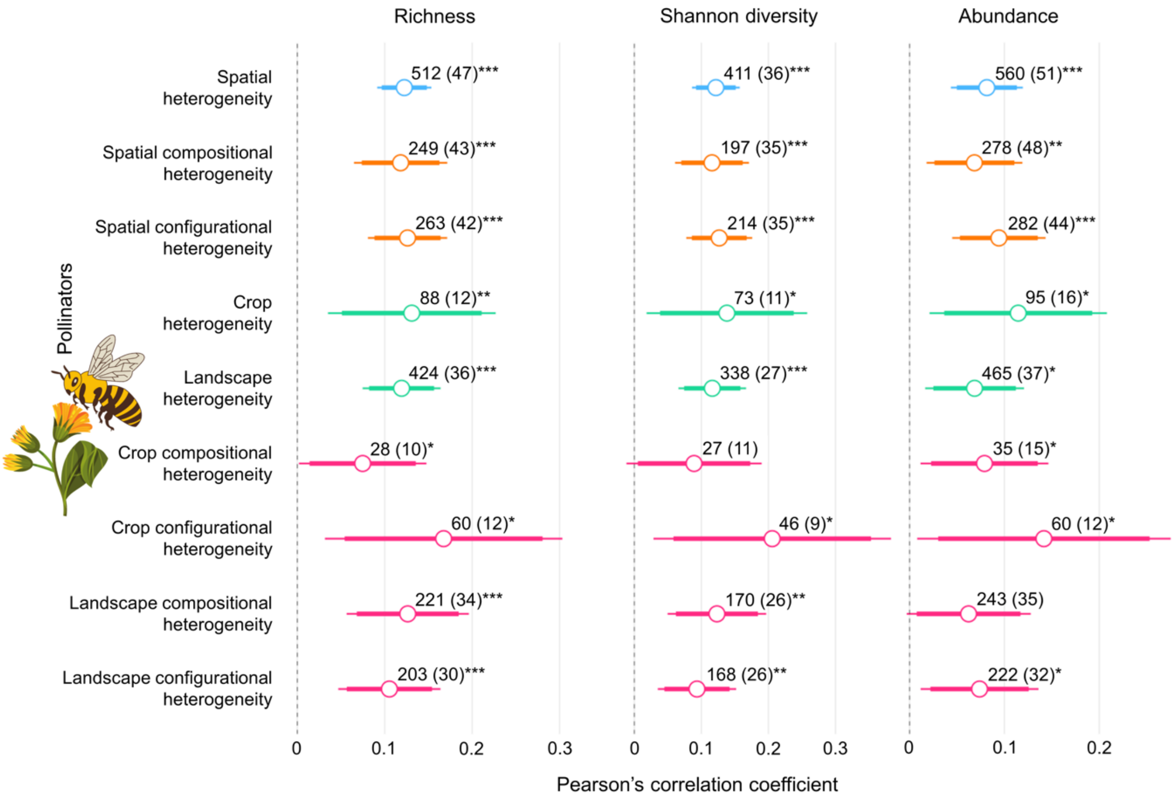

Figure 4. Estimated average Pearson’s correlation coefficients among heterogeneity components and pollinator biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 2. See Table S8, for detailed statistics.

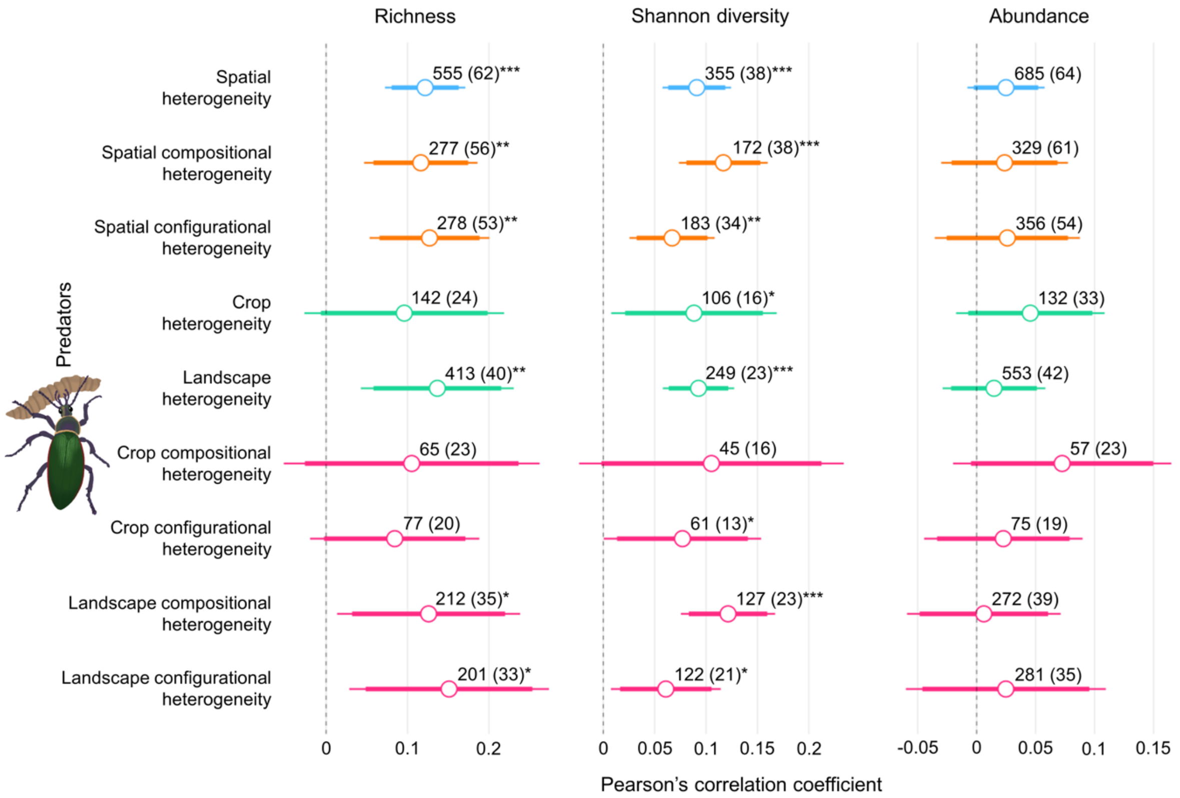

Figure 5. Estimated average Pearson's correlation coefficients among heterogeneity components and predator biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 2. See Table S9, for detailed statistics.

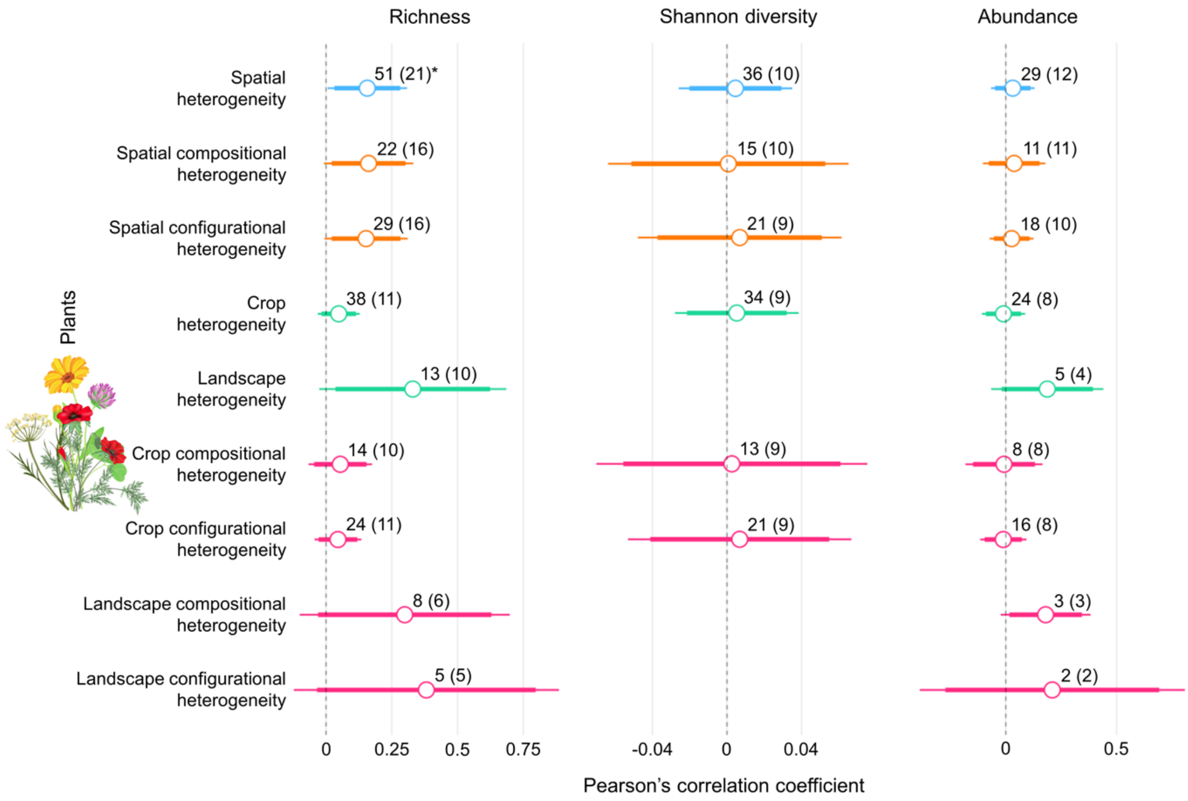

Figure 6. Estimated average Pearson's correlation coefficients among heterogeneity components and plant biodiversity, with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 2. See Table S10, for detailed statistics.

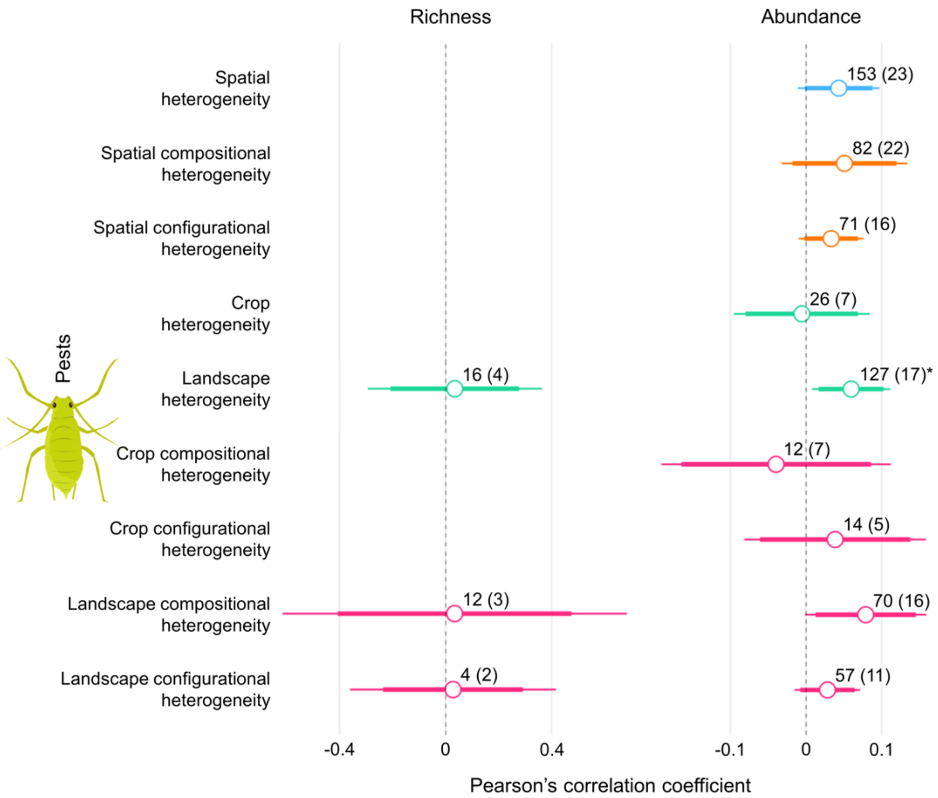

Figure 7. Estimated average Pearson's correlation coefficients among heterogeneity components and pest abundance (pest richness results were not interpreted due to the smaller number of studies, i.e., >5), with 90% (thicker bars) and 95% (thinner bars) Confidence Intervals (CIs). Other details analogous to those in Figure 2. See Table S11, for detailed statistics.