Direct and cascading impacts of landscape heterogeneity and agrochemical use on multi-trophic biodiversity in the patchy agroecosystem

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ABSTRACT

Farmland biodiversity is declining globally due to intensified agricultural practices, landscape homogenization, and simplification. However, the direct and cascading effects of landscape heterogeneity and agrochemical use on various interacting taxa and trophic levels remain unclear. This study investigated the richness and abundance of taxa across trophic levels, including weeds, epigeic invertebrates, and birds, within a patchy agroecosystem in Pengzhou, Sichuan, China. Structural equation modeling was used to analyze the responses of multi-taxa and trophic levels to agrochemical use, edge density and cropland diversity, and quantify the direct and indirect effects therein. Results showed that landscape heterogeneity and agrochemicals influenced the abundance and richness of weeds, epigeic invertebrates, and birds through direct impacts and bottom-up cascading effects. Agrochemicals negatively affected weeds and invertebrates at lower trophic levels, while edge density had positive effects. Both factors also exerted cascading effects on invertebrates and birds, and the magnitude of net effects diminished as trophic level increased. Cropland diversity reduced weed and invertebrate abundance, likely through competition between weeds and crops and frequent soil disturbances during farming, but exerted positive effect on crop-feeding birds probably due to additional food supply. These findings reveal varied responses of trophic groups with distinctive traits in size, mobility, and resource utilization to landscape heterogeneity and agrochemical use, and highlight the importance of biotic interactions in regulating these ecological processes. This study indicates that reducing agrochemicals use alongside enhancing landscape heterogeneity can promote multi-trophic biodiversity and sustain ecosystem services in patchy agroecosystems.

1. Introduction

Agricultural expansion and intensification have profoundly altered the structure of agro-ecosystems, posing significant threats to biodiversity (Fahrig, 2003; Wan et al., 2021; Laurance et al., 2014), and their associated ecosystem services such as pollination and biological pest control (Redlich et al., 2018; Raderschall et al., 2021). The conversion of natural habitats to farmland monocultures reduces the diversity of agricultural landscapes (i.e., compositional heterogeneity), thereby affecting the niche availability for various biological taxa (Marcacci et al., 2022; Salek et al., 2025). Additionally, configurational heterogeneity, i.e., the spatial arrangement of landscape elements, impacts the taxonomic and functional diversity of these taxa through edge and spillover effects (Fahrig et al., 2011). Locally, agricultural managements, such as agrochemical use, brings about different ecological consequences at the field level. While effectively controlling target

species by increasing mortality and reducing fecundity of weeds and herbivorous invertebrates (Griffiths et al., 2008), the agrochemicals simultaneously exert negative impacts on non-target organisms, potentially disrupting ecological stability (Wan et al., 2025). These managements are being increasingly intensified to meet growing demands for effective pest control and crop yield (Tscharntke et al., 2005; 2007). Therefore, addressing the impacts of agricultural landscape heterogeneity and agrochemical use on multi-trophic biodiversity and their underlying mechanisms is the top priority, especially concerning the increasing global food demand.

While researches have explored how agricultural landscape structure and management intensity would affect diversity across taxa, including small mammals (Coda et al., 2015), birds (Guerrero et al., 2011), invertebrates (Benton et al., 2002), and plants (Newbold et al., 2015; Carmona et al., 2020), these investigations have predominantly focused on narrow taxonomic groups and limited trophic-level coverage within

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each taxon (Liere et al., 2015). Further, the findings often vary by taxon and trophic group, probably due to their distinctive life history, dispersal capacity, size, and ecological niche (Leyequien et al., 2010; Vanbergen et al., 2010; Molina et al., 2016). For instance, habitat complexity supports a diverse community of birds and butterflies, but not fruit bats (Azhar et al., 2015). The loss of native vegetation in agroecosystems negatively impacted predatory invertebrates and decomposers, whereas herbivorous invertebrates were less affected (Attwood et al., 2008). Similarly, agrochemical use has varying effects on different invertebrate groups (Meehan et al., 2011), with predators and decomposers often being more negatively affected than herbivores (Attwood et al., 2008). Although numerous studies have shown that farmland reduces invertebrate diversity through habitat filtration, an increase in farmland area promotes pest populations depending on farmland habitats (Wan et al., 2021). Despite these insights, most studies are restricted to a single taxonomic or trophic group, overlooking biotic interactions within complex multi-trophic communities (but see Martin et al. 2019; Tortosa et al. 2022). Trophic cascade is defined as the transmission of indirect effects between trophic levels within a food web or food chain (Wan et al., 2020; Wan et al., 2024). Perturbations at specific trophic levels can affect the diversity and resources use of adjacent levels through bottom-up or/and top-down cascading effects, which may either amplify or counterbalance the direct impacts of agricultural intensification (Barnes et al., 2017). For example, Carbonne et al. (2022) demonstrated that intensive field management directly exerted a toxic effect on low-trophic weeds while indirectly impacting higher-trophic carabids through resource depletion. Conversely, Barnes et al. (2017) found that intensified land-use directly reduced detritivore richness by 66 %, but indirectly increased it by boosting microbial richness. Wan et al. (2020); (2022) suggested that both species diversity and genetic diversity of plants enhance the diversity of natural enemies, such as invertebrate predators and parasites, thereby improving plants viability. These findings highlight the significance of teasing apart direct and indirect effects of biotic interactions on multi-trophic groups (Denno et al., 2002; Scherber et al., 2010; Haddad et al., 2011; Borer et al., 2012). Unfortunately, these direct and cascading processes have rarely been examined and compared in field studies, especially in agroecosystems with patchy landscapes and high trophic complexity (Gagic et al., 2011). Unlike continuous stands of monocultures with large and regular-shaped fields, small-holder patchy farmlands have the potential to maintain a high biodiversity by providing diverse habitats and resources but have been largely overlooked (Li et al., 2020). These intrinsic differences between the two agricultural systems may influence how trophic groups respond to landscape heterogeneity or agricultural management (Benton et al., 2003; Fahrig et al., 2011).

China, with its extensive agricultural history, has preserved numerous traditional small-holder agricultural systems (Li et al., 2020). These systems hold significant biodiversity conservation value and provide an excellent platform for studying the impacts of landscape heterogeneity and agricultural management on complex multi-trophic biodiversity (Lee and Goodale, 2018). Revealing these impacts and their underlying pathways could allow stakeholders to identify conservation priority, such as taxa with especially importance in regulating the structure of food web or provide most important ecosystem services, thereby benefitting biodiversity conservation and agricultural management efforts in these small-holder patchy agroecosystems.

Here, we explored the direct and cascading effects of landscape heterogeneity and agrochemical use on the richness and abundance (or coverage) of weeds, invertebrates, and birds in a typical patchy agroecosystem of South China, which is composed of fine-grained agricultural landscapes with an average patch size of 0.07 ha (Fig. S1).The structural equation models (SEMs), as the most extensively used path models (Duflot et al., 2022), were applied to examine the direct effects of landscape heterogeneity and agrochemical use on weeds, invertebrates, and birds (Fig. 1a), and the indirect cascading effects among different taxa across multiple trophic levels (Fig. 1b), and their individual (i.e.,
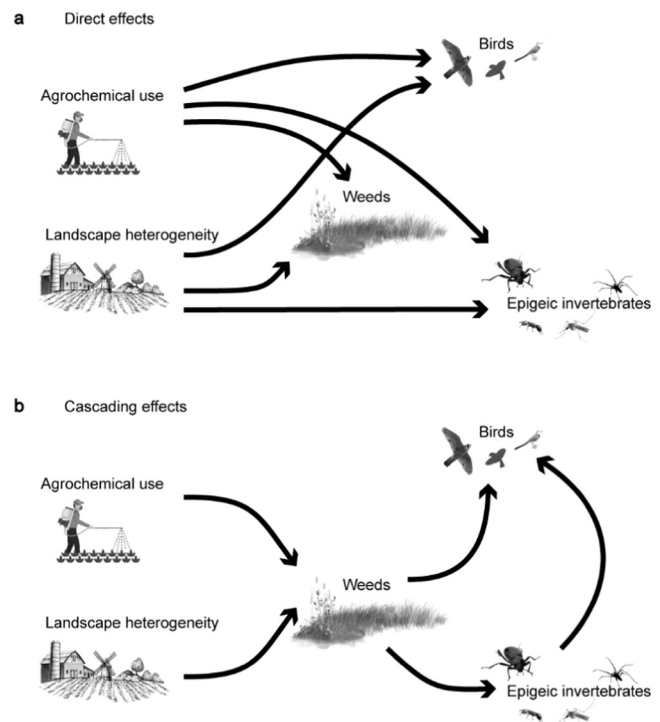

Fig. 1. Hypothesized causal relationships of (a) direct effects of landscape heterogeneity and agrochemicals use on weeds, epigeic invertebrates and birds, and (b) their bottom-up cascading effects on high trophic-level taxa via weeds and/or invertebrates.

direct and cascading effects) and combined impacts on different biological communities and trophic levels were quantified. We predict that increasing landscape heterogeneity would benefit all taxa across trophic levels (Benton et al., 2003), and agrochemicals would negatively affect low-trophic groups (i.e., weeds and herbivorous invertebrates), and exert cascading effects on high-trophic groups including predatory epigeic invertebrates and birds depending on biotic interactions (Carbonne et al., 2022).

2. Materials and methods

2.1. Study area and sampling design

The study was carried out in Pengzhou city, Sichuan Province of China, a typical agricultural region characterized by smallholder and traditional manual farming practices. The average annual temperature of Pengzhou is 15.9°C, and the annual precipitation is 867 mm (China Meteorological Information Center, 2021). The area is occupied by many small-scale farms owned by individual families, primarily cultivating cereals such as rice, corn, and soybeans, and numerous vegetable types including cabbages, broad beans, potatoes, scallions, radishes, cucumbers, etc. Crops are mainly monocultured in three-months rotations or intercropped with vegetables in small field patches. Pesticide use is common, with documented annual pesticide consumption of 12.3 kg/ha reported (Sichuan Agricultural Census 2020), and commonly applied pesticides include imidacloprid (INS) and glyphosate (HBC) to maintain yield and control pests. In May 2021, we randomly set up 23 plots in the study area, with a size of 1 ha (100 m × 100 m; Fig. S1) each, and the interval between adjacent plots is greater than 1 km. The field survey was conducted monthly from May to September, for a total of five times during the study period.

2.2. Weed coverage and richness

Weeds are unwanted herbaceous plants in cultivated fields, which reduce crop yields by competing for resources (Radosevich et al., 2007; Zimdahl, 2018). Weed surveys were conducted once per month for each plot from May to September. Each 1 ha plot was equally divided into 25 grids (20 m × 20 m), and a fixed 1 m × 1 m subplot was set in the center of each grid (Fig. S2). Within each 1 m² subplot, weeds were identified to the species level to count the weed richness, and the coverage of each weed species was visually estimated by the projection method (Aguilar et al., 2022). A total of 205 weed species were recorded.

2.3. Epigeic invertebrate abundance and richness

Field surveys were performed monthly from May to September because the richness, abundance and activity of invertebrates in farmland reached their peaks during the period (Zhu et al., 2018). Epigeic invertebrates were sampled using pitfall traps. Specifically, three trap cups were deployed on the diagonal of each subplot, that is, a 1 ha plot has 75 invertebrate collection points (Fig S2). Pitfall trap was carried out with a plastic beaker (7.8 cm in diameter, 10.8 cm in depth) and half-filled with 75 % ethanol and glycerol mixed (5:1 v/v; Long et al., 2017), and a plastic cover was placed above each pitfall trap to avoid the influence of raindrops and litterfall. All pitfall traps setup spanned three days, and invertebrate specimens were collected from the traps seven days after their placement and stored in 75 % ethanol. All invertebrates were identified to the family level under the stereoscope (Nikon SMZ745T, Nikon Co., China) according to their morphological characteristics, and assigned to one of four feeding guilds, i.e., detritivores, herbivores, omnivores and predators according to Barnes et al. (2017). A total of 272,188 invertebrate specimens belonging to 271 families were sampled.

2.4. Bird abundance and species richness

Bird survey was performed monthly at each 1 ha plot using a combination of 10 min-point counts and 5 min-area search methods, with each survey lasting for one week (Bibby et al., 1992; Smith et al., 2019). The point count was conducted with the observer positioned at the center of the plot, and the area-based search covered the entire 1 ha plot following a circular pattern expanding outward from the center. In the early morning and late evening on each sampling day, all visually and aurally detected birds within the plot were recorded. All surveys were conducted under favorable weather conditions, without rain or strong wind. Flyovers and migratory birds were excluded from the subsequent analysis, because these birds occurred occasionally and seldom relate to local landscapes and agricultural management (Šálek et al., 2018). Finally, a total of 48 bird species were recorded and divided into three main feeding guilds (Tobias et al., 2022): herbivores, predators, and omnivores.

2.5. Landscape heterogeneity and agrochemical use

All land covers within each 1 ha plot were mapped and manually digitized using Ovey software and ArcGIS v10.5, based on the monthly actual observation records with satellite images from the Copernicus Open Access Hub. The land cover types in this study include cropland, forest, grassland, settlement, shrubland, and water, following the classification framework established by the Copernicus Climate Change Service (2019). To assess cropland diversity, we classified cropland patches based on the crop categories (detailed classifications are provided in Supporting Information Table S9). The determination of different cropland patches was conducted during monthly field surveys to record crop types, patch areas, and distribution. Then, we used the software Fragstats 4.2 (McGarigal and Ene, 2013) to calculate (a) Shannon Wiener index of cropland (SHDIcrop) and (b) patch richness of

cropland (PRcrop) based on crop patches, as well as calculated (c) density of edges between patches (edge density, ED) and (d) mean area of patches (AREA_MN) based on all land cover types. All landscape parameters are described in Supplementary Table S1.

We used the dosage of pesticides applied to evaluate the overall impact of agrochemical use (Ferraro et al., 2003). During the sampling period, the total pesticides applied (g) to all crops in each plot in each sampling month was recorded through interview surveys. The details on the investigation and calculation of agrochemical use were provided in the Supporting Information S1.

2.6. Soil sampling and measurements

To investigate the potential impact of soil conditions on epigeic invertebrate communities, particularly detritivorous invertebrates whose abundance and richness are greatly influenced by soil properties (Coleman et al., 2017), we measured several soil physicochemical parameters, including soil moisture, bulk density, pH, and key soil nutrients (inorganic nitrogen, total carbon, and nitrogen content). In each subplot, soil samples were collected using a soil auger (5 cm in internal diameter) by obtaining 3 intact soil samples with a depth of 10 cm. One intact soil sample was used for the determination of soil moisture and bulk density, and the others were thoroughly mixed, with visible stones and debris manually removed, and divided into two parts: one was stored at 4°C to determine soil inorganic nitrogen content, and the remaining were air-dried for the measurements of soil pH, total carbon and nitrogen content.

Soil moisture and bulk density were determined via drying fresh intact soil at 105℃ to a constant weight (Bao, 2012). Soil pH was measured in a soil: deionized water suspension (1:2.5) using a pH meter (Sartorius PB-10, pH) (Lu, 2000). Soil total carbon and nitrogen were measured using an elemental analyzer (FlashSMART, USA). Soil inorganic nitrogen was extracted with 1 mol/L potassium chloride and then measured using a flow analyzer (SEAL AutoAnalyzer3, Germany; Yu and Zhang, 2013). In order to get more streamlined data on soil properties, a principal component analysis (PCAs) was performed to convert the variables of soil properties to fewer integrated ones (Fig S3). Soil PC1 (46.8 % variation explained) reflects an increase in pH, total carbon, and nitrogen along the positive axis, while PC2 (25.8 % variation explained) represents an increase in inorganic nitrogen along the negative axis (Fig. S3).

2.7. Statistical analysis

Before modeling, subplot-level invertebrate abundance and weed coverage were aggregated to the plot level. Weed and invertebrates that occurred in the 25 subplots of each plot were counted to calculate the species richness per plot. To avoid collinearity problems, a Spearman correlation was used to examine the correlations among landscape heterogeneity, agrochemical use and soil variables. After removing the highly correlated variables ($r \geq 0.7$, Table S2; Dormann et al., 2013), five variables were left for the subsequent analysis: agrochemical use, SHDIcrop, ED, PC1 and PC2 of soil.

In this study, piecewise SEMs were used to test the direct and indirect effects of landscape heterogeneity and agrochemical use on multitrophic biodiversity due to the comparatively low sample size (N = 115, i.e., 23 plots × 5 sampling months). The method has been successfully applied to test the cascading effects in complex communities in many observational studies (e.g., Carbonne et al., 2022; Barnes et al., 2017). Specifically, we incorporated sampling month as a random effect and f fitted 16 LMMs with each corresponding to a unique dependent variable within the piecewise SEM framework (Table S3). To ensure the normality of model residuals, logarithmic transformations were performed for weed coverage, invertebrate, and bird abundance in all LMMs. We used automatic backward step selection to simplify each model with the function *steps* in the R package 'lMertest' (Table S3), and

then performed multicollinearity tests on the simplified models using the *vif* function in the R package 'car' to ensure all VIF values < 5 (O'brien, 2007). We additionally tested the spatial autocorrelation by performing a Moran's I test on each trophic taxon, and the results showed that the spatial autocorrelation would not affect the LMMs results in path models ($P > 0.05$ for all Moran's I test results; Table S4). Finally, the overall fitness of piecewise SEMs was assessed with Fisher's C (Shipley, 2013), and the *P*-value > 0.05 (Shipley, 2009). To estimate the strength of cascading effects in a multi-trophic community, we multiplied the coefficients of the interacting taxa along the paths in the path model (Grace, 2006; Olobatuyi, 2006). Then the total effects of each agricultural variable on each biological group and each trophic level were estimated by summing the direct and cascading effect sizes, respectively.

3. Results

3.1. The direct effects and bottom-up cascading effects on different trophic groups

Agrochemical use had a significant negative impact on the richness (mean standardized effect size = -0.45) and coverage of weeds (-0.32), and similarly reduced herbivorous invertebrates (-0.22 and -0.27 in richness and abundance, respectively; Fig. 2 and Fig. S4). However, there was no significantly direct effect on birds (Fig. 2). Further, agrochemical use led to declines across all trophic groups of invertebrates indirectly, with the effect sizes of -0.23 and -0.12 for carnivorous

invertebrate richness and abundance, -0.15 and -0.18 for omnivorous invertebrate richness and abundance, respectively (Fig. 2 and Fig. S4). Herbivore invertebrate richness (-0.11) and detritivore invertebrate richness and abundance (-0.12 and -0.05, respectively) were indirectly reduced by agrochemical use, mediated through agrochemical-induced reductions in weed diversity and its positive relationship with invertebrates (Fig. S4). Bird diversity indirectly reduced by agrochemicals through distinct trophic pathways: carnivore bird abundance declined via reduced detritivore invertebrate richness (-0.02), omnivore bird richness decreased with diminished omnivorous invertebrate abundance (-0.04), while herbivore bird richness suffered from weed richness suppression (-0.10, Fig. S4).

Edge density (ED) positively influenced the richness and abundance of different trophic groups, with effect sizes of 0.27 and 0.32 for weeds, 0.22 and 0.50 for detritivorous invertebrates (Fig. 2; Fig. S4). It also enhanced the richness (0.26) and abundance of herbivorous invertebrates (0.26), and the abundance of omnivorous invertebrates (0.19; Fig. 2 and Fig. S4). ED exerted indirect positive effects on invertebrate diversity through distinct trophic pathways (Fig. 2 and Fig. S4). Detritivores (richness: 0.07; abundance: 0.03) and herbivores (richness: 0.07) benefited primarily through enhanced weed richness. However, carnivores (richness: 0.33; abundance: 0.25) and omnivores (richness: 0.28; abundance: 0.18) were influenced through more complex pathways involving both weed-mediated effects and interactions with detritivorous and herbivorous invertebrates. Additionally, bird diversity showed positive responses to ED (Fig. 2 and Fig. S4). Carnivore abundance increased through combined effects on weeds and detritivorous
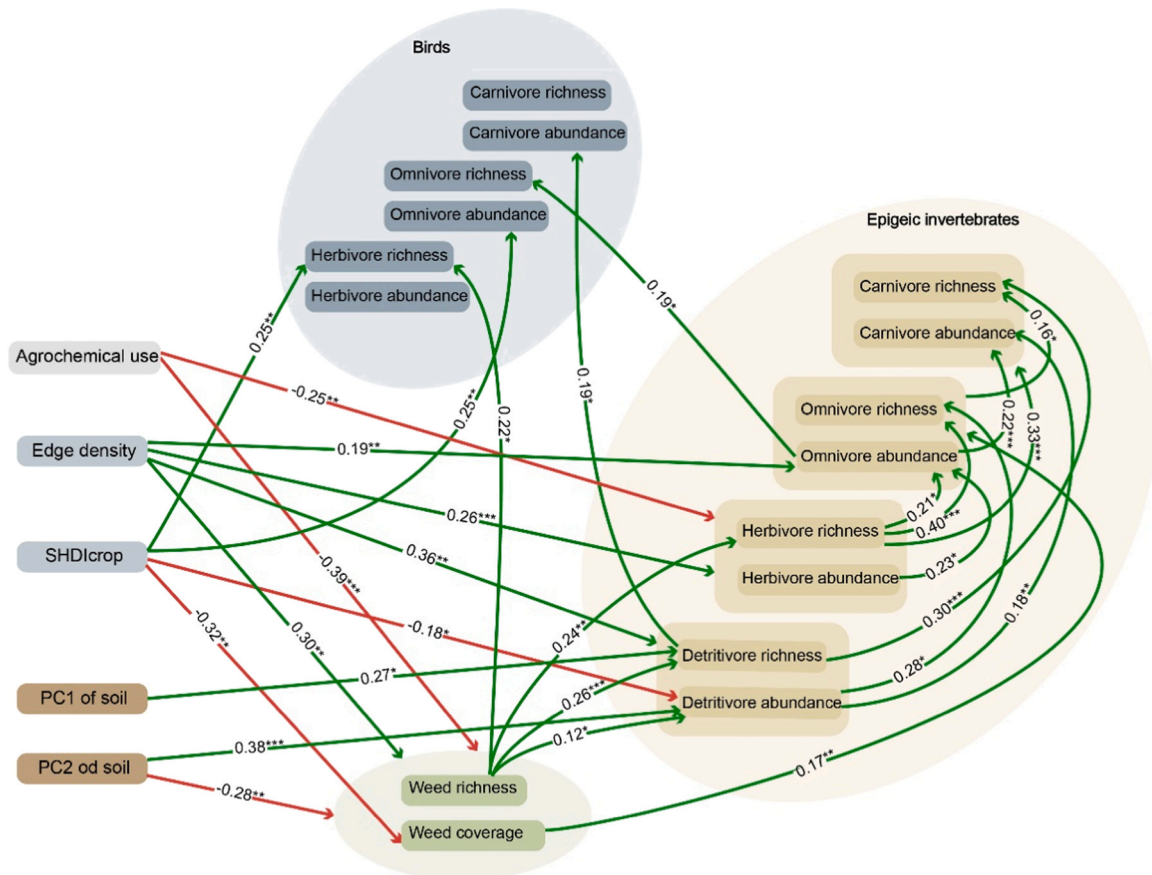

Fig. 2. Path model of direct and bottom-up cascading effects of landscape heterogeneity and agrochemical use on multi-trophic biodiversity (χ^2 =212.917, df = 222, $P = 0.657$). The green and red arrows indicate all significantly positive and negative effects, respectively. An arrow pointing to an ellipse indicates the combined effects of a variable on the richness and abundance of a taxonomic group, while an arrow pointing to a lighter-colored box represents the combined effects of a variable on the richness and abundance of a trophic group. SHDICrop: Shannon-Wiener Habitat Diversity Index of Cropland. Asterisks denote significance levels: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

invertebrates (0.05), omnivore richness positively responded to multi-trophic interactions involving weeds, detritivorous, herbivorous and omnivorous invertebrates (0.07), while herbivore richness was primarily mediated by weeds (0.06).

Increased SHDIcrop boosted herbivorous bird richness (0.25) and omnivorous bird abundance (0.25), but it decreased the abundance of detritivorous invertebrates (-0.18) and weeds (-0.32; Fig. 2 and S4). It also had a weak indirect effect on omnivorous bird richness (-0.01; Fig. S4). Additionally, SHDIcrop indirectly reduced the diversity of omnivorous invertebrates (-0.05 for both richness and abundance) and carnivorous invertebrates (-0.02 and −0.04 for richness and abundance, respectively) through its impact on weed coverage (Fig. 2 and Fig S4).

Detritivorous invertebrates, acting as decomposers, were significantly influenced by soil properties (Fig. 2). The PCA results showed that soil PC1 was associated with higher pH, total carbon, and nitrogen, while PC2 was linked to increased inorganic nitrogen (Fig S3). Detritivorous invertebrates exhibited a positive correlation with soil PC1 and PC2, which means that total carbon and soil pH positively affected, but soil inorganic nitrogen negatively affected detritivores (Fig. 2). In addition, PC2 of soil was negatively correlated with the richness and coverage of weeds (Fig. 2).

3.2. The interaction of direct and cascading effects across biological groups and trophic levels

The overall effects of landscape heterogeneity and agrochemical use on multi-trophic communities revealed that agrochemicals exerted pronouncedly negative effects (-0.43), while dramatically positive influences of ED (0.43), and SHDIcrop had a relatively weak and negative impact (-0.03, Fig. 3a). Teasing apart the responses of three biological groups (weeds, invertebrates, and birds), we found that different

biological groups respond differently to agrochemical use and landscape heterogeneity (Fig. 3b). Although agrochemicals and ED consistently showed negative or positive net effects across all biological groups; their impacts magnitude were notably greater on weeds (-0.38, 0.29, respectively) and invertebrates (-0.38, 0.46, respectively) than birds (-0.05, 0.06, respectively, Fig. 3b). Birds were not directly affected by agrochemicals and ED, and only received a weak impact indirectly (-0.05, 0.06, respectively, Fig. 3b). The net impacts of SHDIcrop were opposite between different biological groups, with a negative effect on weeds (-0.32) and invertebrates (-0.22) but positive on birds (0.24, Fig. 3b). Thus, these opposing effects on different biological groups resulted in a total direct effect close to zero when aggregated (Fig. 3a). The cascading effects of SHDIcrop on biological groups were limited, only showing a weak and negative bottom-up cascading effect on invertebrates (-0.04, Fig. 3b). Additionally, we observed that weeds and invertebrates seemed to be more influenced by local agricultural factor (i.e., agrochemical use), whereas birds were more significantly affected by landscape variables (ED and SHDIcrop; Fig. 3b).

By separating these effects into different trophic levels, we observed that agrochemical impacts predominantly acted on lower trophic levels, exerting negative cascading effects on higher trophic levels (carnivorous and omnivorous birds and invertebrates), with the overall negative impact diminishing with increasing trophic level (Fig. 4). In contrast, the net effect of ED was consistently positive across all trophic levels, while effects peaked at intermediate levels (0.42, Fig. 4). Notably, the direct effects of agrochemicals and ED decreased with increasing trophic level, while the indirect effects show an upward trend from levels 2–4. SHDIcrop negatively affected weeds directly, but this negative impact shifted to positive direct effects at higher trophic levels (omnivorous birds) (Fig. 4). Additionally, SHDIcrop exhibited a negative cascade effect at trophic levels 3 and 4 (-0.05, −0.03, respectively, Fig. 4),
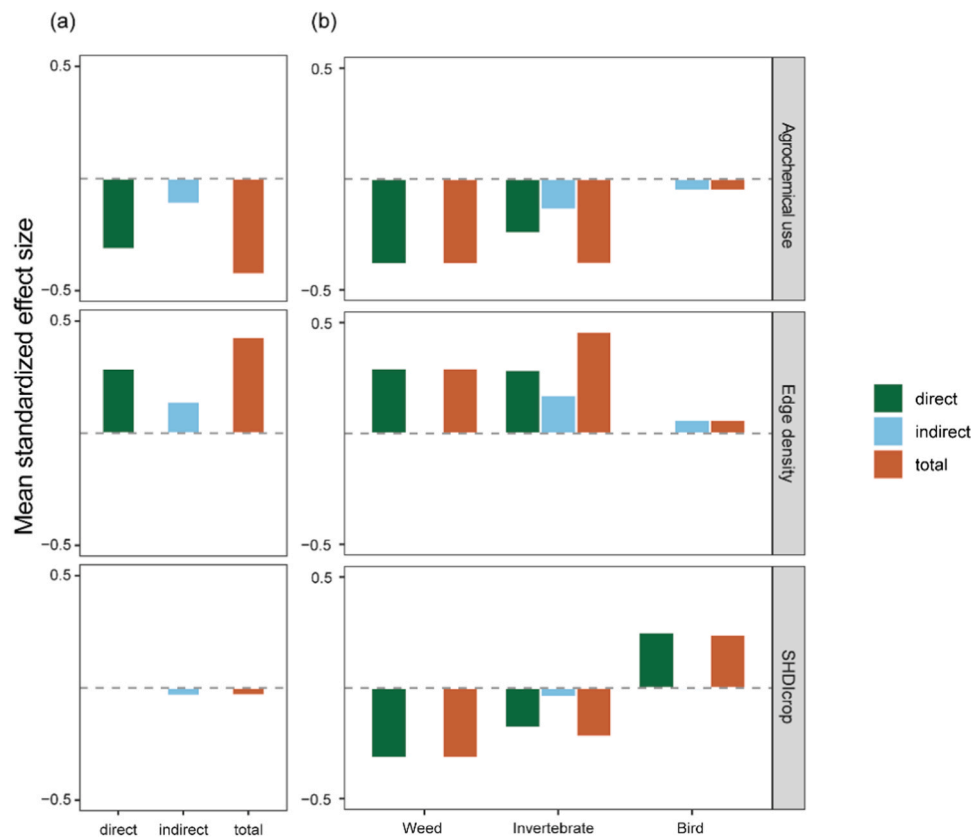

Fig. 3. (a) The effects of landscape heterogeneity and agrochemical use on multi-trophic biodiversity. (b) The effects of landscape heterogeneity and agrochemical use on different biological taxa. Cascading effects were estimated by multiplying coefficients along pathways of interacting taxa in the path model, and total effects were estimated by summing the direct and cascading effect sizes of landscape heterogeneity or agrochemical use on each taxon.
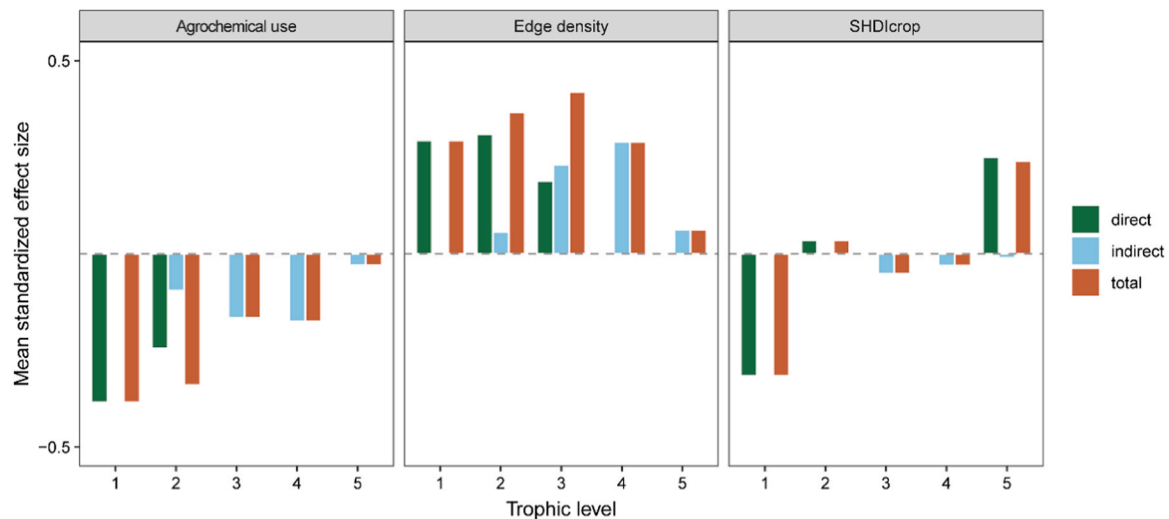
Fig. 4. The effects of landscape heterogeneity and agrochemical use on different trophic levels. Trophic levels: (1) weeds, (2) invertebrate detritivores and herbivores, bird herbivores (3) invertebrate omnivores, (4) invertebrate carnivores, and (5) bird carnivores and omnivores.

mediated by low-trophic weeds.

4. Discussion

Our SEM results revealed strong and direct negative effects of agrochemicals on their main targets (weeds and herbivorous invertebrates), and that the richness and abundance of higher trophic invertebrates and birds were also reduced through cascading effects. Agrochemicals, such as glyphosate disrupts the metabolic processes of weeds and ultimately causes their withering (Duke and Powles, 2008). Long-term agrochemical use probably damages seed production and soil seedbanks, thus reducing the weed diversity (Smith et al., 2016; Carbonne et al., 2022). Additionally, agrochemicals directly affect invertebrates with toxicity, disrupting physiological processes, and altering reproductive success (Navntoft et al., 2006; Goulson, 2013). More seriously, these direct impacts cascaded to higher trophic levels, indicating the reduction in weeds and herbivores may limit food resources for predatory invertebrates and birds, leading to their population declines even without direct agrochemical exposure (Boatman et al., 2004). Our findings also suggest that these indirect effects on other invertebrates and birds may be as significant as, or even exceed, the directly lethal effects of agrochemicals (Thorbek and Bilde, 2004; Morris et al., 2005; Hatten et al., 2007). Such detrimental cascading effects of agrochemicals, however, would remain undetected without considering biotic interactions, which had been neglected in the previous studies.

Our findings revealed distinct response to agrochemical use between trophic levels. The direct effects of agrochemicals were only evident at lower trophic levels when analyzing these effects across broad trophic levels. The indirect bottom-up cascading effects played a main role at higher trophic levels, and the magnitude of these effects diminished progressively with increasing trophic levels. The results can be explained by differences in mobility and size between organisms occupying different trophic levels, and the scale on which the organisms operate (Schweiger et al., 2005; Harsimran Kaur and Harsh, 2014). Relatively stationary weeds and herbivorous invertebrates exhibit the strongest direct responses to agrochemical use, while birds with greater mobility are less directly exposed to and can more easily avoid the effects of agrochemicals (Harsimran Kaur and Harsh, 2014; Janssen et al., 2021). Bird communities are more likely to be affected by changes in landscape traits exceeding 1 ha spatial scale, and less sensitive to the local-scaled effects of agricultural management within the plot (Tscharntke et al., 2005). Importantly, our pathway analysis further

confirmed that the negative impacts of agrochemicals on higher trophic levels, such as predatory birds, act primarily through resource depletion rather than direct toxicity compared with lower trophic levels (Desneux et al., 2007; Harsimran Kaur and Harsh, 2014). Mitigation strategies, such as crop diversification, can be applied to attenuate these harmful impacts of agrochemicals at various trophic level without compromising agricultural productivity and farmland stability (Wan et al., 2020; Wang et al., 2025).

The two landscape heterogeneity variables (edge density and cropland diversity) influenced multi-trophic groups in different ways, but both included direct effects and cascading effects. Among them, edge density (ED) positively affects weeds, herbivorous, detritivorous, and omnivorous invertebrates, with the direct effects generally overriding the indirect ones (Fig. 2). An increase in ED implies an expansion of landscape boundaries, facilitating the movement of organisms between landscape patches, and thereby enhances access to diverse food and habitat resources (Piha et al., 2007; Fahrig et al., 2011). Ecological corridors along patch edges strengthen habitat connectivity, promoting the mobility of invertebrates between patches, and accelerating species turnover (Crowther et al., 2023). These benefits are particular for species with limited or no flight capabilities, such as Heteroptera, enabling them to disperse from their original habitats into other areas via interpatch corridors (Schweiger et al., 2005). Additionally, the rise in ED enhances 'spillover effects' by decreasing the center-edge ratio, allowing certain invertebrate groups to disperse from core areas into surroundings, influencing the diversity of other taxonomic groups (Fahrig et al., 2011). We also observed that the indirect effects of ED exceeded the direct effects at middle and high trophic levels, indicating that omnivorous and predatory invertebrates benefit from ED through the bottom-up cascading forces of prey resources. The reliance of herbivorous, omnivorous and predatory invertebrates on weeds or prey resources, combined with the direct effects of ED, enables these trophic groups as sensitive to ED as, or even more sensitive than lower trophic groups like weeds. However, for the highest trophic level in the study (i. e., carnivorous and omnivorous birds), the beneficial effect of ED was limited likely due to their mobility and requirement for broad foraging ranges, reducing their dependency on localized edge and spillover effects. Although some studies have demonstrated that birds are strongly affected by ED, it is often observed in forests, grasslands, or farmlands with continuously distributed and much larger landscape patches (Ekroos et al., 2019; Sasaki et al., 2020). The positive effects of ED on birds seem to dimmish with decreasing patch size (Reino et al., 2009). Our study is located in a highly patchy agroecosystem with an average

patch size of 0.07 ha. This is significantly smaller than the typical patch size in other studies (e.g., European agroecosystems in Carbonne et al. (2022), which ranges from 50 to 200 ha). The relatively fine scale of our study area may limit the effectiveness of ED on birds. As a result, most birds can easily forage and inhabit across different landscape patches. Perhaps because resource accessibility across landscape patches is no longer a limiting factor for birds, the beneficial effects of ED are less pronounced for birds compared to invertebrates and weeds, particularly in terms of the direct impacts.

The effects of cropland diversity varied among different taxa, showing positive impacts on birds but negative on weeds and invertebrates with different causes. The negative relationship between weed coverage and cropland diversity is probably due to light, water, and nutrients competition between crops and weeds. Polyculture improves the efficiency of light energy interception through canopy complementarity, and simultaneously, root niche differentiation strengthens the nutrient uptake, both suppressing weed growth (Mahaut et al., 2019). Additionally, higher crop diversity often involves more diverse crop rotations, which can benefit weed control in the long-term through disrupting weed establishment and reducing weed competitiveness (Weisberger et al., 2019). As a result, increasing crop diversity not only reduces resource availability for weeds but also lead to their long-term suppression. For detritivorous invertebrates, their negative response to SHDIcrop may be explained by changes in soil organic matter and soil microhabitat. Detritivorous invertebrates mainly inhabit on the soil surface, and their abundance is highly dependent on the humus resource and soil environment (Swift et al., 1979; Lavelle and Spain, 2001). Polyculture is often accompanied by frequent tillage, reclamation and harvesting, which are common agricultural practices in our study area. These activities would reduce the availability of humus for detritivorous invertebrates (Blanco-Canqui et al., 2008; Adamczewska-Sowińska and Sowiński, 2020; Hu et al., 2022). Moreover, our results also indicate that detritivorous invertebrate diversity increased with rising soil PC1 (mainly explained by soil C and pH) and PC2 (negative inorganic nitrogen). The result reflects the differentiation of resource utilization strategies between decomposers and crops, where detritivorous invertebrates are greatly driven by organic matters as food resource, while crops are often limited by inorganic nitrogen in soil (Lavelle and Spain, 2001). However, polyculture is often accompanied by the application of inorganic nitrogen fertilizer, typically leading to an increase in soil inorganic nitrogen concentrations (Robertson and Groffman, 2024). The excess nitrogen input disrupts the soil carbon-to-nitrogen (C:N) balance and utilization of organic matters for detritivorous invertebrates, ultimately having a negative impact on their populations (Fierer and Jackson, 2006; Zhang et al., 2020). In addition, nitrogen fertilization can lead to soil acidification, further creating unfavorable conditions for the survival of many invertebrates (Guo et al., 2010). Reduced soil organic matter and labile soil microhabitat in diverse croplands lead to significant depletion of detritivorous invertebrates. This decline consequently triggers bottom-up cascading effects, compromising prey availability for omnivorous and carnivorous invertebrates and ultimately reduces their diversity. Not like the weak effects of ED, cropland diversity induced strong direct effects on birds, especially herbivores and omnivores. Promoting crop diversity can provide more food choices for crop-feeding birds, consequently attracting more herbivorous and omnivorous birds to these patches and further optimizing their pest control efficiency (Lee and Goodale, 2018; Redlich et al., 2018). The result further implies that resource abundance would be more critical than resource accessibility for birds in these fine-scale mosaic landscapes (Zheng et al., 2015).

Finally, the combined effect of cropland diversity on the whole multi-trophic biodiversity was weakly negative, counterbalanced by the strong negative impact on the low trophic level (i.e., weeds and detritivorous invertebrates) and positive effect on the high trophic level (i.e., omnivorous and predatory birds). Lower trophic groups declined due to resource competition and environmental changes, while higher trophic

groups benefited from resource enrichment. This suggests that future agricultural management should optimize crop layout, reduce tillage disturbances to mitigate losses at lower trophic levels while maintaining diversity at higher trophic levels, thereby fostering a more stable community in the agroecosystems.

5. Conclusions

In summary, our study demonstrates that agrochemical use and landscape heterogeneity educe widespread ecological responses across various interactive taxa and multiple trophic levels through both direct and bottom-up cascading effects. The findings shed light on the role of biotic interactions in modulating agricultural intensification impacts on biodiversity within complex communities. The results also underscore the critical role of increasing landscape heterogeneity in biodiversity conservation programming even in highly patchy farmland, despite their contributions being variable among trophic groups. Enhancing patch edge density and adopting polyculture can serve as alternative strategies of improving semi-natural habitats to achieve the dual goals of agricultural development and biodiversity conservation in small-holder patchy farmlands.

CRediT authorship contribution statement

Jianghong Ran: Writing – review & editing, Supervision, Conceptualization. **Xuewei Geng:** Investigation, Data curation. **Pei Zhang:** Writing – review & editing, Conceptualization. **Jing Liao:** Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109832.

Data availability

Data will be made available on request.

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