Woodlands as refuges and resources for paddy spider communities: Varying importance with land consolidation intensity

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ABSTRACT

Land consolidation (LC) is vital for addressing land fragmentation and enhancing agricultural mechanisation, but it is often associated with farmland biodiversity loss. Preserving semi-natural habitats has been proposed as a solution, but their relative importance as refuges or resource providers for biodiversity at different LC intensities remains unclear. In a well-facilitated farmland demonstration area with high-intensity LC and the surrounding agricultural areas with low-intensity LC, we surveyed epigeic spiders in rice paddies and nearby semi-natural woodlands. We examined how LC intensity affected (1) spider communities activity density, species richness, and community composition in paddies and woodlands and (2) the influence of surrounding woodlands on spiders in paddies. Spider activity density in woodlands was higher than in paddies at high LC intensity but not at low LC intensity. Although spider species composition in paddies altered with LC intensity, that in woodlands remained unaffected. In the species-habitat network of generalist spiders, paddies with low LC intensity showed stronger interactions with woodlands than those with high LC intensity. While paddy spider species richness increased with landscape-scale woodland cover, their activity density increased only at low LC intensity. These results suggested that at high LC intensity, woodlands supported a larger proportion of spider communities across habitats, acting as more important refuges. At low LC intensity, woodlands benefited paddy spiders more effectively, serving as more important resources. These findings highlight the importance of preserving and managing semi-natural habitats in agricultural landscapes, considering their varying roles across LC intensities, to support biodiversity-friendly LC design and restoration.

1. Introduction

Land consolidation (LC) is a land management approach which involves defragmenting smaller fields into larger ones. It is widely adopted to address land fragmentation and promote agricultural mechanisation (Demetriou, 2016). Amid the growing population and climate change, LC has been crucial in boosting agricultural productivity and ensuring food security (Duan et al., 2021). However, these benefits are accompanied by considerable ecological trade-offs. Numerous studies have reported that LC negatively impacts semi-natural habitats and the diversity of wild species, including plants (Osawa, et al., 2016), birds (Denac and Kmecl, 2021), pollinator insects (Shi et al., 2021), spiders (Plath et al., 2021; Yang et al., 2025) and other natural enemy

arthropods (Gong et al., 2024). These would further threaten essential ecosystem services for sustainable agriculture, such as pollination and biological pest control (Felipe-Lucia et al., 2020; Yang et al., 2025).

In China, traditional agricultural landscapes are predominantly characterised by very small and irregular fields and abundant semi-natural habitats (Zou, 2023). Over 90 % of farmland fields in China are smaller than 1 ha (Ritchie and Roser, 2021), and more than 70 % are smaller than 0.64 ha. In contrast, only 13 % of farmland fields in Europe and 4 % in the United States are smaller than 0.64 ha (Lesiv et al., 2019). Due to severe land fragmentation and the pressing need for rural development, China is rapidly advancing LC efforts. China aims to develop 71.7 million ha of well-facilitated farmland by 2025 and 80 million ha by 2030, with LC being considered the most fundamental and

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crucial undertaking (Ministry of Agriculture and Rural Affairs of the People's Republic of China, 2021). However, achieving eco-friendly and sustainable LC remains a significant challenge in China (Tang et al., 2019).

In response to this challenge, studies have suggested controlling LC to a suitable intensity and conserving semi-natural habitats as potential solutions (Li et al., 2019; Zou, 2023; Yang et al., 2025). During the process of LC, semi-natural habitats are often removed, with linear habitats such as field margins and hedgerows being particularly affected. These linear habitats are typically eliminated to enlarge field size, construct concrete irrigation channels, or establish machinery access roads (Li et al., 2019). On the other hand, large semi-natural habitats such as woodlands and grasslands, which are not part of cultivated fields, are less affected by LC (Zou, 2023). Therefore, in theory, large semi-natural habitats can be more feasible for mitigating biodiversity loss associated with LC.

Nevertheless, LC could also affect the roles of large semi-natural habitats in supporting biodiversity in agricultural landscapes. Large semi-natural habitats play two key roles: (1) they act as primary reserves and refuges that sustain local biodiversity within themselves by providing shelter and nesting sites; and (2) they provide resources that enhance biodiversity in surrounding croplands and other habitats through supplying food resources, overwintering sites and species spillover (Tscharntke et al., 2005). On the other hand, linear semi-natural habitats mainly function as dispersal corridors and provide additional food and nesting resources (Fischer et al., 2013). By reducing linear habitats and making croplands less suitable for wild species, LC reshapes landscape-scale species distributions (Tscharntke et al., 2012) and their proportion supported by large semi-natural habitats. This could alter the relative importance of large semi-natural habitats as refuges. Furthermore, LC disrupts the connectivity between crop fields and large semi-natural habitats and changes the dependence of farmland biodiversity on the resources from these large habitats. This potentially changes the role of large semi-natural habitats as resource providers.

Although many studies have focused on LC's effects on local biodiversity in croplands (e.g. Shi et al., 2022; Gong et al., 2024), there has been far less attention on how large semi-natural habitats contribute to biodiversity in consolidated landscapes and how their roles may vary under different LC intensity. A better understanding of this question could help design more effective LC-associated conservation strategies and policy instruments to conserve biodiversity.

Rice (*Oryza sativa* L.) is one of the most important staple crops, consumed regularly by 50 % of the world's population (Fukagawa and Ziska, 2019). China is the world's largest rice producer and consumer (Xin et al., 2020). In rice agroecosystems, spiders play a crucial role as natural enemies of key pests such as leafhoppers (Radermacher et al., 2020) and planthoppers (Baba et al., 2018), which can strongly affect rice yields. As one of the most abundant and diverse invertebrate groups in agricultural landscapes (Michalko et al., 2019), spiders' sensitivity to environmental changes makes them reliable bio-indicators in studies investigating biodiversity in agricultural landscapes (Clough et al., 2005; Duan et al., 2019; Li et al., 2024). The diversity and abundance of spiders are strongly affected by the loss and degradation of semi-natural habitats (Gagic et al., 2018), especially linear habitats such as grassy field margins (Plath et al., 2021) and hedgerows (Fischer et al., 2013). As LC frequently entails the removal of these habitats, spiders have been effectively employed as indicator species to evaluate the ecological consequences of LC (e.g., Plath et al., 2021; Yang et al., 2025).

In Chengdu Plain, one of China's key rice production regions, we surveyed epigeic spiders in rice paddies and nearby woodlands within a well-facilitated farmland demonstration area with high-intensity LC, as well as in its surrounding agricultural areas with low-intensity LC. In China, woodlands are among the most widely distributed terrestrial large semi-natural habitats in agricultural landscapes and are favourable for spiders (Guo et al., 2022). This study focuses on how the role of woodlands in supporting paddy spider communities is influenced by different levels of LC intensity. We ask:

(1) How does the role of woodlands as refuges vary with LC intensity? Specifically, we examine how activity density, species richness and community composition of spiders in woodlands change with increasing LC intensity, using paddies as a comparative baseline.
(2) Does the role of woodlands in providing resources vary with LC intensity? Specifically, does LC intensity moderate how spider communities in paddies are influenced by surrounding woodlands? Here, we examined how LC intensity affects spider dispersal between habitats. We also investigated how LC intensity affects the relationship between paddy spiders and the distribution of surrounding woodlands at the landscape scale.

2. Methods

2.1. Study region and sampling design

This study was conducted in the agricultural area west of Chengdu Plain, Sichuan Province, China (N30.41° – N30.47°, E103.62°– E103.71°). This region has a subtropical humid monsoon climate, with an annual average temperature of 16 °C and precipitation of 1114.7 mm, ideal for crop growth. The arable land here is primarily used for rice cultivation. Before 2013, the rice paddies were highly fragmented, and the mean field size was only 0.086 ha. In 2013, the government initiated a well-facilitated farmland and grain-economic industry comprehensive demonstration area project. This project involved high-intensity LC, resulting in most paddies exceeding 0.67 ha in field size, with some surpassing 2 ha. In contrast, areas outside the demonstration project underwent only low-intensity LC, with paddy fields typically being smaller than 0.2 ha now.

To answer the question (1), we first selected five paddies with high-intensity LC (mean paddy field size in 100 m radius: 0.326 – 1.411 ha) in the well-facilitated farmland demonstration area, and five paddies with low-intensity LC (0.075 – 0.193 ha) in the surrounding agricultural areas. We use their mean field size at the landscape scale as a proxy of LC intensity because the primary goal of LC is to defragment smaller fields into larger ones (Demetriou, 2016). At multiple landscape scales (within radii of 100 m, 200 m, 300 m, 400 m, and 500 m), the mean paddy field sizes around high-intensity LC paddies consistently exceeded those around low-intensity LC paddies (Fig. S1A). Additionally, paddy edges (including paddy ridges, grassy ditch margins, and grassy roadsides) were less dense around high-intensity LC paddies than low-intensity LC paddies (Fig. S1B). Soil properties of paddies were similar across the LC intensity levels (Table S1), indicating that their management regimes were also similar. Secondly, for each sampled paddy, we selected the nearest woodland. These woodlands were secondary forest patches larger than 0.4 ha, with no human management or disturbance.

To address the question (2), we randomly selected an additional 20 paddies, bringing the total to 30 paddies, covering a gradient of LC intensity. The average paddy field size within a 100 m radius of these paddies ranged from 0.075 to 1.411 ha (mean ± SD: 0.267 ± 0.291 ha), with similar gradients observed at other radii (Table S2). Average paddy field size and paddy edge density were strongly correlated at multiple landscape scales (Table S2). To avoid spatial autocorrelation, the distance between every two paddies exceeded 1 km.

2.2. Data collection

We surveyed epigeic spiders in 2021 over three rounds, from late May to early September, covering the entire rice-growing period, using pitfall traps. Each round lasted for two weeks, with a two-week interval between rounds. We placed six pitfall traps in each sampling habitat. At the centre of each woodland, traps were arranged in two parallel lines (2 × 3 traps), spaced 2 m apart. Since pitfall traps could not be placed

within flooded paddies, we instead set them on the ridges flanked by rice paddy fields on both sides (Kagawa and Maeto, 2014) in a single line (1 × 6 traps). Previous studies have shown that spider community composition does not differ between paddy ridges and field interiors (Tahir and Butt, 2009) due to the frequent movement of spiders between them. Therefore, placing traps on the ridges is considered a representative method for sampling epigeic spiders in paddy ecosystems and has been successfully applied in previous studies (e.g., Barrion et al., 2012; Li et al., 2018; Duan et al., 2019).

Each trap comprised a buried opaque plastic cup (7.8 cm diameter and 10.8 cm depth) filled with saturated salt solution and a few drops of detergent. An aluminium rain cover (12 cm × 12 cm) was placed 5 cm above each trap. We replaced the solution and collected spiders once a week. The captured spiders were preserved in 80 % ethanol in the laboratory. Only adult spiders were identified to the species level and included in the analysis.

We categorised the spider species based on their habitat specialisation (Fischer et al., 2013), inferred from their relative occurrence in paddies and woodlands observed in our study. They were grouped as generalists ($\frac{1}{5} \leq$ average activity density in woodlands/ average activity density in paddies ≤ 5, with no distinct habitat preferences), forest species (> 5, associated with forests), and open-habitat species ($< \frac{1}{5}$, associated with open habitats). We calculated the activity density and species richness of overall spiders, as well as of each habitat specialisation group using data pooled over six pitfall traps and three survey rounds in each selected paddy and woodland.

We also surveyed ground vegetation twice (in early July and September) to gauge local habitat quality. Herb communities can approximately reflect local land use intensity and habitat quality, such as herbicide usage and the frequency of ploughing (Petit et al., 2015; Wu et al., 2019). We identified herbaceous plant species and estimated their cover within a 10 m² plot surrounding the six pitfall traps in each paddy ridge (0.5 m × 20 m) or woodland (2 m × 5 m).

We used DJI drones to capture high-resolution (approximately 0.2 m) orthophotos within a 500 m radius around each sampling paddy. Using ArcGIS 10.3.1 (ESRI, 2015), we calculated the mean paddy field size, paddy edge density, and woodland cover within radii of 100 m, 200 m, 300 m, 400 m, and 500 m around each paddy. Previous studies have indicated that the 500 m radius is sufficiently large to describe the landscape relevant to spiders (Schmidt and Tscharntke, 2005).

2.3. Data analysis

All analyses were performed using R version 3.6.0 (R Core Team, 2019).

2.3.1. Examining the role of woodlands as refuges across LC intensities

To address the first question, we analysed how LC intensity affects spider communities in paddies and woodlands. Firstly, we built linear mixed models (LMMs) using the "nlme" package (Pinheiro et al., 2022) for spider activity density and species richness of the 10 paddy-woodland pairs. The full LMMs included "habitat type" (woodland vs. paddy), "LC intensity" (high vs. low) and their interaction as fixed factors. "Paddy-woodland pair" (1 – 10) was included as a random variable to account for the paired design.

At the group level, these analyses were conducted for overall spiders as well as for each habitat specialisation group. At the species level, we examined the activity density responses of the four most frequently captured species: *Pardosa laura* (generalist, 1405 individuals), *Trochosa ruricoloides* (generalist, 860 individuals), *Ummeliata insecticeps* (open-habitat, 815 individuals), and *Ummeliata feminea* (forest, 436 individuals). Other species were not included in species-level analyses because of too many zero values. Models containing all possible combinations of variables and the null model were then ranked based on AICc using the package MuMIn (Bartoń, 2022). We averaged all the

models with △AICc < 2 to estimate the model parameters. If only one model had △AICc < 2, it was selected as the final model. All the models were checked for homoscedasticity and normality.

Secondly, we compared the spider species composition between woodlands and paddies with high and low LC intensity using PERMANOVA (Permutational Multivariate Analysis of Variance, permutations = 999) based on Bray-Curtis distance through the "vegan" package (Jari et al., 2022). The explanatory variables included "habitat type" and "LC intensity" and their interaction. Pairwise post-hoc tests were then conducted using the "pairwiseAdonis" package (Pedro Martinez, 2017). Non-metric multidimensional scaling (NMDS) was performed to visualise spider species composition grouped by habitat types and LC intensities.

2.3.2. Examining the role of woodlands as resources across LC intensities

Open-habitat species and forest species are not considered in this part of the analysis because they are intrinsically linked to certain habitat types. In contrast, generalists are more likely to move between woodlands and paddies, utilising resources from both habitat types. Focusing on this group, we identified two dominant generalists, including *Pardosa laura* (1405 individuals captured in this study) and *Trochosa ruricoloides* (860 individuals). Other generalists ($\leq$ 66 individuals of each species) were grouped as non-dominant generalists.

To investigate the role of woodlands in boosting spiders in paddies, we first applied the species-habitat network of each paddy-woodland pair and computed the Müller index using the "bipartite" package (Carsten et al., 2008). The Müller index, also known as the Potential for Apparent Competition (PAC) metric, was initially developed to study the apparent competition in host-parasitoid networks, taking into account the potential relative number of attacks by shared parasitoids between "source" hosts and "target" hosts (Müller et al., 1999; Morris et al., 2004; Miller et al., 2021). This index has been applied successfully to quantify the contribution of one "source" patch to species in another "sink" patch in species-habitat networks (Nardi and Marini, 2021). In this context, the Müller index could be considered a measure of colonisation potential dependent on the species shared by each possible pair of interacting patches (Lami et al., 2021).

We calculated the woodland-to-paddy Müller index for overall spiders, generalists, and non-dominant generalists, treating woodlands as source habitats and paddies as sinks to represent the potential spillover from woodlands to paddies. We also computed the paddy-to-woodland Müller index to assess movement in the opposite direction, i.e., from paddies to woodlands. Furthermore, we compared these indices between high and low LC intensity levels using two-sample t-tests.

We also examined how LC intensity moderated the influence of landscape-scale woodland cover on spiders in paddies. We built linear models (LMs) for spider activity density and species richness in the 30 paddies. These LMs included LC intensity, woodland cover, and their interaction as explanatory variables, as well as local herb cover and species richness in paddies as covariates. We used the landscape-scale mean paddy field size (logX transformed to improve the normality) as a proxy of LC intensity. The radius of landscape context (200 m, 300 m, 400 m or 500 m) was determined by comparing model fit using package MuMIn and the one producing the lowest AICc was included. 100 m was not considered because woodland cover at this scale contains too many zeros. Model parameters were estimated using the same model-averaging approach used in 2.3.1. We assessed the collinearity of full models based on the variance inflation factor (VIF). The highest VIF of the main factors was 1.73, below the threshold of 3 (Zuur et al., 2007), indicating no collinearity. To help understand how LC intensity moderates the influence of woodland cover on spiders through reducing paddy edge, we also analysed the effects of paddy edge density, landscape-scale woodland cover, and their interaction on spiders using similar methods. All the models were checked for homoscedasticity and normality.

3. Results

3.1. The captured spiders

A total of 5199 adult spider individuals comprising 66 species were collected. 32 species (1212 individuals) were categorised as forest spiders, 21 species (1356 individuals) as open-habitat species and 13 species (2631 individuals) as generalists.

3.2. The role of woodlands as refuges across LC intensities

LC intensity significantly moderated the habitat contrast between woodlands and paddies in the activity density of overall spiders and generalists (Table 1). The overall spider activity density was higher in woodlands than in paddies at high LC intensity. In contrast, at low LC intensity, there were no significant differences between habitat types (Fig. 1A). Generalist spider activity density, on the other hand, was lower in woodlands than in paddies at low LC intensity. As LC intensity increased, activity density of generalists significantly rose in woodlands. At high LC intensity, generalist spider activity density in woodlands did not differ significantly from that in paddies (Fig. 1B). The activity density and species richness of open-habitat species and forest species were higher in their associated habitats regardless of LC intensity (Fig. S1).

Species richness of other groups and overall spiders showed no significant response in LMMs (Table 1, $p > 0.05$).

At the species level, the activity densities of the generalists *Pardosa laura* and *Trochosa ruricoloides* were significantly influenced by the interaction between LC intensity and habitat type. Both species were more abundant in paddies than in woodlands at low LC intensity. As LC intensity increased, their activity density in paddies declined, while *Pardosa laura* increased in woodlands. Consequently, at high LC intensity, *Pardosa laura* was more abundant in woodlands, while *Trochosa ruricoloides* showed no significant difference between habitats (Fig. 1C and D). Independent of LC intensity, *Ummeliata insecticeps* (an open-habitat species) exhibited significantly higher activity density in paddies (Fig. 1E), whereas *Ummeliata feminea* (a forest species) was more abundant in woodlands (Fig. 1F).

The interaction between habitat type and LC intensity significantly influenced the species composition of overall spiders ($R^2 = 0.12$, $F = 3.74$, $p = 0.004$) generalists ($R^2 = 0.19$, $F = 4.94$, $p = 0.001$), and forest species ($R^2 = 0.09$, $F = 2.47$, $p = 0.019$). In paddies, the species composition of these groups varied significantly with increasing LC intensity, while in woodlands, it remained unaffected. The species composition of open-habitat species remained consistent across LC intensities in both habitats. All groups showed significantly different species composition regardless of LC intensity between paddies and

Table 1

Results of linear mixed models examining the effects of habitat type (woodland vs. paddy), LC intensity (high vs. low) and their interaction on activity density and species richness of spiders and their habitat specialisation groups and species level activity density of the four most frequently captured species.

Fixed factor		Estimate	Std. Error	Adjusted SE	z/t value	p	Relative importance
Active density							
Overall spiders							
Habitat type	at Low LC intensity	43.07	27.64	30.00	1.44	0.1510	1
	at High LC intensity	**78.53**	**27.64**	**30.00**	**2.62**	**0.0089**	
LC intensity	in Paddy	−64.60	35.28	41.50	1.56	0.1196	0.45
	in Woodland	14.20	35.28	41.50	0.34	0.7322	.
Habitat type: LC intensity		**78.80**	**28.65**	**33.71**	**2.34**	**0.0194**	0.45
Generalists (log(X + 1) transformed)							
Habitat type	**at Low LC intensity**	**−1.18**	**0.44**	**0.52**	**2.28**	**0.0225**	0.4
	at High LC intensity	0.79	0.44	0.52	1.52	0.1291	
LC intensity	in Paddy	−0.86	0.44	0.52	1.65	0.0990	0.4
	in Woodland	**1.11**	**0.44**	**0.52**	**2.15**	**0.0316**	
Habitat type: LC intensity		**1.97**	**0.62**	**0.73**	**2.69**	**0.0072**	0.4
Open-habitat species							
Habitat type		**−36.10**	**6.41**	——	**−5.63**	**0.0003**	——
Forest species							
Habitat type		**104.70**	**16.26**	**18.76**	**5.58**	**< 0.0001**	**1**
LC intensity		−24.30	16.30	19.18	1.27	0.2050	0.35
Pardosa laura (generalists, log(X + 1) transformed)							
Habitat type	**at Low LC intensity**	**−1.14**	**0.46**	——	**−2.46**	**0.0396**	——
	at High LC intensity	**3.11**	**0.46**	——	**−6.69**	**0.0002**	——
LC intensity	**in Paddy**	**−2.67**	**0.61**	——	**−4.37**	**0.0024**	——
	in Woodland	**1.58**	**0.61**	——	**−2.60**	**0.0316**	——
Habitat type: LC intensity		**4.25**	**0.66**	——	**6.46**	**0.0002**	——
Trochosa ruricoloide (generalists)							
Habitat type	**at Low LC intensity**	**−26.05**	**9.16**	**9.94**	**2.62**	**0.0088**	1
	at High LC intensity	5.75	9.16	9.94	0.58	0.5629	
LC intensity	**in Paddy**	**−15.60**	**6.60**	**7.76**	**2.01**	**0.0445**	0.7
	in Woodland	13.40	6.60	7.76	1.73	0.0843	
Habitat type: LC intensity		**29.00**	**9.33**	**10.98**	**2.64**	**0.0083**	0.7
Ummeliata insecticeps (open-habitat species, log(X + 1) transformed)							
Habitat type		**−1.97**	**0.33**	——	**−6.05**	**0.0002**	——
Ummeliata feminea (forest species)							
Habitat type		**2.54**	**0.37**	**0.43**	**5.95**	**< 0.0001**	**1**
Intensity		0.68	0.53	0.62	1.10	0.2730	0.29
Species richness							
Overall spiders							
Habitat type		2.30	1.78	2.06	1.12	0.2640	0.33
Generalists							
Habitat type		−0.60	0.73	——	−0.83	0.4297	——
Open-habitat species							
Habitat type		**−3.70**	**0.56**	——	**−6.62**	**0.0001**	——
Forest species							
Habitat type		**6.60**	**1.09**	——	**6.07**	**0.0002**	——
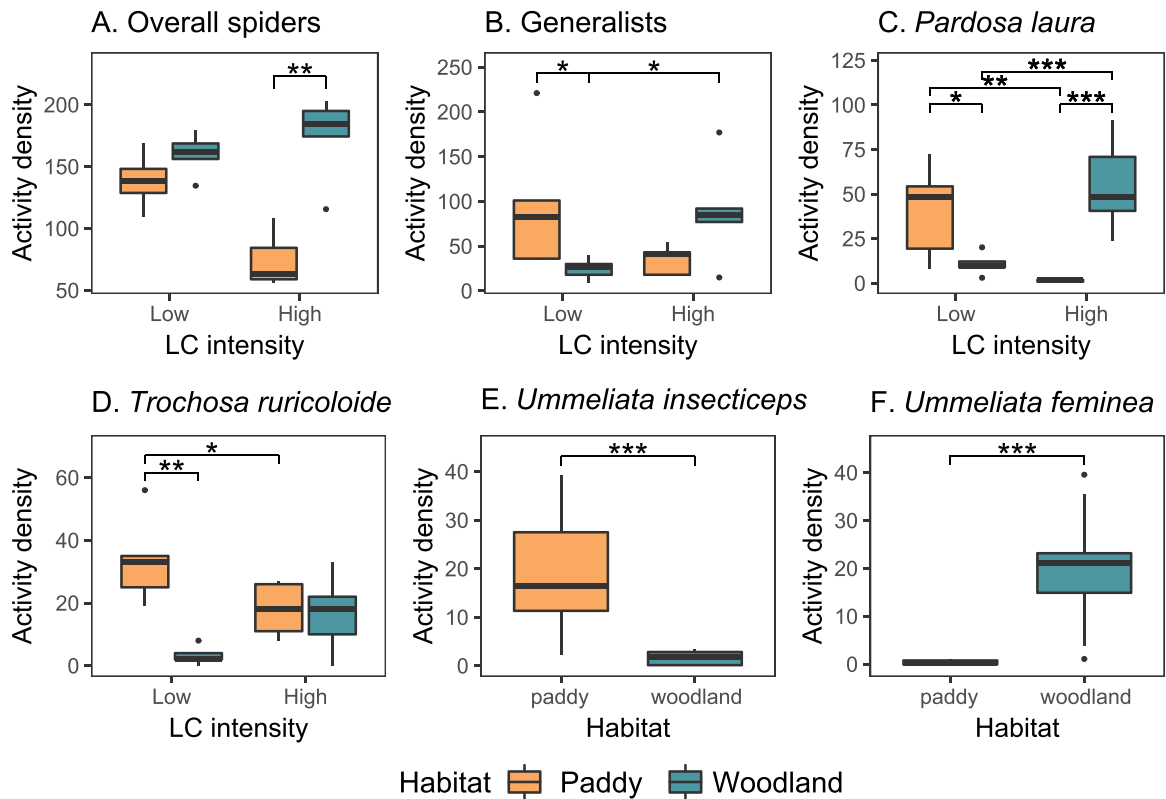
Fig. 1. Response of spider activity density of overall spiders (A), spider habitat generalists (B) and dominant species (C–F) to LC intensity, habitat type and their interaction. Asterisks denote significant differences: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
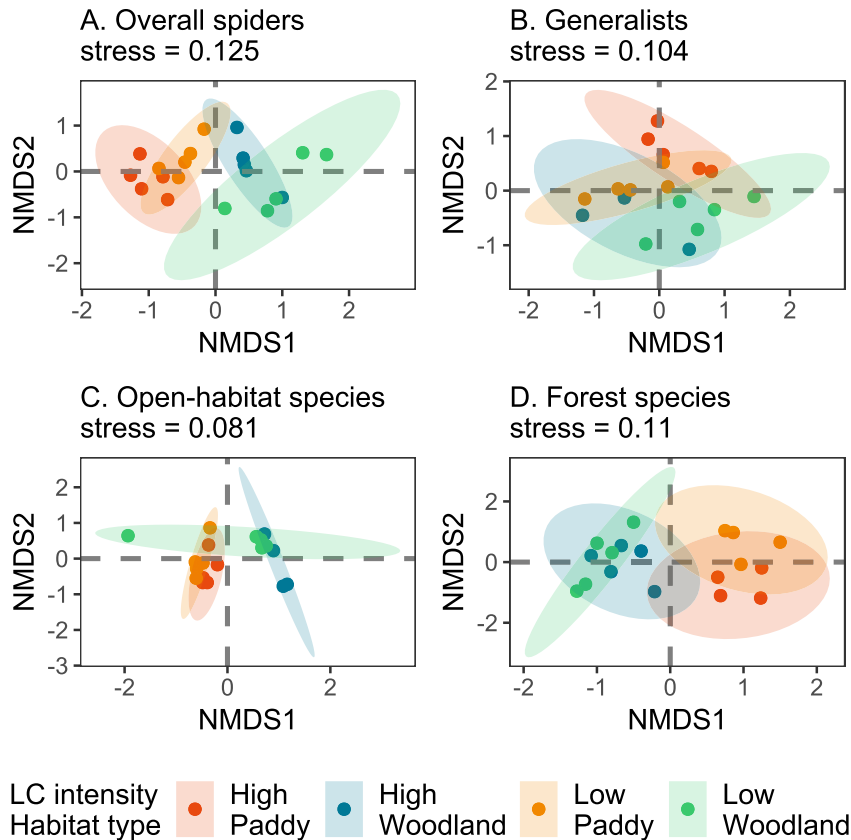
Fig. 2. Non-metric multidimensional scaling (NMDS) of spider species grouped by LC intensities and habitat types.

woodlands. An exception was observed between low-LC paddies and high-LC woodlands, where species composition of generalists showed no significant difference (Table S3, Fig. 2).

3.3. The role of woodlands as resources across LC intensities

The paddy-to-woodland Müller index for generalists and the woodland-to-paddy Müller index for non-dominant generalists were significantly higher in species-habitat networks at low LC intensity than those at high LC intensity (Table 2, Figs. 3 and 4). In contrast, no significant differences in the Müller indices were observed for overall spiders or other group-direction combinations (Table 2, $p > 0.05$).

The activity density of overall spiders, generalists, and non-dominant generalists in the 30 paddies was significantly influenced by the interaction between LC intensity (using paddy field size as a proxy) and landscape-scale woodland cover (Table 3). In paddies at low LC intensity, their activity density increased with increasing woodland cover, while in paddies at high LC intensity, it remained unchanged (Fig. 5 A-C). At the species level, the activity density of the generalist species *Pardosa laura* and *Trochosa ruricoloides* exhibited similar response patterns (Table 3, Fig. 5D and E). Species richness of overall spiders and generalists was positively linked with woodland cover regardless of LC intensities (Table 3, Fig. 6), whereas species richness of non-dominant generalists was not significantly affected (Table 3).

Models incorporating field edge density (an alternative proxy of LC intensity), woodland cover, and their interaction as explanatory variables produced largely consistent results with those based on paddy field size as the proxy of LC intensity (Table S4, Fig. S3). Although the interaction between field edge density and woodland cover did not significantly influence the activity density of *Pardosa laura* and *Trochosa ruricoloides* when analysed separately at the species level, it significantly affected their combined activity density (Table S4).

4. Discussion

LC is a key component of China's food security and rural revitalisation strategy (Lu, 2021). However, mitigating its negative impacts on biodiversity presents a significant challenge in many agricultural regions (Tang et al., 2019). Landscape-scale semi-natural habitats, especially large habitats such as woodlands that are not directly influenced by LC, have been suggested as a solution (Li et al., 2019; Zou, 2023; Yang et al., 2025). However, it remains largely unexplored how varying LC intensity influences the roles of woodlands as refuges and resources in enhancing biodiversity. Using epigeic spiders as indicator species and paddies as baseline habitats, this study reveals the varying roles of woodlands in supporting spider communities across LC intensities. At high LC intensity, woodlands function as more important refuges to sustain local spider communities, while at low LC intensity, they serve as more important resources to benefit spiders in surrounding paddies.

4.1. Woodlands are more important refuges at high LC intensity

Previous studies have reported negative effects of LC on wild species in crop fields (e.g. Denac and Kmecl, 2021; Gong et al., 2024). Our study partly confirmed these findings, showing altered spider species

Table 2
T-test results for Müller indices of species-habitat networks under high and low LC intensities.

Groups	Müller indices	t	*p*
Overall spiders	Woodland-to-paddy	0.802	0.4601
	Paddy-to-woodland	−1.649	0.1403
Generalists	Woodland-to-paddy	1.429	0.2078
	Paddy-to-woodland	**−7.064**	**0.0001**
Non-dominant generalists	**Woodland-to-paddy**	**−3.226**	**0.0130**
	Paddy-to-woodland	−0.097	0.9272

composition and a decreasing trend of spider activity density in paddies with increasing LC intensity. Biodiversity loss in consolidated fields was hypothesised to be linked to the degradation and decrease of vegetated field edges during LC (Shi et al., 2021), as these field edges provide essential habitats and food resources for wild species (Rischen et al., 2021). However, quantifying these narrow features in the smallholder agricultural landscapes in China has been challenging in previous studies (Shi et al., 2022). Our study used high-resolution aerial drone imagery to measure the field edge density and verified its relationship with LC intensity (Fig. S1) and spiders (Table S4). These results support the hypothesis of Shi et al. (2021) that biodiversity loss in consolidated fields is linked to the decrease of vegetated field edges.

However, in our study, overall spider activity density and species richness of all the groups did not show a significant response to LC intensity (Tables 1 and 3, Fig. 1). This discrepancy may arise from our methodology, which compared varying intensities, while previous studies compared fields with and without LC (e.g. Denac and Kmecl, 2021; Shi et al., 2022; Gong et al., 2024). This could also be attributed to the long agricultural history of Chengdu Plain, which may have limited the spider species pool to those well-adapted to human disturbances (Duan et al., 2019; Yang et al., 2025). Our study recorded only 66 species from 5199 adult spider individuals, whereas Hu et al. (2022) identified 175 species from 5144 spiders, and Galloway et al. (2021) observed 352 species among 3681 spiders. Another possible explanation is that the LC projects in our study region were completed seven years before our field survey, potentially allowing spider species richness to stabilise.

Spiders in woodlands exhibited a different response to LC intensity compared with those in nearby paddies (Table 1, Fig. 1). This is somewhat similar to the findings of Li et al. (2020), which indicated that as intensifying management regimes led to a decline in biodiversity in agricultural land, nearby field boundaries maintained unaffected biodiversity, thereby supporting an increasing proportion of biodiversity across habitats and becoming increasingly important refuges. In our study, as LC intensity increased, the spider species composition in paddies was altered but remained unchanged in woodlands. Moreover, woodlands supported a higher spider activity density than paddies at high LC intensity, while at low LC intensity, no significant difference was observed between the two habitats. This is likely because large semi-natural habitats, such as woodlands, are less directly affected by LC (Zou, 2023) compared to croplands. As LC intensity increased, the distribution of open-habitat species and forest species across habitats was not significantly affected (Table 1, Fig. S2), as these species are highly associated with their respective habitat types (Fischer et al., 2013). In contrast, generalists might relocate from paddies to nearby woodlands in search of refuges, as their activity density increases in woodlands and tends to decrease in paddies with the increasing LC intensity (Table 1, Fig. 1). This is further supported by our finding that high-LC woodlands and low-LC paddies harboured similar spider community compositions (Table S3, Fig. 2B). As a result, at high LC intensity, woodlands support a larger proportion of spider community across habitats. These results suggest the greater importance of woodlands as refuges for spiders at high LC intensity.
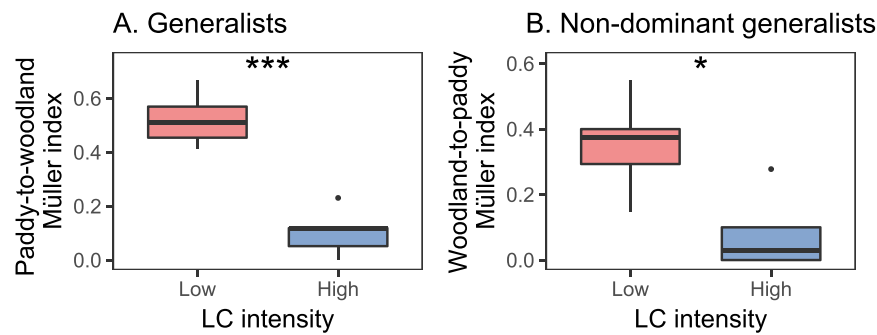
4.2. Woodlands are more important resources at low LC intensity

Previous studies reported that landscape-scale semi-natural habitats enhance natural enemy abundance (Gong et al., 2024) and pollinator species richness (Shi et al., 2021) in both consolidated and traditional fields. In these studies, LC intensity was low, as it primarily transformed traditional irregular-shaped fields into standardised rectangular fields to facilitate machinery use without notably increasing field size (Zou, 2023). However, our study area experienced a significant increase in field size (Yang et al., 2025). Consistent with these previous findings, our results showed that paddy spider species richness increased with landscape-scale woodland cover (Table 3, Fig. 5). Spider activity in
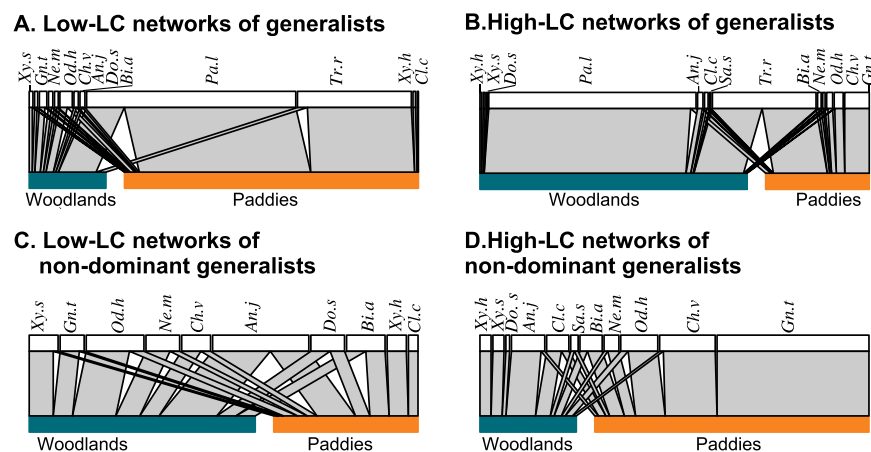
Fig. 3. Boxplots of Müller indices quantifying the relationships between woodlands and paddies in the species-habitat networks of spiders. Asterisks and carets denote significant differences between high and low LC intensities: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Fig. 4. Species-habitat networks of spider generalists in woodlands and paddies with high and low LC intensity. The upper level represents spider species, and the lower level represents habitat types. The width of the links corresponds proportional to spider activity density. Data were pooled over the study sites with the same LC intensity levels to illustrate the average influence. Spider species: *Od.h = Odontodrassus hondoensis, Ne.m = Nesticella mogera, Pa.l = Pardosa laura, Xy.h = Xysticus hedini, Xy.s = Xysticus sp. 1, Bi.a = Bianor angulosus, Do.s = Dolomedes sp. 1, An.j = Anahita jinsi, Tr.r = Trochosa ruricoloides, Ch.v = Chinattus validus, Gn. t = Gnathonarium taczanowskii, Sa.s = Salticus sp. 1, Cl.c = Clubiona corrugata.*

paddies also increased accordingly, but this relationship was observed only at low LC intensity and was absent at high LC intensity (Table 3, Fig. 5).

This positive relationship between spider activity density in paddies and landscape-scale woodland cover under low, but not high, LC intensity was primarily driven by generalist species. These species are more capable of moving between habitats and utilising resources from both woodlands and paddies than open-habitat, or forest specialists (Fischer et al., 2013), and their distribution is more sensitive to changes in LC intensity (Table 1; Fig. 1B and S2).

A similar response pattern was observed in both the two dominant and the 11 non-dominant generalist species. For non-dominant generalists, this pattern may reflect stronger spillover from woodlands into paddies, as indicated by the higher woodland-to-paddy Müller index at low LC intensity (Table 2, Fig. 3A, Fig. 4A and B). In contrast, the two dominant species appeared to treat paddies as their primary habitat at low LC intensity, as they showed higher activity density in low-LC paddies than in nearby woodlands (Table 1, Fig. 1D and F). At low intensity, their increasing activity density in paddies with woodland cover may result from active foraging in nearby woodlands to supplement resources, as supported by the higher paddy-to-woodland Müller index of generalists (primarily dominant species in abundance) at low LC intensity (Table 2, Figs. 3B, 4C and D).

The reduced Müller index and benefits of paddy spider activity from woodlands at high LC intensity may result from the decline in paddy edge density. As LC intensity increases, paddy field size increases, while paddy edge density decreases accordingly (Table S2). These linear

habitats are crucial dispersal corridors for spiders (Schirmel et al., 2016; Gallé et al., 2018), and their loss may hinder the spillover and resource acquisition of these spiders from woodlands to paddies. This is also supported by our results that the relationship between paddy spiders and woodland cover was similarly moderated by paddy edge density and paddy field size (Table S3; Fig. S2).

Another possible explanation is that paddy spiders, especially generalists, may have relocated to woodlands in search of new refuges, as reflected by the opposite responses of spider activity density and community species composition to LC intensity observed between woodlands and paddies (Table 1; Figs. 1 and 2). However, the species richness of overall spiders and generalists remained largely unaffected by LC intensity in both paddies and woodlands (Table 1). This stability may explain why the positive relationship between woodland cover and the species richness of overall spiders and their generalists was consistent across varying levels of LC intensity. These results suggest that woodlands surrounding paddies served as effective resources that enhanced paddy spider species richness, regardless of LC intensity. Species richness is important for farmland biodiversity conservation, but from an ecosystem service perspective, spider activity density is considered more critical (Kleijn et al., 2015). From this viewpoint, our results suggest that woodlands act as more effective resources for promoting paddy spider activity density and associated functional benefits under low LC intensity.

The intermediate landscape-complexity hypothesis proposed by Tscharntke et al. (2005) suggests that the effectiveness of local habitat allocation or biodiversity conservation management in

Table 3

Results of linear models examining the effects of landscape-scale woodland cover (%), paddy field size (m², log x transformed, a proxy of LC intensity) and their interaction on activity density and species richness of overall spiders and spider habitat generalists and activity density of dominant species captured in the 30 sampling paddies. Local herb cover and species richness were included as covariates. The landscape radius was determined by the model with the lowest AICc.

Explanatory	Estimate	Std. Error	Adjusted SE	z/t value	p	Relative importance
Activity density						
Overall spiders (log(X + 1) transformed)						
Woodland cover (400 m)	**1.22**	**0.58**	——	**2.12**	**0.0442**	——
Field size (400 m)	**1.83**	**0.56**	——	**3.29**	**0.0029**	——
Woodland cover: field size	**−0.23**	**0.07**	——	**−3.14**	**0.0041**	——
Generalists (log(X + 1) transformed)						
Field size (300 m)	**1.24**	**0.43**	——	**2.90**	**0.0078**	——
Woodland cover (300 m)	**2.10**	**0.48**	——	**4.38**	**0.0002**	——
Herb species richness	−0.02	0.02	——	−0.81	0.4252	——
Herb cover	**0.01**	**0.00**	——	**3.07**	**0.0053**	——
Woodland cover: field size	**−0.26**	**0.06**	——	**−4.26**	**0.0003**	——
Non-dominant generalists (log(X + 1) transformed)						
Herb cover	0.01	0.01	0.01	1.78	0.0758	0.66
Woodland cover (300 m)	**1.67**	**0.63**	**0.66**	**2.52**	**0.0118**	**0.65**
Field size (300 m)	1.10	0.80	0.81	1.36	0.1726	0.34
Woodland cover: field size	**−0.21**	**0.08**	**0.08**	**2.51**	**0.0121**	**0.34**
Pardosa laura (generalists, log(X + 1) transformed)						
Field size (500 m)	3.27	2.03	——	1.61	0.1196	——
Woodland cover (500 m)	**5.59**	**1.99**	——	**2.82**	**0.0093**	——
Heb cover	**0.03**	**0.01**	——	**3.18**	**0.0039**	——
Woodland cover: field size	**−0.71**	**0.26**	——	**−2.71**	**0.0121**	——
Trochosa ruricoloides (generalists, log(X + 1) transformed)						
Woodland cover (200 m)	**17.26**	**6.54**	**6.85**	**2.52**	**0.0117**	**0.75**
Field size (200 m)	1.40	7.10	7.25	0.19	0.8469	1.00
Woodland cover: field size	**−2.16**	**0.83**	**0.87**	**2.49**	**0.0128**	**0.75**
Herb cover	0.10	0.07	0.07	1.41	0.1585	0.31
Herb species richness	−0.51	0.36	0.38	1.33	0.1851	0.39
Species richness						
Overall spiders						
Woodland cover (200 m)	**0.38**	**0.14**	——	**2.66**	**0.0129**	——
Generalists						
Herb cover	0.03	0.01	0.01	1.91	0.0568	0.77
Woodland cover (200 m)	**0.23**	**0.11**	**0.11**	**2.07**	**0.0381**	**0.85**
Field size (200 m)	0.76	0.65	0.68	1.12	0.2642	0.21
Non-dominant generalists						
Herb cover	0.02	0.01	0.01	1.56	0.1190	0.52
Woodland cover (400 m)	0.23	0.15	0.16	1.45	0.1470	0.48

human-dominated landscapes is highest in simple landscapes (1–20 % semi-natural habitat cover) and lower in both cleared landscapes (<1 %) and complex landscapes (>20 %) (Tscharntke et al., 2012). This hypothesis has been supported by numerous studies (e.g., Scheper et al., 2013; Zirbel et al., 2019). In this framework, landscape complexity primarily refers to landscape composition. This hypothesis focuses on the local biodiversity occurring within semi-natural habitats and local management maintaining areas when considering their effectiveness in conserving biodiversity. However, in our study, increasing LC intensity, along with associated changes in field size and paddy edge density, primarily reflected a change in the complexity of landscape configuration rather than composition. Moreover, we consider not only the role of woodlands as refuges supporting local biodiversity but also their role as resources enhancing biodiversity in nearby croplands.

Consistent with the intermediate landscape-complexity hypothesis, we found that woodlands functioned as more important refuges at high LC intensity; that is, they played a greater role in maintaining local biodiversity in landscapes with simple configurations than those with complex configurations. A possible explanation is that increasing configurational heterogeneity can promote biodiversity in crop fields (Rischen et al., 2023), thereby reducing the relative contribution of landscape-scale population supported by semi-natural habitats. In contrast to the hypothesis, we also observed that woodlands served as more important resource providers at low LC intensity, playing a stronger role in enhancing biodiversity in surrounding crop fields in landscapes with complex configurational and better connectivity. Our study may offer a new perspective on the intermediate landscape-complexity hypothesis. However, this interpretation requires

further validation, as our study was limited in geographic scope, taxonomic coverage, and temporal scale.

5. Conclusion

Our study demonstrates that woodlands play crucial roles across different LC intensities. Woodlands effectively function as resources, enhancing spider activity density in paddies at low LC intensity. As LC intensity increases, this benefit diminishes and spider species composition in paddies changes. However, woodlands serve as more important refuges at high LC intensity, supporting a higher spider activity density than paddies and preserving the spider community composition similar to that at low LC intensity. These findings reflect the reduced field edge density associated with high-intensity LC, which not only impacts local spider communities in croplands but also increases their isolation from surrounding large semi-natural habitats. Therefore, the design and restoration of LC should comprehensively consider the conservation and management of both large and linear semi-natural habitats and their varying roles across LC intensities. Given that these response patterns may differ among indicator groups and habitat types, long-term, multiple-taxa, and comprehensive assessments are recommended in further studies.
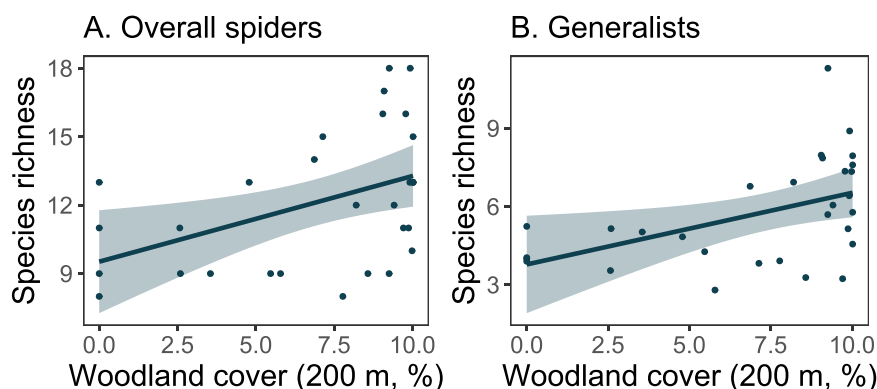
CRediT authorship contribution statement

Meichun Duan: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization. **Ruxia Qin:** Methodology, Formal analysis, Data curation. **Mingzhu**
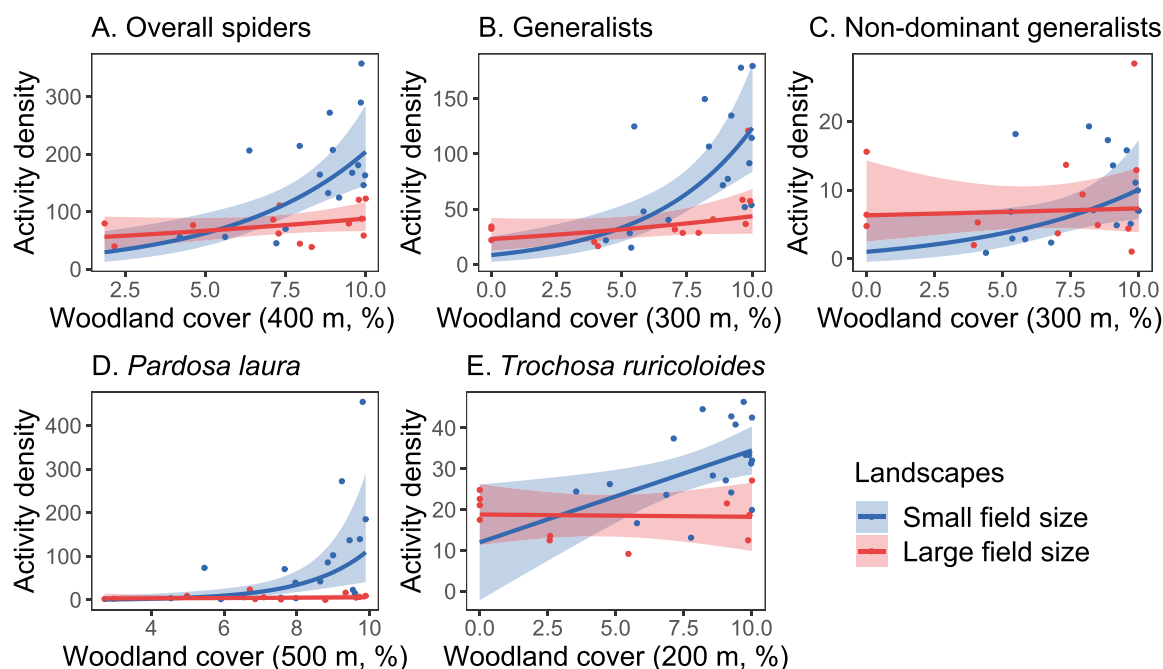
Fig. 5. Response of spider activity density to woodland cover (%), paddy field size (m², log (x) transformed, a proxy of LC intensity) and their interaction. Shaded areas indicate 95 % confidence intervals. Plotted points show back-transformed partial residuals. The landscape radius was determined by the model with the lowest AICc. For visualisation, paddy field size was divided into small and large groups based on the median of the log-transformed values (7.3329 at a 400 m radius; 7.3793 at a 300 m radius).

Fig. 6. Response of spider species richness to woodland cover (%) or field size and landscape scale. Shaded areas indicate 95 % confidence intervals. Plotted points show back-transformed partial residuals. The landscape radius was determined by the model with the lowest AICc.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109815.

Data Availability

Data will be made available on request.

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