# Perennial crops can complement semi-natural habitats in enhancing ground beetle (Coleoptera: Carabidae) diversity in agricultural landscapes

Meina Wang [a], Jan Christoph Axmacher [b,c], Zhenrong Yu [a], Xuzhu Zhang [a,d], Meichun Duan [a,e], Panlong Wu [a], Yi Zou [f], Yunhui Liu [a,*]

[a] *Beijing Key Laboratory of Biodiversity and Organic Farming, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China*
[b] *UCL, Department of Geography, University College London, London WC1E 6BT, United Kingdom*
[c] *Agricultural University of Iceland, Keldnaholt, Reykjavik, Iceland*
[d] *School of Landscape and Ecological Engineering, Hebei University of Engineering, Hebei 056038, China*
[e] *College of Agronomy and Biotechnology, Southwest University, Chongqing 400715, China*
[f] *Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou 215123, China*

## ABSTRACT

Agricultural intensification has caused losses of global biodiversity and associated ecological services. Agro-ecological landscape assessments are therefore often based on the area of remaining semi-natural habitats due to their ability to promote biodiversity. Due to their structural diversity and often less intensive management in comparison to annual crops, perennial cropland could fulfil similar roles. However, comparisons of the ability of perennial cropland versus semi-natural habitat to maintain agricultural diversity are scarce. Here, we conduct such an assessment, in comparing functional group-specific patterns in ground beetles (Coleoptera: Carabidae) as indicators of anthropogenic land-use impacts on biodiversity and biological pest control. Carabid assemblages were compared between annual cropland (56 plots), perennial cropland (24 plots) and semi-natural habitats (74 plots) of varying plant diversity across nine study regions situated in Eastern China. Our results indicated that perennial crops sustained a greater carabid species richness than semi-natural habitats, whereas assemblages of semi-natural habitats contained greater proportions of large and predatory carabids. Plant species richness positively affected the overall diversity of carabids, with the strongest effects again observed in perennial cropland. Abundance-based and species-based proportions of large carabids were positively linked to plant diversity in perennial cropland and semi-natural habitats, but negatively in annual cropland. A similar response was observed for predatory carabid abundance. Perennial crops might therefore fulfil complementary roles to semi-natural habitats in agricultural biodiversity conservation. Given common trade-offs between biodiversity conservation and agricultural production, promoting perennial cropland in particular in combination with management that increases plant diversity, could enable increases in the sustainability of agricultural production systems particularly in areas with high food demand, but limited availability of arable land. Notwithstanding, semi-natural habitats remain crucial particularly with view of enhancing biological pest control services.

## 1. Introduction

Land use change is a key driver of biodiversity losses (Bongaarts, 2019), not least through the loss and fragmentation of natural and semi-natural habitats and the intensification of agricultural production systems (Chiron et al., 2014; Baude et al., 2016). To counteract losses of biodiversity and associated ecosystem services, conservation and re-establishment of semi-natural habitats and less intensively managed habitat patches (e.g. wildflower strips and hedgerows) has been encouraged in agricultural landscapes across the European Union in Agri-Environmental Schemes (AES) (Hülber et al., 2017; Dadam and Siriwardena, 2019). Perennial cropping systems such as fruit orchards are also believed to potentially promote biodiversity and related ecosystem services in intensively managed agricultural landscapes, as these habitat are commonly less intensively managed and harbor more diverse and structurally complex vegetation compared to other cropping systems (Boller et al., 2004; Gurr et al., 2004). Nonetheless, studies evaluating links between landscape structure and biodiversity often

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focus on the area of semi-natural habitats as main indicator. Especially in regions containing few semi-natural habitat remnants, perennial cropland might nonetheless be able to serve as an alternative to semi-natural habitats in promoting biodiversity conservation. Few studies have specifically compared the potential of perennial cropland to maintain and promote biodiversity in direct comparison to annual cropland and semi-natural habitats (Fox et al., 2016).

The effectiveness of measures or landscape structures promoting biodiversity in agricultural landscapes are often related to taxon- and functional group-specific response patterns (Tscharntke et al., 2012). Functional trait-specific responses in turn are reflected in distinct changes of the functional trait composition of assemblages and in the provision of associated ecological services (Newbold et al., 2018).

Carabids (Coleoptera: Carabidae) are one of the most species-rich invertebrate families. Mainly composed of predatory and omnivorous species, carabids play important roles in ecosystems, including in the biological control of pest species, and they are often used in studies evaluating impacts of anthropogenic disturbances on agriculture ecosystems (Knapp et al., 2015). Carabid body size and trophic guild are two functional traits that are commonly used in studies of the response of carabids to environmental change and human disturbances (Lövei & Sunderland, 1996; Zou et al., 2019). This reflects the fact that these traits can be directly linked to beetle stress tolerance against land use intensity, their movement range, habitat and diet preference, as well as their respective life-cycle (Ribera et al., 2001). In heavily disturbed and fragmented homogenized modern agricultural landscapes, populations of predatory and large carabids are assumed to be most vulnerable to extinction (da Silva et al., 2017). This relates to their generally greater mobility, longer larval stages and overall life cycles, and their requirement of large habitat patches (Lövei and Sunderland, 1996; Cole et al., 2002). Accordingly, predatory and large species are often more diverse and dominant in assemblages inhabiting less intensively managed land-use types (Lövei and Sunderland, 1996; Boetzl et al., 2019).

Careful manipulation of the vegetation (determining tolerable 'weed' densities or a desirable vegetation composition) has been suggested as potential measures to enhance the diversity of carabid assemblages and associated ecosystem services in croplands (Lee et al., 2001; Fiedler et al., 2008). Plant diversity can directly benefit the diversity of invertebrate taxa, including carabids, by providing more heterogeneous food resources ('Resource Specialization Hypothesis' and 'Taxonomic Diversity Hypothesis', see Murdoch et al., 1972; Strong et al., 1984; Siemann, 1998), and indirectly via an increased structural habitat heterogeneity mediated by diverse plant communities ('Structural Heterogeneity Hypothesis', Murdoch et al., 1972; Hertzog et al., 2016). However, some studies also have shown a negative correlation (Axmacher, et al., 2004; Zou et al., 2013), as well as no association, between plant diversity and the richness of some predatory invertebrate species (Axmacher et al., 2011). Positive relationships between plant diversity and predatory arthropods could be indirectly driven by the availability of resources provided by herbivores (Brose, 2003; Jacquot et al., 2019), or again directly by the structural diversity of diverse plant communities (Strong et al., 1984). As a result, diverse and structurally complex plant communities are likely to contain larger abundances of predatory carabids (Zou et al., 2019) and exert a stronger "top-down" control effect, resulting in a better suppression of herbivore populations according to the 'Natural Enemy Hypothesis' (Root, 1973; Lubchenco, 1978). At the same time, the strength of positive "bottom-up" effects linking plant diversity with the diversity of herbivorous carabids and other herbivorous arthropods (Honek et al., 2003; Diehl et al., 2012) can be expected to be more pronounced in simple-structured annual cropland (Koricheva et al., 2018), than in generally more complex perennial cropland and semi-natural habitats (Denno et al., 2002).

Positive links between the diversity of plant and carabid assemblages will also vary with land-use type. Compared with natural ecosystems, perennial systems with their optimized productivity will commonly attract herbivorous and omnivorous carabids, as well as other herbivorous arthropods, since they provide more resources like plant biomass and fallen fruits (Söderström et al., 2001; Albertini et al., 2017), with this promotion of herbivorous arthropods ultimately also promoting predatory carabids (Haddad et al., 2001; O'Brien et al., 2017). Perennial cropping systems also have a more persistent vegetation cover and experiencing far less physical disturbances than annual cropping systems (Boller et al., 2004). Therefore, responses of species to changes in land-use and in the vegetation, both in terms of plant diversity and structural complexity, can be expected to be functional trait-specific, which means that management effects will similarly have differential effects on their functional groups.

Perennial systems are commonly experiencing advantageous low-intensity management practices compared to other cropping systems (Gurr et al., 2004). This habitat can be used for long-term planning of the establishment and maintenance of ecological infrastructure, such as the selection of ecological plants and the planning of mowing regimes, which shows a good development potential for supporting target functional groups. Nonetheless, this in turn raises the question how local plant diversity interacts with land use type in determining biodiversity patterns of carabids, an important biological control taxon, across agricultural landscapes in accordance to individual species' functional traits. To date, studies investigating this question have commonly been conducted on small spatial scales (Duan et al., 2016; Baulechner et al., 2019), while we still lack a clear understanding of the intricate inter-linkages between vegetation, land-use and diversity across functional guilds for large geographical scales.

In this study, we set out to fill prevailing knowledge gaps with regards to these links across large geographic scales, compiling data collected from multiple study sites located in Eastern China's main agriculture production areas. We aim to investigate responses of different functional groups in carabid assemblages to the (interactive) effects of land use types and plant diversity – differentiating between semi-natural habitats, perennial cropland and areas cultivated with annual crops. We firstly hypothesize that, compared with intensively managed, simplified annual cropping systems, perennial crops and semi-natural habitats harbor a greater carabid species richness, with these latter assemblages also containing a greater proportion of species and abundance of large and predatory carabids. This hypothesis is based on the assumption that, when compared with annual crops, the extensive management and more complex vegetation structure in perennial cropland and semi-natural habitats provides more stable resources that particularly favor large and predatory species that are known to be more susceptible to disturbance and environmental changes. We secondly hypothesize that with increasing plant diversity, species richness and abundance of the overall carabid assemblages will increase. This link is assumed due to the increase in available resources provided by both plants and herbivorous species, and the high structural habitat heterogeneity. Again, we also predict that the proportion of species and the abundance of large-sized and predatory carabids in perennial cropland and semi-natural habitats will show these trends in a particularly pronounced way. Finally, we hypothesize that the positive effects of plant diversity on both species richness and abundance of overall carabids are less pronounced in semi-natural habitats that are generally high in plant species diversity when compared to perennial and annual crops because these latter habitats are generally species-poor, so that an increase in plant diversity will lead to a very distinct and immediate increase in habitat heterogeneity and also in the diversity of available food resources, with these trends feeding through all the different trophic levels present in these habitats.

## 2. Materials and methods

### 2.1. Study area

Our data covers nine study sites distributed from central to northern parts of Eastern China (29°05′N ∼ 42°51′N, 108°21′E ∼ 122°22′E)
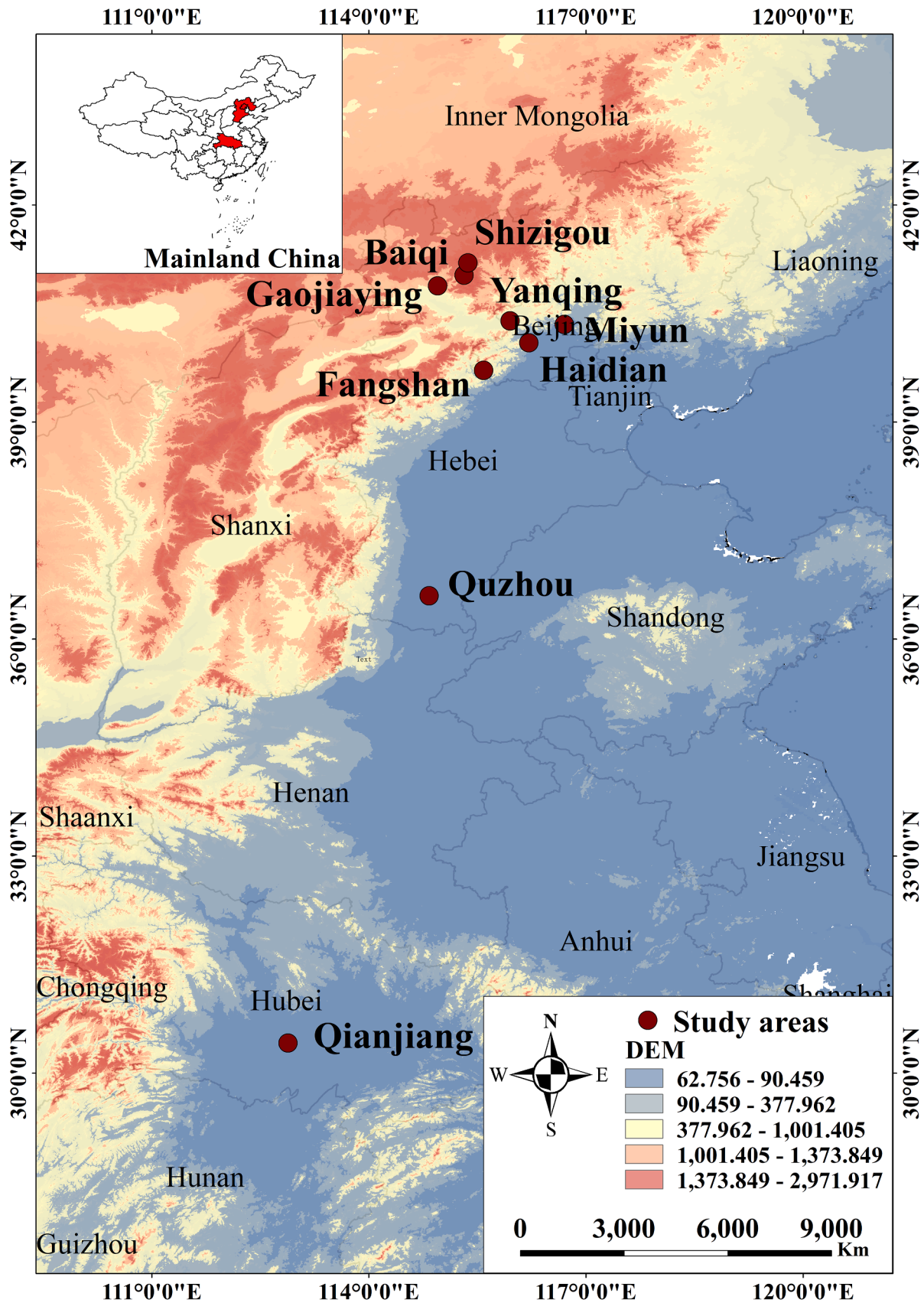
**Fig. 1.** Location of study areas.

(Fig. 1). Among them, study regions at Baiqi, Gaojiaying and Shizigou in the North of Hebei province and Yanqing in Beijing represent typical landscapes in the cropland-pasture transition zone characterized by a continental monsoon climate. Study regions at Haidian, Miyun and Quzhou represent landscape settings typical for the Northern China Plain, the main cereal production area in China dominated by winter wheat-summer maize rotation systems and characterized by a temperate semi-humid continental monsoon climate. Fangshan, located to the Southwest of Beijing, represents a mountainous area dominated by agroforestry and orchard systems. Qianjiang in Hubei province on the middle Yangtze floodplain is dominant by rice fields and characterized by a subtropical monsoon climate. Overall, the study region covers a distance of about 1200 km in a N - S direction and 370 km in a E - W direction. More detailed information about the sampling sites is presented in Table S1 and in publications from members of our author group (see Liu et al., 2010, 2012, 2015; Duan et al., 2016, 2019; Zhang et al., 2017).

In each study area, we sampled beetles and plants in both semi-natural habitats (74 plots) and farmland habitats (80 plots), resulting in a total of 154 plots surveyed across all study regions (Table S1). Farmland habitats were further differentiated into annual crops (56 plots) and perennial crops (24 plots), with cultivated crops varying between study areas. Annual cropping systems across our wider study region generally represent intensively managed annual crop monocultures, our study plots also experience significant regular mechanical/physical disturbances, with crops including wheat/maize rotation, peanut, potato and cabbage fields. Some small herbaceous weeds can also be encountered in this habitat type. Perennial cropping systems considered in this study include walnut groves and fruit orchards (mainly apple, pear, apricot and plum), with a herbaceous plant layer permanently covering the ground around the trees. Some of these systems also represent intercropping systems using a variety of low-growing crops like potatoes, carrots or onions that are conventionally treated with pesticides and fertilizers, while walnut is intercroped with chrysanthemum on the plantations in our study areas, too. Semi-natural habitats in our study included grassland, field margins, windbreaks, woodland and plantation forests. Woodland was planted with *Populus tomentosa* (Miyun, Quzhou), *Larix principis rupprechtii* Mayr. (Baiqi, Haidian, Shizigou, Yanqing), as well as *Metasequoia glyptostroboides* Hu and W. C. Cheng (Qianjiang). The Fangshan region was dominated by secondary forest, primarily composed of the native walnut *Juglans mandshurica* Maximowicz and *L. principis-rupprechtii* Mayr (Tables S2 and S3).

### 2.2. Recording of carabids and plants

Carabids were captured using pitfall traps that consisted of plastic beakers with a diameter of 8 cm and a depth of 11.5 cm, with ~ 2/3 of the capacity of the beakers filled with a 75% vol alcohol solution to preserve the specimens. All study areas were sampled from May to October over one (Haidian, Miyun and Qianjiang) or two years (all other sites). At most sites, eight pitfall traps were placed at a distance of 4 m and 7 m from the plot center along N - S and E - W facing diagonal lines intersecting in the center of the plot. In contrast, five pitfall traps were placed in a straight line in the middle of each plot at Fangshan and Qianjiang because of the smaller size of fields in these two regions. Pitfall traps were operated for 6 days each month (with the exception of Qianjiang, where they were set for only 4 days, and Quzhou, where trapping lasted for 10 days). Specimens caught in the same plot were pooled for analysis. The body size of each individual specimen, measured as the distance from the tip of the mandibles to the end of the abdomen, was recorded with a precision of 1 mm using a Vernier Caliper.

Plant species richness and % coverage were surveyed in June and September at all sites. At each plot, herb species were recorded in four randomly selected 1 m × 1 m sub-plots, while trees and shrubs were surveyed in four randomly selected 5 m × 5 m sub-plots. Data sets for each plot were combined, and the maximum cover value for each species at the two sampling events was used in the analysis.

### 2.3. Data analysis

Carabid species were divided into strictly predatory and "other" (herbivorous and omnivorous) species according to their predominantly feeding traits throughout their lifetime. According to the mean body sizes, carabid species were also classified into small (<12 mm) and large (≥12 mm) according to their body size distribution graph (Fig. S1).

We used rarefied species richness to evaluate relative differences in carabid species richness for our samples that differed strongly in overall sample size. The logarithm of sampling trap * days was used as an offset variable in the analysis of carabid abundances to account for the difference in sampling days between sites. Plots with < 20 carabid specimens (41 plots) were excluded from analysis, as the sample sizes of these pots were likely too small to generate a meaningful result (see also Zou et al., 2019). Relative proportions based on species numbers and abundance (number of individuals) were used to investigate changes in carabid communities, with this approach being robust towards differences in sampling efforts. Generalized linear mixed models (GLMMs) were used to evaluate responses in the diversity of different carabid functional groups and the composition of the beetle assemblages to different land use types, plant diversity and their interaction. In all models, land use types (annual crops/perennial crops/semi-natural habitats), plant species richness, as well as their interaction were used as predictor variables. The study region was set as random variable.

The following variables are used as response variables in our models: (1) Carabid rarefied species richness (Gaussian, identity-link, log-transformed); (2) Carabid abundance (Quasipoisson, log-link, log-transformed 'sampling trap * days' was set as offset); (3) Proportion of large carabid abundance (Binomial, logit-link); (4) Proportion of large carabid species richness (Binomial, logit-link); (5) Proportion of predatory carabid abundance (Binomial, logit-link); (6) Proportion of predatory carabid species richness (Binomial, logit-link). Additionally, we also ran the same model approaches for the same set of response variables for small and non-predatory carabids (Fig. S2-S4).

Calculations and analysis were calculated in R software version 3.4.4 (R Core Team, 2018). Model performance was validated based on the residual distribution using diagnostic plots to ensure that deviance residuals met normality and homoscedasticity assumptions (Zuur et al., 2009). Spatial autocorrelation was assessed by calculating Moran's I index and the diversity variables of different carabid functional groups using the package 'spdep' (Bivand, 2018), and no significant spatial autocorrelation was found to exist in the models. In addition, the Wald chi-squared tests were used to test the significance of predictor variables ('car' package, Fox and Weisberg, 2010). Rarefied species richness was calculated using the 'vegan' package (Oksanen et al., 2014). GLMMs were computed based on the 'glmmPQL' function in the MASS package (Venables and Ripley, 2002).

## 3. Results

### 3.1. Species composition of carabids

A total of 9115 carabids representing 119 species were sampled (Table S4). Samples included 61 small species (3499 individuals) and 58 large carabid species (5616 individuals). For feeding groups, 5 morphospecies (21 individuals) could not be associated with a clear feeding trait, while 67 species were classed as chiefly predatory (5741 individuals), and the remaining 47 species were considered to be omnivorous or even herbivorous (3353 individuals). The most dominant species, encountered at all study sites apart from Qianjiang, was *Harpalus pallidipennis*, accounting for 10.07% of all collected specimens.

## 3.2. Effects of land use types, plant species richness and their interaction on the diversity of carabids

The rarefied species richness of carabids was significantly greater in perennial crops (Mean ± SE: 6.70 ± 0.42) than in semi-natural habitats (5.84 ± 0.26), while annual crops occupied an intermediate position between these two (6.25 ± 0.31), but showing no significant differences to either of them (Tables 1 and 2, Fig. 2a).

The abundance-based proportion of large carabids was significantly greater in semi-natural habitats (74.86 ± 0.32%) and perennial crops (61.73 ± 0.33%) than in annual crops (39.58 ± 0.32%) (Table 1 and 2, Fig. 2b). In contrast, species-based proportions did not differ significantly between the three differentiated land-use types (Tables 1 and 2).

Similar to large carabids, proportions based on both, predatory carabid abundances and species numbers were significantly greater in semi-natural habitats (78.26 ± 0.27% (abundance)/57.32 ± 0.12% (species)) as compared to annual (54.59 ± 0.31%/45.81 ± 0.16%) and perennial crops (53.54 ± 0.29%/44.15 ± 0.15%), while no significant differences were observed between the two crop types (Tables 1 and 2, Fig. 2c and d).

Plant species richness showed significant positive links with the abundance-based proportion of large beetles (Table 1, Fig. 3a) and with the rarefied species richness of carabids in all land use types (Table 1, Fig. 3b). Concomitantly, the positive relationship was less pronounced in semi-natural habitats compared to annual and perennial crops. Except for the species richness-based proportion of predatory carabids, plant species richness was positively linked to all other response variables in perennial crops and semi-natural habitats, but showed negative links for annual crops (Table 1, Fig. 3c–e). The species richness-based proportion of predatory carabids responded positively to plant species richness in semi-natural habitats, only, but declined in annual cropland and perennial cropland (Table 1, Fig. 3f).

**Table 1**
Results of generalized linear mixed models showing the effects of land use types and plant species richness on carabids. Significance of variables were tested with ANOVA. Significance numbers were printed in bold (PSR = Plant species richness).

| Response variable | Explanatory variables | Chisq | P (>Chisq) |
|---|---|---|---|
| Carabid rarefied species richness | **Land use Types** | **10.377** | **0.006** |
| | PSR | 0.032 | 0.858 |
| | **Land use Types * PSR** | **6.879** | **0.032** |
| Carabid abundance | Land use Types | 1.490 | 0.475 |
| | PSR | 0.015 | 0.902 |
| | Land use Types * PSR | 3.231 | 0.199 |
| Proportion of large carabids (Abundance) | **Land use Types** | **7.127** | **0.028** |
| | **PSR** | **6.474** | **0.011** |
| | **Land use Types * PSR** | **36.809** | **<0.001** |
| Proportion of large carabids (Richness) | Land use Types | 0.691 | 0.708 |
| | PSR | 0.916 | 0.339 |
| | **Land use Types *PSR** | **7.914** | **0.019** |
| Proportion of predatory carabids (Abundance) | **Land use Types** | **12.115** | **0.002** |
| | PSR | 1.348 | 0.246 |
| | **Land use Types * PSR** | **6.214** | **0.045** |
| Proportion of predatory carabids (Richness) | **Land use Types** | **11.942** | **0.003** |
| | PSR | 1.891 | 0.169 |
| | **Land use Types * PSR** | **6.740** | **0.034** |

## 4. Discussion

Agricultural intensification is considered to be the dominant pressure on biodiversity in human-dominated landscapes (Bongaarts, 2019; Brasil et al., 2020). In these landscapes, semi-natural habitats are believed to play a key role for the conserving of agricultural biodiversity, often providing shelter and diverse food resources (Cole et al., 2002; Boetzl et al., 2019). Nonetheless, and contrary to our first hypothesis, semi-natural habitats harbored an overall lower carabid species richness when compared to perennial crops in the agricultural landscapes across our study regions in Eastern China. This surprising observation may partly be related to the long agricultural history in China. In our study region, semi-natural habitats are commonly composed of vegetation that is homogenous in both structure and species composition (Cao, 2008; Xu, 2011). Often, these semi-natural habitats furthermore experience surprisingly intensive human activities such as grazing and mowing, which further limits their potential role in biodiversity conservation (Wu et al., 2019). However, semi-natural habitats were shown to still play an important role in sustaining a high diversity and local abundance of predatory and large-sized ground beetles - trait groups that contribute strongly to biological pest control and are vulnerable to the highly frequent disturbances occurring on arable land (Lövei and Sunderland, 1996; da Silva et al., 2017). Based on our results and on previous studies (Liu et al., 2015; Li et al., 2018), the pest control service linked to carabid assemblages could likely be further bolstered if management intensity and, more generally, human-induced disturbances in the semi-natural habitats were reduced, allowing the restoration of a more diverse and structurally heterogeneous native vegetation in these habitats (Hua et al., 2016; Boinot et al., 2019), with this heterogeneity further promoting stable populations of predatory and large species.

The peak in overall species richness of carabids in perennial cropland could partly be associated with specific traits, but also the actual native ranges of the crops and weeds. Certain non-native plant species may actually benefit the populations of natural enemies (Fiedler and Landis, 2007). In this context, the herbaceous layers in perennial cropping systems commonly contained more non-native plant species than semi-natural habitats, such as the often very abundant *Amaranthus retroflexus* and *Hibiscus trionum*, both native to Africa (Table S2). Such plants might provide distinctly different food resources for herbivores than the native community, benefiting not only this community, but leading to cascading effects that also trigger benefits for predators (Lau and Strauss, 2005). This can result in an enhanced beneficial effect of diet-mixing (Karban et al. 2010). This effect could be further strengthened by an increased productivity of these habitats from human interventions (Rosas-Ramos et al., 2018). Furthermore, the relative openness of perennial cropland under the crowns of the woody vegetation also enhances the ease of movement and hence the activity radii and likeliness of trapping of carabids (Andersen, 2000). Perennial cropland habitats also harbor an overall heterogeneous and relatively species-rich vegetation – especially when compared to annual cropland (Risch et al., 1983). This might explain the greater proportion of large carabids, with their populations also benefiting from less intensive management in plots representing this habitat type. Overall, our results suggest that perennial croplands could indeed serve as an alternative to standard semi-natural habitat - focused AES practice in biodiversity conservation and enhancing of associated ecosystem services, while optimizing trade-offs between conservation and production in these agricultural landscapes (Boller et al., 2004). They represent a measure particularly relevant in regions with high food demand, but a limited area of potential arable land. Future research could also ascertain the role non-native plant species play in agricultural plant communities, allowing the identification of species potentially suitable in attracting natural enemies into perennial cropping systems (Fiedler and Landis, 2007). Given that the perennial cropland habitats at least in Eastern China create similar benefits for carabid assemblages to semi-natural habitats, our study furthermore suggests that it might be more meaningful to

**Table 2**

Effects of different land use types on carabid diversity – values show mean values and standard errors, while letters indicate significant differences.

| Functional traits | Species richness (mean ± SE) | | | Abundance (mean ± SE) | | |
|---|---|---|---|---|---|---|
| | Annual crops | Perennial crops | Semi-natural habitats | Annual crops | Perennial crops | Semi-natural habitats |
| Overall carabids | 6.25 ± 0.31ab | 6.70 ± 0.42a | 5.84 ± 0.26b | 74.65 ± 7.05a | 90.35 ± 18.33a | 70.00 ± 7.67a |
| Proportion of large-sized carabid (%) | 51.08 ± 0.15a | 60.80 ± 0.14a | 69.67 ± 0.12a | 39.58 ± 0.32b | 61.73 ± 0.33a | 74.86 ± 0.32a |
| Proportion of predatory carabid (%) | 45.81 ± 0.16b | 44.15 ± 0.15b | 57.32 ± 0.12a | 54.59 ± 0.31b | 53.54 ± 0.29b | 78.26 ± 0.27a |
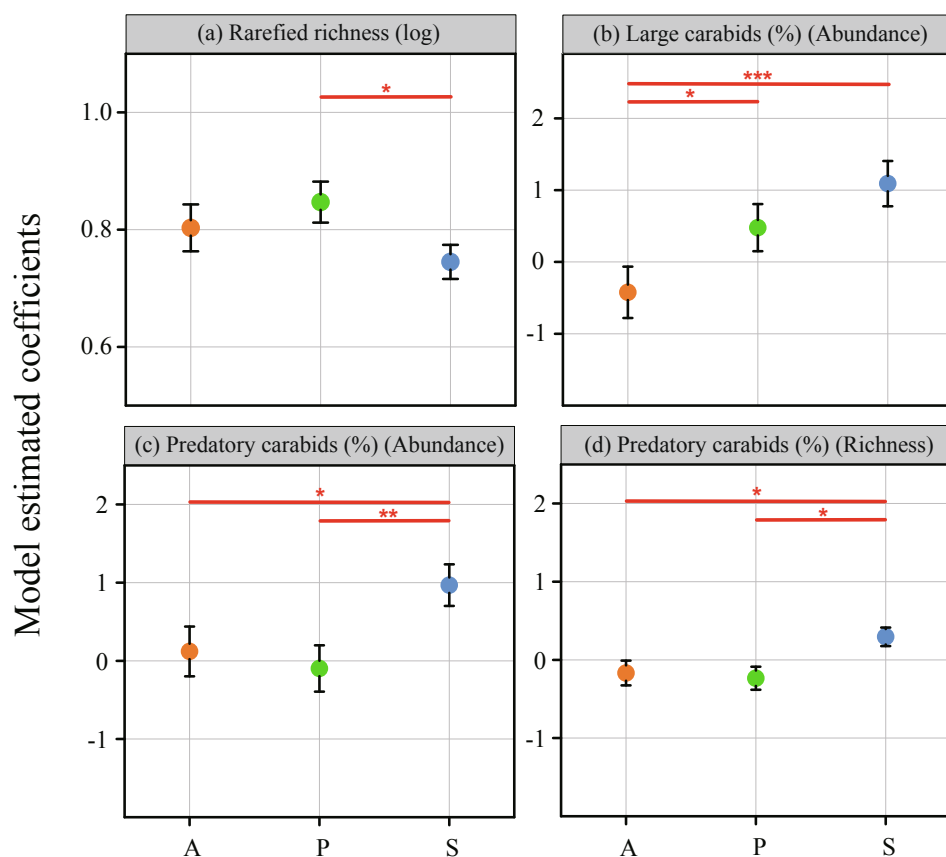


**Fig. 2.** Estimated coefficients from generalized linear mixed models showing the differences between assemblages in different land use types (A: annual crops; P: perennial crops; S: semi-natural habitats): (a) rarefied species richness of carabids (b) proportion of large-sized carabid abundance (c) proportion of predatory carabid abundance (d) proportion of predatory carabid species richness; error bars refer to the SE of estimates, and asterisks indicate a significant difference based on the models (*≤0.05; **≤0.01; ***<0.001).

combine these two habitat types and contrast them with the area covered in annual cropland, or clearly differentiate between these three habitat types, in studies linking biodiversity with agricultural landscape structures.

In addition, our results confirmed the importance of high plant diversity to optimize conservation outcomes. These positive effects on overall carabid diversity were strongest in perennial cropland than annual cropland, but weakest in semi-natural habitats. Previous studies revealed that the positive impact of plant diversity on groups at higher trophic levels gradually decreased with an increasing trophic distance from plant diversity via herbivore diversity to predator diversity (Haddad et al., 2001; O'Brien et al., 2017). This might explain the relatively small impact of plant diversity on large and predatory carabid species in semi-natural habitats. Meanwhile, less intensively managed semi-natural habitats are generally structurally richer than ground-cover vegetation of cropping systems where increases in plant diversity additionally increase both the diversity of food resources and habitat heterogeneity. In contrast, croplands are generally species-poor, so that an increase in plant diversity will lead to a very distinct and immediate increase in these habitat resources. Additionally, strong correlations between overall carabid diversity and plant diversity in perennial cropland could be related to the higher productivity of these agricultural habitats compared to semi-natural habitats, with perennial crops

providing a higher plant biomass, not least in the form of fallen fruits (Söderström et al., 2001; Albertini et al., 2017), while also having a more persistent vegetation cover and experiencing far less physical disturbances than annual systems (Boller et al., 2004). These factors likely come into play in explaining the great potential for areas covered in perennial crops to harbor diverse assemblages under suitable habitat conditions (Simon et al., 2010). Allowing the persistence of some plant species of no direct agricultural use in croplands, and especially in perennial cropland, furthermore appears to allow for strong increases in the diversity of target functional groups like ground beetles with their associated pest control functions (Wyss, 1995) that are considered critical for a sustainable agricultural production (Gurr et al., 2004).

Nonetheless, we also found that the abundance- and species-based proportions of large carabids responded positively to plant diversity only in perennial cropland and semi-natural habitats, but negatively in annual cropland. A similar response was also observed for predatory carabid abundance, somewhat highlighting the fact that many predatory carabid species also tend to be large in size (Liu et al., 2015). This pattern in our view reflects the potential sensitivity of large and predatory carabids especially to disturbance events, with perennial cropland and semi-natural habitats experiencing less intensive human disturbances in our study areas, while also possessing a complex habitat structure and diverse sets of food resources associated with diverse plant
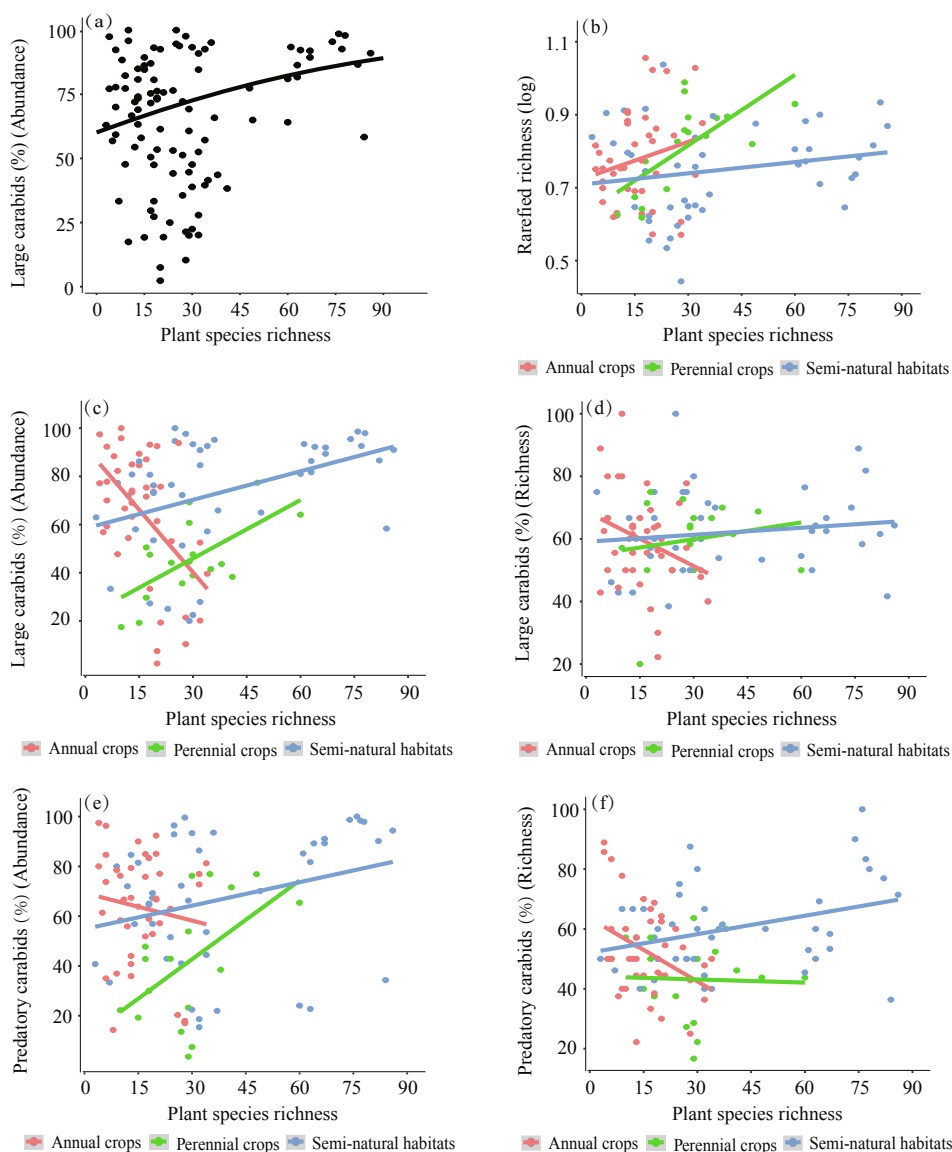
**Fig. 3.** Effects of the plant species richness on the proportion of large carabid abundance (a); and effects of the interaction between land use types and plant species richness on the rarefied species richness of carabids (b), proportion of large-sized carabids based on abundance (c) and species richness (d), and proportion of predatory carabids based on abundance (e) and species richness (f).

communities and their respective herbivorous prey assemblages (Lubchenco, 1978; Srivastava and Lawton, 1998). Results from our study further emphasize the potential of perennial cropland to serve as an alternative habitat type to semi-natural habitats in promoting biodiversity and carabid beetle - related biological pest control, although predatory carabid species had a lower dominance in this habitat type than in semi-natural habitats. However, perennial crops are still of high value as a complementary measure or a compromise between agricultural productivity and biodiversity conservation. Clearly, this potential can be further enhanced by careful management of the vegetation to further boost natural enemies by enhancing habitat quality.

The negative responses of large and predatory carabid abundance and species richness to increased plant diversity in annual crops may be caused by the complex set of factors differentiating different annual crop types not least related to the intensity of management (Lundgren et al., 2006). Differences in local management intensities applied to different crops due to their specific needs, structure and phenology, will trigger differential responses in carabid species (Rivers et al., 2018). Annual crops with the highest plant diversity in our study area were vegetable fields, while cereal crops were linked with lower overall plant species

richness (Table S3). At the same time, vegetable production in China is linked to higher levels of pesticide applications per ha than cereal production (Huang et al., 2000), a trend potentially responsible for the negative links between plant diversity and the abundance and diversity of large and predatory carabids in annual crops. To optimize the pest control services linked to annual crops hence potentially requires a careful selection of the cropping system, and the reduction, where possible, of pesticide applications (Rivers et al., 2017). Small and herbivorous beetles were generally much more dominant in communities inhabiting the simple-structured annual crop land where they can directly benefit from an increased plant species richness according to the 'Resource Specialization Hypothesis' and the 'Taxonomic Diversity Hypothesis' (Murdoch et al., 1972; Strong et al., 1984; Siemann, 1998), which may further explain the inverse relationships between plant diversity and large and predatory carabid assemblage dominance since these groups do not benefit equally from the enhanced plant diversity in habitats of this type. These results confirm that, while plant diversity is an important factor in shaping diversity and composition of carabid assemblages in agricultural landscapes, the response patterns of the beetles are highly complex, as they vary with habitat and crop type, local

management intensity and are further differentiated by feeding guilds.

The important potential contribution of natural enemies to pest control in orchards has already been demonstrated (Solomon et al., 2000; Shaltiel and Coll, 2004). In agroecosystem, the conservation of biodiversity and promotion of biological pest control services within perennial systems is therefore an important issue warranting thorough evaluation. Ecological 'compensation areas' where management intensity is locally reduced - or intensive cultivation is ceased – could further enhance biological control of pests across the agricultural landscape and increase overall biodiversity (Simon et al., 2010). Studies differentiating between functional traits when focusing on the relationships between carabid assemblages and land-use intensity are therefore particularly meaningful when focusing not only on biodiversity patterns, but also on the provision of associated ecosystem services in agricultural landscapes. Perennial cropland in this regard can be seen as particularly promising in matching agricultural production, conservation of biodiversity and provision of biological pest control (Boller et al., 2004). To further strengthen the role of these habitat types, it seems essential to consider targeted habitat type-specific adaptations to their management and to their vegetation composition - with view of promoting specific guilds within carabid communities linked to specific ecological services. In turn, this will increase the ecological sustainability of the agricultural production systems.

## 5. Conclusion

In the context of agricultural intensification, the response pattern of carabid functional groups to agricultural landscape patterns is indicative of the relationship between biodiversity or ecosystem functioning and land-use change. In this context, perennial cropland appears to provide stable resources for a wide range of carabid species. Surprisingly, this resulted in semi-natural habitats not routinely harboring the highest carabid species richness across the different habitat types in Eastern China's agricultural landscapes, but still played an important role in promoting a particularly high diversity and local abundance of predatory and large-sized carabids. Species of these two functional groups furthermore showed positive responses to increasing plant diversity in both perennial cropland and semi-natural habitats. These observations suggested that perennial cropland could serve as a beneficial complementary habitat type to semi-natural habitats in AES, representing a compromise measure that combines agricultural productivity with biodiversity conservation. Particularly in combination with management efforts to obtain a high plant diversity, perennial cropland could therefore be promoted in addition to semi-natural habitats particularly to promote biodiversity and ecosystem services like biological pest control across intensively managed agricultural landscapes.

## CRediT authorship contribution statement

**Meina Wang:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Jan Christoph Axmacher:** Methodology, Supervision, Writing - review & editing. **Zhenrong Yu:** Investigation, Resources, Supervision, Funding acquisition. **Xuzhu Zhang:** Investigation. **Meichun Duan:** Investigation, Writing - review & editing. **Panlong Wu:** Writing - review & editing. **Yi Zou:** Methodology, Writing - review & editing. **Yunhui Liu:** Conceptualization, Investigation, Writing - review & editing, Resources, Supervision, Project administration, Funding acquisition.

## Declaration of Competing Interest

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

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107701.

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