



Effects of plant diversity, habitat and agricultural landscape structure on the functional diversity of carabid assemblages in the North China Plain

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Abstract. 1. This study investigated the effects of plant diversity, habitat type and landscape structure on the functional diversity of the carabid assemblages in the agro-landscape of the North China Plain. We hypothesise (i) small, herbivorous and omnivorous carabids are more strongly affected by local plant diversity, while large and predatory carabids are strongly affected by landscape structure, and (ii) habitat type influences the diversity across functional groups.

2. In 2010, carabid beetles were sampled by pitfall traps in six typical habitats of the agro-landscape: wheat/maize fields, peanut fields, orchards, field margins, windbreaks and woodland.

3. Our results showed that (i) habitat type played a predominant role in driving the changes in the diversity of carabid assemblages, followed by local plant diversity while the landscape structure had little effect; (ii) small and omnivorous carabid were strongly affected by local plant diversity, while the composition of large and predatory carabid was strongly associated with the landscape structure; and (iii) habitats dominated by woody species harboured different assemblages to habitats dominated by herbaceous plants for overall carabids and three functional groups excluding omnivorous beetles.

4. Informed by our results, we suggest the differentiated responses between functional groups should be appreciated in conservation management. In the intensively managed agro-landscape, maintenance of diverse habitats and creating a more complex vegetation structure would be the most efficient measures to enhance the diversity of carabid assemblages. Particularly, the maintenance of extensively managed habitats coupled with a targeted increase in the local plant diversity is crucial to optimise the biological pest control by carabid assemblages.

Key words. Functional groups, ground beetles, landscape heterogeneity, vegetation.

Introduction

Agricultural landscapes account for more than 40% of the global land area and play a significant role in sustain-

ing global biodiversity including conserving endangered species (Tscharntke *et al.*, 2005; Norris, 2008). Accordingly, the implications of agricultural management for the protection of biodiversity and associated ecosystem services in the agricultural landscape are increasingly recognised. A variety of factors ranging from the complexity of the landscape structure (Weibull *et al.*, 2000; Aavik & Liira, 2010), habitat diversity (Hendrickx *et al.*, 2007) as well as vegetation structure and composition (Thomas & Marshall, 1999; Söderström *et al.*, 2001) strongly influence

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the community structure and diversity of invertebrate (Weibull *et al.*, 2000; Söderström *et al.*, 2001; Hendrickx *et al.*, 2007), vertebrate (Söderström *et al.*, 2001) and plant species assemblages (Aavik & Liira, 2010) at different spatial scales. In particular, complex structured landscapes with high proportions of non-crop habitat can enhance local diversity, where source populations can spill over into cropland and therefore provide spatio-temporal insurances (Tschardt *et al.*, 2012). Diverse habitats support higher species richness due to the widespread existence of strong species-habitat associations (Willand *et al.*, 2011). Habitat management intensity can also affect biodiversity, with less intensive managed habitat commonly sustaining a greater diversity (Yu *et al.*, 2006). Plant communities determine the physical structure, niche and food resource in most habitats and therefore exert considerable influence on the distributions and interactions of animal species considerably (Bazzaz, 1975; Lawton, 1983; McCoy & Bell, 1991). In recognition of the importance of the agricultural landscape context, research emphasis has started to shift from centring on individual species and species assemblages, protected area management and farm practice improvements to more holistic perspectives considering conservation and sustainable management of larger regions containing a diversity of different landscape elements (Bennett *et al.*, 2006; Wu, 2008). Targeted modifications of these factors are believed to potentially provide an effective approach to compensate for negative effects from intensive modern agricultural practices (Tschardt *et al.*, 2005; Fischer *et al.*, 2006).

In Europe, environmental and agricultural policies have strongly promoted measures to increase landscape heterogeneity, habitat diversity and vegetation diversity to foster regional biodiversity and ecosystem service provision. Agri-environment schemes in England, for example, encourage the establishment of ecological corridors, extensively managed field margins, wildflower strips and 'beetle banks' to foster regional biodiversity and ecosystem service provision (<http://www.naturalengland.org.uk>). Recent debates, however, have put the effectiveness of such landscape development approaches in promoting biodiversity into question (Kleijn & Sutherland, 2003; Roth *et al.*, 2008). Discrete and even diverging responses to changes in landscape structure (Burel *et al.*, 2004; Aviron *et al.*, 2005), habitat type (Gabriel *et al.*, 2010; Liu *et al.*, 2012) and vegetation (Woodcock *et al.*, 2009; Tischler *et al.*, 2013) have emerge when comparing diversity responses of different organism groups, especially where these also differ in their functional traits (Aviron *et al.*, 2005; Woodcock *et al.*, 2009; Liu *et al.*, 2012). Body size and feeding habit, for example, are factors potentially leading divergent responses to environmental factors (Henle *et al.*, 2004; Jetz *et al.*, 2004). Larger species are expected to be more susceptible to larger scale landscape changes than small species (Concepción & Díaz, 2011), because they have a longer duration of juvenile stages and large home ranges (Blake *et al.*, 1994; Lövei & Magura, 2006; Concepción & Díaz, 2011). Species at higher trophic levels are

suggested to be more susceptible to changes in environmental conditions than species at lower levels, because these species commonly have lower population densities, longer juvenile stages or larger home ranges (Gard, 1984; Holt, 1996; Lövei & Magura, 2006). They are also believed to be more severely affected by the larger scale landscape structure than herbivorous and omnivorous species (Ritchie & Olf, 1999; Purtauf *et al.*, 2005a). These trends reflect highly complex and spatially specific taxon response patterns to environmental change, requiring the development of a functional-group specific management and to identify the appropriate scale for more effective conservation measures (Yaacobi *et al.*, 2006; Gabriel *et al.*, 2010; Batáry *et al.*, 2012).

In China, with more than 50% of its terrestrial land area under agricultural use, the intensification of agricultural production in recent decades has had strong negative effects on agricultural biodiversity (Xu & Wilkes, 2004). In the key cereal production area, the North China Plain (NCP), a significant intensification in agricultural production (Ju *et al.*, 2006; Guo *et al.*, 2010) has been associated with a high risk of biodiversity loss. Unfortunately, biodiversity conservation in the agricultural landscape has so far received limited attention (but see Liu *et al.*, 2006, 2010, 2012), with very limited information available on the connections between landscape structure and biodiversity (EBIBAG, 2009) or on differential responses of functional groups to environmental change at different scales. An understanding of the spatial scale-dependent effects of land-use patterns on the diversity in China's agricultural landscape is nonetheless vital to promote a more sustainable landscape management and the conservation of high levels of biodiversity (EBIBAG, 2009).

Our study aims to address current knowledge deficits, investigating how variations in local plant diversity, habitat type and landscape structure affect the diversity of the carabid assemblages in the agricultural landscape of the NCP. We also explore how functional grouping influences species-environment relationships. Carabid beetles were chosen as focal taxon as they play multiple important ecological roles in agro-ecosystems especially in controlling biological pests (Kromp, 1999) and weed species (Bohan *et al.*, 2011; Jonason *et al.*, 2013). We classified carabids into two binomial functional groups according to body size (large vs. small) and main feeding traits during their life cycle (predatory vs. omnivorous). Previous studies indicated strong effects of landscape structure (de la Peña *et al.*, 2003; Purtauf *et al.*, 2005b) or both local and landscape-scale factors on carabid assemblages (Aviron *et al.*, 2005; Werling and Gratton 2008). Beetle responses have been suggested to vary with functional traits such as body size, feeding habit or habitat affinity (Aviron *et al.*, 2005; Batáry *et al.*, 2007; Clough *et al.*, 2007). Predatory carabid species have been reported to be more affected by changing landscape structure than herbivorous and omnivorous species (Purtauf *et al.*, 2005a). We hypothesise that carabid beetles response to environmental factors depend on their functional traits. Predatory and large

species, which have good dispersal abilities, large home range sizes, long life cycles and are hence more susceptible to human disturbances, are believed to be more strongly affected by the overall landscape structure and more abundant in less intensively managed habitats. In contrast, omnivorous and small beetles are hypothetically more strongly linked to local plant diversity because of their lower dispersal ability, smaller home ranges and lower sensitivity to disturbance. Finally, the habitat type is hypothesised to influence the diversity across the functional groups.

Materials and methods

Study area and site selection

This study was conducted at Xitiange village in Northeastern Miyun County (40°21'–40°25'N, 116°42'–116°47'E) near the northern boundary of the NCP. The area is situated about 70 km north of Beijing city centre. The local climate is continental, with an annual temperature of 11.5 °C and an average annual precipitation of ~700 mm.

The sampling sites were located in the plain area that covers about 27% of Xitiange village mainly to the south of the village centre. In this area, agricultural land accounts for about 55% of the total area, while residential and roads account for a further 21% (Fig. 1). The most common agricultural crops are winter wheat/summer maize and peanuts, with large areas also used as fruit orchards. Semi-natural land, which mainly consists of woodland, windbreaks, field margins, weeds

land, accounts for about 12% of the sampled landscape.

The six most common habitats in the research region: wheat/maize rotation fields, peanut fields, woodland, windbreaks, field margins and orchards, were selected for beetle sampling. Field margins were defined as linear non-cropping areas with a naturally colonised grass-dominated vegetation covering a width >2 m between fields. Windbreaks consisted of poplar tree lines planted between fields. Woodland was also planted with *Populus* spp., but had a much greater width with an overall area exceeding 1 ha.

In maize/wheat fields, about 300 kg ha⁻¹ of N fertilizer and 110 kg ha⁻¹ of P₂O₅ were applied during two growing seasons. Herbicides were applied after each crop sowing and pesticides were applied once in spring and autumn respectively. In peanut fields, about 60 kg ha⁻¹ of N fertilizer and 170 kg ha⁻¹ of P₂O₅ were applied in addition to herbicides and fungicides, which were sprayed after sowing and flowering respectively. No fertilizer was applied in the orchards, while fungicide was sprayed after the flowering. No agro-chemicals were used in woodland, windbreaks and on the field margins.

Beetle and plant surveys

Beetles were sampled over periods of 6 days every month between the beginning of May and the end of September 2010 using a total of five pitfall traps at each plot. Arrangements of pitfall traps were adjusted according to the shape of habitat to enable more typical catchment of fauna (Kotze *et al.*, 2011) and also to limit the edge effect

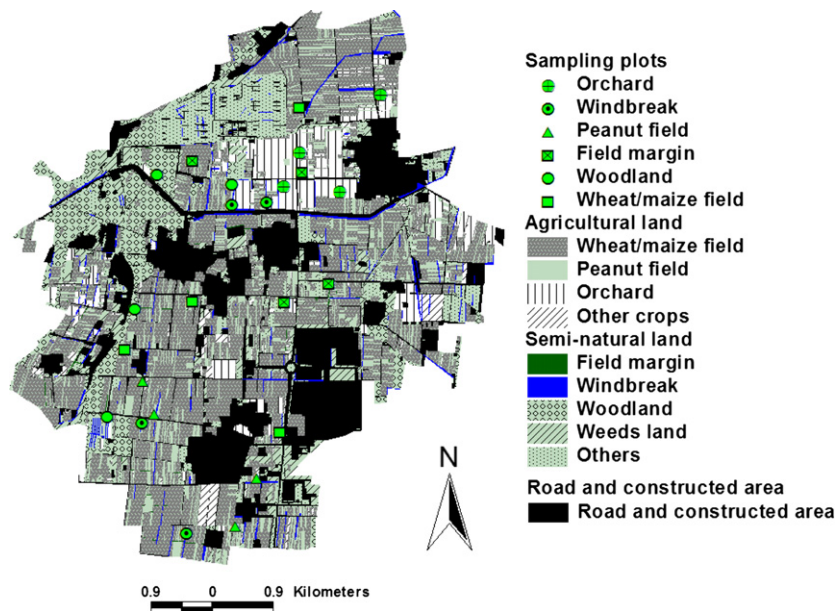


Fig. 1. Map of land-use and sampling plots in Xitiange village, Miyun county, Beijing (2010).

in linear habitats. At the agricultural fields, orchards and in woodland, plots measuring $20 \times 20 \text{ m}^2$ were established, and five pitfall traps were placed at the centre of each of these plots and at a distance of 5 m from the plot centre along N–S and E–W facing diagonal lines. At field margins and windbreaks, plots were established at the centre of these linear habitats to minimise edge effects. To achieve comparative results across the different habitats, five traps in these linear habitats were placed with a distance of 5 m between individual pitfall traps as in agricultural lands.

The % cover of vascular plant species was surveyed in June and September 2010. Within each plot, all tree and shrub species were recorded in four randomly selected $1 \text{ m} \times 5 \text{ m}$ sub-plots, while herb species were surveyed in four randomly selected $1 \text{ m} \times 1 \text{ m}$ sub-plots. Data sets in both seasons for each plot were combined, allocating the maximum % cover recorded at these two sampling events to each plant species.

Landscape data

Land-use types in the study region were digitised based on an extensive field mapping surveys in combination with high-resolution Quickbird satellite imagery (resolution 0.6 m) during sampling season. Landscape metrics within a radius of 300 m were considered in this study as it was supposed that most carabid beetles disperse within the limited distance of up to 50 m (Welsh, 1990) and respond to landscape structure at fine spatial scales (Aviron *et al.*, 2005; Batáry *et al.*, 2007). Shannon Diversity Index was selected as an indicator for the heterogeneity of landscape structure as it is widely applied in research on landscape–biodiversity relationships (Concepción *et al.*, 2008; Bassa *et al.*, 2011), and it was calculated using FRAGSTATS 3.3 (Mcgarigal *et al.*, 2002).

Data analysis

Carabid beetles were divided into small (<15 mm) and large species (>15 mm) (Cole *et al.*, 2002) according to their averaged body size measured using a vernier calliper. They were also divided into predators and omnivores according to their predominantly feeding traits during their entire life cycle (Antonenko, 1980; Yu, 1980, 1981; Deng, 1983; Deng *et al.*, 1985; Liang & Yu, 2000; Sasakawa, 2007, 2009). As little information is available for the feeding habits of Chinese carabids, we categorised them depending on assumptions on the basis of taxonomic affinity in the cases where information for a specific species was lacking. Accordingly, *Amara* spp. was assumed to be omnivorous (Hürka & Jarošík, 2003). *Harpalus* spp., which tends to be granivorous, but is also known to utilise other food sources (Brandmayr, 1990; Deng 1983; Kirk, 1973; Liang & Yu, 2000; Lund & Turpin, 1977; Yu, 1981), was categorised as omnivorous.

Beetle data for each plot were pooled for subsequent analysis. Non-metric multidimensional scaling based on Chord distances was applied to analyse species turnover rates of different carabid groups between sites using PAST (Hammer *et al.*, 2001). Species richness was calculated using EstimateS V9.1.0 (Colwell, 2013) based on the Chao1 species richness estimator to account for the inevitable confounding effects of sample size resulting from the varied shapes of investigated habitats and arrangement of pitfall traps. The Gini-Simpson diversity index which emphasises ‘evenness’ of the community and varies between 0 and 1 was calculated to characterise the diversity of the plant communities using the statistical package PAST (Hammer *et al.*, 2001).

To investigate the effects of landscape structure, habitat type and local plant diversity on the activity-abundance and estimated species richness of each beetle group, linear mixed effect models with fixed variance (glms, nlme package version 3.1-108 in R) (Pinheiro *et al.*, 2013) were used in R 2.15.2 (R Core Team, 2012). Landscape diversity, habitat type as well as local plant diversity were used as fixed predictors, and the model was simplified using the step-AIC function in the package MASS (Venables & Ripley, 2002). The normality of the distribution of the raw-dependent variables was assessed using QQ-plots. Data were \log_{10} -transformed or sqrt-transformed where necessary. To account for spatial autocorrelation, we fitted gls models to response variables with Gauss–Krüger coordinates treated as spatial covariates, assuming a spherical spatial correlation structure (Pinheiro & Bates, 2000), but no spatial autocorrelation was found.

Three separate partial redundancy analyses (pRDA) were used to investigate the separate effects of local plant diversity, habitat type and landscape diversity on species composition of the all beetle assemblages and the four functional groups when combining the other two variables as conditional variables. Prior to the analyses, the beetle species matrix was modified using Hellinger transformation (Legendre & Gallagher, 2001) in preparation for the use in PCA and RDA. Pseudo-F values and the corresponding significance levels were calculated based on 999 Monte-Carlo permutations. Finally, spatial autocorrelations of plots were diagnosed using the mso function, but no spatial patterns were apparent. Calculations were performed using the vegan package (version 2.0-2) in R (Oksanen *et al.*, 2012).

Results

Species composition and turnover

A total of 1750 carabids representing 17 species and 9 genera were caught during the sampling season (Table 1). Among these, 11 species with a total of 1246 individuals were smaller than 15 mm, while the remaining six species representing 504 individuals were classified as large beetles (>15 mm). Furthermore, six species representing 781

Table 1. Effects of landscape diversity, habitat type and local plant diversity on the activity-abundance and species richness of different carabid groups.

Depend variable	Functional group	Explanatory variables	d.f.	AIC	F-value	P-value
Activity-abundance	Overall carabids	Habitat type	5, 18	120.612	4.405	0.009
	Large carabids	Habitat type	5, 18	92.757	5.840	0.002
	Small carabids	Habitat type	5, 18	18.961	5.040	0.005
	Predatory carabids	Habitat type	5, 18	17.232	8.256	<0.0001
	Omnivorous carabids	Habitat type	5, 18	17.547	6.134	0.002
Species richness (Chao1)	Overall carabids	Habitat type	5, 18	-13.262	2.875	0.044
	Large carabids	Habitat type	5, 18	65.838	4.893	<0.005
	Small carabids	Plant diversity	1, 22	-12.680	4.383	0.048
	Predatory carabids	Habitat type	5, 18	66.653	3.712	0.018
	Omnivorous carabids	Plant diversity	1, 22	-4.498	2.878	0.104

individuals were predatory, while the remaining 12 species accounting for 969 individuals were classed as omnivores. Among the omnivorous carabids, more than 97% of the individuals were also small species. Accordingly, more than 75% of small carabids were omnivorous. On the other hand, 94% of large individuals were classed as predatory, but only 61% of the predatory individuals represented large species. *Harpalus pastor*, *Dolichus halensis*, *Chlaenius posticalis* and *Harpalus pallidipennis* were the four most common species in the sampled agricultural landscape, accounting for 43.3%, 21.3%, 17.5% and 8.2% of all sampled individuals respectively.

The NMDS ordination showed that plots dominated by woody plants including orchards, windbreaks and woodland harboured distinctly different carabid species assemblage from the plots dominated by herbaceous plants, including wheat/maize fields, peanut fields and field margins (Fig. 2a). This distinction was also evident for large carabids (Fig. 2b), small carabids (Fig. 2c) and predators (Fig. 2d). In contrast, all sampling plots for omnivorous carabids were closely clustered together with an exception of four plots, indicating a more homogenous composition of omnivorous carabid species across the sampled habitats (Fig. 2e).

Effects of local plant diversity, habitat type and landscape structure on abundance and diversity

Activity-abundance and species richness. The activity-abundance of the overall carabid assemblage and of the four functional groups were strongly influenced by the difference in habitat types, but not by landscape diversity and local plant diversity (Table 1). Peanut fields generally harboured the lowest activity-abundance, followed generally by woodland activity-abundance levels (Fig. 3a). Field margins in contrast were characterised by a high activity-abundance of large and predatory carabids, and in orchards a high activity-abundance of carabid species across all four groups.

Differences in species richness for the overall carabid assemblages, large and predatory carabid functional groups were all strongly associated with differences in habitat type,

but no differences were observed for the species richness of both small and omnivorous carabids (Table 1). Peanut fields harboured the lowest species richness for the overall carabid assemblage and all functional groups (Fig. 3b). Wheat/maize field, field margins and orchard harboured a large species richness of both large and predatory carabids, while woodland assemblages contained a large number of predatory carabids (Fig. 3b). In addition, species richness of small carabid was positively associated with plant diversity (Table 1; Fig. 4), while omnivorous species richness responded to none of the parameters landscape structure, habitat type or local plant diversity (Table 1).

Species composition. The partial RDA ordination plots indicate varied responses of beetle assemblages to the individual variable of landscape diversity, habitat type and plant diversity across the different functional carabid groups when the effects of the other two of these three variables were excluded (Table 2). The overall carabid assemblage was significantly associated with habitat type and local plant diversity, but not with landscape diversity. Large carabid assemblages changed significantly only between habitat types, while shifts in small and omnivorous carabid assemblages were again associated with both changes in habitat type and local plant diversity. Predatory carabid turnover finally was not significantly associated with any of the factors. Habitat type was the variable that explained the overall greatest amount in variation (>21%) in the species composition across all carabid groups; species composition of overall, small and omnivorous assemblages were much more closely linked to plant diversity than by landscape structures. In contrasted, large and predatory carabid assemblages, whose species compositions were much more explained by landscape structure than by local plant diversity.

Discussion

Effects of plant diversity

The taxonomic diversity of plant species is commonly suggested to be directly and indirectly linked to the

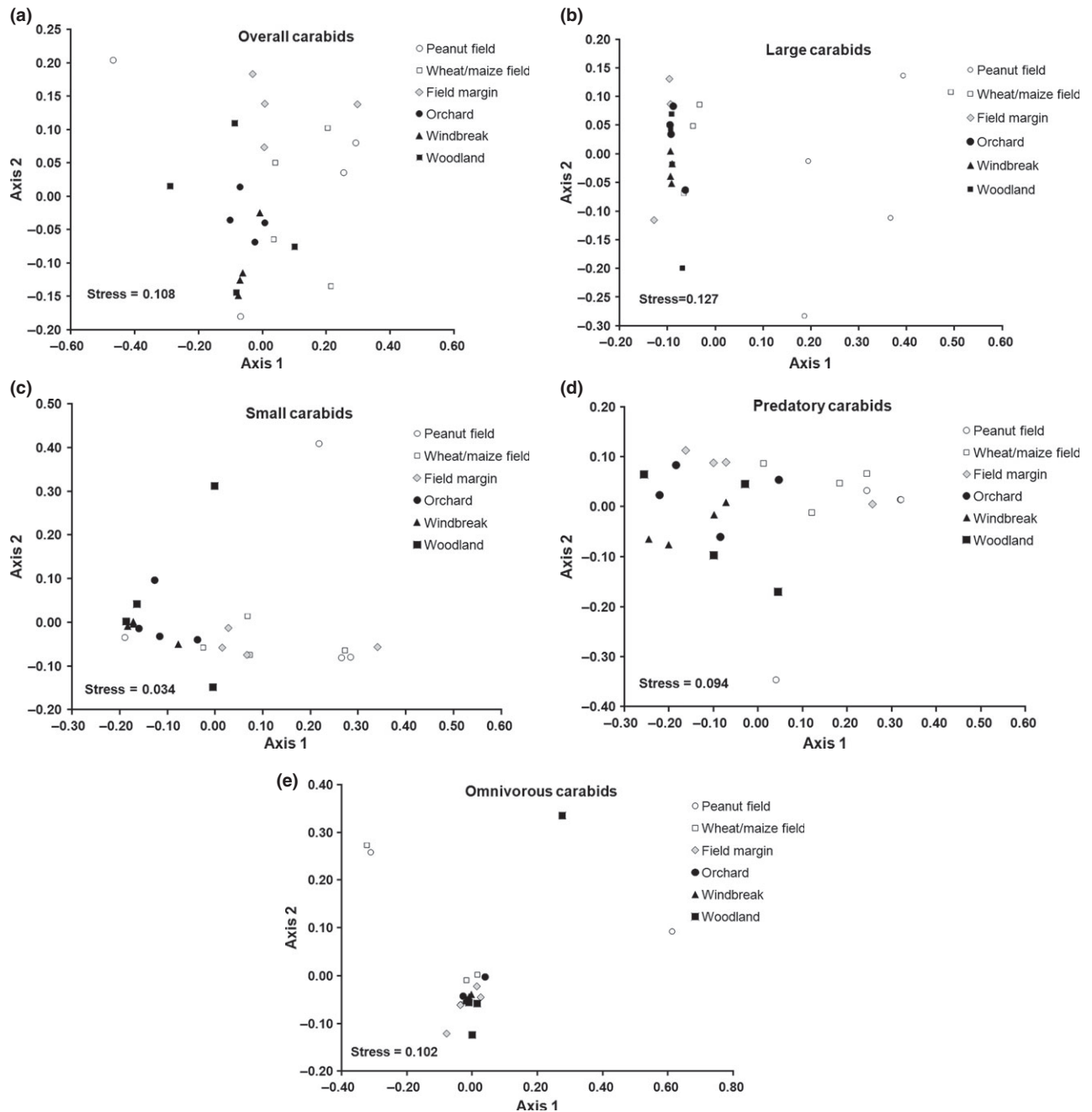


Fig. 2. Nonlinear two-dimensional scaling of different carabid groups based on the Chord distance: (a) Overall carabids; (b) Large carabids; (c) Small carabids; (d) Predatory carabids; (e) Omnivorous carabids.

diversity of invertebrate taxa (Kareiva, 1983; Siemann, 1998). On one hand, increasing in plant species richness can potentially support increasing numbers of specialised consumers (Murdoch *et al.*, 1972; Siemann *et al.*, 1998), which in turn can encourage a greater diversity of predators through cascade effects (Hunter & Price, 1992). On the other hand, plant communities can impact consumer diversity indirectly by mediating the physical structure of

the environment, which again increases in heterogeneity with increasing plant species richness, with implications for distribution and interactions of species in the increased niche spaces (Lawton, 1983; McCoy & Bell, 1991). The strong association observed between changes in overall beetle and plant species composition in our study could be explained by either of these direct and indirect effects, especially in relation to the strong correlation between

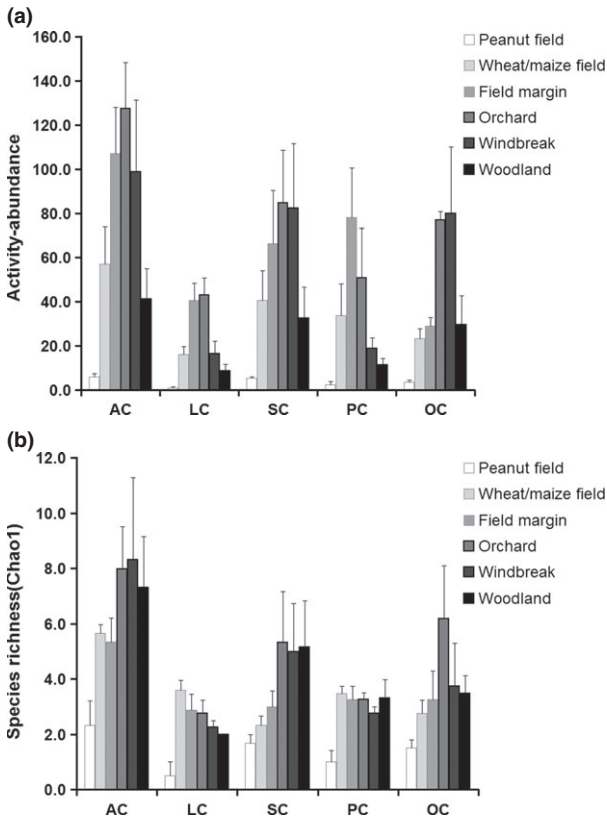


Fig. 3. Abundance and species richness of carabid groups in the different habitats. AC, Overall carabids; LC, Large carabids; SC, Small carabids; PC, Predatory carabids; OC, Omnivorous carabids. Bars indicate standard error (1 SE).

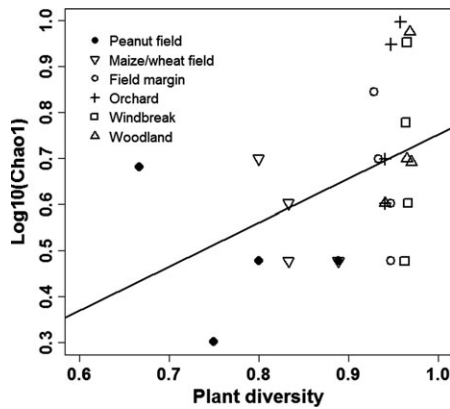


Fig. 4. Relationship between species richness of small carabids and plant diversity based on generalised least square model results.

plant diversity and small carabid assemblage structure, and to the strongly differentiated species composition between habitats dominated by woody versus herbaceous plants.

Table 2. Species composition of carabid functional groups: percentage of variance explained by partial redundancy analyses (pRDA).

Explanatory	Overall carabids	Large carabids	Small carabids	Predatory carabids	Omnivorous carabids
Landscape diversity 5.1 Pseudo-F(1,16) = 1.601; P = 0.16 32.3 Pseudo-F(5,16) = 2.041; P = 0.008 9.5 Pseudo-F(1,16) = 3.007; P = 0.035	4.4 Pseudo-F(1,16) = 0.931; P = 0.438 24.0 Pseudo-F(5,16) = 1.907; P = 0.022 0.6 Pseudo-F(1,16) = 0.231; P = 0.871	5.6 Pseudo-F(1,16) = 1.788; P = 0.163 35.2 Pseudo-F(5,16) = 2.241; P = 0.012 12.3 Pseudo-F(1,16) = 3.899; P = 0.023	3.8 Pseudo-F(1,16) = 1.419; P = 0.239 21.0 Pseudo-F(5,16) = 1.556; P = 0.112 0.5 Pseudo-F(1,16) = 0.181; P = 0.919	5.6 Pseudo-F(1,16) = 1.671; P = 0.152 30.2 Pseudo-F(5,16) = 1.795; P = 0.042 21.3 Pseudo-F(1,16) = 5.915; P = 0.013	

The significant association between the functional groups of both omnivores and small carabids, but not predatory or large beetles, with plant diversity is congruent with observations made in previous studies (Harvey *et al.*, 2008; Šerić Jelaska *et al.*, 2010). The previous studies suggested that herbivore diversity is affected predominantly by bottom-up effects related to resource availability, a trend commonly reported in environments with poor plant species diversity, while top-down effects are believed to become more pronounced in environments with high-quality plants or in high-productivity (Hunter & Price, 1992; Stiling & Rossi, 1997; Denno *et al.*, 2002). As seed feeding species contribute strongly to the groups of omnivores and small carabid beetles in this study, their strong association with plant diversity could indeed be explained by bottom-up effects of resource availability. Top-down effects related to predation pressure might also be at work. For example, in the case of peanut fields, very low plant coverage could lead to small beetles being more prone to attack from their natural enemies.

It is remarkable that predatory and large beetles did not show any significant links with plant diversity in this study. Predators are often assumed to be more abundant and more diverse in species-rich plant communities with a greater variety of habitats and more availability of prey according to the natural enemy hypothesis (Jactel *et al.*, 2005). Scherber *et al.* (2010) however, showed that the links between plant diversity and arthropod diversity dampen with increasing trophic level. The lack of correlation between plant diversity and predatory and large beetles could be explained by the poor habitat quality of some of the investigated habitats so that they were unable to support sufficient numbers of herbivores to sustain large predator assemblages, or by predatory and large beetles having strong dispersal ability, enabling them to use resources at large spatial scales. Vegetation structure still appears to play a role in affecting the composition of predatory and large beetles, as indicated by the differential species composition between habitats dominated by woody and herbaceous plant species for both predatory and large beetles.

Effects of habitat

In accordance with our initial hypothesis, habitat type presented a key factor in determining the overall diversity of carabids. As also mentioned above, the distinct plant structure of the different habitats determines the availability of both structural niches and environmental resources required by the different carabid species (Bazzaz, 1975; Mortimer *et al.*, 1998; Brose, 2003; Asteraki *et al.*, 2004; Axmacher *et al.*, 2009). This is further supported by the observed distinct species assemblages supported by the structurally more complex woody habitats, which also tended to support a greater taxonomic diversity of plant species. Habitat types are also closely linked to disturbance intensity and productivity (Murison *et al.*, 2007;

Liu *et al.*, 2012). Agricultural intensification is commonly seen as a main cause of biodiversity loss (Matson *et al.*, 1997; Wilson *et al.*, 1999), despite observations that intensively managed habitats can sometimes support diverse and abundant populations of ground beetles when they provide large quantities of potential resources in some cases (Tschardtke *et al.*, 2005; Liu *et al.*, 2010). Carabids are nonetheless generally known to show higher diversity levels in habitats with less intensive management (Carcamo *et al.*, 1995; Pfiffner & Luka, 2003). Therefore, the low activity-abundance and species richness of the overall carabid assemblages in peanut fields could be further contributed to higher management intensity and much simpler and more homogenous vegetation structure in these habitats. The heterogeneous carabid species composition of large and predatory species as well as in the overall species assemblage for habitats dominated by herbaceous plants could similarly be related to the stronger gradient in management intensity. Furthermore, the cultivation of annual crops on these sites will strongly influence their microclimatic conditions, which form a further, important factor determining carabid distribution (Thiele, 1977). It is therefore likely that the significant influence of the habitat type on the diversity of all carabid groups can be attributed to the interaction of several factors including plant diversity and plant structure, productivity, land-use intensity and microclimate conditions. This complex interaction appears to lead to a strong similarity in activity-abundance and species richness between the intensively managed, more productive wheat/maize fields and extensively managed, more structurally complex habitats, such as orchards, field margins and woodland.

Effects of landscape structure

Wider landscape structure has been demonstrated to significantly affect carabid species richness and density (Burel *et al.*, 1998; Purtauf *et al.*, 2005a,b; Batáry *et al.*, 2007; Diekötter *et al.*, 2010), as well as on ground beetle species composition (de la Peña *et al.*, 2003; Aviron *et al.*, 2005; Diekötter *et al.*, 2010). Carabids with different traits also show different responses to landscape structure, with species richness of carnivorous and phytophagous carabid species decreasing with a decrease in non-cropping area in the landscape, while no effects on species richness were observed for omnivorous species (Purtauf *et al.*, 2005a). The relative abundance of large species (>15 mm) was also found to significantly correlate with the proportion of woody elements in the landscape, whereas small species were not similarly affected (Aviron *et al.*, 2005).

In contrast to the above published results, landscape structure did not show any significant effects on abundance or species richness of the overall carabid assemblage and the four functional groups investigated in our study. Although consistent with our hypothesis that landscape structure showed a greater relative impact on the species composition of large and predatory carabid in

comparison to small and omnivorous species, landscape structure explained very small percentage of the variance in species composition of both large and predatory carabid assemblages (<6%). Compared to earlier studies reporting strong positive effects of a heterogeneous landscape on local arthropod diversity (see also Weibull *et al.*, 2000; Clough *et al.*, 2005; Batáry *et al.*, 2007), the landscape investigated in this study was overall rather homogenous and had experienced serious semi-natural loss and fragmentation for several millennia due to strong anthropogenic influences, leaving no natural residual habitats. The substantial habitat loss and fragmentation would result dramatic loss of biodiversity before this investigation. The most 'natural' habitats in the landscape we investigated are mainly formed by monotonous monocultures of poplar (woodland and windbreak) or secondary herbaceous vegetation, largely restricted to 'edge' environments of a lower habitat 'quality' than pristine habitats would have contained. Overall, any habitat specialists specialised on the potential natural vegetation will have been lost, and the resulting assemblages are predominantly composed of generalist species which are at least partly adapted to crop land (Tscharrntke *et al.*, 2012). The lack of any natural habitat in the wider vicinity of the study area would rule out any cross-habitat spillover from natural habitats into the agricultural landscape. With more than 75% of the total landscape being under cultivation or classed as residential and roads areas and another 12% being covered in semi-natural habitats, the local traits and quality of habitats can therefore be expected to be more important than the surrounding landscape matrix in determining the ground beetle species composition and diversity (Tscharrntke *et al.*, 2005).

Effects of sampling methods

Although pitfall trapping is the most commonly used the method in to gain standardised quantitative samples of carabid beetles in ecological studies, its effective capture rates depend both on activity patterns and population densities of the captured species (Mitchell, 1963; Greenslade, 1964). Habitat-related or traits-related differences in the activity patterns of carabid species therefore somewhat complicate direct comparisons of pitfall trapping results (Spence & Niemelä, 1994), and the subsequent analysis of assemblage data (Kotze *et al.*, 2011). Unfortunately, these drawbacks in pitfall-trapped samples remain unresolved (Kotze *et al.*, 2011). The different arrangement of pitfall traps between different habitat types in our investigation will further affect the results as well, although these were necessary to ensure the collection of representative samples for the different habitat types (see also Kotze *et al.*, 2011), and we used the estimated species richness was used to eliminate the effects of differences in our sampling sizes. It is nonetheless important to recognise that there are inherent limitations to the accuracy of

results obtained solely from pitfall trapping. Combinations with other sampling methods should therefore be considered in future research to further substantiate our results (Liu *et al.*, 2007).

Implications for conservation

With a long history of agricultural use, little natural or even semi-natural residual habitats remaining in this key area of China's cereal production. A first important measure to support and enhance the existing regional biodiversity in the region should therefore focus on improvements at small spatial scales. As our study indicates, the habitat type and plant diversity currently play an important role in driving the diversity of the overall carabid assemblages. A diverse range of cropping systems in the landscape is therefore seen as critical for enhancing the carabid diversity. Specifically, extensively managed orchards appear to be of high value for carabid conservation particularly when there is a high production pressure on the land due to food requirements and to ensure the farmers' income. Field margins which are allowed to go through succession to increase in complexity and in their proportion of woody plant components could also be an economic and efficient way to promote the abundance particularly of large and predatory carabids, which are the key group in arthropod pests control (Yu *et al.*, 2006). In addition, given the strong effects of the plant community on overall ground beetle diversity, future management of non-cropping habitats should be aimed towards creating a more complex vegetation structure with higher levels of plant diversity. Specifically, habitats containing woody vegetation such as orchard, woodland and windbreak in addition to semi-natural field margins, should be maintained and sustainably managed as a further loss of such habitat would be detrimental to the biological control service in the agricultural landscape. At the same time, the plant species composition should be carefully managed (Landis *et al.*, 2000; Fiedler *et al.*, 2008), as particularly small and omnivorous ground beetle species, which show strong association with plant diversity in our study, are known to form agricultural pests themselves in some circumstances (Yu, 1980). Given our substantial knowledge gaps in this area, a better understanding of plant–insect relationships is critical to formulate clear guidance for the enhancement of biodiversity and associated ecosystem services in the agricultural landscape.

Despite a less pronounced effect of the landscape structure on carabid assemblages in comparison to habitat and plant diversity and the scarcity of any pristine habitats in the study area, maintaining landscape heterogeneity is particularly important to support the biological pests control function of ground beetles. This is crucially important for predatory carabid since variation in predatory carabid assemblage was much more strongly linked to landscape structure than local plant diversity. On the other hand,

the 17 species sampled in six different habitats during a period of 30 sampling days between May and September indicated an overall very low level of species richness in the local carabid species pool compared to other regions (Liu *et al.*, 2012) or even to other villages in the same area (Yu *et al.*, 2006 – unfortunately these study sites have now been replaced by a residential area due to the rapid urbanisation of Beijing). On a longer term, measures at larger scales, like ecological networks connecting agricultural land with high-quality natural or semi-natural habitats, could be effective steps for the recovery of the remaining biodiversity in the entire region (Jones-Walters, 2007).

Conclusion

The key finding of this study is that it is habitat and local plant diversity rather than landscape structure are driving the changes in diversity of carabid assemblages; and carabid beetles, response patterns to local plant diversity and landscape structure depending on their functional traits. Small and omnivorous carabid assemblages are more affected local plant diversity, while large and predatory carabid assemblages are more strongly associated with landscape structure. Conservation management needs to consider these spatially varied responses of functional groups to optimise diversity and biological pest control service. In the intensively managed agricultural landscape of the NCP, a tailored increase in habitat diversity and local plant diversity can therefore provide a good starting point to support the carabid diversity and assemblage structure. In the long term, the establishment of a protected area network specifically based on strongly degraded agricultural habitats left to natural vegetation succession and linking the overall agricultural landscape with remnants of pristine habitats could enable the future enhancement of the carabid biodiversity and their biological pest control service.

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References

Aavik, T. & Liira, J. (2010) Quantifying the effect of organic farming, field boundary type and landscape structure on the

vegetation of field boundaries. *Agriculture, Ecosystems & Environment*, **135**, 178–186.

- Antonenko, O.P. (1980) Remove from marked Records Biological peculiarities of predacious carabids and their role in the reduction of numbers of the noxious pentatomid (*Eurygaster integriceps*) in the Saratov region. *Zoologicheskii Zhurnal*, **59**, 1634–1643.
- Asteraki, E.J., Hart, B.J., Ings, T.C. & Manley, W.J. (2004) Factors influencing the plant and invertebrate diversity of arable field margins. *Agriculture, Ecosystems and Environment*, **102**, 219–231.
- Aviron, S., Burel, F., Baudry, J. & Schermann, N. (2005) Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems & Environment*, **108**, 205–217.
- Axmacher, J.C., Brehm, G., Hemp, A., Tünte, H., Lyaruu, H.V.M., Müller-Hohenstein, K. & Fiedler, K. (2009) Determinants of diversity in afrotropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography*, **36**, 337–349.
- Bassa, M., Boutin, C., Chamorro, L. & Sans, F.X. (2011) Effects of farming management and landscape heterogeneity on plant species composition of Mediterranean field boundaries. *Agriculture, Ecosystems & Environment*, **141**, 455–460.
- Batáry, P., Báldi, A., Szé, G., Podlussány, A., Rozner, I. & Erdős, S. (2007) Responses of grassland specialist and generalist beetles to management and landscape complexity. *Diversity and Distribution*, **13**, 196–202.
- Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tschardtke, T. (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture, Ecosystems and Environment*, **146**, 130–136.
- Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, **56**, 485–488.
- Bennett, A.F., Radford, J.Q. & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, **133**, 250–264.
- Blake, S., Foster, G.N., Eyre, M.D. & Luff, M.L. (1994) Effects of habitat type and grassland management practice on the body size distribution of carabid beetles. *Pedobiologia*, **28**, 502–512.
- Bohan, D.A., Boursault, A., Brooks, D.R. & Sandrine, P. (2011) National-scale regulation of the weed seed bank by carabid predators. *Journal of Applied Ecology*, **48**, 888–898.
- Brandmayr, T.Z. (1990) Sperophagous (seed-eating) ground beetles: first comparison of the diet and ecology of the Harpaline genera *Harpalus* and *Ophonus* (Col.: Carabidae). *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. by N.E. Stork), pp. 307–316. Intercept, Andover, Hampshire, UK.
- Brose, U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, **135**, 407–413.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., The-nail, C., Brunel, E. & Lefeuvre, J.C. (1998) Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica*, **19**, 47–60.
- Burel, F., Butet, A., Delettre, Y.R. & de la Peña, N.M. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning*, **67**, 195–204.

- Carcamo, H.A., Niemala, J.K. & Spence, J.R. (1995) Farming and ground beetles – effects of agronomic practice on populations and community structure. *Canadian Entomologist*, **127**, 123–140.
- Clough, Y., Kruess, A., Kleijn, D. & Tscharrntke, T. (2005) Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *Journal of Biogeography*, **11**, 2007–2014.
- Clough, Y., Kruess, A. & Tscharrntke, T. (2007) Organic versus conventional arable farming systems: functional grouping helps understand staphylinid response. *Agriculture, Ecosystems & Environment*, **118**, 285–290.
- Cole, L.J., McCracken, D.I., Nennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J. & Waterhouse, T. (2002) Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. *Agriculture, Ecosystems & Environment*, **93**, 323–336.
- Colwell, R.K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. <<http://purl.oclc.org/estimates>> 16th September 2013.
- Concepción, E.D. & Díaz, M. (2011) Field, landscape and regional effects of farmland management on specialist open-land birds: does body size matter? *Agriculture, Ecosystems and Environment*, **142**, 303–310.
- Concepción, E.D., Díaz, M. & Baquero, R.A. (2008) Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology*, **23**, 135–148.
- Deng, D. (1983) The feeding habits of thirteen species of ground beetles (Coleoptera: Carabidae). *Acta Entomologica Sinica*, **26**, 356–357.
- Deng, D., Wang, G. & Li, J. (1985) Bionomics of predacious carabids in Heilongjiang. *Acta Entomologica Sinica*, **28**, 281–287.
- Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, **83**, 1443–1458.
- Diekötter, T., Wamser, S., Wolters, V. & Birkhofer, K. (2010) Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems & Environment*, **137**, 108–112.
- EBIBAG (Editor Board for Inventory on the biodiversity in agricultural region) (2009) *Inventory on the Biodiversity in Agricultural Region*. Chinese Environmental Sciences Press, Beijing, China.
- Fiedler, A.K., Landis, D.A. & Wratten, S.D. (2008) Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biological Control*, **45**, 254–271.
- Fischer, J., Lindenmayer, D.B. & Manning, A.D. (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, **4**, 80–86.
- Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, **13**, 858–869.
- Gard, T.C. (1984) Persistence in food webs. *Mathematical Ecology* (ed. by S.A. Levin and T.G. Hallam), pp. 208–219. Springer Verlag, Berlin, Germany.
- Greenslade, P.J.M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301–310.
- Guo, J.H., Liu, X.J., Zhang, Y., Shen, J.L., Han, W.X., Zhang, W.F., Christie, P., Goulding, K.W.T., Vitousek, P.M. & Zhang, F.S. (2010) Significant acidification in major Chinese croplands. *Science*, **327**, 1008–1010.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: paleontological statistics software package for education and data analysis. <http://palaeo-electronica.org/2001_1/past/issue1_01.htm> 12th October 2009.
- Harvey, J.A., van der Putten, W.H., Turin, H., Wagenaar, R. & Bezemer, T.M. (2008) Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds. *Agriculture, Ecosystems and Environment*, **127**, 100–106.
- Hendrickx, F., Maelfait, J., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V. & Bugter, R. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340–351.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity Conservation*, **13**, 207–251.
- Holt, R.D. (1996) Food webs in space: an island biogeographic perspective. *Food Webs: Integration of Patterns and Dynamics* (ed. by G.A. Polis and K.O. Winemiller), pp. 313–323. Chapman & Hall, New York City, New York.
- Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.
- Hürka, K. & Jarošík, V. (2003) Larval omnivory in *Amara aenea* (Coleoptera: Carabidae). *European Journal of Entomology*, **100**, 329–335.
- Jactel, H., Brockerhoff, E.G. & Duelli, P. (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects in insect pest infestations, and re-examination of responsible factors. *Forest Diversity and Function: Temperate and Boreal Systems* (ed. by M. Scherer-Lorenzen, Ch. Körner and E.D. Schulze), pp. 235–261. Springer, Berlin, Heidelberg, Germany.
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, **306**, 266–268.
- Jonason, D., Smith, H.G., Bengtsson, J. & Birkhofer, K. (2013) Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae). *Landscape Ecology*, **28**, 487–494.
- Jones-Walters, L. (2007) Pan-European ecological networks. *Journal for Nature Conservation*, **15**, 262–264.
- Ju, X.T., Kou, C.L., Zhang, F.S. & Christie, P. (2006) Nitrogen balance and groundwater nitrate contamination: Comparison among three intensive cropping systems on the North China Plain. *Environmental Pollution*, **143**, 117–125.
- Kareiva, P. (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. *Variable Plants and Herbivores in Natural and Managed Systems* (ed. by R.F. Denno and M.S. McClure), pp. 259–289. Academic Press, New York City, New York.
- Kirk, V.M. (1973) Biology of a ground bootle, *Harpalus pensylvanicus*. *Annals of the Entomological Society of America*, **66**, 513–518.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.

- Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., De-koninck, W., Koivula, M.J., Lövei, G.L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. & Zetto, T. (2011) Forty years of carabid beetle research in Europe—from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, **100**, 55–148.
- Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment*, **74**, 187–228.
- Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve Natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.
- Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.
- Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.
- Liang, H. & Yu, P. (2000) Species of ground beetles (Coleoptera: Carabidae) predating oriental armyworm (Lepidoptera: Notuidae) in China. *Journal of Environmental Entomology*, **22**, 160–167.
- Liu, Y., Axmacher, J.C., Wang, C., Li, L. & Yu, Z. (2007) Ground beetle (Coleoptera: Carabidae) inventories: a comparison of light and pitfall trapping. *Bulletin of Entomological Research*, **97**, 577–583.
- Liu, Y., Axmacher, J.C., Wang, C., Li, L. & Yu, Z. (2010) Ground beetles (Coleoptera: Carabidae) in the intensively cultivated agricultural landscape of Northern China - implications for biodiversity conservation. *Insect Conservation and Diversity*, **3**, 34–43.
- Liu, Y., Axmacher, J.C., Wang, C., Li, L. & Yu, Z. (2012) Ground beetle (Coleoptera: Carabidae) assemblages of restored semi-natural habitats and intensively cultivated fields in Northern China. *Restoration Ecology*, **20**, 234–239.
- Liu, Y., Yu, Z., Gu, W. & Axmacher, J.C. (2006) Diversity of carabids (Coleoptera, Carabidae) in the desalinized agricultural landscape of Quzhou county, China. *Agriculture, Ecosystems & Environment*, **113**, 45–50.
- Lövei, G.L. & Magura, T. (2006) Body size changes in ground beetle assemblages—a reanalysis of Braun *et al.* (2004)'s data. *Ecological Entomology*, **31**, 411–414.
- Lund, R.D. & Turpin, F.T. (1977) Carabid damage to weed seeds found in Indiana cornfields. *Environmental Entomology*, **6**, 695–698.
- Matson, P.A., Parton, W.J., Power, A. & Swift, M. (1997) Agricultural intensification and ecosystem properties. *Science*, **277**, 504–509.
- McCoy, E.D. & Bell, S.S. (1991) Habitat structure: the evolution and diversification of a complex topic. *Habitat Structure: The Physical Arrangement of Objects in Space* (ed. by S.S. Bell, E.D. McCoy and H.R. Mushinsky), pp. 3–27. Chapman and Hall, London, UK.
- Megarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: Spatial Pattern Analysis Program for categorical maps. <<http://www.umass.edu/landeco/research/fragstats/fragstats.html>> 12th May 2013
- Mitchell, B. (1963) Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schränk). II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. *Journal of Animal Ecology*, **32**, 377–392.
- Mortimer, S.R., Hollier, J.A. & Brown, V.K. (1998) Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in Southern Britain. *Applied Vegetation Science*, **1**, 101–114.
- Murdoch, W.W., Evans, F.C. & Peterson, C.H. (1972) Diversity and pattern in plants and insects. *Ecology*, **53**, 819–829.
- Murison, G., Bullock, J.M., Underhill-Day, J., Langston, R., Brown, A.F. & Sutherland, W.J. (2007) Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler *Sylvia undata*. *Ibis*, **149**(Suppl. 1), 16–26.
- Norris, K. (2008) Agriculture and biodiversity conservation: opportunity knocks. *Conservation Letters*, **1**, 2–11.
- Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2012) Vegan: Community Ecology Package. R package version 2.0-5. <<http://CRAN.R-project.org/package=vegan>> 10th March 2013.
- de la Peña, N.M., Butet, A., Delettre, Y., Morant, P. & Burel, F. (2003) Landscape context and carabid beetles (Coleoptera: Carabidae) communities of hedgerows in western France. *Agriculture, Ecosystems and Environment*, **94**, 59–72.
- Piffner, L. & Luka, H. (2003) Effects of low-input farming systems on carabids and epigeal spiders - a paired farm approach. *Basic and Applied Ecology*, **4**, 117–127.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-plus*. Springer, New York City, New York.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D.; R Core Team (2013) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-108. <http://cran.r-project.org/web/packages/nlme/index.html> 10th January 2013.
- Purtauf, T., Dauber, J. & Wolters, V. (2005a) The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, **142**, 458–464.
- Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tschirntke, T. & Wolters, V. (2005b) Landscape context of organic and conventional farms: influences on carabid beetle diversity. *Agriculture, Ecosystems & Environment*, **108**, 165–174.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ritchie, M. & Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, **400**, 557–560.
- Roth, T., Amrhein, V., Peter, B. & Weber, D. (2008) A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. *Agriculture, Ecosystems and Environment*, **125**, 167–172.
- Sasakawa, K. (2007) Laboratory studies on larval feeding habits of *Amara macronota* (Coleoptera: Carabidae: Zabrinini). *Applied Entomology and Zoology*, **42**, 669–674.
- Sasakawa, K. (2009) Effects of maternal diet on fecundity and larval development in the 'primitive' granivorous carabid *Amara (curtonotus) macronota*. *Entomologia Experimentalis Et Applicata*, **130**, 106–112.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D., Roscher, E., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher,

- J., Temperton, V.M. & Tscharrntke, T. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.
- Šerić Jelaska, L., Ješovnik, A., Jelaska, S.D., Pirnat, A., Kučinić, M. & Durbešić, P. (2010) Variations of carabid beetle and ant assemblages, and their morpho-ecological traits within natural temperate forests in Medvednica Nature Park. *Šumarski list*, **134**, 475–486.
- Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057–2070.
- Siemann, E., Tilman, D., Haarstad, D.J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, **152**, 738–750.
- Söderström, B., Svensson, B., Vessby, K. & Glimskär, A. (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity & Conservation*, **10**, 1839–1863.
- Spence, J.R. & Niemelä, J.K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist*, **126**, 881–894.
- Stiling, P. & Rossi, A.M. (1997) Experimental manipulations of topdown and bottom-up factors in a tri-trophic system. *Ecology*, **78**, 1602–1606.
- Thiele, H.U. (1977) *Carabid Beetles in their Environments – A Study on Habitat Selection by Adaptations in Physiology and Behavior*. Springer-Verlag, New York City, New York.
- Thomas, C.F.G. & Marshall, E.J.P. (1999) Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems & Environment*, **72**, 131–144.
- Tischler, M., Christopher, R., Dickmanand, C.R. & Wardle, G.M. (2013) Avian functional group responses to rainfall across four vegetation types in the Simpson Desert, central Australia. *Austral Ecology*, **38**, 809–819.
- Tscharrntke, T., Klein, A.M., Kruss, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, **8**, 857–874.
- Tscharrntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews*, **87**, 661–685.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York City, New York.
- Weibull, A.C., Bengtsson, J. & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, **23**, 743–750.
- Welsh, R.C. (1990) Dispersal of invertebrates in the agricultural environment. *Species Dispersal in Agricultural Habitats* (ed. by R.G.H. Bunce and D.C. Howard), pp. 203–218. Belhaven Press, London, UK.
- Werling, B.P. & Gratton, C. (2008) Influence of field margins and landscape context on ground beetle diversity in Wisconsin (USA) potato fields. *Agriculture, Ecosystems and Environment*, **128**, 104–108.
- Willand, J.E., Wodicka, B.R., Palmer, J., Jenkins, S.E. & Mccravy, K.W. (2011) Diversity of ground beetles (Coleoptera: Carabidae) in relation to habitat type in West-central Illinois. *The American Midland Naturalist*, **166**, 266–282.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment*, **75**, 13–30.
- Woodcock, B.A., Potts, S.G., Tscheulin, T., Pilgrim, E., Ramsey, A.J., Harrison-Cripps, J., Brown, V.K. & Tallowin, J.R. (2009) Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology*, **46**, 920–929.
- Wu, J.G. (2008) Changing perspectives on biodiversity conservation: from species protection to regional sustainability. *Biodiversity Science*, **16**, 205–213.
- Xu, J. & Wilkes, A. (2004) Biodiversity impact analysis in northwest Yunnan, southwest China. *Biodiversity & Conservation*, **13**, 959–983.
- Yaacobi, G., Ziv, Y. & Rosenzweig, M.L. (2006) Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape Ecology*, **22**, 687–703.
- Yu, P. (1980) Preliminary study on Chinese carabid beetles as grain crop pests. *Entomotaxonomia*, **2**, 81–84.
- Yu, P. (1981) Key to genera of phytophagous carabidae. *Entomotaxonomia*, **3**, 153–154.
- Yu, Z., Liu, Y.H. & Axmacher, J.C. (2006) Field margins as rapidly evolving local diversity hotspots for ground beetles (Coleoptera: Carabidae) in Northern China. *The Coleopterists Bulletin*, **60**, 135–143.

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Appendix**Table A1.** Individuals and traits of carabid species caught during the sampling season in 2010.

Species	Body size (mm)	Feeding	Total individuals
<i>Amara</i> sp.	6.0	Omnivorous	1
<i>Calosoma denticolle</i> Gebler, 1833	22.2	Predatory	1
<i>Chlaenius micans</i> (Fabricius), 1792	15.7	Predatory	9
<i>Chlaenius posticalis</i> Motschulsky, 1853	12.8	Predatory	306
<i>Curtonotus giganteus</i> Motschulsky, 1844	21.3	Omnivorous	15
<i>Cymindis daimio</i> Bates, 1873	9.2	Predatory	1
<i>Dolichus halensis</i> (Schaller), 1783	17.3	Predatory	372
<i>Harpalus bungii</i> Chaudoir, 1844	6.5	Omnivorous	10
<i>Harpalus corporosus</i> (Motschulsky, 1861)	13.5	Omnivorous	5
<i>Harpalus crates</i> Bates, 1883	9.3	Omnivorous	1
<i>Harpalus lumbaris</i> Mannerheim, 1825	10.4	Omnivorous	3
<i>Harpalus pallidipennis</i> Morawitz, 1862	8.5	Omnivorous	144
<i>Harpalus griseus</i> (Panzer, 1796)	9.6	Omnivorous	10
<i>Harpalus pastor</i> Motschulsky, 1844	11.4	Omnivorous	758
<i>Harpalus simplicidens</i> Schaubberger, 1929	11.2	Omnivorous	7
<i>Pterostichus gebleri</i> Dejean, 1831	16.4	Predatory	92
<i>Scarites terricola</i> Bonelli, 1813	17.9	Omnivorous	15