Different response patterns of epigaeic spiders and carabid beetles to varying environmental conditions in fields and semi-natural habitats of an intensively cultivated agricultural landscape

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Abstract

Agricultural intensification has resulted in major losses of biodiversity due to landscape homogenization and an increasing use of agrochemicals. It has often been assumed that associated changes in environmental conditions are impacting composition and diversity of two main ground-dwelling generalist predator taxa, carabid beetles and epigaeic spiders, in similar ways. Here, we test how variations in environmental conditions at local scales (plant diversity and total soil nitrogen, N_{tot}) and landscape-scale (mean patch size) affect species composition, richness and abundance of ground beetles and epigaeic spiders in semi-natural and cultivated habitats of an agricultural landscape. We specifically test the hypotheses that both taxa are more diverse in semi-natural than cultivated habitats, but that due to their weaker dispersal ability, ground beetles are more strongly linked to local factors than spiders. Our results indicate that in our study area, carabid diversity shows no significant difference between semi-natural habitats and cropland, while spider abundance is significantly enhanced in semi-natural habitats. N_{tot} significantly affected carabid species richness and abundance, but had a limited influence on spider abundances. The species composition of both carabids and spiders was influenced by plant diversity, while N_{tot} played a significant role in determining spider assemblages but not carabid composition. There was no significant effect of the mean patch size in the surroundings landscape on either spider or carabid species. Nonetheless, in landscapes with small patch sizes, spider abundance decreased with increasing N_{tot}, while in landscapes with large sized patches, this relationship was reversed. The differences in responses of these taxa to local and landscape-scale environmental factors suggests that scale- and taxon-specific targets need to be established to improve the efficiency of measures aimed at enhancing ecosystem services provisions by these key pest control agents.

Keywords: Landscape fragmentation; Intensification; Semi-natural habitat; Carabid assemblages; Epigaeic spiders

1.Introduction

Agricultural biodiversity has greatly suffered due to intensification of agricultural practices (Grez *et al.*, 2008; Tscharntke *et al.*, 2012a; Perrings and Halkos, 2015). Apart from direct effects associated with agro-chemical applications linked with these practices, arthropod communities are further influenced by additional environmental drivers like plant diversity and vegetation structure, general habitat type and management, as well as the overall landscape configuration - that all act on distinctly different spatial scales (Horvath *et al.*, 2015).

A species-rich vegetation can potentially support a large number of specialized herbivores (Murdoch et al., 1972; Siemann et al., 1998), in turn supporting a high diversity of predators. Plant communities can furthermore indirectly influence diversity at higher trophic levels through alterations of the physical habitat structure (Lawton, 1983). In agricultural landscapes, semi-natural habitats with their often greatly enhanced plant diversity in comparison to surrounding fields, could hence be expected to also host more diverse predator communities through the provision of a diverse range of prey, as well as of shelter and generally a more heterogeneous habitat structure (Duflot *et al.*, 2015). Assemblages in unmanaged semi-natural habitats often also experience stable environmental conditions, while managed agricultural habitats undergo regular disturbances. In heterogeneous agricultural landscapes, natural enemies may colonize cropland while conditions are favorable and retreat to semi-natural habitats when field conditions become hostile (Horvath *et al.*, 2015). These movements and spillover effects between different habitat in complex landscapes are important for habitat complementarity effects, evolving source-sink relationships and re-colonization processes (Dunning *et al.*, 1992), enhancing the sustainable provision of ecosystem services. Hence, semi-natural habitats are considered not only important for harboring diverse local communities, but also for their contribution to maintaining diverse species assemblages on cultivated lands (e.g. MacLeod *et al.*, 2004). While positive effects of diverse agro-landscapes containing a significant proportion of semi-natural habitats have been widely reported, the influence of individual environmental factors like plant diversity and the wider landscape composition on arthropod assemblages requires further in-depth investigations. The general importance of landscape-level factors in this context is being increasingly recognized (Tscharntke et al., 2012; Horvath et al., 2013), with studies on effects the fragmentation of semi-natural habitats has on agricultural biodiversity providing strong indications for a decreasing α-diversity with increasing fragmentation (e.g. Yang and Da-Han, 2006; Davis, 2009; Vieira *et al.*, 2009).

With numerous studies of cropland species showing effects of plant diversity, habitat and landscape fragmentation on arthropod diversity, their relative importance has again remained poorly understood (Jamoneau *et al.*, 2012), particularly in view of their potential differential influence on different taxonomic groups. However, this understanding is essential for the design of efficient management strategies that improve cropland biodiversity and associated ecosystem service provisions alike.

China has experienced rapid agricultural intensification over the past decades, with widely unknown consequences for agricultural biodiversity and associated ecosystem services. Large knowledge gaps prevail with regard to the current status of biodiversity across virtually all invertebrate taxa in the resulting intensively cultivated landscape, for example in relation to agriculture management and planting patterns (Liu *et al.*, 2006; Liu *et al.*, 2009; Liu *et al.*, 2013; Luo *et al.*, 2014). This is particularly true for investigations of diversity patterns across taxonomic groups, and we here present a rare example of research simultaneously looking into spiders and carabid beetles as two species-rich taxonomic groups that are both relatively well known taxonomically and ecologically (Wise, 1995; Powell, 2009) and have been proven to be the excellent indicator taxa to evaluate effects of agriculture intensification on biodiversity (Perner and Malt, 2003). In our study, we therefore address persisting knowledge gaps, providing insights into the responses of spider and beetles as key biological pest control agents to local factors of fertilizer application, plant diversity and habitat type, as well as to landscape-scale fragmentation, in a typical, intensively cultivated agricultural landscape located in Hubei province in the central Yangtse Plain of China.

Some spiders like linyphiids are known to frequently use ballooning for dispersal (Oleszczuk and Karg, 2012), allowing them to disperse over large areas, whereas ground-dwelling carabids, although regularly still in possession of functioning wings, appear to move on the ground as their preferred mode of more limited and targeted dispersal (Venn, 2016). This, as well as differences in their feeding habits and associated diversity of hunting approaches, mean that spiders will likely react more strongly to the configuration of the wider landscape, as also indicated by Gardiner *et al.* (2010), whereas carabids will likely respond more strongly to factors at local scale than spiders.

In this study, we specifically test the hypotheses that both spiders and carabid beetles are more diverse in semi-natural habitats than in cropland due to the higher diversity of plant species and resulting higher structural diversity in the former habitat types, but that due to the greater dispersal ability of spiders, this taxon is less strongly affected by local factors, instead responding to changes in the overall landscape configuration, while we hypothesize that carabids respond more strongly to local factors like plant diversity and the application of agro-chemicals on the studied habitat patches.

2. Materials and methods

2.1 Study area and sampling plot

The study region is located at Qianjiang (30°25′ ~ 30°23′ N，112° 50′ ~112° 53′ E), Hubei province, a region characterized by sandy to loam-dominated soils on the central Yangtse Plain. The region experiences a sub-tropical climate, with a mean annual temperature of ~ 16°C and the mean annual precipitation exceeding 1100 mm. The dominating rice paddy fields are sown at the beginning of May and harvested in the middle of October, while rainfed fields are cultivated for oilseed rape/peanut and oilseed rape/soybean rotation double cropping systems, as well as for rotations of rape, wheat and soybean and the cultivation of cotton.

Fig.1. Map of land-use and sampling plots in Qianjiang, Hubei province, China (2013).

In recent decades, the Jianghan Plain, where our study region is located, has experienced a rapid urbanization and agricultural intensification. According to the Statistical Yearbook of Hubei Province (http://www.stats-hb.gov.cn/info/iList.jspcat_id10554), the cultivated land on the Jianghan Plain increased by 362.2%, while the area of construction land increased by 1089.7%，between 1993 and 2013. In our study region, analysis of aerial photos and remotely sensed images indicates that the agricultural land area actually decreased by a more moderate 37%, while the area occupied by semi-natural habitats decreased by 38% and the land area used for construction increased by 84%.

Eight common habitat types were selected for sampling: four cultivated habitats (vegetable fields, paddy fields [rice/broad bean cultivation], rainfed fields [soybean/wheat cultivation], and tidal flat fields [peanut/wheat cultivation]) and four semi-natural habitats (field margins, woodland, grassland, shelterbelt). Three separate 20×20 m^2 plots in different patches of each habitat type were established as the basis for carabid, spider and vegetation recording, resulting in a total of 12 study plots, each, representing cultivated and semi-natural habitats, respectively. Sample plots were spread out across the study area, resulting in a minimum distance of more than 500 m between individual plots.

2.2 Beetle and spider sampling

Carabids and spiders were sampled over 4-day periods in the middle of each month from May to October 2013 using pitfall traps. Sets of three pitfall traps were placed in parallel lines 5 m and 10 m from the field margin, with distances between individual traps along the lines also of 5 m. All pitfall transects established in the field were also positioned in N-S direction. The pitfall traps themselves measured 7 cm in diameter and 14 cm in depth, and they were filled with 75% alcohol and a few drops of detergent to break the water surface tension. All adult spiders and carabid beetles contained in the pitfall traps were identified to species level.

2.3 Environmental variables

The coverage and species richness of vascular plants was surveyed in June and September 2013, one to two weeks before harvesting. Each 20×20 m^2 plot was divided into 4 10×10 m^2 sub-plots. All trees and shrubs were recorded in the sub-plots, and herbaceous species were recorded in four randomly placed 1 m^2 plots, one within each sub-plot. We recorded all plant species using the six-point Braun-Blanquet-scale (Braun-Blanquet *et al.*, 1979) to quantify species abundance.

Land-use types in the study region were digitized in extensive field mapping surveys based on high-resolution 2013 Quick Bird satellite images (resolution 0.6 m). Landscape metrics within a radius of 250 m were considered in this study. This scale has been recommended as an appropriate scale at which many carabids and spiders are affected by the patterns of the agriculture landscapes (Maisonhaute *et al.*, 2010; Gallé and Schweger, 2014). The Mean Patch Size (MPS)-index calculated across overall landscape was selected as an indicator for the landscape fragmentation (Hargis *et al.*, 1998; Carranza *et al.*, 2015). The land-use maps we used in our analysis were based on field surveys, and the landscape metrics were calculated using FRAGSTATS 4.2 (McGarigal and Ene, 2015).

Total soil nitrogen (N_{tot}) was measured from composite soil samples collected in October 2013 as an indicator of fertilization use intensity, since it is commonly highly correlated with the amount of fertilizers applied and productivity (Steckler *et al.*, 2008). Five randomly selected soil samples were taken at 0–20 cm depth using a 50-mm diameter sand auger at each plot. Samples were sieved (<2 mm) to remove roots and other large organic debris, homogenized, and air-dried prior to chemical analysis. We pooled dried samples within each plot and ground each one in a ball mill until the material had a talcum powder consistency. We then analysis N_{tot} using the Kjeldahl-Method (Kirk, 1950).

2.4 Data analysis

The ‘true’ species richness of carabids and spiders was calculated based on the Chao-1 estimator (Chao, 1984) for each plot using PAST 3.08 (Hammer *et al.*, 2001). Carabid and spider abundance and richness was then compared between semi-natural habitat and cropland types using one-way ANOVA, with environmental data being log-transformed for analysis. In a second step, the species richness and abundance of carabid and spider assemblages were treated as dependent variables, and their change linked to potential environmental predictor variables on the local (total soil nitrogen, plant diversity) and landscape (mean patch size) scale in a set of Generalized Least Squares models (GLSMs) with fixed variance (gls, nlme package) (Pinheiro *et al.*, 2015) in R 3.1.2 (R Development Core Team, 2015). For this analysis, the full model containing all environmental factors was fitted first. A forward model selection based on the values for the corrected Akaike Information Criterion (AIC_C) was then used to identify the model with the lowest AIC_C as the final model. To account for spatial autocorrelation, we fitted the gls models to response variables with Gauss–Krüger coordinates treated as spatial covariates, assuming a spherical spatial correlation structure (Pinheiro *et al.*, 2015). This approach indicated that no significant spatial auto-correlation was contained in the data-sets.

In a final step, we analyzed the effects of the local and landscape-level factors on the composition of dominant species (all species >10individuals) using a redundancy analysis (RDA). Biplot scaling in the ordination was focused on inter-species distances. In addition, three separate partial redundancy analyses (pRDA) were calculated to investigate the independent effects of local plant diversity, N_{tot} and mean patch size on species composition of the carabid and spider assemblages when controlling for variations in the respective other two variables. Prior to the analyses, the carabid and spider species matrix were modified using a Hellinger transformation in preparation for the use in the RDA (Legendre and Gallagher, 2001), and RDA Pseudo-F values and the corresponding significance levels were calculated using 999 Monte-Carlo permutations. This analysis was conducted using Canoco5 (Braak and Šmilauer, 2012).

3. Results

A total of 978 individuals of 53 carabid species and 2427 individuals of 67 spider species were recorded in the study area. There were no significant differences in either species richness (p=0.82) or number of individuals (p=0.20) of carabid beetles between semi-natural habitats and cropland (Fig. 2). The spider species richness between cropland and semi-natural habitats again showed no significant differences, while semi-natural habitats harbored a significantly higher abundance of spiders than cropland habitats (p=0.01) (Fig.2).

The GLSMs indicated a significant negative link between N_{tot} and both the abundance (p=0.02) and species richness (p=0.05) of carabids, whereas links to all other factors were non-significant (Table1). The abundance of spiders was significantly related to plant diversity and to the interactive effect between mean patch size and N_{tot} (Table 1). The model prediction showed that spider abundance was negatively associated with N_{tot} in landscapes characterized by small mean patch sizes, but positively correlated with N_{tot} in landscapes with large mean patch sizes (Fig.4).

The RDA biplot showed that the changes in composition of carabid assemblages were significantly associated only with the plant diversity, with this local factor explaining 7.7% of the overall variation in species composition (Fig. 5). Most of the omnivorous species like *Harpalus pastor* and *H. tridens* were positively associated with plant diversity, while a number of predators like the members of the genus *Chlaenius*, *C. leucops*,*C. micans, C. nigricans* and *C. aspericollis*, were more abundant on plots with a low plant diversity.

For spider assemblages, both N_{tot} (8.8% explained variance) and plant diversity (9.7% explained variance) were associated with changes in their species composition, explaining 17.5% of the overall community variation. Three common wolf spiders that occurred both in cropland and semi-natural habitats, *Pardosa nebulosa, P. mionebulosa and Trochosa wuchangensis*, were positively associated with plots characterized by high N_{tot}. Three common spider species, *Ozyptila wuchangensis (Nesticidae)*, *Pirata tenuisetaceus (Lycosidae)* and *Piratula procurvus (Lycosidae)* that chiefly occurred in the semi-natural habitats (Appendix A) were strongly associated with high plant diversity.

The partial RDA results confirmed the aforementioned, significant associations of changes in the cararbids assemblages with plant diversity and of changes in spider assemblages with both plant diversity and N_{tot} (Table 2).

Fig.2. Abundance of carabid and spider in the different habitat categories (“semi-natural” and “cropland” habitats).

*:$p<0.05$

Table 1 Relationship between the number of carabid individuals, estimated carabid species richness (Chao-1), spider individuals, estimated spider species richness (Chao-1) and environmental factors at different scales (plot and landscape).

Significant negative (-) and significant positive (+) relationships are marked in bold.

Fig.3. Relationship between N_{tot} and estimated carabid species richness (a), estimated spider species richness (b), carabid abundance (c), and the relationship between the plant diversity and spider individuals (d).

Fig.4. Contrasting effects of the N_{tot} on spider abundance (log_{10}-transformed) in landscapes with small (a) and large (b) patch sizes. Results are predictions from generalized least squares models.

Table 2 Species composition of carabids and spiders: percentage of variance explained by partial redundancy analysis (pRDA)

Fig.5. Redundancy analysis performed on carabid species (a, pseudo-F=1.6, P=0.018) and spider species (b, pseudo-F=3.2, P=0.032) composition in response to environment factors acting at different spatial scales (plot and landscape).

Discussion

In different habitat

In contrast to previous studies (Hendrickx *et al.*, 2007) and our first hypothesis, we found no significant difference in carabid diversity between semi-natural habitats and cropland, and only spider abundance, but not species richness, was significantly higher in semi-natural habitats compared to agricultural fields. For carabid beetles, semi-natural habitats hence cannot be assumed to permanently support higher levels of diversity than cropland since fields can at least temporarily provide large, sparsely vegetated areas as ideal hunting areas for these mobile ground-dwelling soil arthropods, as well as potentially harboring very high densities of prey like aphids, eggs, larvae and pupae of dipterans or chrysomelid larvae (Kromp, 1999; Batary *et al.*, 2012). Agricultural carabid assemblages commonly consist of carnivores, omnivores and generalist herbivores, but contain only a small number of specialist species. In terms of α-diversity, non-carnivore carabids could be assumed to be more abundant in semi-natural habitats than in cropland due to bottom-up effects of resource availability, but if conditions are right, then herbivorous carabids, and particularly granivorous species within this guild, can become very abundant also on cereal fields (Diehl *et al.*, 2012). In addition, plant diversity is not always linked to heterogeneity of microclimatic conditions, and it has been shown in previous studies to poorly predict carabid activity abundance and α-diversity (Zou *et al.*, 2013). This could be due to the fact that carabids are chiefly ground-dwelling and rarely live in plant foliage, and therefore are relatively insensitive to changes in plant structure apart from the density of plant stems and culms at ground level.

In this study, the carabid samples are dominated by carnivorous species, accounting for about 77% of caught individuals, while most of the captured spiders are wolf spiders (lycosids), and accounting for 91% of the catch. Both carabids and lycosids prey on a wide spectrum of crop pests (Kremen, 1993), and studies usually state that carnivorous carabids and wolf spiders have similar feeding habits and patterns of movement, both actively hunting prey on the ground. The resulting expected similarity in occupied niche space could indicate that they also show similar responses to environmental factors (Snyder and Wise, 1999). Nonetheless, according to our result, carnivorous carabids were slightly more abundant in cropland than in semi-natural habitats, whereas wolf spiders showed the opposite patterns, although the overall abundance patterns of the two taxa were not significantly negatively correlated (Spearman Rank Correlation, P=0.36), indicative of only a limited direct competitive exclusion between the two taxa. Different responses between them could alternatively be explained by their different dispersal abilities. At least some wolf spider species are known to use ballooning in their dispersal as an extremely effective approach to large-distance travel (Pedley and Dolman, 2014), and a large number of lycosid species are diurnal active-hunting spiders with a very high mobility, compared to the often nocturnal carnivorous carabids (Kruse *et al.*, 2008). Wolf spiders can hence be expected to more easily move between fields and semi-natural habitats even over relatively large distances, for example when conditions in the fields become less favorable due to the application of pesticides killing off their prey (Oleszczuk and Karg, 2012).

Effects of environmental factors

While carabid species richness and abundance showed significant negative responses to fertilizer applications indicated by N_{tot}, the composition of ground beetle assemblages appears widely unaffected by intensive management as indicated by the minor influence of N_{tot} on the assemblage patterns (see also Diekotter *et al.*, 2010). This suggests that the observed changes in α-diversity relate to assemblages in high nitrogen environments forming impoverished subsets both in terms of species and abundance to assemblages in low-nitrogen environments, irrespective of the habitat type. This might be a reflection of a dense vegetation growth occurring in response to higher soil N levels that potentially limits the hunting ability of these chiefly predatory or omnivorous insects (Wolak, 2002; Bultman and DeWitt, 2008).

Overall, responses in diversity of both carabid beetles and spiders were negatively correlated with N_{tot}, to a certain extent indicating a negative response of both taxa to intensive application of fertilizers, which is often also linked to the amount of pesticide and herbicide applications and to management-related disturbances like tillage. The negative general effects of intensive farming practices on carabids and spiders is in agreement with previous studies (Schmidt *et al.*, 2005; Flohre *et al.*, 2011). Nonetheless, at least in our study, spider abundance was unaffected by N_{tot}. It therefore appears that the dominating wolf spider species can cope well with intensive agricultural management, as well as having a good dispersal ability that allows them to establish high abundances in regularly disturbed agricultural fields and semi-natural habitats without being heavily impeded by agro-chemical applications (Hendrickx *et al.*, 2007; Horvath *et al.*, 2015), with Patrick et al (2012) even reporting a positive response of spider abundance to fertilization in temperate grassland ecosystems.

The significant changes in the species composition of both carabid and spider species composition in response to changes in plant diversity represents a trend that could be related to indirect bottom-up effects, with high plant diversity leading to shifts in the species richness and abundance patterns of herbivore assemblages forming the prey for both study taxa (Moreira *et al.*, 2016). Furthermore, this pattern could also reflect changes in the microhabitat structure that are likely to occur in plant-diverse habitats. The vegetation structure is a key factor, affecting for example potential predator–prey interactions, the presence and abundance of ovipositioning sites and microclimatic conditions (Dennis *et al.*, 1994). A strong association between ground-dwelling arthropod assemblages and plant diversity is confirmed by a number of previous studies (Dennis *et al*. 2001; Schaffers et al. 2008), particularly in relation to species turnover (Liu *et al.*, 2015), while α-diversity often remains unaffected, or links between insect and plant diversity are even negative (Axmacher *et al.*, 2011). The local plant species composition is believed to be is the most effective predictor of arthropod assemblage (Schaffers *et al.*, 2008).

Classic island biogeography theory (Mac Arthur and Wilson, 1967) suggests that landscape fragmentation will negatively affect species richness, with larger, interconnected patches supporting a greater diversity than small, isolated patches. Nonetheless, this hypothesis does not align with our observations that mean patch sizes in the landscape matrix did not generally affect spider nor carabid diversity. Instead, the positive response in spider abundance to the interactive effect of patch size and N_{tot} might be related to the fact that in our study region, in the landscapes characterized by larger patch sizes, large patches were predominantly covered by woodland and grassland habitats. These large non-cropped, permanent semi-natural habitats can potentially form a crucial source area for the colonization of more habitat-specialized, disturbance-sensitive spider species across the wider landscape, since these spiders likely require a certain habitat size to build up viable populations (Galle, 2008). On the landscape scale, the existence of large, permanent semi-natural habitats may hence partly compensate for negative effects from intensive agricultural practices in the surrounding field matrix. Because large non-crop habitat patches in agricultural landscapes additionally provide refuges and overwintering habitats, hence enhancing the overall diversity in complex agricultural landscapes (Schmidt et al., 2005), these habitat patches can therefore function as sources for species colonization to more heavily disturbed conventional fields. Previous studies have shown that highly specialized species tend to be particularly area-sensitive and hence mostly confined to large fragments (Lasky and Keitt, 2013). It can be assumed that spider assemblages could keep traveling until find a right place to settle down. The lack of a similar response in carabids could be interpreted in view of their dispersal ability. Due to the generally more limited long-distance movement of carabids, these species can be assumed more reliant on resources, or at least keep moving between cropland and semi-natural habitat nearby, with resulting beetle assemblages more strongly dominated by generalists throughout the different landscape settings. Resulting assemblages will not only have a high tolerance towards agricultural practices, but also be less demanding toward habitat characteristics (Winqvist *et al.*, 2011).

Implication for conservation

Many studies and conservation strategies consider spider and carabid species as widely equivalent indicators of biodiversity and effectiveness of biological pest control agents in agriculture landscapes (Jeanneret *et al.*, 2003; Knapp and Rezac, 2015), and a majority of studies focuses only on one of these two taxa. Our results nonetheless indicate that using single-taxon approaches does not allow for a comprehensive appreciation of the abundance and diversity patterns of pest control agents in agricultural landscapes, and their resulting effectiveness in biological pest control, with both studied taxa widely considered as crucial due to both their great abundance and species richness across agricultural landscapes (Sunderland et al., 2000). Since spider and carabid species assemblages are clearly affected differently by environmental factors at local and landscape scales, biodiversity responses to landscape and habitat changes will also result in different patterns in these groups, and the assessment of overall changes requires a multi-taxon approach. The promotion of biological pest control using specific agricultural management practices equally requires full consideration of the specific requirements of both taxa. Furthermore, the different responses of biodiversity components linked to species richness, abundance and community structure show that these three factors need to be considered in conjunction to optimize the success of any targeted management (Isbell *et al.*, 2011; Batary *et al.*, 2012; Liu *et al.*, 2014). Our research furthermore suggests that maintaining a high plant diversity at local scales could generally increase the abundance of natural enemies and enhance their species diversity at the landscape scale, hence potentially mitigating some of the negative effects related to intensive cropping.

While yield optimization is crucially important in view of an increasing human population, the optimization of ecosystem services like biological pest control and pollination requires that high yields are insured in a way that simultaneously strengthens the populations of insect assemblages providing these services, for example via the targeted creation of suitable semi-natural habitat patches and an overall reduction of agro-chemical applications according to site-specific crop needs. Larger scale monitoring and replication across habitats or regions would be very helpful to better assess population trends and further describe trends in potentially sensitive taxa. More detailed studies of different species and species groups could help us better understand their niche breadth (trait variance) and potential sensitivity to different environmental factors. Overall, the preservation of large patches of semi-natural habitats such as woodlots and grassland is vital, because these habitats can serve as colonization sources for the surrounding cropland and could help to dampen effects of intensive farming activities and of landscape fragmentation.

Conclusion

Our results show that semi-natural habitats containing relatively high plant diversity and a varied vegetation structure primarily influences the abundance of spiders, but is a poor predictor of the species richness and abundance in carabid beetles. Members of this taxon appear more sensitive to management intensity. The different response of these two taxa can partly be explained by their different dispersal ability, as well as by differences in the balance between habitat specialists and generalists. While landscape fragmentation does not show a strong influence on either of the two assemblages, mean patch size interacts with N_{tot} influencing spider abundance. In general we suggest that measures to enhance predator biodiversity in agricultural landscapes needs to take full account of the diverging requirements of the key taxonomic groups involved. Following approaches used in Europe, targeted financial incentives for farmers could be considered in exchange for alterations of their agricultural landscape management and for the creation of semi-natural habitats. In combination with ongoing urbanization and the resulting changes to the wider landscape allowing for more large-scale management, such an approach could allow Chinese agriculture to make significant progress towards an increasing sustainability, and enhance the country's movement towards an ecological civilization.

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Appendix A

Dominate carabid species in different habitat

Appendix B

Dominate spider species in different habitat

Appendix C

Carabid and spider abundance changes in different months

Figure caption

Fig.1. Map of land-use and sampling plots in Qianjiang, Hubei province, China (2013). Different shapes of black symbols represent sampling points in different habitats, and patches with different colors represent different types of land use.

Fig.2. Abundance of carabid and spider in the different habitat categories (“semi-natural” and “cropland” habitats). “*” indicates a statistically significant difference ($p<0.05$).

Fig.3. Relationship between N_{tot} and carabid species richness (a), spider species richness (b), carabid abundance (c), and the relationship between plant diversity and spider individuals (d).

Fig.4. Contrasting effects of the N_{tot} on spider abundance (log10-transformed) in landscapes with large and small patch sizes. Results are predictions from generalized least squares models.

Fig.5. Redundancy analysis performed on carabid species (a, 7.63% variance explained by Axis 1, 27.05% variance explained by Axis 2 , pseudo-F=1.6, P=0.018) and spider species (b, 13.80% variance explained by Axis 1, 3.67% variance explained by Axis 2, pseudo-F=3.2, P=0.032) composition in response to environment index in factors acting at different spatial scales (plot and landscape). Closed triangles represent species and arrows represent environmental factors.

Table 1 Relationship between the number of carabid individuals, estimated carabid species richness (Chao-1), spider individuals, estimated spider species richness (Chao-1) and environmental factors at different scales (plot and landscape).

Taxa group	Depend variable	Explanatory variables	d.f.	F-value	P-value
Carabid	Individuals	**Total soil nitrogen (-)**	**1,22**	**5.821**	**0.02**
	Species richness (Chao-1)	**Total soil nitrogen (-)**	**1,22**	**3.798**	**0.05**
Spider	Individuals	Mean patch size (n.s.)	1,19	0.711	0.12
		Total soil nitrogen (n.s.)	1,19	3.988	0.44
		Plant diversity (+)	**1,19**	**2.582**	**0.02**
		Mean patch size × Total soil nitrogen (+)	**1,19**	**4.128**	**0.03**
	Species richness (Chao-1)	Mean patch size (n.s.)	1.21	1.992	0.15
		Total soil nitrogen (-)	**1.21**	**4.934**	**0.05**

Significant negative (-) and significant positive (+) relationships are marked in bold.

Table 2 Species composition of carabids and spiders: percentage of variance explained by partial redundancy analysis (pRDA)

Explanatory	Carabid species			Spider species		
	Explains %	pseudo-F	P	Explains %	pseudo-F	P
N_{tot}	4.8	1.1	0.270	**7.8**	**2.0**	**0.054**
Plant diversity	**7.7**	**1.8**	**0.044**	**9.7**	**2.4**	**0.018**
Patch size	5.4	1.3	0.208	1.7	0.4	0.940

Tables
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Appendix A

Dominate carabid species in different habitat

Feeding habit	Species	Number of individuals	
		Semi-natural habitat	Cropland
Carnivore	*Chlaenius aspericollis*	4	11
Carnivore	*Chlaenius leueops*	15	0
Carnivore	*Chlaenius micans*	13	93
Carnivore	*Chlaenius nigricans*	8	18
Carnivore	*Dolichus halensis*	10	0
Omnivore	*Harpalus bungii*	13	0
Omnivore	*Harpalus chalcentus*	3	10
Omnivore	*Harpalus pastor*	25	4
Omnivore	*Harpalus sinicus*	6	42
Omnivore	*Harpalus sp.*	19	2
Carnivore	*Harpalus tridens*	47	0
Carnivore	*Lesticus magnus*	5	8
Carnivore	*Patrobus flavipes*	1	11
Omnivore	*Pheropsophus jessoensis*	45	331
Carnivore	*Scarites difficilis*	2	14
Carnivore	*Scarites terricola*	15	5
Carnivore	*Tachys sp.*	2	20

Appendix B

Dominate spider species in different habitat

Family	Species	Number of individuals	
		Semi-natural habitat	Cropland
Lycosidae	*Arctosa recurva*	12	22
Lycosidae	*Arctosa springiosa*	15	4
Gnaphosidae	*Gnaphosa kompirensis*	21	0
Gnaphosidae	*Odontodrassus hondoensis*	8	6
Nesticidae	*Ozyptila wuchangensis*	53	0
Thomisidae	*Pardosa astrigera*	1	17
Lycosidae	*Pardosa laura*	256	147
Lycosidae	*Pardosa mionebulosa*	238	35
Lycosidae	*Pardosa nebulosa*	20	27
Lycosidae	*Pardosa pseudoannulata*	1	10
Lycosidae	*Pirata subpiraticus*	5	11
Lycosidae	*Pirata tenuisetaceus*	17	15
Lycosidae	*Piratula piratoides*	68	140
Lycosidae	*Piratula procurvus*	113	2
Lycosidae	*Trochosa wuchangensis*	14	9
Lycosidae	*Ummeliata insecticeps*	7	19

Figure
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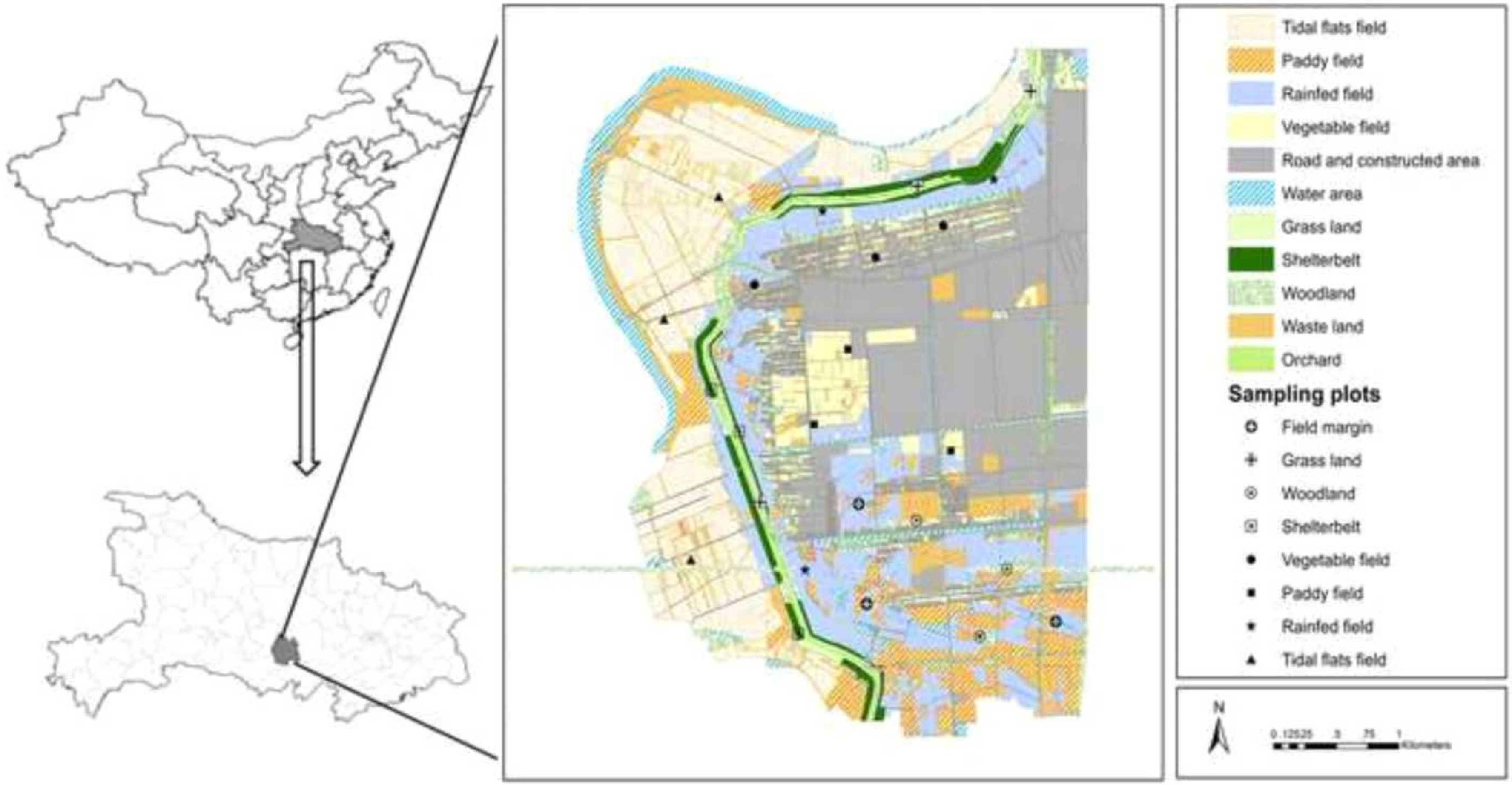
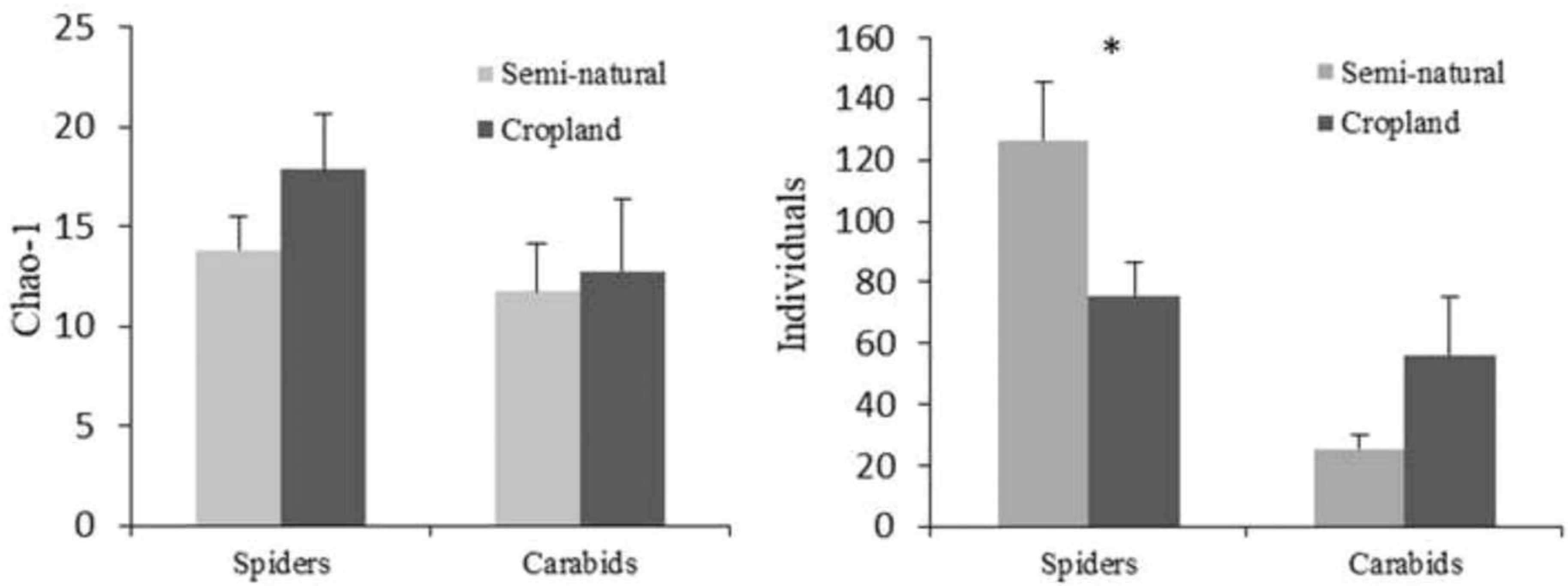


Figure


Chao-1
25
20
15
10
5
0
Semi-natural
Cropland
Spiders
Carabids
Individuals
160
140
120
100
80
60
40
20
0
*
Semi-natural
Cropland
Spiders
Carabids

Figure

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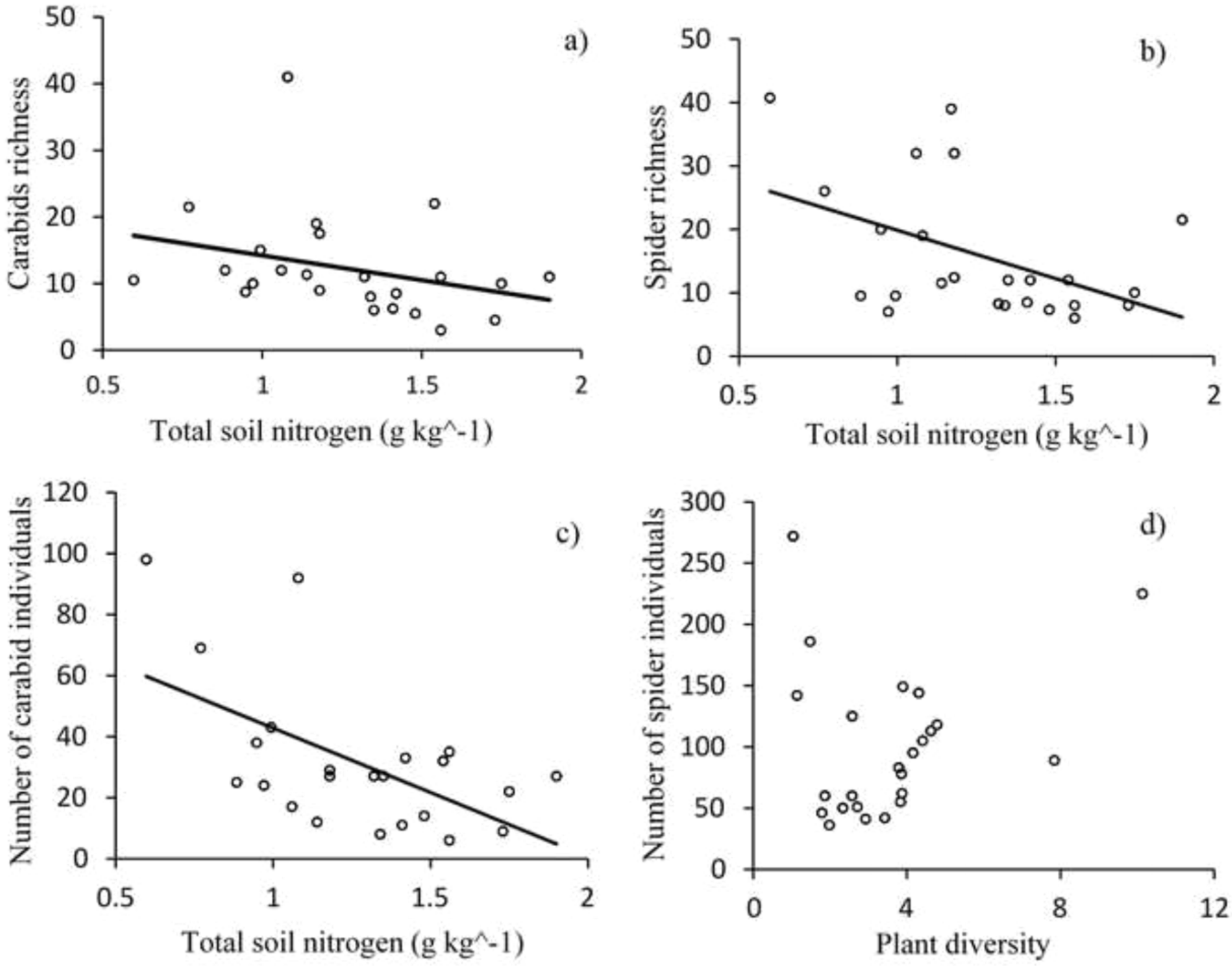

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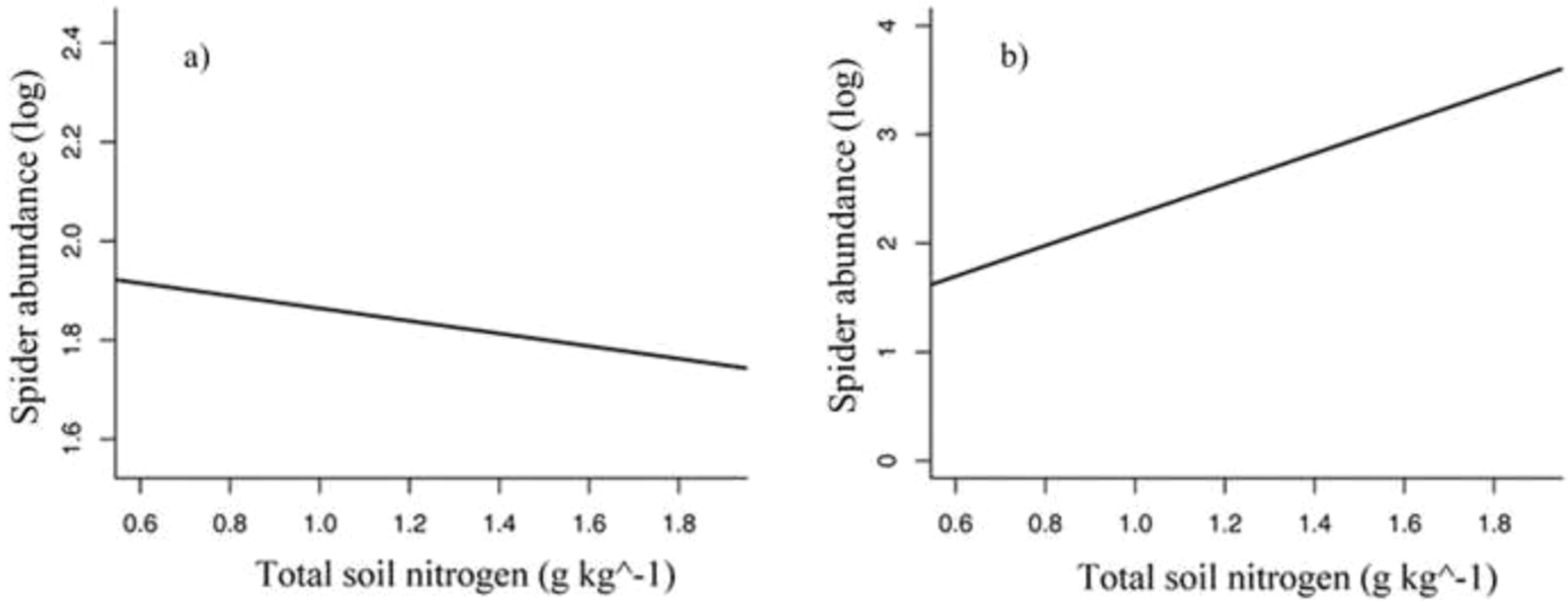

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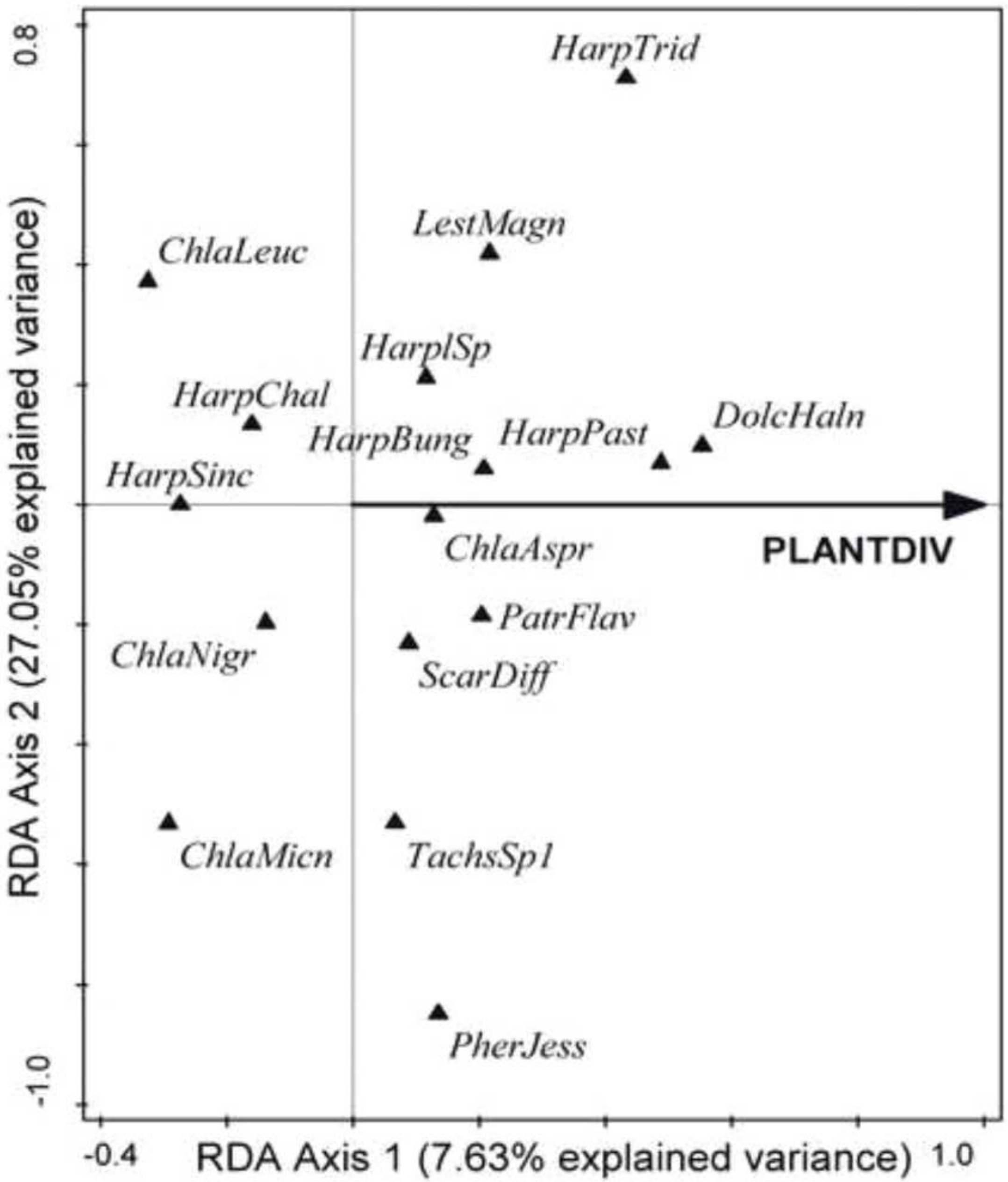
HarpTrid
LestMagn
ChlaLeuc
HarplSp
HarpChal
HarpBung
HarpPast
DolcHaln
HarpSinc
ChlaAspr
PLANTDIV
PatrFlav
ChlaNigr
ScarDiff
ChlaMicn
TachsSp1
PherJess
0.8
-1.0
-0.4
1.0
RDA Axis 2 (27.05% explained variance)
RDA Axis 1 (7.63% explained variance)

Figure
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