Plant and carabid assemblages are determined at proximal levels

Moth assemblages are strongly associated with regional landscape characteristics

Semi-natural habitats in the plot vicinity benefit plant and carabid diversity

Responses to environmental variables are highly taxon-specific

Landscape-scale approaches are crucial for insect conservation
Environmental factors acting at multiple scales determine assemblages of insects and plants in agricultural mountain landscapes of northern China

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Abstract

Mountainous regions harbor high levels of biodiversity, while often experiencing substantial pressure from agricultural production. Our current understanding of factors driving changes in the highly diverse species assemblages of these regions is generally limited. We used variance partitioning based on redundancy analysis to establish the effects of environmental variables on the species composition of vascular plants and three insect taxa (Geometridae, Arctiinae and Carabidae). These environmental determinants are linked to three distinct spatial levels: the regional level - the four study regions positioned at ~ 400m altitudinal intervals, the landscape level - the landscape structure in the vicinity of each study plot, and the plot level - the environmental conditions at individual sampling locations. Our results showed that variations in the species composition of vascular plants and carabids were more closely linked to plot-level characteristics than to regional-level factors, while the opposite trend was observed for the two moth taxa. When effects explicitly linked to the four study regions were controlled, plant and carabid assemblages showed strong links to the percentage of semi-natural habitat at the landscape level, while geometrid and arctiinid assemblages were affected primarily by the overall plant species richness and plant coverage at the plot level. Overall, the variations in the species composition of different taxa can be explained by varying sets of environmental variables acting at different spatial scales, and the relative role of these variables is highly taxon-specific.

Regional-scale approaches are crucial for biodiversity conservation in mountainous agricultural landscapes, as exemplified by the responses in the two moths taxa, while a high proportion of semi-natural habitats in the agricultural landscape is not only linked to a diverse vegetation, but
also to species-rich carabid assemblages.

Key words: Arctiinae; β-diversity; Carabidae; Geometridae; vascular plants
Mountainous areas are known to harbor high levels of biodiversity, partly due to a substantial
species turnover along the steep environmental gradients typical for these areas (Körner, 2004;
Viterbi et al., 2013). In many parts of the world, mountainous regions have experienced significant
environmental change, habitat degradation and fragmentation linked to the expansion of
agricultural areas (Batáry et al., 2012; Brooks et al., 2012; Nogués-Bravo et al., 2008). Modern
agricultural production in general is seen as a key threat to global and regional biodiversity (Fox,
2013; McMahon et al., 2012; Norris, 2008), but in some cases, agricultural landscapes can also
support high levels of biodiversity (Burel et al., 2013b; Sturaro et al., 2013; Tscharntke et al.,
2005).

Mutual benefits for biodiversity and agricultural production can be achieved for example
through the targeted support of functional groups like pollinators or biological control agents
(Altieri, 1999; Schirmel et al., 2015). It is therefore essential to understand the distribution of
biodiversity in mountainous agricultural landscapes and its response to both natural and
anthropogenic factors to develop and optimize sustainable approaches to landscape management
that also enhance the provision of ecosystem services (Körner, 2007; Tews et al., 2004;
Tscharntke et al., 2012). In view of prevailing knowledge gaps and anthropogenic pressures,
studies investigating biodiversity patterns of agricultural mountainous landscapes are of particular
importance in temperate regions of Asia (Tang et al., 2006; Wang et al., 2012).

In China, more than 44% of the country’s cultivated land is located in mountainous regions.
Many of these regions also harbor high level of biodiversity and are priorities for biodiversity
At the same time, these mountain regions are inhabited by >30 million people, with rural communities strongly relying on agricultural production for their survival (Jiang et al., 2012). This pattern is exemplified by the mountainous agricultural landscapes located between Beijing and the Bashang Plateau that also harbor important animal and plant genetic resources (Li, 2006). The entire area has experienced a serious degradation of its natural ecosystems due to overgrazing and the transformation of natural habitats into cultivated land. These developments are still rapidly progressing, and the area under very intensive management for vegetable production has increased by 21% from spring 2013 to spring 2014. The regional biodiversity is additionally under pressure from the region’s rapidly developing tourism industry. However, research on this region’s biodiversity and its response to environmental changes is scarce (Axmacher et al., 2011; Yuan et al., 2006).

Environmental factors acting on different spatial scales play a variety of roles in explaining the distribution of diversity (Batáry et al., 2008; Clough et al., 2005; Kinnunen et al., 2001; Liu et al., 2015). Regional species pools that form the foundation of local species assemblages are determined by environmental conditions acting on regional scales, with potential drivers including large-scale land use patterns, topography and climatic conditions (Holzschuh et al., 2007; Liu et al., 2014; Schweiger et al., 2005). The landscape structure in the vicinity of sampling plots further moderates the population dynamics and functional trait selection in species assemblages (Burel et al., 2013a; Holzschuh et al., 2009; Tscharntke et al., 2012), while factors characterizing the actual habitat at individual sampling plots, including microclimatic and soil conditions as well as the management regime, are also seen as important in determining the composition of assemblages at
individual the sampling plots (Aviron et al. 2005; Batáry et al. 2008; Liu et al., 2012, 2015).

Species-specific traits such as a species’ position in trophic guilds and its dispersal ability further affect its distribution and response to environmental factors across spatial scales (Burel et al., 2004; Hendrickx et al., 2007; Jeanneret et al., 2003; Merckx et al., 2012). Species occupying high trophic levels are more prone to respond to regional environmental changes, partly because they commonly have large home ranges in which they occur at low population densities (Liu et al., 2014). Species with strong dispersal abilities are influenced by environmental conditions at larger spatial scales when compared to weak dispersers that respond strongly to local factors like habitat conditions and farming practices (Dauber et al., 2005; Gabriel et al., 2010; Weibull and Östman, 2003). This means that different taxa are expected to show distinct and often complex response patterns in response to a wide variety of different pressures and environmental gradients occurring and interacting at different spatial scales (Axmacher et al., 2011; Batáry et al., 2012; Clough et al., 2007; McMahon et al., 2012). Conservation strategies aimed at preserving a wide range of taxa and associated ecosystem service provision therefore require a profound understanding not only of biodiversity patterns across the different taxa, but also of the strength of links between biodiversity patterns and environmental factors acting at different spatial scales (Billeter et al., 2007; Fahrig et al., 2011; Petit et al., 2013; Viterbi et al., 2013). Studies in mountainous agricultural landscapes are in this regard extremely valuable, as they can provide insights into biodiversity changes in species-rich assemblages along pronounced environmental gradients (Chemini and Rizzoli, 2003; Wang et al., 2012).

In our study, we address the prevailing knowledge gaps related to changes in the species
composition of diverse arthropod taxa and the vegetation in agricultural mountainous landscapes.

We selected the four species-rich taxa, vascular plants, geometrid and arctiinid moths and ground beetles, as focal groups to investigate their taxon-specific responses to environmental factors acting at different spatial scales. Vascular plant communities as the main producers in terrestrial ecosystems are often hypothesized to be strongly linked with the species composition of consumers via bottom-up control or various top-down effects (Scherber et al., 2010; Yanahan and Taylor, 2014). Both geometrid and arctiinid moths represent herbivorous insect taxa with a strong flight ability (Hilt, 2005) that also serve as pollinators (Fox, 2013; Merckx et al., 2012) and whose overall distribution in agricultural landscapes is currently poorly understood (Fuentes-Montemayor et al., 2011; Ricketts et al., 2001). Carabids have been extensively used as bioindicators (Schirmel et al., 2015). As a chiefly predatory taxon, these beetles are used to control crop pests such as slugs, snails, caterpillars and aphids (Kromp, 1999; Rouabah et al., 2015). They contain a number of flightless species and are overall more limited in their flight ability in comparison to the two moth taxa (Schirmel et al., 2015).

In our study, we specifically focused on the spatial changes in species composition, since these are highly sensitive to environmental change and closely associated with ecosystem functioning (Jeanneret et al., 2003; Weibull and Östman, 2003). Due to the different life histories and dispersal abilities of the four target taxa, their responses to environmental changes was expected to be governed by distinctly different sets of predictor variables (Billeter et al., 2007; Burel et al., 2004; Merckx et al., 2012). We aimed to determine the nature and strength of links between the species composition changes in our four target taxa and a set of environmental
predictors that act at regional, landscape and plot levels. We hypothesized that factors on all three
spatial scales would significantly affect the species composition of the four taxa, and that the
species composition in all taxa was most strongly linked to changes at the regional level that also
reflected distinct shifts in elevation. Plot-level parameters were assumed to chiefly impact the two
taxa of low mobility, vascular plants and ground beetles, whereas the landscape-level variables
were hypothesized to be more closely associated with the composition of geometrid and arctiid
moth assemblages due to the greater mobility and distinct resource requirements of these insects.

2 Materials and Methods

2.1 Study sites and plot selection

The study area (40°23’ - 41°12’ N, 114° 57’ - 115°57’ E) is located within the mountain
ranges between Beijing and the Inner Mongolian Plateau in northern China. This area represents
the transition zone between temperate and sub-temperate climate and is strongly affected by
monsoon weather patterns, with rainfall amounts typical for the transition zone between
sub-humid and semiarid conditions. This area is also an important transition zone between
agricultural cropland and pasturing regimes. The altitude rises from about 50 m to >2000 m, with
substantial changes in the composition of the agricultural landscapes occurring along this steep
altitudinal gradient. For our study, we selected four distinct regions along the altitudinal gradient
that represent four distinctly different agricultural landscapes. These four study regions were
located in the vicinity of four villages, Dayushu, Gaojiaying, Baiqi and Shizigou, at elevations of
about 500 m, 800 m, 1200 m and 1650 m, respectively (Figure 1).
Within each study region, three representative habitats were subsequently selected according to the typical management intensity, dominant natural vegetation and farming regime encountered (Table 1). These habitat types were selected from four wider habitat categories. Intensely cultivated fields that were regularly treated with chemical pesticides and fertilizers, plowed and cropped with maize, oat, potato or vegetables formed the first category. Orchards planted with fruit trees and with intercropping of a variety of products treated with pesticides and fertilizers formed a second habitat category, while grassland represented the third habitat category. The grassland habitats remained widely unmanaged, since livestock grazing was prohibited, but occasional intrusion from livestock was observed. Planted woodlands formed the final habitat category. These woodlands were dominated by broadleaved or conifer trees and not commonly used by local residents and their livestock. For each habitat type, four plots measuring 20 m × 20 m were randomly established on separate habitat patches to minimize pseudo-replication. The mean distance between individual plots in each study region was 213.2m, ranging from 60.4m to 684.1m. Overall, twelve plots were selected within each study region, with 48 plots sampled in total.
2.2 Recording of vegetation and insects

Surveys of the % cover of all vascular plant species were conducted in June and September 2007. Trees and shrubs were recorded on the entire plots, while herbaceous species were recorded at five 2×2m² subplots located in the center and at the four corners of each plot. Data from both seasons were combined, allocating the maximum % cover recorded during either of the two surveys to each plant species to establish their maximum ‘importance’ in the plot vegetation.

Automatic light traps were used for moth sampling between May and October in both 2006 and 2007. These traps consisted of a 12 V battery-operated UV light tube (Sylvania black light-blue, F15W/BLB-TB; Osram, Munich) placed above a plastic funnel leading into a plastic bucket (Axmacher et al., 2011). To avoid the effect of strong moonlight (Yela and Holyoak, 1997), sampling occurred at 6-day periods around the new moon. Moths were sampled twice per sampling period on each plot, with a single light trap operated in the center of each plot. Four plots were sampled simultaneously in each sampling night at each study region. We restricted sampling to the peak time of moth activity between 19:00 h and 23:00 h local time (Axmacher et al., 2009; Hilt, 2005). Although this approach excludes some species that are active later at night, our approach was standardized across our study regions, allowing for direct comparisons in our analysis.

Ground beetles were sampled using pitfall traps set over 6 day-periods every month between the beginning of May and early October in both 2006 and 2007. On each plot, eight pitfall traps were placed at a distance of 4 m and 7 m from the plot center along N–S and E–W facing diagonal lines intersecting in the middle of the plot. Pitfall traps were formed of cups 8 cm in diameter and
11.5 cm in depth, and partly filled with 75% alcohol to kill and preserve the specimens (Southwood, 1978). Each trap was protected from rain by an aluminum roof positioned about 5 cm above the trap.

2.3 Recording of environmental parameters

In our analysis, environmental variables were divided according to the spatial levels on which they act: regional- (R), landscape- (L) or plot-level (P) variables. At the regional level, each of the four regions, as four categorical variables, were used as regional variables and included in the analysis to estimate account for the influence of the regional context (Aviron et al., 2005; Clough et al., 2005; Ter Braak and Šmilauer, 2002). They were linked to the four study villages and positioned at altitudinal intervals of ~ 400m that also represent distinct agricultural landscapes. Landscape-level variables included the proportion of semi-natural land, the proportion of cultivated land and the Shannon-Wiener landscape diversity index as measures of the overall landscape heterogeneity (Heikkinen et al., 2004). Furthermore, the largest patch index and the mean perimeter area ratio were also included as measures of the configurational landscape heterogeneity (Fuentes-Montemayor et al., 2011). Landscape-level variables were recorded using detailed 100 m × 100 m land-use maps centered on each sampling plot. The land-use maps we used in our analysis were based on field surveys, where land-use was differentiated into five cultivated land habitat types (maize, oat, vegetable and potato fields as well as orchards), three semi-natural habitats (woodland, bushland and grassland), and other habitats (including roads and buildings). Only land-use patches exceeding 2m ×2m in size were included on the maps. The
landscape metrics were analyzed using Fragstats 3.3 (Mcgarigal et al., 2002).

Plot level variables included the habitat type, vegetation and soil properties. Each habitat type was included in the statistical analysis as a categorical variable (Dauber et al., 2005; Weibull and Östman, 2003). The vegetation was characterized based on plant species richness and total % cover of all plant species. The soil properties we recorded were soil organic matter content (SOM), total nitrogen and soil pH, as these factors are believed to directly influence the vegetation and partly also invertebrate assemblages (Petit et al., 2013; Schirmel et al., 2015; Yanahan and Taylor, 2014). Five soil sub-samples were randomly taken from the upper 20 cm of the mineral soil at each plot and mixed prior to the analysis. We used the rapid dichromate oxidation method and Kjeldahl method to measure SOM and total nitrogen, respectively (see Axmacher et al., 2011 for more details on the laboratory analysis).

2.4 Data analysis

Prior to the statistical analyses, the 2006 and 2007 insect data was pooled for each sampling plot and Hellinger-transformed to allow their use in the Redundancy Analysis (RDA), as initial data-sets contained many zero values (Legendre and Gallagher, 2001). Quantitative environmental variables were either log-transformed or, for proportional data, arcsine-transformed to align values more closely to a normal distribution. All environmental variables were standardized to avoid scale-dependent distortions due to the use of different units. Variation partitioning was used to determine the relative importance of certain groups of explanatory variables for the species composition of the different taxa, using selected groups of
explanatory variables as constrains and the remaining groups as covariates in the RDA. The same
sets of explanatory variables were used for all RDAs and partial RDAs to allow reliable
comparisons between taxa (Schweiger et al., 2005). We differentiated the following eight fractions
in this initial analysis: (1) independent effects linked uniquely to regional-level variables (R); (2)
independent effects of landscape-level variables (L); (3) independent effects of plot-level variables
(P); (4) combined effects of regional- and landscape-level variables (R+L); (5) combined effects
of regional- and plot-level variables (R+P); (6) combined effects of landscape- and plot-level
variables (L+P); (7) combined effects of all variables across the three levels (R+L+P); and (8)
unexplained variance (Heikkinen et al., 2004).

In a three steps analysis, a series of separate RDAs and partial RDAs were computed to
identify the individual factors that significantly determined the species composition in the
different taxa. Firstly, separate RDAs were conducted to detect the effects of regional-, landscape-
and plot-level variables on each taxon, respectively (Aviron et al. 2005; Batáry et al. 2008). All
variables not contributing significantly (P > 0.05, Monte-Carlo test with 999 permutations) to the
variation in species composition were excluded from further analysis (Heikkinen et al., 2004; Ter
Braak and Šmilauer, 2002). Secondly, regional-level variables were used as covariates in
subsequent partial RDAs to exclude the effect of the large-scale spatial factors on the species
composition (Batáry et al., 2012). Stepwise forward selection was chosen for the regression
analysis to select models with reduced predictive redundancy (co-linearity) to ensure that
explanatory variables included in the model were independent (Lepš and Šmilauer, 2003;
Maisonhaute et al., 2010). In a final step, explanatory variables that contributed significantly to the
variation in species composition in these partial RDAs were selected as a basis for ordination diagrams visualizing the taxon-specific responses to the environmental predictor parameters 

(Aviron et al., 2005; Batáry et al., 2008; Jeanneret et al., 2003; Weibull and Östman, 2003). All ordinations were performed using CANOCO 4.5 (Ter Braak and Šmilauer, 2002).

3 Results

3.1 Overall Species richness

In total, 415 plant species were recorded in the study areas. The light traps yielded a total of 14,692 specimens representing 110 species of geometrids and 1,543 individuals representing 20 arctiid species (Appendix A). Furthermore, 3,663 individuals representing 73 carabid species were caught in the pitfall traps on the 48 sampling plots.

3.2 Variation partitioning

Based on combinations of the contributions by all predictor variables, the overall explained variation in species compositions in the four taxa ranged between 60.7% and 66.4% (Table 2). Results indicated significant impacts of factors representing all three spatial scales. The regional- and plot-level variables showed particularly strong individual links with the assemblage changes in all four taxa, with the combined effect of regional- and plot-level variables (R+P) explaining an additional large proportion (11.4-22.5%) of the variation in the three insect assemblages. Overall, variations in species composition of vascular plants and carabids were much more closely linked
to the individual effects of plot-level variables (P) than to regional-level factors (R), while composition changes in both moth taxa were much better explained by changes in the respective study region (R). Although the independent effect of landscape-level variables (L) only explained between 6.0-7.3% of the changes in the assemblage structure of all four taxa and did therefore not have a significant individual effect at P<0.05, the combined component of landscape- and plot-level variables (L+P) explained 23.6% and 7.4% of the total variation in the composition of vascular plants and carabids, respectively. The remaining combinations of variables explained no more than 7% of the variations in the species composition of each of the four taxa.

3.3 Species-environment relationships

When variables with no significant contribution towards the explained variation in the species composition were excluded in separate RDAs and regional-level variables (R) (the four categorical variables representing the four different study regions) were used as covariates, the percentage of semi-natural area, Shannon-Wiener landscape diversity and SOM contents significantly contributed towards changes in the vegetation composition, explaining 9.6%, 3.1%, and 2.9% of the variance, respectively, while the two habitat types ‘cultivated land’ and ‘orchard’ explained 19.7% and 4.9%, respectively (Table 3). The first ordination axis (22.5% explained variance) in the associated partial RDA was closely linked to plot-level variables, while the second axis (10.1 % explained variance) chiefly represented the landscape-level variables (Figure 2A). The ordination diagram (Fig. 2A) showed that plots of grassland and woodland formed a cluster clearly separated from plots representing cultivated land and orchards, which indicates a strong
The plot-level variables including plant species richness (4.2%), soil pH (2.0%), and the habitat type ‘cultivated land’ (2.1%), explained the greatest part of the variation in the geometrid species composition accounted for by the partial RDA (Table 3). In the respective ordination diagram, 16 cultivated plots formed a separate cluster to the remaining plots representing grassland, orchards and woodland, which indicates a differentiation of geometrid assemblages between cropland on one hand and orchards, semi-natural and natural habitats on the other (Figure 2B).

Species assemblages of Arctiinae showed similar responses to changes in the landscape structure and plot characteristics as Geometridae. Nonetheless, only the habitat type ‘cultivated land’ (2.6%) and the plant species coverage (2.5%) showed significant effects on the variation in the arctiinid species composition (Table 3). Furthermore, all plots with the exception of cultivated land clustered together (Figure 2C) in the partial RDA, indicating a similar composition of arctiinid assemblages on these plots, with a distinct, second set of assemblages present on cultivated land.

A significant part of the variation (4.4%) in the carabid composition was explained by the
percentage of semi-natural land in the partial RDA. Furthermore, habitat type (cultivated land
9.0% and grassland 2.9%) as well as plant coverage (2.6%) showed significant links to the ground
beetle assemblage structure (Table 3). In the respective ordination plot (Fig. 2D), the first axis
(11.5% explained variance) was closely linked to differences in habitat type. The second axis
(4.6% explained variance) was related to landscape structure and plant coverage (Figure 2D).
Grassland plots at Gaojiaying and cultivated plots clustered together, while orchards formed
another cluster, indicating distinct carabid assemblages encountered within these habitats.

4 Discussion

The high degree of variation (60.7 - 66.4%) explained by the sets of environmental variables
demonstrates that all investigated taxa responded strongly to the selected environmental factors
across the different spatial scales, with additional substantial effects observed for the combined
variable groups acting on different spatial scales. These results highlight the importance of
considering the spatial scale in regional biodiversity assessments (Gabriel et al., 2010;
Maisonhaute et al., 2010; Petit et al., 2013). In addition to the strong links between all four taxa
and regional variations, their highly variable responses to the remaining environmental variables
support our initial hypothesis that organisms may vary considerably in their reactions to changes
in environmental variables across spatial scales (Burel et al., 2004; Clough et al., 2005; Kinnunen
et al., 2001; Liu et al., 2014). This confirms that a ‘one size fits all’ approach for the conservation
of extremely species-rich insect taxa is unlikely to be effective (Axmacher et al., 2011; Burel et al.,
2013a; Gabriel et al., 2010).
The significant links between regional-level variables and the species composition of all four taxa may mainly relate to the altitudinal gradient along which the four study regions are positioned. Climatic drivers such as temperature, humidity and precipitation that are strongly associated with shifts in altitude have commonly been identified as dominant drivers for changes in the species composition of insects and plants in mountainous regions (Axmacher et al., 2009; Körner, 2004; Viterbi et al., 2013; Zou et al., 2014) and are believed to strongly underpin the differentiation in our regional species pools (see also Petit et al., 2013; Wang et al., 2012). Land use history and large-scale landscape structure and heterogeneity, levels of land use intensification and the differentiation of farming systems associated with study region are additional key potential causes of changes in assemblage structures at the regional scale (Aviron et al., 2005; Burel et al., 2013a; Clough et al., 2005). These significant shifts in the species composition with changes in altitude need to be fully considered in conservation planning, requiring a large-scale view of conservation activities across mountain ranges, rather than focusing for example on selected altitudinal bands. In contrast to our initial hypothesis, changes in the species composition of both plants and carabids were more strongly differentiated by plot-level parameters in comparison to regional-level factors. This supports the suggestions by Dauber et al. (2005), who argue that variables describing smaller-scale variations like local habitat characteristics are more strongly associated with variations in the species composition of weak dispersers like many plant and ground beetle species in our study. However, the strong effects of plot characteristics could also be explained by habitat management intensity in our mountainous agricultural landscapes, especially
on cultivated land. Although partly different habitat types were sampled in the different study regions, somewhat limiting the ability to perfectly separate effects of study region and habitat type, this was mainly related to the scarcity of orchards at high elevations, while cultivated land was sampled across all four study regions.

Cultivated land experiences very intensive management regimes, including substantial applications of agro-chemicals and farming practices that directly impact on the vegetation and carabids (Clough et al., 2007; Petit et al., 2013). On farmland, assemblages will chiefly be composed of highly disturbance-tolerant generalists, such as typical agricultural weeds and small carabid species with a strong flight ability (Aavik and Liira, 2010; Hendrickx et al., 2007; Liu et al., 2015; Rouabah et al., 2015). In contrast, habitats experiencing little anthropogenic management like grassland and woodland allow for the persistence of a wide range of plant species (Aavik and Liira, 2010; Weibull and Östman, 2003) and favor large-bodied and predatory carabid species (Aviron et al., 2005; Burel et al., 2004). The significant association between the two moth taxa and ‘cultivated land’ can be partly linked to the nectar feeding-habits of adult moths (Axmacher et al., 2011; Fuentes-Montemayor et al., 2011), as intensively cultivated land strongly lacks flowering plants as well as larval food plants (Fox, 2013; Merckx et al., 2012; Petit et al., 2013). When also taking account of results generated earlier from the study region (Axmacher et al., 2011; Liu et al., 2012) that reported a significantly higher plant diversity and higher activity density of predatory and large carabids in both woodland and grassland than in cultivated land (also see Appendix A), it can be concluded that a further expansion of intensively cultivated land such as vegetable fields will likely have strong negative impacts on the
biodiversity and, in relation to carabids, also the biological pest control across the agricultural
landscape, while restoration of grassland and woodland should be further promoted (Liu et al.,
2012; Schirmel et al., 2015; Schweiger et al., 2005).

The other plot-level factors explaining variations in species composition vary strongly
between taxa. SOM is known to play a key role in the storage and provision of nutrients for plant
growth and could in turn favor carabids by promoting a greater diversity of shelter and food
resources or the buffering of extreme microclimatic conditions (Thiele, 1977; Williams et al.,
2010). Nonetheless, SOM did not appear to strongly affect the composition in any of the three
insect taxa in our study. Soil pH significantly influenced the composition of three insect
assemblages. This could be partly related to the high correlation of soil pH with altitude (|r|> 0.7,
p<0.001). The contrast between arctiinid moths that responded more strongly to the overall plant
coverage and geometrid moths that were more strongly linked to overall plant species richness
could be explained by a higher degree of oligophagy in geometrids. The species composition in
this latter family therefore changed more strongly in response to vegetation changes (see
Axmacher et al., 2011; Merckx et al., 2012; Scherber et al., 2010). The plant coverage at the plot
level finally might have increased the heterogeneity in available resources, such as foraging
resources or microclimatic refuges, which increased the overall niche space for arciinids (Hilt,
2005), but also for carabids (Rouabah et al., 2015; Schirmel et al., 2015; Yanahan and Taylor,
2014).

Landscape-level variables finally explained the smallest proportion of the variation in the
species composition of all taxa. This somehow contradicts results from earlier studies
investigating changes in the vegetation (Aavik and Liira, 2010; Petit et al., 2013), carabid (Aviron et al., 2005; Burel et al., 2013a), and moth assemblages (Fuentes-Montemayor et al., 2011; Merckx et al., 2012). The limited effects of landscape-level variables could be explained by the difficulty in clearly distinguishing landscape-scale effects from regional factors, since the overall landscape structure changed between study regions, which impacted the measured landscape metrics, while some of the variables measured in the 1 ha quadrates surrounding the sampling plots also showed links to plot-level variables like the specific habitat type. However, the landscape-level variable ‘proportion of semi-natural land’ had a significant effect on the species composition of both carabids and plants, confirming the importance of a diverse, heterogeneous landscape structure containing semi-natural habitat for the two taxa (Gabriel et al., 2010).

Semi-natural habitats could also have provided carabids with shelter, overwintering sites or supplementary food sources (Aviron et al., 2005; Burel et al., 2013a; Weibull and Östman, 2003), in turn serving as source areas for the colonization of carabids into neighboring plots, as most carabid species are known to chiefly disperse over limited distances of only up to 50m (Welsh, 1990). The lack of observed links between the moth assemblage structures and the landscape-level variables could be seen as surprising, given the dependency of many moth species on multiple, distinct habitats during their lifecycle (Fahrig et al., 2011; Fuentes-Montemayor et al., 2011; Merckx et al., 2012). We believe that this observation could relate to the relatively small area used in our landscape structure analysis, because moths with their generally strong flight ability can easily cover large distances (Merckx et al., 2012; Ricketts et al., 2001). The landscape structure could more strongly affect assemblages of these taxa if a larger landscape context was considered.
with 200 ha suggested by Merckx et al. (2012), and a 20 ha circle around the respective study plots by Fuentes-Montemayor et al. (2011). This further highlights the importance of defining the right spatial scale when assessing the effects of landscape structure on different taxa (Aviron et al., 2005; Batáry et al., 2012; Fuentes-Montemayor et al., 2011; Merckx et al., 2012).

5 Conclusion

The four species-rich taxa we investigated strongly varied in their overall distribution patterns and their response to changes in environmental factors across the agricultural mountainous landscape, where both region-and plot-level characteristics were identified as important predictors for changes in the species composition across all taxa. Within these taxa, variations in the composition of vascular plants and carabids were best explained by plot-level characteristics, while geometrid and arctiid assemblages reacted more strongly to regional-level factors. An effective conservation strategy for the biodiversity linked to these four taxa in this agricultural mountainous landscape needs to address the varying requirements of both, the mega-diverse arthropod taxa and the vegetation, across multiple spatial scales. At least in the context of conserving the diversity of flying moths, regional-scale conservation approaches appear clearly superior to the conservation of small protected areas, while increasing the landscape heterogeneity by promoting an increase in the proportion semi-natural habitats can strongly benefit both the vegetation and carabid assemblages.
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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://
References


and spider biodiversity to local and landscape scale management intensity in cereal crops and

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J.,
Bukacek, R., Burel, F., 2007. Indicators for biodiversity in agricultural landscapes: a

Chapman, J.W., 2012. Large carabid beetle declines in a United Kingdom monitoring
network increases evidence for a widespread loss in insect biodiversity. J. Appl. Ecol. 49,
1009-1019.

Burel, F., Aviron, S., Baudry, J., Le Féon, V., Vasseur, C., 2013a. The structure and dynamics of
agricultural landscapes as drivers of biodiversity, in: Fu, B., Jones, K.B. (Eds.), Landscape


Burel, F., Lavigne, C., Marshall, E., 2013b. Landscape ecology and biodiversity in agricultural

Ecol. 7 (Suppl.), 1-7.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I.,


structure and spatial variables on the abundance of birds in an agricultural- forest mosaic. J.

Appl. Ecol. 41, 824-835.

Hendrickx, F., Maelfait, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S.,

Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T.I.M., Dirksen, J.,


structure, land-use intensity and habitat diversity affect components of total arthropod

Hilt, N., 2005. Diversity and species composition of two different moth families (Lepidoptera:

Arctiidae vs. Geometridae) along a successional gradient in the Ecuadorian Andes. PhD
dissertation. University of Bayreuth, Bayreuth, Germany.


bees in cereal fields: effects of farming system, landscape composition and regional context.


Holzschuh, A., Steffan- Dewenter, I., Tscharntke, T., 2009. How do landscape composition and
configuration, organic farming and fallow strips affect the diversity of bees, wasps and their


Jiang, Q., Deng, X., Yan, H., Liu, D., Qu, R., 2012. Identification of food security in the
mountainous guyuan prefecture of China by exploring changes of food production. J. Food Agric. Environ. 10, 210-216.


Table 1

Characterization of the study regions positioned at ~400m altitudinal intervals that also represent distinct agricultural landscapes. Three common habitats with different dominant vegetation and management intensity were selected for sampling within each study region as indicated under ‘habitat type’.

<table>
<thead>
<tr>
<th>Study region</th>
<th>Elevation (m)</th>
<th>Habitat type</th>
<th>Dominant plant species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Orchard</td>
<td><em>Prunus armeniaca</em> L., <em>Malus pumila</em> Mill., <em>P. salicina</em> L.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Orchard</td>
<td><em>Prunus armeniaca</em> L., <em>Malus pumila</em> Mill., <em>P. salicina</em> L.</td>
</tr>
</tbody>
</table>
Table 2
Partitioning of the explained variance in the species composition of vascular plant, moths and carabids by the independent and combined effects of regional- (R), landscape- (L) and plot-level variables (P).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Independent components (%)</th>
<th>Combined components (%)</th>
<th>Unexplained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>L</td>
<td>P</td>
</tr>
<tr>
<td>Vascular plant</td>
<td>10.5**</td>
<td>6.1</td>
<td>20.4**</td>
</tr>
<tr>
<td>Geometridae</td>
<td>15.1**</td>
<td>6.0</td>
<td>10.3*</td>
</tr>
<tr>
<td>Arctiinae</td>
<td>15.6**</td>
<td>7.6</td>
<td>12.6*</td>
</tr>
<tr>
<td>Carabidae</td>
<td>11.2**</td>
<td>6.3</td>
<td>17.6**</td>
</tr>
</tbody>
</table>

Levels of statistical significance (Monte-Carlo test) for independent components:*p<0.05, **p<0.01
Table 3

Percentage of variance in the compositions of vascular plant, moths and carabids communities explained by separated RDAs and partial RDAs. Separate RDAs were calculated for regional-, landscape- and plot-level variable groups, respectively. The environmental variables that significantly influenced species composition changes in the separate RDAs were used as variables in subsequent partial RDAs, with the study regional level variables as covariates.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Vascular plant</th>
<th>Geometridae</th>
<th>Arctiinae</th>
<th>Carabidae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Separate</td>
<td>Partial</td>
<td>Separate</td>
<td>Partial</td>
</tr>
<tr>
<td><strong>RDA % of variation</strong></td>
<td></td>
<td></td>
<td><strong>RDA % of variation</strong></td>
<td></td>
</tr>
<tr>
<td>Regional level - study region</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dayushu (D)</td>
<td>1.3</td>
<td>—</td>
<td>16.1**</td>
<td>—</td>
</tr>
<tr>
<td>Gaojiaying (G)</td>
<td>—</td>
<td>—</td>
<td>15.6**</td>
<td>—</td>
</tr>
<tr>
<td>Baiqi (B)</td>
<td>9.0**</td>
<td></td>
<td>8.9**</td>
<td>—</td>
</tr>
<tr>
<td>Shizigou (S)</td>
<td>6.1**</td>
<td>—</td>
<td>—</td>
<td>17.8**</td>
</tr>
<tr>
<td>Total</td>
<td>16.3**</td>
<td>40.6**</td>
<td>45.9**</td>
<td>32.6**</td>
</tr>
</tbody>
</table>

Landscape level - landscape structure
<table>
<thead>
<tr>
<th></th>
<th>1.9</th>
<th>2.1</th>
<th>2</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largest patch index (LPI)</td>
<td></td>
<td></td>
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<tr>
<td>Shannon-Wiener diversity (SHDI)</td>
<td>4.0*</td>
<td>3.1*</td>
<td>2</td>
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<tr>
<td>Mean of perimeter area ratio (PM)</td>
<td>1.6</td>
<td>2.6</td>
<td>4.1</td>
<td>1.6</td>
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<tr>
<td>Semi-natural land % (SNP)</td>
<td>16.9**</td>
<td>9.6**</td>
<td>5.8**</td>
<td>1.4</td>
</tr>
<tr>
<td>Cultivated land % (FP)</td>
<td>8.8**</td>
<td>0.8</td>
<td>4.3**</td>
<td>1.5</td>
</tr>
<tr>
<td>Total</td>
<td>33.2**</td>
<td>16.7**</td>
<td>15.2</td>
<td>23.7**</td>
</tr>
</tbody>
</table>

**Plot level - plot characteristics**

<table>
<thead>
<tr>
<th></th>
<th>17.1**</th>
<th>19.7**</th>
<th>5.9**</th>
<th>2.1**</th>
<th>3.0*</th>
<th>2.6**</th>
<th>9.5**</th>
<th>9.0**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cultivated land (CL)</td>
<td></td>
<td></td>
<td>2.6*</td>
<td>1.1</td>
<td>5.0*</td>
<td>2.5</td>
<td>5.6**</td>
<td>2.6*</td>
</tr>
<tr>
<td>Orchard (OR)</td>
<td>10.7**</td>
<td>4.1**</td>
<td>2.9*</td>
<td>1.1</td>
<td>1.6</td>
<td>1.2</td>
<td>1.2</td>
<td>1.2</td>
</tr>
<tr>
<td>Woodland (WL)</td>
<td>6.3**</td>
<td>1.4</td>
<td>1.6</td>
<td>5.2**</td>
<td>1.2</td>
<td>1.2</td>
<td>1.2</td>
<td>1.2</td>
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<tr>
<td>Grassland (GL)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant coverage (Cov)</td>
<td>—</td>
<td>—</td>
<td>2.6*</td>
<td>1.1</td>
<td>5.0*</td>
<td>2.5</td>
<td>5.6**</td>
<td>2.6*</td>
</tr>
<tr>
<td>Plant species richness (Ric)</td>
<td>—</td>
<td>—</td>
<td>5.0**</td>
<td>4.2**</td>
<td>4.4*</td>
<td>1.4</td>
<td>3.2**</td>
<td>1.3</td>
</tr>
<tr>
<td>Soil pH value (pH)</td>
<td>2.1</td>
<td>14.1**</td>
<td>2.0*</td>
<td>15.2**</td>
<td>0.6</td>
<td>5.1**</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Soil organic matter content (SOM)</td>
<td>7.5**</td>
<td>2.9*</td>
<td>1.9</td>
<td>2.4</td>
<td></td>
<td>10.7**</td>
<td>1.2</td>
<td>1.2</td>
</tr>
<tr>
<td>Soil total nitrogen (SN)</td>
<td>1.8</td>
<td>2.2</td>
<td>3.5*</td>
<td>0.8</td>
<td>1.2</td>
<td>1.2</td>
<td>1.2</td>
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<td>--------</td>
<td>--------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>45.5**</td>
<td>36.3**</td>
<td>40.3**</td>
<td>43.4**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total (Partial ordination)</td>
<td>41.5**</td>
<td>13.4**</td>
<td>9.2*</td>
<td>24.7**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1

The location of four villages (white circles: (1) Dayushu, (2) Gaojiaying, (3) Baiqi and (4) Shizigou) in the mountainous agro-landscape of northern China.

Figure 2

Partial RDA biplots showing significant effects of selected variables on the species composition of vascular plants (A), Geomtridae (B), Arctiinae (C) and Carabidae (D). 48 sampling plots use Samp scores to display the variability in the species composition.
Environmental variable
- Quantitative variable
  - Cov - Plant coverage
  - pH - Soil pH
  - Ric - Plant species richness
  - SHDI - Shannon-Wiener diversity
  - SNP - % Semi-natural area
  - SOM - Soil organic matter content
- Categorial variable
  - CL - Cultivated land
  - GL - Grassland
  - OR - Orchard

Sampling plots
- Cultivated land at Dayushu
- Orchard at Dayushu
- Woodland at Dayushu
- Cultivated land at Gaojiaying
- Orchard at Gaojiaying
- Grassland at Gaojiaying
- Cultivated land at Baiqi
- Grassland at Baiqi
- Woodland at Baiqi
- Cultivated land at Shizigou
- Grassland at Shizigou
- Woodland at Shizigou
Appendix A. Supplementary data

Total species richness (Plot mean ± SE) for each taxon at each habitat type and study region.

<table>
<thead>
<tr>
<th>Study region</th>
<th>Habitat type</th>
<th>Vascular plants</th>
<th>Carabidae</th>
<th>Geometridae</th>
<th>Arctiinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xingbaozhuang</td>
<td>Cultivated land</td>
<td>30 (17.50±1.04)</td>
<td>24 (12.00±0.91)</td>
<td>30 (12.75±0.85)</td>
<td>7 (3.00±1.08)</td>
</tr>
<tr>
<td></td>
<td>Orchard</td>
<td>50 (22.25±1.93)</td>
<td>11 (5.00±1.08)</td>
<td>44 (22.25±1.70)</td>
<td>9 (4.25±0.47)</td>
</tr>
<tr>
<td></td>
<td>Woodland</td>
<td>88 (40.00±3.62)</td>
<td>17 (6.75±2.83)</td>
<td>56 (33.50±1.84)</td>
<td>10 (4.75±1.18)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>117 (26.58±3.18)</td>
<td>32 (7.91±1.31)</td>
<td>65 (22.83±2.67)</td>
<td>11 (4.00±0.55)</td>
</tr>
<tr>
<td>Wulahada</td>
<td>Cultivated land</td>
<td>47 (23.25±2.92)</td>
<td>23 (10.50±0.86)</td>
<td>34 (16.50±2.72)</td>
<td>10 (3.50±0.64)</td>
</tr>
<tr>
<td></td>
<td>Orchard</td>
<td>96 (46.00±5.36)</td>
<td>27 (16.50±1.65)</td>
<td>43 (21.75±3.22)</td>
<td>8 (4.25±0.47)</td>
</tr>
<tr>
<td></td>
<td>Meadow</td>
<td>186 (91.00±3.24)</td>
<td>21 (9.25±1.54)</td>
<td>61 (37.00±2.41)</td>
<td>11 (7.25±0.75)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>251 (53.41±8.74)</td>
<td>44 (12.08±1.20)</td>
<td>66 (25.08±3.00)</td>
<td>14 (5.00±0.59)</td>
</tr>
<tr>
<td>Baiqi</td>
<td>Cultivated land</td>
<td>65 (25.50±2.50)</td>
<td>38 (19.25±2.49)</td>
<td>45 (23.00±2.61)</td>
<td>11 (6.50±0.86)</td>
</tr>
<tr>
<td></td>
<td>Meadow</td>
<td>127 (64.75±1.43)</td>
<td>28 (16.00±1.08)</td>
<td>61 (37.50±2.49)</td>
<td>12 (8.00±0.40)</td>
</tr>
<tr>
<td></td>
<td>Woodland</td>
<td>153 (80.50±2.21)</td>
<td>26 (12.50±1.44)</td>
<td>73 (41.75±2.75)</td>
<td>12 (7.25±1.31)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>220 (56.91±7.05)</td>
<td>50 (15.91±1.24)</td>
<td>83 (34.16±2.79)</td>
<td>16 (7.25±0.52)</td>
</tr>
<tr>
<td>Shihao</td>
<td>Cultivated land</td>
<td>68 (29.50±5.6)</td>
<td>29 (12.50±1.25)</td>
<td>40 (21.00±3.53)</td>
<td>10 (4.50±0.28)</td>
</tr>
<tr>
<td></td>
<td>Meadow</td>
<td>165 (63.00±8.86)</td>
<td>32 (10.75±1.10)</td>
<td>46 (23.25±1.43)</td>
<td>11 (5.00±0.40)</td>
</tr>
<tr>
<td></td>
<td>Woodland</td>
<td>145 (58.25±3.14)</td>
<td>19 (10.75±2.25)</td>
<td>36 (21.25±2.39)</td>
<td>11 (6.00±1.47)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>245 (50.25±5.55)</td>
<td>44 (11.33±0.88)</td>
<td>50 (21.83±1.39)</td>
<td>13 (5.16±0.50)</td>
</tr>
</tbody>
</table>

Total number of species 415 (46.79±3.57) 73 (11.81±0.70) 110 (25.97±1.42) 20 (5.35±0.31)