

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

1 **Environmental factors acting at multiple scales determine assemblages of insects and plants**
2 **in agricultural mountain landscapes of northern China**

3 Meichun Duan^{ab}, Yunhui Liu^{a*}, Zhenrong Yu^a, Liangtao Li^c, Changliu Wang^d, Jan C. Axmacher^e

4

5 ^aChina Agricultural University, College of Agricultural Resources and Environmental Sciences, 2

6 Yuanmingyuanxilu, Beijing 100193, China

7 ^bFrench National Institute of Agronomic Research (INRA), UR 980 SAD-Paysage, 65 rue de St

8 Brieuc CS 84215, 35042 Rennes Cedex, France

9 ^cHebei University of Engineering, College of Agriculture, 199 Guangming South Street, Handan

10 056038, China

11 ^dSouthwest University for Nationalities, Department of Architecture and Urban Planning, 16

12 South Section, 1st Ring Road, Chengdu 610041, China

13 ^eUniversity College London (UCL), Department of Geography, Pearson Building, Gower Street,

14 London WC1E 6BT, UK

15 * Corresponding author. Tel: +86-10-62734819/fax: +86-10-62731293

16 E-mail: liuyh@cau.edu.cn

17

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20 **Abstract**

21 Mountainous regions harbor high levels of biodiversity, while often experiencing substantial
22 pressure from agricultural production. Our current understanding of factors driving changes in the
23 highly diverse species assemblages of these regions is generally limited. We used variance
24 partitioning based on redundancy analysis to establish the effects of environmental variables on
25 the species composition of vascular plants and three insect taxa (Geometridae, Arctiinae and
26 Carabidae). These environmental determinants are linked to three distinct spatial levels: the
27 regional level - the four study regions positioned at ~ 400m altitudinal intervals, the landscape
28 level - the landscape structure in the vicinity of each study plot, and the plot level - the
29 environmental conditions at individual sampling locations. Our results showed that variations in
30 the species composition of vascular plants and carabids were more closely linked to plot-level
31 characteristics than to regional-level factors, while the opposite trend was observed for the two
32 moth taxa. When effects explicitly linked to the four study regions were controlled, plant and
33 carabid assemblages showed strong links to the percentage of semi-natural habitat at the landscape
34 level, while geometrid and arctiid assemblages were affected primarily by the overall plant
35 species richness and plant coverage at the plot level. Overall, the variations in the species
36 composition of different taxa can be explained by varying sets of environmental variables acting at
37 different spatial scales, and the relative role of these variables is highly taxon-specific.
38 Regional-scale approaches are crucial for biodiversity conservation in mountainous agricultural
39 landscapes, as exemplified by the responses in the two moths taxa, while a high proportion of
40 semi-natural habitats in the agricultural landscape is not only linked to a diverse vegetation, but

41 also to species-rich carabid assemblages.

42

43 **Key words:** Arctiinae; β -diversity; Carabidae; Geometridae; vascular plants

44

45 **1 Introduction**

46 Mountainous areas are known to harbor high levels of biodiversity, partly due to a substantial
47 species turnover along the steep environmental gradients typical for these areas (Körner, 2004;
48 Viterbi et al., 2013). In many parts of the world, mountainous regions have experienced significant
49 environmental change, habitat degradation and fragmentation linked to the expansion of
50 agricultural areas (Batáry et al., 2012; Brooks et al., 2012; Nogués-Bravo et al., 2008). Modern
51 agricultural production in general is seen as a key threat to global and regional biodiversity (Fox,
52 2013; McMahon et al., 2012; Norris, 2008), but in some cases, agricultural landscapes can also
53 support high levels of biodiversity (Burel et al., 2013b; Sturaro et al., 2013; Tschardtke et al.,
54 2005).

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

64 In China, more than 44% of the country's cultivated land is located in mountainous regions.
65 Many of these regions also harbor high level of biodiversity and are priorities for biodiversity

66 conservation (Tang et al., 2006; Wu et al., 2014). [At the same time, these mountain regions are](#)
67 [inhabited by >30 million people, with rural communities](#) strongly relying on agricultural
68 production for their survival (Jiang et al., 2012). This pattern is exemplified by the mountainous
69 agricultural landscapes located between Beijing and the Bashang Plateau that also harbor
70 important animal and plant genetic resources (Li, 2006). The entire area has experienced a serious
71 degradation of its natural ecosystems due to overgrazing and the transformation of natural habitats
72 into cultivated land. These developments are still rapidly progressing, and the area under very
73 intensive management for vegetable production has increased by 21 % from spring 2013 to spring
74 2014. [The regional biodiversity is additionally under pressure from the region's rapidly](#)
75 [developing tourism industry.](#) However, research on this region's biodiversity and its response to
76 environmental changes is scarce (Axmacher et al., 2011; Yuan et al., 2006).

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

87 individual the sampling plots (Aviron et al. 2005; Batáry et al. 2008; Liu et al., 2012, 2015).
88 Species-specific traits such as a species' position in trophic guilds and its dispersal ability further
89 affect its distribution and response to environmental factors across spatial scales (Burel et al., 2004;
90 Hendrickx et al., 2007; Jeanneret et al., 2003; Merckx et al., 2012). Species occupying high
91 trophic levels are more prone to respond to regional environmental changes, partly because they
92 commonly have large home ranges in which they occur at low population densities (Liu et al.,
93 2014). Species with strong dispersal abilities are influenced by environmental conditions at larger
94 spatial scales when compared to weak dispersers that respond strongly to local factors like habitat
95 conditions and farming practices (Dauber et al., 2005; Gabriel et al., 2010; Weibull and Östman,
96 2003). This means that different taxa are expected to show distinct and often complex response
97 patterns in response to a wide variety of different pressures and environmental gradients occurring
98 and interacting at different spatial scales (Axmacher et al., 2011; Batáry et al., 2012; Clough et al.,
99 2007; McMahon et al., 2012). Conservation strategies aimed at preserving a wide range of taxa
100 and associated ecosystem service provision therefore require a profound understanding not only of
101 biodiversity patterns across the different taxa, but also of the strength of links between biodiversity
102 patterns and environmental factors acting at different spatial scales (Billetter et al., 2007; Fahrig et
103 al., 2011; Petit et al., 2013; Viterbi et al., 2013). Studies in mountainous agricultural landscapes
104 are in this regard extremely valuable, as they can provide insights into biodiversity changes in
105 species-rich assemblages along pronounced environmental gradients (Chemini and Rizzoli, 2003;
106 Wang et al., 2012).

107 In our study, we address the prevailing knowledge gaps related to changes in the species

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

122 In our study, we specifically focused on the spatial changes in species composition, since
123 these are highly sensitive to environmental change and closely associated with ecosystem
124 functioning (Jeanneret et al., 2003; Weibull and Östman, 2003). Due to the different life histories
125 and dispersal abilities of the four target taxa, their responses to environmental changes was
126 expected to be governed by distinctly different sets of predictor variables (Billeter et al., 2007;
127 Burel et al., 2004; Merckx et al., 2012). We aimed to determine the nature and strength of links
128 between the species composition changes in our four target taxa and a set of environmental

129 predictors that act at regional, landscape and plot levels. We hypothesized that factors on all three
130 spatial scales would significantly affect the species composition of the four taxa, and that the
131 species composition in all taxa was most strongly linked to changes at the regional level that also
132 reflected distinct shifts in elevation. Plot-level parameters were assumed to chiefly impact the two
133 taxa of low mobility, vascular plants and ground beetles, whereas the landscape-level variables
134 were hypothesized to be more closely associated with the composition of geometrid and arctiid
135 moth assemblages due to the greater mobility and distinct resource requirements of these insects.

136

137 **2 Materials and Methods**

138 2.1 Study sites and plot selection

139 The study area (40°23' - 41°12' N, 114° 57' - 115°57' E) is located within the mountain
140 ranges between Beijing and the Inner Mongolian Plateau in northern China. This area represents
141 the transition zone between temperate and sub-temperate climate and is strongly affected by
142 monsoon weather patterns, with rainfall amounts typical for the transition zone between
143 sub-humid and semiarid conditions. This area is also an important transition zone between
144 agricultural cropland and pasturing regimes. The altitude rises from about 50 m to >2000 m, with
145 substantial changes in the composition of the agricultural landscapes occurring along this steep
146 altitudinal gradient. For our study, we selected four distinct regions along the altitudinal gradient
147 that represent four distinctly different agricultural landscapes. These four study regions were
148 located in the vicinity of four villages, Dayushu, Gaojiaying, Baiqi and Shizigou, at elevations of
149 about 500 m, 800 m, 1200 m and 1650 m, respectively (Figure 1).

150

151 Figure 1 approximately here#

152

153 Within each study region, three representative habitats were subsequently selected according
154 to the typical management intensity, dominant natural vegetation and farming regime encountered
155 (Table 1). These habitat types were selected from four wider habitat categories. Intensely
156 cultivated fields that were regularly treated with chemical pesticides and fertilizers, plowed and
157 cropped with maize, oat, potato or vegetables formed the first category. Orchards planted with
158 fruit trees and with intercropping of a variety of products treated with pesticides and fertilizers
159 formed a second habitat category, while grassland represented the third habitat category. The
160 grassland habitats remained widely unmanaged, since livestock grazing was prohibited, but
161 occasional intrusion from livestock was observed. Planted woodlands formed the final habitat
162 category. These woodlands were dominated by broadleaved or conifer trees and not commonly
163 used by local residents and their livestock. For each habitat type, four plots measuring 20 m × 20
164 m were randomly established on separate habitat patches to minimize pseudo- replication. The
165 mean distance between individual plots in each study region was 213.2m, ranging from 60.4m to
166 684.1m. Overall, twelve plots were selected within each study region, with 48 plots sampled in
167 total.

168

169 # Table1 approximately here#

170

171 2.2 Recording of vegetation and insects

172 Surveys of the % cover of all vascular plant species were conducted in June and September
173 2007. Trees and shrubs were recorded on the entire plots, while herbaceous species were recorded
174 at five 2×2m² subplots located in the center and at the four corners of each plot. Data from both
175 seasons were combined, allocating the maximum % cover recorded during either of the two
176 surveys to each plant species to establish their maximum ‘importance’ in the plot vegetation.

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

188 Ground beetles were sampled using pitfall traps set over 6 day-periods every month between
189 the beginning of May and early October in both 2006 and 2007. On each plot, eight pitfall traps
190 were placed at a distance of 4 m and 7 m from the plot center along N–S and E–W facing diagonal
191 lines intersecting in the middle of the plot. Pitfall traps were formed of cups 8 cm in diameter and

192 11.5 cm in depth, and partly filled with 75% alcohol to kill and preserve the specimens
193 (Southwood, 1978). Each trap was protected from rain by an aluminum roof positioned about 5 cm
194 above the trap.

195

196 2.3 Recording of environmental parameters

197 In our analysis, environmental variables were divided according to the spatial levels on which
198 they act: regional- (R), landscape- (L) or plot-level (P) variables. At the regional level, each of the
199 four regions, as four categorical variables, were used as regional variables and included in the
200 analysis to estimate account for the influence of the regional context (Aviron et al., 2005; Clough
201 et al., 2005; Ter Braak and Šmilauer, 2002). They were linked to the four study villages and
202 positioned at altitudinal intervals of ~ 400m that also represent distinct agricultural landscapes.

203 Landscape-level variables included the proportion of semi-natural land, the proportion of
204 cultivated land and the Shannon-Wiener landscape diversity index as measures of the overall
205 landscape heterogeneity (Heikkinen et al., 2004). Furthermore, the largest patch index and the
206 mean perimeter area ratio were also included as measures of the configurational landscape
207 heterogeneity (Fuentes-Montemayor et al., 2011). Landscape-level variables were recorded using
208 detailed 100 m × 100 m land-use maps centered on each sampling plot. The land-use maps we
209 used in our analysis were based on field surveys, where land-use was differentiated into five
210 cultivated land habitat types (maize, oat, vegetable and potato fields as well as orchards), three
211 semi-natural habitats (woodland, bushland and grassland), and other habitats (including roads and
212 buildings). Only land-use patches exceeding 2m × 2m in size were included on the maps. The

213 landscape metrics were analyzed using Fragstats 3.3 (Mcgarigal et al., 2002).

214 [Plot level variables included the habitat type, vegetation and soil properties.](#) Each habitat type
215 was included in the statistical analysis as a [categorical](#) variable (Dauber et al., 2005; Weibull and
216 Östman, 2003). The vegetation was characterized based on plant species richness and total %
217 cover of all plant species. The soil properties we recorded were soil organic matter content (SOM),
218 total nitrogen and soil pH, as these factors are believed to directly influence the vegetation and
219 partly also invertebrate assemblages (Petit et al., 2013; Schirmel et al., 2015; Yanahan and Taylor,
220 2014). Five soil sub-samples were randomly taken from the upper 20 cm of the mineral soil at
221 each plot and mixed prior to the analysis. [We used the rapid dichromate oxidation method and](#)
222 [Kjeldahl method to measure SOM and total nitrogen, respectively](#) (see Axmacher et al., 2011 for
223 more details on the laboratory analysis).

224

225 2.4 Data analysis

226 Prior to the statistical analyses, the 2006 and 2007 insect data was pooled for each sampling
227 plot and Hellinger-transformed to allow their use in the Redundancy Analysis (RDA), as initial
228 data-sets contained many zero values (Legendre and Gallagher, 2001). Quantitative environmental
229 variables were either log-transformed or, for proportional data, arcsine-transformed to align values
230 more closely to a normal distribution. All environmental variables were standardized to avoid
231 scale-dependent distortions due to the use of different units.

232 Variation partitioning was used to determine the relative importance of certain groups of
233 explanatory variables for the species composition of the different taxa, using selected groups of

234 explanatory variables as constrains and the remaining groups as [covariates](#) in the RDA. The same
235 sets of explanatory variables were used for all RDAs and partial RDAs to allow reliable
236 comparisons between taxa (Schweiger et al., 2005). We differentiated the following eight fractions
237 in this initial analysis: (1) [independent effects linked uniquely to](#) regional-level variables (R); (2)
238 [independent](#) effects of landscape-level variables (L); (3) [independent](#) effects of plot-level variables
239 (P); (4) combined effects of regional- and landscape-level variables (R+L); (5) combined effects
240 of regional- and plot-level variables (R+P); (6) combined effects of landscape- and plot-level
241 variables (L+P); (7) combined effects of all variables across the three levels (R+L+P); and (8)
242 unexplained variance (Heikkinen et al., 2004).

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

255 variation in species composition in these partial RDAs were selected as a basis for ordination
256 diagrams visualizing the taxon-specific responses to the environmental predictor parameters
257 (Aviron et al., 2005; Batáry et al., 2008; Jeanneret et al., 2003; Weibull and Östman, 2003). All
258 ordinations were performed using CANOCO 4.5 (Ter Braak and Šmilauer, 2002).

259

260 **3 Results**

261 3.1 Overall Species richness

262 In total, 415 plant species were recorded in the study areas. The light traps yielded a total of
263 14,692 specimens representing 110 species of geometrids and 1,543 individuals representing 20
264 arctiid species ([Appendix A](#)). Furthermore, 3,663 individuals representing 73 carabid species
265 were caught in the pitfall traps on the 48 sampling plots.

266

267 3.2 Variation partitioning

268 Based on combinations of the contributions by all predictor variables, the overall explained
269 variation in species compositions in the four taxa ranged between 60.7% and 66.4% (Table 2).
270 Results indicated [significant impacts of factors](#) representing all three spatial scales. The regional-
271 and plot-level variables showed particularly strong individual links with the assemblage changes
272 in all four taxa, with the combined effect of regional- and plot-level variables (R+P) explaining an
273 additional large proportion (11.4-22.5%) of the variation in the three insect assemblages. Overall,
274 variations in species composition of vascular plants and carabids were much more closely linked

275 to the individual effects of plot-level variables (P) than to regional-level factors (R), while
276 composition changes in both moth taxa were much better explained by changes in the respective
277 study region (R). Although the independent effect of landscape-level variables (L) only explained
278 between 6.0-7.3% of the changes in the assemblage structure of all four taxa and did therefore not
279 have a significant individual effect at $P < 0.05$, the combined component of landscape- and
280 plot-level variables (L+P) explained 23.6% and 7.4% of the total variation in the composition of
281 vascular plants and carabids, respectively. The remaining combinations of variables explained no
282 more than 7% of the variations in the species composition of each of the four taxa.

283

284 3.3 Species-environment relationships

285 When variables with no significant contribution towards the explained variation in the
286 species composition were excluded in separate RDAs and regional-level variables (R) (the four
287 categorical variables representing the four different study regions) were used as covariates, the
288 percentage of semi-natural area, Shannon-Wiener landscape diversity and SOM contents
289 significantly contributed towards changes in the vegetation composition, explaining 9.6%, 3.1%,
290 and 2.9% of the variance, respectively, while the two habitat types 'cultivated land' and 'orchard'
291 explained 19.7% and 4.9%, respectively (Table 3). The first ordination axis (22.5% explained
292 variance) in the associated partial RDA was closely linked to plot-level variables, while the second
293 axis (10.1 % explained variance) chiefly represented the landscape-level variables (Figure 2A).
294 The ordination diagram (Fig. 2A) showed that plots of grassland and woodland formed a cluster
295 clearly separated from plots representing cultivated land and orchards, which indicates a strong

296 separation between plant assemblages on agricultural land and semi-natural habitats.

297

298 # Table 3 approximately here#

299

300 # Figure 2 approximately here#

301

302 The plot-level variables including plant species richness (4.2%), soil pH (2.0%), and the

303 habitat type 'cultivated land' (2.1%), explained the greatest part of the variation in the geometrid

304 species composition accounted for by the partial RDA (Table 3). In the respective ordination

305 diagram, 16 cultivated plots formed a separate cluster to the remaining plots representing

306 grassland, orchards and woodland, which indicates a differentiation of geometrid assemblages

307 between cropland on one hand and orchards, semi-natural and natural habitats on the other (Figure

308 2B).

309 Species assemblages of Arctiinae showed similar responses to changes in the landscape

310 structure and plot characteristics as Geometridae. Nonetheless, only the habitat type 'cultivated

311 land' (2.6%) and the plant species coverage (2.5%) showed significant effects on the variation in

312 the arctiid species composition (Table 3). Furthermore, all plots with the exception of cultivated

313 land clustered together (Figure 2C) in the partial RDA, indicating a similar composition of

314 arctiid assemblages on these plots, with a distinct, second set of assemblages present on

315 cultivated land.

316 A significant part of the variation (4.4%) in the carabid composition was explained by the

317 percentage of semi-natural land in the partial RDA. Furthermore, habitat type (cultivated land
318 9.0% and grassland 2.9%) as well as plant coverage (2.6%) showed significant links to the ground
319 beetle assemblage structure (Table 3). In the respective ordination plot (Fig. 2D), the first axis
320 (11.5% explained variance) was closely linked to differences in habitat type. The second axis
321 (4.6% explained variance) was related to landscape structure and plant coverage (Figure 2D).
322 Grassland plots at Gaojiaying and cultivated plots clustered together, while orchards formed
323 another cluster, indicating distinct carabid assemblages encountered within these habitats.

324

325 **4 Discussion**

326 The high degree of variation (60.7 - 66.4%) explained by the sets of environmental variables
327 demonstrates that all investigated taxa responded strongly to the selected environmental factors
328 across the different spatial scales, with additional substantial effects observed for the combined
329 variable groups acting on different spatial scales. These results highlight the importance of
330 considering the spatial scale in regional biodiversity assessments (Gabriel et al., 2010;
331 Maisonhaute et al., 2010; Petit et al., 2013). In addition to the strong links between all four taxa
332 and regional variations, their highly variable responses to the remaining environmental variables
333 support our initial hypothesis that organisms may vary considerably in their reactions to changes
334 in environmental variables across spatial scales (Burel et al., 2004; Clough et al., 2005; Kinnunen
335 et al., 2001; Liu et al., 2014). This confirms that a 'one size fits all' approach for the conservation
336 of extremely species-rich insect taxa is unlikely to be effective (Axmacher et al., 2011; Burel et al.,
337 2013a; Gabriel et al., 2010).

338 The significant links between regional-level variables and the species composition of all four
339 taxa may mainly relate to the altitudinal gradient along which the four study regions are positioned.
340 Climatic drivers such as temperature, humidity and precipitation that are strongly associated with
341 shifts in altitude have commonly been identified as dominant drivers for changes in the species
342 composition of insects and plants in mountainous regions (Axmacher et al., 2009; Körner, 2004;
343 Viterbi et al., 2013; Zou et al., 2014) and are believed to strongly underpin the differentiation in
344 our regional species pools (see also Petit et al., 2013; Wang et al., 2012). Land use history and
345 large-scale landscape structure and heterogeneity, levels of land use intensification and the
346 differentiation of farming systems associated with study region are additional key potential causes
347 of changes in assemblage structures at the regional scale (Aviron et al., 2005; Burel et al., 2013a;
348 Clough et al., 2005). These significant shifts in the species composition with changes in altitude
349 need to be fully considered in conservation planning, requiring a large-scale view of conservation
350 activities across mountain ranges, rather than focusing for example on selected altitudinal bands.

351 In contrast to our initial hypothesis, changes in the species composition of both plants and
352 carabids were more strongly differentiated by plot-level parameters in comparison to
353 regional-level factors. This supports the suggestions by Dauber et al. (2005), who argue that
354 variables acting at larger spatial scales tend to be associated with stronger dispersers, whereas
355 variables describing smaller-scale variations like local habitat characteristics are more strongly
356 associated with variations in the species composition of weak dispersers like many plant and
357 ground beetle species in our study. However, the strong effects of plot characteristics could also be
358 explained by habitat management intensity in our mountainous agricultural landscapes, especially

359 on cultivated land. Although partly different habitat types were sampled in the different study
360 regions, somewhat limiting the ability to perfectly separate effects of study region and habitat type,
361 this was mainly related to the scarcity of orchards at high elevations, while cultivated land was
362 sampled across all four study regions.

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

380 biodiversity and, in relation to carabids, also the biological pest control across the agricultural
381 landscape, while restoration of grassland and woodland should be further promoted (Liu et al.,
382 2012; Schirmel et al., 2015; Schweiger et al., 2005).

383 The other plot-level factors explaining variations in species composition vary strongly
384 between taxa. SOM is known to play a key role in the storage and provision of nutrients for plant
385 growth and could in turn favor carabids by promoting a greater diversity of shelter and food
386 resources or the buffering of extreme microclimatic conditions (Thiele, 1977; Williams et al.,
387 2010). Nonetheless, SOM did not appear to strongly affect the composition in any of the three
388 insect taxa in our study. Soil pH significantly influenced the composition of three insect
389 assemblages. This could be partly related to the high correlation of soil pH with altitude ($|r| > 0.7$,
390 $p < 0.001$). The contrast between arctiinid moths that responded more strongly to the overall plant
391 coverage and geometrid moths that were more strongly linked to overall plant species richness
392 could be explained by a higher degree of oligophagy in geometrids. The species composition in
393 this latter family therefore changed more strongly in response to vegetation changes (see
394 Axmacher et al., 2011; Merckx et al., 2012; Scherber et al., 2010). The plant coverage at the plot
395 level finally might have increased the heterogeneity in available resources, such as foraging
396 resources or microclimatic refuges, which increased the overall niche space for arctiinids (Hilt,
397 2005), but also for carabids (Rouabah et al., 2015; Schirmel et al., 2015; Yanahan and Taylor,
398 2014).

399 Landscape-level variables finally explained the smallest proportion of the variation in the
400 species composition of all taxa. This somehow contradicts results from earlier studies

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

411 Semi-natural habitats could also have provided carabids with shelter, overwintering sites or
412 supplementary food sources (Aviron et al., 2005; Burel et al., 2013a; Weibull and Östman, 2003),
413 in turn serving as source areas for the colonization of carabids into neighboring plots, as most
414 carabid species are known to chiefly disperse over limited distances of only up to 50m (Welsh,
415 1990). The lack of observed links between the moth assemblage structures and the landscape-level
416 variables could be seen as surprising, given the dependency of many moth species on multiple,
417 distinct habitats during their lifecycle (Fahrig et al., 2011; Fuentes-Montemayor et al., 2011;
418 Merckx et al., 2012). We believe that this observation could relate to the relatively small area used
419 in our landscape structure analysis, because moths with their generally strong flight ability can
420 easily cover large distances (Merckx et al., 2012; Ricketts et al., 2001). The landscape structure
421 could more strongly affect assemblages of these taxa if a larger landscape context was considered,

422 with 200 ha suggested by Merckx et al. (2012), and a 20 ha circle around the respective study
423 plots by Fuentes-Montemayor et al. (2011). This further highlights the importance of defining the
424 right spatial scale when assessing the effects of landscape structure on different taxa (Aviron et al.,
425 2005; Batáry et al., 2012; Fuentes-Montemayor et al., 2011; Merckx et al., 2012).

426

427 **5 Conclusion**

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

441

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448

449 **Appendix A. Supplementary data**

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

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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'.

Study region	Elevation	Habitat type	Dominant plant species
Dayushu	518-526m	Cultivated land	<i>Zea mays L.</i> , <i>Potentilla anserina L.</i> , <i>Chenopodium album L.</i>
		Orchard	<i>Prunus armeniaca L.</i> , <i>Lepidium apetalum Willd.</i> , <i>Convolvulus arvensis L.</i>
		Woodland	<i>Populus cathayana Rehd.</i> , <i>Cynodon dactylon (L.) Pers.</i> , <i>Vitex negundo L.</i>
Gaojiaying	874-936m	Cultivated land	<i>Zea mays L.</i> , <i>Chenopodium album L.</i> , <i>Amaranthus retroflexus L.</i>
		Orchard	<i>Prunus armeniaca L.</i> , <i>Malus pumila Mill.</i> , <i>P. salicina L.</i>
		Grassland	<i>Carex humilis Leyss.</i> , <i>Ulmus pumila L.</i> , <i>Armeniaca sibirica(L.) Lam.</i>
Baiqi	1365-1419m	Cultivated land	<i>Avena sativa L.</i> , <i>Solanum tuberosum L.</i> , <i>Brassica napus L.</i>
		Grassland	<i>Ulmus pumila L.</i> , <i>Artemisia brachyloba Franch.</i> , <i>Aster altaicus Willd.</i>
		Woodland	<i>Larix principis-rupprechtii Mayr.</i> , <i>Carex humilis Leyss.</i> , <i>Ulmus davidiana Planch.</i>
Shizigou	1621-1679m	Cultivated land	<i>Brassica rapa L. var. glabra Regel.</i> , <i>S. tuberosum L.</i> , <i>Malva crispa L.</i>
		Grassland	<i>Chamaerhodos erecta (L.) Bge.</i> , <i>Artemisia annua L.</i> , <i>Plantago depressa Willd.</i>
		Woodland	<i>Larix principis-rupprechtii Mayr.</i> , <i>Carex humilis Leyss.</i> , <i>Populus simonii Carr.</i>

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).

Taxon	Independent components (%)			Combined components (%)				Unexplained (%)
	R	L	P	R+L	R+P	L+P	R+L+P	
Vascular plant	10.5**	6.1	20.4**	4.3	2.3	23.6	-0.8	33.6
Geometridae	15.1**	6.0	10.3*	3.3	18.6	3.9	3.5	39.3
Arctiinae	15.6**	7.6	12.6*	2.4	22.5	-0.2	5.4	34.1
Carabidae	11.2**	6.3	17.6**	3.1	11.4	7.4	6.9	36.1

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

645 **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](#).

Environmental variables	Vascular plant		Geometridae		Arctiinae		Carabidae	
	Separate	Partial	Separate	Partial	Separate	Partial	Separate	Partial
	RDA % of variation	RDA % of variation	RDA % of variation	RDA% of variation	RDA % of variation	RDA% of variation	RDA % of variation	RDA% of variation
Regional level - study region								
Dayushu (D)	1.3	—	16.1**	—	23.1**	—	16.8**	—
Gaojiaying (G)		—	15.6**	—	5**	—	11.4**	—
Baiqi (B)	9.0**	—	8.9**	—		—	4.4**	—
Shizigou (S)	6.1**	—		—	17.8**	—		—
Total	16.3**		40.6**		45.9**		32.6**	
Landscape level - landscape structure								

Largest patch index(LPI)	1.9		2.1		2		2	
Shannon-Wiener diversity(SHDI)	4.0*	3.1*	2		3.2		2.9	
Mean of perimeter area ratio(PM)	1.6		2.6		4.1		1.6	
Semi-natural land %(SNP)	16.9**	9.6**	5.8**	1.4	2.5		7.8**	4.4**
Cultivated land %(FP)	8.8**	0.8	4.3**	1.5	3.4		9.3**	1.7
Total	33.2**		16.7**		15.2		23.7**	
Plot level - plot characteristics								
Cultivated land (CL)	17.1**	19.7**	5.9**	2.1**	3.0*	2.6**	9.5**	9.0**
Orchard (OR)	10.7**	4.1**	2.9*	1.1	1.6		2.5	
Woodland(WL)	6.3**	1.4	1.6		5.2**	1.2		
Grassland (GL)							4.8**	2.9**
Plant coverage(Cov)	—	—	2.6*	1.1	5.0*	2.5*	5.6**	2.6*
Plant species richness(Ric)	—	—	5.0**	4.2**	4.4*	1.4	3.2**	1.3
Soil pH value(pH)	2.1		14.1**	2.0*	15.2**	0.6	5.1**	1.6
Soil organic matter content (SOM)	7.5**	2.9*	1.9		2.4		10.7**	1.2
Soil total nitrogen (SN)	1.8		2.2		3.5*	0.8	2.1	

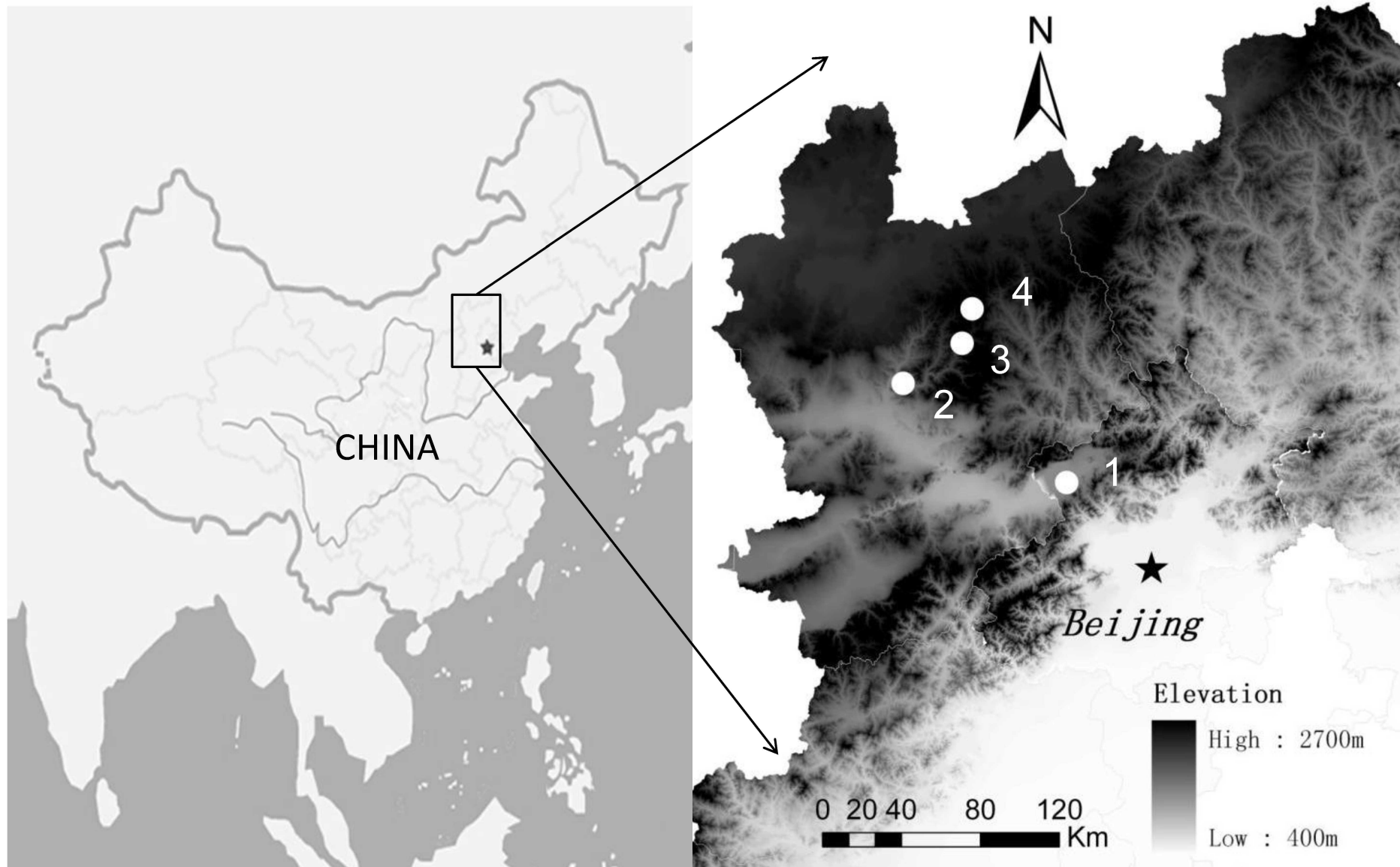
Total	45.5**	36.3**	40.3**	43.4**
Total (Partial ordination)	41.5**	13.4**	9.2*	24.7**

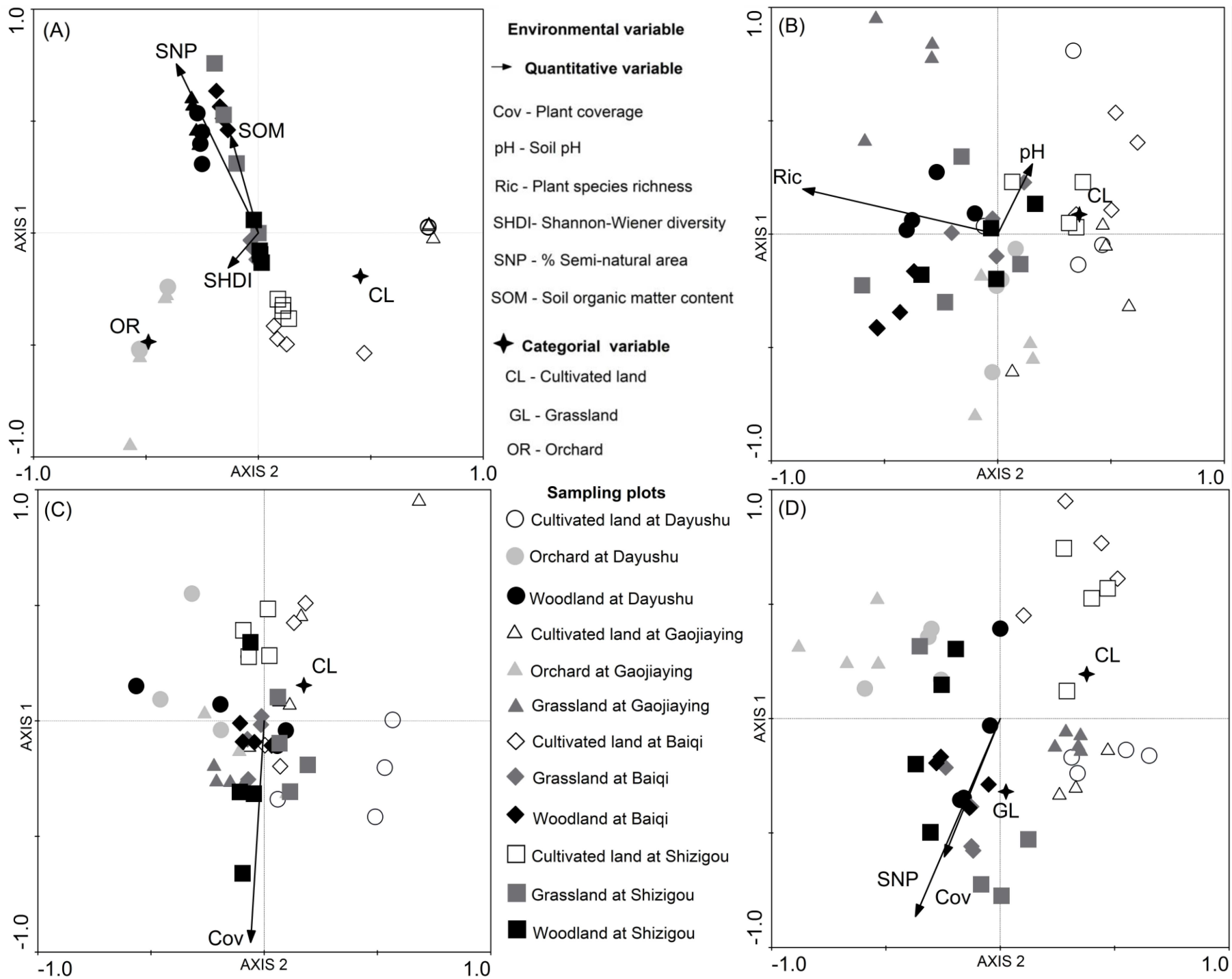
Figure 1

650 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.





Appendix A. Supplementary data

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

Study region	Habitat type	Vascular plants	Carabidae	Geometridae	Arctiinae
Xingbaozhuang	Cultivated land	30 (17.50 \pm 1.04)	24 (12.00 \pm 0.91)	30 (12.75 \pm 0.85)	7 (3.00 \pm 1.08)
	Orchard	50 (22.25 \pm 1.93)	11 (5.00 \pm 1.08)	44 (22.25 \pm 1.70)	9 (4.25 \pm 0.47)
	Woodland	88 (40.00 \pm 3.62)	17 (6.75 \pm 2.83)	56 (33.50 \pm 1.84)	10 (4.75 \pm 1.18)
	Total	117 (26.58 \pm 3.18)	32 (7.91 \pm 1.31)	65 (22.83 \pm 2.67)	11 (4.00 \pm 0.55)
Wulahada	Cultivated land	47 (23.25 \pm 2.92)	23 (10.50 \pm 0.86)	34 (16.50 \pm 2.72)	10 (3.50 \pm 0.64)
	Orchard	96 (46.00 \pm 5.36)	27 (16.50 \pm 1.65)	43 (21.75 \pm 3.22)	8 (4.25 \pm 0.47)
	Meadow	186 (91.00 \pm 3.24)	21 (9.25 \pm 1.54)	61 (37.00 \pm 2.41)	11 (7.25 \pm 0.75)
	Total	251 (53.41 \pm 8.74)	44 (12.08 \pm 1.20)	66 (25.08 \pm 3.00)	14 (5.00 \pm 0.59)
Baiqi	Cultivated land	65 (25.50 \pm 2.50)	38 (19.25 \pm 2.49)	45 (23.00 \pm 2.61)	11 (6.50 \pm 0.86)
	Meadow	127 (64.75 \pm 1.43)	28 (16.00 \pm 1.08)	61 (37.75 \pm 2.49)	12 (8.00 \pm 0.40)
	Woodland	153 (80.50 \pm 2.21)	26 (12.50 \pm 1.44)	73 (41.75 \pm 2.75)	12 (7.25 \pm 1.31)
	Total	220 (56.91 \pm 7.05)	50 (15.91 \pm 1.24)	83 (34.16 \pm 2.79)	16 (7.25 \pm 0.52)
Shihao	Cultivated land	68 (29.50 \pm 5.6)	29 (12.50 \pm 1.25)	40 (21.00 \pm 3.53)	10 (4.50 \pm 0.28)
	Meadow	165 (63.00 \pm 8.86)	32 (10.75 \pm 1.10)	46 (23.25 \pm 1.43)	11 (5.00 \pm 0.40)
	Woodland	145 (58.25 \pm 3.14)	19 (10.75 \pm 2.25)	36 (21.25 \pm 2.39)	11 (6.00 \pm 1.47)
	Total	245 (50.25 \pm 5.55)	44 (11.33 \pm 0.88)	50 (21.83 \pm 1.39)	13 (5.16 \pm 0.50)
Total number of species		415 (46.79 \pm 3.57)	73 (11.81 \pm 0.70)	110 (25.97 \pm 1.42)	20 (5.35 \pm 0.31)