

1 Taxon- and functional group-specific responses of ground beetles and
2 spiders to landscape complexity and management intensity in apple
3 orchards of the North China Plain

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12 Abstract

13 Agricultural intensification has caused severe declines in ground-dwelling arthropods
14 and associated ecosystem services. The conservation and re-establishment of semi-
15 natural habitats in agricultural landscapes represent widely accepted measures to
16 counter these declines. The effectiveness of these measures nonetheless varies
17 between target taxa and their functional traits, while also being affected by local
18 management. Here, we studied how species richness and abundance of different
19 functional groups of carabid beetles and spiders in apple orchards were affected by
20 landscape complexity (% semi-natural habitat) and local management intensity
21 (mowing and soil total nitrogen (STN) content). Both abundance and species richness

22 of non-carnivorous carabids and carabids overall were negatively affected by STN,
23 while the abundance of carnivorous carabids and carabids overall was affected by
24 interactive effects of mowing and landscape complexity, showing a positive response
25 to mowing where semi-natural habitats are scarce, but negative responses in
26 landscapes with a higher proportion of semi-natural habitats. The abundance of
27 ground-hunting spiders and spiders overall was generally positively related to %
28 semi-natural habitats, while the abundance of web-building spiders and the species
29 richness of ground-hunting spiders showed a positive correlation with STN at
30 landscapes with a low or medium abundance of semi-natural habitats, but a negative
31 correlation where semi-natural habitats were more abundant. Non-carnivorous carabid
32 diversity benefitted from low nitrogen application, while carnivorous carabid
33 abundance benefitted from mowing intensity especially in simple and structurally
34 homogenous agricultural landscapes. Both web-building and ground-hunting spiders
35 positively responded to low nitrogen applications and intermediate landscape
36 complexity. Overall, a low local management intensity promoted carabid beetles,
37 while spiders were favored by increasing landscape complexity. We conclude that
38 taxon- and functional group- specific, multi-scale conservation strategies are therefore
39 required to conserve invertebrate predators in apple orchards.

40 Keywords

41 Agricultural intensification; semi-natural habitats; generalist predators; functional
42 traits

43 1. Introduction

44 Agricultural intensification is regarded as a key driver of global biodiversity
45 declines (Tilman, 2017; IPBES, 2019). Intensive farming practices, dominated by
46 monocropping systems that require high levels of agro-chemical application and
47 heavy machinery-reliant rotary tillage or mowing, have been recognized as a main
48 driver of ground-dwelling arthropod losses and the associated degradation of
49 ecological services like biological pest control (Power, 2010; Garratt et al., 2011;
50 Boetzl et al., 2020). High applications of nitrogen fertilizers for example negatively
51 impact on ground-dwelling arthropods (Li et al., 2018), with nitrogen enrichment
52 causing soil acidification and eutrophication as well as the mobilization of potentially
53 toxic aluminum ions, therefore harming the resource habitat of ground-dwelling
54 predators (Likens et al., 1996; Paoletti et al., 1996; Haddad et al., 2000). A decreased
55 plant species richness under high nitrogen loading can also indirectly reduce ground-
56 dwelling arthropod diversity (Bobbink et al., 1998; Haddad et al., 2000), since it has
57 been positively associated with local plant diversity and vegetation coverage (Winter
58 et al., 2018). While the vegetation composition directly affects the diversity of
59 herbivores (Siemann, 1998), predator diversity is also impacted through bottom-up
60 cascade effects (Jacquot et al., 2019; Grettenberger & Tooker, 2020). Here, plant
61 diversity benefits diverse predator assemblages by providing both abundant
62 herbivorous prey and a heterogeneous mosaic of microhabitats (Paredes et al., 2013).
63 Arthropod predation furthermore decreases with high mowing frequency (Meyer et
64 al., 2019) that homogenizes microhabitat conditions.

65 At larger spatial scales, landscape complexity, commonly characterized as % semi-
66 natural habitat, also plays an important role in affecting ground-dwelling arthropod
67 diversity (Bianchi et al., 2006). An increase in the proportion of semi-natural habitats
68 in the landscape is widely assumed to benefit ground-dwelling arthropod diversity
69 (Alignier et al., 2014; Fusser et al., 2017). Nonetheless, some studies have shown a
70 neutral or even negative correlation between the proportion of semi-natural habitats
71 and generalist predator diversity (Riggi et al., 2017; Zhang et al., 2020).

72 In Europe, the re-establishment of semi-natural habitats and wildlife-friendly
73 farming approaches are promoted as important components in Agri-Environment
74 Schemes (AES) to booster the biodiversity in agricultural landscape (Tscharntke et al.,
75 2005). However, the effectiveness of these measures can vary greatly in agricultural
76 landscapes differing in landscape complexity, indicating that interactive effects
77 between local management intensity and landscape complexity determine the ground-
78 dwelling arthropod diversity in farmland areas (Lee et al., 2001; Cardarelli &
79 Bogliani, 2014). Potential negative impacts of localized intensive management on
80 ground-dwelling arthropods could therefore be partly compensated in complex
81 landscapes where particularly semi-natural habitats provide alternative food sources
82 and shelter and can act as species source habitats (Tscharntke et al., 2012). In
83 addition, the effects that local management and landscape complexity have on
84 ground-dwelling arthropods vary between taxa and functional groups (Schmidt et al.,
85 2005, 2008; Batary et al., 2012; Caprio et al., 2015). For instance, organic agricultural
86 management positively affected the species richness of non-carnivorous carabids and

87 ground-hunting spiders, but not that of grasshoppers or web-building spiders (Batary
88 et al., 2012), while the proportion of non-cropped habitats positively affected species
89 richness of hunting spiders, but not of web-building spiders (Schmidt et al., 2005,
90 2008).

91 Overall, the development of sustainable, environmentally friendly farming
92 approaches that combine sustained or even increased production with reduced agro-
93 chemical inputs remains a key challenge facing humanity (Power, 2010). Such
94 farming approaches will require a shift from a chemical and mechanical
95 intensification to an ecological intensification of agricultural production (Kleijn et al.,
96 2019). The success of these approaches in conserving ground-dwelling arthropod
97 diversity and associated ecosystem services also depends on balancing landscape
98 complexity with impacts of localized high management intensities and agro-chemical
99 applications required by some crops. While positive effects of landscape complexity
100 on diversity and abundance of many ground-dwelling arthropods have been reported
101 for a wide range of agricultural landscapes (Alignier et al., 2014; Fusser et al., 2017;
102 Seree et al., 2020), the extent of these positive effects compensating for the negative
103 effects of intensive farming practices on different taxa and functional groups of
104 ground-dwelling arthropods still requires urgent attention (Cardarelli & Bogliani,
105 2014).

106 Carabid beetles and spiders, two highly species-rich ground-dwelling arthropod
107 taxa, are relatively well known both taxonomically and ecologically (Knapp & Rezac,
108 2015). Both groups are important biological control agents in agricultural landscapes,

109 with many species feeding, as generalist predators, on Collembola, Diptera and
110 Hemiptera, where high rates of aphid (Hemiptera) predation and attacks especially on
111 nascent aphid populations early in the season are known to limit pest outbreaks
112 (Sunderland et al. 1987; Harwood et al., 2004). Herbivorous carabids can destroy the
113 seeds of weeds that would otherwise compete with crops for nutrients and water
114 (Diehl et al., 2012).

115 Furthermore, carabids and spiders show strong, taxon- or traits-specific responses
116 to landscape composition and management intensity (Batary et al., 2012; Zhang et al.,
117 2020). Species requiring specific resource conditions or have low dispersal abilities
118 are more vulnerable to intensive management, whereas generalists and highly mobile
119 species generally cope better with land-use changes (Woodcock et al., 2010). Earlier
120 studies indicate that, reflecting their greater dispersal abilities, spiders are more
121 strongly influenced by the wider landscape configuration than carabids (Bell et al.,
122 2005; Li et al., 2018). Species at high trophic levels are often assumed to have greater
123 dispersal abilities, but they require larger habitat patches than omnivorous or
124 herbivorous species (Lövei & Sunderland, 1996; Cole et al., 2002). By contrast,
125 especially herbivorous carabid species with low dispersal abilities are strongly
126 affected by management intensity (Lövei & Sunderland, 1996; Meiss et al., 2010;
127 Woodcock et al., 2010). Furthermore, ballooning provides web-building spiders with
128 greater dispersal abilities than ground-hunting spiders, reflected in a more
129 homogenous or random landscape-scale distribution of web-building compared to
130 ground-hunting spiders (Weyman et al., 2002; Graham et al., 2003; Bell et al., 2005).

131 In turn, web-building spiders are locally sensitive to mowing as it removes physical
132 structures required for the webs (Pajunen et al. 1995; Diehl et al., 2013).

133 In our study area, both mowing and high nitrogen applications are conventional
134 farming practices in apple orchards. As a major apple-producing country, China's
135 harvest accounts for ~35% of the global apple production (Chen et al., 2010),
136 highlighting the great national importance of this crop. However, little is known about
137 the interactive effects of landscape complexity and farming intensities on ground-
138 dwelling arthropods in apple orchards, or whether these interactive effects change
139 across taxa and functional groups (Caprio et al., 2015; Zhang et al., 2020). We aim to
140 address these persisting knowledge gaps in this study. We hypothesize that, based on
141 their strong dispersal ability and habitat requirements, (1) spider diversity across
142 functional groups responds positively to an increased proportion of semi-natural
143 habitats, while web-building spider diversity is negatively affected by local mowing
144 intensity. We further hypothesize that (2) the diversity of carabids decreases with
145 increasing local management intensity (increased mowing intensity and soil nitrogen
146 content), with effects especially visible in functional groups with low dispersal ability
147 and occupying a low trophic level. Where interactions between local management and
148 landscape complexity are concerned, we finally hypothesize that (3) both, carabids
149 and spiders, show strong negative responses to STN and mowing especially in
150 landscapes where semi-natural habitats are scarce, while the impacts of local
151 management interventions are much less pronounced in landscapes with a high
152 proportion of semi-natural habitats.

153 2. Materials and methods

154 2.1 Study area, sampling plots and landscape analysis

155 This study was conducted in Changping District (40°2'-40°23' N, 115°50'-116°29'
156 E) in Northwest Beijing, China, in 2019 (Fig. 1). The area is located within the
157 mountain ranges between Taihang and Yanshan mountains at the northern boundary of
158 the North China Plain, with elevation decreasing from north to south. The local climate
159 is classified as a semi-humid continental monsoon climate, with a mean annual
160 temperature of ~12°C and an annual precipitation of ~550 mm. The piedmont alluvial
161 plain is relatively warm and rich in water resources, favoring fruit production.
162 Accordingly, the plain area in the district with an elevation ranging from 30 to 100 m
163 is dominated by a mosaic of orchards, planted forest and settlement areas. The
164 surrounding mountains are dominated by natural forest and shrubland, with elevations
165 reaching up to 1000 m. Intensively managed apple orchards form the dominant
166 agricultural land-use type in the region. Since 2012, forest plantations mainly consisting
167 of *Platycladus orientalis*, *Pinus tabulaeformis* or *Populus tomentosa*, are occupying
168 increasingly large areas in the region, too. In the mountains, the main vegetation is
169 comprised of *Vitex negundo*, *Ziziphus jujuba*, *Spiraea salicifolia* and *Pennisetum*
170 *centrasiaticum* at elevations below 800 m; whereas above this altitude, *Abelia biflora*,
171 *Corylus mandshurica* and *Lespedeza bicolor* form the main components of the natural
172 shrubland.

173 We selected 23 “Fuji” apple orchards along a landscape complexity gradient (based

174 on % semi-natural habitats), using circles with 500 m radius to characterize the
175 surrounding landscape. This scale was selected as it was shown to be highly suitable
176 to describe patterns in agriculture landscapes that influence the species richness and
177 abundance of both, carabids and spiders (Batáry et al., 2012; Mader et al., 2016;
178 Zhang et al., 2020). The distance between neighboring sampled orchards in the study
179 area was 800~1000 m. Landscape composition was digitized following field
180 inspections based on a set of high-resolution 2019 Worldview-2 satellite images
181 (resolution 0.46 m). ArcGIS 10.2 (ESRI, 2014) was then used to calculate the relative
182 coverage of the different land-use types in the landscape, and to quantify the
183 landscape complexity as the proportion of semi-natural habitats (comprising
184 grassland, plantation forests, windbreak and shrubland habitat patches).

185 2.2 Carabid and spider sampling

186 Carabids and spiders were sampled over 6-day periods in the middle of each month
187 from April to October 2019 using pitfall traps. In each selected orchard, a 20×20 m²
188 plot was established for the sampling of these ground-dwelling arthropods. Three
189 parallel transects of 20 m length were set up along two opposite boundary lines and
190 the center of each plot. Each transect was also located at least 15 m from the edge of
191 the orchard. On each of the three transects, two pitfall traps were installed at a
192 distance of 20 m. The 6 pitfall trap samples per plot were then aggregated to create
193 total richness and abundance measures. The pitfall traps consisted of plastic cups with
194 an 8 cm diameter and 13.8 cm depth, and they were filled with 150 ml of saturated

195 salt solution (26.47%) and a drop of detergent to break the water surface tension. An
196 aluminum roof of 5×5 cm² was placed above each trap to protect it from rain. All
197 carabid and spider specimens were identified to species level based on the taxonomic
198 literature (Song & Zhu, 1997; Song, 1999; Zhu et al., 1999; Shi, 2013).

199 2.3 Environmental and management intensity

200 All orchards were managed conventionally. We recorded the number of mowing
201 events from April to October 2019 and measured the soil total nitrogen (STN) in
202 September 2019 as local management intensity indicators on each orchard (Table S1),
203 with the mowing representing the key disturbance factor, while STN strongly reflects
204 the amount of fertilizer applied (Herzog et al., 2006). For STN measurements, soil
205 samples were taken from the upper 20 cm of the soil at five randomly selected
206 locations near the four corners and the center of the sampled orchard using an auger
207 with 50 mm diameter. The five soil samples were then mixed to measure STN using
208 the Kjeldahl method (Carter & Gregorich, 2007).

209 2.4 Data analysis

210 We divided Carabids into two feeding trait groups: carnivorous and non-
211 carnivorous (combining chiefly granivorous, omnivorous or herbivorous) species,
212 while spiders were divided into the trait groups of web-building and ground-hunting
213 species according to their adult hunting strategy.

214 Generalized linear models based on a negative binomial distribution were used for

215 the analysis (Zuur et al., 2009), employing the package ‘MASS’ (Ripley et al., 2018).
216 Abundance and species richness of each functional group of carabids and spiders were
217 included as response variables, respectively, with landscape complexity (% semi-
218 natural habitat), management intensity (mowing frequency and STN) and the
219 interactions between landscape complexity and local management intensity (mowing
220 frequency or STN, respectively) included as explanatory variables. For spiders, the
221 abundance data combined adult and juvenile spiders, while the species richness data
222 was based on adults, only. We computed the variance inflation factors (VIF) between
223 explanatory variables using the ‘usdm’ package (Naimi et al., 2014) to detect possible
224 collinearity between explanatory variables, and to determine the stability of the
225 resulting models. With the interaction term responsible for high VIFs in the
226 generalized linear models, we centred each variable by subtracting the mean from all
227 observed values of that variable. No collinearity was found between standardized
228 explanatory variables ($VIF \leq 1.80$ in all cases, Table S2). The dredge function (R
229 package ‘MuMIn’, Barton, 2018) was then used to identify the final models based on
230 the corrected Akaike Information Criterion (AICc). We used the model average
231 function to estimate the model parameters if several models showed a $\Delta AICc < 2$
232 and calculated the relative importance of each variable for these models. If no model
233 had a $\Delta AICc < 2$, then the model with the lowest $\Delta AICc$ was selected. To
234 establish that homoscedasticity assumptions and deviance residuals met normality, we
235 used diagnostic plots validating model performance based on residual distributions
236 (Zuur et al., 2009). Moran’s I coefficient was used to test for spatial autocorrelation in

237 model residuals ('spdep' package, Bivand, 2018), and no spatial autocorrelation was
238 detected. All analysis was performed in R 3.6.0 (R Core Team, 2019).

239

240 3. Results

241 3.1. Species composition

242 Overall, the pitfall traps collected 660 carabid specimens representing 34 species
243 (Table S3). Among these, 17 carabid species were classified as non-carnivorous
244 (omnivores/herbivores, 260 individuals), while the remaining 17 species were
245 classified as carnivorous (400 individuals). The dominant species were *Harpalus*
246 *bungii* and *Oxycentrus jelineki*, accounting for 22.88% and 20.30% of the total
247 sampled specimens, respectively.

248 The spider samples contained 1868 individuals, including 1293 adult spiders (53
249 species) and 575 juvenile spiders (Table S4 & S5). Among juvenile spiders, 78
250 individuals were classified as web-building, while 497 individuals were classified as
251 ground-hunting spiders. Among adult spiders, 18 species were classified as web-
252 building (439 individuals), while the remaining 35 species were classified as ground-
253 hunting spiders (854 individuals). The dominant species were *Ummeliata feminea* and
254 *Piratula piratoides*, accounting for 21.81% and 19.57% of the total sampled
255 specimens, respectively.

256 3.2. Effects of landscape complexity, management intensity and their interaction on
257 the diversity of carabids and spiders

258 The abundance and species richness of overall and non-carnivorous carabids were
259 negatively correlated with STN (Table 1, Fig. 2), while the interactive effect of
260 landscape complexity and mowing significantly affected the abundance of
261 carnivorous carabids and carabids overall (Table 1). For landscapes with a low
262 proportion of semi-natural habitats, mowing positively affected overall and
263 carnivorous carabid abundance, whereas this trend was reversed where semi-natural
264 habitats covered medium or high levels of the landscape (Fig. 3). Carnivorous carabid
265 richness was not significantly correlated with any of the explanatory variables.

266 The abundance of ground-hunting spiders and spiders overall were positively
267 correlated with the proportion of semi-natural habitat in the landscape (Table 2, Fig.
268 4). Furthermore, the interaction between landscape complexity and STN showed
269 significant correlations with the abundance of web-building spiders and the species
270 richness of ground-hunting spiders (Table 2). Where the proportion of semi-natural
271 habitats reached low or medium levels, STN was positively correlated with the
272 abundance of web-building spiders and the species richness of ground-hunting
273 spiders, whereas this trend was reversed where semi-natural habitats covered large
274 proportions of the landscape (Fig. 5). Neither the diversity of web-building spiders
275 nor the species richness of spiders overall were significantly correlated with any
276 explanatory variable.

277 4. Discussion

278 4.1 Effects of local management and landscape complexity on total carabid richness
279 and on their functional groups

280 Our results showed that local nitrogen applications had strong negative effects on
281 abundance and species richness of non-carnivorous carabids and carabids overall, but
282 not on carnivorous carabids. Negative effects of the local management intensity on
283 carabids have also been reported in previous studies where impacts of fertilizer inputs
284 were correlated with intensive human management interventions (Flohre et al., 2011;
285 Li et al., 2018). In line with our observations for non-carnivorous species, the impact
286 of intensive nitrogen applications appears generally particularly pronounced for
287 species at low trophic levels (Haddad et al., 2000). This can be explained by high
288 nitrogen input leading to a reduction in plant species richness (Tilman, 1993; Maskell
289 et al., 2010; Dise et al., 2011) that reduces the diversity of food resources especially
290 for specialist herbivores (Haddad et al., 2000). On the other hand, high levels of soil
291 nitrogen leads to soil acidification and the mobilization of potentially toxic aluminum
292 ions that can contaminate the habitat of ground-dwelling arthropods, a trend again
293 particularly affecting non-carnivorous carabids since these commonly show low
294 dispersal abilities (Likens et al., 1996; Paoletti et al., 1996). Carnivorous carabids in
295 turn will only be indirectly affected by reduced plant diversity and can more easily
296 escape to less impacted habitats due to their generally greater mobility (Lövei &
297 Sunderland, 1996; Cole et al., 2002; Brose, 2003).

298 Falsifying our hypothesized trends, landscape complexity did not compensate for
299 the negative impact of a high local management intensity on carabids. We sampled
300 carabids between April and October when many generalist predators have cyclic
301 colonization patterns characterized by migrations between annual cropland and
302 perennially vegetated habitats (Öberg & Ekbom, 2006). These effects are particularly
303 pronounced for carnivorous carabids whose active hunting is facilitated by their high
304 mobility, potentially allowing them to disperse across large habitat patches (Lövei &
305 Sunderland, 1996; Cole et al., 2002). When the landscape complexity is at medium
306 and high levels, resulting in high proportions of semi-natural habitat, mowing-related
307 disturbances will likely result in carnivorous carabids' movement from orchards into
308 surrounding semi-natural habitats to obtain shelters and food (Rand & Louda, 2006).
309 Semi-natural habitats in this scenario chiefly provide temporary sink habitats. When
310 landscape complexity is low, chances of evasive migration are limited. Thus, mowing
311 will likely enhance mobility of carnivorous species and increase pitfall capture
312 efficiency. (Batáry et al., 2012; Birkhofer et al., 2015). Furthermore, physical
313 disturbances can facilitate the recolonization of disturbed habitats by highly mobile
314 species, potentially resulting in cyclic colonization patterns (Pedley et al., 2013). No
315 effect of mowing on non-carnivorous carabids is surprising. A possible explanation
316 might be related to specific feeding traits of the dominant non-carnivorous carabid
317 species. *H. bungii* that accounted for 58.08% of all non-carnivorous carabid
318 specimens, has a highly varied omnivorous diet, feeding on insect, seedlings, but also
319 on leaves of food crops like Chinese cabbage or turnips (Habu, 1973). Such highly

320 omnivorous species can adapt their diet according to available resources and for
321 example feed on seeds and leaves on the ground following the mowing.

322 4.2 Effects of local management and landscape complexity on total spider richness
323 and on their functional groups

324 We found strong effects of landscape complexity, reflected by the overall
325 proportion of semi-natural habitats, on the abundance of spiders overall as well as of
326 ground-hunting spiders, but not on web-building spiders. Spider hunting strategies are
327 strongly linked to their relative dispersal ability, since web-building spiders
328 commonly disperse widely using ballooning (Weyman et al., 2002; Bell et al., 2005),
329 while most ground-hunting spiders lack this ability. The large-scale dispersal
330 mechanism of ballooning may lead to dispersal patterns in web-building spiders that
331 are only visible at scales much larger than the 500 m radius used in our study. In
332 addition, the dispersal of this functional group is widely random, with dispersing
333 individuals unable to accurately orientate themselves towards favorable semi-natural
334 habitats (Schmidt et al., 2005). In contrast, the cursorial movement of ground-hunting
335 spiders is active and targeted, allowing them to potentially be widely distributed
336 across heterogeneous landscapes where, following local disturbances, they can easily
337 re-colonize habitat patches from more stable nearby patches of semi-natural habitat
338 (Schmidt et al., 2008; Feber et al., 2015). In turn, this allows ground-hunting spiders
339 to establish high abundances in regularly disturbed agricultural cropland near semi-
340 natural habitat, leaving them less strongly affected by local agricultural management

341 activities like the application of agro-chemicals or mowing (Horváth et al., 2015; Li
342 et al., 2018). A similar, positive effect of landscape complexity on ground-hunting,
343 but not web-building spiders, has been reported by Schmidt et al. (2005). They
344 suggested that a positive effect of high landscape complexity for these taxa related to
345 the higher availability of non-cropped habitat patches acting as refuges (Schmidt et
346 al., 2005; 2008).

347 In addition to direct effects of landscape complexity on ground-hunting spiders
348 and, as a result, spider overall, spiders were also substantially affected by interactive
349 factors between landscape complexity and local soil nitrogen. In contrast to our
350 hypothesis, landscape complexity could not compensate for the negative effects of
351 local management intensity on spiders. Instead, negative responses in the abundance
352 of web-building spiders and the species richness of ground-hunting spiders to soil
353 total nitrogen in complex landscapes can be linked to migrations from the affected
354 orchard into surrounding semi-natural habitats. However, where the landscape
355 complexity is lower, an increase in plant productivity and quality linked to higher soil
356 total nitrogen (Lukina et al., 2000) might exert positive impacts on spiders through
357 bottom-up cascade effects (Siemann, 1998; Brose, 2003; Theron et al., 2020) coupled
358 with a lack of opportunities for evasive movement into ‘better’ habitat patches
359 following disturbances. Increased plant growth with increasing nitrogen levels can
360 also increase the availability of microhabitats suitable for web construction, thus
361 enhancing the density of web-building spiders (Alderweireldt, 1994; Samu et al.,
362 1996). Such high plant productivity and associated diversification of microhabitats

363 might even attract spiders to orchard from surrounding semi-natural habitats.

364 4.3 Contrasting the responses of carabids and spiders to environmental variables

365 acting at different scales

366 As hypothesized, landscape complexity had a stronger effect on spiders than
367 carabids. This may be explained by their cursorial (walking) and ballooning behaviors
368 which increase their dispersal abilities compared to carabids (Simpson, 1995; Bell et
369 al., 2005; Feber et al., 2015). Different taxa therefore respond to their environment at
370 different scales, making it impossible to comprehensively evaluate impacts of
371 management or landscape structure on the effectiveness of biological pest control in
372 agricultural landscapes by studying exclusively a single taxon or studying effects on a
373 single spatial scale (Fischer et al., 2013). The spatial scale at which species are
374 influenced strongly depends on their activity range, which is determined by their
375 dispersal abilities which in turn is linked to their specific feeding guild and trophic
376 level, and to the associated food resource distribution in the landscape (Ribera et al.,
377 2001). Accordingly, carabid species with a generally lower dispersal ability are more
378 vulnerable to local factors like nitrogen applications and mowing, with that
379 vulnerability increasing for species at low trophic levels, whereas the generally more
380 mobile spiders appear to be able to cope well even under intensive management
381 where conditions allow for compensation effects through landscape complexity (Li et
382 al., 2018; Wamser et al., 2010; Varet et al., 2011). Therefore, comprehensive measures
383 to enhance predator populations need to comprise a variety of taxon-specific and

384 multiple-scale approaches.

385 Nonetheless, one overarching trend reflected also in our data is the positive impact
386 of landscape complexity that is linked to opportunities of recolonization and
387 population exchanges for predator species, therefore improving their chance to
388 recover even from severe localized disturbances (Tschardt et al., 2012). Predator
389 groups can therefore be greatly enhanced through appropriate restoration and creation
390 of semi-natural habitats as stepping stones in intensively managed agricultural
391 landscapes (Gruttke & Willecke, 2000), while carabids require to consider more finely
392 grained farming practices than spiders on a local scale. In combination, an
393 intermediate landscape complexity, a low to medium application of nitrogen fertilizers
394 and low mowing intensity at local scales appears as the best approach in enhancing
395 predator assemblages as a prerequisite for a more sustainable management of apple
396 orchards (Fig. S1 & Fig. S2).

397 5. Conclusion

398 Different carnivorous taxa respond to their environment on different scales, with
399 further complexity linked to interactive effects between different environmental
400 variables that lead to differentiations related to spatial configurations and management
401 intensities. Comprehensive measures to enhance ground-dwelling generalist predators
402 and therefore biological pest control in agricultural landscapes therefore requires a
403 diversity of targeted, taxon- and functional group-specific approaches targeting
404 relevant spatial scales. In this context, maintaining at least an intermediate complexity

405 of agricultural landscapes appears efficient to increase spider diversity especially
406 when combined with relatively low to medium levels of nitrogen fertilizer
407 applications in orchard, while low mowing frequencies especially in landscapes with a
408 low proportion of semi-natural habitats benefits ground beetles. Low nitrogen
409 fertilizer input helps carabids, while spiders appear to show a greater tolerance to
410 nitrogen applications than carabids.

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419 Appendix A. Supplementary data

420 Supplementary material related to this article can be found in the online version...

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667 Table 1 Model-averaged coefficients and relative variable importance for abundance
668 and species richness of carabids from different functional groups. Significance
669 numbers were printed in bold. Mo=Mowing (times), % SNH =% Semi-natural habitat,
670 STN= Soil total nitrogen (g. kg⁻¹).

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672 Table 2. Model-averaged coefficients and relative variable importance for abundance
673 and species richness of spiders from different functional groups. Significance
674 numbers were printed in bold. Mo=Mowing (times), % SNH =% Semi-natural habitat,
675 STN= Soil total nitrogen (g. kg⁻¹).

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689 Fig. 1. Distribution of sampling plots in the study region.

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691 Fig. 2. Effects of local nitrogen application measured as soil total nitrogen (STN) on
692 abundance of (a) carabids overall; (b) non-carnivorous carabids, and species richness
693 of (c) carabids overall and (d) non-carnivorous carabids. Lines with 95% confidence
694 intervals show predictions of negative binomial generalized linear models.

695

696 Fig. 3. Effects of the interaction between mowing and landscape complexity (% semi-
697 natural habitats: % SNH) on abundance of (a) carabids overall and (b) carnivorous
698 carabids. Lines with 95% confidence intervals show predictions of negative binomial
699 generalized linear models at 20% (low), 50% (medium) and 80% (high) quantiles of
700 the % SNH.

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702 Fig. 4. Effects of landscape complexity (% semi-natural habitats: % SNH) on
703 abundance of (a) spiders overall and (b) ground-hunting spiders. Lines with 95%
704 confidence intervals show predictions of negative binomial generalized linear models.

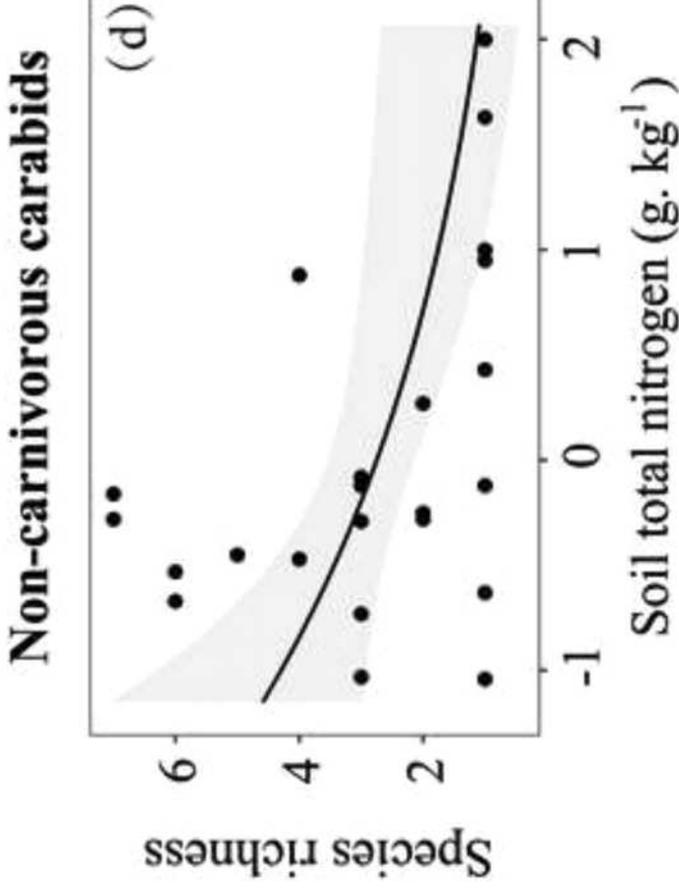
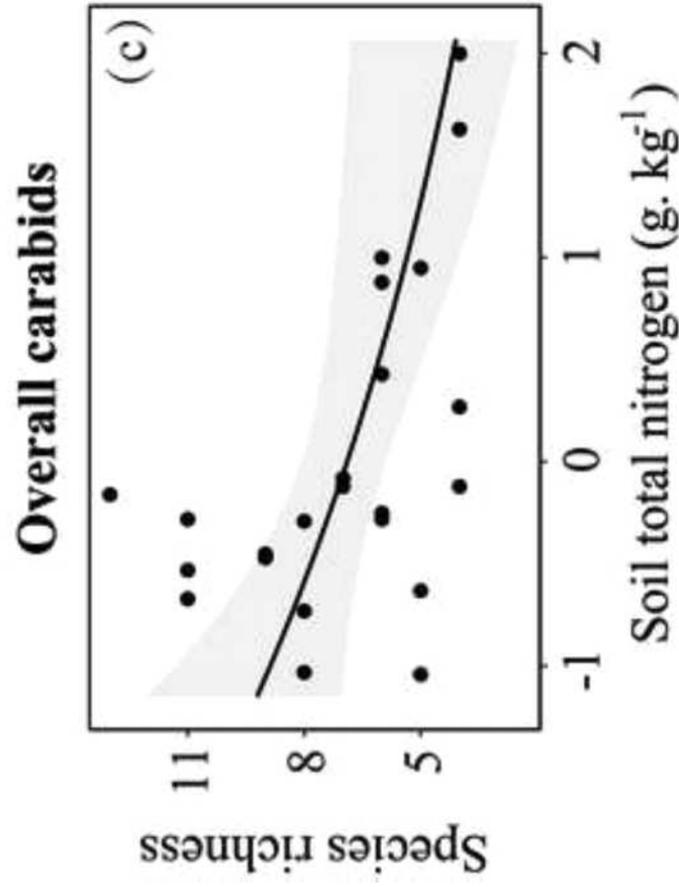
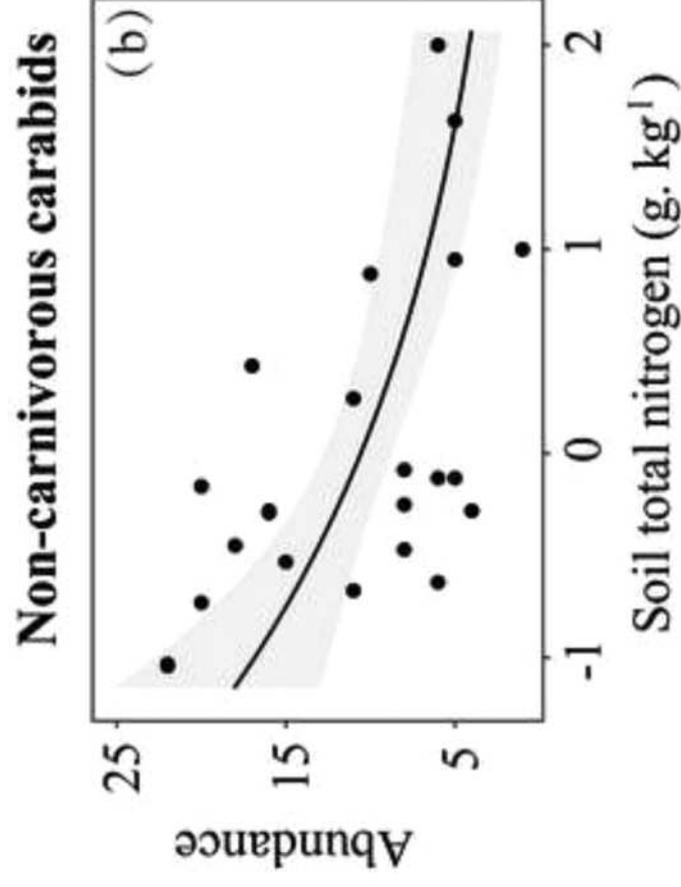
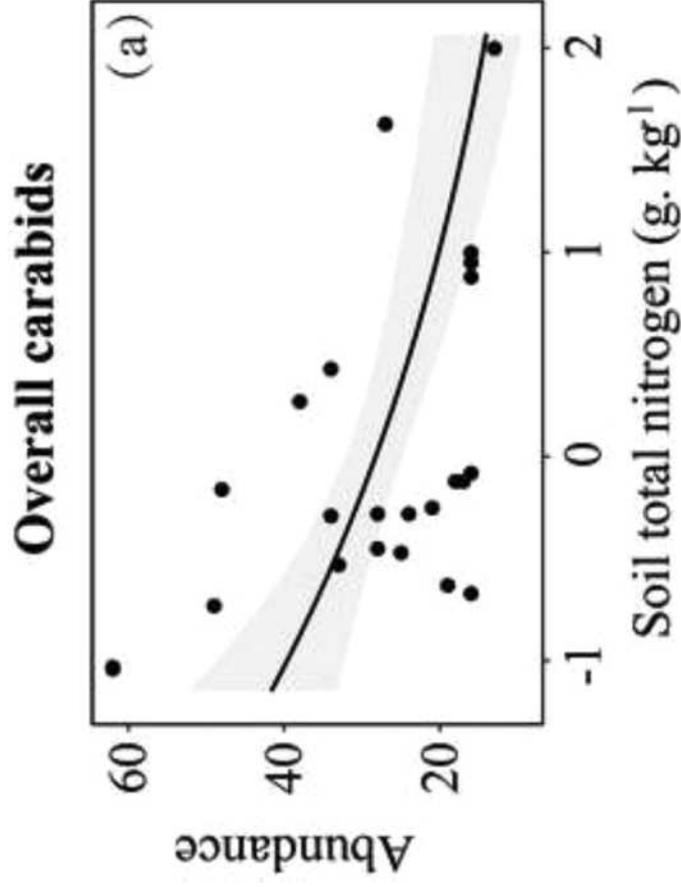
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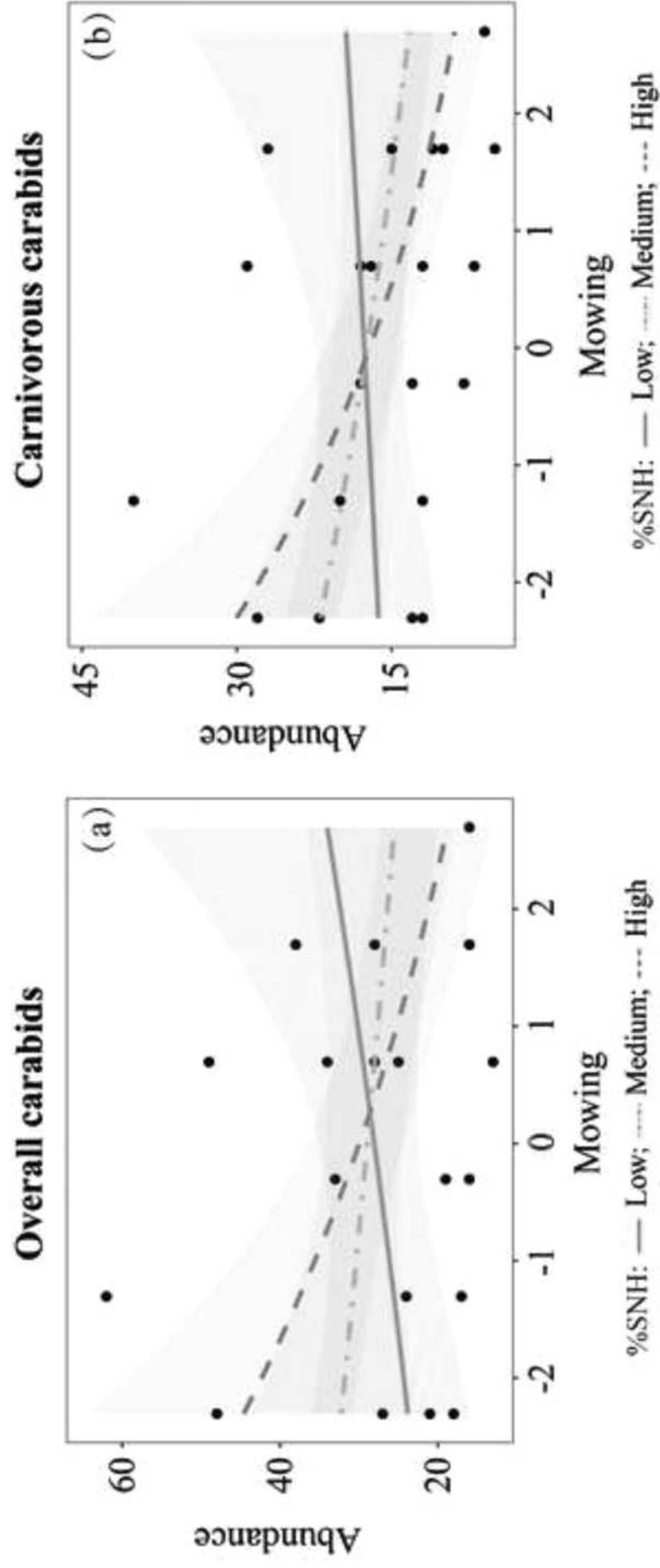
706 Fig. 5. Effects of the interaction between soil total nitrogen (STN) and landscape
707 complexity (% semi-natural habitats: % SNH) on abundance of (a) web-building
708 spiders, and species richness of (b) ground-hunting spiders. Lines with 95%
709 confidence intervals show predictions of negative binomial generalized linear models
710 at 20% (low), 50% (medium) and 80% (high) quantiles of the % SNH.

Table 2. Model-averaged coefficients and relative variable importance for abundance and species richness of spiders from different functional groups. Significance numbers were printed in bold. Mo=Mowing (times), % SNH =% Semi-natural habitat, STN= Soil total nitrogen (g. kg⁻¹).

Response variable	Explanatory variable	Estimate	Std. error	Adjusted SE	Z-value	Pr (> z)	Relative variable importance
Overall spider abundance	(Intercept)	4.2748	0.1206	0.1281	33.3690	<0.0001	
	Mo	0.0367	0.0807	0.0859	0.4280	0.6690	0.17
	% SNH	0.0381	0.0084	0.0089	4.2890	0.0002	1.00
	STN	0.0273	0.1542	0.1641	0.1660	0.8680	0.16
Overall spider richness	(Intercept)	2.4517	0.0861	0.0913	26.8570	<0.0001	
	Mo	0.0855	0.0556	0.0590	1.4490	0.1470	0.31
	% SNH	0.0057	0.0059	0.0063	0.9000	0.3680	0.15
	STN	0.1152	0.1068	0.1133	1.0170	0.3090	0.17
Web-building spider abundance	(Intercept)	3.0135	0.1456	0.1544	19.5200	<0.0001	
	% SNH	0.0130	0.0091	0.0097	1.3400	0.1803	0.65
	% SNH×STN	-0.0317	0.0124	0.0133	2.3920	0.0167	0.65
Web-building spider richness	(Intercept)	1.3396	0.1069	0.1132	11.8320	<0.0001	
	STN	-0.1539	0.1447	0.1535	1.0020	0.3160	0.32
Ground-hunting spider abundance	(Intercept)	3.8808	0.1687	0.1792	21.6560	<0.0001	
	Mo	0.0495	0.1129	0.1201	0.4120	0.6800	0.17
	% SNH	0.0518	0.0117	0.0125	4.1550	0.0003	1.00
	STN	0.0886	0.2150	0.2288	0.3870	0.6980	0.16
Ground-hunting spider richness	(Intercept)	2.0097	0.1134	0.1202	16.7180	<0.0001	
	Mo	0.0969	0.0751	0.0797	1.2160	0.2239	0.18
	% SNH	0.0098	0.0074	0.0078	1.2530	0.2104	0.31
	STN	0.1531	0.1396	0.1478	1.0360	0.3003	0.39
	% SNH×STN	-0.0192	0.0085	0.0091	2.1120	0.0347	0.18







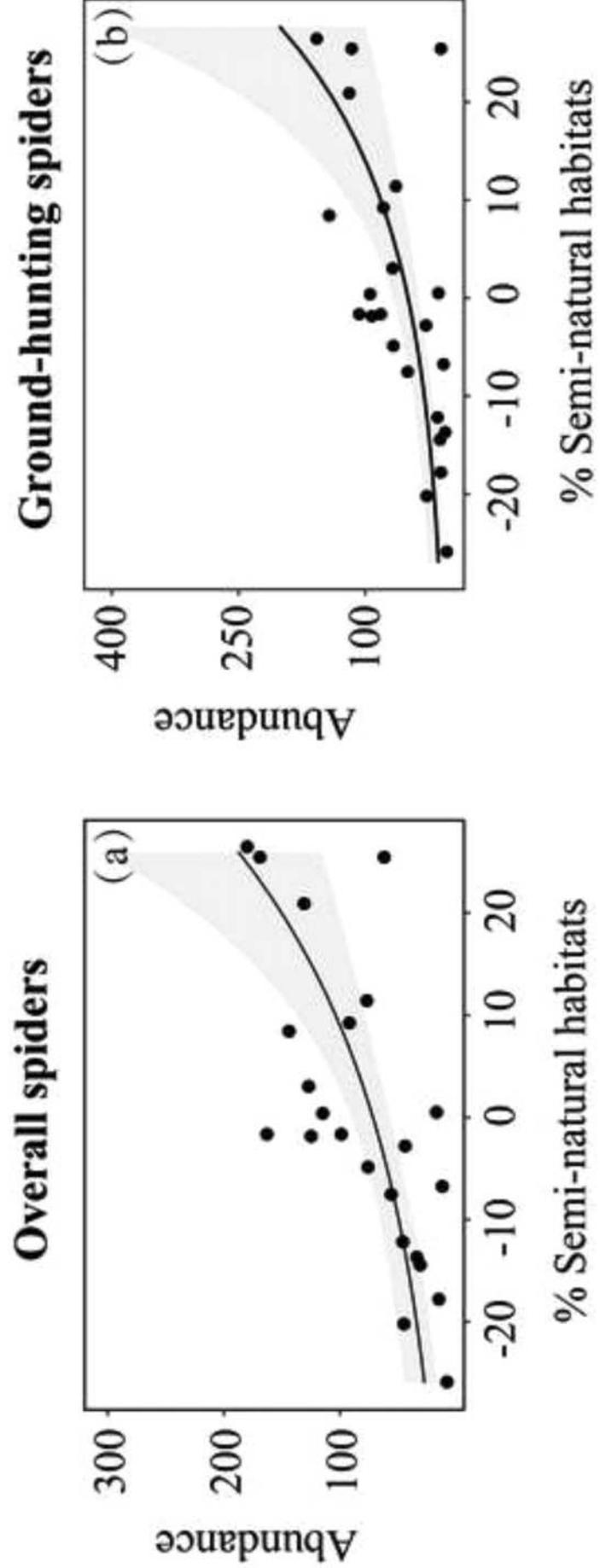
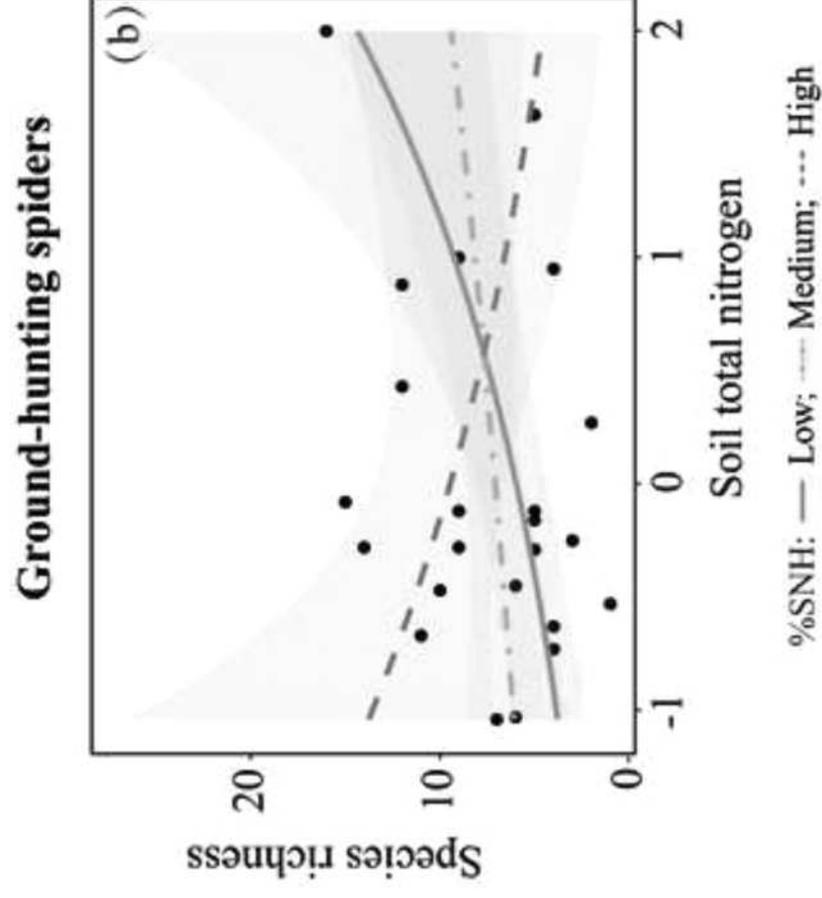
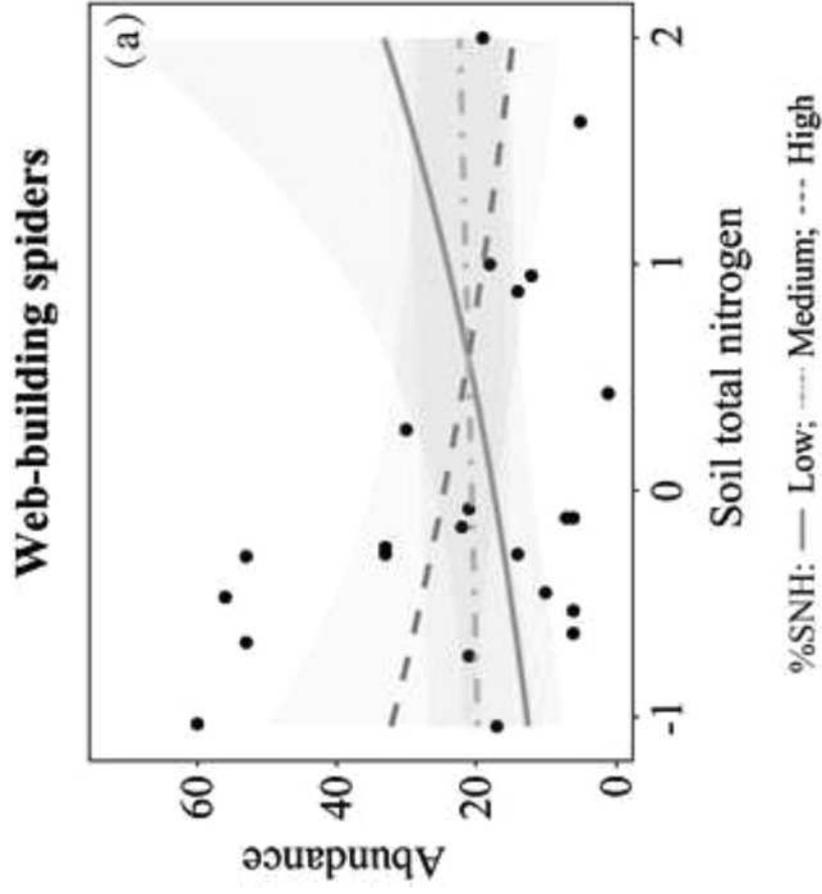


Figure 4



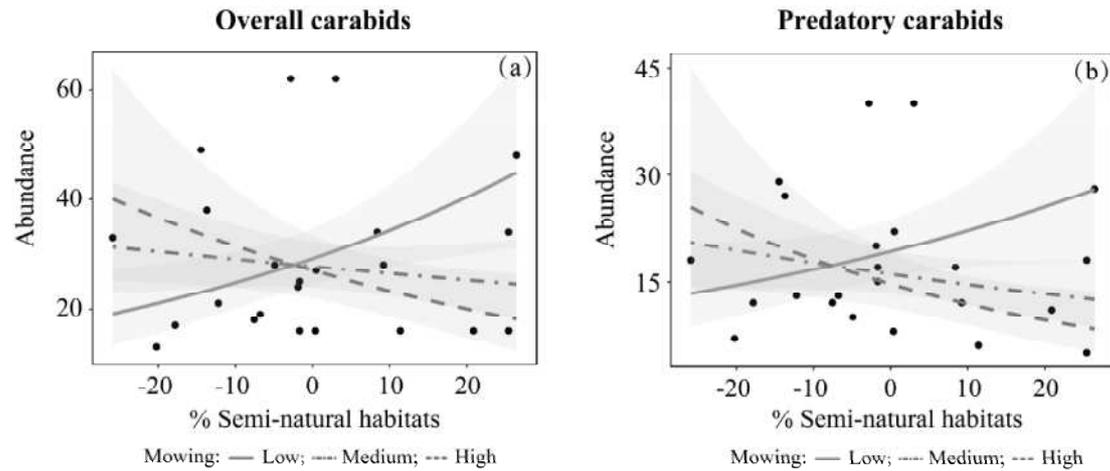


Fig. S1. Effects of the interaction between landscape complexity (% semi-natural habitats: % SNH) and mowing on abundance of (a) carabids overall; (b) carnivorous carabids. Lines with 95% confidence intervals show predictions of negative binomial generalized linear models at 20% (low), 50% (medium) and 80% (high) quantiles of the mowing.

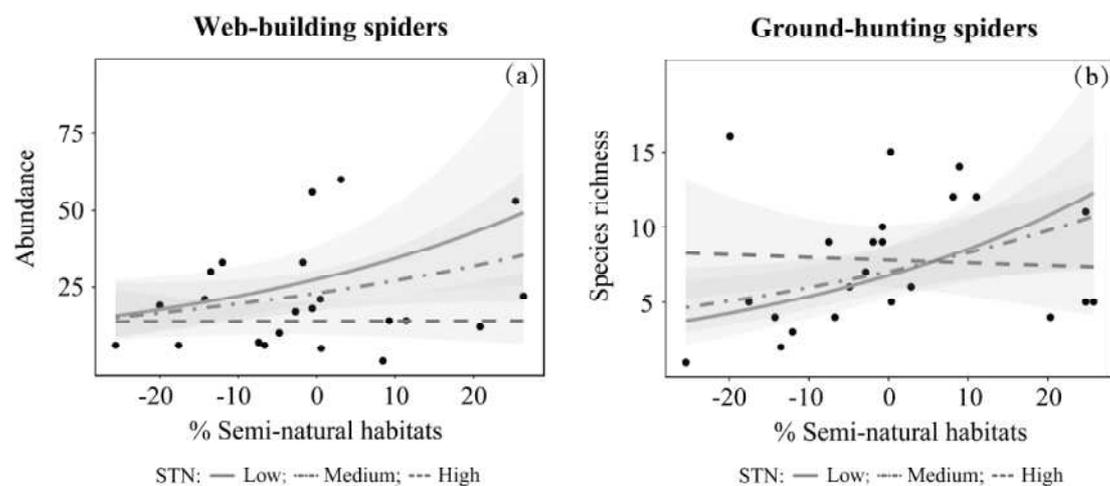


Fig. S2. Effects of the interaction between landscape complexity (% semi-natural habitats: % SNH) and soil total nitrogen (STN) on abundance of (a) web-building spiders, and species richness of (b) ground-hunting spiders. Lines with 95% confidence intervals show predictions of negative binomial generalized linear models at 20% (low), 50% (medium) and 80% (high) quantiles of the STN.

Table S1. Environmental and management intensity parameters. Mo=Mowing (times), SNH =%Semi-natural habitats, STN= Soil total nitrogen (g. kg⁻¹).

Habitat type	Mean±SD	Min	Max
Mo	3.3±1.6	1.0	6.0
%SNH	31.6±14.8	5.7	58.1
SNT	2.2±0.8	1.2	4.2

Table S2. Collinearity among explanatory variables based on variance inflation factors (VIF) in the generalized linear model. Mo=Mowing (times), SNH =%Semi-natural habitats, STN= Soil total nitrogen (g. kg⁻¹).

	Mo	SNH	STN	Mo×SNH	Mo×STN	SNH×STN
Overall carabid abundance	1.17	1.03	1.12	1.11	1.05	1.12
Overall carabid richness	1.21	1.08	1.05	1.16	1.04	1.11
Predatory carabid abundance	1.17	1.02	1.15	1.13	1.07	1.16
Predatory carabid richness	1.22	1.05	1.08	1.14	1.05	1.10
Non-predatory carabid abundance	1.20	1.07	1.12	1.12	1.03	1.12
Non-predatory carabid richness	1.25	1.18	1.04	1.22	1.06	1.23
Overall spider abundance	1.25	1.06	1.15	1.13	1.08	1.15
Overall spider richness	1.29	1.11	1.25	1.17	1.11	1.20
Web-building spider abundance	1.22	1.06	1.22	1.12	1.06	1.17
Web-building spider richness	1.12	1.04	1.80	1.08	1.03	1.18
Ground-hunting spider abundance	1.25	1.06	1.14	1.13	1.09	1.14
Ground-hunting spider richness	1.34	1.15	1.27	1.20	1.13	1.21

Table S3. Species list of carabids

Family	Species	Individuals	traits
Amara	<i>Amara (Amara) obscuripes</i> Bates, 1873	2	Non-predatory
Amara	<i>Amara (Curtonotus) gigantea</i> Motschulsky, 1844	11	Non-predatory
Amara	<i>Amara (Curtonotus) macronota</i> Solsky 1875	7	Non-predatory
Anisodactylus	<i>Anisodactylus signatus</i> Panzer, 1797	2	Non-predatory
Asaphidion	<i>Asaphidion semilucidum</i> Motschulsky, 1862	1	Non-predatory
Badister	<i>Badister marginellus</i> Bates, 1873	8	Predatory
Carabus	<i>Carabus (Cathaicus) brandti</i> Faldermann, 1835	3	Predatory
Carabus	<i>Carabus (Coptolabrus) smaragdinus</i> Fischer von Waldheim, 1823	5	Predatory
Chlaenius	<i>Chlaenius (Achlaenius) micans</i> Fabricius, 1792	17	Predatory
Chlaenius	<i>Chlaenius (Lissauchenius) posticalis</i> Motschulsky, 1854	10	Predatory
Diplocheila	<i>Diplocheila zeelandica</i> Redtenbacher, 1867	5	Predatory
Dolichus	<i>Dolichus halensis</i> Schaller, 1783	24	Predatory
Dyschirius	<i>Dyschirius (Dyschirius) amurensis</i> Fedorenko, 1991	18	Predatory
Harpalus	<i>Harpalus (Harpalus) bungii</i> Chaudoir, 1844	151	Non-predatory
Harpalus	<i>Harpalus (Harpalus) chalcensus</i> Bates, 1873	14	Non-predatory
Harpalus	<i>Harpalus (Harpalus) corporosus</i> Motschulsky, 1861	7	Non-predatory
Harpalus	<i>Harpalus (Harpalus) pallidipennis</i> Morawitz, 1862	36	Predatory
Harpalus	<i>Harpalus (Harpalus) tarsalis</i> Mannerheim, 1825	2	Non-predatory
Harpalus	<i>Harpalus (Pseudoophonus) griseus</i> Panzer, 1796	22	Non-predatory
Harpalus	<i>Harpalus (Pseudoophonus) pastor</i> Motschulsky, 1844	5	Non-predatory
Harpalus	<i>Harpalus (Pseudoophonus) roninus</i> Bates, 1873	3	Predatory
Harpalus	<i>Harpalus (Pseudoophonus) simplicidens</i> Schaubberger, 1929	5	Non-predatory
Harpalus	<i>Harpalus (Zangoharpalus) microdemas</i> Schaubberger, 1932	16	Non-predatory
Harpalus	<i>Harpalus (Zangoharpalus) tinctulus luteicornoides</i> Breit, 1913	3	Non-predatory
Nipponoharpalus	<i>Nipponoharpalus discrepans</i> Morawitz, 1862	48	Predatory
Oxycentrus	<i>Oxycentrus jelineki</i> Ito 2006	134	Predatory
Poecilus	<i>Poecilus (Poecilus) gebleri</i> Dejean, 1828	2	Non-predatory
Poecilus	<i>Poecilus (Poecilus) nitidicollis</i> Motschulsky, 1844	5	Non-predatory
Pterostichus	<i>Pterostichus (Rhagadus) microcephalus</i> Motschulsky, 1860	65	Predatory
Pterostichus	<i>Pterostichus (Rhagadus) solskyi</i> Chaudoir, 1878	4	Predatory
Scaritis	<i>Scaritis terricola</i> Bonelli, 1810	5	Non-predatory
Syntomus	<i>Syntomus pallipes</i> Dejean, 1825	9	Predatory
Tachyura	<i>Tachyura gradate</i> Bates 1873	9	Predatory
Trechoblemus	<i>Trechoblemus postilenatus</i> Bates, 1873	2	Predatory

Table S4. Species list of adult spiders.

Family	Species	Individuals	traits
Atypidae	<i>Atypus heterothecus</i> Zhang, 1985	2	web-building
Clubionidae	<i>Clubiona pseudogermanica</i> Schenkel, 1936	1	ground-hunting
Ctenidae	<i>Anahita fauna</i> Karsch, 1879	10	ground-hunting
Ctenizidae	<i>Latouchia pavlovi</i> Schenkel, 1953	3	web-building
Dictynidae	<i>Cicurina</i> sp.	4	web-building
Gnaphosidae	<i>Cladothela joannisi</i> Schenkel, 1963	2	ground-hunting
Gnaphosidae	<i>Drassyllus vinealis</i> Kulczyński, 1897	8	ground-hunting
Gnaphosidae	<i>Gnaphosa kansuensis</i> Schenkel, 1936	39	ground-hunting
Gnaphosidae	<i>Gnaphosa licenti</i> Schenkel, 1953	37	ground-hunting
Gnaphosidae	<i>Gnaphosa sinensis</i> Simon, 1880	13	ground-hunting
Gnaphosidae	<i>Micaria dives</i> Lucas, 1846	22	ground-hunting
Gnaphosidae	<i>Trachyzelotes jaxartensis</i> Kroneberg, 1875	1	ground-hunting
Gnaphosidae	<i>Zelotes davidi</i> Schenkel, 1963	14	ground-hunting
Gnaphosidae	<i>Zelotes exiguus</i> Müller & Schenkel, 1895	3	ground-hunting
Gnaphosidae	<i>Zelotes wuchangensis</i> Schenkel, 1963	3	ground-hunting
Gnaphosidae	<i>Zelotes zhaoi</i> Platnick & Song, 1986	5	ground-hunting
Gnaphosidae	<i>Zelotes</i> sp.	1	ground-hunting
Linyphiidae	<i>Agyneta nigra</i> Oi, 1960	36	web-building
Linyphiidae	<i>Ceratinella plancyi</i> Simon, 1880	2	web-building
Linyphiidae	<i>Erigone prominens</i> Bösenberg & Strand, 1906	58	web-building
Linyphiidae	<i>Ummeliata feminea</i> Bösenberg & Strand, 1906	282	web-building
Linyphiidae	<i>Walckenaeria antica</i> Wider, 1834	1	web-building
Lycosidae	<i>Alopecosa albostrigata</i> Grube, 1861	9	ground-hunting
Lycosidae	<i>Alopecosa licenti</i> Schenkel, 1953	9	ground-hunting
Lycosidae	<i>Pardosa astrigera</i> L. Koch, 1878	51	ground-hunting
Lycosidae	<i>Pardosa hedinii</i> Schenkel, 1936	160	ground-hunting
Lycosidae	<i>Pardosa multivaga</i> Simon, 1880	2	ground-hunting
Lycosidae	<i>Pardosa taczanowskii</i> Thorell, 1875	68	ground-hunting
Lycosidae	<i>Piratula piratoides</i> Bösenberg & Strand, 1906	253	ground-hunting
Lycosidae	<i>Trochosa terricola</i> Thorell, 1856	16	ground-hunting
Mimetidae	<i>Ermetus koreanus</i> Paik, 1967	1	web-building
Nemesiidae	<i>Sinopesa sinensis</i> Zhu & Mao, 1983	18	web-building
Nesticidae	<i>Nesticella mogera</i> Yaginuma, 1972	8	web-building
Oecobiidae	<i>Uroctea lesserti</i> Schenkel, 1936	1	web-building
Philodromidae	<i>Thanatus miniaceus</i> Simon, 1880	7	ground-hunting
Pholcidae	<i>Pholcus zichyi</i> Kulczyński, 1901	1	web-building
Phrurolithidae	<i>Orthobula crucifera</i> Bösenberg & Strand, 1906	1	ground-hunting
Phrurolithidae	<i>Phrurolithus sinicus</i> Zhu & Mei, 1982	24	ground-hunting

Phrurolithidae	<i>Phrurolithus</i> sp.	2	ground-hunting
Salticidae	<i>Asianellus festivus</i> C. L. Koch, 1834	16	ground-hunting
Salticidae	<i>Euophrys frontalis</i> Walckenaer, 1802	6	ground-hunting
Salticidae	<i>Evarcha albaria</i> L. Koch, 1878	3	ground-hunting
Salticidae	<i>Sitticus fasciger</i> Simon, 1880	2	ground-hunting
Salticidae	<i>Sitticus sinensis</i> Schenkel, 1963	2	ground-hunting
Tetragnathidae	<i>Pachygnatha tenera</i> Karsch, 1879	2	web-building
Theridiidae	<i>Enoplognatha gramineusa</i> Zhu, 1998	1	web-building
Theridiidae	<i>Paidiscura subpallens</i> Bösenberg & Strand, 1906	2	web-building
Theridiidae	<i>Stemmops nipponicus</i> Yaginuma, 1969	16	web-building
Theridiidae	<i>Theridion hotanense</i> Zhu & Zhou, 1993	1	web-building
Thomisidae	<i>Ozyptila</i> sp.	25	ground-hunting
Thomisidae	<i>Xysticus ephippiatus</i> Simon, 1880	26	ground-hunting
Thomisidae	<i>Xysticus pseudobliteus</i> Simon, 1880	5	ground-hunting
Titanoecidae	<i>Nurscia albofasciata</i> Strand, 1907	8	ground-hunting

Table S5. Species list of juvenile spiders.

Family	Individuals	traits
Agelenidae	8	web-building
Araneidae	1	web-building
Clubionidae	8	ground-hunting
Ctenidae	7	ground-hunting
Gnaphosidae	78	ground-hunting
Linyphiidae	12	web-building
Lycosidae	312	ground-hunting
Nemesiidae	52	web-building
Philodromidae	2	ground-hunting
Phrurolithidae	1	ground-hunting
Salticidae	41	ground-hunting
Theridiidae	5	web-building
Thomisidae	48	ground-hunting