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## Crop heterogeneity may not enhance biological control of rice pests in landscapes rich in semi-natural habitats

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1 **Title: Crop heterogeneity may not enhance biological control of rice pests in landscapes rich in**  
2 **semi-natural habitats**

3

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16

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18

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20

21

22 **Abstract**

23 Agricultural landscapes are undergoing profound changes worldwide, including crop homogenization  
24 and loss of semi-natural habitats, which may be detrimental to arthropod natural enemies of crop pests,  
25 although interactive effects between these drivers remain understudied. We assessed the relative  
26 contribution of crop diversity, mean field size and the proportion of semi-natural habitats on the  
27 abundance and diversity of rice pests and their arthropod natural enemies (predators versus parasitoids)  
28 across four spatial scales (100, 250, 500 and 1000 m) in 17 rice fields in Hainan Island, China. The  
29 overall low abundance of pests and natural enemies measured in rice fields could indicate high biological  
30 control level. Semi-natural habitats (including some recently restored ones) were largely represented in  
31 the studied landscapes (average proportion of 65%) and may be biodiversity reservoirs. Indeed,  
32 decreased mean field size and increased semi-natural habitat proportion promoted rice pests at the largest  
33 spatial scale only, possibly by enhancing their mobility and use of alternative resources. Predators'  
34 response was weak and indicated a positive influence of semi-natural habitats (or crop diversity in  
35 absence of semi-natural habitats) at small spatial scales. Parasitoid abundance was low, but tended to  
36 support the resource concentration hypothesis (reduced by crop diversity and increased by mean field  
37 size). Overall, crop heterogeneity favoured pests, but not natural enemies, its two components reduced  
38 mean field size and increased crop diversity were somewhat complementary and modulated by the  
39 proportion of semi-natural habitats but depended on spatial scale.

40

41 **Keywords:** agroecosystem; biocontrol; crop diversity; landscape complexity; landscape composition  
42 and configuration; mean field size; pest management.

43

44

## 45 **1 Introduction**

46 Agricultural intensification is a major cause of biodiversity loss worldwide due to landscape  
47 simplification and heavy reliance of inputs such as pesticides (Tscharntke et al. 2005; van Klink et al.  
48 2020; Wagner 2020). Insecticides are massively used because of pest problems causing heavy yield  
49 losses, despite their negative impacts on the environment, non-target species including pests' natural  
50 enemies, and human health (Stehle and Schulz, 2021). In addition, agricultural landscapes worldwide  
51 have been undergoing profound changes, including reduced crop heterogeneity through a decreased  
52 diversity in arable crops and increased mean field size, but also a decrease in semi-natural habitat areas  
53 (Tscharntke et al. 2005, 2021; Clough et al. 2020). These changes have caused significant declines in  
54 the abundance and diversity of natural enemies of crop pests, weakening biological pest control services  
55 (Rusch et al. 2016; Seibold et al. 2019).

56

57 To promote the conservation of natural enemies and biological pest control services, landscape  
58 complexity can be restored by (i) restoring semi-natural habitats (Tscharntke et al. 2005; Gurr et al. 2017;  
59 Yang et al. 2021, 2023); and (ii) increasing the heterogeneity of the crop mosaic itself through increased  
60 crop diversity and reduced mean field size (Sirami et al. 2019). While the importance of semi-natural  
61 habitats for natural enemy conservation has been relatively well studied, but comes at a cost of reducing  
62 agricultural land, the effect of manipulating crop heterogeneity across spatial scales to enhance natural  
63 enemies and biological pest control remains less understood (Jaworski et al. 2023). In particular, the  
64 interactive effects of increased crop heterogeneity and proportion of semi-natural habitats are difficult  
65 to predict and often non-linear (Jaworski et al. 2023).

66

67 Landscape heterogeneity has two key components: landscape composition, i.e., the diversity of  
68 different crop types and non-crop patches, and landscape configuration, i.e., the shape and spatial  
69 arrangement of these different patches (Fahrig et al. 2011). These two components influence pest  
70 suppression through trophic interactions between pests and their natural enemies, predators and  
71 parasitoids. Increasing crop diversity can provide multiple habitat and food resources and increase the  
72 temporal continuity of these resources to generalist predators including ladybugs (aphid specialists also

73 using floral resources), predatory bugs (feeding on aphids, planthoppers, floral resources, etc.), spiders  
74 (generalist prey hunters; Ratnadass et al. 2012; Jaworski et al. 2022). Conversely, crop diversity may be  
75 detrimental to parasitoids, which are specialists (attacking a restricted range of host species), and  
76 therefore tend to concentrate where host resources are important (i.e., in large monocultures; resource  
77 concentration hypothesis; Pareja et al. 2008; Gagic et al. 2012). Increased crop diversity may also cause  
78 locally higher pest densities, i.e. the crowding of host crop patches (Schneider et al. 2015). Therefore,  
79 increasing crop diversity may not necessarily result in improved biological pest control (Tscharrntke et  
80 al. 2016; Jaworski et al. 2022).

81

82 Insect pests and natural enemies often move back and forth between crop fields and surrounding  
83 semi-natural habitats (Schellhorn et al. 2014). Therefore, the proportion of semi-natural habitats in a  
84 landscape can significantly affect the abundance of crop pests and of natural enemies (Schneider et al.  
85 2016). Semi-natural habitats such as flower strips, forests and grasslands provide alternative food  
86 resources and shelter and create microclimate for natural enemies, which can promote pest control  
87 (González et al. 2015; Gurr et al. 2017; Yang et al. 2023). However, such semi-natural habitats may also  
88 be used by crop pests as alternative feeding, reproduction, and overwintering sites, promoting pest  
89 occurrence (Laterza et al. 2023; Thomine et al. 2023). Landscape configurational heterogeneity (e.g.,  
90 decreased mean field size) may also benefit natural enemies by increasing their capacity to colonize  
91 crop fields from semi-natural habitats, or by improving access to resource spatio-temporal continuity  
92 over shorter spatial scales (Schneider et al. 2016; Sirami et al. 2019; Jaworski et al. 2022). Therefore,  
93 benefits of increased crop diversity and semi-natural habitat proportion interactively affect natural  
94 enemy abundance, and crop diversity tends to promote natural enemies in landscapes with intermediate  
95 proportions of semi-natural habitats (between 20 and 50%; Jaworski et al. 2023).

96

97 Effects of landscape composition and configuration on pest control vary across spatial scales, due  
98 to the dispersal capacity and ecology of crop pests and their natural enemies (Chaplin-Kramer et al.  
99 2011; Haan et al. 2020). For instance, increased mean field size was often found to correlate to increased  
100 pest problems (Larsen and Noack, 2017; Tscharrntke et al. 2021), but not at very small spatial scales (e.g.,

101 from 0.1 to <0.5 ha; Jaworski et al. 2022; Rosenheim et al. 2022). In a multi-scale analysis, densities of  
102 generalist arthropod predators increased with increased crop diversity over small spatial scales (100-  
103 250 m radius, i.e., 3-20 ha), while densities of aphid specialist parasitoids increased with increased crop  
104 diversity over very large spatial scales (2,000-3,000 m radius, i.e., 1,000-3,000 ha; Redlich et al. 2018).  
105 In another study, ladybird abundances in cotton fields were not increased with increasing crop diversity  
106 at very small spatial scale (from 0.025 to 2 ha; Jaworski et al. 2022). Conversely, Thomine et al. (2023)  
107 found that lacewing abundance - but not ladybug abundance - increased with increasing edge density (a  
108 measure of landscape configuration), but not with increasing crop diversity in cotton fields at an  
109 intermediate spatial scale (500 m radius, i.e., 80 ha). The effects of semi-natural habitat on natural  
110 enemies also depend on the spatial scale considered (Jaworski et al. 2023). Therefore, understanding the  
111 interactive effects of crop diversity, mean field size, and semi-natural habitat proportion on natural  
112 enemy functional groups across spatial scales is key to restore biological pest control services.

113

114 Rice is one of the three main staple food crops (maize, wheat) worldwide, but more than 20% of  
115 rice yield is lost due to insect pests (Huang et al. 2014). The main insect rice pests are the specialist  
116 planthoppers (*Sogatella furcifera*; Hemiptera: Delphacidae) and generalist leafhoppers (*Nephotettix* spp.;  
117 Hemiptera: Cicadellidae), and the generalist true bugs (Hemiptera) and locusts (Orthoptera). Their  
118 natural enemies include generalist predators such as spiders and predatory bugs, which have a strong  
119 dispersal capacity, as well as specialist parasitoids, which tend to have a smaller dispersal capacity (Zhu  
120 et al. 2023). Rice agroecosystems are undergoing profound changes with reduced crop heterogeneity  
121 and the reduction of semi-natural habitat areas (GRiSP, 2013; Zou et al. 2020; Gong et al., 2024).  
122 Restoring semi-natural habitats around rice fields has been shown to conserve natural enemies and  
123 increased pest suppression (Ali et al. 2019; Gurr et al. 2016). However, to our knowledge, the interactive  
124 effects of semi-natural habitats and crop heterogeneity on pest-natural enemy interactions in rice  
125 cropping systems have not been investigated across spatial scales. This limits the potential to restore  
126 rice agrosystems for conservation biological control.

127

128 We investigated the interactive effects of crop heterogeneity (crop diversity and mean field size)

129 and semi-natural habitat proportion on biological pest control across four spatial scales (100, 250, 500,  
130 1,000 m radius circles) in 17 rice fields in the northeast part of Hainan Island, a biodiversity hotspot  
131 (Myers et al. 2000). We measured the abundance and diversity of arthropod rice pests and natural  
132 enemies. We asked: i) Do increased crop diversity and reduced mean field size interactively enhance  
133 pest suppression? ii) Is such effect of crop heterogeneity regulated by the proportion of semi-natural  
134 habitats? iii) Do these effects depend on the spatial scale considered?

135

136

## 137 **2 Materials and methods**

### 138 **2.1 Study area and experimental design**

139 The study took place in 2022 in a cultivated region of 80 × 40 km in Wenchang City, Hainan Island,  
140 southeast China (**Fig. S1**). This region has a tropical monsoon climate. The average temperature was  
141 23.83 °C and the total precipitation was 898.70 mm at Wenchang City during the early rice stage (January  
142 to May) in 2022. A diversity of arable crops is cultivated in Hainan Island, including rice, soybean and  
143 especially high-input industrial crops such as lychee, areca and mango. 17 rice fields were selected  
144 (**Fig. S1**) along orthogonal gradients of crop diversity and mean field size as much as possible across  
145 four spatial scales (100 m, 250 m, 500 m and 1000 m; **Figs. S1-S5**), and also encompassing a gradient  
146 of semi-natural habitat proportion. Rice field size ranged from 0.04 to 0.11 ha with an average of  
147 0.083 ha (**Table S1**). Rice fields were managed using standard commercial practices, with no pesticide  
148 application during the whole growing season.

149

### 150 **2.2 Crop heterogeneity and semi-natural habitat variables**

151 We used high-resolution (0.8 m) remote sensing data of Wenchang City in 2021. We delineated  
152 all fields and attributed each field to one of the following 19 crop types, including rice, soybean, sweet  
153 potato, cassava, areca, coconut, jackfruit, litchi, orange, pomegranate, longan, dragon fruit, pineapple,  
154 grapefruit, jujube, pepper, chili, wax gourd, and mixed vegetables (**Fig. 1, Fig. S6**). We also delineated  
155 non-crop patches, including semi-natural habitats, urbanized habitats, and waterbody (**Fig. S6**). Crop

156 diversity was calculated across four spatial scales (100, 250, 500, and 1000 m radii from the centre of  
157 each field) as Shannon Wiener Index; it ranged from 0.068 to 0.932 (**Table S1**). Mean field size was  
158 defined as the average size of all crop fields in each landscape at each spatial scale; it ranged from 0.2  
159 to 6.0 ha (**Table S1**). Semi-natural habitat proportion ranged from 0 to 85% of the area across landscapes  
160 and spatial scales, with an average of 52% (**Table S1**); it was composed mainly of forest (57% in  
161 average), grassland (41%), and a small portion of shrubland (<1%; **Table S2**). China has already  
162 recently implemented extensive plans to return farmland to forests to restore semi-natural habitats,  
163 explaining these relatively high values (Tong et al. 2023); it is therefore essential to test the efficiency  
164 of such measures in promoting biological pest control in this area. The largest selected spatial scale of  
165 1 km as well as smaller spatial scales of 100 and 250 m are commonly used to study the relationships  
166 between landscape structure and arthropod abundances in crop fields (Bosem et al. 2017; Sirami et al.  
167 2019).

168

### 169 **2.3 Sampling of arthropod pests and natural enemies**

170 Arthropod communities in each field were sampled during the dry season (March to May 2022),  
171 in three rounds coinciding with the rice jointing, filling, and mature stages to reflect the occurrence and  
172 diversity of insect pests and natural enemies. In each rice field, three sampling points were placed  
173 equitably distributed along a transect covering field length (at roughly  $\frac{1}{4}$ ,  $\frac{1}{2}$  and  $\frac{3}{4}$  of the distance of the  
174 field's long side) and at least 5 m apart from the field border to minimize edge effects (Rand et al. 2006).  
175 They were marked with sticks for later resampling. At each sampling point, a nylon mesh enclosure  
176 (0.35 m  $\times$  0.35 m  $\times$  0.93 m) was placed above rice plants and arthropods were collected using a Vortis  
177 insect suction sampler (Burkard Manufacturing Company Limited) for 1 min (Zhou et al. 2016; Dominik  
178 et al. 2018). Rice herbivore and natural enemy arthropod specimens preserved in 75% ethanol were  
179 classified and identified to the species level (or morphospecies where specimens could not be adequately  
180 identified to the species level) using a binocular microscope and referring to the taxonomic books of He  
181 and Pang (1986) and Institute of Zoology, Chinese Academy of Sciences (1987). Natural enemies were  
182 divided into two groups: predators and parasitoids. Samples from the three rounds from each sampling  
183 point were pooled to obtain three values of total abundance and three values of Shannon Index for the



184 three functional groups of rice herbivores, predators and parasitoids for each field.

185

## 186 **2.4 Statistical analysis**

187 All analyses were performed using R Core Team (2020) version 4.0.2. The responses of rice  
188 arthropods to crop heterogeneity variables - crop diversity (CD) and mean field size (MFS) - and semi-  
189 natural habitat proportion (SNH) were analysed using a linear mixed-effect model for each response  
190 variable at each spatial scale (R package ‘lme4’; Bates et al. 2015). The response variables were the  
191 abundance or Shannon Index of each functional group and were log-transformed (natural constant  $e$ )  
192 prior to analyses to meet normality assumptions (Pinheiro et al. 2016). The fixed effects were CD, MFS,  
193 SNH and their interactions CD:MFS, CD:SNH, MFS:SNH, and CD:MFS:SNH. The random effect was  
194 the sampling field. The “check\_collinearity” function from the ‘performance’ R package (Lüdecke et al.  
195 2015) was used to check for multicollinearity among the three landscape predictors (CD, MFS, and  
196 SNH). Low correlation was found (all VIFs < 2.14, **Table S3**). Spatial autocorrelation among the three  
197 landscape predictors was also assessed for each spatial scale (**Figs. S2-S5**). When predictors were  
198 correlated at a given spatial scale, they were tested in alternative models, as detailed in **Table S4**. All  
199 models were verified for the absence of excessive discreteness (**Table S5**).

200

201 An information-theoretic approach was used to quantify the strength of alternative competing  
202 models with  $\Delta AICc < 7$  (Burnham et al. 2011). Estimates with 95% confidence intervals (95% CIs) for  
203 each predictor were calculated through model averaging across the model sets., using the ‘MuMIn’ R  
204 package (Barton 2013). Using the package ‘glmm.hp’ (Lai et al. 2022), we further calculated the  
205 contribution of each fixed effect and random effect to the variance in each alternative model, for each  
206 response variable and scale. Because this function requires at least two fixed effects implemented in the  
207 model to compute predictor relative contributions, CD was added as fixed effect in addition to SNH for  
208 the 1000 m spatial scale.

209

## 210 **3 Results**

211 In total, we collected 1,292 arthropod specimens, for an average of  $8.4 \pm 0.7$  [95%CI: 6.8, 9.7]

212 specimens per sampling point per date. Out of these, 699 were neither rice pests nor natural enemies.  
213 Among the remaining 593 individuals, 358 were rice herbivorous pests (60%), 147 were predators (25%),  
214 and 88 were parasitoids (15%). Rice herbivorous pests were dominated by green leafhoppers  
215 (Cicadellidae, 150 individuals); whitebacked planthoppers were the second most abundant (*S. furcifera*,  
216 19 individuals). The most abundant predators were rove beetles (Staphylinidae, 41 individuals), dwarf  
217 spiders (Linyphiidae, 22 individuals), wolf spiders (Lycosidae, 17 individuals), long-jawed orb weavers  
218 (Tetragnathidae, 7 individuals), and the mirid bug *Cyrtorhinus lividipennis* (4 individuals). Finally, the  
219 most abundant families of parasitoids were Braconidae (19 individuals), Diapriidae (13 individuals) and  
220 Pteromalidae (16 individuals). The abundance and diversity of all rice arthropods (herbivores, predators,  
221 parasitoids and neutral insects) marginally significantly increased with the increase of semi-natural  
222 habitat proportion at large scales (500 m for abundance, 1000 m for diversity; **Fig. S8**).

223

224 The relative size effect (**Figs. 2-3**) and importance (**Figs. S9-S14**) of crop diversity, mean field size,  
225 semi-natural habitat proportion and their interactions varied across the four spatial scales for each  
226 functional group (herbivores, predators and parasitoids), and were overall quite similar between  
227 abundance and Shannon Index metrics. Overall, the best models (lowest AICc, **Figs. 2-3, Table S6**)  
228 coincided with the 1000 m scale, except for predator abundance (all scales equivalent), for parasitoid  
229 abundance (500 m yielded lowest AICc), and for parasitoid Shannon Index (all scales equivalent).

230

### 231 **3.1 Herbivores**

232 Increased mean field size had a negative effect on herbivore abundance at a 1000 m scale, but this  
233 was not true for smaller spatial scales (**Fig. 2A-D, Table S6**). Conversely, increased semi-natural habitat  
234 proportion had a marginally significant positive effect on herbivore abundance at a 1000 m scale, but  
235 this effect was lessened at a 500 m scale, and not different from zero at even smaller spatial scales. Mean  
236 field size explained 9% of variance in model 1, and semi-natural habitat proportion explained 8% of  
237 variance in model 2 at a 1000 m scale (**Fig. S9**). All other predictors had no significant effects on  
238 herbivore abundance, however the spatial scale considered.

239

240 Similar to herbivore abundance, decreased mean field size had a negative effect on herbivore  
241 Shannon Index, but only at a 1000 m scale (**Fig. 3A-D, Table S6**). It explained 11% of variance in model  
242 1 (**Fig. S11**). All other predictors had no significant effects on herbivore abundance, however the spatial  
243 scale considered.

244

### 245 **3.2 Predators**

246 Predator abundance was marginally significantly influenced by the interaction between mean field  
247 size and semi-natural habitat proportion (MFS:SNH) at a 100 m scale, but not at larger spatial scales  
248 (**Fig. 2E-H, Table S6**). This was because increasing mean field size in landscapes with low SNH tended  
249 to yield higher values of predator abundance, but not in landscapes with higher SNH (**Fig. 4A**). Predator  
250 abundance was marginally significantly influenced by the interaction between crop diversity and mean  
251 field size (CD:MFS) at a 250 m scale, but not at other spatial scales. This was because crop diversity  
252 increased predator abundance in landscapes with smaller mean field size only (**Fig. 6B**). However,  
253 MFS:SNH explained only 2% of variance in model 2 at a 100 m scale, and CD:MFS explained only 2%  
254 of variance at a 250 m scale (**Table S7; Fig. S10**). All other predictors had no significant effects on  
255 predator abundance, however the spatial scale considered. Exactly the same trends were found for  
256 predator Shannon Diversity Index, except that MFS:SNH had a stronger, significant effect and explained  
257 5% of variance in model 1 (**Table S7; Fig. S13**) at a 100 m scale, while CD:MFS explained 2% of  
258 variance at a 250 m scale (**Figs. 3E-H, S12**).

259

### 260 **3.3 Parasitoids**

261 Parasitoid abundance was significantly influenced by the interaction between crop diversity and  
262 semi-natural habitat proportion (CD:SNH) at a 500 m spatial scale but not at other spatial scales  
263 (**Figs. 2I-L, 4D**). This was because parasitoid abundance decreased with increasing crop diversity only  
264 in landscapes with low SNH. In addition, crop diversity had a marginally significant negative effect on

265 parasitoid abundance at a 500 m scale. Both effects were only true at a 500 m scale, where CD:SNH and  
266 CD explained 6% and 9% of total variance, respectively (**Fig. S11**). Finally, at a 250 m scale, mean field  
267 size had a marginally significant positive effect on parasitoid abundance, where it explained 6% of  
268 variance, but this was not true at other spatial scales.

269

270 Unlike predators, landscape predictors had a very different effect on parasitoid Shannon Diversity  
271 Index compared to parasitoid abundance (**Fig. 3I-L**). At a 250 m scale only, CD:SNH had a marginally  
272 significant effect on parasitoid diversity, explaining 1% of variance (**Fig. S14**). Specifically, parasitoid  
273 diversity increased with increased crop diversity in landscapes with low SNH only (**Fig. 4F**). At a 100 m  
274 scale only, MFS:SNH had a marginally significant effect on parasitoid diversity, explaining 3% of  
275 variance (**Fig. 4E**). This was because parasitoid diversity tended to decrease with increasing mean field  
276 size in landscapes with high, but not low SNH.

277

278

#### 279 **4 Discussion**

280 Our study explored whether increasing crop heterogeneity - by increasing crop diversity (CD) and  
281 reducing mean field size (MFS) - can enhance rice pest suppression depending on the semi-natural  
282 habitat proportion (SNH) and across spatial scales. Overall, the effects of these landscape predictors  
283 were weak and varied across spatial scales. Herbivores only responded at the largest spatial scale of  
284 1,000 m: increased MFS significantly reduced their abundance and diversity, while increased SNH  
285 marginally increased their abundance. Conversely, predators responded at the two smallest spatial scales,  
286 with marginally significant negative effects of the interactions between CD and MFS at 250 m, and  
287 between MFS and SNH at 100 m; these effects were similar for predator abundance and diversity.  
288 Finally, parasitoids responded at intermediate spatial scales, where crop diversity reduced parasitoid  
289 abundance only in landscapes with low SNH at 500 m, while increased MFS tended to increase  
290 parasitoid abundance at 250 m. However, they responded differently in terms of diversity, with a  
291 positive effect of increased MFS at 100 m and a positive effect of crop diversity at 250 m in landscapes  
292 with low to intermediate SNH only. Our results show that it is fundamental to take into account the

293 spatial scale considered to restore landscapes promoting efficient ecosystem services.

294

295 One key result is that the majority (54%) of arthropods caught in the suction samplings were neither  
296 rice herbivorous pests nor natural enemies of rice pests, and this despite the validity of our sampling  
297 method, calibrated on recommended durations for sampling efficiency (Zhou et al. 2016). Contrary to  
298 similar studies on landscape-scale crop diversity effects (e.g., Redlich et al. 2018), rice was not a  
299 massively dominant crop in this region (in average, 56% of the crop area, and 10% of the total area at a  
300 1,000 m scale), while semi-natural habitat proportion was relatively high (in average 65% at a 1,000 m  
301 scale), potentially explaining the low prevalence of rice pests and their natural enemies in rice field  
302 catches in our study. It would be interesting, in future studies, to compare abundances of herbivores  
303 (including crop pests) and their natural enemies in crop fields and in surrounding semi-natural habitats.  
304 Also, and despite Hainan Island is embedded into a biodiversity hotspot (Myers et al. 2000; Liu et al.  
305 2018), large portions of these semi-natural habitats in the study area have been restored only recently in  
306 this part of the island (Tong et al. 2023); therefore, it is possible that they have not yet reached their full  
307 potential in hosting arthropod biodiversity.

308

309 We found that herbivorous pests only responded to landscape predictors at the largest spatial scale  
310 (1 km), which was also found by Zhang et al. (2020). According to the resource concentration hypothesis,  
311 pests should be more abundant in large monocultures (Root 1973). However, at large scale (1000 m),  
312 we found that both increased crop configurational heterogeneity (reduced mean field size) and increased  
313 semi-natural habitat proportion promoted rice herbivores, which were mostly polyphagous pests  
314 (**Figs. 2D, 3D**). In our landscapes, smaller fields could have promoted rice pest dispersal across patches  
315 with favourable resources (Sirami et al. 2019), such as rice crops but also grasses - abundant in semi-  
316 natural habitats (**Tables S1-S2**) - used by leafhoppers and grasshoppers (McNeill et al. 2021). These  
317 polyphagous pests have a strong dispersal capacity, which might explain why they responded to  
318 landscape predictors at the largest spatial scale only.

319

320 The ecology of natural enemies (such as feeding habits and mobility) led to important differences

321 in their responses to crop diversity, as previously reported (Jaworski et al. 2022). In general, generalist  
322 predators have strong dispersal capacity (Symondson et al. 2002). In our study, most predators were  
323 generalists, such as spiders and rove beetles, and they had a weak response to landscape predictors, at  
324 small spatial scales only. This could indicate that they use multiple habitats over short temporal scales,  
325 moving back and forth between different habitat patches - including SNH - to find alternative resources  
326 and/or shelter (Schellhorn et al. 2014; Gurr et al. 2017; Gallé et al. 2018). Specifically, we found that  
327 increased mean field size tended to reduce predator diversity and abundance in rice fields in landscapes  
328 with high SNH only, at a 100 m scale. This could be because they would not spillover far from the edge  
329 into large fields in landscapes with high SNH availability if such habitats can provide suitable resources  
330 (Woodcock et al. 2016). Conversely, increased crop diversity tended to increase predator abundance and  
331 diversity in landscapes with low SNH only, at a 250 m scale. This could be because crop diversity could  
332 partially compensate for reduced semi-natural habitat availability in promoting generalist predators by  
333 providing access to and spatio-temporal continuity of alternative resources (Jaworski et al. 2023). Rice  
334 pest incidence is generally low in the region, and farmers do not need to use large amounts of insecticides  
335 (authors' pers. obs.). This could further explain the low prevalence of natural enemies in rice fields if  
336 host / prey resources are low compared to adjacent semi-natural habitats. A reliance of predators on  
337 semi-natural habitats over short time scales would also explain why landscape effects were apparent at  
338 small spatial scales only.

339

340 Parasitoids had a very distinct response from that of predators in our study. Parasitoid abundance  
341 responded to landscape predictors at intermediate spatial scales only. At 250 m, it was promoted by  
342 increased mean field size, which is in line with the resource concentration hypothesis, where rice  
343 specialist parasitoids could be attracted to large patches of host resources (Pareja et al. 2008; Gagic et  
344 al. 2012; Jaworski et al. 2022). At a 500 m spatial scale, parasitoid abundance was significantly increased  
345 by crop diversity in habitats with high SNH only, but was otherwise reduced by crop diversity. A negative  
346 effect of crop diversity on parasitoid abundance can also be explained by the resource concentration  
347 hypothesis, where increased crop diversity would dilute the concentration of host resources (Jaworski  
348 et al. 2022). However, a positive interactive effect of crop diversity and SNH may suggest that

349 parasitoids can become more abundant in very diverse landscapes, potentially through the use of  
350 alternative resources such as nectariferous flower resources (Gurr et al. 2017). Similar to predators, crop  
351 diversity effects may not be visible at a smaller spatial scale where crop diversity is too constrained by  
352 field size.

353

354 Parasitoid diversity had a different response to landscape predictors than parasitoid abundance,  
355 and only at the smallest spatial scales. It tended to be reduced by increased mean field size at a 100 m  
356 scale, and by increased crop diversity at a 250 m scale, but only in landscapes with high SNH. While  
357 increased mean field size would reduce the diversity of host resources, and thereby the diversity of  
358 specialist parasitoids, increased crop diversity would be expected to have an opposite effect, especially  
359 for parasitoids of polyphagous pests. In addition, if semi-natural habitats provide host resources, they  
360 should also boost parasitoid diversity, and therefore parasitoid diversity would be expected to be higher,  
361 not lower, in landscapes with high SNH. Our unexpected results may be an artifact of the small parasitoid  
362 sampling sizes, and of the diversity metrics calculated based on identification to the family level.

363

364 Increasing crop heterogeneity does not necessarily lead to improved pest control services,  
365 particularly in landscapes with high proportions of semi-natural habitats (reviewed in Jaworski et al.,  
366 2023): in our study, we found that it promoted pests (likely because they were polyphagous pests), but  
367 with no strong benefits for natural enemies. It would be interesting to replicate the study in landscapes  
368 widely dominated by rice crops, as well as in landscape with lower proportions of semi-natural habitat,  
369 and with more ancient semi-natural habitat, as these may all have significantly shaped the outcomes of  
370 our study. In the other hand, and likely best suited in regions with high crop diversity, it could be useful  
371 to consider agroecosystem restoration promoting biological pest control services across all crop types  
372 (not just on one focus crop) at the landscape level. The characteristics of the agroecosystems, including  
373 crop diversity and mean field size but also semi-natural habitat quantity, quality and connectivity all  
374 interact to shape arthropod abundances and diversity and ultimately ecosystem services. Although we  
375 still lack a fine understanding of - and testable ecological hypotheses on - the processes that determine  
376 the responses of specific arthropod functional groups to landscape predictors, it is necessary to take into

377 account the multiple dimensions of landscape complexity across spatial scales to inform landscape  
378 management promoting efficient biological pest control services.

379

380

381 **Supplementary information** The online version contains supplementary material available at xxx.

382

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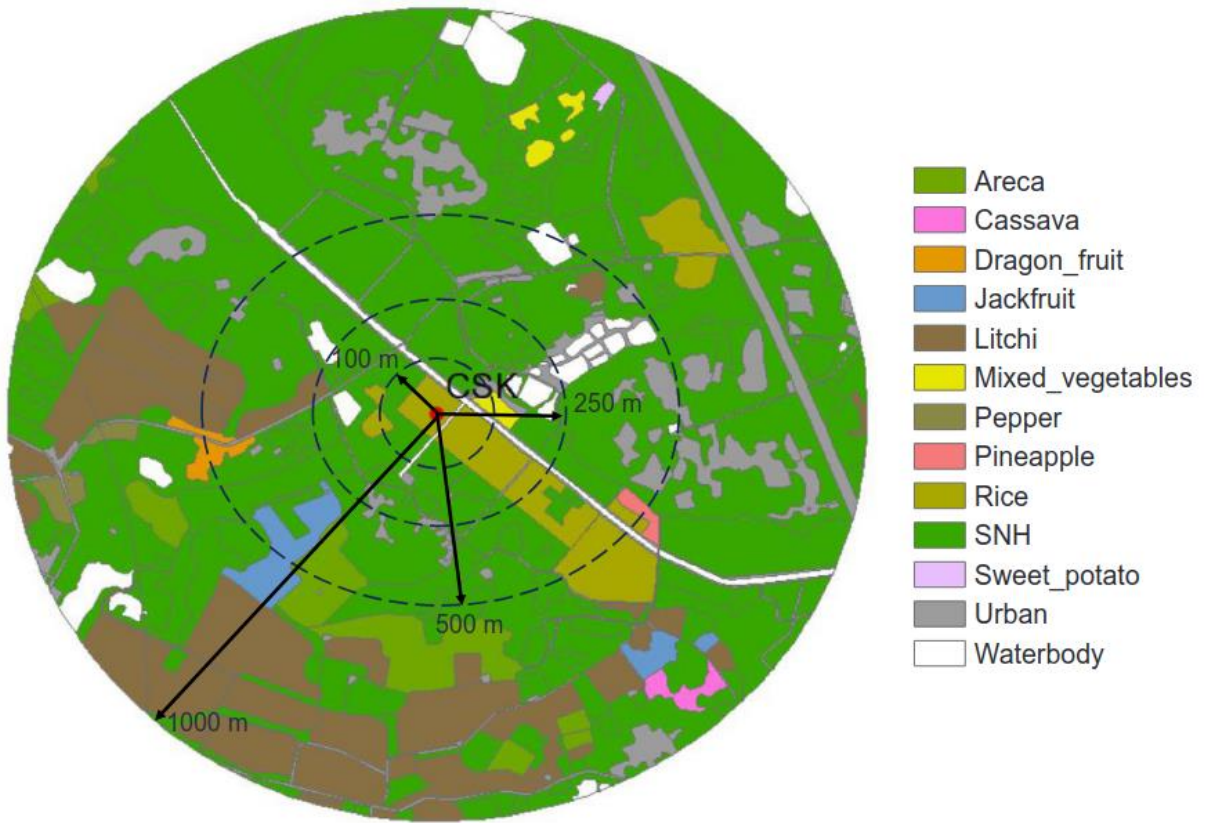
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## 555 FIGURES

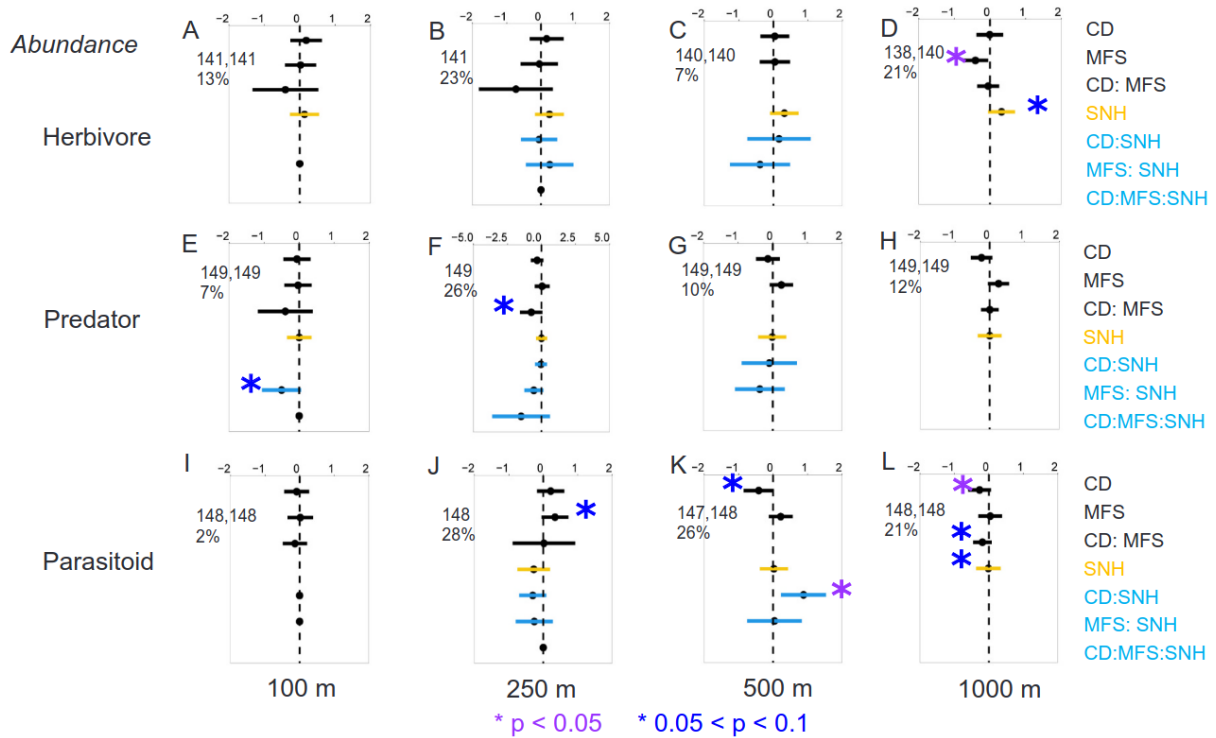
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558 **Fig. 1.** Example of a land cover map used to calculate landscape predictors within each landscape and each  
 559 spatial scale (shown with concentric circles). Maps of the 17 study sites are shown in Fig. S6.

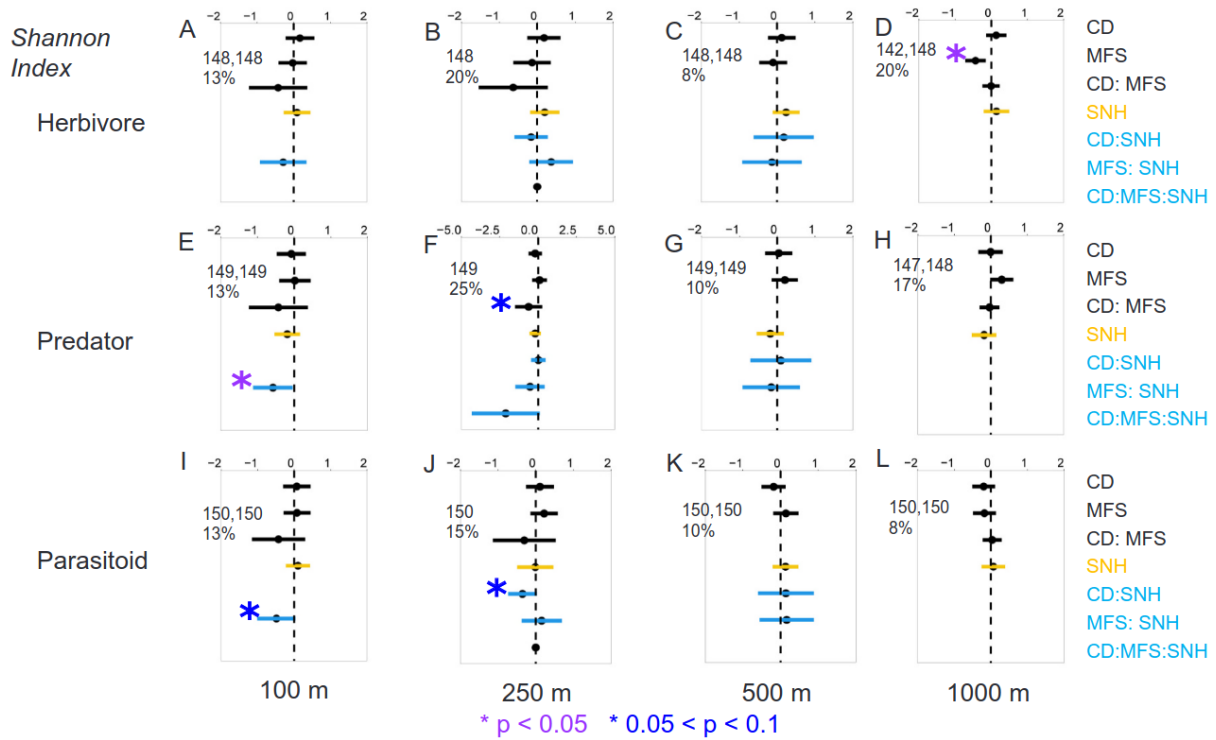
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562 **Fig. 2.** Relative effect estimates of crop diversity (CD), mean field size (MFS), and semi-natural habitat  
 563 proportion (SNH), as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH,  
 564 CD:MFS:SNH) on the total abundance of (A-D) rice herbivores, (E-H) predators, and (I-L) parasitoids across  
 565 four spatial scales: (A,E,I) 100 m, (B,F,J) 250 m, (C,G,K) 500 m, and (D,H,L) 1000 m. Predictor estimates  
 566 (plain dots) and 95 % CI (horizontal arrows) and names are shown in three colours: black = crop  
 567 heterogeneity (CD, MFS), gold = semi-natural habitat proportion (SNH), cyan = interactive effects between  
 568 crop heterogeneity and SNH (CD: MFS, CD: SNH, CD: MFS: SNH). AIC values of models 1 and 2 (Table  
 569 S4) are shown in each panel along with the total contribution of fixed effects (CD, MFS, SNH and their  
 570 interactions) to the variance.

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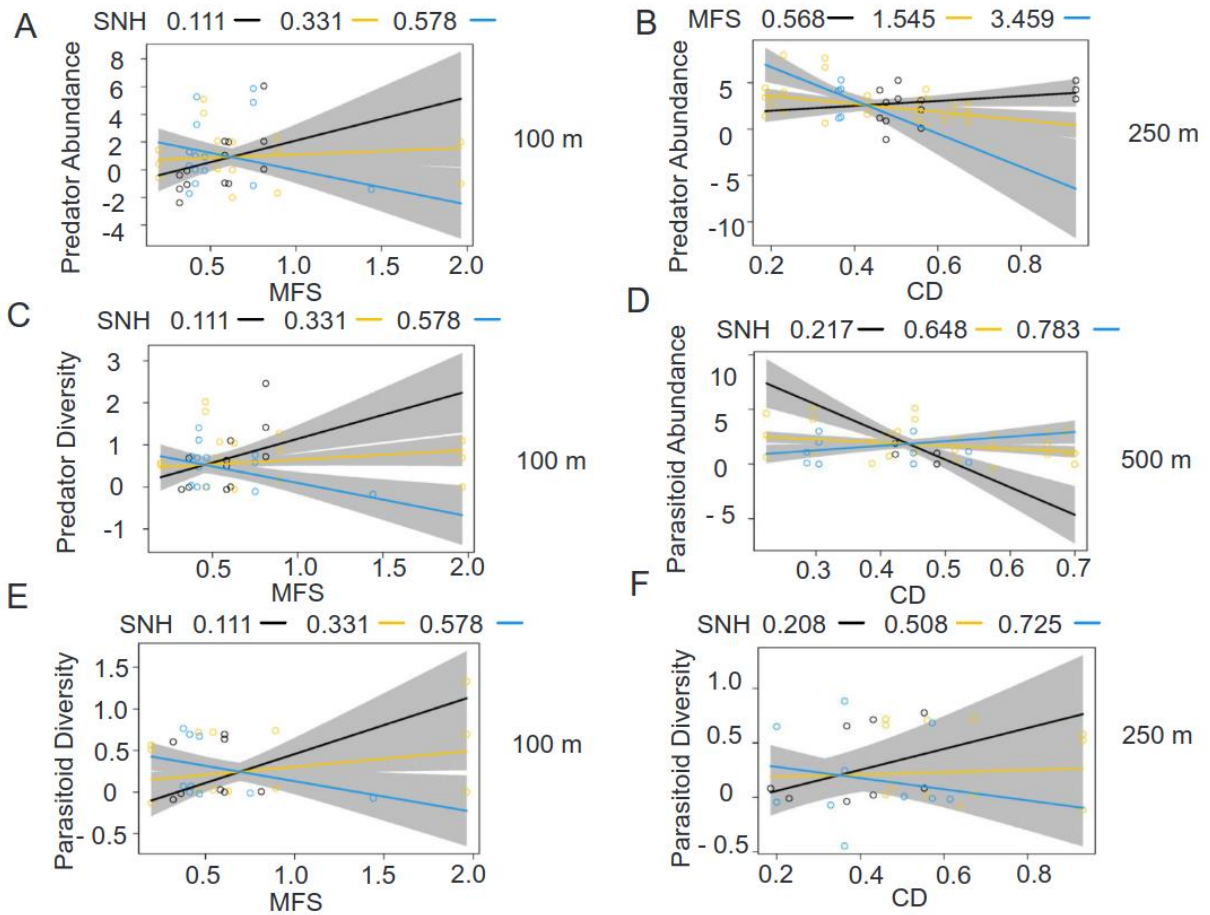


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573 **Fig. 3.** Relative effect estimates of crop diversity (CD), mean field size (MFS), and semi-natural habitat  
 574 proportion (SNH), as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH,  
 575 CD:MFS:SNH) on the Shannon Diversity Index of (A-D) rice herbivores, (E-H) predators, and (I-L)  
 576 parasitoids across four spatial scales: (A,E,I) 100 m, (B,F,J) 250 m, (C,G,K) 500 m, and (D,H,L) 1000 m.  
 577 Predictor estimates (plain dots) and 95 % CI (horizontal arrows) and names are shown in three colours: black  
 578 = crop heterogeneity (CD, MFS), gold = semi-natural habitat proportion (SNH), cyan = interactive effects  
 579 between crop heterogeneity and SNH (CD: MFS, CD: SNH, CD: MFS:SNH). AIC values of models 1 and  
 580 2 (Table S4) are shown in each panel along with the total contribution of fixed effects (CD, MFS, SNH and  
 581 their interactions) to the variance.

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584

585 **Fig. 4.** Interactive effects of (A) MFS and SNH and (B) CD and MFS on predator abundance, (C) MFS and  
 586 CD on predator Shannon Index, (D) CD and SNH on parasitoid abundance, and (E) MFS and SNH and (F)  
 587 CD and SNH on parasitoid Shannon Index. Corresponding spatial scales are shown to the right of each panel.  
 588 Only significant ( $p < 0.05$ ; D) or marginally significant ( $p < 0.1$ ; A-C,E-F) interactive effects are shown (Figs.  
 589 2–3). MFS: mean field size; SNH: semi-natural habitat proportion; CD: crop diversity.

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## Supporting Information for the article:

### Crop heterogeneity may not enhance biological control of rice pests in landscapes rich in semi-natural habitats

Quanfeng Yang, Coline C. Jaworski, Zhi Wen, Nicolas Desneux, Fang Ouyang, Xuhuan Dai, Lijuan Wang, Jiao Jia, & Hua Zheng\*

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## Supplementary tables

**Table S1. Crop heterogeneity gradients in 17 rice landscapes.**

#	Village	Acron ym	longitude	latitude	Size of focal rice field (ha)	% rice area at 1000 m scale	Crop diversity (Shannon-Wiener Index)				Mean field size (hectares)				Proportion of semi-natural habitats			
							100 m	250 m	500 m	1000 m	100 m	250 m	500 m	1000 m	100 m	250 m	500 m	1000 m
1	Nanxin Xia	NXX	110.839	19.719	0.0754	4.9	0.644	0.560	0.387	0.468	0.376	0.668	0.851	1.415	0.4811	0.5078	0.6657	0.7269
2	Baocai Nan	BCN	110.905	19.789	0.109	0.11	0.530	0.505	0.536	0.457	0.420	0.543	0.788	1.612	0.4676	0.6263	0.7520	0.7156
3	Feng Ming	FM	110.869	19.771	0.0609	0.50	0.357	0.615	0.451	0.419	1.441	1.609	1.131	1.812	0.5356	0.7040	0.7580	0.8149
4	Po Liu	PL	110.902	19.644	0.0672	5.9	0.293	0.362	0.223	0.213	1.964	5.988	7.440	1.147	0.3314	0.6199	0.6163	0.6543
5	Baodian Xi	BDX	110.872	19.682	0.0847	3.0	0.353	0.329	0.286	0.188	0.750	2.084	3.137	1.580	0.4899	0.7245	0.7945	0.8650
6	Tian Dui	TD	110.832	19.654	0.112	12.6	0.515	0.638	0.515	0.469	0.362	1.071	1.858	2.191	0.1335	0.4154	0.5738	0.7038
7	Song Shu	SS	110.788	19.656	0.0485	9.5	0.572	0.671	0.658	0.520	0.411	1.523	1.278	2.070	0.5780	0.5423	0.5689	0.6536
8	Xia Yuan	XY	110.752	19.639	0.0862	10.2	0.284	0.553	0.413	0.372	0.319	1.164	1.384	1.576	0.2166	0.3486	0.4708	0.5264
9	Dong Keng	DK	110.721	19.703	0.0535	4.8	0.283	0.200	0.305	0.352	0.466	1.545	0.962	1.657	0.6182	0.8279	0.7829	0.6684
10	Changshi Keng	CSK	110.692	19.756	0.0699	3.8	0.361	0.476	0.700	0.794	0.628	0.568	0.662	1.059	0.2578	0.6011	0.6494	0.5992
11	Mei De	MD	110.666	19.750	0.111	44.5	0.068	0.186	0.423	0.605	0.583	1.822	3.470	2.584	0.0000	0.0337	0.1126	0.3422
12	Shang Zhai	SZ	110.777	19.779	0.110	8.9	0.210	0.461	0.426	0.600	0.606	0.894	0.877	1.514	0.1114	0.4920	0.6477	0.6558
13	Long Dui	LD	110.740	19.838	0.0840	6.5	0.452	0.572	0.574	0.510	0.893	1.675	1.711	1.463	0.4309	0.7157	0.7117	0.6759
14	Shan Tou	ST	110.717	19.853	0.0776	2.1	0.616	0.932	0.687	0.407	0.196	0.673	0.891	1.315	0.4450	0.4880	0.6484	0.7296
15	Hou Po	HP	110.796	19.868	0.108	0.11	0.196	0.230	0.487	0.627	0.813	1.790	2.775	3.204	0.1305	0.2079	0.2166	0.3585
16	Paigang Zhong	PGZ	110.674	19.992	0.107	0.11	0.341	0.431	0.453	0.435	0.542	1.984	2.531	2.808	0.2560	0.3555	0.4636	0.5484
17	Hen Chan	HC	110.677	20.041	0.0445	0.05	0.360	0.368	0.295	0.148	0.459	3.459	4.257	2.810	0.2841	0.2160	0.5308	0.7080
Mean ± SE					0.083 ± 0.006	10.406 ± 2.990	0.379 ±0.038	0.476 ± 0.046	0.460 ±0.034	0.446 ± 0.040	0.661 ±0.107	1.709 ±0.320	2.118 ±0.423	1.872 ± 0.154	0.339 ±0.044	0.496 ±0.052	0.586 ±0.046	0.644 ±0.033

**Table S2. The proportion of forest, grassland and shrubland in semi-natural habitats around each rice field across the four spatial scales.**

#	Village	Acronym	Scale	Forest	Grassland	Shrubland
1	Nanxin Xia	NXX	100 m	0.4774	0.0012	0.0025
2	Baocai Nan	BCN		0.0931	0.3745	0
3	Feng Ming	FM		0.0365	0.4991	0
4	Po Liu	PL		0.0353	0.2961	0
5	Baodian Xi	BDX		0.1801	0.3098	0
6	Tian Dui	TD		0.1278	0.0057	0
7	Song Shu	SS		0.5130	0.0650	0
8	Xia Yuan	XY		0	0.2166	0
9	Dong Keng	DK		0.3670	0.2511	0
10	Changshi Keng	CSK		0	0.2578	0
11	Mei De	MD		0	0	0
12	Shang Zhai	SZ		0.1114	0	0
13	Long Dui	LD		0.1577	0.2733	0
14	Shan Tou	ST		0.0877	0.2982	0.0591
15	Hou Po	HP		0.0470	0.0835	0
16	Paigang Zhong	PGZ		0.1713	0.0847	0
17	Hen Chan	HC		0.2841	0	0
1	Nanxin Xia	NXX	250 m	0.4904	0.0102	0.0072
2	Baocai Nan	BCN		0.3374	0.2889	0
3	Feng Ming	FM		0.3776	0.3264	0
4	Po Liu	PL		0.2934	0.3266	0
5	Baodian Xi	BDX		0.4069	0.3177	0
6	Tian Dui	TD		0.3239	0.0915	0
7	Song Shu	SS		0.5124	0.0299	0
8	Xia Yuan	XY		0.0322	0.3073	0.0092
9	Dong Keng	DK		0.4166	0.4113	0
10	Changshi Keng	CSK		0.0281	0.5176	0.0555
11	Mei De	MD		0.0327	0.0011	0
12	Shang Zhai	SZ		0.3386	0.1533	0
13	Long Dui	LD		0.4586	0.2571	0
14	Shan Tou	ST		0.3530	0.0809	0.0541
15	Hou Po	HP		0.0199	0.1880	0
16	Paigang Zhong	PGZ		0.2630	0.0805	0.0120
17	Hen Chan	HC		0.0917	0.0344	0.0899
1	Nanxin Xia	NXX	500 m	0.4706	0.1819	0.0132
2	Baocai Nan	BCN		0.4558	0.2962	0
3	Feng Ming	FM		0.5149	0.2430	0
4	Po Liu	PL		0.4554	0.1599	0.0010
5	Baodian Xi	BDX		0.4166	0.3779	0
6	Tian Dui	TD		0.3621	0.2117	0
7	Song Shu	SS		0.5219	0.0337	0.0132
8	Xia Yuan	XY		0.1901	0.2698	0.0109
9	Dong Keng	DK		0.3828	0.4001	0
10	Changshi Keng	CSK		0.3092	0.3177	0.0225
11	Mei De	MD		0.0949	0.0177	0
12	Shang Zhai	SZ		0.4128	0.2329	0.0020

#	Village	Acronym	Scale	Forest	Grassland	Shrubland
13	Long Dui	LD		0.4852	0.2222	0.0043
14	Shan Tou	ST		0.4513	0.1648	0.0324
15	Hou Po	HP		0.1244	0.0902	0.0019
16	Paigang Zhong	PGZ		0.2579	0.1959	0.0098
17	Hen Chan	HC		0.1184	0.3548	0.0576
1	Nanxin Xia	NXX		0.4250	0.2888	0.0132
2	Baocai Nan	BCN		0.4787	0.2349	0.0020
3	Feng Ming	FM		0.4725	0.3370	0.0055
4	Po Liu	PL		0.3859	0.2628	0.0056
5	Baodian Xi	BDX		0.4856	0.3771	0.0023
6	Tian Dui	TD		0.3533	0.3457	0.0047
7	Song Shu	SS		0.4861	0.1530	0.0145
8	Xia Yuan	XY		0.3443	0.1572	0.0248
9	Dong Keng	DK	1000 m	0.3745	0.2939	0
10	Changshi Keng	CSK		0.2850	0.2723	0.0419
11	Mei De	MD		0.2393	0.1023	0.0005
12	Shang Zhai	SZ		0.3869	0.2546	0.0143
13	Long Dui	LD		0.4207	0.2409	0.0144
14	Shan Tou	ST		0.5493	0.1627	0.0176
15	Hou Po	HP		0.2403	0.1080	0.0102
16	Paigang Zhong	PGZ		0.2661	0.2595	0.0228
17	Hen Chan	HC		0.1900	0.4781	0.0399

**Table S3. Multicollinearity check between the three landscape predictors.**

Analyses of collinearity between the three landscape predictors studied for each spatial scale (CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion).

Spatial scale	Results	Variable	VIF	VIF 95% CI	Increased SE	Tolerance	Tolerance 95% CI
100 m	Low Correlation	CD	1.91	[1.43, 2.91]	1.38	0.52	[0.34, 0.70]
		MFS	1.25	[1.06, 2.06]	1.12	0.8	[0.49, 0.94]
		SNH	1.71	[1.31, 2.62]	1.31	0.58	[0.38, 0.76]
250 m	Low Correlation	CD	1.22	[1.05, 2.06]	1.11	0.82	[0.49, 0.96]
		MFS	1.17	[1.03, 2.13]	1.08	0.86	[0.47, 0.98]
		SNH	1.05	[1.00, 12.01]	1.02	0.95	[0.08, 1.00]
500 m	Low Correlation	CD	1.74	[1.33, 2.66]	1.32	0.58	[0.38, 0.75]
		MFS	1.91	[1.43, 2.92]	1.38	0.52	[0.34, 0.70]
		SNH	1.19	[1.03, 2.09]	1.09	0.84	[0.48, 0.97]
1000 m	Low Correlation	CD	1.53	[1.21, 2.36]	1.24	0.65	[0.42, 0.83]
		MFS	1.58	[1.24, 2.42]	1.26	0.63	[0.41, 0.81]
		SNH	2.13	[1.56, 3.26]	1.46	0.47	[0.31, 0.64]

**Table S4. Tested models for each spatial scale.**

Landscape predictors included in tested models for the total abundance or Shannon Index of herbivores, predators and parasitoids at each spatial scale. When landscape predictors were significantly correlated at a given spatial scale, they were included in alternative models 1 and 2. CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion.

Scale	Tested models
100 m	model 1 <- CD + MFS + CD:MFS model 2 <- SNH + MFS + SNH:MFS
250 m	model 1 <- CD*MFS*SNH
500 m	model 1 <- CD + SNH + CD:SNH model 2 <- MFS + SNH + MFS:SNH
1000 m	model 1 <- CD + MFS + CD:MFS model 2 <- SNH

**Table S5. Results of excessive discreteness tests at each spatial scale and for each response variable.**

Note: “model 1” and “model 2” are detailed in **Table S2**.

<b>Response variable</b>	<b>Spatial scale</b>	<b>Alternative model</b>	<b>Chisq</b>	<b>Ratio</b>	<b>rdf</b>	<b>P</b>
Herbivore abundance	100 m	model 1	20.07	0.45	45	1.00
		model 2	19.91	0.44	45	1.00
	250 m	model 1	19.39	0.47	41	1.00
		model 2	20.16	0.45	45	1.00
	500 m	model 1	20.26	0.45	45	1.00
		model 2	20.44	0.45	45	1.00
1000 m	model 1	20.78	0.44	47	1.00	
	model 2	20.78	0.44	47	1.00	
Parasitoid abundance	100 m	model 1	30.92	0.69	45	0.95
		model 2	30.98	0.69	45	0.94
	250 m	model 1	30.70	0.75	41	0.88
		model 2	34.02	0.76	45	0.88
	500 m	model 1	31.31	0.70	45	0.94
		model 2	32.37	0.72	45	0.92
1000 m	model 1	32.24	0.69	47	0.95	
	model 2	32.24	0.69	47	0.95	
Predator abundance	100 m	model 1	34.41	0.76	45	0.87
		model 2	35.32	0.78	45	0.85
	250 m	model 1	35.12	0.86	41	0.73
		model 2	34.24	0.76	45	0.88
	500 m	model 1	35.27	0.78	45	0.85
		model 2	36.04	0.80	45	0.83
1000 m	model 1	35.72	0.76	47	0.89	
	model 2	35.72	0.76	47	0.89	
Herbivore diversity	100 m	model 1	31.04	0.69	45	0.94
		model 2	30.65	0.68	45	0.95
	250 m	model 1	29.57	0.72	41	0.91
		model 2	31.14	0.69	45	0.94
	500 m	model 1	30.95	0.69	45	0.95
		model 2	33.48	0.74	45	0.90
1000 m	model 1	31.92	0.68	47	0.95	
	model 2	31.92	0.68	47	0.95	
Parasitoid diversity	100 m	model 1	37.84	0.84	45	0.77
		model 2	39.07	0.87	45	0.72
	250 m	model 1	35.62	0.87	41	0.71
		model 2	37.80	0.84	45	0.77
	500 m	model 1	37.78	0.84	45	0.77
		model 2	38.27	0.85	45	0.75
1000 m	model 1	39.13	0.83	47	0.79	
	model 2	39.13	0.83	47	0.79	
Predator diversity	100 m	model 1	32.58	0.72	45	0.92
		model 2	34.17	0.76	45	0.88
	250 m	model 1	32.90	0.80	41	0.81
		model 2	32.59	0.72	45	0.92
	500 m	model 1	32.98	0.73	45	0.91
		model 2	33.32	0.74	45	0.90
1000 m	model 1	34.22	0.73	47	0.92	
	model 2	34.22	0.73	47	0.92	

**Table S6. Estimates and model weights.**

$\Delta AICc < 7$  for the four spatial scales (100m, 250m, 500m, 1000m) for abundance of herbivore, predator and parasitoid, and Shannon diversity of herbivores, predators and parasitoids. Models are listed in descending order according to their  $\Delta AICc$ . Standardized parameter estimates, degrees of freedom (df), Akaike's Information Criterion with small-sample size adjustment (AICc),  $\Delta AICc$  and Akaike weights ( $w_i$ ) of each explanatory variable for the set of top models for each scale based on model averaging are reported. 'NA' parameters not selected in set of top models. The space indicated that the model doesn't select this landscape factor. CD: crop diversity; MFS: mean field size; SNH: semi-natural habitats. Estimates with shaded with gray color indicated that this landscape factor was selected in model 2 again. The AICc value with blue color corresponds to the minimum AICc in this model.

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight	
<b>Herbivore</b>															
<b>Abundance</b>															
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA	NA				3	-67.862	140.813	0	0.500	
		2	0	0.191	NA	NA				4	-68.097	142.233	1.420	0.246	
		3	0	NA	0.016	NA				4	-68.538	143.232	2.419	0.149	
		4	0	0.219	0.087	NA				5	-68.639	144.625	3.812	0.074	
		8	-0.128	0.027	-0.035		-0.406			6	-68.106	146.405	5.592	0.031	
	<b>model 2</b>	1	0		NA	NA			NA		3	-67.862	140.813	0	0.552
		3	0		NA	0.134			NA		4	-68.325	142.749	1.935	0.210
		2	0		0.016	NA			NA		4	-68.538	143.232	2.419	0.165
		4	0		0.008	0.134			NA		5	-68.983	145.332	4.519	0.058
		8	0.005		0.030	0.120			-0.087		6	-69.044	148.022	7.209	0.015
<b>250 m</b>	<b>model 1</b>	1	0	NA	NA	NA	NA	NA	NA	3	-67.862	140.813	0	0.255	
		5	0	NA	NA	0.261	NA	NA	NA	4	-67.689	141.307	0.493	0.199	
		2	0	0.218	NA	NA	NA	NA	NA	4	-67.956	141.912	1.099	0.147	

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		6	0	0.170	NA	0.225	NA	NA	NA	5	-68.017	143.038	2.225	0.084
		3	0	NA	-0.017	NA	NA	NA	NA	4	-68.537	143.231	2.418	0.076
		7	0	NA	-0.005	0.261	NA	NA	NA	5	-68.390	143.891	3.078	0.055
		4	0	0.247	0.076	NA	NA	NA	NA	5	-68.503	144.352	3.539	0.043
		12	-0.236	-0.011	-0.233	NA	-0.635	NA	NA	6	-67.504	145.328	4.515	0.027
		16	-0.309	-0.159	-0.339	0.303	-0.830	NA	NA	7	-67.094	145.392	4.579	0.026
		8	0	0.197	0.068	0.222	NA	NA	NA	6	-68.583	145.675	4.861	0.022
		22	0.012	0.169	NA	0.176	NA	-0.057	NA	6	-68.431	145.740	4.926	0.022
		39	0.012	NA	-0.082	0.206	NA	NA	0.255	6	-68.265	145.948	5.135	0.020
		40	0.010	0.172	-0.004	0.183	NA	NA	0.207	7	-68.534	148.162	7.349	0.006
		48	-0.291	-0.157	-0.359	0.279	-0.795	NA	0.105	8	-67.199	148.436	7.623	0.006
		32	-0.321	-0.165	-0.346	0.332	-0.844	0.032	NA	8	-67.519	148.552	7.738	0.005
		24	0.011	0.195	0.067	0.176	NA	-0.054	NA	7	-68.965	148.578	7.765	0.005
		56	0.022	0.170	-0.005	0.135	NA	-0.056	0.208	8	-68.889	151.282	10.469	0.001
		64	-0.302	-0.162	-0.364	0.305	-0.809	0.028	0.103	9	-67.583	151.855	11.041	0.001
		128	-0.318	-0.167	-0.363	0.365	-0.829	0.061	0.263	10	-66.154	155.507	14.694	0
<b>500 m</b>	<b>model 1</b>	3	0	NA		0.308		NA		4	-67.328	<a href="#">140.489</a>	0	0.404
		1	0	NA		NA		NA		3	-67.862	140.813	0.324	0.344
		4	0	0.049		0.309		NA		5	-68.024	142.998	2.510	0.115
		2	0	0.043		NA		NA		4	-68.519	143.190	2.701	0.105
		8	0.003	-0.004		0.338		0.163		6	-67.842	145.593	5.104	0.032
	<b>model 2</b>	3	0		NA	0.308		NA		4	-67.328	<a href="#">140.489</a>	0	0.397
		1	0		NA	NA		NA		3	-67.862	140.813	0.324	0.337
		4	0		0.066	0.328		NA		5	-67.955	142.948	2.460	0.116
		2	0		-0.033	NA		NA		4	-68.528	143.209	2.720	0.102

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		8	-0.115	0.149	0.475		-0.387			6	-67.474	144.688	4.199	0.049
<b>1000 m</b>	<b>model 1</b>	3	0	NA	-0.411	NA				4	-66.212	137.960	0	0.602
		4	0	-0.008	-0.411	NA				5	-67.012	140.543	2.583	0.165
		1	0	NA	NA	NA				3	-67.862	140.813	2.853	0.145
		8	0.001	-0.013	-0.400		-0.052			6	-67.928	143.154	5.194	0.045
		2	0	-0.013	NA	NA				4	-68.539	143.235	5.275	0.043
	<b>model 2</b>	2	0			0.324				4	-67.183	140.160	0	0.581
		1	0		NA					3	-67.862	140.813	0.653	0.419
<b>Predator</b>														
<b>Abundance</b>														
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA	NA				3	-72.260	149.226	0	0.572
		3	0	NA	-0.040	NA				4	-73.104	151.588	2.362	0.176
		2	0	-0.040	NA	NA				4	-73.104	151.589	2.363	0.176
		4	0	-0.059	-0.059	NA				5	-73.838	154.049	4.823	0.051
		8	-0.126	-0.246	-0.178		-0.397			6	-73.343	155.502	6.276	0.025
	<b>model 2</b>	1	0		NA	NA		NA		3	-72.260	149.226	0	0.544
		2	0		-0.040	NA		NA		4	-73.104	151.588	2.362	0.167
		3	0		NA	0.023		NA		4	-73.122	151.630	2.404	0.164
		8	0.029		0.085	-0.057		-0.503		6	-72.740	153.090	3.864	0.079
		4	0		-0.042	0.026		NA		5	-73.931	154.147	4.921	0.046
<b>250 m</b>	<b>model 1</b>	2	0	-0.242	NA	NA	NA	NA	NA	4	-72.042	149.181	0	0.184
		1	0	NA	NA	NA	NA	NA	NA	3	-72.260	149.226	0.045	0.180
		3	0	NA	0.182	NA	NA	NA	NA	4	-72.533	150.294	1.114	0.106
		48	-0.335	-0.483	-0.114	0.138	-0.832	NA	-0.540	8	-70.599	150.790	1.609	0.082
		12	-0.240	-0.464	-0.208	NA	-0.644	NA	NA	6	-71.449	151.047	1.866	0.072



		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		5	0	NA	NA	-0.091	NA	NA	NA	4	-72.987	151.323	2.142	0.063
		4	0	-0.202	0.105	NA	NA	NA	NA	5	-72.694	151.326	2.145	0.063
		39	-0.023	NA	0.320	0.018	NA	NA	-0.472	6	-72.168	151.555	2.374	0.056
		6	0	-0.233	NA	-0.041	NA	NA	NA	5	-72.899	151.691	2.510	0.052
		7	0	NA	0.178	-0.082	NA	NA	NA	5	-73.291	152.590	3.409	0.034
		40	-0.021	-0.139	0.257	0.037	NA	NA	-0.433	7	-72.673	153.660	4.479	0.020
		16	-0.244	-0.473	-0.215	0.019	-0.656	NA	NA	7	-72.326	153.989	4.808	0.017
		8	0	-0.191	0.107	-0.045	NA	NA	NA	6	-73.524	153.998	4.817	0.017
		64	-0.352	-0.490	-0.122	0.177	-0.852	0.043	-0.544	9	-71.333	154.140	4.960	0.015
		22	0.011	-0.234	NA	-0.087	NA	-0.053	NA	6	-73.492	154.376	5.195	0.014
		128	-0.278	-0.466	-0.125	-0.090	-0.761	-0.105	-1.257	10	-69.376	154.391	5.211	0.014
		56	-0.011	-0.141	0.255	-0.002	NA	-0.045	-0.432	8	-73.302	156.771	7.590	0.004
		24	0.010	-0.193	0.106	-0.087	NA	-0.049	NA	7	-74.097	156.889	7.708	0.004
		32	-0.251	-0.476	-0.219	0.036	-0.664	0.019	NA	8	-72.942	157.160	7.979	0.003
<b>500 m</b>	<b>model 1</b>	1	0	NA		NA		NA		3	-72.260	<a href="#">149.226</a>	0	0.520
		2	0	-0.142		NA		NA		4	-72.771	150.834	1.608	0.233
		3	0	NA		-0.050		NA		4	-73.089	151.555	2.329	0.162
		4	0	-0.143		-0.052		NA		5	-73.587	153.306	4.080	0.068
		8	-0.002	-0.111		-0.071		-0.100		6	-73.574	155.984	6.758	0.018
	<b>model 2</b>	1	0		NA	NA		NA		3	-72.260	<a href="#">149.226</a>	0	0.370
		2	0		0.238	NA		NA		4	-72.078	149.262	0.036	0.363
		3	0		NA	-0.050		NA		4	-73.089	151.555	2.329	0.115
		4	0		0.245	0.025		NA		5	-72.928	151.822	2.596	0.101
		8	-0.111		0.326	0.167		-0.374		6	-72.489	153.205	3.979	0.051
<b>1000 m</b>	<b>model 1</b>	4	0	-0.238	0.257		NA			5	-71.664	<a href="#">148.637</a>	0	0.279

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		3	0	NA	0.254	NA				4	-71.919	148.903	0.266	0.244
		1	0	NA	NA	NA				3	-72.260	149.226	0.589	0.208
		2	0	-0.235	NA	NA				4	-72.105	149.323	0.687	0.198
		8	0	-0.238	0.256	0.002				6	-72.839	151.398	2.761	0.070
	<b>model 2</b>	1	0		NA					3	-72.260	149.226	0	0.771
		2	0		0					4	-73.132	151.652	2.426	0.229
<b>Parasitoid</b>														
<b>Abundance</b>														
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA	NA				3	-71.737	148.268	0	0.568
		2	0	-0.086	NA	NA				4	-72.447	150.425	2.157	0.193
		3	0	NA	0.023	NA				4	-72.557	150.674	2.407	0.171
		4	0	-0.088	-0.005	NA				5	-73.194	153.009	4.741	0.053
		8	-0.054	-0.168	-0.056	-0.171				6	-73.075	155.555	7.287	0.015
	<b>model 2</b>	1	0		NA	NA		NA		3	-71.737	148.268	0	0.538
		3	0		NA	-0.134		NA		4	-72.275	150.035	1.767	0.222
		2	0		0.023	NA		NA		4	-72.557	150.674	2.407	0.162
		4	0		0.031	-0.136		NA		5	-73.072	152.584	4.316	0.062
		8	0.001		0.037	-0.139		-0.022		6	-73.312	155.340	7.072	0.016
<b>250 m</b>	<b>model 1</b>	3	0	NA	0.278	NA	NA	NA	NA	4	-71.224	147.655	0	0.171
		1	0	NA	NA	NA	NA	NA	NA	3	-71.737	148.268	0.613	0.126
		4	0	0.201	0.354	NA	NA	NA	NA	5	-71.390	148.684	1.030	0.102
		24	0.063	0.241	0.355	-0.474	NA	-0.302	NA	7	-70.938	148.957	1.303	0.089
		7	0	NA	0.269	-0.166	NA	NA	NA	5	-71.600	149.007	1.353	0.087
		8	0	0.249	0.362	-0.215	NA	NA	NA	6	-71.413	149.230	1.575	0.078

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		5	0	NA	NA	-0.179	NA	NA	NA	4	-72.034	149.490	1.836	0.068
		56	0.049	0.274	0.451	-0.420	NA	-0.299	-0.277	8	-70.791	150.342	2.688	0.045
		2	0	0.066	NA	NA	NA	NA	NA	4	-72.495	150.534	2.879	0.040
		40	-0.014	0.283	0.459	-0.161	NA	NA	-0.282	7	-71.256	150.665	3.010	0.038
		39	-0.010	NA	0.331	-0.123	NA	NA	-0.203	6	-71.700	151.083	3.429	0.031
		12	-0.040	0.157	0.301	NA	-0.108	NA	NA	6	-71.284	151.367	3.712	0.027
		6	0	0.109	NA	-0.203	NA	NA	NA	5	-72.656	151.626	3.971	0.023
		22	0.065	0.103	NA	-0.473	NA	-0.313	NA	6	-72.243	151.861	4.206	0.021
		32	0.133	0.317	0.442	-0.507	0.178	-0.320	NA	8	-70.799	151.872	4.218	0.021
		16	0.012	0.263	0.377	-0.218	0.032	NA	NA	7	-71.329	152.182	4.527	0.018
		64	0.083	0.309	0.489	-0.438	0.086	-0.308	-0.266	9	-70.703	153.712	6.058	0.008
		48	-0.037	0.257	0.431	-0.154	-0.062	NA	-0.290	8	-71.146	153.817	6.163	0.008
		128	0.063	0.303	0.489	-0.363	0.061	-0.267	-0.068	10	-69.550	157.223	9.568	0.001
<b>500 m</b>	<b>model 1</b>	8	0.017	-0.495		0.103		0.885		6	-69.704	<a href="#">146.618</a>	0	0.512
		1	0	NA		NA		NA		3	-71.737	148.268	1.650	0.224
		2	0	-0.206		NA		NA		4	-71.854	149.081	2.464	0.149
		3	0	NA		-0.054		NA		4	-72.519	150.589	3.972	0.070
		4	0	-0.208		-0.058		NA		5	-72.641	151.534	4.916	0.044
	<b>model 2</b>	1	0		NA	NA		NA		3	-71.737	<a href="#">148.268</a>	0	0.429
		2	0		0.222	NA		NA		4	-71.739	<a href="#">148.821</a>	0.553	0.325
		3	0		NA	-0.054		NA		4	-72.519	150.590	2.322	0.134
		4	0		0.226	0.015		NA		5	-72.537	151.398	3.130	0.090
		8	0.012		0.217	-0.001		0.041		6	-72.561	154.145	5.878	0.023

			(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
<b>1000 m</b>	<b>model 1</b>	2	0	-0.266	NA		NA				4	-71.344	147.926	0	0.383
		1	0	NA	NA		NA				3	-71.737	148.268	0.342	0.322
		4	0	-0.266	0.030		NA				5	-72.204	150.473	2.546	0.107
		3	0	NA	0.027		NA				4	-72.554	150.667	2.741	0.097
		8	0.002	-0.285	0.072		-0.187				6	-72.323	150.802	2.876	0.091
	<b>model 2</b>	1	0				NA				3	-71.737	148.268	0	0.770
		2	0				-0.015				4	-72.562	150.685	2.418	0.230
		<b>Herbivore Shannon</b>													
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA		NA				3	-71.633	148.074	0	0.471
		2	0	0.189	NA		NA				4	-71.873	149.183	1.109	0.271
		3	0	NA	-0.034		NA				4	-72.436	150.459	2.385	0.143
		4	0	0.198	0.030		NA				5	-72.631	151.736	3.662	0.076
		8	-0.134	-0.002	-0.097		-0.424				6	-72.065	153.047	4.974	0.039
	<b>model 2</b>	1	0		NA	NA			NA		3	-71.633	148.074	0	0.558
		3	0		NA	0.093			NA		4	-72.317	150.188	2.114	0.194
		2	0		-0.034	NA			NA		4	-72.436	150.459	2.385	0.169
		4	0		-0.039	0.095			NA		5	-73.088	152.717	4.643	0.055
		8	0.017		0.033	0.049			-0.286		6	-72.913	154.430	6.356	0.023
<b>250 m</b>	<b>model 1</b>	1	0	NA	NA	NA	NA	NA	NA	NA	3	-71.633	148.074	0	0.182
		2	0	0.247	NA	NA	NA	NA	NA	NA	4	-71.426	148.170	0.096	0.174
		5	0	NA	NA	0.238	NA	NA	NA	NA	4	-71.509	148.358	0.284	0.158
		6	0	0.206	NA	0.194	NA	NA	NA	NA	5	-71.628	149.222	1.148	0.103
		3	0	NA	-0.086	NA	NA	NA	NA	NA	4	-72.337	150.233	2.160	0.062
		7	0	NA	-0.075	0.234	NA	NA	NA	NA	5	-72.265	150.717	2.644	0.049

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		4	0	0.251	0.009	NA	NA	NA	NA	5	-72.203	150.752	2.678	0.048
		39	0.019	NA	-0.196	0.149	NA	NA	0.402	6	-71.609	150.981	2.908	0.043
		22	0.036	0.203	NA	0.045	NA	-0.173	NA	6	-71.924	151.162	3.089	0.039
		16	-0.266	-0.100	-0.349	0.263	-0.715	NA	NA	7	-71.043	151.553	3.479	0.032
		12	-0.203	0.029	-0.257	NA	-0.546	NA	NA	6	-71.348	151.670	3.597	0.030
		8	0	0.207	0.002	0.194	NA	NA	NA	6	-72.415	151.984	3.910	0.026
		40	0.017	0.164	-0.121	0.126	NA	NA	0.356	7	-71.982	152.902	4.828	0.016
		48	-0.219	-0.094	-0.400	0.202	-0.625	NA	0.275	8	-70.913	153.332	5.259	0.013
		24	0.036	0.202	-0.002	0.045	NA	-0.173	NA	7	-72.696	154.122	6.048	0.009
		32	-0.226	-0.082	-0.328	0.168	-0.667	-0.105	NA	8	-71.537	154.390	6.317	0.008
		56	0.054	0.159	-0.126	-0.026	NA	-0.176	0.359	8	-72.260	155.120	7.046	0.005
		64	-0.173	-0.075	-0.378	0.094	-0.569	-0.117	0.284	9	-71.374	156.298	8.225	0.003
		128	-0.192	-0.081	-0.378	0.160	-0.591	-0.081	0.460	10	-70.152	159.884	11.811	0
<b>500 m</b>	<b>model 1</b>	1	0	NA		NA		NA		3	-71.633	<a href="#">148.074</a>	0	0.368
		3	0	NA		0.239		NA		4	-71.502	148.342	0.269	0.322
		2	0	0.128		NA		NA		4	-72.192	149.906	1.832	0.147
		4	0	0.133		0.241		NA		5	-72.054	150.201	2.127	0.127
		8	0.003	0.075		0.274		0.178		6	-71.977	152.696	4.622	0.036
	<b>model 2</b>	1	0		NA	NA		NA		3	-71.633	<a href="#">148.074</a>	0	0.380
		3	0		NA	0.239		NA		4	-71.502	148.342	0.269	0.333
		2	0		-0.137	NA		NA		4	-72.152	149.815	1.741	0.159
		4	0		-0.072	0.217		NA		5	-72.227	150.738	2.664	0.100
		8	-0.040		-0.043	0.268		-0.135		6	-72.204	153.345	5.271	0.027
<b>1000 m</b>	<b>model 1</b>	3	0	NA	-0.435		NA			4	-68.680	<a href="#">141.946</a>	0	0.602
		4	0	0.135	-0.436		NA			5	-69.266	143.430	1.484	0.287

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		8	0	0.134	-0.435					6	-70.509	146.190	4.244	0.072
		1	0	NA	NA					3	-71.633	148.074	6.128	0.028
		2	0	0.129	NA					4	-72.187	149.894	7.947	0.011
	<b>model 2</b>	1	0		NA					3	-71.633	148.074	0	0.699
		2	0		0.143					4	-72.127	149.758	1.684	0.301
<b>Predator Shannon</b>														
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA					3	-71.981	148.718	0	0.573
		2	0	-0.054	NA					4	-72.778	151.033	2.315	0.180
		3	0	NA	-0.011					4	-72.825	151.139	2.421	0.171
		4	0	-0.064	-0.032					5	-73.526	153.584	4.866	0.050
		8	-0.136	-0.268	-0.161					6	-72.943	154.879	6.161	0.026
	<b>model 2</b>	1	0		NA	NA		NA		3	-71.981	148.718	0	0.433
		3	0		NA	-0.149		NA		4	-72.451	150.291	1.573	0.197
		8	0.034		0.144	-0.244		-0.579		6	-71.549	150.398	1.680	0.187
		2	0		-0.011	NA		NA		4	-72.825	151.139	2.421	0.129
		4	0		-0.002	-0.149		NA		5	-73.287	152.875	4.157	0.054
<b>250 m</b>	<b>model 1</b>	1	0	NA	NA	NA	NA	NA	NA	3	-71.981	148.718	0	0.229
		5	0	NA	NA	-0.217	NA	NA	NA	4	-72.008	149.287	0.569	0.173
		2	0	-0.175	NA	NA	NA	NA	NA	4	-72.301	149.951	1.233	0.124
		3	0	NA	0.143	NA	NA	NA	NA	4	-72.483	150.364	1.646	0.101
		6	0	-0.135	NA	-0.188	NA	NA	NA	5	-72.545	151.125	2.407	0.069
		7	0	NA	0.132	-0.210	NA	NA	NA	5	-72.567	151.126	2.408	0.069
		39	-0.018	NA	0.248	-0.128	NA	NA	-0.384	6	-71.971	151.462	2.744	0.058

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		4	0	-0.142	0.089	NA	NA	NA	NA	5	-72.958	152.262	3.544	0.039
		12	-0.230	-0.393	-0.212	NA	-0.618	NA	NA	6	-71.889	152.619	3.901	0.033
		8	0	-0.098	0.096	-0.191	NA	NA	NA	6	-73.187	153.539	4.821	0.021
		22	-0.014	-0.134	NA	-0.131	NA	0.066	NA	6	-73.099	153.771	5.053	0.018
		48	-0.274	-0.334	-0.079	-0.039	-0.677	NA	-0.456	8	-71.457	154.191	5.473	0.015
		40	-0.018	-0.054	0.223	-0.121	NA	NA	-0.369	7	-72.699	154.305	5.587	0.014
		128	-0.228	-0.325	-0.111	-0.279	-0.620	-0.059	-1.476	10	-69.128	154.675	5.957	0.012
		16	-0.197	-0.325	-0.163	-0.140	-0.529	NA	NA	7	-72.387	154.734	6.016	0.011
		24	-0.015	-0.096	0.098	-0.131	NA	0.070	NA	7	-73.712	156.368	7.650	0.005
		64	-0.333	-0.359	-0.107	0.100	-0.749	0.151	-0.468	9	-71.836	156.811	8.093	0.004
		56	-0.033	-0.052	0.225	-0.058	NA	0.073	-0.370	8	-73.240	157.325	8.607	0.003
		32	-0.246	-0.347	-0.190	-0.022	-0.588	0.130	NA	8	-72.787	157.431	8.713	0.003
<b>500 m</b>	<b>model 1</b>	1	0	NA		NA		NA		3	-71.981	<a href="#">148.718</a>	0	0.462
		3	0	NA		-0.196		NA		4	-72.163	149.638	0.920	0.291
		2	0	0.045		NA		NA		4	-72.794	151.069	2.351	0.143
		4	0	0.041		-0.195		NA		5	-72.992	152.155	3.437	0.083
		8	0.002	0.010		-0.178		0.095		6	-72.976	154.843	6.125	0.022
	<b>model 2</b>	1	0		NA	NA		NA		3	-71.981	<a href="#">148.718</a>	0	0.363
		2	0		0.214	NA		NA		4	-72.026	149.328	0.610	0.267
		3	0		NA	-0.196		NA		4	-72.163	149.638	0.920	0.229
		4	0		0.171	-0.144		NA		5	-72.511	151.105	2.387	0.110
		8	-0.047		0.205	-0.084		-0.158		6	-72.493	153.638	4.920	0.031
<b>1000 m</b>	<b>model 1</b>	3	0	NA	0.299		NA			4	-71.182	<a href="#">147.415</a>	0	0.494
		1	0	NA	NA		NA			3	-71.981	148.718	1.303	0.258
		4	0	-0.006	0.299		NA			5	-72.104	149.999	2.583	0.136

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		2	0	-0.003	NA		NA			4	-72.827	151.143	3.728	0.077
		8	0	-0.010	0.307		-0.036			6	-73.163	152.667	5.252	0.036
	<b>model 2</b>	1	0				NA			3	-71.981	<b>148.718</b>	0	0.633
		2	0				-0.185			4	-72.239	149.811	1.093	0.367
<b>Parasitoid</b>														
<b>Shannon</b>														
<b>100 m</b>	<b>model 1</b>	1	0	NA	NA		NA			3	-72.592	<b>149.807</b>	0	0.538
		2	0	0.088	NA		NA			4	-73.359	151.902	2.095	0.189
		3	0	NA	0.060		NA			4	-73.436	152.077	2.270	0.173
		4	0	0.119	0.099		NA			5	-74.035	154.102	4.296	0.063
		8	-0.136	-0.083	-0.030		-0.429			6	-73.434	155.131	5.325	0.038
	<b>model 2</b>	1	0		NA	NA		NA		3	-72.592	<b>149.807</b>	0	0.472
		3	0		NA	0.130		NA		4	-73.180	151.497	1.690	0.203
		2	0		0.060	NA		NA		4	-73.436	152.077	2.270	0.152
		8	0.028		0.175	0.047		-0.486		6	-72.798	152.634	2.827	0.115
		4	0		0.053	0.127		NA		5	-74.029	153.959	4.152	0.059
<b>250 m</b>	<b>model 1</b>	1	0	NA	NA	NA	NA	NA	NA	3	-72.592	<b>149.807</b>	0	0.217
		3	0	NA	0.211	NA	NA	NA	NA	4	-72.612	150.210	0.404	0.177
		4	0	0.182	0.280	NA	NA	NA	NA	5	-72.889	151.375	1.568	0.099
		5	0	NA	NA	0.108	NA	NA	NA	4	-73.282	151.728	1.922	0.083
		2	0	0.076	NA	NA	NA	NA	NA	4	-73.396	151.987	2.180	0.073
		7	0	NA	0.217	0.118	NA	NA	NA	5	-73.267	152.108	2.301	0.069
		24	0.073	0.152	0.269	-0.215	NA	-0.351	NA	7	-72.731	152.194	2.387	0.066
		22	0.075	0.048	NA	-0.214	NA	-0.360	NA	6	-73.228	153.075	3.268	0.042
		12	-0.114	0.057	0.131	NA	-0.307	NA	NA	6	-72.587	153.414	3.607	0.036



		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
		8	0	0.162	0.277	0.087	NA	NA	NA	6	-73.664	153.756	3.949	0.030
		6	0	0.055	NA	0.096	NA	NA	NA	5	-74.100	154.185	4.379	0.024
		39	0.009	NA	0.163	0.081	NA	NA	0.178	6	-73.451	154.302	4.495	0.023
		32	-0.020	0.051	0.153	-0.172	-0.237	-0.327	NA	8	-72.548	154.864	5.058	0.017
		56	0.080	0.135	0.219	-0.244	NA	-0.353	0.143	8	-73.042	154.886	5.079	0.017
		16	-0.144	-0.004	0.087	0.124	-0.387	NA	NA	7	-73.186	155.601	5.795	0.012
		40	0.007	0.146	0.229	0.061	NA	NA	0.137	7	-73.920	156.369	6.562	0.008
		64	0.002	0.054	0.132	-0.202	-0.197	-0.332	0.117	9	-72.869	157.977	8.170	0.004
		48	-0.128	-0.002	0.070	0.104	-0.357	NA	0.091	8	-73.484	158.628	8.821	0.003
		128	0.002	0.054	0.132	-0.202	-0.197	-0.332	0.118	10	-71.778	161.705	11.899	0.001
<b>500 m</b>	<b>model 1</b>	1	0	NA		NA		NA		3	-72.592	149.807	0	0.427
		2	0	-0.181		NA		NA		4	-72.862	150.777	0.970	0.263
		3	0	NA		0.125		NA		4	-73.204	151.552	1.745	0.179
		4	0	-0.178		0.121		NA		5	-73.496	152.661	2.854	0.103
		8	0.003	-0.225		0.148		0.144		6	-73.515	155.222	5.415	0.029
	<b>model 2</b>	1	0		NA	NA		NA		3	-72.592	149.807	0	0.470
		2	0		0.125	NA		NA		4	-73.204	151.551	1.744	0.197
		3	0		NA	0.125		NA		4	-73.204	151.552	1.745	0.197
		4	0		0.179	0.179		NA		5	-73.499	152.785	2.978	0.106
		8	0.049		0.144	0.117		0.165		6	-73.512	155.272	5.465	0.031
<b>1000 m</b>	<b>model 1</b>	1	0	NA	NA		NA			3	-72.592	149.807	0	0.352
		2	0	-0.198	NA		NA			4	-72.728	150.472	0.666	0.252
		3	0	NA	-0.176		NA			4	-72.892	150.845	1.038	0.210

		(Intercept)	CD	MFS	SNH	CD: MFS	CD: SNH	MFS:SNH	CD:MFS: SNH	df	logLik	AICc	delta	weight
	4	0	-0.196	-0.174		NA				5	-73.040	151.554	1.748	0.147
	8	0	-0.192	-0.182		0.036				6	-74.148	154.212	4.405	0.039
<b>model 2</b>	1	0			NA					3	-72.592	149.807	0	0.752
	2	0			0.069					4	-73.414	152.028	2.221	0.248

**Table S7. Model-averaged estimates with unconditional lower and upper 95% confidence intervals.**

Model-averaged estimates with unconditional lower (LC95) and upper (UC95) 95% confidence intervals for the abundance of herbivores, predators and parasitoids, and Shannon diversity of herbivores, predators and parasitoids as a function of landscape predictors at each spatial scale in alternative models 1 and 2 (see **Table S2**). Model averaging was based on a set of top models ( $\Delta AIC_c < 7$ ). CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion. Estimates are highlighted in bold if 95% confidence intervals do not overlap with zero. Grey cells coincide with predictors not included to either model due to collinearity. The italicized row (model 2) corresponds to the common landscape predictor between model 2 and model 1.

	Model	Landscape predictor	Estimate	LC95	UC95
<b>Herbivore abundance</b>					
<b>100 m</b>					
	model 1 <- CD + MFS + CD:MFS	CD	0.182	-0.261	0.626
		MFS	0.031	-0.411	0.472
		CD:MFS	-0.406	-1.337	0.525
	model 2 <- SNH + MFS + SNH:MFS	SNH	0.134	-0.277	0.545
		<i>MFS</i>	<i>0.014</i>	<i>-0.402</i>	<i>0.430</i>
		MFS:SNH	0	0	0
		CD:SNH			
		CD:MFS:SNH			
<b>250 m</b>					
	model 1 <- CD*MFS*SNH	CD	0.164	-0.330	0.657
		MFS	-0.050	-0.592	0.493
		CD:MFS	-0.731	-1.808	0.346
		SNH	0.247	-0.170	0.665
		CD:SNH	-0.057	-0.584	0.471
		MFS:SNH	0.255	-0.438	0.949
		CD:MFS:SNH	0	0	0
<b>500 m</b>					
	model 1 <- CD + SNH + CD:SNH	CD	0.040	-0.379	0.458
		SNH	0.310	-0.078	0.698
		CD:SNH	0.163	-0.753	1.080
	model 2 <- MFS + SNH + MFS:SNH	MFS	0.043	-0.398	0.484
		<i>SNH</i>	<i>0.326</i>	<i>-0.087</i>	<i>0.739</i>
		MFS:SNH	-0.387	-1.257	0.482
		CD:MFS			
		CD:MFS:SNH			
<b>1000 m</b>					
	model 1 <- CD + MFS + CD:MFS	CD	-0.009	-0.387	0.368
		<b>MFS</b>	<b>-0.411</b>	<b>-0.769</b>	<b>-0.052</b>

	Model	Landscape predictor	Estimate	LC95	UC95
		CD:MFS	-0.052	-0.360	0.256
	model 2 <- SNH	SNH	0.324	-0.054	0.702
		CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			
<b>Herbivore Shannon</b>					
<b>100m</b>					
		CD	0.171	-0.220	0.563
	model 1 <- CD + MFS + CD:MFS	MFS	-0.025	-0.412	0.362
		CD:MFS	-0.424	-1.218	0.370
	model 2 <- SNH + MFS + SNH:MFS	SNH	0.090	-0.272	0.452
		MFS	-0.029	-0.396	0.339
		MFS:SNH	-0.286	-0.919	0.347
		CD:SNH			
		CD:MFS:SNH			
<b>250m</b>					
		CD	0.180	-0.258	0.618
		MFS	-0.136	-0.628	0.356
		CD:MFS	-0.635	-1.546	0.276
	model <- CD*MFS*SNH	SNH	0.196	-0.190	0.581
		CD:SNH	-0.163	-0.604	0.277
		MFS:SNH	0.368	-0.208	0.945
		CD:MFS:SNH	0	0	0
<b>500m</b>					
		CD	0.124	-0.237	0.485
	model 1 <- CD + SNH + CD:SNH	SNH	0.242	-0.100	0.584
		CD:SNH	0.178	-0.614	0.970
	model 2 <- MFS + SNH + MFS:SNH	MFS	-0.105	-0.475	0.264
		SNH	0.236	-0.118	0.589
		MFS:SNH	-0.135	-0.921	0.651
		CD:MFS			
		CD:MFS:SNH			
<b>1000m</b>					
		CD	0.134	-0.148	0.417
	model 1 <- CD + MFS + CD:MFS	MFS	<b>-0.435</b>	<b>-0.716</b>	<b>-0.154</b>
		CD:MFS	-0.005	-0.241	0.231
	model 2 <- SNH	SNH	0.143	-0.208	0.494
		CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			
<b>Predator</b>					

	<b>Model</b>	<b>Landscape predictor</b>	<b>Estimate</b>	<b>LC95</b>	<b>UC95</b>
<b>abundance</b>					
<b>100m</b>		CD	-0.064	-0.452	0.323
	model 1 <- CD + MFS + CD:MFS	MFS	-0.058	-0.424	0.309
		CD:MFS	-0.397	-1.181	0.387
		SNH	0.002	-0.348	0.352
	model 2 <- SNH + MFS + SNH:MFS	MFS	-0.007	-0.371	0.357
		MFS:SNH	-0.503	-1.062	0.057
		CD:SNH			
		CD:MFS:SNH			
<b>250m</b>		CD	-0.316	-0.770	0.138
		MFS	0.050	-0.501	0.601
		CD:MFS	-0.746	-1.568	0.076
	model <- CD*MFS*SNH	SNH	0.006	-0.395	0.407
		CD:SNH	-0.035	-0.467	0.397
		MFS:SNH	-0.561	-1.256	0.134
		CD:MFS:SNH	-1.491	-3.597	0.616
<b>500m</b>		CD	-0.141	-0.483	0.202
	model 1 <- CD + SNH + CD:SNH	SNH	-0.052	-0.397	0.293
		CD:SNH	-0.100	-0.902	0.701
		MFS	0.248	-0.086	0.582
	model 2 <- MFS + SNH + MFS:SNH	SNH	0.020	-0.375	0.414
		MFS:SNH	-0.374	-1.094	0.345
		CD:MFS			
		CD:MFS:SNH			
<b>1000m</b>		CD	-0.237	-0.545	0.071
	model 1 <- CD + MFS + CD:MFS	MFS	0.255	-0.053	0.563
		CD:MFS	0.002	-0.250	0.255
		SNH	0	-0.341	0.341
	model 2 <- SNH	CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			
<b>Predator Shannon</b>					
<b>100m</b>		CD	-0.078	-0.477	0.321
	model 1 <- CD + MFS + CD:MFS	MFS	-0.031	-0.410	0.348
		CD:MFS	-0.431	-1.232	0.371
		SNH	-0.189	-0.539	0.160

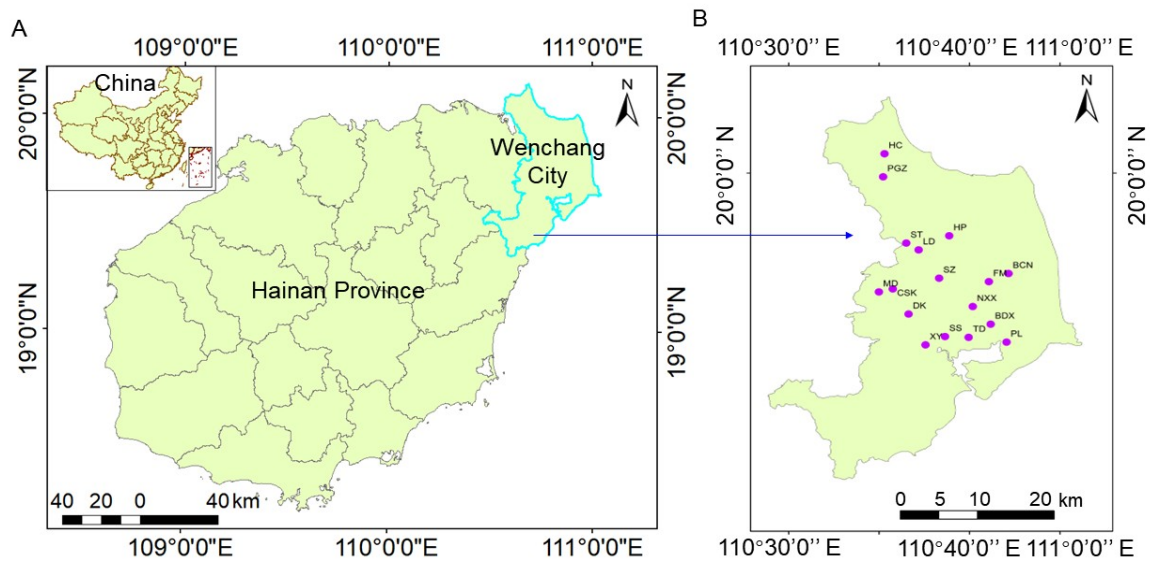
	<b>Model</b>	<b>Landscape predictor</b>	<b>Estimate</b>	<b>LC95</b>	<b>UC95</b>
	SNH:MFS	MFS	0.069	-0.309	0.447
		<b>MFS:SNH</b>	<b>-0.579</b>	<b>-1.117</b>	<b>-0.041</b>
		CD:SNH			
		CD:MFS:SNH			
<b>250m</b>		CD	-0.189	-0.616	0.238
		MFS	0.095	-0.386	0.575
		CD:MFS	-0.617	-1.508	0.275
	model <- CD*MFS*SNH	SNH	-0.187	-0.557	0.183
		CD:SNH	0.018	-0.444	0.480
		MFS:SNH	-0.522	-1.473	0.430
		CD:MFS:SNH	-2.109	-4.320	0.103
<b>500m</b>		CD	0.040	-0.318	0.398
	model 1 <- CD + SNH + CD:SNH	SNH	-0.195	-0.535	0.145
		CD:SNH	0.095	-0.712	0.902
		MFS	0.202	-0.143	0.547
	model 2 <- MFS + SNH + MFS:SNH	SNH	-0.171	-0.531	0.188
		MFS:SNH	-0.158	-0.917	0.601
		CD:MFS			
		CD:MFS:SNH			
<b>1000m</b>		CD	-0.006	-0.340	0.329
	model 1 <- CD + MFS + CD:MFS	MFS	0.299	-0.018	0.617
		CD:MFS	-0.036	-0.310	0.237
	model 2 <- SNH	SNH	-0.185	-0.522	0.151
		CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			
<b>Parasitoid abundance</b>					
<b>100m</b>		CD	-0.086	-0.447	0.275
	model 1 <- CD + MFS + CD:MFS	MFS	0.016	-0.348	0.381
		CD:MFS	-0.134	-0.487	0.218
		SNH			
	model 2 <- SNH + MFS + SNH:MFS	MFS	0.025	-0.333	0.383
		MFS:SNH	0	0	0
		CD:SNH			
		CD:MFS:SNH			

	Model	Landscape predictor	Estimate	LC95	UC95
<b>250m</b>		CD	0.216	-0.182	0.614
		MFS	0.341	-0.049	0.730
		CD:MFS	0.020	-0.889	0.928
	model <- CD*MFS*SNH	SNH	-0.277	-0.747	0.193
		CD:SNH	-0.305	-0.698	0.089
		MFS:SNH	-0.261	-0.799	0.277
		CD:MFS:SNH			
<b>500m</b>		CD	-0.416	-0.852	0.020
	model 1 <- CD + SNH + CD:SNH	SNH	0.074	-0.269	0.417
		<b>CD:SNH</b>	<b>0.885</b>	<b>0.231</b>	<b>1.538</b>
		MFS	0.222	-0.126	0.570
	model 2 <- MFS + SNH + MFS:SNH	SNH	-0.024	-0.403	0.355
		MFS:SNH	0.041	-0.754	0.836
		CD:MFS			
	CD:MFS:SNH				
<b>1000m</b>		CD	-0.269	-0.600	0.062
	model 1 <- CD + MFS + CD:MFS	MFS	0.042	-0.304	0.388
		CD:MFS	-0.187	-0.454	0.080
	model 2 <- SNH	SNH	-0.015	-0.371	0.341
		CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			
<b>Parasitoid Shannon</b>					
<b>100m</b>		CD	0.072	-0.303	0.448
	model 1 <- CD + MFS + CD:MFS	MFS	0.057	-0.296	0.409
		CD:MFS	-0.429	-1.160	0.302
		SNH	0.104	-0.226	0.433
	model 2 <- SNH + MFS + SNH:MFS	MFS	0.099	-0.248	0.446
		MFS:SNH	-0.486	-1.007	0.035
		CD:SNH			
	CD:MFS:SNH				
<b>250m</b>		CD	0.113	-0.260	0.487
		MFS	0.223	-0.141	0.588
	model <- CD*MFS*SNH	CD:MFS	-0.303	-1.139	0.533
		SNH	-0.012	-0.493	0.470
		CD:SNH	-0.351	-0.734	0.032

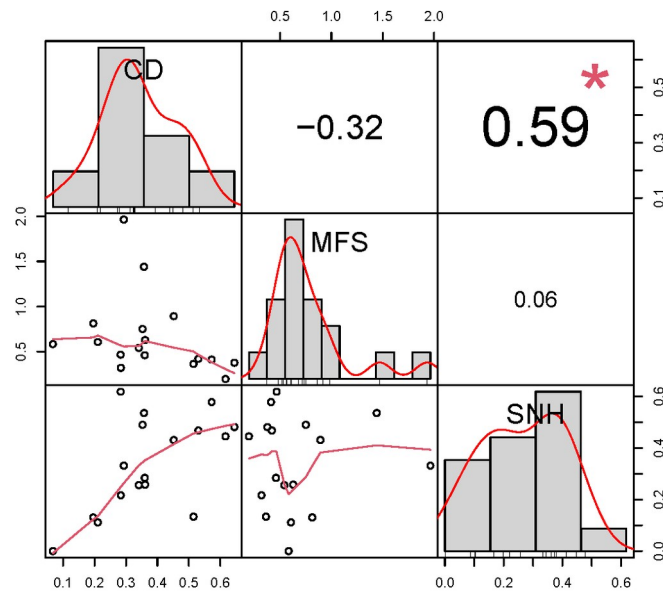
	<b>Model</b>	<b>Landscape predictor</b>	<b>Estimate</b>	<b>LC95</b>	<b>UC95</b>
		MFS:SNH	0.158	-0.374	0.691
		CD:MFS:SNH			
<b>500m</b>		CD	-0.183	-0.507	0.140
	model 1 <- CD + SNH + CD:SNH	SNH	0.126	-0.198	0.450
		CD:SNH	0.144	-0.595	0.884
	model 2 <- MFS + SNH + MFS:SNH	MFS	0.144	-0.191	0.479
		SNH	0.141	-0.201	0.483
		MFS:SNH	0.165	-0.557	0.886
		CD:MFS			
		CD:MFS:SNH			
<b>1000m</b>		CD	-0.197	-0.507	0.114
	model 1 <- CD + MFS + CD:MFS	MFS	-0.176	-0.489	0.137
		CD:MFS	0.036	-0.223	0.296
	model 2 <- SNH	SNH	0.069	-0.257	0.394
		CD:SNH			
		MFS:SNH			
		CD:MFS:SNH			



## Supplementary Figures

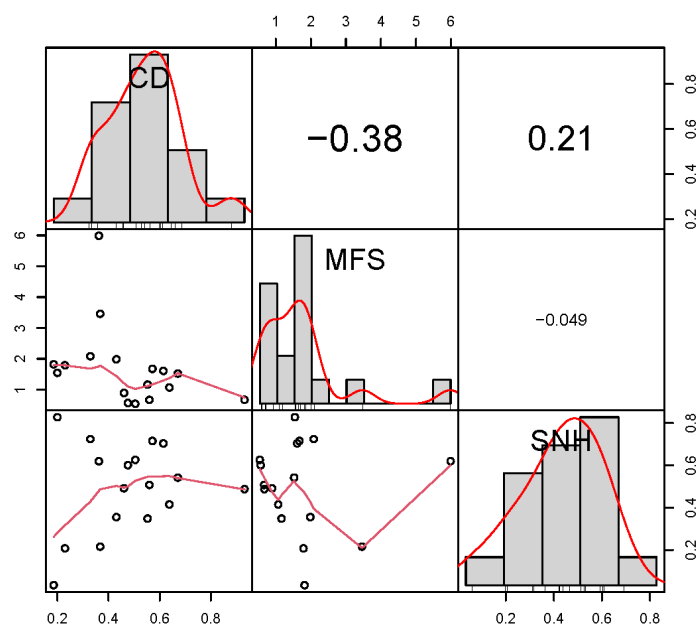


**Fig. S1.** (A) Research area (Hainan province) and (B) the location of the 17 sampled rice fields.



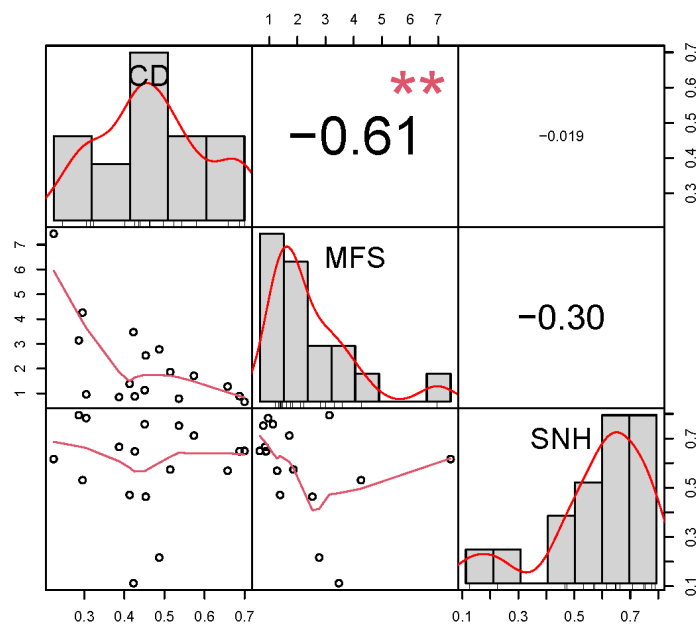
**Fig. S2.** Correlation graphs between the second-order interaction terms CD:MFS, CD:SNH, and MFS:SNH at the 100 m spatial scale.

CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion.



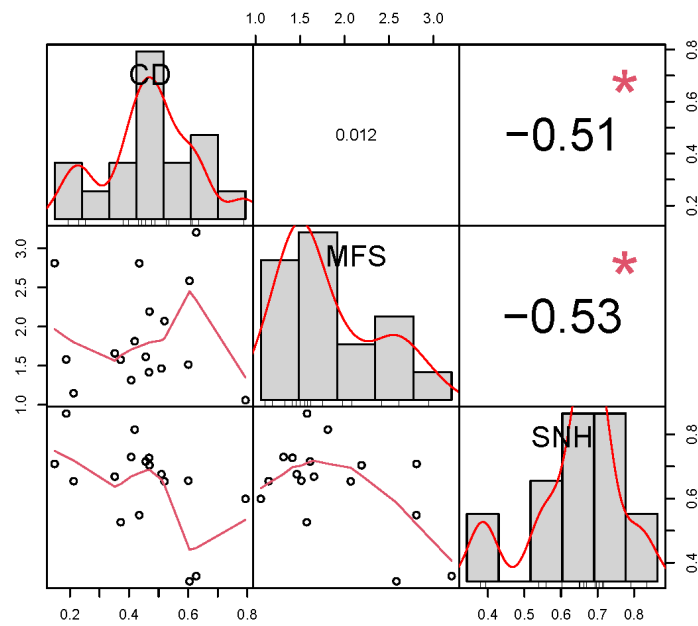
**Fig. S3.** Correlation graphs between the second-order interaction terms CD:MFS, CD:SNH, and MFS:SNH at the 250 m spatial scale.

CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion.



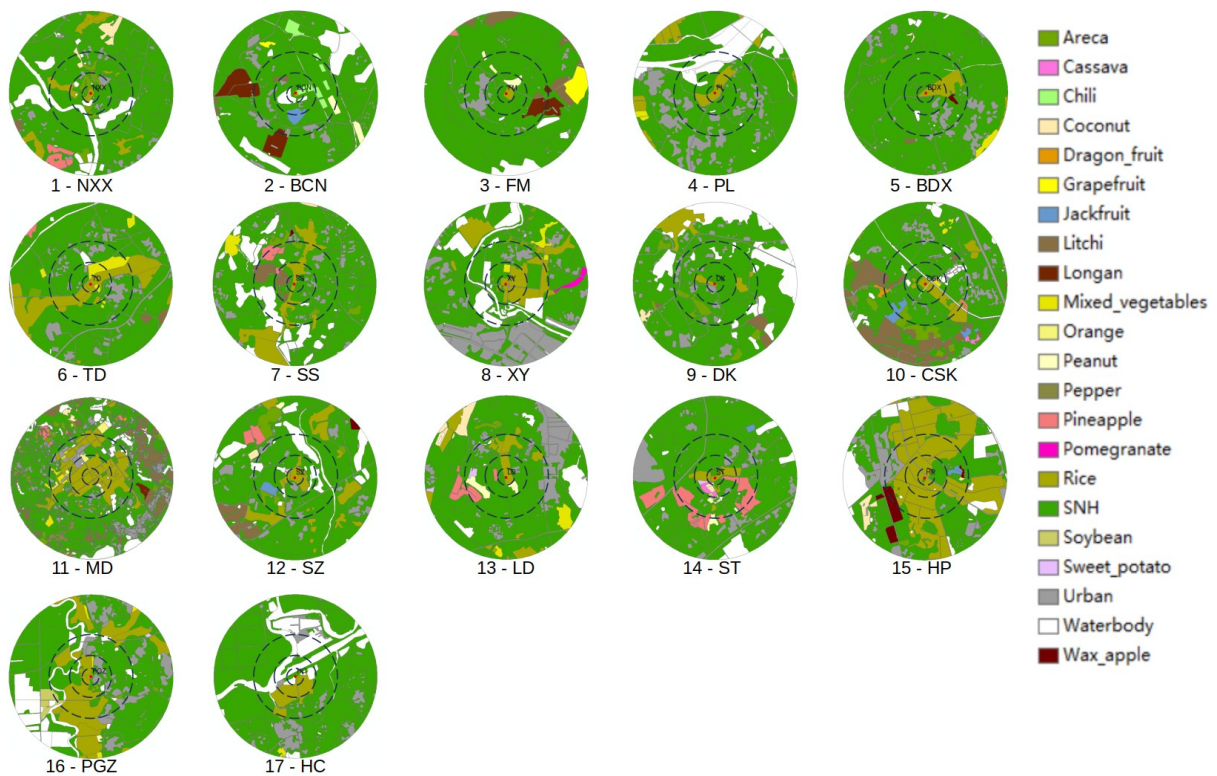
**Fig. S4.** Correlation graphs between the second-order interaction terms CD:MFS, CD:SNH, and MFS:SNH at the 500 m spatial scale.

CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion.



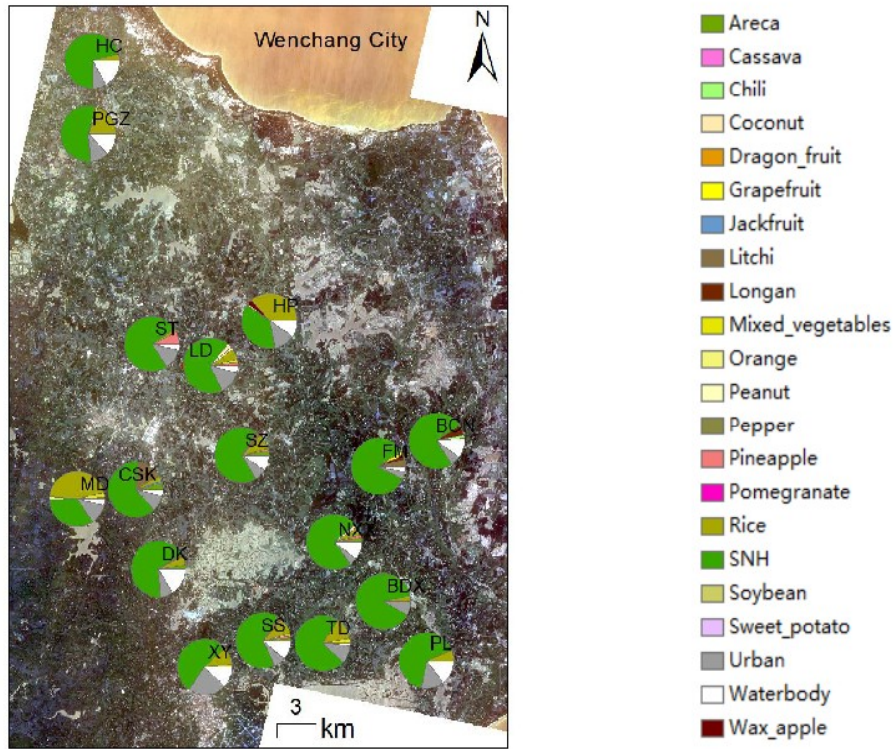
**Fig. S5.** Correlation graphs between the second-order interaction terms CD:MFS, CD:SNH, and MFS:SNH at the 1000 m spatial scale.

CD: crop diversity; MFS: mean field size; SNH: semi-natural habitat proportion.

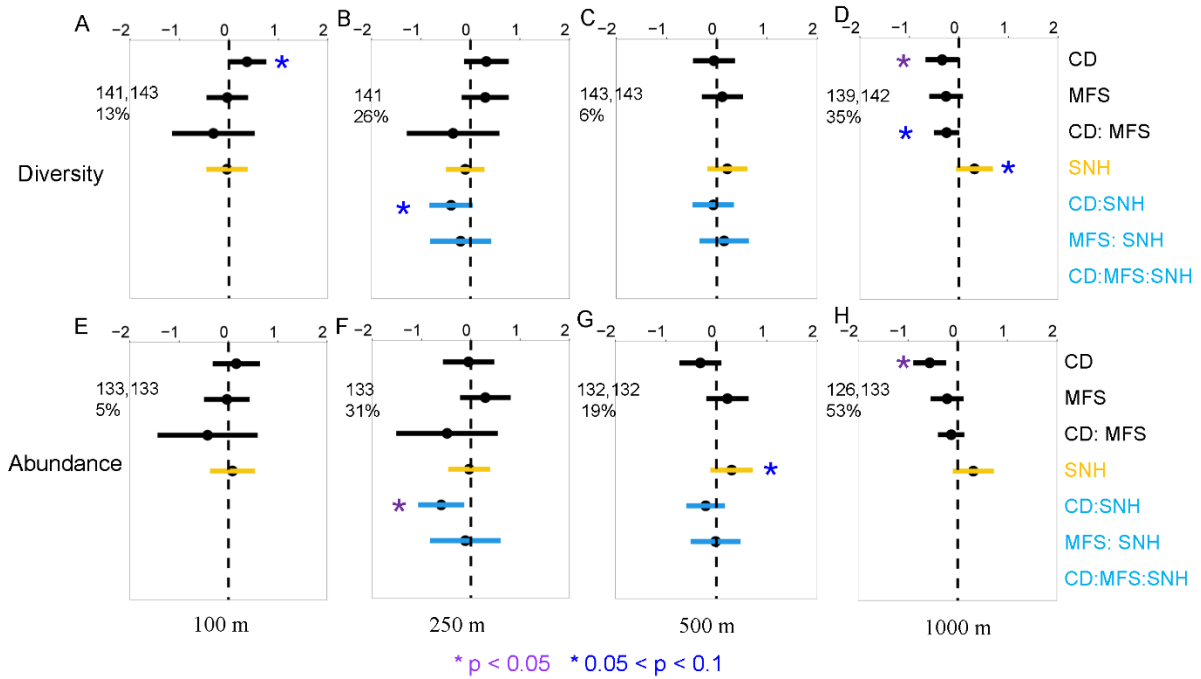


**Fig. S6.** Landcover maps of the 17 study sites.

Wenchang City, Hainan Province, China. Landscape 10 is also shown in **Fig. 1**.

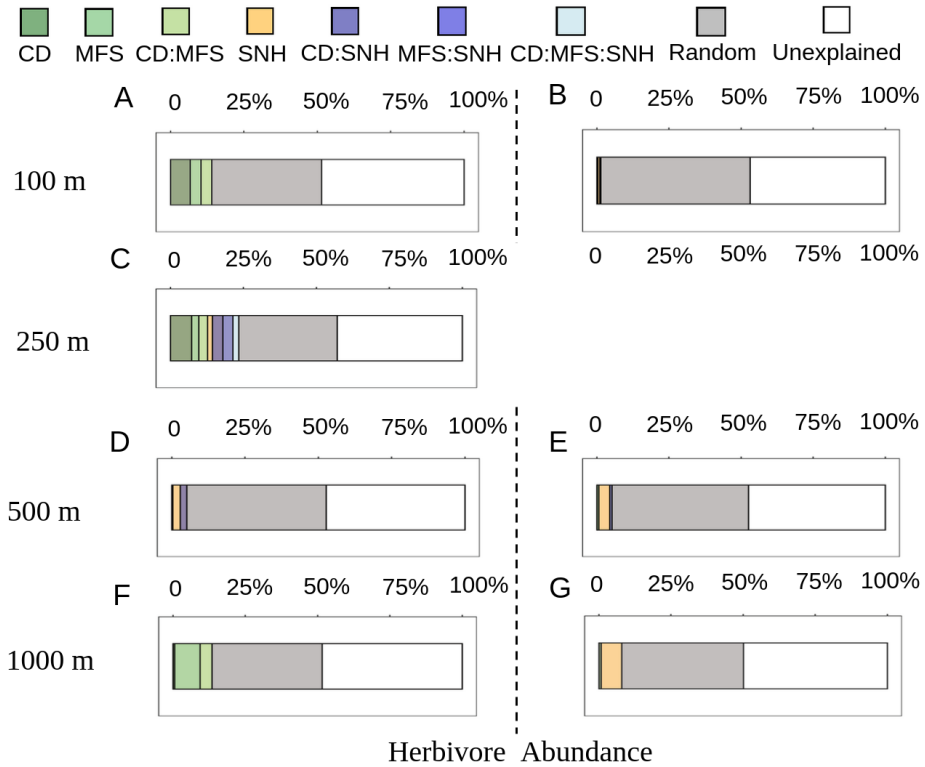


**Fig. S7.** Location and landscape composition (1,000 m scale) of the 17 study sites. Wenchang City, Hainan Province, China.



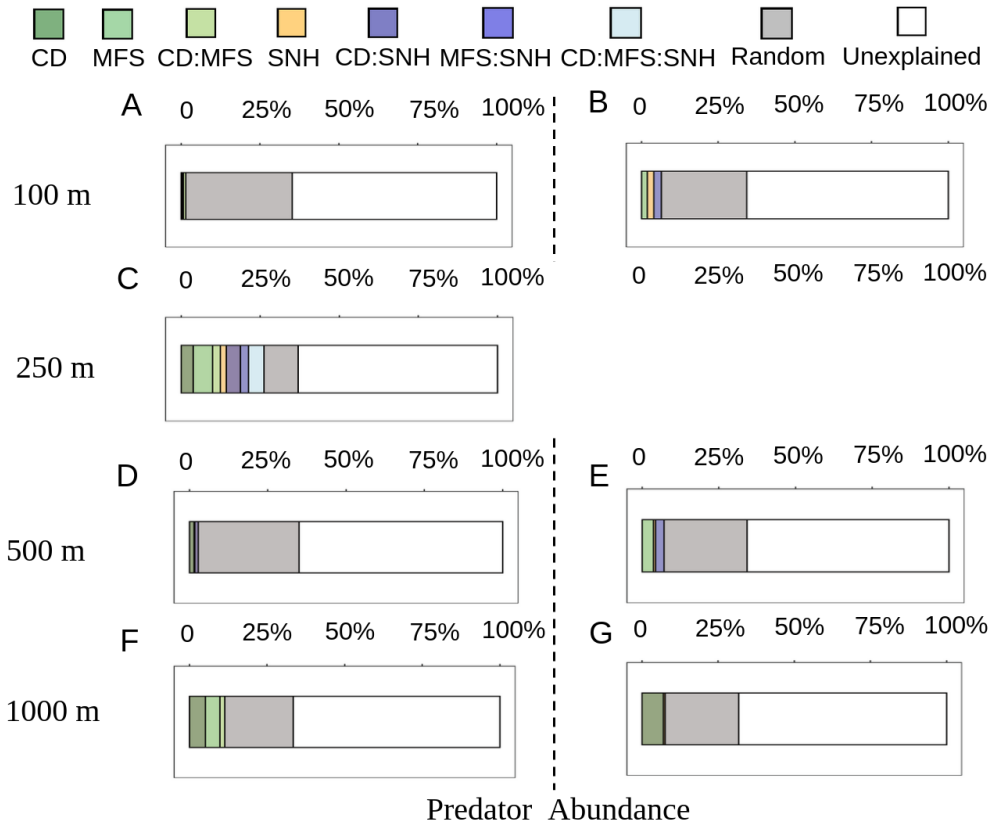
**Fig. S8.** Relative effects of landscape predictors on the diversity and total abundance of all arthropods caught in rice fields (herbivores, predators, parasitoids and neutral insects).

Relative effect estimates of crop diversity (CD), mean field size (MFS), and semi-natural habitat proportion (SNH), as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) on the diversity (A-D) and total abundance (E-H) of all arthropods across four spatial scales: (A, E) 100 m, (B, F) 250 m, (C, G) 500 m, and (D, H) 1000 m. Predictor estimates (plain dots) and 95% CI (horizontal arrows) and names are shown in three colours: black = crop heterogeneity (CD, MFS), gold = semi-natural habitat proportion (SNH), cyan = interactive effects between crop heterogeneity and SNH (CD:MFS, CD:SNH, CD:MFS:SNH). AIC values of models 1 and 2 (Table 2) are shown in each panel along with the total contribution of fixed effects (CD, MFS, SNH and their interactions) to the variance.



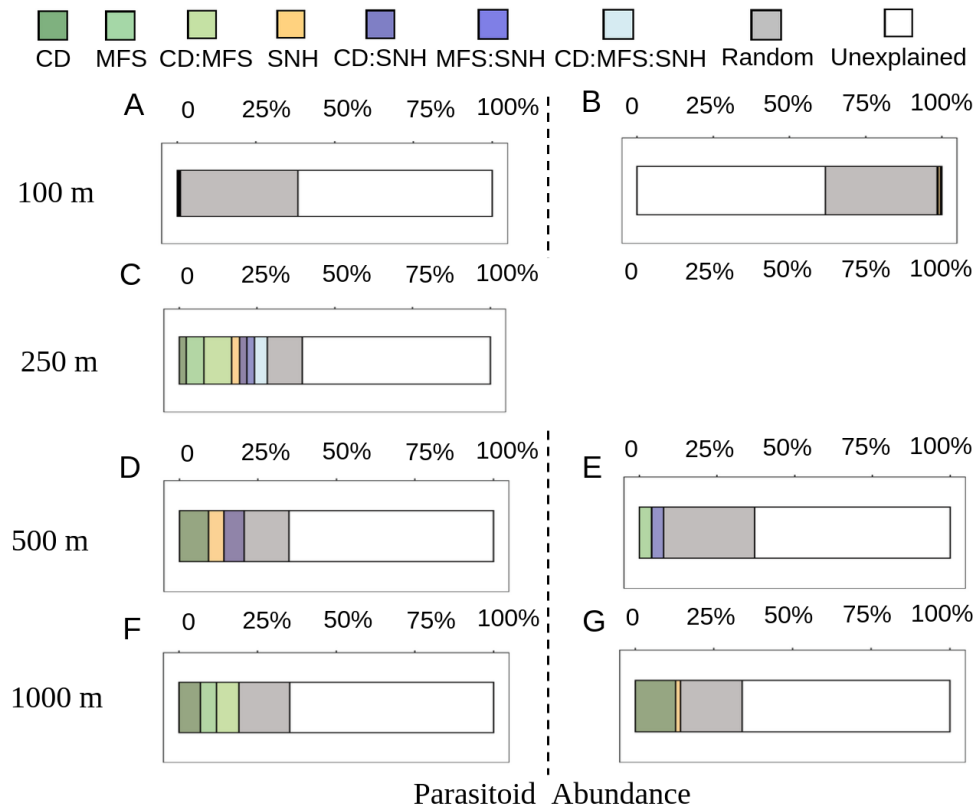
**Fig. S9. Relative importance of landscape predictors on rice herbivore abundance.**

Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **rice herbivore abundance** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glm.hp analysis).



**Fig. S10. Relative importance of landscape predictors on predator abundance.**

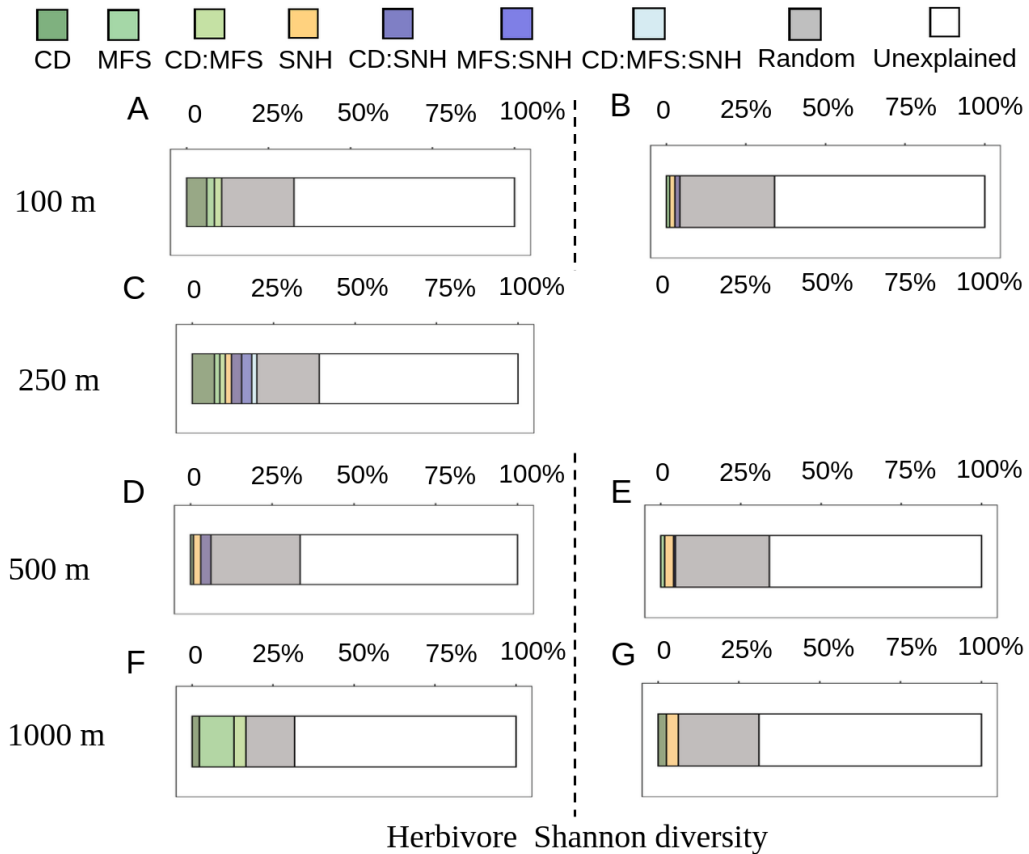
Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **predator abundance** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glmm.hp analysis).



**Fig. S11. Relative importance of landscape predictors on parasitoid abundance.**

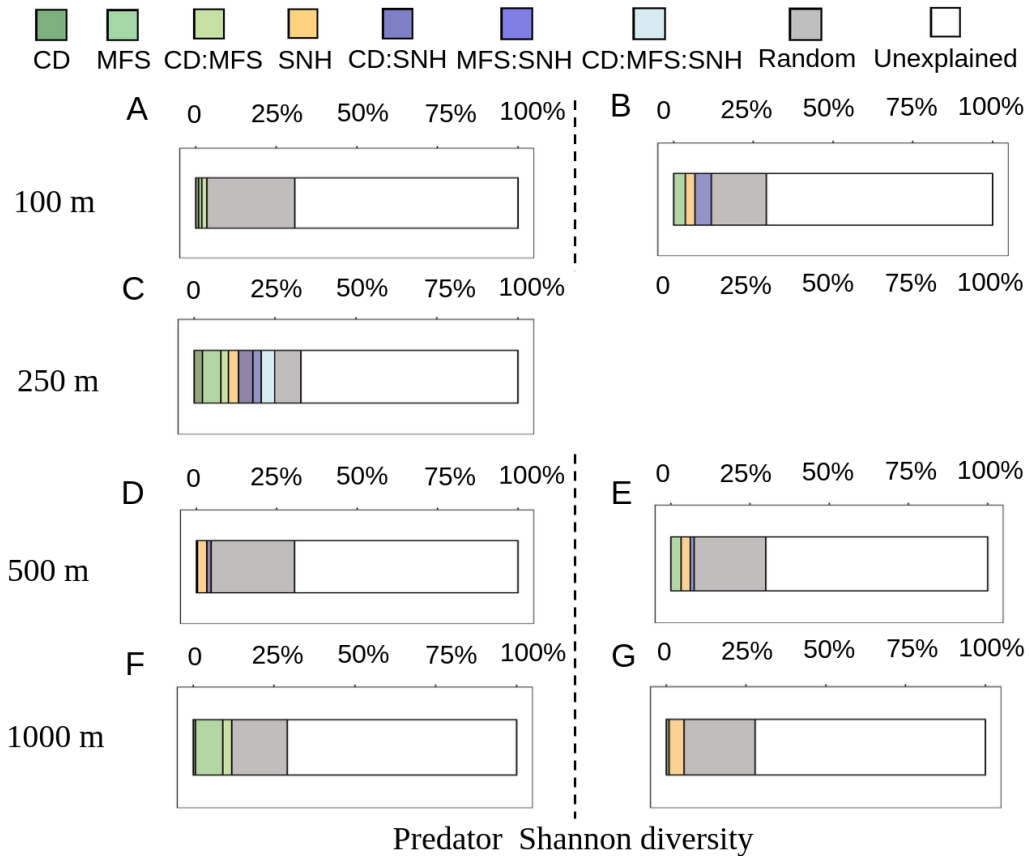
Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **parasitoid abundance** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glmm.hp analysis).





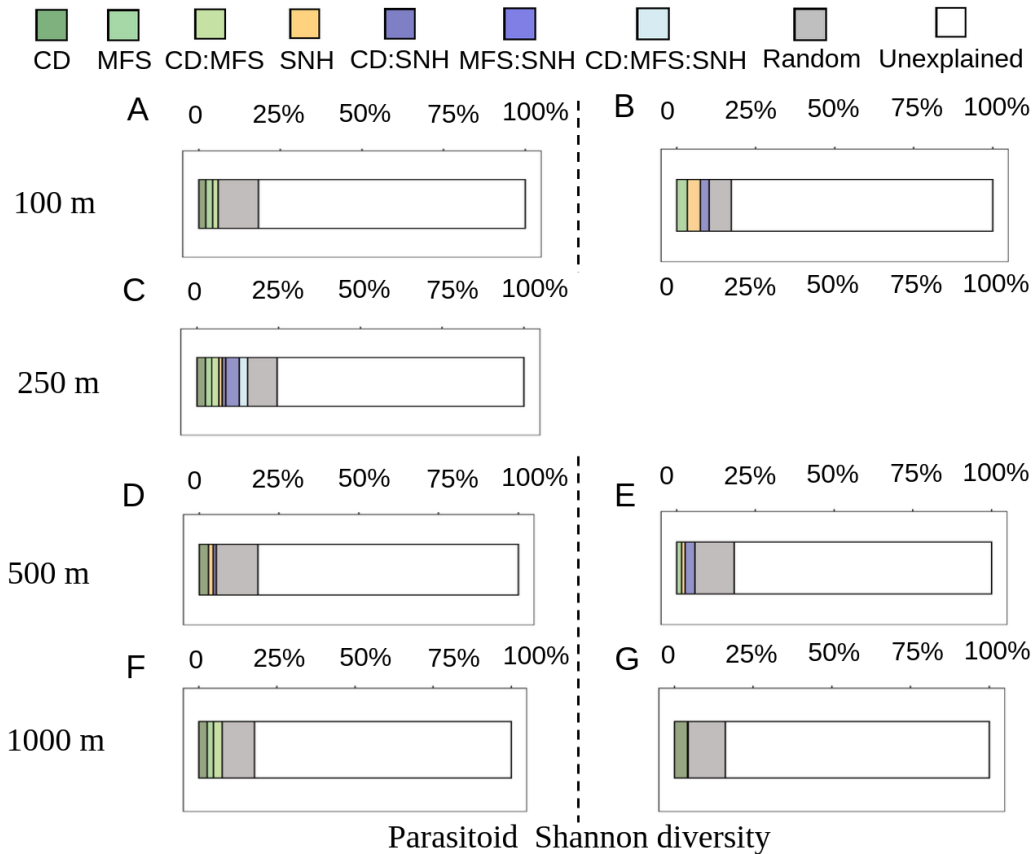
**Fig. S12. Relative importance of landscape predictors on Shannon diversity of rice herbivores.**

Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **Shannon diversity of rice herbivores** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glmm.hp analysis).



**Fig. S13. Relative importance of landscape predictors on Shannon diversity of predators.**

Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **Shannon diversity of predators** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glmm.hp analysis).



**Fig. S14. Relative importance of landscape predictors on Shannon diversity of parasitoids.**

Relative importance of crop diversity (CD), mean field size (MFS), and proportion of semi-natural habitat (SNH) predictors, as well as the second-order and third-order interaction terms (CD:MFS, MFS:SNH, CD:MFS:SNH) used in alternative models 1 (left) and models 2 (right) on **Shannon diversity of parasitoids** across the 4 spatial scales (100, 250, 500 and 1000 m). Note: the alternative models 1 and 2 for each spatial scale are detailed in **Table S4**. CD was included in model 2 for the 1000 m spatial scale to calculate the relative importance of SNH (a minimum of two predictors is required to run the glmm.hp analysis).