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## Landscape heterogeneity as an ecological filter of species traits

Rémi Duflot, Romain Georges, Aude Ernoult, Stéphanie Aviron, Françoise Burel

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1 **Title**

2 Landscape heterogeneity as an ecological filter of species traits

3

4 **Author names and affiliations**

5 Rémi Duflot <sup>a,b</sup> \*(e-mail: duflot.remi@gmail.com);

6 Romain Georges <sup>a</sup> \* (e-mail: romaingeorges@live.fr);

7 Aude Ernoult <sup>a</sup> (e-mail: aude.ernoult@univ-rennes1.fr);

8 Stéphanie Aviron <sup>b</sup> (e-mail: stephanie.aviron@rennes.inra.fr);

9 Françoise Burel <sup>a</sup> (e-mail: francoise.burel@univ-rennes1.fr)

10

11 \* These authors contributed equally to this work

12 RD and RG designed the experiment, collected data, performed statistical analyses, and wrote  
13 the manuscript. Other authors participated in designing the experiment, data collection and  
14 writing the manuscript.

15

16 <sup>a</sup> CNRS, UMR 6553 Ecobio, Université de Rennes 1

17 Campus de Beaulieu, 35042 Rennes Cedex, France

18

19 <sup>b</sup> INRA, UR 980, SAD-Paysage

20 65 Rue de Saint Briec, CS 84215, 35042 Rennes Cedex, France

21

22 **Corresponding author**

23 Rémi Duflot

24 e-mail: duflot.remi@gmail.com

25 phone: +33-223-236-663 / fax: +33-223-235-026

26 **Abstract**

27 Landscape heterogeneity is a major driver of biodiversity in agricultural areas and represents  
28 an important parameter in conservation strategies. However, most landscape ecology studies  
29 measure gamma diversity of a single habitat type, despite the assessment of multiple habitats  
30 at a landscape scale being more appropriate. This study aimed to determine the effects of  
31 landscape composition and spatial configuration on life-history trait distribution in carabid  
32 beetle and herbaceous plant communities. Here, we assessed the gamma diversity of carabid  
33 beetles and plants by sampling three dominant habitats (woody habitats, grasslands and crops)  
34 across 20 landscapes in western France. RLQ and Fourth Corner three-table analyses were  
35 used to assess the association of dispersal, phenology, reproduction and trophic level traits  
36 with landscape characteristics. Landscape composition and configuration were both  
37 significant in explaining functional composition. Carabid beetles and plants showed similar  
38 response regarding phenology, i.e. open landscapes were associated with earlier breeding  
39 species. Carabid beetle dispersal traits exhibited the strongest relationship with landscape  
40 structure; for instance, large and apterous species preferentially inhabited woody landscapes,  
41 whereas small and macropterous species preferentially inhabited open landscapes. Heavy  
42 seeded plant species dominated in intensified agricultural landscapes (high % crops), possibly  
43 due to the removal of weeds (which are usually lightweight seeded species). The results of  
44 this study emphasise the roles of landscape composition and configuration as ecological filters  
45 and the importance of preserving a range of landscape types to maintain functional  
46 biodiversity at regional scales.

47

48 **Keywords:** agriculture, assemblage, carabidae, community, flora, landscape ecology

## 49 **1. Introduction**

50

51 Agricultural landscapes occupy approximately 75% of Europe (Robinson and  
52 Sutherland, 2002), and support a high amount of plant and animal total biodiversity (Benton  
53 et al., 2003). Agricultural intensification and land-use changes represent major causes of  
54 biodiversity decline in agricultural landscapes (Strijker, 2005). Since the 2000s, maintaining  
55 biodiversity in agricultural landscapes has become an important social and economic issue,  
56 with a focus on preserving ecosystem functioning and ecosystem services provision (Kleijn  
57 and Sutherland, 2003; Le Roux et al., 2008; Millennium Ecosystem Assessment, 2005).

58 Spatio-temporal landscape heterogeneity strongly influences the species richness and  
59 composition of communities, and is consequently an important parameter that should be  
60 considered in biodiversity conservation (Fahrig et al., 2011; Huston, 1995; Turner, 1987). In  
61 agricultural landscapes, short-term (crop rotation) and long-term (agricultural intensification)  
62 temporal changes represent important drivers of biodiversity (Ernault et al., 2006; Le Feon et  
63 al., 2013). Diversity is also influenced by spatial heterogeneity, which is defined as a  
64 combination of two components, compositional and configurational heterogeneity (Duelli,  
65 1992; Fahrig et al., 2011). Landscape composition affects diversity as habitat diversity  
66 influences plant, vertebrate and invertebrate diversity (Benton et al., 2003; Poggio et al.,  
67 2010; Robinson et al., 2001; Woodcock et al., 2010). Landscape configuration which can be  
68 measured from the length of edges (or boundaries), influences species movements and  
69 spillovers (Blitzer et al., 2012; Brudvig et al., 2009; Concepcion et al., 2012; Tschardt et  
70 al., 2005). However, high landscape heterogeneity may also increase fragmentation *per se* and  
71 have negative effects on biodiversity. Hence, biodiversity is expected to peak at intermediate  
72 levels of heterogeneity. Yet, it remains unclear which ecological processes drive species  
73 response to landscape heterogeneity components in agricultural areas (Fahrig et al., 2011).

74           It is generally accepted that functional traits control species responses to landscape  
75 heterogeneity gradients (Barbaro and van Halder, 2009; Vallet et al., 2010), and are readily  
76 linked with ecological processes (Díaz and Cabido, 2001). Dispersal traits are considered to  
77 be the main traits affected by landscape heterogeneity (Hendrickx et al., 2009; Piessens et al.,  
78 2004). The phenology (Silvertown and Charlesworth, 2001; Tremlova and Munzbergova,  
79 2007) and longevity (Lindborg, 2007) of plants are also highly sensitive to landscape  
80 fragmentation. Therefore, in addition to local abiotic and biotic factors, landscape  
81 heterogeneity may be considered as an ecological filter (Tonn et al., 1990), which selects or  
82 excludes species from the regional pool according to particular functional traits (Keddy, 1992;  
83 Lomba et al., 2011). The species filtered by landscape composition and configuration  
84 represent the landscape species pool, with species being further selected by habitat type and  
85 local factors to form local species composition and diversity. Hence, it is essential to obtain  
86 knowledge about the landscape scale to describe the processes that govern ecological  
87 communities from the regional to the local scales.

88           In recent literature, some studies investigated the effect of landscape heterogeneity on  
89 gamma diversity, i.e. the “whole” diversity measured at a landscape scale (Bennett et al.,  
90 2006). Traditionally, the dominant “focal patch” approach has been used, which only tests the  
91 influence of landscape heterogeneity on a single site/patch (for a review see Thornton et al.,  
92 2011). In contrast, the assessment of gamma diversity allows the resulting overall diversity to  
93 be viewed, rather than the response of only one patch (Bennett et al., 2006). However, most  
94 existing studies that have used this approach, are focussing on a single habitat  
95 (Grasslands: Dauber et al., 2003; woodlands: Radford et al., 2005; hedgerows: Ernoult and  
96 Alard, 2011; Millan-Pena et al., 2003; crops: Concepcion et al., 2012). Such gamma diversity  
97 measures may be referred as “single-habitat gamma diversity”. However, landscapes are  
98 mosaics of different habitats, supporting communities of varying species composition.

99 Therefore, single-habitat gamma diversity only partially reflects overall landscape diversity,  
100 with the study of total landscape scale diversity being required to consider the diversity of  
101 multiple habitats, which we termed “multi-habitat gamma diversity”. Such measure of  
102 landscape-level gamma diversity hierarchically depends on local diversity (alpha) and beta  
103 diversity among patches of the same habitat types (beta patch) and among habitat types (beta  
104 habitat (Crist et al. 2003, Diekötter et al., 2008). Although mosaic-level diversity monitoring  
105 is important from a conservation and landscape planning perspective, there are limited studies  
106 using this approach (but see Liira et al., 2008).

107 Here, we investigated the distribution of dispersal, phenology, reproduction and  
108 trophic traits for carabid beetles and herbaceous plants along a gradient of spatial  
109 heterogeneity in typical western European agricultural landscapes. We evaluated multi-habitat  
110 gamma diversity, including crop habitats, to determine i) whether landscape heterogeneity  
111 (composition and configuration) serves as an environmental filter for species, ii) which  
112 functional traits are affected by the landscape heterogeneity, and iii) whether the observed  
113 response patterns could be extended to different species groups (i.e. across taxa).

114

## 115 **2. Materials and methods**

116

### 117 *2.1. Study area*

118

119 The study was conducted in hedgerow network agricultural landscapes located in the  
120 west of France (Fig. 1). These landscapes are typical of western Europe (Baudry et al., 2000)  
121 and have been subject to major modifications since the middle of the twentieth century  
122 because of agriculture intensification (Baudry and Papy, 2001; Meeus, 1993). The study area  
123 is located in a region where dominant agriculture is mixed dairy farming. The farmlands

124 contain annual crops (mostly winter cereals, but also corn), along with temporary and  
125 permanent grasslands, and are separated by woodlands and hedgerows (termed woody  
126 elements here). These two types of grasslands are comparable in this area, as they are often  
127 similarly managed (Roche et al., 2010).

128

## 129 *2.2. Sampling design*

130 Twenty square-shaped landscape sites of 1 km<sup>2</sup> were selected to maximise landscape  
131 compositional and configurational heterogeneity (Fig. 1). From a regional habitat map derived  
132 from remote sensing data (COSTEL Land-cover map, Hubert-Moy et al., 2012), landscapes  
133 were selected based on the percentage of semi-natural covers (composition) and the length of  
134 edges between semi-natural covers and farmland (configuration).

135 Within each studied landscape, we sampled carabid beetle and plant communities in  
136 the three characteristic habitats of the study area: crop, grassy, and woody habitats. Two  
137 patches of each habitat type were sampled in each landscape, i.e. two patches of the most  
138 abundant crop (winter cereals), two patches of grassland, and two patches of woody habitat.  
139 The variability in the types of woody habitat was addressed by sampling one hedgerow patch  
140 and one woodland patch. A total of 120 patches were sampled (6 in each landscape, Fig. 1).  
141 The sampled crop, grassland and woodland patches had an average area of 37.8 ha, 9.5 ha and  
142 3.4 ha respectively. The sampled hedgerows were, on average, 132 m long.

143 Carabid beetles were sampled using two pitfall traps per patch. The traps were  
144 positioned 10 m from the patch margins. Traps were collected every two weeks, after being  
145 open for seven consecutive days. There were two sampling seasons: from May to June 2011  
146 (containing four sampling periods), and September 2011 (containing 2 sampling periods),  
147 except for winter cereal patches, which were harvested in July. This sampling regime was  
148 designed to encompass the two main seasons during which carabid beetles emerge (Kromp,

149 1999). Data from each trapping period were pooled by sampled patch, and carabid species  
150 were identified following Roger et al. (2010).

151 Herbaceous plant species were sampled using three quadrats, the total area of which  
152 corresponded to the minimal recommended area of each habitat type (Mueller-Dombois and  
153 Ellenberg, 1974). These quadrats were distributed along transects from the margin to the  
154 centre of the patch to sample edge and interior species. Grasslands and winter cereal crops  
155 were sampled using 2 m x 2 m quadrats, established at 2, 6 and 10 m from the patch margin.  
156 Woodlands and hedgerows were sampled using respectively 5 m x 5 m and 5 m x 2 m  
157 quadrats, which were separated by a distance of 5 m. Data from the three quadrats were  
158 pooled for each sampled patch.

159 We pooled data from the three habitats for every landscape to obtain the multi-habitat  
160 gamma diversity. We used specific occurrence within each landscape site, with every plant  
161 and carabid species being assigned a value from 0 to 6 (0 indicated absent from every cover  
162 type, and 6 indicated present in the two patches x three cover types). Occurrence was the  
163 selected measure because it allows the diversity of habitats to be considered.

164

### 165 2.3. *Species traits*

166

167 We selected four carabid beetle life-history traits (Table 1) that are associated with  
168 vital functions (breeding phenology, diet and dispersal). First, we removed rare carabid  
169 species (less than 5 individuals found across all sampling sites, following Barbaro and van  
170 Halder, 2009). We then extracted the selected trait values from previous studies (Barbaro and  
171 van Halder, 2009; Ribera et al., 2001), and from a database currently under construction  
172 (BETSI, 2012). Finally, we checked that no trait categories contained too few species to avoid



173 any statistical bias. Sixty-two carabid beetle species were included in the analyses, which  
174 represented 84.9% of the total sampled carabid species.

175 For plants, we extracted trait values from existing databases (the Bioflor database,  
176 Kuhn et al., 2004, and the LEDA traitbase, Kleyer et al., 2008) to describe nine plant life-  
177 history traits that included phenology, reproduction and dispersal (Table 2). Species for which  
178 trait data were not available were excluded from the analyses. We analysed 153 herbaceous  
179 plant species, representing 88% of the total sampled herbaceous species. This ratio was  
180 consistent with Romermann et al. (2009), who retained at least 80% of the species pool. To  
181 avoid statistical bias, categories with too few species were merged with the closest ecological  
182 category (Barbaro and van Halder, 2009).

183

#### 184 *2.4. Landscape descriptors*

185

186 Descriptors of landscape heterogeneity were computed from detailed land-cover maps  
187 of each 1 km<sup>2</sup> landscape with Chloe 3.1 software (Baudry et al., 2006). Six landscape  
188 descriptors were computed to quantify variability in landscape composition and configuration.  
189 Composition was estimated using the percentage coverage in woody (woodlands and  
190 hedgerows), grassy (permanent and temporary grasslands) and crop habitats. Landscape  
191 spatial configuration was evaluated using the length of the three edge types among the three  
192 habitat categories ('woody.crop', 'woody.grassy', 'grassy.crop').

193

#### 194 *2.5. Statistical analyses*

195

196 Two complementary types of three-table analysis method were conducted to associate  
197 carabid and plant traits with landscape descriptors (Dziöck et al., 2011; Dray et al., *in press*).

198 Specifically, we used RLQ analysis (Doledec et al., 1996) to obtain a graphic display, and  
199 Fourth Corner analysis (Dray and Legendre, 2008) for statistical power. All analyses were  
200 computed using the ‘ade4’ package in R 3.00 software.

201 RLQ analysis was used to provide simultaneous ordination, and to analyse the joint  
202 structure of the three datasets: R (landscape descriptors), L (carabid beetles and plant  
203 occurrence data) and Q (species traits). First, all tables were analysed separately using the  
204 appropriate ordination method. Correspondence Analysis (CA) was used to analyse the L-  
205 species table. The R-landscape descriptors table was analysed using Principal Component  
206 Analysis (PCA), with the CA site scores being used as row weighting to couple R and L. The  
207 Q-trait tables for carabid beetles and plants were analysed respectively by Multiple  
208 Correspondence Analysis (MCA), and by a Hill Smith PCA, which combines quantitative and  
209 qualitative variables, using CA species scores as a column weighting to couple Q and L.  
210 Subsequently, RLQ analysis was used to combine the independent analyses in a simultaneous  
211 ordination. We tested the significance of the relationship between species traits and landscape  
212 descriptors (significance level at  $\alpha = 0.05$ ) using a Monte Carlo test (999 permutations). To  
213 determine which traits influenced the most the species distributions across landscapes,  
214 correlation ratios were calculated between traits and species ordination along the first and  
215 second RLQ axes (Doledec et al., 1996; Barbaro and van Halder, 2009).

216 Fourth Corner analysis was used to quantify and test the correlation between each trait  
217 category and each landscape descriptor. Two permutation tests were applied to determine  
218 correlation significance (Models 2 and 4, as recommended by Dray and Legendre, 2008).  
219 First, we tested the null hypothesis that “species assemblages are randomly attributed to sites,  
220 irrespective of the site characteristics” using 9999 permutations of site vectors (rows of L).  
221 Then, we tested the null hypothesis that “species are distributed irrespective of their traits”  
222 using 9999 permutations of species vectors (columns of L). From these two randomisation

223 models, the largest p-value was selected to establish significant correlations. The use of  
224 multiple landscape descriptors in the R-landscape descriptors table required Bonferroni  
225 correction. Furthermore, because two permutation models were used, we used the square root  
226 of this corrected alpha level (Dray and Legendre, 2008; Dziock et al., 2011). Therefore, the  
227 alpha value used to determine statistical significance in the Fourth Corner analysis was  $\alpha <$   
228 0.091.

229

### 230 **3. Results**

231

#### 232 *3.1. Global effects of landscape heterogeneity on species trait distributions*

233

234 RLQ analysis showed that carabid beetle and plant functional compositions were  
235 significantly related with landscape descriptors (permutation test, p-value = 0.020 and 0.019  
236 respectively). The two first RLQ analysis axes accounted for 91.4% of total carabid  
237 community variance (75.2 and 16.2%, respectively; Fig. 2a), and 82.5% of the total plant  
238 community variance (42.4 and 40.1%, respectively; Fig. 2b).

239 For both taxa, landscape composition and configuration descriptors correlated  
240 significantly with the first two RLQ analysis axes (Fig. 2). For carabid beetles (Fig. 2a), the  
241 first ordination axis of functional traits distribution contrasted more forested landscapes to  
242 open ones, dominated by grasslands and crops. The second axis differentiated landscapes with  
243 large areas of grassland from landscapes supporting other habitat types (crops and  
244 woodlands). For plants (Fig.2b), on the first axis, landscape descriptors associated with  
245 functional trait distributions were the descriptors associated to grasslands *versus* descriptors  
246 associated to crops. The second axis differentiated landscapes supporting increased woody  
247 habitats area from open landscapes with many grasslands and crops.

248           The highest correlation ratios between RLQ analysis axes and species traits were  
249   obtained for carabid beetle body size, wing system and breeding season (Table 3). The plant  
250   traits showed a weaker association to the RLQ analysis axes (Table 3). Plant seed mass, seed  
251   bank longevity, beginning of flowering and type of reproduction were associated with one of  
252   the two RLQ analysis axes. In addition, plant dissemination and pollen vector were equally  
253   correlated with the two axes (Table 3).

254

### 255 *3.2. Relationships between trait categories and landscape descriptors*

256

257           The results of the RLQ analyses were combined with Fourth Corner analysis. The  
258   latter showed significant correlations for landscape descriptors with carabid beetle and plant  
259   trait categories (p-value < 0.091, Table 4 and 5). The traits that were associated to the RLQ  
260   analysis axes were also significantly associated to the landscape descriptors in Fourth Corner  
261   analyses, except for plant dissemination and pollen vector. Therefore, these traits were not  
262   considered to be affected by landscape heterogeneity.

263           In wooded landscapes, carabid communities were dominated by apterous species,  
264   along with summer and autumnal breeders. In comparison, landscapes supporting a lower  
265   amount of woody habitats contained more spring breeders and macropterous species (Table  
266   4). These results are supported by the distribution of these traits along the first axis of the  
267   RLQ analysis (Fig. 2a). Regarding body size, medium-sized carabid beetles were significantly  
268   less common in landscapes with more ‘woody.grassy’ edges (Table 4). In addition, the RLQ  
269   analysis showed that ‘very large’ and ‘large’ sized carabid species were associated with  
270   wooded landscapes. In comparison, medium and small sized species were associated with  
271   landscapes characterised by higher crop percentages and greater lengths of ‘grassy.crop’  
272   edges (Fig. 2a).

273 For plants, landscapes with increased edge lengths between grasslands and crops  
274 enhanced species that have an intermediate flowering period. In comparison, late flowering  
275 species favoured woody landscapes (Table 5; opposite responses to ‘grassy.crop’ and  
276 ‘woody’). Species that primarily reproduce with seeds and that have high seed bank longevity  
277 were associated with woody landscapes. In comparison, species that mostly used vegetative  
278 reproduction and that have transient seeds were less common in these landscapes (Table 5).  
279 The trends observed from the Fourth Corner analyses were consistent with the trait  
280 distributions along the second axis of the RLQ analysis (Fig. 2b). In addition, plant species  
281 with lightweight seeds were associated with landscapes supporting a high proportion of grassy  
282 habitats (‘grassy’), whereas heavy seeded species were associated with highly cultivated  
283 landscapes (‘crop’) and greater ‘woody.crop’ length edges (Table 5). These results match the  
284 variation in seed mass that was observed along the first axis of the RLQ analysis (Fig. 2b).

285

#### 286 **4. Discussion and Conclusions**

287

##### 288 *4.1. Landscape composition and configuration: two drivers of functional composition*

289

290 This study shows that landscape heterogeneity acts as an ecological filter on the  
291 functional composition of landscape-level diversity. We found that the two landscape  
292 heterogeneity components (i.e. composition and configuration) contributed in the selection of  
293 species based on their phenology, reproduction and dispersal traits. Previous studies have  
294 already reported such landscape filtering on carabid wing systems (Hendrickx et al., 2009;  
295 Wamser et al., 2012), breeding season (Purtauf et al., 2005) and body size (Kotze and O'Hara,  
296 2003), in addition to plant seed mass (Tremlova and Munzbergova, 2007; Westoby et al.,  
297 1996), beginning of flowering (Silvertown and Charlesworth, 2001) and seed bank longevity

298 (Tremlova and Munzbergova, 2007). However, these studies focused on one particular habitat  
299 (e.g. grasslands or crops), whereas the current study detected these relationships for multi-  
300 habitat gamma diversity. Thus, we show that the dominance of a given trait category in a  
301 given landscape type indicates that all local community types tend to contain a greater  
302 frequency of species from a considered group, irrespective of habitat type. This observation  
303 implies that such species selection does not only occur within each habitat type, but also at the  
304 landscape scale.

305         There is a limited number of studies that addressed the question of landscape filter  
306 effects on multi-habitat gamma diversity (but see Liira et al., 2008 and Lomba et al., 2011).  
307 However, we used different traits compared to the previous studies; for instance, the  
308 mentioned studies did not include dispersal traits (dissemination type and seed mass). Hence,  
309 our study provides novel information about the landscape filtering effects on dispersal, which  
310 is a major landscape-level ecological process. In addition, the type of statistical analysis used  
311 by the previous studies did not explicitly quantify which traits caused the greatest species  
312 response to landscape heterogeneity gradients. In the current study, we used RLQ and Fourth  
313 Corner analyses to overcome this limitation, leading us to identify the reproduction period and  
314 dispersal capacity as the main traits that are affected by landscape heterogeneity.

315         Our results highlight the importance of taking compositional and configurational  
316 landscape heterogeneity into account, as both components played a significant role in  
317 landscape filtering effects. However, landscape composition and configuration had different  
318 effects and relative importance on carabid and plant diversity, showing, as discussed below,  
319 that distinct mechanisms drive the response of these two taxa (Fahrig, 2011). The importance  
320 of considering both landscape components was particularly noticeable for carabid and plant  
321 dispersal traits. Indeed, experimental-based and theoretical-based literature usually considers  
322 a major influence of landscape configuration on dispersal (see e.g. Hendrickx et al., 2009 for

323 carabids or Piessens et al., 2004). However, the present study showed that the two landscape  
324 heterogeneity components influenced dispersal traits selection at the landscape level (gamma  
325 diversity). This may be due to correlations between descriptors of composition and  
326 configuration, but, as all descriptors were included, their relative importance in driving  
327 functional composition could be identified (Smith et al., 2009). For instance, prior studies  
328 showed that landscape configuration had an effect on plant dispersal (Tremlova and  
329 Munzbergova, 2007; Westoby et al., 1996); however, the current study showed that  
330 compositional heterogeneity was the main factor influencing plant dispersal traits. The  
331 functional composition of the plant community at the landscape level (i.e. for all considered  
332 habitats) might largely depend on the dominant habitat type. Therefore, changes in habitat  
333 dominance along the composition gradient are expected to have a major influence on total  
334 functional composition, including dispersal traits.

335

#### 336 *4.2. Landscape stability: an ecological filter of carabid beetles and herbaceous plants*

337

338         This study showed that two landscape heterogeneity gradients influenced the  
339 functional composition of carabid beetle and plant communities in the studied landscapes.  
340 Some traits were selected along a gradient of increasing landscape openness (opposing woody  
341 landscapes to landscapes dominated by open habitats). In comparison, other traits were  
342 distributed along a gradient of increasing agricultural use (grassland vs. annual crops). These  
343 gradients may be considered as gradients of landscape stability. Indeed, open landscapes tend  
344 to be more disturbed due to intensified farming, whereas woody landscapes support greater  
345 amounts of stable habitats and less intensified farming systems (Baudry and Papy, 2001;  
346 Meeus, 1993). In addition, farming practices (such as ploughing and pesticide use) are more  
347 frequent in annual crops, which also have a faster turnover due to crop rotation compared to

348 grasslands. These inter- and intra- annual disturbances alter the stability of landscapes that  
349 have greater amounts of open habitats and where the annual crops dominate over grasslands.  
350 Hence, landscape stability, representing a measure of temporal heterogeneity, seems to exert a  
351 selective pressure on both carabid and plant species according to their phenology and  
352 dispersal capacity. This relationship between landscape openness and landscape stability  
353 should be tested by analysing land cover time series and surveying agricultural practices.  
354 Further research is also needed to better determine biodiversity response to temporal  
355 heterogeneity.

356         The gradient related to landscape openness selected early reproductive species for both  
357 carabid beetles and plants (breeding season and beginning of flowering). In the more  
358 disturbed landscapes, these species may reproduce before the onset of the main agricultural  
359 disturbances (e.g. mowing, grazing, pesticide spraying and harvest), resulting in higher  
360 reproductive success and persistence. This hypothesis is supported by local-scale studies  
361 showing that spring breeding carabid species are more abundant in open landscapes (Barbaro  
362 and van Halder, 2009; Purtauf et al., 2005) and that early flowering plants are selected in  
363 managed and disturbed sites (Ollerton and Lack, 1992; Silvertown and Charlesworth, 2001).  
364 Landscape openness also selected plant species with vegetative reproduction and transient  
365 seeds. In unstable open landscapes, transient seeded species might benefit their quick  
366 emergence rates, enabling them to develop before destruction or predation. Vegetative-  
367 reproducing species are adapted to disturbances, as they are able to reproduce and continue  
368 developing even when cut (harvest, mowing) or grazed. The similar trends observed for these  
369 two ecologically different taxonomic groups (herbaceous plants and carabid beetles) indicates  
370 that strong landscape filtering on the reproduction period at the scale of gamma diversity  
371 could be generalised to other taxonomic groups.



372 Carabid beetles and plant species experienced contrasting filtering effects on their  
373 dispersal traits with respect to landscape stability gradients. Carabid beetle dispersal traits  
374 were mainly selected by the landscape openness gradient. Landscapes dominated by annual  
375 crops and grasslands selected highly mobile carabid species (small, macropterous), which are  
376 able to adapt to rapidly changing spatial distributions in resources (Holland, 2002). In these  
377 landscapes, a high amount of edges between grasslands and annual crops may favour  
378 movement between highly disturbed crops and more stable grasslands, which act as  
379 temporary refuges or permit complementation (Purtauf et al., 2005). Low mobility species  
380 (large, apterous) were associated with stable landscapes, where they probably benefited from  
381 higher amounts of woody habitats (Kromp, 1999). These species that often need a  
382 combination of both woody and crop habitats might also benefit from edges between woody  
383 habitats and crops in these landscapes (Tschardt et al., 2005). In contrast, plant dispersal  
384 traits (i.e. seed mass) were selected by the gradient of agricultural use (grasslands vs. crops).  
385 Landscapes with increased amounts of more stable habitats (grassland) favoured lightweight  
386 seeded species. In comparison, heavy weight seeded species were favoured in landscapes with  
387 an increased proportion of annual crops and ‘woody.crop’ edges length. These landscapes are  
388 subject to higher herbicide use, and are characterised by a low diversity and abundance of  
389 arable weeds (Storkey et al., 2012), which largely support lightweight seeds. Moreover,  
390 farmers commonly use herbicides on the adjacent hedgerows or woodlot edges of crop fields  
391 to reduce colonisation by non-crop plants (Jamoneau et al., 2011). These practices reduce the  
392 quantity of weeds, and explain the effect of ‘woody.crop’ edges. Plant dispersal modes were  
393 not influenced by landscape structure, which contradicted most previous studies (Piessens et  
394 al., 2004; Tremlova and Munzbergova, 2007), except a recent one (Alignier et al., 2012). Our  
395 results may be due to the fact that dispersal is not a limiting factor at the scale (1km<sup>2</sup>) or in the  
396 landscape type (hedgerow landscapes) of the study. Also, as we studied several traits

397 simultaneously, it is possible that the landscape heterogeneity filtering of plant species  
398 according to their dispersal mode was hidden by much stronger effects on other traits (e.g.  
399 phenology).

400

#### 401 *4.3 Conclusions*

402

403 We used multi-habitat gamma diversity to study variation in plant and carabid beetle  
404 functional composition across a landscape heterogeneity gradient. As a result, we  
405 demonstrated the role of landscape stability as an ecological filter of carabid beetles and  
406 herbaceous plants in relation to their dispersal and phenology traits. We suggest that future  
407 work focused on studying the role of landscape as ecological filter of gamma diversity, should  
408 compare the response of multiple taxa by grouping ecological traits within shared ecological  
409 functions. Such research would help identify general rules about species responses to  
410 landscape heterogeneity, in addition to linking these effects to ecosystem functioning. We  
411 found that different landscapes support different sets of functional groups, indicating that all  
412 functional groups cannot be preserved at the same time, which is an important issue for  
413 conservation management. Hence, it seems that it is necessary to preserve a diversity of  
414 landscape types to preserve functional biodiversity at a regional scale.

415

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425

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612

613 **TABLES**614 **Table 1:** Categories of life history traits used for carabid beetle species

Vital function	Carabid species traits	Categories	Code
Trophic level	Diet	Generalist predators*	D_pred_g
		Specialist predators*	D_pred_s
		Phytophagous	D_phyto
Dispersion	Wing system	Apterous	W_apr
		Dimorphic	W_dim
		Macropterous	W_macro
	Body size (length in mm)	Very small (< 6 mm)	BS_VS
		Small (6 -7.9 mm)	BS_S
		Medium (8 - 9.9 mm)	BS_M
		Large (10 -11.9 mm)	BS_L
		Very large (> 12 mm)	BS_VL
Phenology	Breeding season	Spring	BrS_spr
		Summer	BrS_sum
		Autumn	BrS_aut

615 \* The “Generalist predators” diet category refers to carabid species which are opportunist  
616 predators and have a wide diet, while “Specialist predators” refers to species that feed  
617 only/mostly on collembola.

618 **Table 2:** Categories of life history traits used for herbaceous plant species

Vital function	Plant species traits	Categories	Code
Dispersion	Seed mass	Continuous trait	Seed_mass
	Dissemination	Anemochory	D_an
		Barochory	D_ba
		Zoochory	D_zoo
		Other dispersal mode	D_other
Phenology	Seed bank longevity	Transient	SBL_trans
		Short term	SBL_short
		Long term	SBL_long
	Age of first flowering	Within 1 year	AOF_early
		More than 1 year	AOF_late
	Life span	Annual and biannual	LS_a
		Perennial	LS_p
	Beginning of flowering	[January-March]	BOF_early
		[May-June]	BOF_med
		[July-September]	BOF_late
	Duration of flowering (nb. of months)	Very short (< 3)	DOF_VS
		Short ([3-4])	DOF_S
Long (> 4)		DOF_L	
Reproduction	Type of reproduction	Only by seed	TR_s
		Mostly by seed, rarely vegetatively	TR_ssv
		By seed and vegetatively	TR_sv
	Pollen vector	Insect	PV_in
		Selfing	PV_se
		Wind	PV_wi
		Various pollen vectors	PV_var

619 **Table 3:** Correlation ratios (CR) between carabid beetle traits (a) or herbaceous plant traits  
 620 (b) and the two first axes of RLQ analysis. Traits with highest correlation ratio are in bold.

	Species trait	CR Axis 1	CR Axis 2
(a) Carabid beetles	Diet	0.03	0.02
	<b>Wing system</b>	<b>0.13</b>	0.01
	<b>Body size</b>	<b>0.18</b>	0.10
	<b>Breeding season</b>	<b>0.24</b>	0.01
(b) Herbaceous plants	<b>Seed mass</b>	<b>0.03</b>	0.01
	<b>Dissemination</b>	<b>0.02</b>	<b>0.02</b>
	<b>Seed bank longevity</b>	0.00	<b>0.04</b>
	Age of first flowering	0.02	0.00
	Life span	0.00	0.03
	<b>Beginning of flowering</b>	0.00	<b>0.07</b>
	Duration of flowering	0.02	0.00
	<b>Type of reproduction</b>	<b>0.03</b>	0.02
<b>Pollen vector</b>	<b>0.02</b>	<b>0.02</b>	

621

622 **Table 4:** Fourth Corner analysis of the effects of landscape descriptors on carabid beetle  
623 traits. + and - symbols correspond to positive and negative correlations between the  
624 considered trait category and landscape descriptor. Only the significant correlations (p-values  
625 < 0.091, see methods section for explanation) are reported, empty cells represent non-  
626 significant correlations. See Table 1 for trait codes. In bold are the traits that were correlated  
627 with RLQ axes and showing significant correlation with Fourth Corner.

		Woody	Grassy	Crop	Woody.Grassy	Grassy.Crop	Woody.Crop
Diet	D_pred_g						
	D_pred_s						
	D_phyto						
<b>Wing System</b>	W_apr		+				
	W_dim						
	W_macro		-				
<b>Body Size</b>	BS_VS						
	BS_S						
	BS_M				-		
	BS_L						
	BS_VL						
<b>Breeding Season</b>	BrS_spr		-				
	BrS_sum		+				
	BrS_aut		+				

628 **Table 5:** Fourth Corner analysis of the effects of landscape descriptors on herbaceous plant  
629 traits. + and - symbols correspond to positive and negative correlations between the  
630 considered trait category and landscape descriptor. Only the significant correlations ( $p$ -values  
631  $< 0.091$ , see methods section for explanation) are reported, empty cells represent non-  
632 significant correlations. See Table 2 for trait codes. In bold are the traits that were correlated  
633 with RLQ axes and showing significant correlation with Fourth Corner.

		Woody	Grassy	Crop	Woody.Grassy	Grassy.Crop	Woody.Crop
<b>Seed Mass</b>	Seed_mass		-	+			+
Dissemination	D_an						
	D_ba						
	D_other						
	D_zoo						
<b>Seed Bank Longevity</b>	SBL_long	+					
	SBL_short						
	SBL_trans	-					
Age of First Flowering	AOF_early				-		
	AOF_late				+		
Life Span	LS_a	+					
	LS_p	-					
<b>Beginning Of Flowering</b>	BOF_early						
	BOF_late	+				-	
	BOF_med	-				+	
Duration Of Flowering	DOF_L						
	DOF_S						+
	DOF_VS						-
<b>Type of Reproduction</b>	TR_s	+					
	TR_ssv						+
	TR_sv						
Pollen Vector	PV_in						
	PV_se						
	PV_var						
	PV_wi						

634



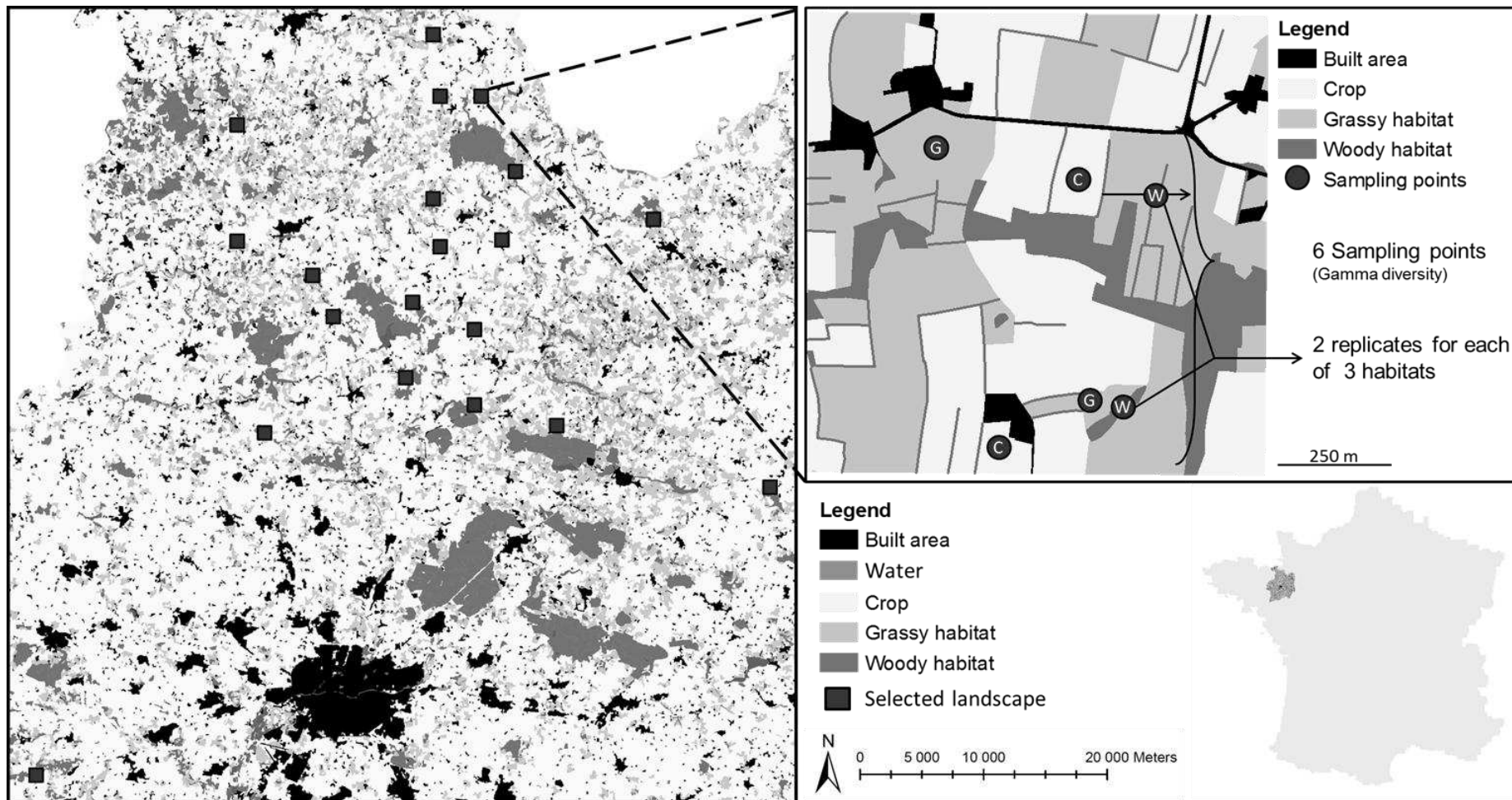
635 **FIGURE CAPTIONS**

636

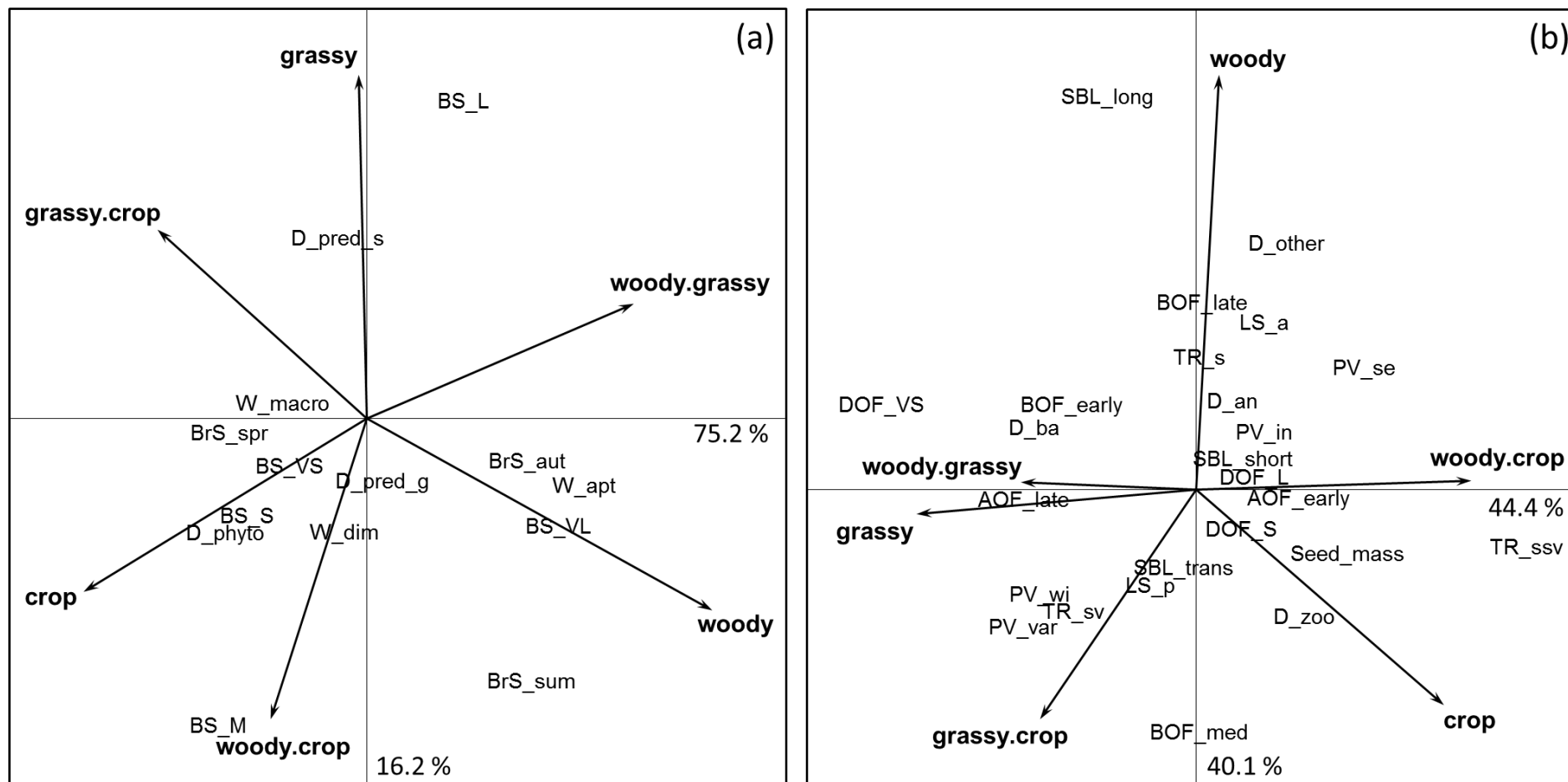
637 **Figure 1:** Map of the study area showing the 20 x 1km<sup>2</sup> selected landscapes (a) and the  
638 hierarchical sampling design of one of these landscapes (b). The sampled cover types are W:  
639 woody habitat, G: grassland and C: winter cereal crop.

640

641 **Figure 2:** Ordination of landscape descriptors and species trait categories along the two first  
642 axes of the RLQ analysis, for carabid beetles (a) and herbaceous plants (b). Numbers  
643 represent percentages of variance explained by each axes. See Table 1 and 2 for trait category  
644 codes.



648 **Figure 2**



649