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1 **Title**

2 Landscape heterogeneity as an ecological filter of species traits

3

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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 km² 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 km² 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 (1km²) 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 |
| | Wing system | 0.13 | 0.01 |
| | Body size | 0.18 | 0.10 |
| | Breeding season | 0.24 | 0.01 |
| (b) Herbaceous plants | Seed mass | 0.03 | 0.01 |
| | Dissemination | 0.02 | 0.02 |
| | Seed bank longevity | 0.00 | 0.04 |
| | Age of first flowering | 0.02 | 0.00 |
| | Life span | 0.00 | 0.03 |
| | Beginning of flowering | 0.00 | 0.07 |
| | Duration of flowering | 0.02 | 0.00 |
| | Type of reproduction | 0.03 | 0.02 |
| Pollen vector | 0.02 | 0.02 | |

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 | | | | | | |
| Wing System | W_apr | + | | | | | |
| | W_dim | | | | | | |
| | W_macro | - | | | | | |
| Body Size | BS_VS | | | | | | |
| | BS_S | | | | | | |
| | BS_M | | | | - | | |
| | BS_L | | | | | | |
| | BS_VL | | | | | | |
| Breeding Season | 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 |
|-------------------------------|-----------|-------|--------|------|--------------|-------------|------------|
| Seed Mass | Seed_mass | | - | + | | | + |
| Dissemination | D_an | | | | | | |
| | D_ba | | | | | | |
| | D_other | | | | | | |
| | D_zoo | | | | | | |
| Seed Bank | SBL_long | + | | | | | |
| Longevity | SBL_short | | | | | | |
| | SBL_trans | - | | | | | |
| Age of First Flowering | AOF_early | | | | - | | |
| | AOF_late | | | | + | | |
| Life Span | LS_a | + | | | | | |
| | LS_p | - | | | | | |
| Beginning Of Flowering | BOF_early | | | | | | |
| | BOF_late | + | | | | - | |
| | BOF_med | - | | | | + | |
| Duration Of Flowering | DOF_L | | | | | | |
| | DOF_S | | | | | | + |
| | DOF_VS | | | | | | - |
| Type of Reproduction | TR_s | + | | | | | |
| | TR_ssv | | | | | | + |
| | TR_sv | | | | | | |
| Pollen Vector | PV_in | | | | | | |
| | PV_se | | | | | | |
| | PV_var | | | | | | |
| | PV_wi | | | | | | |

634

635 **FIGURE CAPTIONS**

636

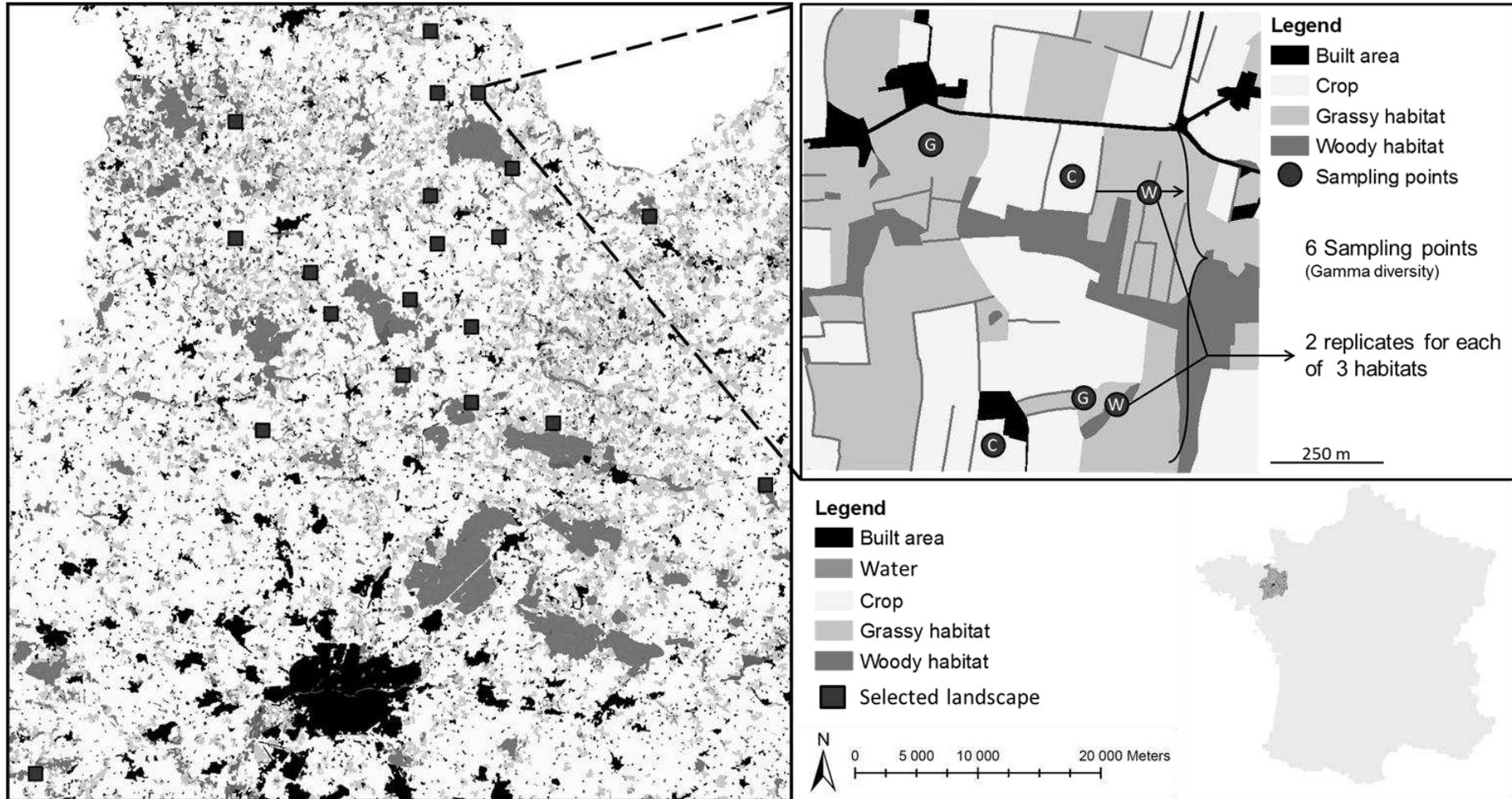
637 **Figure 1:** Map of the study area showing the 20 x 1km² selected landscapes (a) and the
638 hierarchical sampling design of one of these landscapes (b). The sampled cover types are W:
639 woody habitat, G: grassland and C: winter cereal crop.

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.

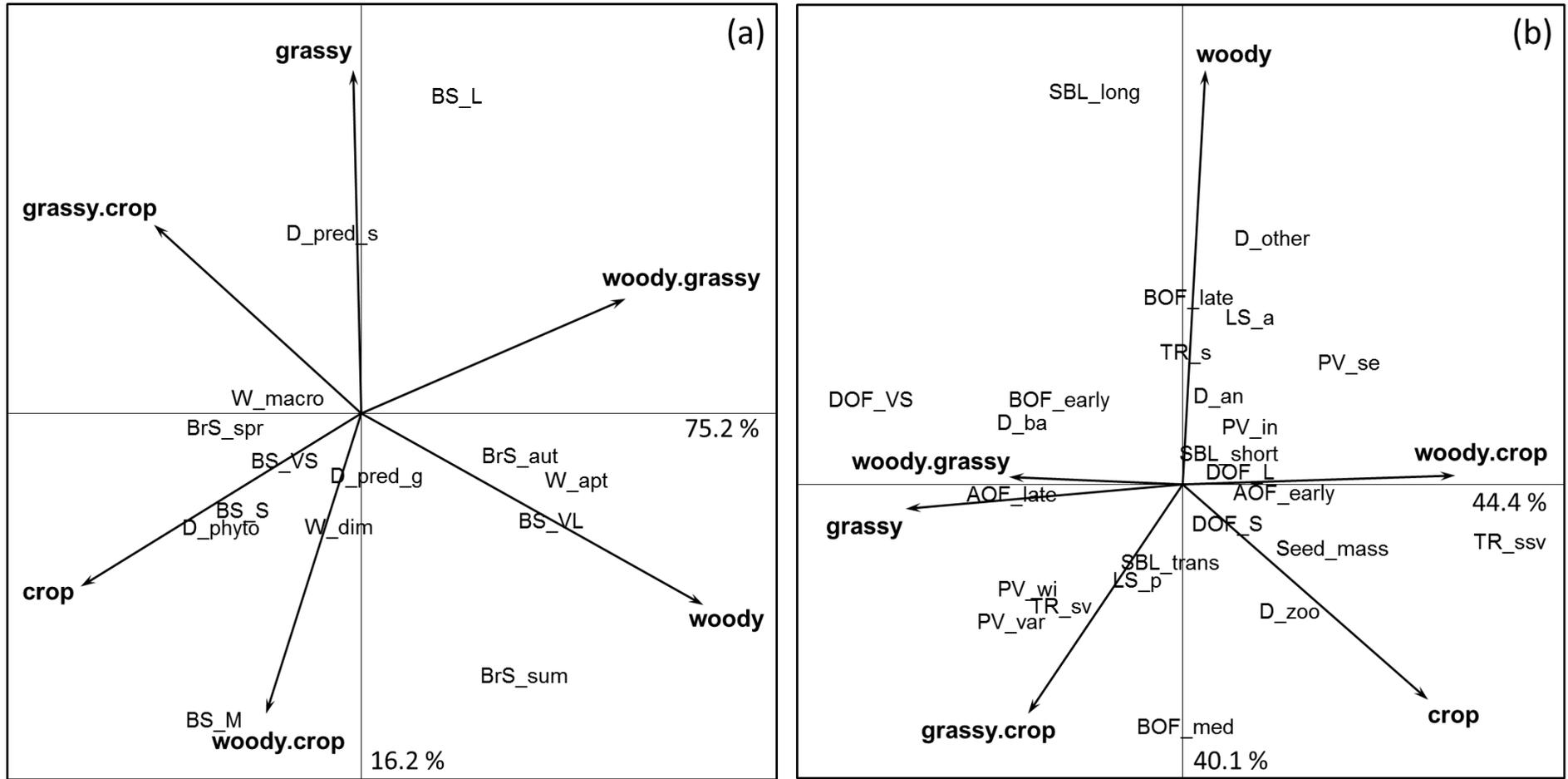
645 FIGURES

646 Figure 1



647

648 **Figure 2**



649