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Adjacent woodlands rather than habitat connectivity influence grassland plant, carabid and bird assemblages in farmland landscapes

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5 **Title:**

6 Adjacent woodlands rather than habitat connectivity influence grassland plant, carabid and bird
7 assemblages in farmland landscapes

8

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19

20 **Abstract**

21 One response to biodiversity decline is the definition of ecological networks that extend beyond
22 protected areas and promote connectivity in human-dominated landscapes. In farmland, landscape
23 ecological research has focused more on wooded than open habitat networks. In our study, we
24 assessed the influence of permanent grassland connectivity, described by grassland amount and spatial
25 configuration, on grassland biodiversity. We selected permanent grasslands in livestock farming areas
26 of north-western France, which were sampled for plants, carabids and birds. At two spatial scales we
27 tested the effects of amount and configuration of grasslands, wooded habitats and crops on richness
28 and abundance of total assemblages and species ecological groups. Grassland connectivity had no
29 significant effects on total richness or abundance of any taxonomic group, regardless of habitat affinity
30 or dispersal ability. The amount of wooded habitat and length of wooded edges at the 200 m scale
31 positively influenced forest and generalist animal groups as well as grassland plant species, in
32 particular animal-dispersed species. However, for animal groups such as open habitat carabids or
33 farmland bird specialists, the same wooded habitats negatively influenced richness and abundance at
34 the 500 m scale. The scale and direction of biodiversity responses to landscape context were therefore
35 similar among taxonomic groups, but opposite for habitat affinity groups. We conclude that while
36 grassland connectivity is unlikely to contribute positively to biodiversity, increasing or maintaining
37 wooded elements near grasslands would be a worthwhile conservation goal. However, the
38 requirements of open farmland animal species groups must be considered, for which such action may
39 be deleterious.

40

41 **Key words**

42 Multi-taxon biodiversity; habitat network; random forests; multi-model inference; dispersal;
43 hedgerow; human-dominated landscapes

44

45 **Highlights**

46 Permanent grassland connectivity had little effect on biodiversity

47 Wooded habitats in the landscape influenced grassland plants, carabids and birds

48 Open habitat animal specialists avoided landscapes with woods and hedgerows

49 Response to landscape was more dependent on habitat affinity than on taxonomic group

50 Increasing or maintaining wooded elements near grasslands may be good policy

51

52 **1. Introduction**

53 In human-dominated, highly fragmented landscapes, site protection alone is unlikely to achieve the
54 objective of stopping or reversing biodiversity declines (Bennett and Saunders 2010). Rather
55 enhancing habitat connectivity or linkages, such as ecological corridors and networks, will be needed
56 to ensure the viability of plant and animal populations (Crooks and Sanjayan 2006). This connectivity
57 depends on the amount (area) and spatial configuration of suitable habitat as well as on matrix
58 permeability (Bennett 2003). Nature conservation policy has accordingly evolved towards the
59 implementation of habitat networks (ecological networks or greenveining), which are increasingly
60 integrated into international, national or regional planning; particularly in Europe (Boitani et al. 2007;
61 Jongman et al. 2011). For example, since 2009 in France, it has become a legal requirement that
62 habitat networks be established at national, regional and local levels (Vanpeene-Bruhier and
63 Amsallem, 2014). Most territory may potentially be concerned by this policy's implementation,
64 including areas subject to more or less intense human activity. The need to develop nature
65 conservation outside protected areas has been accompanied by the recognition that most conservation
66 efforts have tended to focus on rare species and habitats, sometimes to the detriment of common
67 biodiversity (Inger et al. 2015). However, such biodiversity dominates ecosystem composition and
68 makes an important contribution to ecosystem functioning (Gaston and Fuller 2008; Gaston 2008).
69
70 Agriculture is clearly one of the major human activities to be concerned by these shifts in policy.
71 Farming landscapes occupy large areas of land (approximately 75% in Europe, Robinson and
72 Sutherland 2002, and up to 40% globally, Foley et al. 2005) and are associated with a valuable and
73 partly typical flora and fauna (Benton et al. 2003), which has declined severely over the past few
74 decades (Chamberlain et al. 2000; Donald et al. 2001; Lira et al. 2008). There is some consensus on
75 the importance of landscape complexity, or the amount of semi-natural habitat, in determining levels
76 of biodiversity in farmland landscapes (Benton et al. 2003; Tschardt et al. 2012). In this context,
77 attempts are being made to preserve and enhance semi-natural habitats of ecological value, like
78 hedgerows and permanent grasslands. These habitats have generally diminished (Meeus 1993) and are

79 the focus of some considerable attention in the context of nature conservation in farming areas. For
80 instance, in France permanent grasslands declared by farmers represented 6.7 million ha of agricultural
81 land at national scale in 2006. By 2010 6.3% of them had been lost, replaced by temporary grasslands
82 or scrubland (Faïq et al. 2013). Enhanced connectivity of these semi-natural habitats is expected to
83 counteract the negative effects of such reductions in biodiversity (e.g. Hendrickx et al. 2007).
84
85 Studies of connectivity effects in farmland contexts have tended to focus on wooded habitat types (e.g.
86 Gil-Tena et al. 2014; Neumann et al. 2016). The effectiveness of linear woodland habitats, like
87 hedgerows, as corridors facilitating forest specialist dispersal has been demonstrated for a diversity of
88 taxonomic groups: birds (Davies and Pullin 2007), arthropods (e.g. carabid beetles, Petit 1994; Millan-
89 Pena et al. 2003), plants (Jamoneau et al. 2011) and small mammals (Gelling et al. 2007). Meanwhile
90 the possible effects of increasing permanent grassland connectivity for farmland biodiversity have
91 received relatively less attention. Most studies of grassland connectivity have concentrated on rarer
92 grasslands of high conservation value, such as wet grasslands (e.g. Lafage et al. 2015), calcareous
93 grasslands (e.g. Brückmann et al. 2010; Rösch et al. 2013), heathland (e.g. Piessens et al. 2005),
94 species-rich grasslands at higher altitudes (e.g. Marini et al. 2008) or indigenous grasslands
95 fragmented by commercial forestry (e.g. Samways & Pryke, 2016). These studies, involving a
96 diversity of taxonomic groups, have shown that species of open, grassland habitats may respond
97 positively to increasing grassland connectivity. Common permanent grasslands of agricultural
98 mosaics, which are mesophilic, managed grasslands that have not been ploughed for several years,
99 have been understudied in landscape connectivity research. With their lack of vertical heterogeneity
100 and dependence on highly variable forms of management, such grasslands are difficult to describe
101 (Allen et al. 2011) and until the recent focus on common biodiversity may have been expected to
102 harbour few species of conservation interest. Only a few studies in Europe have begun to explore how
103 connectivity of more managed grasslands may influence arthropods and plant assemblages (Öckinger
104 et al. 2012; Wamser et al. 2012; Villemey et al. 2015). These studies found contrasting effects of
105 grassland connectivity on species richness. Thus, it is important to further explore to what extent

106 connectivity of common permanent grassland contributes to maintaining biodiversity in farmland
107 mosaics.

108

109 The effects of landscape context depend on the varying scales of perception of taxa with differing
110 dispersal abilities (Jackson and Fahrig 2012) and within-taxa differences in dispersal ability may
111 potentially obscure the effects of connectivity at assemblage level (e.g. Wamser et al. 2012). In
112 addition, species with different habitat affinities may display opposing responses to landscape
113 structure (Mauremooto et al. 1995; Thomas et al. 1998; Filippi-Codaccioni et al. 2010). Therefore,
114 using two spatial scales, we aimed to assess how variation in grassland connectivity (amount and
115 spatial configuration) influenced the richness and abundance of various taxonomic groups with
116 potentially different scales of landscape perception: plants, carabids and birds observed in common,
117 mesophilic, permanent grasslands. We hypothesized that grassland connectivity would increase
118 richness and / or abundance of these assemblages. We also looked at the richness and abundance of
119 species groups based on habitat affinity and dispersal ability, and compared the influence of grasslands
120 with that of wooded habitats and crops in the surrounding landscape. We further hypothesized that
121 grassland specialist or open habitat species would benefit most from grassland connectivity or amount
122 of crops. Wooded habitats (particularly hedgerows) may act as barriers for these species, while they
123 may help forest species to disperse and therefore increase richness and abundance of this group in
124 grasslands. We expected a stronger influence of landscape structure on species with low dispersal
125 ability.

126

127 **2. Method**

128 2.1. Study areas and permanent grassland selection

129 The study was conducted in north-western France, where farmland landscapes contain annual crops
130 (mostly winter cereals, but also spring maize and oilseed rape), along with temporary and permanent
131 grasslands (not ploughed for at least 5 years), separated by woodland and hedgerow networks (which
132 will be referred to as wooded habitats). We selected four study areas located close to Nantes, Angers,

133 La-Roche-sur-Yon and Rennes which shared the same climate (temperate oceanic), geo-morphological
134 conditions (acidic substrate: schists, granites, sandstones) and a similar agricultural history of mixed
135 dairy farming systems (Appendix 1A). In these areas, we selected permanent grasslands to maximize
136 variation in the proportion of permanent grassland in the surrounding landscape. These production
137 grasslands were originally established by farmers, using a mixture of sown species of grasses and
138 sometimes clover, but most plant species were native. In western Europe and elsewhere, such
139 grasslands have a long history of agricultural management, and their biodiversity has long been
140 determined by the dynamics of regular mowing and grazing. To minimise other sources of variation,
141 we excluded wet grassland and grasslands that were close to major roads or urban infrastructure. All
142 were grazed, as this factor is known to have a strong influence on grassland plant assemblages
143 (Gaujour et al., 2012).

144

145 2.2. Sampling and biodiversity measures

146 Biodiversity was sampled in between 21 and 55 permanent grasslands, depending on taxonomic
147 group. The proportion of grassland in the landscape surrounding sampled grasslands (200m-radius
148 buffer) ranged from 12 to 85% for plant, from 10 to 58% for carabids and 28 to 85% for birds. Plants
149 were sampled in 55 permanent grasslands (4 Nantes, 18 Angers, 14 La Roche-sur-Yon, 19 Rennes).
150 Each grassland was visited once between 2011 and 2015, in the late spring or summer (May –July).
151 All vascular species were listed within 3 quadrats of 2 x 2m per grassland, placed at least 2 m from the
152 field edge, and these were subsequently pooled for calculation of species richness measures.

153

154 Carabid beetles were sampled in 40 permanent grasslands (40 Rennes), using pitfall traps. Two pitfall
155 traps per grassland were located 1m from each other and 10m from grassland edge. Carabids were
156 sampled during six sampling periods, two per month in May, June and September 2011, to coincide
157 with the seasons during which carabid beetles emerge (spring and late summer). Traps were collected
158 every two weeks, after being open for seven consecutive days. Eliminating a few lost traps (destroyed
159 by cattle), we measured activity-density as the number of individuals per trap per week and we

160 checked that the number of valid traps did not influence species richness. The six sampling periods
161 were then pooled to calculate species richness and activity-density measures for each grassland.

162

163 Birds were sampled in 21 permanent grasslands (10 Angers, 11 La Roche-sur-Yon) and their
164 associated field margin vegetation, using standard territory mapping (Bibby et al. 2000). The
165 grasslands were visited six times per breeding season in 2014 and 2015 (between mid-March and mid-
166 June). All bird surveys were carried out by a single observer between 1 and 4 hours after sunrise, on
167 days without continuous rain or wind. Species defending one or more territories in at least one of the
168 two years were considered to be breeding birds. The two years were pooled for calculation of species
169 richness measures while abundance values corresponded to the maximum number of territories a
170 species defended over the two years.

171

172 Plants, carabids and birds were classified according to their habitat affinity (generalists, grassland or
173 open farmland specialists, woodland specialists) or to their dispersal ability (dispersal mode for plants,
174 wing system for carabids and a morphological dispersal ability predictor for birds; see below). Species
175 richness and abundance (for carabids and birds) were calculated for each habitat affinity or dispersal
176 ability group. Plant ecological preferences were adapted from Baseflor database (Julve, 1998) and
177 plant dispersal mode extracted from Bioflor (Kuhn et al. 2004) and Baseflor (Julve 1998) databases
178 (Appendix 1B). Carabid habitat affinity data were adapted from Neumann et al. (2016) and Roger et
179 al. (2010). Carabid species dispersal ability was estimated by the wing system (Kotze and O'Hara
180 2003; Purtauf et al. 2004) using information from Barbaro and van Halder (2009), Ribera et al. (2001),
181 and BETSI database (2012, Appendix 1C). Bird habitat affinity groups were based on analysis of
182 national bird monitoring data (Jiguet 2010) except for 14 missing species, for which we used regional
183 atlas descriptions of habitat use (Marchadour 2014). Bird dispersal ability was estimated by using the
184 quotient of Kipp's distance (distance between the tip of the first primary feather to the tip of the wing)
185 and bill depth (measured at the proximate edge of the nostrils), which has been shown to be a good
186 surrogate for natal dispersal distance in European passerines (Dawideit et al. 2009). Biometric data
187 were provided by the Senckenberg Biodiversity and Climate Research Centre in Frankfurt, Germany

188 (for details, see Laube et al. 2013). Based on the obtained dispersal ability predictor we classified birds
189 into 4 dispersal categories (low, medium, high and long distance) using Jenks natural breaks
190 (Appendix 1D). Some bird ecological groups containing very few species, at low levels of frequency
191 or abundance, were excluded from analysis (urban species and long-distance dispersers).

192

193 2.3. Land-cover maps and landscape descriptors

194 We produced land-cover maps of the four study areas using existing land cover databases coupled
195 with automatic classification of satellite imagery, and corrected by photo-interpretation and ground-
196 truthing. Land-cover classification was as follows: built-up area (roads and buildings), water bodies,
197 crop fields, permanent grasslands, and wooded habitats (woodland and hedgerows). We paid particular
198 attention to the accurate estimation of permanent grassland distribution, using photo-interpretation and
199 the Land Parcel Identification System (i.e. Registre Parcellaire Graphique), where farmers subsidised
200 by the Common Agricultural Policy (CAP) declare field use. These maps were produced using QGIS
201 (QGIS Development Team, 2015).

202

203 Landscape descriptors were calculated from these maps within 200m and 500m radius, circular buffers
204 centred on each sampled grassland, in order to describe two components of the connectivity of
205 permanent grassland, i.e. grassland amount and grassland configuration. These circular buffers were
206 centred on field centroids for plants and birds, or on exact trap locations for carabids (recorded with a
207 GPS). The choice of two spatial scales was to account for expected differing grains of landscape
208 perception between plants, carabids and birds (Jackson and Fahrig, 2012). Amount of permanent
209 grassland was described as the proportion of surface area covered by these habitats in buffers.

210 Configuration of permanent grassland was assessed via three contrasting landscape descriptors, chosen
211 to investigate the possible influence of different forms of spatial arrangement: largest grassland patch
212 area, length of permanent grassland edges and a grassland connectivity index (derived from Hanski
213 1999, see Steffan-Dewenter 2003):

$$214 C_k = \sum_i^n e^{-D_{ik}} A_i$$

215 where k is the focal sampled permanent grassland, n the number of other (non-sampled) permanent
216 grasslands in the 200 m or 500 m scale landscape, D_{ik} is the distance between the sampled grasslands k
217 and the neighbouring permanent grassland i and A_i the area of the neighbouring permanent grassland i .
218 This measure of connectivity increases when many, large, permanent grasslands are located near the
219 sampled grassland. The proportion of other main habitat types was also calculated for the two buffer
220 sizes: wooded habitat (woodlands + hedgerows), and crops (including temporary grasslands which are
221 part of crop rotations). Total length of wooded habitat edges was also measured as it reflects
222 fragmentation of open habitats and adjacencies between open and wooded habitats. In the studied
223 landscapes, wooded habitat edges mostly corresponded to the presence of hedgerows. Landscape
224 descriptors were calculated at the two spatial scales using Chloé 2012 (Boussard and Baudry 2014).
225 The extent of variation in each landscape descriptor, obtained at each scale and for each study taxon, is
226 presented in Appendices 1E and 1F.

227

228 2.4. Statistical analyses

229 To test the representativeness of our sampled communities compared to potential richness, we
230 calculated non-parametric species richness estimators of Chao2 across all grasslands (Chao, 1987).
231 These estimated richness values were compared to the observed total number of species, for each
232 taxon. We tested the effect of landscape descriptors on biodiversity measures using two successive
233 steps (e.g. see Puech et al. 2014, Aviron et al. 2016): (i) preselection of landscape descriptors with
234 random forest procedure, (ii) multi-model inference (MMI) and averaging of multiple regression
235 models. Pearson's correlations between landscape descriptors and across scales are presented in
236 Appendices 1G-I.

237

238 All seven landscape descriptors at both scales (14 variables) were included in a random forest analysis
239 (Breiman 2001; Strobl et al. 2009), a recursive partitioning method recommended to deal with “small
240 n large p problems” (i.e. few replicates and many environmental variables), complex interactions and
241 correlated environmental variables (Strobl et al. 2008). For each biodiversity measure, 10,000 trees
242 were grown and landscape descriptor importance was evaluated as the difference in model accuracy

243 before and after 10 permutations of values of the considered descriptor, averaged over all trees.
244 Conditional importance that adjusts for correlations between environmental variables was used. The
245 absolute importance value of the lowest negative-scoring landscape descriptor was used as a threshold
246 to determine relevant and informative variables to retain for regression models (for full details, see
247 Strobl et al. 2008, 2009). Landscape descriptors selected for each biodiversity measure may be found
248 in Appendices 1J-L. To assess the influence of landscape descriptors on the global assemblage, the
249 conditional importance values of each variable were averaged across the biodiversity measures for
250 each taxon.

251

252 The selected landscape descriptors were then included in multiple regression models, which was
253 analysed using multi-model inference (MMI) and model averaging. MMI analysis deals with model
254 selection uncertainty (Burnham and Anderson 2002; Arnold 2010) and is robust against correlation
255 among descriptors (Smith et al. 2009, 2011). All landscape descriptors were mean-centred and divided
256 by the standard deviation to make the coefficients comparable (Smith et al. 2009, 2011). Following the
257 MMI procedure, we created linear models for each possible combination of landscape descriptors and
258 ranked them based on the corrected Akaike information criterion (AICc). Then, we computed
259 standardised average regression coefficients weighted by the Akaike weights across supported best
260 models ($\Delta AICc < 4$) and tested their significance using unconditional 95 % confidence intervals
261 (Burnham and Anderson 2002; Smith et al. 2009, 2011). Averaged model coefficients and their 95 %
262 confidence intervals are presented in Appendices 1M-P. We also checked that the detected effects
263 were consistent across all individual models included in model averaging (appendix 2). We more
264 specifically looked at the correct estimation of relative effects of correlated landscape descriptors
265 (grassland-related vs. wooded habitat descriptors, composition vs. configuration descriptors, and
266 between scales).

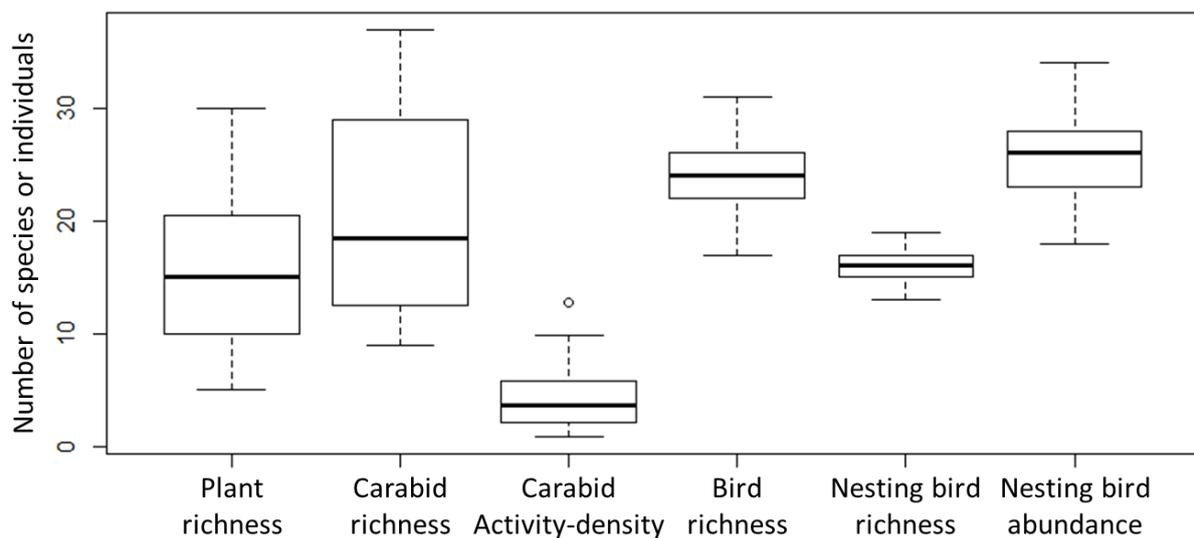
267

268 Residuals of averaged models were tested for normality (Shapiro-Wilcoxon test and quantile-quantile
269 plots) and spatial auto-correlation (Moran correlogram). When residuals were not normally distributed
270 a new average model was built using the adequate distribution using a generalized linear model, either

271 Poisson distribution for non-overdispersed data or negative binomial distribution for overdispersed
 272 data (Crawley 2007; Bouche et al. 2009). No model showed spatial auto-correlation. Models included
 273 study area (plants and birds) or locality (carabids) as random factors (mixed models). All statistical
 274 tests were performed using R software 3.3.1 (R Core Team 2016) using the ‘vegan’ package for Chao2
 275 estimation (Oksanen et al. 2013), the ‘party’ package for random forest analyses (Hothorn et al. 2013),
 276 the ‘MuMin’ package for MMI analyses (Barton 2016), and the ‘lme4’ package for generalized linear
 277 mixed-effects models (Bates et al. 2015), the ‘qcc’ package for over-dispersion testing (Scrucca 2004),
 278 and the ‘nfc’ package for spatial-autocorrelation test (Bjornstad 2016).
 279

280 3. Results

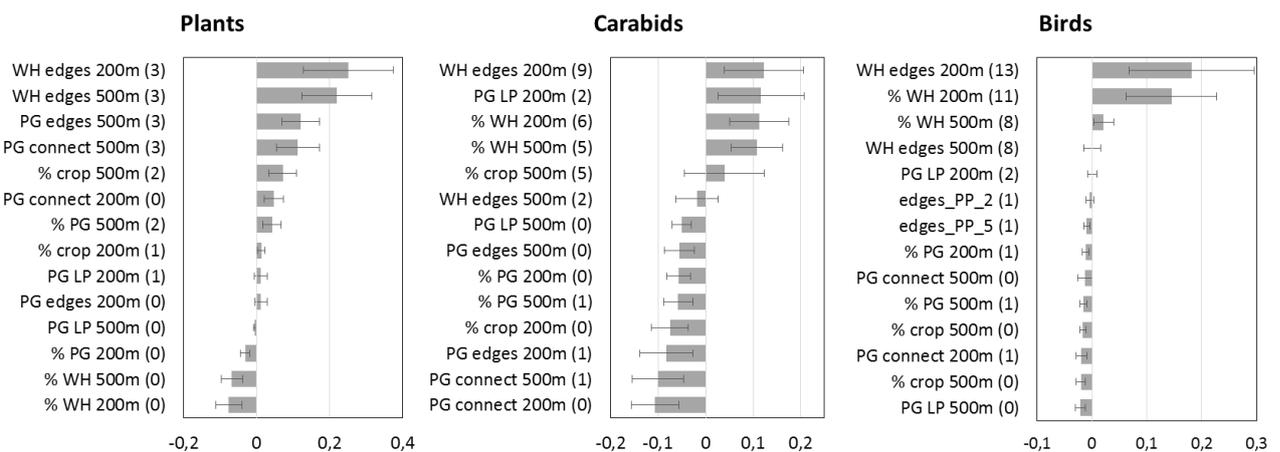
281 In total, we sampled 108 plant species (Chao2 = 125.0 ± 8.2), 76 carabid beetle species (Chao2 = 84.3
 282 ± 5.5 , 1922 individuals) and 63 bird species (Chao2 = 73.4 ± 7.3), 41 of which were breeding (Chao2
 283 = 54.7 ± 10.7 , 672 breeding territories). Observed species richness was therefore close to expected for
 284 all taxonomic groups, indicating that the sampling intensity was adequate.



285 **Figure 1.** Boxplot of plant, carabid and bird biodiversity measures per sampled permanent
 286 grassland, all species included.
 287
 288

289 Measures of richness and abundance at the assemblage level varied between sampled permanent
 290 grasslands (Fig. 1), but could not be explained by permanent grassland connectivity. Proportion and
 291 spatial configuration descriptors of permanent grassland were sometimes selected by the random forest

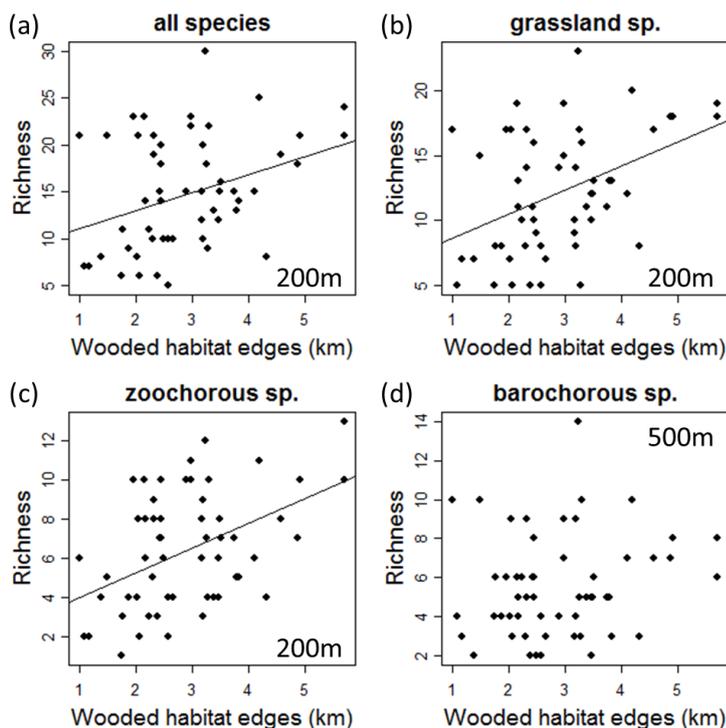
292 analysis, at both spatial scales, but they had limited explanatory power for carabid and bird
 293 assemblages (Fig. 2). The only exception was largest grassland patch area at the 200m scale for
 294 carabids, but this descriptor was selected only twice (Fig. 2). For plants, grassland-related descriptors
 295 were of higher importance than for the animal groups and were often selected, particularly the
 296 configuration descriptors at the 500m scale (Fig. 2). However, they never significantly affected total
 297 species richness or activity-density / abundance of plants, carabids or birds (Appendices 1M-P). Nor
 298 did they have any significant influence on species richness or abundance measures of the different
 299 ecological groups, based on habitat affinity or dispersal ability. The only exception was a nearly
 300 significant negative effect of largest grassland patch area on total richness of forest bird specialists, at
 301 the 200m scale (Appendix 1O). So, despite considerable variation in the amount and configuration of
 302 permanent grasslands across sampled grasslands (e.g. 10-80 % of permanent grassland for plants at the
 303 200 m scale, Appendix 1E), these factors had little or no influence on the different taxonomic groups.



304
 305 **Figure 2.** Conditional importance scores of landscape descriptors provided by random forest
 306 analyses, averaged across biodiversity measures for each studied taxon. Error bars are the
 307 standard errors. $n = 7$ for plants, 16 for carabids and 21 for birds. In brackets are the
 308 number of times the considered landscape descriptor was selected by the random forest
 309 procedure. Detailed results on landscape descriptors selected for each biodiversity measure
 310 may be found in Appendices 1J-K. % PG: proportion of permanent grassland (%), PG
 311 connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch
 312 (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%),
 313 WH edges: wooded habitat edges (km), % crops: proportion of crop (%). “200m” and
 314 “500m” indicate the scale at which the considered landscape descriptor was measured.
 315

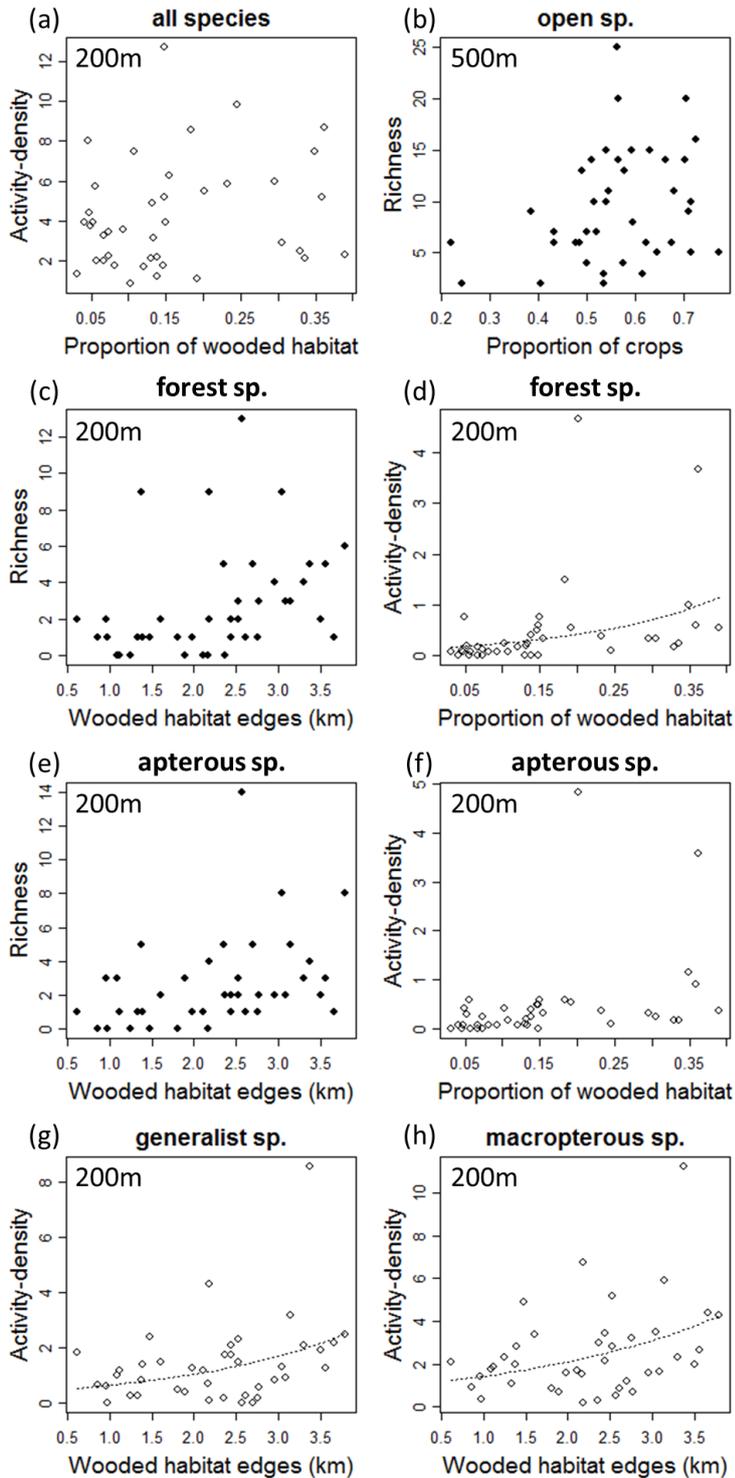
316 Instead, the grassland assemblages of the three studied taxa were significantly influenced by wooded
 317 habitats. Random forest results showed that landscape descriptors related to wooded habitats were

318 amongst those that explained the most variation in biodiversity measures, for the three taxa (Fig. 2).
 319 Significant relationships between landscape descriptors and biodiversity measures are shown
 320 graphically in Figures 3-5 and relationships that fell just short of the 95% confidence level are also
 321 displayed, but without a trend line. The latter relationships are henceforth referred to as nearly
 322 significant (near. sig.). Wooded habitats had a particularly strong influence at the 200m scale for birds
 323 and, to a lesser extent, carabid assemblages. Total plant species richness and richness of grassland
 324 plant specialists increased with increasing length of wooded habitat edges at the 200m scale (Fig. 3a/b,
 325 Appendix 1M). These two biodiversity measures responded similarly as most plant species were
 326 grassland specialists (Appendix 1B). The length of wooded habitat edges significantly positively
 327 influenced animal-dispersed plant species richness at the 200 m scale and gravity-dispersed plant
 328 species richness (near.sig.), at the 500 m scale (Fig. 3c/d, Appendix 1M). Ruderal and wind-dispersed
 329 plant species were unaffected by landscape descriptors.



330
 331 **Figure 3.** Graphical representation of significant and nearly significant results for plants
 332 biodiversity measures. Barochorous: gravity-dispersed, zoochorous: animal-dispersed. Scale
 333 of effects is indicated on each graph corner as the radius of buffers surrounding sampled
 334 permanent grasslands. Plain lines are given for illustrative purposes (only for significant
 335 results). Coefficients from average models are used for drawing linear and exponential lines
 336 (Appendix 1M). Linear lines are used for biodiversity measures analysed with Gaussian
 337 distribution.
 338

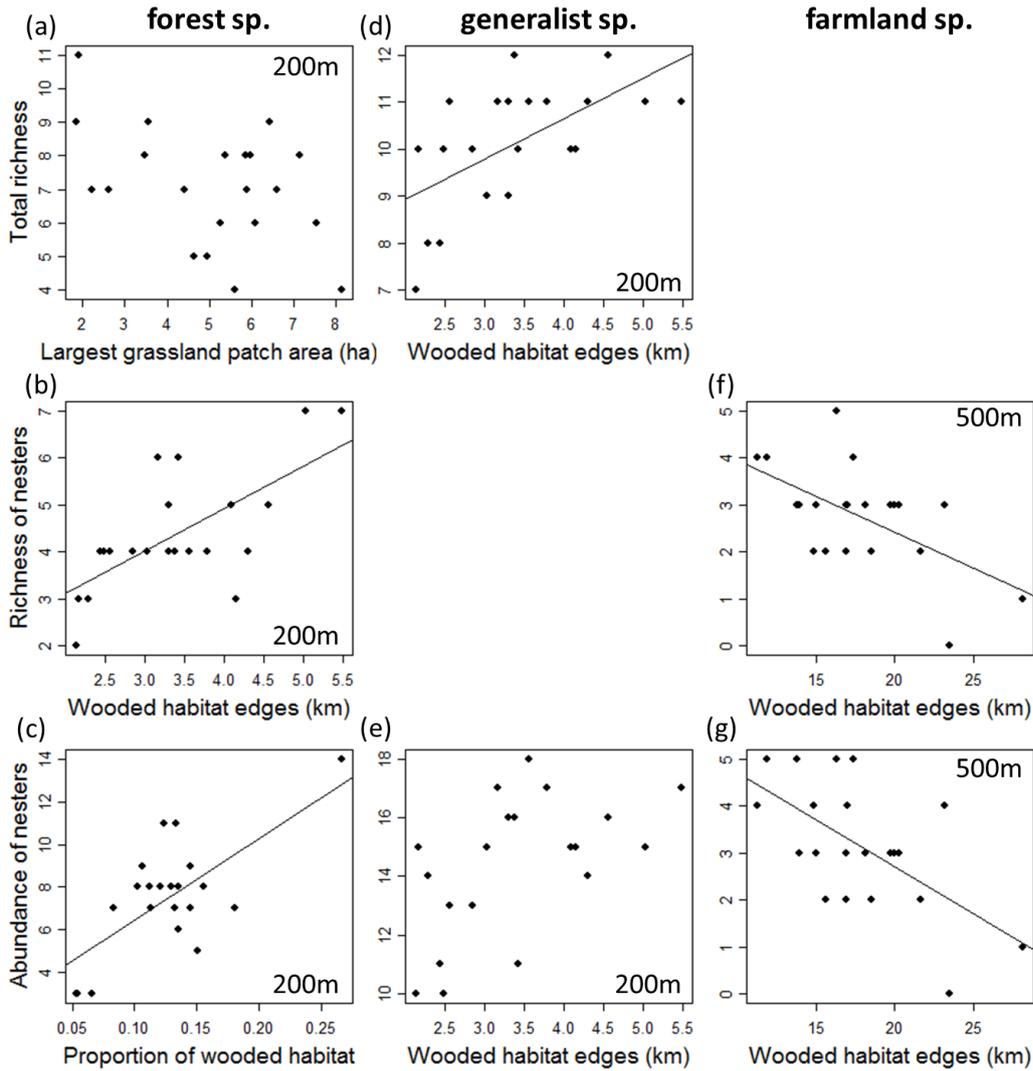
339 Total activity-density of carabid beetles tended to increase with increasing proportion of wooded
340 habitats (near.sig. Fig. 4a, Appendix 1N). Richness of open habitat carabids increased with increasing
341 proportion of crops area at the 500m scale (near. sig. Fig. 4b, Appendix 1N) which was strongly
342 negatively correlated with the proportion of wooded habitats at this scale ($r_s = - 0.83$, Appendix 1H).
343 Species richness of forest carabid specialists increased with increasing length of wooded habitat edges
344 and activity-density of the same group significantly increased with increasing proportion of wooded
345 habitats, both at the 200m scale (Fig. 4c/d, Appendix 1N). Apterous carabid species, which are mostly
346 forest specialists (Appendix 1C), followed the same trends (near. sig. Fig. 4e/f, Appendix 1N).
347 Activity-density of carabid generalist and macropterous species were positively influenced by
348 increasing length of wooded habitat edges, also at the 200m scale (Fig. 4g/h, Appendix 1N).



349

350 **Figure 4.** Graphical representation of significant and nearly significant results for carabid
 351 beetle biodiversity measures. Full dots are used for species richness, while empty dot and
 352 dashed lines are used for activity-density. Activity-density is expressed as number of
 353 individuals / valid trap / week. Scale of effects is indicated on each graph corner as the radius
 354 of buffers surrounding sampled permanent grasslands. Lines are given for illustrative
 355 purposes (only for significant results). Coefficients from average models are used for drawing
 356 linear and exponential lines (Appendix 1N). Exponential lines are used for Poisson and
 357 Negative Binomial distributions (log link functions).

358 For birds, richness of breeding forest specialists increased with increasing length of wooded habitat
359 edges at the 200m scale while their abundance was positively influenced by proportion of wooded
360 habitats also at the 200 m scale (Fig. 5b/c, Appendix 1O). As mentioned above, total richness of forest
361 specialist bird species was the only biodiversity measure to be influenced by a grassland landscape
362 descriptor, i.e a nearly significant negative influence of large grassland patch area (Fig 5a, Appendix
363 1O). Similarly, total richness and abundance of breeding generalist birds increased with increasing
364 length of wooded habitat edges at the 200m scale (Fig. 5d/e, Appendix 1O). Conversely, richness and
365 abundance of breeding farmland bird specialists decreased with increasing length of wooded habitat
366 edges, this time at the 500m scale (Fig. 5f/g, Appendix 1O). Birds with limited dispersal were not
367 affected by landscape descriptors, while medium and high dispersal groups responded significantly
368 (Appendix 1P) but this seems to have been more related to habitat affinity of the forest specialist or
369 generalist species dominating these dispersal groups, than to dispersal ability per se, and so these
370 results are not shown graphically.



371 **Figure 5.** Graphical representation of significant and nearly significant results for bird
 372 habitat affinity groups. Scale of effects is indicated on each graph corner as the radius of
 373 buffers surrounding sampled permanent grasslands. Lines are given for illustrative purposes
 374 (only for significant results). Coefficients from average models are used for drawing linear
 375 (Appendix 10), all models followed Gaussian distribution.
 376
 377

378 4. Discussion

379 The substantial variation in biodiversity between sampled permanent grasslands was not explained by
 380 the connectivity of permanent grassland, either amount or spatial configuration, in the landscape, at
 381 least at the two spatial scales considered (200 and 500 m). It should be kept in mind that overall
 382 diversity in such human-modified landscapes is low (see Irmiler & Hoernes, 2003), but our sampling
 383 protocol enabled us to detect a high proportion of the expected species pool for each taxonomic group.
 384 Many species were not considered to be grassland specialists, particularly in the animal groups, so the

385 lack of response of these assemblages as a whole is perhaps not surprising. However, contrary to our
386 hypothesis, even grassland specialist groups were unaffected. The lack of response of grassland
387 assemblages to grassland amount was also noted by Soderstrom et al. (2001), who found no effect on
388 either species richness or composition of plants, ground beetles and other insects (butterflies, bumble
389 bees, dung beetles), and birds . However, in their study the proportion of grassland varied only from 0
390 to 17%, while in this study it varied from at least 10 to 58% at the 200m scale and 4 to 32% at the
391 500m scale, and despite this, there was still little response from the different groups. In our study,
392 grassland connectivity index (*sensu* Hanski 1999) also varied (0-7) without significantly influencing
393 the grassland assemblages. Similarly, Öckinger et al. (2012) found grassland isolation (inverse of
394 Hanski index) had no effect on either total species richness of plants and insects (butterflies, bees or
395 hoverflies), or on richness of grassland specialist groups. One could argue that if we had used a wider
396 range of connectivity indices we might have found different effects. However Villemey et al. (2015)
397 explored a much wider range of connectivity measures including Hanski index but also nearest
398 Euclidean distance, graph-based measures with cost (least-cost path) or resistance (circuit theoretic)
399 distances, only to come to the same conclusion for the butterfly assemblages they studied. The only
400 group to respond to any measure of grassland connectivity was the total species richness of forest
401 birds, which included 6 species not breeding in our study area, while the richness of breeding forest
402 species alone did not. This suggests that certain species with a greater affinity for forest habitats may
403 avoid very open areas, even when engaged in more temporary activities than breeding, such as
404 dispersal or foraging. Configuration of grassland at 500m was sometimes selected by random forest
405 procedures for plant assemblages. However, as for the other taxa, the effects of these descriptors were
406 not significant.

407

408 Grassland specialists dominated plant assemblages, forming on average 83% of total species richness.
409 Both grassland and total species richness were positively influenced by wooded habitats in the
410 landscape as also shown by Soderstrom et al. (2001) and Ernoult et al. (2006). One hypothesis is that
411 landscapes with more wooded habitats tend to be less disturbed and more species rich, and that
412 wooded edges, particularly hedgerows, have well-developed herbaceous strata which may act as

413 sources. Plant dispersal groups varied in their response to wooded habitats, independently from habitat
414 affinity groups. Wind-dispersed species were unaffected by landscape context, in agreement with
415 Piessens et al. (2005). However, we might have expected that wooded edges would inhibit flow of
416 wind-dispersed seeds by forming physical barriers or reducing wind speed (Gaujour et al. 2012).
417 Wooded habitat edges did promote animal-dispersed species, probably because seed-dispersing
418 animals (birds, mammals, insects) tend themselves to follow woodland edges and hedgerows as they
419 move.

420

421 In the case of carabids, the lack of grassland connectivity effects might be explained by the limited
422 number of true grassland specialists (Roger et al. 2010; Neumann et al. 2016). Although grassland
423 assemblages are clearly different from those observed in crop fields or wooded habitats (Duflot et al.
424 2015) some species considered to be crop or forest specialists are known to utilize permanent
425 grasslands. Richness of open habitat carabid species tend to increase in landscapes with a greater
426 proportion of crops, where a greater amount and diversity of complementary resources may be
427 available (Duflot et al. 2016). Richness and activity-density of forest specialist species were higher in
428 landscapes with more wooded habitat or edges (presence of hedgerows), which is a general
429 observation for carabid assemblages found in farmland habitats (e.g. Millan-Pena et al. 2003; Aviron
430 et al. 2005; Duflot et al. 2014). This is probably why total activity-density tended to increase with the
431 proportion of wooded habitat in the landscape. Meanwhile, activity-density of generalist carabid
432 species increased with increasing length of hedgerows, known to be overwintering sites for these
433 species (Sotherton 1985; Thorbek and Bilde 2004). These results concur with studies in other contexts
434 showing that carabid assemblages are strongly influenced by habitats adjacent to the focal habitat
435 (Schneider et al. 2016; Yekwayo et al. 2016).

436

437 The majority of sampled birds were contacted in hedgerows delimiting each grassland or in trees or
438 shrubs within, with relatively few observations of foraging in grasslands and < 1 breeding territory per
439 hectare within the grassland habitat itself (data not shown). Therefore, it is not surprising that
440 landscape descriptors of wooded habitat amount and configuration best explained distributions of

441 observed assemblages and more specifically of generalist and forest birds. Species more typical of
442 open farmland habitats including grasslands are known to be negatively impacted by wooded or
443 shrubby habitats in the landscape (Besnard et al. 2016) and we too found that wooded habitat edges
444 reduced farmland bird richness and abundance of breeding farmland birds. Hedgerow avoidance
445 behaviour of ground-nesting farmland birds is common and is partly due to increased predation risks
446 associated with hedgerows and woodland edges (Besnard et al. 2016). The low dispersal ability group,
447 which was composed of species with a diversity of habitat affinities, was not significantly affected by
448 landscape context, although this group was expected to be the most sensitive to habitat connectivity.
449 This study focused on breeding birds and we cannot rule out effects of landscape structure on this low
450 dispersal group outside the breeding season and at wider geographical scales.

451

452 Given the composition of the sampled animal assemblages, it proved difficult to construct dispersal
453 ability groups that would be independent from species habitat affinity and that would be comparable
454 with other taxa. Although effects on plant dispersal groups were clearer, the positive, nearly
455 significant, influence of wooded habitats on plant species dispersed by barochory was also difficult to
456 explain. As Piessens et al. (2005) has highlighted, some plant species may disperse in a variety of
457 ways making it difficult to define dispersal groups and to link dispersal processes with landscape
458 structure.

459

460 Contrary to expectations, all three taxa responded mainly to landscape variables at the same 200 m
461 scale. As the scale of landscape perception is expected to be between 4 to 9 times the average dispersal
462 distance (Jackson and Fahrig 2012), the response of plant and carabids at the finer scale is less
463 surprising than that of birds. It should be noted that most of the significant bird-landscape relationships
464 related to breeding birds only, which are sedentary during the sampling season. Further investigation
465 of a wider range of spatial scales of influence may yield different results. For both animal taxa,
466 landscape configuration had opposite effects on open habitat and farmland species compared to forest
467 and generalist species, and at different spatial scales. Farmland or open specialists seemed to have a
468 wider scale of perception (500 m) than forest specialists and generalists (200 m), which suggests that

469 response to landscape context was more dependent on habitat affinity than taxonomic group.
470 However, in the case of plants, ruderal species, more adapted to human disturbance and that included
471 crop weeds, did not respond to increasing proportion of crops and/or decreased wooded habitats at the
472 500m scale. Interestingly, for both animal groups richness of forest species of tended to increase with
473 connectivity of wooded habitats (i.e. hedgerows), while their abundance or activity-density increased
474 with resource availability (i.e. amount of wooded habitat).

475

476 **5. Conclusion**

477 We found no evidence that increasing connectivity of common, mesophilic, permanent grassland
478 would have positive or indeed negative effects on plant and animal assemblages of such grassland
479 habitats. Hence conservation planning to enhance the surface area and linkages between such
480 grasslands within agricultural landscapes alone is unlikely to produce biodiversity increases, at least as
481 far as our three study taxa are concerned. Instead, studied assemblages responded mostly to wooded
482 habitats surrounding sampled grasslands, including hedgerows. Lengths of wooded habitat edges were
483 often more important than the amount of wooded habitat itself, although collinearity between these
484 landscape descriptors made it difficult to disentangle their independent effects. For grassland plant
485 assemblages as a whole, or for the generalist or forest specialist components of the grassland animal
486 assemblages, more woodland habitat in the landscape matrix is generally positive. Preserving or re-
487 creating landscapes composed of permanent grasslands interspersed with woodlands and hedgerows
488 may be good policy, especially in regions where such forms of landscape organisation have been
489 historically present and match with established and adapted biodiversity. Therefore, schemes aiming to
490 reintroduce landscape complexity to farmland areas through hedge and tree planting should enhance
491 biodiversity. However, the presence of open habitat carabids as well as farmland specialist birds
492 depended on sufficiently large expanses of open land, free of wooded habitats. So, though increasing
493 the area of common, permanent, mesophilic grassland did not influence these groups, maintaining
494 sufficient areas of open land is crucial and potentially contradictory with the objectives of policies
495 aiming to restore semi-natural, wooded habitats in farmland. These results illustrate the importance of

496 balancing landscape conservation planning in agricultural contexts, and of using multi-taxon
497 approaches, to meet the needs of contrasting ecological groups.

498

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506

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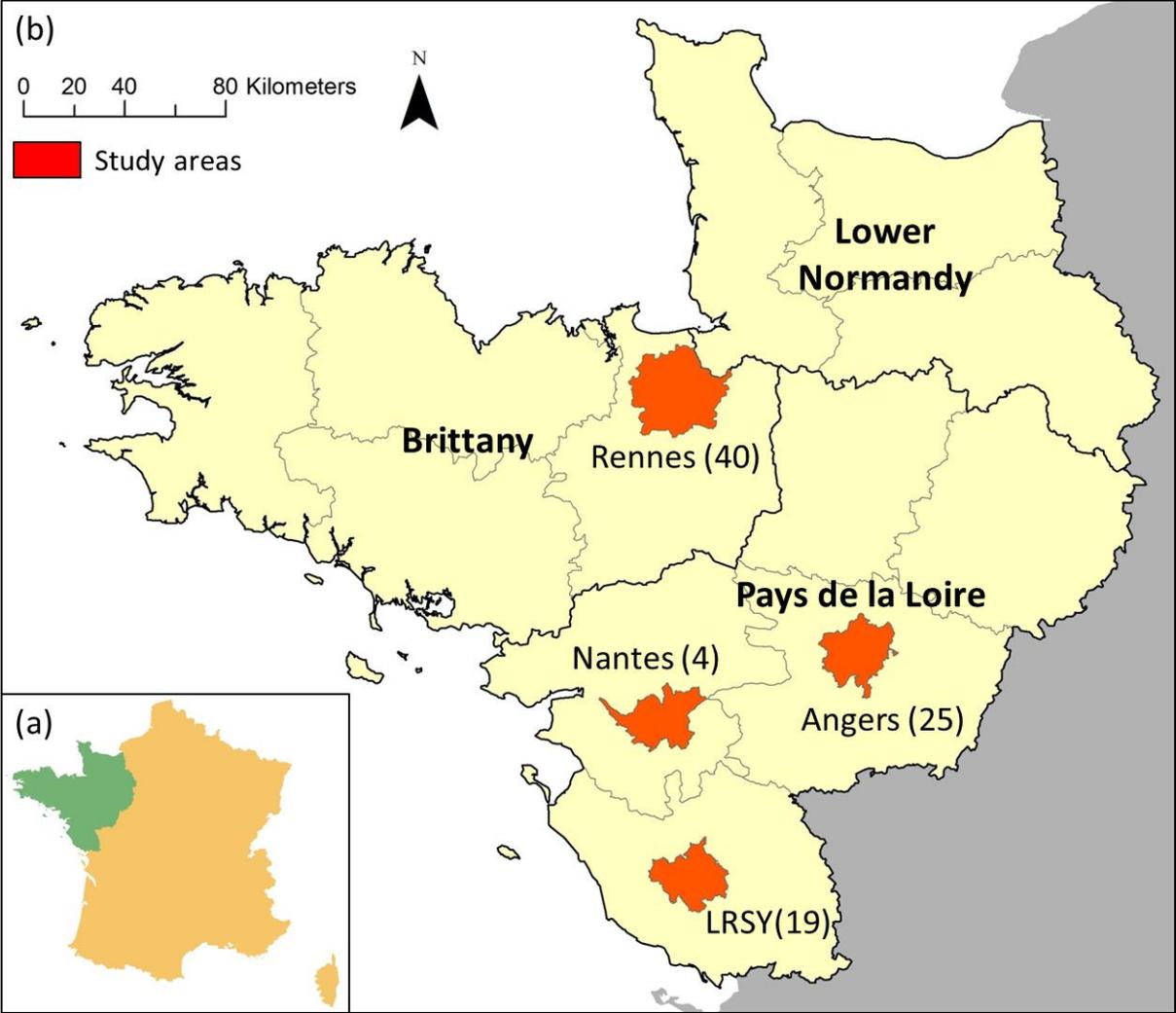
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Online appendixes 1

Appendix 1A

Map of the study areas. (a) Geographical location of the study region in France. (b) Geographical location of the four study areas in north-western France. In brackets, the number of sampled grasslands in each study area (LSRY = La Roche-sur-Yon).



Appendix 1B

Distribution of plant species among the different biological groups within the sampled permanent grasslands. Species occurrence is the number of species observations across all sampled permanent grasslands (maximum occurrence = 55). Anemochorous: wind-dispersed, barochorous gravity-dispersed, zoochorous: animal-dispersed. NA: species for which data were not available, others: autochorous and hydrochorous.

Species number

	anemochorous	barochorous	zoochorous	NA / others	Total
forest	3	4	6	1	14
grassland	10	25	23	1	59
ruderal	5	8	12	1	26
NA		1	2	6	9
Total	18	38	43	9	108

Summed species occurrences

	anemochorous	barochorous	zoochorous	NA / others	Total
forest	6	11	21	1	39
grassland	131	243	296	2	672
ruderal	17	49	37	1	104
NA		1	2	7	10
Total	154	304	356	11	825

Appendix 1C

Distribution of carabid beetle species among the different biological groups within the sampled permanent grasslands. Species occurrence is the number of species observations across all sampled permanent grasslands (maximum occurrence = 40). Apterous: windless, dimorphic: undeveloped wings, macropterous: winged. Activity-density is expressed as number of individuals / valid trap / week. NA: species for which data were not available.

Species number

	apterous	dimorphic	macropterous	NA	Total
crop	2	2	11		15
forest	8	6	1		15
generalist	1	1	5		7
open habitat		7	11		18
NA	3	3	14	1	21
Total	14	19	42	1	76

Summed species occurrences

	apterous	dimorphic	macropterous	NA	Total
crop	7	15	92		114
forest	79	29	3		111
generalist	14	1	152		167
open		184	194		378
NA	6	7	34	3	50
Total	106	236	475	3	820

Summed activity-density

	apterous	dimorphic	macropterous	NA	Total
crop	0.70	1.62	15.20		17.51
forest	15.84	3.26	0.25		19.35
generalist	1.82	0.10	53.86		55.77
open habitat		44.96	27.90		72.86
NA	0.61	0.63	3.65	0.27	5.16
Total	18.96	50.57	100.86	0.27	170.66

Appendix 1D

Distribution of bird species among the different biological groups within the sampled permanent grasslands, for total species pool and nesters. Species occurrence is the number of species observations across all sampled permanent grasslands (maximum occurrence = 21). Dispersal ability groups were obtained by splitting a dispersal ability predictor into categories using natural breaks (Jenks). NA: species for which data were not available. * unstudied biological groups.

Species number						
	low	medium	high	long distance*	NA	Total
farmland	2	4	6	2	3	17
forest	5	8	6			19
generalist	6	4	6	2	2	20
urban*	3	1	5	2		11
NA					5	5
Total	16	17	23	6	10	72

Summed species occurrences						
	low	medium	high	long distance*	NA	Total
farmland	23	40	21	23	9	116
forest	29	90	61			180
generalist	112	78	35	33	2	260
urban*	23	7	22	16		68
NA					7	7
Total	187	215	139	72	18	631

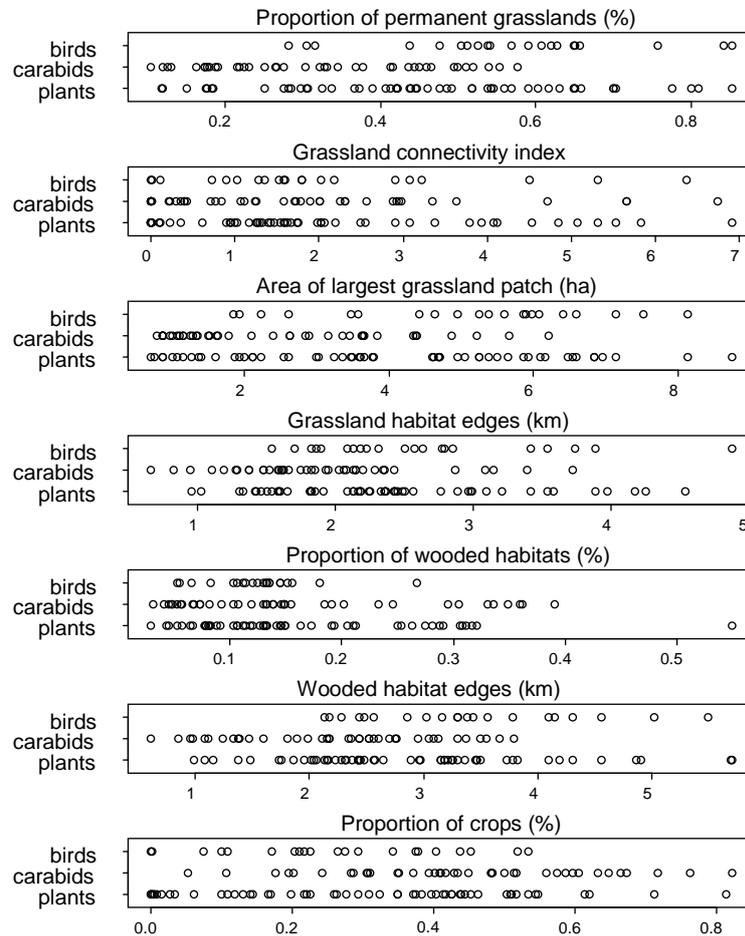
Nesting species number						
	low	medium	high	long distance*	NA	Total
farmland	2	4	3	2	1	12
forest	1	7	5			13
generalist	5	4	4	2		15
urban*	3	1	2			6
NA					1	1
Total	11	16	14	4	2	47

Summed nesting species occurrences						
	low	medium	high	long distance*	NA	Total
farmland	21	29	9	8	1	68
forest	24	65	25			114
generalist	98	66	25	18		207
urban*	13	4	7			24
NA					1	1
Total	156	164	66	26	2	414

Nesting species summed abundance						
	low	medium	high	long distance*	NA	Total
farmland	23	35	9	8	1	76
forest	42	126	30			198
generalist	182	131	37	21		371
urban*	15	4	7			26
NA					1	1
Total	262	296	83	29	2	672

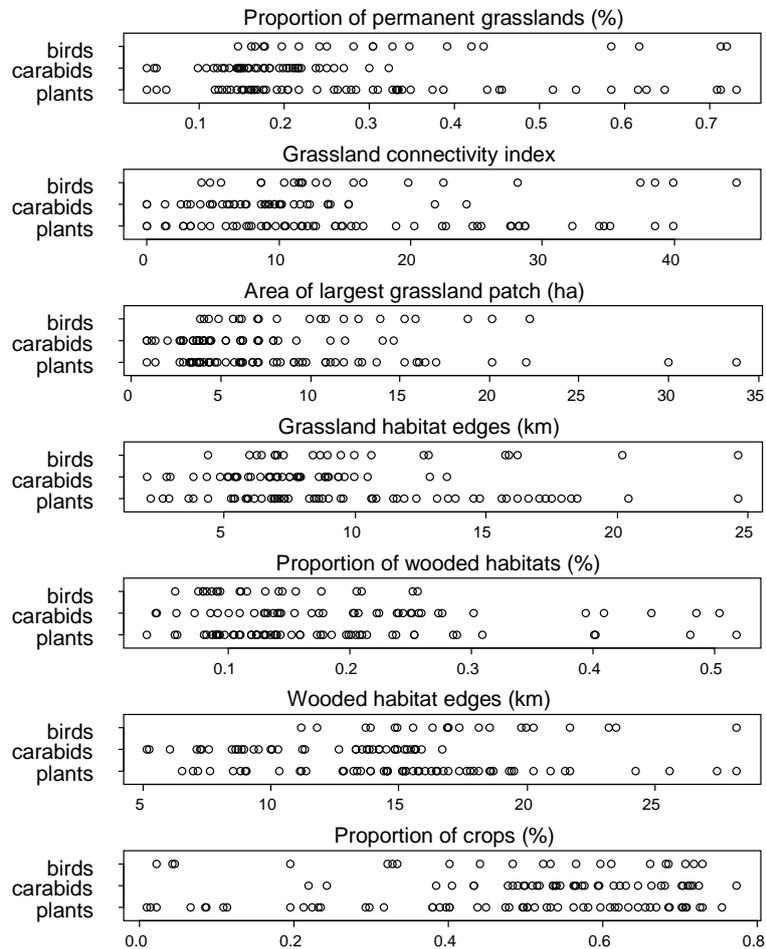
Appendix 1E

Range of values of studied landscape descriptors, in a 200m-radius buffer surrounding sampled permanent grasslands, for each taxon. Each dot represents a landscape. Proportions are expressed as percentage.



Appendix 1F

Range of values of studied landscape descriptors, in a 500m-radius buffer surrounding sampled permanent grasslands for each taxon. Each dot represents a landscape. Proportions are expressed as percentage.



Appendix 1G

Pearson correlation coefficient for all pairs of landscape descriptors measured for plant-sampled permanent grasslands (n = 55). Highest correlation coefficients (> |0.7|) are indicated in bold characters. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

	200m							500m						
	% PG	PG connect	PG LP	PG edges	% WH	WH edges	% crops	% PG	PG connect	PG LP	PG edges	% WH	WH edges	
200m														
% PG														
PG connect	0.39													
PG LP	0.79	-0.19												
PG edges	0.66	0.78	0.18											
% WH	-0.12	0.19	-0.20	0.19										
WH edges	0.13	0.38	-0.10	0.55	0.38									
% crops	-0.83	-0.49	-0.59	-0.70	-0.33	-0.29								
500m														
% PG	0.81	0.37	0.58	0.55	-0.02	0.21	-0.71							
PG connect	0.68	0.63	0.33	0.69	0.13	0.33	-0.69	0.87						
PG LP	0.70	0.05	0.68	0.21	-0.25	-0.03	-0.48	0.81	0.49					
PG edges	0.68	0.54	0.34	0.71	0.20	0.43	-0.74	0.88	0.88	0.53				
% WH	-0.18	0.09	-0.21	0.02	0.72	0.15	-0.22	-0.07	0.02	-0.26	0.13			
WH edges	0.36	0.33	0.18	0.48	0.34	0.74	-0.48	0.48	0.52	0.20	0.67	0.21		
% crops	-0.63	-0.37	-0.43	-0.52	-0.35	-0.31	0.79	-0.85	-0.78	-0.58	-0.88	-0.42	-0.57	

Appendix 1H

Pearson correlation coefficient for all pairs of landscape descriptors measured for carabid-sampled permanent grasslands. (n = 40) Highest correlation coefficients (> |0.7|) are indicated in bold. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

	200m							500m					
	% PG	PG connect	PG LP	PG edges	% WH	WH edges	% crops	% PG	PG connect	PG LP	PG edges	% WH	WH edges
200m													
% PG													
PG connect	0.54												
PG LP	0.76	-0.09											
PG edges	0.64	0.83	0.14										
% WH	-0.03	0.33	-0.26	0.41									
WH edges	-0.10	0.28	-0.34	0.42	0.70								
% crops	-0.80	-0.69	-0.42	-0.81	-0.46	-0.23							
500m													
% PG	0.64	0.40	0.43	0.53	0.06	0.10	-0.51						
PG connect	0.42	0.84	-0.04	0.66	0.26	0.12	-0.54	0.48					
PG LP	0.52	-0.08	0.69	0.18	-0.16	-0.28	-0.27	0.66	-0.01				
PG edges	0.39	0.55	0.04	0.66	0.28	0.42	-0.45	0.84	0.63	0.29			
% WH	0.08	0.16	-0.03	0.12	0.49	0.28	-0.36	-0.08	0.02	-0.11	-0.09		
WH edges	-0.04	0.33	-0.30	0.41	0.60	0.76	-0.24	0.10	0.22	-0.29	0.46	0.28	
% crops	-0.42	-0.36	-0.21	-0.41	-0.42	-0.23	0.60	-0.45	-0.28	-0.31	-0.34	-0.83	-0.22

Appendix 1I

Pearson correlation coefficient for all pairs of landscape descriptors measured for bird-sampled permanent grasslands (n = 21). Highest correlation coefficients (> |0.7|) are indicated in bold characters. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

	200m							500m					
	% PG	PG connect	PG LP	PG edges	% WH	WH edges	% crops	% PG	PG connect	PG LP	PG edges	% WH	WH edges
200m													
% PG													
PG connect	0.49												
PG LP	0.60	-0.40											
PG edges	0.65	0.73	0.01										
% WH	0.23	0.46	-0.17	0.53									
WH edges	0.24	0.47	-0.19	0.63	0.76								
% crops	-0.93	-0.58	-0.45	-0.75	-0.42	-0.35							
500m													
% PG	0.83	0.53	0.38	0.62	0.18	0.24	-0.84						
PG connect	0.69	0.68	0.09	0.65	0.20	0.29	-0.75	0.93					
PG LP	0.72	0.08	0.69	0.35	0.05	0.01	-0.63	0.69	0.40				
PG edges	0.76	0.67	0.19	0.76	0.32	0.44	-0.82	0.93	0.89	0.55			
% WH	0.45	0.46	0.05	0.58	0.72	0.62	-0.60	0.58	0.55	0.29	0.70		
WH edges	0.28	0.52	-0.18	0.52	0.49	0.70	-0.39	0.38	0.42	0.04	0.64	0.75	
% crops	-0.82	-0.49	-0.42	-0.66	-0.30	-0.33	0.88	-0.97	-0.88	-0.67	-0.92	-0.69	-0.45

Appendix 1J

List of landscape descriptors retained for regression models after the random forest procedure for each plant biodiversity measure. The retained variables are those whose relative importance value was higher than the absolute importance value of the lowest negative-scoring landscape descriptor.

Biodiversity measure	200m							500m						
	% PG	PG connect	PG LP	PG edges	% WH	WH edges	% crops	% PG	PG connect	PG LP	PG edges	% WH	WH edges	% crops
all species richness						X			X				X	
forest richness								X	X		X			X
grassland richness						X			X				X	
ruderal richness			X				X	X						
anemochorous richness														
barochorous richness											X		X	X
zoochorous richness						X					X			

Appendix 1M

Estimate and 95% confidence intervals from model averaging for plant biodiversity measures. Significant results, i.e. estimates whose 95 % confidence interval do not include zero, are in bold. Near significant results are shown with a “X” sign. All models were performed using a Gaussian distribution except for biodiversity measures with *, for which Poisson distribution was used, and with ** for which a negative binomial distribution was used. Models with only intercept values indicate a null model, i.e. random forest procedure selected no landscape descriptors (see “2.4 Statistical analyses”). Landscape descriptors: % PG: proportion of permanent grassland, PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges, % WH: proportion of wooded habitat, WH edges: wooded habitat edges, % crops: proportion of crop. “200m” and “500m” indicate the scale at which the considered landscape descriptor was measured.

biodiversity measure	landscape descriptor	estimates	lower CI	upper CI	
allspecies richness	(Intercept)	14,74	11,941	17,547	
	WH edges 200m	2,05	0,123	3,983	
	PG connect 500m	0,97	-0,734	2,678	
	WH edges 500m	0,64	-2,046	3,321	
forest richness *	(Intercept)	-0,42	-0,762	-0,074	
	PG edges 500m	0,33	-0,183	0,839	
	PG connect 500m	0,32	-0,180	0,821	
	% crops 500m	-0,25	-0,777	0,267	
	% PG 500m	0,17	-0,394	0,729	
grassland richness	(Intercept)	12,14	10,261	14,024	
	WH edges 200m	1,97	0,488	3,443	
	PG connect 500m	0,66	-0,667	1,986	
ruderal richness **	WH edges 500m	0,12	-1,826	2,072	
	(Intercept)	0,49	0,036	0,940	
	PG LP 200m	0,15	-0,091	0,400	
	% crops 200m	-0,15	-0,413	0,113	
	% PG 500m	0,02	-0,248	0,288	
anemochor richness *	(Intercept)	1,03	0,849	1,189	
barochor richness *	(Intercept)	1,67	1,451	1,887	
	WH edges 500m	0,15	-0,006	0,306	X
	% crops 500m	-0,08	-0,257	0,089	
	PG edges 500m	0,03	-0,195	0,248	
zoochor richness	(Intercept)	6,38	5,208	7,550	
	WH edges 200m	1,36	0,577	2,134	
	PG edges 500m	0,34	-0,461	1,142	

Appendix 1N

Estimate and 95% confidence intervals from model averaging for carabid biodiversity measures. Significant results, i.e. estimates whose confidence interval do not include zero, are in bold. Near significant results are shown with a “X” sign. All models were performed using a negative binomial distribution except for biodiversity measures with *, for which a Gaussian distribution was used and ** for which a Poisson distribution was used. Models with only intercept values indicate a null model, i.e. random forest procedure selected no landscape descriptors (see “2.4. Statistical analyses”). Landscape descriptors: % PG: proportion of permanent grassland, PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges, % WH: proportion of wooded habitat, WH edges: wooded habitat edges, % crops: proportion of crop. “200m” and “500m” indicate the scale at which the considered landscape descriptor was measured.

biodiversity measure	landscape descriptor	estimates	lower CI	upper CI	
allspecies richness	(Intercept)	3,02	2,890	3,153	
activity-density	(Intercept)	1,42	1,224	1,616	
	% WH 200m	0,18	-0,029	0,391	X
crop richness	(Intercept)	1,05	0,803	1,289	
activity-density **	(Intercept)	-0,98	-1,817	-0,514	
forest richness	(Intercept)	0,79	0,39	1,18	
	WH edges 200m	0,38	-0,02	0,78	X
	% WH 200m	0,33	-0,068	0,738	
activity-density	PG edges 200m	0,15	-0,235	0,534	
	(Intercept)	-1,08	-1,802	-0,367	
	% WH 200m	0,56	0,015	1,108	
	% crops 500m	-0,42	-1,050	0,203	
generalist richness *	WH edges 200m	0,45	-0,309	1,200	
	(Intercept)	4,18	3,456	4,894	
	WH edges 200m	0,45	-0,262	1,155	
	PG connect 500m	-0,36	-1,087	0,366	
activity-density	% PG 500m	-0,11	-0,839	0,629	
	(Intercept)	0,18	-0,210	0,561	
	WH edges 200m	0,42	0,078	0,765	
open richness	(Intercept)	2,23	2,050	2,410	
	% crops 500m	0,20	-0,028	0,435	X
	% WH 500m	-0,13	-0,416	0,157	
activity-density	(Intercept)	0,55	0,204	0,814	
apterous richness	(Intercept)	0,82	0,490	1,147	
	WH edges 200m	0,31	-0,064	0,692	X
	% WH 500m	0,24	-0,113	0,592	
	% WH 200m	0,27	-0,112	0,648	
	% crops 500m	-0,21	-0,563	0,147	
	WH edges 500m	0,23	-0,178	0,643	

activity-density	(Intercept)	-1,11	-1,834	-0,389	
	% WH 200m	0,51	-0,063	1,089	X
	% crops 500m	-0,48	-1,147	0,192	
	WH edges 200m	0,40	-0,343	1,151	
	% WH 500m	0,30	-0,513	1,112	
dimorphic richness *	(Intercept)	5,90	4,737	7,063	
	WH edges 200m	-1,38	-3,003	0,234	
	% crops 500m	0,94	-0,700	2,587	
	% WH 500m	-0,62	-2,479	1,243	
	WH edges 500m	-0,76	-2,568	1,058	
	% WH 200m	-0,16	-2,069	1,741	
activity-density	(Intercept)	0,11	-0,279	0,505	
	WH edges 200m	-0,31	-0,649	0,023	
	PG LP 200m	0,06	-0,295	0,405	
macropterous richness	(Intercept)	2,47	2,293	2,645	
	PG LP 200m	-0,14	-0,323	0,049	
	% WH 500m	-0,10	-0,290	0,081	
activity-density	(Intercept)	0,84	0,583	1,105	
	WH edges 200m	0,34	0,086	0,586	

Appendix 10

Estimate and 95% confidence intervals from model averaging for bird biodiversity measures (all species and habitat affinity). Significant results, i.e. estimates whose 95 % confidence interval do not include zero, are in bold. Near significant results are shown with a “X” sign. All models were performed using a Gaussian distribution except for biodiversity measures with *, for which a Poisson distribution was used. Models with only intercept values indicate a null model, i.e. random forest procedure selected no landscape descriptors (see “2.4. Statistical analyses”). Landscape descriptors: % PG: proportion of permanent grassland, PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges, % WH: proportion of wooded habitat, WH edges: wooded habitat edges, % crops: proportion of crop. “200m” and “500m” indicate the scale at which the considered landscape descriptor was measured.

biodiversity measure	Landscape descriptor	estimates	lower CI	upper CI	
all species total richness	(Intercept)	24,29	22,623	25,949	
	WH edges 200m	1,18	-0,508	2,863	
richness of nester	(Intercept)	15,87	14,869	16,865	
	% WH 200m	0,59	-0,270	1,459	
	WH edges 200m	0,52	-0,381	1,431	
abundance of nester	(Intercept)	25,81	24,27	27,35	
	% WH 200m	2,01	-0,31	4,32	
	WH edges 200m	1,60	-0,76	3,95	
	% WH 500m	-0,39	-2,70	1,92	
forest total richness	(Intercept)	7,10	6,345	7,845	
	PG LP 200m	-0,76	-1,526	0,009	X
	WH edges 200m	0,66	-0,155	1,483	
	PG connect 200m	0,52	-0,338	1,381	
	WH edges 500m	0,30	-0,666	1,269	
richness of nester	(Intercept)	4,38	3,934	4,827	
	WH edges 200m	0,85	0,238	1,456	
	% WH 200m	0,74	-0,018	1,504	X
	% WH 500m	-0,30	-0,947	0,349	
abundance of nester	WH edges 500m	-0,19	-0,840	0,455	
	(Intercept)	7,43	5,151	9,710	
	% WH 200m	1,76	0,786	2,734	
	WH edges 200m	0,38	-0,79	1,56	
generalist total richness	% WH 500m	-0,25	-1,432	0,924	
	(Intercept)	10,14	9,639	10,647	
	WH edges 200m	0,81	0,111	1,501	
	% WH 200m	0,62	-0,099	1,330	
	WH edges 500m	-0,44	-1,148	0,268	
richness of nester*	% WH 500m	-0,03	-0,699	0,647	
	(Intercept)	2,08	1,924	2,246	
	WH edges 500m	0,05	-0,116	0,210	
	% WH 500m	0,04	-0,118	0,207	

abundance of nester	(Intercept)	14,48	13,50	15,46	X
	WH edges 200m	1,19	-0,02	2,40	
	% WH 200m	0,63	-0,90	2,15	
	% WH 500m	0,67	-0,68	2,01	
	WH edges 500m	0,27	-1,269	1,818	
farmland total richness*	(Intercept)	1,55	1,338	1,760	
	PG connect 500m	0,09	-0,116	0,300	
	% PG 500m	0,08	-0,132	0,287	
richness of nester	(Intercept)	2,76	2,330	3,194	
	WH edges 500m	-0,62	-1,096	-0,153	
	% WH 500m	-0,40	-1,058	0,250	
	PG edges 500m	-	-	-	
abundance of nester	(Intercept)	3,14	2,631	3,655	
	WH edges 500m	-0,82	-1,389	-0,248	
	% WH 500m	-0,40	-1,282	0,478	

Appendix 1P

Estimate and 95% confidence intervals from model averaging for bird biodiversity measures (dispersal ability). Significant results, i.e. estimates whose confidence interval do not include zero, are in bold. All models were performed using a Gaussian distribution. Models with only intercept values indicate a null model, i.e. random forest procedure selected no landscape descriptors (see “2.4. Statistical analyses”). Landscape descriptors: % PG: proportion of permanent grassland, PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges, % WH: proportion of wooded habitat, WH edges: wooded habitat edges, % crops: proportion of crop. “200m” and “500m” indicate the scale at which the considered landscape descriptor was measured.

Biodiversity measure	landscape descriptor	estimates	lower CI	upper CI
low total richness	(Intercept)	6.81	6.281	7.338
	richness of nester	(Intercept)	5.76	5.297
abundance of nester	WH edges 500m	0.36	-0.058	0.781
	(Intercept)	9.81	8.970	10.649
	WH edges 200m	0.66	-0.184	1.501
medium total richness	(Intercept)	8.43	7.754	9.104
	PG LP 200m	-0.66	-1.332	0.013
	% WH 200m	0.39	-0.314	1.098
	richness of nester	(Intercept)	6.33	5.828
abundance of nester	(Intercept)	11.43	10.339	12.518
	% WH 200m	1.38	0.087	2.682
	WH edges 200m	0.08	-1.811	1.974
high total richness	(Intercept)	5.48	4.820	6.132
	WH edges 200m	0.52	-0.276	1.323
	% WH 200m	-0.07	-1.078	0.942
richness of nester	(Intercept)	2.62	2.129	3.109
	WH edges 200m	0.67	0.046	1.292
	% WH 200m	0.62	-0.004	1.254
	PG edges 200m	-0.19	-0.838	0.467
abundance of nester	(Intercept)	3.33	2.588	4.078
	% WH 200m	0.85	-0.060	1.761
	WH edges 200m	0.76	-0.217	1.745

Appendix 2A

Corrected Akaike information criterion (AIC_c), AIC_c difference with best model (ΔAIC_c), and Akaike weights (w_i) of all supported models ($\Delta AIC_c < 4$) that were included in model averaging for the analysis of plant biodiversity measures. Models are ordered in terms of ΔAIC_c . In bold are the biodiversity measures with significant effects detected. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

Biodiversity measure	Intercept	PG LP 200m	WH edges 200m	% crops 200m	% PG 500m	PG connect 500m	PG edges 500m	WH edges 500m	% crops 500m	AIC_c	ΔAIC_c	w_i
allspecies richness	14.77		2.03			0.99				345.7	0	0.25
	14.76		1.99			0.97		0.08		345.9	0.20	0.23
	14.69		1.92					0.61		346.1	0.45	0.20
	14.76		2.30							346.2	0.47	0.20
	14.75					0.90		1.56		348.6	2.88	0.06
	14.68							2.02		348.7	3.04	0.06
forest richness	-0.42						0.38			119.6	0	0.19
	-0.42					0.38				119.7	0.04	0.19
	-0.41								-0.37	120.3	0.68	0.14
	-0.40				0.33					120.9	1.25	0.10
	-0.43					0.25			-0.17	121.6	1.93	0.07
	-0.43					0.20	0.21			121.6	1.94	0.07
	-0.42						0.28		-0.11	121.9	2.21	0.06
	-0.42				0.04		0.34			122.0	2.31	0.06
-0.42				0.05	0.34				122.0	2.35	0.06	
-0.42				0.12				-0.26	122.4	2.80	0.05	

grassland richness	12.15		2.08				320.5	0	0.33	
	12.15		1.89		0.65		321.0	0.46	0.26	
	12.12		1.90			0.28	321.2	0.66	0.23	
	12.15		1.94		0.67	-0.08	321.7	1.17	0.18	
ruderal richness	0.50						190.7	0	0.24	
	0.49	0.17					190.8	0.13	0.23	
	0.47		-0.16				191.0	0.32	0.21	
	0.50			0.08			192.4	1.75	0.10	
	0.48	0.11	-0.10				192.7	2.06	0.09	
	0.49	0.17		0.00			193.2	2.55	0.07	
	0.47		-0.20	-0.05			193.3	2.63	0.07	
anemochor richness	1.03						199.7			
barochor richness	1.66				0.16		249.6	0	0.38	
	1.66				0.13	-0.05	251.5	1.88	0.15	
	1.68					-0.11	251.7	2.08	0.13	
	1.66			0.02	0.15		251.9	2.27	0.12	
	1.69			0.10			252.4	2.81	0.09	
	1.70						252.7	3.11	0.08	
	1.66				-0.08	0.15	-0.11	253.6	3.94	0.05
zoochor richness	6.38		1.39				268.5	0	0.70	
	6.38		1.26		0.34		270.2	1.71	0.30	

Appendix 2B

Corrected Akaike information criterion (AIC_c), AIC_c difference with best model (ΔAIC_c), and Akaike weights (w_i) of all supported models ($\Delta AIC_c < 4$) that were included in model averaging for the analysis of carabid biodiversity measures. Models are ordered in terms of ΔAIC_c . In bold are the biodiversity measures with significant effects detected. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

Biodiversity measure	Intercept	PG LP 200m	PG edges 200m	% WH 200m	WH edges 200m	% PG 500m	PG connect 500m	% WH 500m	WH edges 500m	% crops 500m	AIC_c	ΔAIC_c	w_i
allspecies richness	3.02										288.7		
activity-density	1.41			0.18							194.2	0	0.65
	1.43										195.4	1.26	0.35
crop richness	1.05										173.5		
activity-density	-0.98										69.3		
forest richness	0.78				0.43						174.3	0	0.33
	0.80			0.40							174.9	0.61	0.24
	0.78			0.22	0.28						176.0	1.68	0.14
	0.78		0.11		0.38						176.6	2.28	0.10
	0.80		0.14	0.35							177.0	2.65	0.09
	0.79										178.0	3.71	0.05
	0.79		0.27								178.2	3.94	0.05
activity-density	-1.06			0.61							76.5	0	0.33
	-1.09			0.49						-0.30	78.1	1.67	0.14
	-1.10				0.60						78.5	2.00	0.12
	-1.11									-0.55	78.5	2.01	0.12

	-1.16		0.49			-0.44	78.6	2.12	0.12	
	-1.09	0.50	0.22				78.8	2.30	0.11	
	-1.00						80.0	3.57	0.06	
generalist richness	4.18						179.5	0	0.38	
	4.18		0.43				180.7	1.22	0.21	
	4.18			-0.34			181.3	1.82	0.15	
	4.18			-0.09			182.1	2.63	0.10	
	4.18		0.48		-0.40		182.3	2.81	0.09	
	4.18		0.45	-0.14			183.4	3.91	0.05	
activity-density	0.17		0.42				124.7	0	1.00	
open richness	2.23					0.21	246.5	0	0.47	
	2.23				-0.18		247.7	1.26	0.25	
	2.24						248.7	2.25	0.15	
	2.23				-0.03	0.18	249.0	2.59	0.13	
activity-density	0.55						142.7			
apterous richness	0.81		0.33		0.24		168.8	0	0.10	
	0.85	0.38					169.0	0.21	0.09	
	0.82		0.40				169.1	0.25	0.09	
	0.81		0.35			-0.23	169.1	0.27	0.09	
	0.80				0.27	0.29	169.7	0.91	0.06	
	0.83	0.23	0.24				170.2	1.37	0.05	
	0.83	0.29			0.19		170.2	1.39	0.05	
	0.81					0.31	-0.26	170.2	1.39	0.05
	0.80				0.35			170.3	1.46	0.05
	0.84	0.31					-0.17	170.4	1.56	0.04
	0.84	0.29				0.19		170.5	1.71	0.04
	0.82					0.37		170.8	1.94	0.04
	0.81						-0.32	171.3	2.46	0.03
	0.80		0.24		0.24	0.12		171.3	2.50	0.03
	0.81	0.11	0.26		0.20			171.3	2.50	0.03

	0.82		0.31		0.13	171.3	2.54	0.03	
	0.82	0.14	0.26			-0.19	171.4	2.61	0.03
	0.81		0.33	0.16		-0.09	171.5	2.64	0.03
	0.81		0.26		0.12	-0.23	171.6	2.74	0.02
	0.82	0.18		0.20	0.20		171.7	2.90	0.02
	0.82	0.20			0.20	-0.18	171.8	3.04	0.02
	0.80			0.20	0.30	-0.09	172.4	3.58	0.02
	0.83	0.22	0.18		0.10		172.8	3.95	0.01
activity-density	-1.07	0.60					75.6	0	0.20
	-1.13					-0.59	76.6	0.98	0.12
	-1.12	0.46				-0.37	76.6	0.98	0.12
	-1.17		0.46			-0.50	77.1	1.42	0.10
	-1.11	0.49		0.25			77.6	1.94	0.07
	-1.13			0.54			77.6	1.94	0.07
	-1.10		0.57				77.7	2.10	0.07
	-1.09	0.50	0.19				78.0	2.39	0.06
	-1.16		0.45	0.40			78.3	2.66	0.05
	-1.02						78.9	3.28	0.04
	-1.14	0.32	0.22			-0.39	79.1	3.45	0.04
	-1.14			0.09		-0.51	79.2	3.57	0.03
	-1.11	0.47		-0.10		-0.45	79.3	3.71	0.03
dimorphic richness	5.90		-1.45			1.00	220.9	0	0.10
	5.90		-1.42	-0.91			221.5	0.56	0.07
	5.90		-1.42	-0.22		0.81	221.7	0.81	0.06
	5.90		-1.16		-0.38	0.98	221.9	1.02	0.06
	5.90		-1.68				222.0	1.04	0.06
	5.90	0.15	-1.54			1.04	222.1	1.22	0.05
	5.90				-1.25	1.05	222.5	1.55	0.04
	5.90		-1.15	-0.88	-0.36		222.5	1.58	0.04
	5.90	0.17	-1.53	-0.96			222.6	1.71	0.04

	5.90		-1.30		-0.49		222.7	1.74	0.04		
	5.90		-1.15		-0.20	-0.37	0.82	222.9	1.99	0.04	
	5.90		-0.38	-1.41				222.9	2.02	0.04	
	5.90				-0.96	-1.22		223.0	2.05	0.03	
	5.90		0.21	-1.55		-0.28		0.83	223.0	2.11	0.03
	5.90				-0.29	-1.22	0.81	223.2	2.29	0.03	
	5.90		0.21	-1.27			-0.41	1.04	223.3	2.35	0.03
	5.90						-1.49		223.6	2.71	0.03
	5.90		0.23	-1.27		-0.95	-0.39		223.8	2.84	0.02
	5.90		-0.30				-1.09	0.96	223.8	2.84	0.02
	5.90		-0.31	-1.12			-0.44		223.8	2.91	0.02
	5.90		-0.73				-1.04		224.1	3.22	0.02
	5.90		-0.26			-0.87	-1.09		224.2	3.30	0.02
	5.90		0.26	-1.28		-0.27	-0.40	0.83	224.3	3.41	0.02
	5.90		-0.97					0.92	224.4	3.45	0.02
	5.90		-0.25			-0.21	-1.09	0.80	224.6	3.72	0.02
	5.90		-1.36						224.7	3.78	0.01
	5.90		-0.95			-0.84			224.8	3.84	0.01
	5.90							1.32	224.9	3.97	0.01
	activity-density		0.12						123.3	0	0.47
			0.11						124.2	0.86	0.30
		0.01							125.9	2.62	0.13
		0.11							126.3	2.95	0.11
	macropterous richness		2.47						265.7	0	0.36
			2.47	-0.13					266.1	0.44	0.29
			2.47				-0.09		267.1	1.40	0.18
			2.46	-0.15			-0.12		267.2	1.49	0.17
	activity-density		0.84						159.4	0	1.00

Appendix 2C

Corrected Akaike information criterion (AIC_c), AIC_c difference with best model (ΔAIC_c), and Akaike weights (w_i) of all supported models ($\Delta AIC_c < 4$) that were included in model averaging for the analysis of bird biodiversity measures. Models are ordered in terms of ΔAIC_c . In bold are the biodiversity measures with significant effects detected. % PG: proportion of permanent grassland (%), PG connect: permanent grassland connectivity index, PG LP: largest permanent grassland patch (ha), PG edges: permanent grassland edges (km), % WH: proportion of wooded habitat (%), WH edges: wooded habitat edges (km), % crops: proportion of crop (%)

Biodiversity measure	Intercept	PG LP 200m	PG edges 200m	% WH 200m	WH edges 200m	% PG 500m	PG connect 500m	% WH 500m	WH edges 500m	AIC_c	ΔAIC_c	w_i
all species total richness	24.29				1.18					118.8	0	0.55
	24.29									119.3	0.44	0.45
richness of nester	15.86									88.0	0	0.35
	15.87			0.64						88.2	0.24	0.31
	15.87				0.60					88.5	0.59	0.26
abundance of nester	15.87			0.42	0.28					90.8	2.86	0.08
	25.81			2.23						115.7	0	0.28
	25.81			1.42	1.07					116.2	0.52	0.21
	25.81				2.15					116.4	0.68	0.20
	25.81			2.57				-0.47		117.0	1.34	0.14
	25.81			1.81	1.19			-0.66		117.8	2.15	0.09
	25.81				2.11			0.06		118.1	2.41	0.08
forest total richness	7.10		-0.82							88.2	0	0.24
	7.10		-0.71		0.60					89.0	0.82	0.16
	7.10				0.74					89.2	1.00	0.14
	7.10									89.8	1.57	0.11

	7.10	0.66				90.0	1.78	0.10
	7.10	0.40	-0.66			90.7	2.52	0.07
	7.10		-0.76		0.35	91.0	2.77	0.06
	7.10				0.49	91.4	3.15	0.05
	7.10	0.40		0.55		91.7	3.48	0.04
	7.10			0.78	-0.06	92.2	3.96	0.03
richness of nester	4.38			0.88		68.9	0	0.44
	4.38		0.84			70.3	1.40	0.22
	4.38		0.41	0.57		71.2	2.32	0.14
	4.38			1.01	-0.22	72.5	3.63	0.07
	4.38			1.01	-0.19	72.5	3.65	0.07
	4.38		1.12		-0.39	72.7	3.83	0.06
abundance of nester	7.43			1.78		90.4	0	0.64
	7.43			1.49	0.38	92.7	2.37	0.19
	7.43			1.98	-0.25	93.0	2.66	0.17
generalist total richness	10.14			0.78		73.6	0	0.44
	10.14		0.73			74.7	1.12	0.25
	10.14			1.09	-0.44	75.7	2.13	0.15
	10.14		0.34	0.52		76.4	2.81	0.11
	10.14			0.80	-0.03	77.6	3.98	0.06
richness of nester	2.09					90.0	0	0.62
	2.08				0.05	92.4	2.38	0.19
	2.08				0.04	92.5	2.42	0.19
abundance of nester	14.48			1.25		97.8	0	0.33
	14.48		1.03			100.0	2.21	0.11
	14.48		0.21	1.09		100.0	2.26	0.11
	14.48			1.01	0.39	100.1	2.29	0.11
	14.48				1.01	100.2	2.40	0.10
	14.48			1.29	-0.05	100.3	2.51	0.09
	14.48				0.85	101.4	3.63	0.05

	14.48				101.5	3.76	0.05	
	14.48	0.64		0.56	101.7	3.95	0.05	
farmland total richness	1.55				85.5	0	0.58	
	1.55		0.09		87.4	1.90	0.22	
	1.55	0.08			87.7	2.15	0.20	
richness of nester	2.76			-0.64	66.8	0	0.64	
	2.76			-0.54	69.3	2.56	0.18	
	2.76			-0.15	-0.53	70.6	3.78	0.10
	2.76				70.7	3.92	0.09	
abundance of nester	3.14			-0.83	73.9	0	0.74	
	3.14			-0.13	-0.74	77.4	3.52	0.13
	3.14			-0.68	77.4	3.53	0.13	