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1 PLANT AND SPIDER COMMUNITIES BENEFIT DIFFERENTLY FROM THE
2 PRESENCE OF PLANTED HEDGEROWS IN HIGHWAY VERGES.

3

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20 PLANT AND SPIDER COMMUNITIES BENEFIT DIFFERENTLY FROM THE
21 PRESENCE OF PLANTED HEDGEROWS IN HIGHWAY VERGES.

22 **Abstract:** Road verges should play a crucial role as a refuge for native flora and fauna
23 in human dominated landscapes. However, the influence of construction choices, such
24 as plantation of woody species, on the biodiversity supported by roadsides has received
25 little attention, although the presence of hedgerows in roadsides is likely to enhance
26 their role as a refuge, notably for woodland species. Using standardised methods, we
27 assessed the impact of planted hedgerows on two taxonomic groups (plants and spiders)
28 inhabiting highway verges within an intensive agricultural landscape. We examined
29 community richness, taxonomic and functional composition in sites with and without
30 planted hedgerows. At the site level, the response of plant and spider communities to
31 the presence of planted hedgerows differed markedly: hedgerows were associated with
32 significantly higher plant richness (higher α -diversity), but similar spider richness. Plant
33 communities in sites without hedgerows appeared as a subset of communities in sites
34 with hedgerows, whereas spider communities in non-planted sites were complementary
35 to that of planted sites (increased β -diversity). The presence of planted hedgerows was
36 also associated with increased taxonomic and functional trait diversity at the landscape
37 level (γ -diversity), through an increased β -diversity in both plants and spiders. Our
38 results thus suggest that a mosaic of planted hedgerows and grassland habitats is crucial
39 for the maintenance of biodiversity at a landscape scale. By providing information for
40 road practitioners and policy makers regarding their potential impact on biodiversity,
41 these results have important direct implications for the management of road networks.

42 **Key words:** α and β -diversity, Biodiversity, Functional traits, Roadside management,
43 Revegetation, RLQ analysis.

44

45 **1. Introduction**

46

47 Road networks, which have expanded over large areas with human population growth
48 (Watts et al., 2007), are known to influence landscape structure and have major negative
49 impacts on ecosystems dynamics (Trombulak and Frissel, 2000). However, the potential
50 biological value of road verges has also long been recognised (Way, 1977) with
51 possible contribution to the conservation of indigenous flora (Spooner et al., 2004;
52 O'Farrell and Milton, 2006) and fauna (Meunier et al., 2000; Ries et al., 2001). This
53 role as a refuge depends on the surrounding landscape: in natural habitats, generally
54 supporting a high species diversity, road verges may not serve as a refuge (O'Farrell
55 and Milton, 2006) and even have negative effects, notably by promoting invasion by
56 non-indigenous species (Hansen and Clevenger, 2005; Brown, 2006). In contrast, in
57 human dominated areas such as intensive agricultural landscapes, where non-
58 agricultural habitats (e.g. edges) are critical to the conservation of biological diversity
59 and ecological processes (Burel, 1996), road verges should play a crucial role as a
60 refuge and as ecological corridors (Tikka et al., 2001; Smart et al., 2006).

61 Road verges support intensively managed habitats, which are artificially created
62 on bare soil after road construction (restoration) and subsequently experience frequent
63 mowing. This has direct consequences on the communities they can support and there is
64 a need to identify and promote biodiversity-friendly construction and management
65 practices, in order to optimise the role of road verges as a refuge for wild flora and
66 fauna. As in any habitat, community composition in road verges is controlled by an
67 array of distinct factors acting as filters at both landscape and local scales (Bochet et al.,
68 2007), few of which can easily be manipulated to optimise biodiversity conservation.

69 There have been extensive studies addressing the influence of management on roadside
70 biodiversity, notably mowing frequency and timing (Schaffers, 2002; Jantunen et al.,
71 2007). In contrast, construction choices have received much less attention, with the
72 exception of revegetation with herbaceous species (Matesanz et al., 2006; Leps et al.,
73 2007). In particular, the role of planted trees in the maintenance of diversity in road
74 verges was never considered to our knowledge, even though the presence of hedgerows
75 along roadsides is likely to enhance their role as a refuge, by increasing the diversity of
76 microhabitats. This role of hedgerows as a refuge however depends on their ability to
77 receive a significant proportion of the local species pool and of the functional diversity
78 they shelter (Roy and de Blois, 2006). Outside of roadsides, hedgerows appear to be a
79 sustainable habitat and even functional corridors (flora: Corbit et al., 1999, Roy and de
80 Blois, 2008; fauna: Maudsley, 2000, Griffiths et al., 2007; Davies and Pullin, 2007 for a
81 review) even though other authors consider hedgerows as sink habitats (McCollin et al.,
82 2000; Sitzia, 2007).

83 The aim of the present study is to evaluate the effect of hedgerows on the
84 surrounding biodiversity of highway verges at different spatial scales, and on the
85 distribution of biodiversity within and among sites in the context of an intensive
86 agricultural landscape. Highway verges offer ideal settings to study the influence of
87 hedgerows, because, in contrast to other habitats, the influence of history on community
88 composition is strongly reduced, due to common history of all study sites. To address
89 the impact of hedgerows on biodiversity, we compared the community richness and
90 composition in sites with and without planted hedgerows for two taxonomic groups
91 (plants and spiders), because no single taxon can inform on the ecological behaviour of
92 other groups (Lowell et al., 2007); In addition, in the context of the search for

93 biodiversity indicators, it is of great importance to better assess the characteristics of
94 different taxa (Pearman and Weber, 2007). These two groups differ in their ecological
95 requirements and dispersal capabilities and are likely differentially affected by the
96 presence of hedgerows: plant community composition is expected to be controlled
97 mostly by soil and light characteristics (Schaffers, 2002) whereas spider communities
98 are known to be highly sensitive to habitat structure and microclimatic conditions (Marc
99 et al., 1999; Entling et al., 2007; see also Beals, 2006) and may exhibit variation on
100 much smaller time scales than plants. By comparing similar grassland habitats in sites
101 with and without planted hedgerows, we specifically examined (1) whether the presence
102 of planted hedgerows influenced the surrounding specific and functional trait diversity,
103 (2) whether plant and spider communities exhibited different environmental patterns,
104 and (3) whether artificial hedgerows resulted in a higher overall biodiversity supported
105 by highway verges.

106

107 **2. Methods**

108

109 **2.1. Study area**

110

111 This study was conducted within a 50 km section of highway A11 (1°39'30''E –
112 48°29'15''N to 1°03'E – 48°14'N) in the Beauce region, an intensive agricultural
113 landscape, West of Paris, France. The Beauce covers about 6 000 km² and is
114 characterised by a temperate climate and high base status soils. This study area is a
115 fairly typical modern open field landscape with a complete absence of hedgerows and

116 very few semi-natural habitats, such as remnant woodland patches. Agricultural
117 practices consist mostly of intensive cereal production.

118 A11 Highway was built thirty years ago and enlarged in 1992. At this time, the
119 newly created verges, devoid of vegetation, were sown with the same seed mixture,
120 including mainly *Leguminosae* and *Poaceae* species (*Festuca rubra*, *Festuca ovina*,
121 *Lolium perenne*, *Festuca arundinacea*, *Bromus inermis*, but also *Medicago lupulina*,
122 *Lotus corniculatus*, *Trifolium arvense* and *Achillea millefolium*), along the whole
123 highway section studied, and were planted with trees at discrete locations (*Cofiroute*
124 construction company, personal communication). In the following, we define
125 hedgerows as linear patches of planted shrubs and trees longer than 150 m, following
126 the definition of Baudry et al. (2000). Sites with and without planted hedgerows are
127 subsequently referred to as “WT” sites and “WO” sites, respectively. Management
128 practices of highway verges depend on distance from the carriageway edge: all verges
129 receive a visibility cut up to 6 m from the road edge twice a year, but areas behind this
130 safety zone are only cut once a year, whereas vegetation growing under planted trees is
131 seldom, if ever, cut.

132

133 **2.2. Field sampling and data collection**

134

135 2.2.1. Field sampling

136 We selected 25 field sites (Fig. 1) based on the following structural and biological
137 criteria: highway sections were “roadcuts” (resulting from excavation), with edges of
138 the same shape (width = 16.1 m \pm 0.7 SE, height = 4 m \pm 0.3 SE), slope ($30^\circ \pm 2.4$ SE)
139 and aspect, and were bordered by crop fields. Within the 50 km study area, we selected

140 11 sites with planted hedgerows (WT) along these criteria, using geomorphic maps,
141 aerial photographs, and field surveys. Hedgerows consisted of mature deciduous trees in
142 the canopy layer, and were on average above 3 meters tall and 5 meters wide (5.2 ± 0.5
143 SE, varying between 3 and 8 meters). They were generally pluri-specific, including
144 most frequently the following planted species: *Acer campestre*, *Acer platanoides*, *Acer*
145 *pseudoplatanus*, *Alnus cordata*, *Betula verrucosa*, *Betula pendula*, *Carpinus betulus*,
146 *Cornus alba*, *Cornus mas*, *Cornus sanguinea*, *Corylus avellana*, *Cotinus coggygria*,
147 *Fraxinus excelsior*, *Prunus avium*, *Prunus mahaleb*, *Prunus padus*, *Prunus spinosa*,
148 *Quercus sessiliflora*, *Quercus robur*, *Robinia pseudo-acacia*, *Salix caprea*, *Sambucus*
149 *nigra*, *Sorbus aucuparia*, *Sorbus torminalis*, *Viburnum lantana*, *Viburnum opulus*.
150 When possible, one site without hedgerows (WO) was chosen within 1.5 km of a given
151 site with hedgerows (WT). We thus selected 7 pairs of geographically close sites with
152 and without hedgerows and completed this sample with isolated WT (n = 4) and WO
153 sites (n = 7), for a total of 25 sampled sites (11 WT - 14 WO). WO sites were always
154 located at least 50 m from the closest tree.

155

156 2.2.2. Data collection

157 All inventories were performed through a 60 m transect running parallel to the
158 carriageway, located at least 7.5 m from the carriageway edge and at 8.2 ± 0.6 SE from
159 the neighbouring crop field. Such location corresponded to extensive management
160 practices. In WT sites, transects were also located 0.5 to 1 m from the canopy of planted
161 trees (vertical projection of lower branches), and started and ended at least 50 m away
162 from the end of the hedgerow, to avoid border effects.

163 For flora, sites were surveyed from May 10th to June 10th 2006. In each site, all
164 vascular plant species were inventoried once in five 1 m² quadrats regularly distributed
165 over the 60 m transect. Almost all taxa were identified to species level according to the
166 International Plant Names Index. A few species that were difficult to distinguish when
167 not in flower or fruit (*Vicia gr tetrasperma-hirsuta* for example) were grouped.

168 Spiders were sampled using five pitfall traps per site. Traps were placed within
169 30 cm of each vegetation quadrat on the 60 m transect and were left in place from May
170 10 to June 10 2006. Each trap was 8.5 cm wide in diameter and 10 cm deep, and
171 contained ethylene glycol, a non-attractive preservative. Two pitfall traps were
172 destroyed and were omitted in the analyses (n = 123). Adult spiders were identified to
173 species level following the nomenclature of Platnick (2007). We failed to identify three
174 individuals to species level; nevertheless, because they were obviously different from
175 other species, they were conserved for analyses. Spider juveniles were generally not
176 identifiable to species level and were not considered.

177 Sites characteristics: sampling design was defined to test impact of hedgerows,
178 so that the variation of other environmental variables was minimised. We recorded sites
179 characteristics and checked the absence of correlation between presence/absence of
180 hedgerows and other environmental factors using pearson correlations, to check that the
181 effects of hedgerows were not confounded with other environmental factors. For each
182 site, we recorded geographic coordinates, verge width (final variation: 10-20 m),
183 adjacent land use type (crop vs. temporary fallow), slope, distance from crop edge,
184 aspect, and soil nutrient status. The latter was characterised via determination of soil
185 pH, as well as phosphorus (P₂O₅, Olsen %), salt (Na₂O), and total nitrogen (%)
186 concentration in a bulked representative soil sample, taken to a depth of 10 cm in each

187 of five plots and subsequently mixed. For each site, we also recorded the distance from
188 the nearest woodland patch ($411.6 \text{ m} \pm 70.4 \text{ SE}$), as well as the total woodland area
189 within 250 m, 500 m and 1 000 m radius buffers, using aerial photographs and the
190 Geographical Information System package ARCGIS 8 (ESRI, 2000). In this open-field
191 system, woodland patches can be considered as the main natural habitat in Beauce.
192 Consequently, we considered that they could be important reservoirs of species
193 compared to others habitats, providing a pool of both plants and spiders from which
194 species were able to disperse and potentially colonise highway verges.

195

196 **2.3. Species attributes**

197

198 To address the influence of hedgerows on community functional composition, we
199 characterised species based on readily available functional traits. As such data were
200 analyzed using multivariate methods that are highly sensitive to “rare” species or
201 classes, we chose to group some classes to minimize the resulting bias (see caption of
202 fig. 2). For plants, these functional traits include Raunkier types, maximum adult height,
203 and seed dispersal mode, scored according to a literature review (supplementary
204 material 1). For spiders, we retained hunting strategies, body size and aerial-dispersal
205 behaviour (ballooning vs. non-ballooning species). Hunting strategies (diurnal cursorial
206 hunters, nocturnal cursorial hunters, ambush hunters, and web-builders) and species-
207 specific body sizes were derived from Roberts (1985, 1987). As body sizes usually
208 differ between sexes, the mean value of male and female median sizes was retained.
209 Species exhibiting aerial dispersal using silk (ballooning) are considered species with
210 great dispersal capabilities (Bell et al., 2005 for review) and were defined using the

211 world species list of ballooning Araneomorphae established by Bell et al. (2005). All
212 species that did not appear in this list were considered “non ballooners”, which may be
213 incorrect because the list is not exhaustive. However, as we worked with common
214 species frequently found in agricultural landscapes and whose biology is generally well-
215 known, we expect that this bias should be small. For both plants and spiders, a given
216 taxon was assigned attributes only when it was identified to species level and observed
217 in more than four instances (quadrats or traps), which yielded a total of 46 plant species
218 (100% of species observed in more than four quadrats) and 56 spider species (84% of
219 species detected in more than four pitfalls) for which all traits were scored.

220

221 **2.4. Data analysis**

222

223 To remove the obvious increase in plant species richness due to the simple presence of
224 planted species and examine solely indirect effects of planted hedgerows on plant
225 community composition, we chose to work with spontaneous plant species only. Hence,
226 unless otherwise stated, shrub or tree species that were observed in the herbaceous strata
227 in a site where they had been planted (as inferred from historical plantation map data,
228 *Cofiroute – Vegetude*) were discarded in subsequent analyses, i.e. they were excluded of
229 this particular site; not however that these species were retained in other sites. In
230 addition, for spider species, we chose to work with presence/absence data only, so that a
231 range of different analyses, some of which valid with presence/absence data only, could
232 be used on the same dataset. With few exceptions, including abundance data yielded
233 very similar results. All analyses were conducted with R (R Development Core Team,
234 2007).

235

236 2.4.1. Species richness

237 To assess the effect of hedgerows at different spatial scales, we considered species
238 richness at the quadrat scale (S_{local} , plants only), at the site scale (S_{site} , in a transect of 60
239 m, plants and spiders) and at the highway section scale, within each type of site (S_{type} ,
240 within WT or WO types of sites, plants and spiders). For plants, we considered local
241 species richness (S_{local}) within quadrats because we assumed that all species were
242 detected, whereas for spiders, pitfall trapping is known to be influenced by the activity-
243 density of species (Melbourne, 1999). In addition, analysis on local spider richness
244 showed no effect of any environmental variable. Comparing observed species richness
245 across sites and habitats might not be valid in case of unequal species detection
246 probabilities (Boulinier et al., 1998; Nichols et al., 1998). We therefore used statistical
247 methods derived from capture-recapture approaches in population or community
248 dynamics to estimate species richness and changes in community composition As in
249 recent studies (Lekve et al., 2002; Doherty et al., 2003; Selmi and Boulinier, 2003;
250 Devictor et al., 2007; Kerbiriou et al., 2008) addressing richness estimation and
251 differences in community composition from species count data, we used the program
252 COMDYN (Hines et al., 1999), based on the jack-knife estimator of Burnham and
253 Overton (1979). To estimate species richness at the site level (S_{site}), we used quadrat or
254 pitfall captures as replicates. To estimate richness at type of site level (S_{type} within WT
255 or WO type of sites), we used sites as replicates ($n = 11$): analyses were based on
256 presence-absence data at the site level, pooled across the five quadrats for plants and the
257 five pitfall traps for spiders. As 11 replicates only were available for WT sites, we
258 sampled randomly without replacement 11 sites out of 14 in the WO group; this

259 sampling procedure was performed 15 times. Each of 15 pairs of (1) 11 sampled WO
260 sites plus (2) the 11 WT sites was input into program COMDYN to obtain estimated
261 richness per type of site. The estimated richness in each type of site was then
262 characterised using the mean and standard error of the 15 outputs.

263 We analysed the combined influence of hedgerows and environmental variables
264 on both local species richness for plants (S_{local}) and estimated richness per site for
265 plants and spiders (S_{site}), using linear models and analyses of variance, as follows: for
266 each taxonomic group (plants and spiders) and dependent variable (S_{local} and S_{site}), we
267 selected the most informative model using a stepwise algorithm based on Akaike
268 Information Criterion (StepAIC, library MASS in R) starting from the most complete
269 model including all environmental variables likely to influence species richness (listed
270 above : see “site characteristics”). Plant richness was included as an additional
271 environmental variable for spiders. Data were log-transformed when necessary to meet
272 normality assumptions; the effects of variables retained by the stepwise algorithm were
273 tested adjusted to others and the nested structure of the data was taken into account
274 (local richness per quadrat nested within site: lme, library nlme in R).

275

276 2.4.2. Species composition

277 We investigated a possible spatial autocorrelation in community composition by
278 performing mantel tests (mantel.randtest, library ade4 in R) to assess the correlation
279 between matrices of geographic vs. specific distances among sites. For plants and
280 spiders, matrices of specific distances across sites were computed with the Jaccard
281 index on presence/absence matrices. This effect was also tested separately within both
282 types of edges (WT and WO sites). For these analyses, all species were retained.

283 We also examined the effect of hedgerows on the composition of plant and
284 spider communities in the herbaceous strata using two types of multivariate analyses:
285 Constrained Analysis of Principal Coordinates (CAP) and partial Constrained
286 Correspondence Analysis (pCCA), followed-up by ANOVA-like permutation tests ($n =$
287 999) to assess significance of effects. CAP (capscale, library vegan in R, see Anderson
288 and Willis, 2003) is an ordination method similar to Redundancy Analysis (RDA), i.e.
289 exploring the relationship between two sets of variables, but allowing non-Euclidean
290 dissimilarity indices. It was used to examine whether species similarity among sites
291 depended on the presence/absence of hedgerows, and on the distance to nearest
292 woodland patch, which was used as a covariable. It was performed on presence/absence
293 matrices across sites, using the Jaccard index. pCCA (cca, library vegan in R, ter Braak,
294 1986) is an ordination method based on CCA, a constrained ordination method
295 developed to relate community composition to known variation in the environment. It is
296 considered as a good choice if the user has clear and strong *a priori* hypotheses on
297 constraints. Here, we used pCCA to test whether the presence of some species was
298 associated with the presence or absence of planted hedgerows. We chose pCCA instead
299 of a simple CCA to remove the effect of the distance to the nearest woodland patch,
300 used as a covariable, as in CAP. As both analyses are sensitive to rare species, we only
301 retained species observed in more than four samples, i.e. 46 plant species and 67 spider
302 species.

303 Third, we examined the complementarity of communities (Nichols et al., 1998)
304 in each type of site (WO type and WT type) using COMDYN with sites as replicates (n
305 = 11). In addition to estimating richness within each type of site (S_{type} within WO and
306 WT type of sites), we obtained the following estimators: complement of “extinction

307 probability” between the two types, Φ (i.e. proportion of WT species present in WO),
308 estimated complement of species “turnover”, γ (i.e. proportion of WO species present in
309 WT), and “estimated local colonising” species, B (i.e. number of species not present in
310 WT but present in WO). As for richness, we compared the mean and standard error
311 (over 15 re-sampling events) of these estimators between WT and WO types.

312

313 2.4.3. Functional trait composition

314 We investigated whether some species attributes were more likely associated with one
315 type of site and distance to neighbouring woody patch (environmental variables). To
316 this end, we used a multivariate ordination analysis, RLQ, which is an extension of
317 coinertia analysis. RLQ performs a double inertia analysis of two arrays (R, here the
318 environmental array and Q, here the trait array), i.e. measures the adequacy between the
319 two arrays, with a link expressed by a contingency table (L, here the species array:
320 matrix of presence-absence of species across sites) (rlq, library ade4 in R, complete
321 description: see Doledec et al., 1996; for an example: Ribera et al., 2001). The general
322 significance of the relationship between environmental variables and species traits was
323 tested using random permutations test ($n = 999$). We also used only species observed in
324 more than four samples to limit the potentially strong effects of rare species.

325

326 **3. Results**

327

328 Across 25 highway verge sites, we observed a total of 85 plant species and 123 different
329 spider species. For spiders, we captured 8 300 individuals, 7 862 of which were adults
330 that could be identified to species level. Only eight of the 85 plant species (A.

331 *campestre*, *A. pseudoplatanus*, *B. pendula*, *F. excelsior*, *P. avium*, *P. padus*, *P. spinosa*,
332 *V. opulus*) were identical to those planted in the immediately neighbouring hedgerow in
333 WT sites and were excluded from most analyses; note however that including them had
334 no effect on the following results.

335

336 **3.1. Species richness**

337

338 3.1.1. Influence of planted hedgerows on plant communities

339 We observed a significant positive effect of the presence of hedgerows (Table 1) on
340 plant richness at the local scale (quadrat level, $n = 125$, $S_{\text{localWT}} = 10.20 \pm 0.46$ SE;
341 $S_{\text{localWO}} = 8.20 \pm 0.47$ SE, $F_{1,20} = 5.79$, $p = 0.026$). We also found a negative effect of
342 distance from crop edge ($F_{1,20} = 5.75$, $p = 0.026$), as well as tendencies for effects of
343 adjacent land use (higher richness with temporary fallow, $F_{1,20} = 4.15$, $p = 0.055$) and
344 phosphorous rate (negative : $F_{1,20} = 4.00$, $p = 0.059$) on local plant richness. In contrast,
345 no effect of hedgerows or any environmental factor was detected on plant richness at the
346 site level ($n = 25$, $S_{\text{siteWT}} = 25.45 \pm 1.66$ SE; $S_{\text{siteWO}} = 23.75 \pm 3.12$ SE) and there was no
347 difference in detection probabilities between the two types of sites. However, at the
348 section level ($n = 11$), the estimated plant richness was 139.16 over all WT sites (S_{typeWT} ,
349 ± 29.20 SE; detection probability $dp = 0.47 \pm 12.42$ SE) vs. 87.51 over all WO sites
350 (S_{typeWO} , ± 19.43 SE; detection probability $dp = 0.68 \pm SE = 0.12$).

351

352 3.1.2. Influence of planted hedgerows on spider communities

353 We found no effect of the presence of planted hedgerows on spider richness at the site
354 level. Spider richness was significantly affected by distance to the nearest woodland

355 patch (negative effect, $F_{1,18} = 5.94$, $p = 0.025$), site slope (positive effect, $F_{1,18} = 4.65$, p
356 $= 0.044$) and plant richness (positive effect, $F_{1,18} = 6.81$, $p = 0.018$). There was no
357 difference in detection probabilities between the two types of sites. At the section level,
358 ($n = 11$), estimated spider richness was 119.3 over all WT sites (S_{typeWT} , ± 19.6 SE;
359 detection probability $dp = 0.80 \pm 0.10$ SE) and 142.0 over all WO sites (S_{typeWO} , ± 27.15
360 SE; detection probability $dp = 0.64 \pm 0.11$ SE).

361

362 **3.2. Community composition**

363

364 3.2.1. Spatial autocorrelation

365 Using Mantel tests on the full dataset, we found significant spatial autocorrelation in
366 plant communities ($p = 0.001$), but not in spider communities ($p = 0.066$). In contrast,
367 within types of site, spatial autocorrelation was observed in plants (WT: $p = 0.006$; WO:
368 $p = 0.001$) and spiders (WT: $p = 0.007$; WO: $p = 0.028$). However, as WO and WT sites
369 were randomly distributed in space (Fig. 1), autocorrelation should not interfere with
370 our main purpose, i.e. to assess the influence of hedgerows on community composition.

371

372 3.2.2. The presence of planted hedgerows influence community composition

373 Sites with and without planted hedgerows supported significantly different plant and
374 spider communities, as shown by CAP (ANOVA-like permutation tests: plants: $F_{1,22} =$
375 2.26 , $p < 0.001$, inertia explained by hedgerows = 9% and by distance to the nearest
376 woodland patch = 4%; spiders: $F_{1,22} = 1.90$, $p = 0.006$, inertia explained = 7% and 6%,
377 respectively). This effect of hedgerows on plant and spider community composition was
378 confirmed by the pCCA analysis (ANOVA-like permutation tests: plants: $F_{1,22} = 2.13$, p

379 < 0.01, inertia explained = 8% and 4% respectively; spiders : $F_{1,22} = 1.81$, $p < 0.005$,
380 inertia explained = 7% and 5% respectively). This method also identified species that
381 seemed preferably associated with WT sites. For plants, these were *A. campestre*, *B.*
382 *pendula*, *Galium mollugo*, *Centaureum erythraea*, *Trifolium repens*, and for spiders,
383 *Panamomops sulcifrons*, *Maso sundevalli*, *Walckenaera dysderoides*, *Ceratinella*
384 *brevis*, and *Drassodes cupreus*. In contrast, the spider species *Tegenaria picta*, *Ero*
385 *furcata*, and *Palliduphantes ericaeus*, were preferably associated with WO sites.

386

387 3.2.3. Nested vs. complementary communities

388 We found that the plant community observed in WO sites was a subset of the plant
389 community in WT sites (Table 1). WO sites did not exhibit any private species: we
390 found 99% of WO sites species in WT sites, so that all WO species were expected in
391 WT sites (COMDYN estimator $B = 0$). The reverse was not true: WT exhibited several
392 private species (14%), with only 86% of WT sites species also observed in WO sites. In
393 contrast, spider communities appeared complementary. Respectively 83% (WT) and
394 77% (WO) of spider species were present in the other type of site, so that each type of
395 sites exhibited private species.

396

397 **3.3. Relationship between species attributes and presence of hedgerows**

398

399 For both plants and spiders, there was a significant relationship between species
400 attributes and environmental variables (Fig. 2; RLQ randtest, $p = 0.001$ and $p = 0.001$).

401 For the two taxa, the presence/absence of planted hedgerows was associated with the
402 first axis, which explained respectively 81% and 80% of the total inertia, whereas the

403 distance to the nearest woodland patch tended to be associated with axis 2 (respectively
404 19% and 20% of inertia). In spontaneous plant species, Raunkier type was influenced by
405 the presence of hedgerows, with Phanerophytes and Chamaephytes (Rank: P) positively
406 associated with WT sites (Fig. 2). In contrast, adult height was not significantly
407 associated with site type. Finally, species with no specific means of dispersal
408 (barochory, autochory) tended to be more present in WT sites than in WO sites, whereas
409 animal-dispersed species (zoochory) were more common in WO than in WT sites;
410 wind-dispersed species were not affected by the presence of hedgerows. In spiders, the
411 mode of dispersal (ballooning vs. non ballooning) was strongly affected by the presence
412 of hedgerows: ballooning species were more likely found in WO sites, and non-
413 ballooning species in WT sites. In addition, web-builders were more common in WT
414 than in WO sites, and diurnal wandering hunters in WO sites. Finally, larger species
415 tended to be more common in WT sites than in WO sites.

416

417 **4. Discussion**

418

419 We addressed the effect of the presence of planted hedgerows on neighbouring plant
420 and spider communities of highway verges. We showed that (1) planted hedgerows
421 were associated with higher species richness, i.e. a higher α -diversity ($\alpha_{WO} < \alpha_{WT}$), for
422 plants, but not for spiders. This was due to the fact that plant communities in sites
423 without hedgerows (WO) were a subset of communities in sites with hedgerows (WT),
424 whereas spider communities in WO sites were complementary to communities in WT
425 sites. Below, we argue that such differences are attributable to different ecological

426 characteristics of species, which is supported by the distribution of functional traits, and
427 derive the consequences in terms of roadside management.

428

429 **4.1. The influence of propagule source vs. local conditions on plant and spider** 430 **community composition**

431

432 Following the environmental filter model (Keddy, 1992), two non-exclusive hypotheses
433 may explain the effect of hedgerows on community composition, depending on
434 taxonomic group. Hedgerows could either be a source of dispersers (“source”
435 hypothesis) or could provide microclimatic conditions that affect the presence of some
436 species due to their environmental requirements (“local conditions” hypothesis).

437

438 4.1.1. “Source” hypothesis and the effect of hedgerows on plant communities

439 The dispersal of some species from neighbouring hedgerows into a suboptimal habitat
440 (grassland) would affect community composition in the suboptimal habitat. This
441 phenomenon, known as the edge effect, has been observed in several taxa: contrasted
442 adjacent habitats supporting distinct species assemblages often mix over a few meters
443 on either side of the interface (see for example Bedford and Usher, 1994). For example,
444 Downie et al. (1996) studying spider community composition across a plantation-
445 pasture ecotone, found that most of the community (70% of species) was formed by the
446 overlap of both pasture and plantation species encroaching across the interface through
447 dispersal or foraging processes. Interface-specialist species were present but contributed
448 less to the interface community content than the other species categories (23% of
449 individuals and 25% of species).

450 Under the “source” hypothesis, communities are therefore expected to exhibit
451 higher species richness in WT vs. WO sites. This was the case for plant communities
452 ($\alpha_{wo} < \alpha_{wt}$), at the quadrat scale, but not at the site level. Another prediction of the
453 source hypothesis is that WO communities should be a subset of WT communities. This
454 was true again for plants: in WT sites, we observed ‘private’ species which were not
455 supported by WO sites, whereas the reverse was not true. Finally, in the case of a higher
456 effect of dispersal vs. local conditions on species distribution within similar habitats, a
457 distance effect can be expected independently of presence/absence of hedgerows. In
458 plant communities, spatial autocorrelation was in fact detected regardless of the
459 presence of hedgerows. These three observations converge to suggest that dispersal is a
460 major driver of community composition in this group.

461 The distribution of plant functional traits is consistent with this role of
462 dispersal. We found that Phanerophytes and Chamaephytes were more represented in
463 WT sites, corresponding mostly to the occurrence of the following species: *A.*
464 *campestre*, *B. pendula*, *C. scoparius*, *F. excelsior* and *P. spinosa*. These species
465 observed in the herbaceous strata most likely originated from seed-bearer trees that
466 grow spontaneously within the otherwise planted hedgerow. Thus, hedgerows offer a
467 sustainable habitat where particular species, and notably woody plants, can grow and
468 reproduce, whereas such species cannot reach maturity within WO sites, due to frequent
469 mowing. The fact that zoochory was more represented in WO sites is however not
470 easily interpreted in this framework.

471

472 4.1.2. Local conditions hypothesis and the effect of hedgerows on spider communities

473 Microclimatic conditions (influenced, among others, by the neighbouring hedgerows)
474 might be responsible for observed community composition, especially in spiders. For
475 example, spider richness within sites was positively correlated with local plant richness;
476 plant community composition and consequently the architecture of habitat are well-
477 known predictors of spider community composition (e.g. Beals, 2006). Moreover,
478 woody hedgerows are known to provide particular microclimate conditions in their
479 neighbourhood (Forman and Baudry, 1984) and most authors agree that those are a
480 major factor controlling spider distribution (see Marc et al., 1999). For example,
481 Downie et al. (1996), examining spider community composition, proposed that close to
482 an interface, the role of vegetation structure is low compared to other factors, including
483 changes in microclimate. Finally, perennial non-crop habitats are known to be used by
484 spiders as overwintering sites and refuges (Oberg et al. 2008). Grassland habitats
485 located next to hedgerows maybe therefore provide better conditions than sites without
486 hedgerows for overwintering, with direct consequences on spider community
487 composition. Thus, neighbouring hedgerows may have an environmental filter effect,
488 which leads to the selection of species with particular ecological requirements.

489 Under the 'local conditions' hypothesis, we expect that sites with and without
490 planted hedgerows support different species. This was the case with spiders: WT and
491 WO communities were complementary instead of nested, thus yielding similar species
492 richness with or without hedgerows. This implies that some spider species occurring in
493 WO sites were absent from planted sites. As the two types of sites offered the same
494 habitat (grassland with similar percentage cover and dominance of graminoids), the
495 observed differences are likely be explained by specific microclimatic conditions
496 created by the neighbouring hedgerows. Finally, the role of hedgerow-induced local

497 conditions in spider community composition is also supported by patterns of spatial
498 autocorrelation: the dominant impact of neighbouring hedgerows on spider community
499 composition removed spatial autocorrelation patterns across all sites, whereas spatial
500 autocorrelation remained significant within WT and WO sites.

501 Despite the significant role of local conditions, spider community composition is
502 also likely affected by dispersal. For example, spider richness within sites was
503 negatively correlated with the distance to the nearest woodland patch. Such effect of
504 distance is well known from the theory of island biogeography (Mac-Arthur and
505 Wilson, 1967) and consistent with results from other field studies: spider species
506 richness in wheat fields has been shown to increase with the proportion of non-crop
507 habitats in the surrounding landscape (Schmidt and Tschardtke, 2005; see also Bianchi
508 et al., 2006 for other groups).

509 Although the observed distribution of species between site types suggests a
510 major role of local conditions, trait analyses outlined that aerial dispersal capabilities are
511 an important factor explaining the interaction between the presence of hedgerows and
512 spider community composition: species exhibiting ballooning behaviour were more
513 represented in WO sites and the reverse was true for non-ballooning species. This result
514 is comparable to that of Bonte et al. (2004), who found that the distribution of 29 spider
515 species inhabiting fragmented grey dunes depended on their aerial dispersal potential, as
516 well as on the interaction between patch connectivity and area. Ballooning is thought to
517 be more common in species from unstable and ephemeral habitats (Bonte et al., 2003;
518 Bell et al., 2005); moreover, high dispersal capabilities are generally dominant in
519 disturbed habitats (e.g. Nyffeler and Sunderland, 2003 for spiders; Ribera et al., 2001
520 for beetles), allowing the maintenance of populations in ephemeral agricultural

521 ecosystems (Weyman et al., 1995). We therefore suggest that the significantly higher
522 proportion of ballooning species in WO sites may be due to the absence of a
523 neighbouring hedgerow, i.e. of a stable habitat. In contrast, species that do not exhibit
524 this behaviour should be more common in WT sites because hedgerow likely provides
525 more stable conditions, both in terms of management (no mowing) and microclimatic
526 variables. Hedgerows would thus be overwintering refuges (see also: Pywell et al.,
527 2005), from which species colonise the surrounding habitats in spring. Sites without
528 planted hedgerows, which receive a cut, generally in autumn, would be poor refuges
529 that are partly recolonised from more distant sources in spring. Hence, they support a
530 higher proportion of species exhibiting large dispersal capabilities, i.e. “ballooners”.
531 Dispersal and local conditions therefore appear to drive spider community composition
532 at different temporal scales.

533 Finally, note that taxonomic differences in composition of spider communities
534 were also associated with differences in hunting strategies: web-builder were more
535 represented in WT sites possibly due to the greatest heterogeneity of support provided
536 by the presence of neighbouring hedgerow and the higher richness of plant whereas
537 diurnal wandering hunter were more abundant in WO sites.

538

539 4.1.3. Conclusions

540 Planting generally increased the γ -diversity of highway verges, via an increase in both
541 taxonomic and functional trait β -diversity between sites with and without hedgerows,
542 but this positive effect was different in the two taxa considered. For plants, it was
543 mostly due to an increase in taxonomic α -diversity within sites with hedgerows,
544 whereas for spiders it was related to a direct increase of taxonomic β -diversity between

545 the two types of sites. Note that this partition of diversity is likely to vary through time
546 as well (e.g. due to overwintering dispersal patterns in spiders), with different temporal
547 scales in the two taxa, but this was not the focus of the present study. From a theoretical
548 viewpoint, the fact that the partitioning of diversity between α and β diversity differed
549 between the two taxa is probably due to the different spatial and temporal scales at
550 which the heterogeneity of interactions between organisms and their environment can
551 be found (see Loreau 2000). According to Loreau (2000), “the challenge now is to
552 understand the relationship between α and β diversity at multiple scales, and the
553 processes that determine it”. In our opinion, comparing the partitioning of diversity
554 among several taxa and functional groups at different spatial scales is therefore a
555 promising way to explore the processes that control the distribution of biodiversity.

556

557 **4.2. Consequences for the management of highway verges**

558

559 Our findings have direct consequences for the management and conservation of
560 highway verges in agricultural landscapes, where most biodiversity is aggregated in
561 more stable non-crop habitats and field edges (Bianchi et al., 2006). Increasing the
562 botanical and structural heterogeneity of hedgerows by planting is likely to have
563 significant beneficial effects on native flora and fauna (Maudsley, 2000). Obviously,
564 plantation increases species richness both directly (introduction of new species) and
565 indirectly, by providing particular environmental conditions within woody hedgerows
566 and thus contributing to the maintenance of some species (e.g. woody plants) in
567 landscapes where they are poorly represented. But our results suggest that planted

568 hedges may also affect community composition of nearby herbaceous strata, enhancing
569 both taxonomic and functional trait γ -diversity along highway verges.

570 In practice, our results highlight the importance of creating a mosaic of planted
571 sites alternating with non planted sites in highly disturbed landscapes. Of course,
572 “natural” dynamics could yield the same results and probably a greater biodiversity as
573 demonstrated by Boutin et al. (2002), who compared natural vs. planted hedgerows.
574 However, in the case of highway verges, natural hedgerows would only arise by
575 recolonisation of the newly created habitats, which involves successional dynamics with
576 intermediate states, and the presence of pioneer species often considered as weeds. In
577 the context of intensive agricultural landscape, where farmers wish to limit weeds in
578 field boundaries as much as possible, planting trees along highway verges appears as a
579 compromise between biodiversity conservation and anthropogenic pressures. The issues
580 of the identity of planted species (which are usually exotic species), of management of
581 hedgerows (Croxtton et al., 2004) and of their spatial arrangement along highway verges
582 (to provide effective corridors) remain to be addressed. Given the urge to conserve
583 biodiversity, especially in the context of climate change, road practitioners should
584 consider plantation not only for esthetical reasons but also as a possibility to increase
585 the role of verges as a refuge and, consequently, landscape connectivity.

586

587

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589

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597

598

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778

779 **Captions**

780

781 **Table 1** - Changes in species composition in the herbaceous strata of highway verges in
782 sites without planted hedgerows (WO) vs. sites with planted hedgerows (WT).

783

784 **Fig. 1**- Location of the 25 study sites.

785

786 **Fig. 2** - RLQ analysis ordination biplot illustrating relationships among environmental
787 parameters and plant species attributes (A) and spider species attributes (B).

788

789 **Table 1** - Change in species composition in the herbaceous strata of highway verges in
790 sites without planted hedgerows (WO) vs. sites with planted hedgerows (WT).

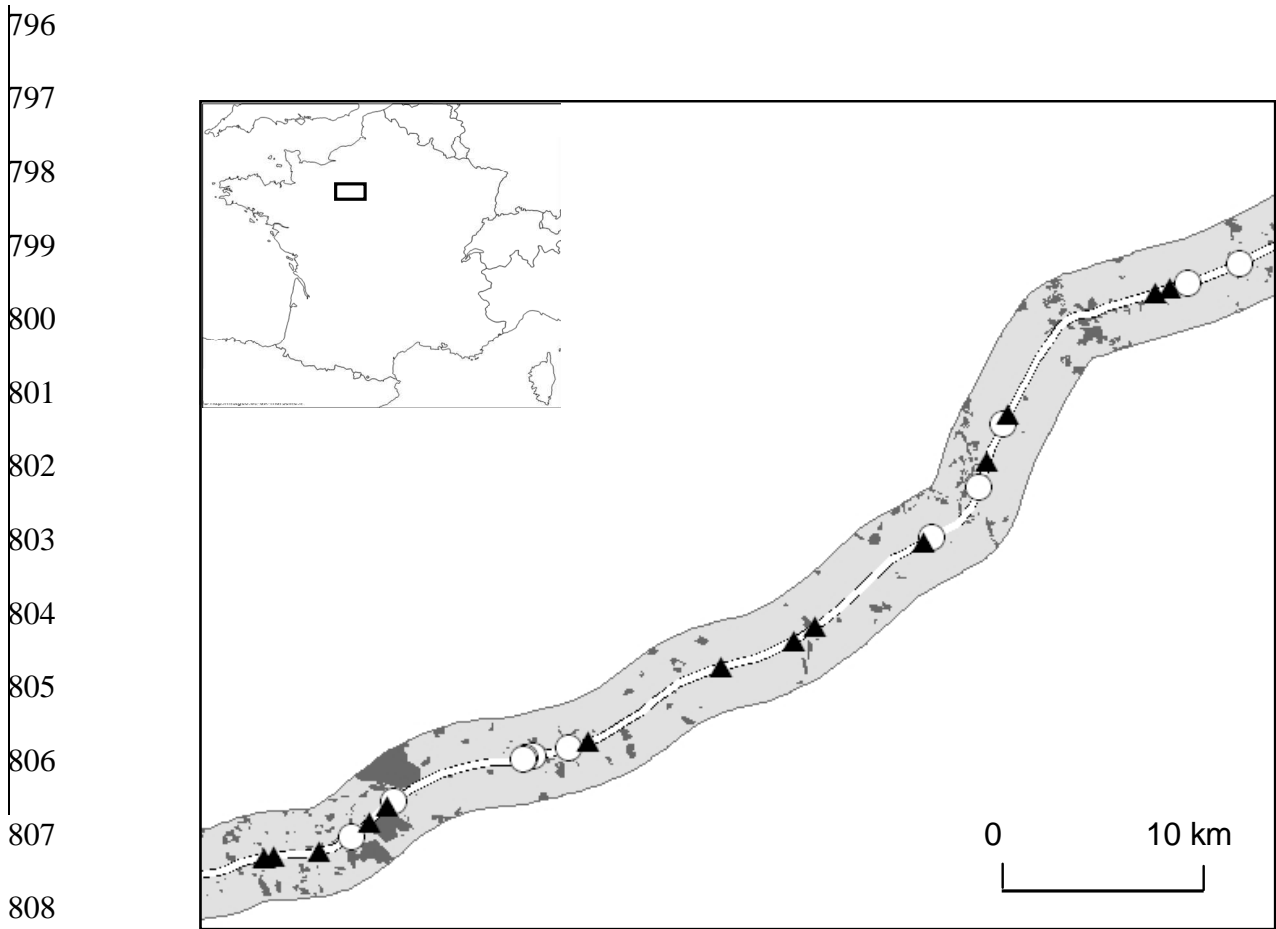
791

	Φ	γ
Plants	0.86 ± 0.11	0.99 ± 0.10
Spiders	0.77 ± 0.09	0.83 ± 0.08

792 Φ is the proportion of WT sites species still present in WO sites and γ is the proportion
793 of WO sites species still present in WT sites.

794

795 **Fig. 1-** Location of the 25 study sites.

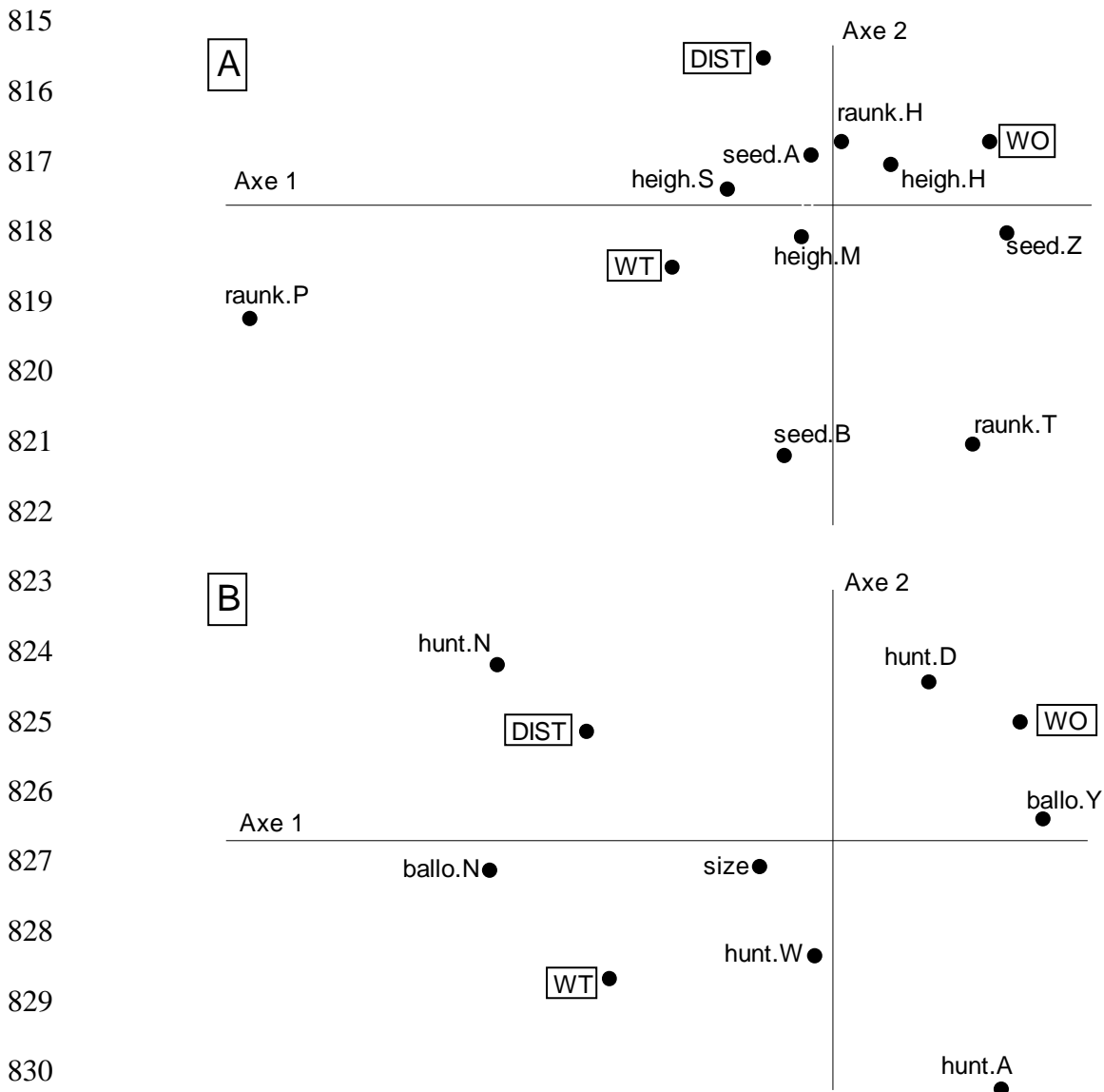


809

810 ▲: sites without hedgerows (WO), ○: sites with planted hedgerows (WT); line: A11
811 highway; grey patches: woodland patches within a 2 000m radius buffer.

812

813 **Fig. 2** - RLQ analysis ordination biplot illustrating relationships between environmental
 814 parameters and plant species attributes (A) and spider species attributes (B).



831 The analysis is based on presence/absence of species with known attributes that were
 832 observed in more than four samples (46 plant species and 56 spider species).

833 1) **Environmental parameters.** WT: sites with planted hedgerows, WO: sites without
 834 hedgerows; dist: distance to the distance to the nearest woodland patch. 2) **Plant traits**
 835 **(A).** rank: raunkier type: H: Hemicryptophytes and Geophytes (28 species), P:
 836 Phanerophytes and Chamaephytes (6), T: Therophytes (12); heigh: maximum adult
 837 height: S: small (0 to 45 cm: 9), M: medium (46 to 100 cm: 19), H: high (100 and more:
 838 18); seed: Seed dispersal: A : anemochory (30), B: barochory and autochory (9), Z:
 839 zoochory (7). 2) **Spider traits (B).** ballo: ballooning behaviour: Y: Yes (30), N: No
 840 (26); size; hunt: hunting strategies: W: diurnal wandering (18); N: nocturnal wandering
 841 (10); W: web-builders (21); A: ambush hunters (7).