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► **To cite this version:**

Axel Hacala, Maxime Le Roy, Jerome Sawtschuk, Julien Pétilion. Comparative responses of spiders and plants to maritime heathland restoration. *Biodiversity and Conservation*, 2020, 29 (1), pp.229-249. 10.1007/s10531-019-01880-y . hal-02355338

HAL Id: hal-02355338

<https://univ-rennes.hal.science/hal-02355338v1>

Submitted on 3 Feb 2020

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**Comparative responses of spiders
and plants to maritime heathland restoration**

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11 **Abstract**

12 Assessment of habitat restoration often rely on single-taxa approach, plants being widely used.
13 Arthropods might yet complement such evaluation, especially in hard, poorly-diversified
14 environments such as maritime clifftops. In this study we compared the responses of spiders
15 and plants (both at species and assemblage levels) to increasing time of heathland restoration.
16 Sampling took place in different sites of Brittany (Western France), using a replicated design
17 of both pitfall traps and phytosociological relevés. A total of 5056 spiders belonging to 160
18 species, and 103 plant species were found. No change in species richness between degradation
19 states was found for spiders. Plant species richness was lower in highly degraded habitats of
20 recently restored sites but was not in the oldest restored one. Species composition greatly
21 changed through turnover mechanisms between all sites and degradation states, for both spider
22 and vegetation. Heterogeneity was higher in references states, and increased over restoration
23 time between sites. The number of indicator species decreased with restoration age for spiders,
24 while no indicator species was found for plants. Restoration is still on-going after 15 years, with
25 no recovery of reference assemblages for both plants and spiders, but there were some signals
26 toward reference in the oldest restoration site. Plants and spiders were proved to be
27 complementary bio-indicators of post disturbance restoration, as they bring different, scale-
28 dependent information on restoration success.

29 **Key-words:** Indicator taxa, species turn-over, Araneae, Ulex, Brittany, clifftop.

30

31

32 **Introduction**

33 Due to strong environmental stresses (mainly wind and salt deposition: Malloch 1972;
34 Sawtschuk 2010), maritime clifftops present particular conditions for flora and fauna, which
35 lead to the establishment of maritime heathlands, a habitat protected by European legislation
36 Natura 2000 (Sawtschuk et al. 2010), under the codes 4030 (European dry heaths) and 4040
37 (dry Atlantic coastal heaths with *Erica vagans*). Despite their high conservation values,
38 maritime clifftops are often degraded along the French East-Atlantic coasts because of
39 important touristic uses, leading to intensive human trampling and/or building constructions
40 (especially since the 50s: Le Fur 2013; Sawtschuk 2010). These habitats have actively been
41 restored since the 90s, first for landscape and then for biodiversity purposes (Le Fur 2013),
42 locally resulting in sites with different state of degradation. In Brittany (Western France), most
43 of restoration projects include passive restoration by precluding areas from human trampling or
44 vehicle access. Some projects also use active restoration methods (e.g. biodegradable geotextile
45 and fascines use) to initiate or accelerate the restoration of degraded sites. Some projects finally
46 include the deconstruction of infrastructures such as building or car parks, together with public
47 access restriction. Since the start of the restoration projects (between 2002 and 2012 for our
48 study sites) vegetation monitoring plots are set up to assess the efficiency of restoration
49 practises (Desdoigts 2000, Le Roy et al. 2019). This has proven that passive restoration, when
50 performed in moderately or lightly degraded areas, is usually enough to create a good
51 restoration dynamic (Sawtschuk et al. 2010). However, this assessment of ecological restoration
52 success mainly relies on vegetation analysis. To the best of our knowledge, no study has been
53 performed to assess the restoration of arthropod assemblages in degraded maritime heathlands
54 yet.

55 Measurements of species diversity and abundance constitute the most widely used indicator of
56 restoration success (Wortley et al. 2013), mainly using plants as bio-indicators (Morrison 1998;

57 Babin-Fenske & Anand 2010; Kollmann et al. 2016). There are different reasons to explain this
58 over-representation of plants, such as the facility to sample this group (Gatica-Saavedra et al.
59 2017) or the lesser impact of seasonality on plant assemblages compared to animal assemblages
60 (Ruiz-Jaen & Aide 2005). Some authors also claimed that restoration of indigenous plants might
61 naturally lead to the restoration of fauna (Young 2000), because of their structural and
62 functional roles (Allen 1998). Fauna and more specifically arthropods are comparatively less
63 used as bio-indicators (Ruiz-Jaen & Aide 2005; Wortley et al. 2013), while they represent more
64 diversified taxonomic and functional groups (Longcore 2003). Using vegetation only as a proxy
65 of global restoration success is thus increasingly criticised in literature (Morrison 1998;
66 Andersen Majer 2004). Arthropods are known to answer differently to restoration (Babin-
67 Fenske & Anand 2010; Feest et al. 2011; Spake et al. 2016), and can actually complement
68 assessments only based on plants (Pétillon et al. 2014). Arthropods are yet under-studied,
69 probably because of their complexity and the specific skills required to identify some taxa
70 (Gerlach et al. 2013). To encourage the use of arthropods in monitoring projects, some authors
71 therefore recommended using bio-indicator taxa instead of the whole arthropod assemblage (
72 Longcore 2003; Pearce & Venier 2006; Gerlach et al. 2013). Monitoring arthropod taxa is thus
73 expected to complete conclusions based on vegetation studies, especially in habitats where
74 specific abiotic conditions lead to specific arthropod assemblages (Leibold et al. 2004; Schirmel
75 et al. 2012). Such taxa have to fulfil a number of criteria to be considered as “good” bio-
76 indicators: nor too rare nor too common, to contain specialised taxa (e.g. by habitat, feeding
77 regime, etc.: Caro & O’Doherty 1999), and easy to sample and to identify. Spiders, dominant
78 arthropod predators in many terrestrial habitats, are one of these taxa described as good bio-
79 indicators (Cristofoli et al. 2010; Gerlach et al. 2013; Ossamy et al. 2016), and also reported to
80 react fast and differently from plants to local habitat disturbance (Lafage et al. 2019). In
81 maritime grasslands and maritime heathlands, extreme conditions such as nutrient-limited and

82 shallow soil (Bourlet 1980), high wind exposure and salt deposit (Malloch 1972; Sawtschuk
83 2010) lead to specific plant assemblages (Bioret & Géhu 2008). The same probably applies for
84 arthropods that have to resist, and likely to be adapted, to these strong constraints.

85 In this study we assess the complementarity of plants and arthropods to monitor the restoration
86 success of degraded maritime heathlands by comparing their patterns in taxonomic diversity
87 (both alpha and beta, i.e. functional and rarity based metrics were not considered here, see e.g.
88 Leroy et al. 2014). We first tested the hypothesis that reference habitats host few but constant
89 specialist species, while degraded habitat host as many, but more context-dependent, generalist
90 or opportunistic species and that their ratio is driven by the intensity of degradation (figure 1).
91 We consequently expect (i) species richness to be similar between degradation states, (ii)
92 species composition to differ between sites, with heterogeneity of assemblages (estimated by
93 β -diversity) increasing with restoration process due to higher species turnover and a constant
94 nestedness (i.e. species pool in degraded habitats is not a subset of species pool in reference
95 habitat: see Baselga 2010) and (iii) a decreasing number of indicator species explained by a
96 higher degradation. Although environmental filters act differently on plants and spiders (see
97 e.g. Klejin et al. 2006), we do not expect significant differences in alpha- and beta-diversity
98 patterns between these taxa (see e.g. Lafage et al. 2015). The number of indicators species in
99 degraded states is expected to increase with time since restoration for both taxa (because pools
100 of generalist species are larger and more site-dependent), while this number should remain
101 constant in reference states. Lastly, we expect more indicator species for plants than for spiders,
102 the latter being more mobile and thus more likely to be found in different adjacent degradation
103 states.

104

105 **Material and Methods**

106 Study sites and sampling design

107 Fieldwork was done in three coastal sites of Brittany, Western France (Appendix 1). Sites were
108 coded using the time (in years) since their restoration (at the time of fieldwork, i.e. 2017).
109 L'Apothicaiererie (S5) (47°21'44.0" N, 3°15'34.9" W) was heavily degraded by infrastructures
110 (mainly car park and hotel) that were removed in 2012. La Pointe de l'Enfer (S11)
111 (47°37'18.3"N 3°27'46.9"W) was degraded by human trampling and by frequent vehicle access.
112 Both degradations sources were removed from the site in 2006. The last site La Pointe de Pen-
113 Hir (S15), located on the mainland (48° 15' 03" N, 4° 37' 25" W), was mainly degraded by
114 human trampling that was reduced in 2002. Therefore S5 is the youngest restoration site with
115 five years of restoration while S15 has the longest restoration time. These sites were selected
116 because of their increasing age of restoration, but also because they all present the same kind
117 of reference vegetation (i.e. without degradation) which is a short and dry heathland dominated
118 by *Erica spp.* and *Ulex spp.* (Appendix 1).

119 On top of the reference (further abbreviated RF) state, two other states were defined according
120 to their morphology and selected at each site: heavily damaged (HD) and moderately damaged
121 (MD). Two 400 m² plots of homogeneous vegetation were designed for each degradation state,
122 and four pitfall traps (80mm in diameters and 100mm deep) were set at each plot. Traps were
123 half-filled of salted solution (250 g.L⁻¹) with a drop of odorless soap and settled 10 meters apart
124 in order to avoid interference and local pseudoreplication (Topping and Sunderland, 1992). This
125 resulted in 71 traps (in one station, the sampling area was too restricted to set 4 traps spaced of
126 10m apart, so 1 was removed) active between mid-March to mid-June 2017, and emptied every
127 two weeks. Total plant cover was estimated in a 5m radius circle around every trap, and all
128 species were identified and their percentage cover estimated. Pitfall samples were sorted,
129 arthropods transferred to ethanol 70°, and stored at the University of Rennes 1. Spiders were

130 identified to species level using keys of Roberts (1985) and Nentwig (2019). Data were pooled
131 together by state of degradation and by site.

132 Data analysis

133 Spider and plant assemblages were consistently analyzed by (1) comparing alpha and beta-
134 diversities between sites and between degradation states within sites, and (2) looking for
135 indicator taxa of specific degradation states. Sampling coverage curves were computed
136 (Appendix 2), and the above 90% values used to check the validity of the sampling protocol,
137 and to assess the overall quality of spider and plant datasets. Site effect was tested through
138 assemblage composition analysis (Anosim), which further determined whether sites were
139 grouped or not in subsequent analyses.

140 We compared alpha-diversity (species richness) between states using estimated richness based
141 on the methods developed by Chao (1984, 1987). The “iNEXT” function from iNEXT package
142 (Chao et al. 2014). This method was selected to account for possible influence of sampling
143 coverage. The test was ran with 40 knots and 200 bootstrap replication. Significant differences
144 were assessed through the absence of overlapping confidence intervals on iNEXT curves (Chao
145 et al. 2014).

146 Assemblages were compared between sites using NMDS with a Sørensen dissimilarity matrix
147 that is not affected by joint absence (Borcard et al. 2011). Data was transformed to
148 presence/absence data to avoid abundance bias from difference in species activity rate and/or
149 in sensitivity to environment structures (Lang 2000). If ANOSIMs were significant, subsequent
150 analyses on beta-diversity and indicator species were performed site by site, if not sites were
151 pooled together for comparing degradation states.

152 Beta-diversities were compared using NMDS and ANOSIM on dissimilarity matrices to
153 identify significant differences between assemblages. NMDS and ANOSIM tests were

154 performed using “MetaMDS” and “anosim” functions of the “vegan” package (Oksanen et al.
155 2019) respectively. When ANOSIMs were performed on pairs of states, level of significance
156 was adjusted using correction (here $\alpha=0.016$). Dissimilarity matrices were calculated with the
157 Sørensen dissimilarity on presence/absence data with the “beta.pair” function (“betapart”
158 package, Baselga et al. 2018). This method assesses for broad dissimilarity and its partition
159 following Baselga (2012). Between-site dissimilarity was calculated to assess beta diversity
160 patterns (Baselga 2010) within degradation states using the “beta.multi” function (“betapart”
161 package, Baselga et al. 2018).

162 IndVal were calculated using presence absence data (Dufrière & Legendre 1997) in order to
163 identify the species representative of each state in terms of fidelity and exclusivity. Significance
164 of IndVal was tested using a random reallocation procedure with 1000 permutations using the
165 “indval” function from “labdsv” package (Roberts 2016). Only taxa both with an IndVal > 0.5
166 and with a significant p-value were considered accurate indicators of their respective
167 degradation state (Pétillon et al. 2010).

168 All analyses were carried out using R software (version 3.2.3 2015/12/10).

169 **Results**

170 5056 adult spiders belonging to 160 species were identified (Appendix 3). The most common
171 species were *Pardosa monticola* (1458 individuals) and *Pardosa nigriceps* (599 individuals).
172 A total of 133 plant species were identified (Appendix 4). The most common species were
173 *Leontodon saxatilis ssp. saxatilis* and *Plantago coronopus*, both found in more than 60% of
174 sampled plots. *Festuca ovina*, *Calluna vulgaris* and *Agrostis stolonifera* were also found in the
175 three sites, and were found in more than 10% of plots.

176

177 Species richness

178 Spider estimated richness showed no significant pattern between degradation states (Figure 2).
179 No statistical differences were found in estimated species richness of spiders, with all
180 confidence intervals overlapping. Plant assemblages showed a lower richness in the most
181 degraded state for both S5 and S11 sites. The oldest restoration site (S15) showed no significant
182 differences in plant species richness between the three states.

183

184 Assemblage composition

185 Both taxa significantly differed in their assemblage composition between sites (ANOSIM on
186 presence / absence data, spider: $R=.76$, $P=0.001$; plants: $R=.69$, $P=0.001$, Figure 3), which can
187 be explained by important differences in species occurrence. S5 was the spider richer site with
188 112 different species, half were found only in this site (Figure 3). Out of the 81 species identified
189 in S11, a third was unique to this site. S15 was the less spider diversified site (57 species), and
190 a fifth of these was found only there. The same pattern was found for plant assemblages (Figure
191 3). Site S5 was indeed the most diversified site (63 species), followed by S11 (48 species) and
192 S15 (39 species), with only 15 species common to the three sites. Half of S5 and S11 plant
193 species were found only on these sites, whereas a quarter of S15 species was unique to this site.
194 Sites were finally ordered by geographic proximity, for both spider and plant assemblages, and
195 total species richness of sites increased from North to South. Because of such strong differences
196 between assemblages of the three studied sites, further analyses on beta-diversities and indicator
197 species were done site by site.

198 RF states had the highest beta-diversities, while degraded states had similar, lower, beta-
199 diversities (Table 1). Patterns in beta-diversities were driven by changes in turn-over, while
200 nestedness was negligible. NMDS displayed results consistent with beta-diversity analyses

201 (Appendix 5), i.e. higher heterogeneity in RF sites. An overlap in species assemblages in the
202 oldest restoration site was finally observed for both plants and spiders (although while spider
203 assemblages between MD and HD in S15 seem closer, they still differ significantly: ANOSIM,
204 $R=0.17$, $P=0.04$).

205

206 Indicator taxa

207 Several significant indicator taxa above the 0.5 IndVal value threshold were found for spiders
208 (Table 2). They were no spider indicator of reference state in S5, 9 in S11 and 1 in S15. Mildly
209 degraded states had 14 indicator spider species in S5, 2 in S11 and 0 in S15. Highly degraded
210 had 4 indicator spider species in S5, 1 in S11 and 0 in S15 (see appendix 3 for species list).
211 There was no significant indicator plant species, i.e. having an IndVal above the 0.5 threshold.

212

213 **Discussion**

214 Species richness

215 Contrary to other studies reporting that species richness follows perturbation or degradation
216 patterns (Varet et al. 2013, Bargmann et al. 2015), species richness remained stable for spider
217 assemblages. This is overall consistent with Bell et al. (1998) who described species richness a
218 quite unreliable metrics for monitoring management effects. Plants responded differently, with
219 a lower richness in highly degraded habitats for the two most recent restored sites and no
220 significant differences for the oldest one, which indicates a success of restoration on this metric
221 over time. Species richness can hardly be used alone as restoration proxy in a maritime cliff-top
222 context, especially for spiders. This result has already been found by other authors (Matthews
223 et al. 2009; Déri et al. 2011), but can hardly be generalized to all ecosystems. Some studies

224 indeed proved the effectiveness of this metric for the same taxa, like Pétilion & Garbutt (2008)
225 for spiders of disturbed salt marshes and Borchard et al. (2014) for plants of degraded mountain
226 heathlands. In a grassland context, spider and plant species richness can also be higher in
227 reference states (Perner & Malt 2003; Borchard et al. 2014; DiCarlo & DeBano 2018).

228

229 Species composition

230 Assemblage compositions of the two taxa (spiders and plants) were very different between the
231 three studied sites. Only a few plant and spider species were common to all sites. Differences
232 between plant assemblages are not surprising, maritime heathland being well differentiated
233 along Brittany's coast (Bioret 1989; Demartini 2016). Differences in spider assemblages
234 between sites is an interesting result that can be partly explained by their great sensitivity to
235 changes in environmental, including climatic, conditions (Pik et al. 2002; Andersen & Majer
236 2004; Pearce & Venier 2006) and by their high diversity (Roberts 1985).

237 Almost all assemblages from the different degradation states within a given site significantly
238 differed between each other. As expected, most of these differences were driven by changes in
239 turnover, nestedness being negligible in most cases. Such a pattern due to turnover is consistent
240 with other studies on spider and plant beta diversity (Schirmel & Buchholz 2011; Rickert et al.
241 2012; Lafage et al. 2015; Coccia & Fariña 2019; see also Almeida-neto et al. 2011).

242 The observed patterns validate our hypothesis of a higher heterogeneity in reference states as
243 compared to references states that also increases over time since restoration. Both spiders and
244 plants displayed this pattern, which is consistent with several previous studies that showed
245 similar responses of these taxa (Perner & Malt 2003; Ilg et al. 2008; Rickert et al. 2012; Lafage
246 et al. 2015).

247 Therefore heterogeneity, as revealed by analyses of beta-diversity, can be used as a restoration
248 criteria of coastal heathland restoration for both spider and plant assemblages. Spiders appear
249 to increase in heterogeneity over time, but without converging toward the same referential state.
250 Differences in sites could explain such a result. It has indeed been shown that spider beta
251 diversity is strongly impacted by landscape-level factors (Carvalho et al. 2011; Lafage et al.
252 2015). The three sampling sites are split between continental (S15) and islands (S5 & S11), and
253 also show a temperature gradient from North to South, which are some example on how site
254 specificity may induce differences in landscape composition. Spider assemblages in all three
255 sites became more and more variable with an increasing restoration level but differently for
256 each site, which is probably driven by site-specific ecological variables. Spider assemblages
257 are known to be shaped by the interplay of environmental structures (Uetz 1991), and to rapidly
258 colonize empty niches (Pearce & Venier 2006; Cristofoli et al. 2010; Borchard et al. 2014). As
259 the environment tends to be more complex along the restoration process, spiders that are known
260 for their high dispersion abilities (e.g. Foelix 2011) colonize habitats from the surrounding
261 landscapes.

262 Contrary to spiders, plant beta diversity is known to be mostly driven by local factors (Lafage
263 et al. 2015). Coastal heathlands are constraining habitats (Bioret & Géhu 2008), which can
264 induce a stable reference state for plants toward which degraded states are converging. The
265 remaining differences with assemblages of reference state could come from the restoration
266 dynamic that stabilized into an alternative stable state (Leroy 2019).

267

268 Indicator taxa

269 Ground-dwelling spiders were both abundant and diverse in pitfall traps (they were actually the
270 dominant predators here: Hacala et al. unpublished data), which confirms their value as

271 potential bio-indicators. The low and inconsistent number of reference indicator species concurs
272 with the hypothesis of a heterogeneous reference habitat driven by site specificity. That was
273 especially true for the site S5, where no indicator species of the reference state was found. This
274 might be due to the fact that the dominant plant species of this habitat was *Erica vagans* that
275 creates more patchy vegetation, hereby inducing more spatial heterogeneity in spider
276 assemblages than in the two other sites and preventing the highlight of indicator species. Since
277 habitat structure is known to be a strong driver of spider assemblages (e.g. Uetz 1991), the
278 heterogeneity in reference state of site S5 may induce variations that prevent indicator species
279 to be detected. The number of indicator species in degraded states decreased with increasing
280 restoration from S5 to S15. This expected shift in assemblage composition with more specialist
281 species in preserved habitats is consistent with other previous studies (Bonte et al. 2006;
282 Cristofoli et al. 2010). The higher number of indicator species in MD than in HD state is
283 probably linked to the greater number of ecological niches in MD, whereas HD state is mostly
284 characterized by high levels of bare grounds. Several indicator species found in this study match
285 well with their known ecology. Degraded habitats were associated with open habitat species
286 like Linyphiidae (e.g. *Erigone dentipalpis*, *Diplostyla concolor* etc.) and reference states were
287 more characterized by plant-dwelling species (e.g. *Pardosa nigriceps*, *Zora spinimana* etc).
288 Finally, the absence of plant indicator species strongly invalidates our hypothesis about the ratio
289 of indicator species between spiders and plants. This result could be due to the relatively low
290 spatial scale of sites together with the high dispersal ability of plants (Dufrêne & Legendre
291 1997).

292

293 Concluding remarks

294 Recovery is still on-going after 15 years after initiating restoration, with no recovery of
295 reference assemblages for both plants and spiders. There were some signals that in the oldest

296 restoration site, HD resembles MD in terms of spider and plant species composition (although
297 the latter was significant different between degradation states), and plant species richness. This
298 study allows us to confirm what has been shown in other ecosystems (Babin-Fenske & Anand
299 2010; Borchard et al. 2014; McCary et al. 2015; Cole et al. 2016), i.e. arthropods strongly
300 responds to disturbance through changes in assemblage composition and species occurrence.
301 Monitoring both these taxa should provide a better understanding of the restoration dynamic
302 (Harry et al. 2019). The use of multiple bio-indicators, as the ones shown in this study, seems
303 to be the best way of assessing restoration operation (Lambeck 1997; Sattler et al. 2013;
304 Fournier et al. 2015; Harry et al. 2019). This was illustrated here by the complementary
305 responses of spiders and plants. Our study is consistent with previous studies that showed
306 arthropod assemblages respond differently to disturbances compared to vegetation (Babin-
307 Fenske & Anand 2010; Feest et al. 2011; Spake et al. 2016, Harry et al. 2019), because of their
308 greater diversity (Longcore 2003) and sensitivity to changes in microhabitat (Pearce & Venier
309 2006). Thus a habitat where vegetation has been restored does not mean that arthropods are
310 restored as well (Pétillon et al. 2014), and the other way around may probably apply.

311 These results stress the need to use multiple taxa in restoration studies as one cannot necessarily
312 be the proxy of others (Coelho et al. 2009; Gerlash et al. 2013). Taxa from various trophic
313 guilds, such as detritivorous, phytophagous or polyphagous arthropods (e.g. weevils, ground
314 beetles or ants respectively), will be studied in the future since they are also likely to display
315 different and complementary information (Lafage et al. 2015; Coccia & Fariña 2019). Such
316 comparisons groups should be done using functional or phylogenetical (Pavoine & Ricotta
317 2014; Cardoso et al. 2015) distances aside from taxonomic one to understand the dynamics of
318 arthropod assemblages, and therefore the ongoing, complex, processes that drive them.

319

320 **Acknowledgements**

321 We thank Denis Lafage and Kaïna Privet for fruitful discussions, Aurélien Ridel and Timothée
322 Scherer for their help in identifying spiders and sorting samples respectively, and “Bretagne
323 Vivante” and “Communauté de communes de Belle-île-en-Mer” for continuous support during
324 fieldwork. Two anonymous reviewers and Marie Handock provided constructive comments on
325 a first draft.

326

327 **Bibliography**

- 328 Almeida-Neto M, Frensel DM, Ulrich W (2011) Rethinking the relationship between nestedness and beta diversity:
329 a comment on Baselga (2010). *Global Ecology and Biogeography* 21(7): 772-777.
- 330 Allen EB (1998) Response. *Restoration Ecology* 6:134–134
- 331 Andersen AN, Majer JD (2004) Ants show the way down under: invertebrates as bioindicators in land
332 management. *Frontiers in Ecology and the Environment* 2:291–298
- 333 Babin-Fenske J, Anand M (2010) Terrestrial insect communities and the restoration of an industrially perturbed
334 landscape: assessing success and surrogacy. *Restoration Ecology* 18:73–84
- 335 Bargmann T, Hatteland BA, Grytnes JA (2015) Effects of prescribed burning on carabid beetle diversity in coastal
336 anthropogenic heathlands. *Biodiversity and Conservation* 24(10):2565-2581
- 337 Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and*
338 *Biogeography* 19:134-143
- 339 Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and
340 nestedness. *Global Ecology and Biogeography* 21:1223-1232
- 341 Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F (2018). betapart: Partitioning Beta Diversity into Turnover
342 and Nestedness Components. R package version 1.5.1. <https://CRAN.R-project.org/package=betapart>
- 343 Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1.
344 <https://CRAN.R-project.org/package=betapart>
- 345 Bell JR, Rod Cullen W, Wheeler P (1998) The structure of spider communities in limestone quarry environments.
346 In *Proceedings of the 17th European Colloquium of Arachnology*. British Arachnological Society,
347 Burnham Beeches, Bucks. 253-259
- 348 Bioret F (1989) Contribution à l'étude de la flore et de la végétation de quelques îles et archipels ouest et sud
349 armoricains. Ph.D. thesis, Université de Nantes, Nantes, France
- 350 Bioret F, Géhu J-M (2008) Révision phytosociologique des végétations halophiles des falaises littorales atlantiques
351 françaises. *Fitosociologia* 45:75–116
- 352 Bonte D, Lens L, Maelfait JP (2006) Sand dynamics in coastal dune landscapes constrain diversity and life-history
353 characteristics of spiders. *Journal of Applied Ecology* 43:735–747
- 354 Borcard D, Gillet F, Legendre P (2011) *Numerical ecology with R*. Springer Science & Business Media.

355 Borchard F, Buchholz S, Helbing F, Fartmann T (2014) Carabid beetles and spiders as bioindicators for the
356 evaluation of montane heathland restoration on former spruce forests. *Biological Conservation* 178:185–
357 192

358 Bourlet Y (1980) Les landes de Bretagne septentrionale. *Etudes de biogéographie végétale*. *Norois* 107:417–432

359 Cardoso P, Rigal F, Carvalho J C (2015). BAT - Biodiversity Assessment Tools, an R package for the measurement
360 and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and*
361 *Evolution* 6(2): 232–236. doi:10.1111/2041-210x.12310

362 Caro TM, O’Doherty G (1999) On the use of surrogate species in conservation biology. *Conservation Biology*
363 13:805–814

364 Carvalho JC, Cardoso P, Crespo LC, Henriques S, Carvalho R, Gomes P (2011) Determinants of beta diversity of
365 spiders in coastal dunes along a gradient of mediterraneity. *Diversity and Distributions* 17(2):225-234

366 Chao A (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of*
367 *Statistics* 11:265-270

368 Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*
369 43:783-791

370 Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation
371 with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological*
372 *Monographs* 84: 45–67

373 Coccia C, Fariña JM (2019) Partitioning the effects of regional, spatial, and local variables on beta diversity of salt
374 marsh arthropods in Chile. *Ecology and Evolution* 9(5): 2575-2587

375 Coelho MS, Quintino AV, Fernandes GW, Santos JC, Delabie JHC (2009) Ants (hymenoptera: formicidae) as
376 bioindicators of land restoration in a Brazilian Atlantic forest fragment. *Sociobiology* 54(1):51-63

377 Cole RJ, Holl KD, Zahawi RA, Wickey P, Townsend AR (2016) Leaf litter arthropod responses to tropical forest
378 restoration. *Ecology and Evolution* 6:5158–5168

379 Cristofoli S, Mahy G, Kekenbosch R, Lambeets K (2010) Spider communities as evaluation tools for wet heathland
380 restoration. *Ecological Indicators* 10:773–780

381 Demartini C (2016) Les végétations des côtes Manche-Atlantique françaises: essai de typologie et de cartographie
382 dynamico-caténales. Ph.D. thesis, Université de Bretagne occidentale - Brest

383 Déri E, Magura T, Horváth R, Kisfali M, Ruff G, Lengyel S, Tóthmérész B (2011) Measuring the short-term
384 success of grassland restoration: The use of habitat affinity indices in ecological restoration. *Restoration*
385 *Ecology* 19:520–528

386 Desdoigts J-Y (2000) L'extrémité du Cap Sizun : restauration de la nature et tourisme. L'opération grand site de
387 la pointe du Raz, de la pointe du Van et de la baie des Trépassés. *Norois* 186:283–293

388 DiCarlo LAS, DeBano SJ (2018) Spider community responses to grassland restoration: balancing trade-offs
389 between abundance and diversity. *Restoration Ecology* 27(1): 210-219

390 Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical
391 approach. *Ecological Monographs* 67:345–366

392 Feest A, Merrill I, Aukett P (2011) Does botanical diversity in sewage treatment reed-bed sites enhance
393 invertebrate biodiversity? *International Journal of Ecology* 1:1-9

394 Foelix R (2011) *Biology of spiders*. OUP USA.

395 Fournier B, Gillet F, Le Bayon RC, Mitchell EA, Moretti M (2015) Functional responses of multitaxa communities
396 to disturbance and stress gradients in a restored floodplain. *Journal of Applied Ecology* 52:1364–1373

397 Gatica-Saavedra P, Echeverría C, Nelson CR (2017) Ecological indicators for assessing ecological success of
398 forest restoration: a world review. *Restoration Ecology* 25:850–857

399 Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available
400 taxonomic groups. *Journal of Insect Conservation* 17:831–850

401 Harry I, Höfer H, Schielzeth H, Assman T (2019) Protected habitats of Natura 2000 do not coincide with important
402 diversity hotspots of arthropods in mountain grasslands. *Insect Conservation and Diversity* 12(4):329-
403 338

404 Ilg C, Dziöck F, Foeckler F, Follner K, Gerisch M, Glaeser J, Rink A, Schanowski A, Scholz M, Deichner O,
405 Henle K (2008) Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain
406 grasslands. *Ecology* 98(9):2392-2398

407 Klejin D, Baquero RA, Clough Y, Días M, De Esteban J, Fernández F, Gabriel D, Herzog F, Holzschuh A, Jöhl
408 R, Knop E, Kruess A, Marshall EJP, Steffan-Dewenter I, Tschardtke T, Verhulst J, West TM, Yela JL
409 (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology*
410 *Lettres* 9:243-254

- 411 Kollmann J, Meyer ST, Bateman R, Conradi T, Gossner MM, de Souza Mendoza Jr. M, Fernandes GW, Hermann
412 J-M, Koch C, Müller SC, Oki Y, Overbeck GE, Paterno GB, Rosenfield MF, Toma TSP, Weisser WW
413 (2016) Integrating ecosystem functions into restoration ecology—recent advances and future directions.
414 *Restoration Ecology* 24:722–730
- 415 Lafage D, Maugenest S, Bouzillé JB, Pétilion J (2015) Disentangling the influence of local and landscape factors
416 on alpha and beta diversities: opposite response of plants and ground-dwelling arthropods in wet meadows.
417 *Ecological Research* 30(6):1025-1035
- 418 Lafage D, Djoudi EA, Perrin G, Gallet S, Pétilion J (2019) Responses of ground-dwelling spider assemblages to
419 changes in vegetation from wet oligotrophic habitats of Western France. *Arthropod-Plant Interactions*, in
420 press. <https://doi.org/10.1007/s11829-019-09685-0>
- 421 Lambeck RJ (1997) Focal Species: A multi-species umbrella for nature conservation. *Conservation Biology*
422 11:849–856
- 423 Lang A (2000) The pitfalls of pitfalls: a comparison of pitfalls trap catches and absolute density estimates of
424 epigeal invertebrate predators in arable land. *Journal of Pest Science* 73(4): 99-106
- 425 Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman
426 D, Loreau M, Gonzales A (2004) The metacommunity concept: a framework for multi-scale community
427 ecology. *Ecology Letters* 7:601–613
- 428 Le Fur Y (2013) La patrimonialisation des grands sites : évolution des doctrines et transformation des espaces :
429 exemple des promontoires littoraux emblématiques bretons. Ph.D. thesis, Université de Bretagne
430 Occidentale, Brest, France
- 431 Le Roy M, Sawtschuk J, Bioret F, Gallet S (2019) Toward a social-ecological approach to ecological restoration:
432 A look back at three decades of maritime cliff-top restoration. *Restoration Ecology* 27(1): 228-238
- 433 Le Roy M (2019) Contribution à la connaissance socio-écologique des opérations de restauration des hauts de
434 falaises littorales de Bretagne. Ph.D. thesis, Université de Bretagne Occidentale, Brest, France
- 435 Leroy B, Le Viol I, Pétilion J (2014) Complementarity of rarity, specialisation and functional diversity metrics to
436 assess community responses to environmental changes, using an example of spider communities in salt
437 marshes. *Ecological Indicators* 46: 351-357.
- 438 Longcore T (2003) Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub
439 (California, U.S.A.). *Restoration Ecology* 11:397–409

- 440 Malloch AJC (1972) Salt-spray deposition on the maritime cliffs of the lizard peninsula. *Journal of Ecology*
441 60:103–112
- 442 Matthews JW, Spyreas G, Endress AG (2009) Trajectories of vegetation-based indicators used to assess wetland
443 restoration progress. *Ecological Applications* 19:2093–2107
- 444 McCary MA, Martinez J-C, Umek L, Heneghan L, Wise DH (2015) Effects of woodland restoration and
445 management on the community of surface-active arthropods in the metropolitan Chicago region.
446 *Biological Conservation* 190:154–166
- 447 Morrison ML (1998) Letter to the editor. *Restoration Ecology* 6:133–133
- 448 Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2019) Version 06.2019. Online at
449 <https://www.araneae.nmbe.ch>, accessed on 19/06/2019. doi: 10.24436/1
- 450 Oksanen J, Blanchet F G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin P R, O'Hara R B, Simpson G
451 L, Solymos P, Stevens H M H, Szoecs E, Wagner H (2019). *vegan: Community ecology package*. R
452 package version 2.5-4. <https://CRAN.R-project.org/package=vegan>
- 453 Minchin P R, O'Hara R B, Simpson G L, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2019). *vegan:*
454 *Community ecology package*. R package version 2.5-4. <https://CRAN.R-project.org/package=vegan>
- 455 Ossamy S, Elbanna SM, Orabi GM, Semida FM (2016) Assessing the potential role of spiders as bioindicators in
456 Ashtoum el Gamil natural protected area, Port Said, Egypt. *Indian J. Arachnol* 5:101
- 457 Pavoine S, Ricotta C (2014) Functional and phylogenetic similarity among communities. *Methods in Ecology and*
458 *Evolution* 5(7):666-675
- 459 Pearce JL, Venier LA (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as
460 bioindicators of sustainable forest management: A review. *Ecological Indicators* 6:780–793
- 461 Perner J, Malt S (2003) Assessment of changing agricultural land use: response of vegetation, ground-dwelling
462 spiders and beetles to the conversion of arable land into grassland. *Agriculture, Ecosystems &*
463 *Environment* 98:169–181
- 464 Pétilion J, Lasne E, Lambeets K, Canard A, Vernon P, Ysnel F (2010) How do alterations in habitat structure by
465 an invasive grass affect salt-marsh resident spiders? *Annales Zoologici Fennici* 47:79–89
- 466 Pétilion J, Garbutt A (2008) Success of managed realignment for the restoration of salt-marsh biodiversity:
467 preliminary results on ground-active spiders. *Journal of Arachnology* 36:388–393

468 Pétillon J, Potier S, Carpentier A, Garbutt A (2014) Evaluating the success of managed realignment for the
469 restoration of salt marshes: Lessons from invertebrate communities. *Ecological Engineering* 69:70–75

470 Pik AJ, Dangerfield JM, Bramble RA, Angus C, Nipperess DA (2002) The use of invertebrates to detect small-
471 scale habitat heterogeneity and its application to restoration practices. *Environmental Monitoring and*
472 *Assessment* 75:179–199

473 Rickert C, Fichtner A, Van Klink R, Bakker JP (2012) α - and β - diversity in moth communities in salt marshes is
474 driven by grazing management. *Biological Conservation* 146:24-31

475 Roberts MJ (1985) *The spiders of Great Britain and Ireland*. Brill Archive

476 Roberts D W (2016). labdsv: Ordination and multivariate analysis for ecology. R package version 1.8-0.
477 <https://CRAN.R-project.org/package=labdsv>

478 Ruiz-Jaen MC, Aide TM (2005) Restoration success: how is it being measured? *Restoration Ecology* 13:569–577

479 Sattler T, Pezzatti GB, Nobis MP, Obrist MK, Roth T, Moretti M (2013) Selection of multiple umbrella species
480 for functional and taxonomic diversity to represent urban biodiversity. *Conservation Biology* 00:1–13

481 Sawtschuk J (2010) Restauration écologique des pelouses et des landes des falaises littorales atlantiques : analyse
482 des trajectoires successioneles en environnement contraint. Ph.D. thesis, Université de Bretagne
483 Occidentale, Brest, France

484 Sawtschuk J, Bioret F, Gallet S (2010) Spontaneous succession as a restoration tool for maritime cliff-top
485 vegetation in Brittany, France. *Restoration Ecology* 18:273–283

486 Schirmel J, Blindow I, Buchholz S (2012) Life-history trait and functional diversity patterns of ground beetles and
487 spiders along a coastal heathland successional gradient. *Basic and Applied Ecology* 13:606–614

488 Schirmel J, Buchholz S (2011) Response of carabid beetles (Coleoptera: Carabidae) and spiders (Araneae) to
489 coastal heathland succession. *Biodiversity and Conservation* 20(7):1469

490 Spake R, Barsoum N, Newton AC, Doncaster CP (2016) Drivers of the composition and diversity of carabid
491 functional traits in UK coniferous plantations. *Forest Ecology and Management* 359:300–308

492 Topping CJ, Sunderland KD (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a
493 study of spiders in a field of winter wheat. *Journal of Applied Ecology* 485-491.

494 Uetz GW (1991) Habitat structure and spider foraging. In *Habitat structure*. Springer, Dordrecht, pp 325-348

495 Varet M, Burel F, Lafage D, Pétillon J (2013) Age-dependent colonization of urban habitats : a diachronic
496 approach using carabid beetles and spiders. *Animal Biology* 63:257–269

- 497 Wickham H (2016) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.
- 498 Wortley L, Hero J-M, Howes M (2013) Evaluating ecological restoration success: A review of the literature.
499 Restoration Ecology 21:537–543
- 500 Young TP (2000) Restoration ecology and conservation biology. *Biological Conservation* 92:73–83
- 501

502 **Tables**

503

504 Table 1. Comparison of partitioned beta-diversities computed using Sørensen dissimilarity
 505 matrices between degradation states (RF: Reference; MD: Midly degraded; HD: Highly
 506 degraded).

507

Spiders		S5	S11	S15
RF	Turnover	0.73	0.67	0.73
	Nestedness	0.03	0.05	0.07
MD	Turnover	0.56	0.63	0.68
	Nestedness	0.04	0.06	0.06
HD	Turnover	0.55	0.67	0.67
	Nestedness	0.15	0.06	0.09
Plants		S5	S11	S15
RF	Turnover	0.65	0.48	0.59
	Nestedness	0.04	0.17	0.07
MD	Turnover	0.66	0.47	0.56
	Nestedness	0.05	0.08	0.04
HD	Turnover	0.49	0.40	0.52
	Nestedness	0.08	0.10	0.11

509

510 Table 2. Number of significant indicator species (IndVal > 0.5, for species names of spiders see
511 appendix 4) of each degradation state (RF: Reference; MD: Moderately degraded; HD: Highly
512 degraded).

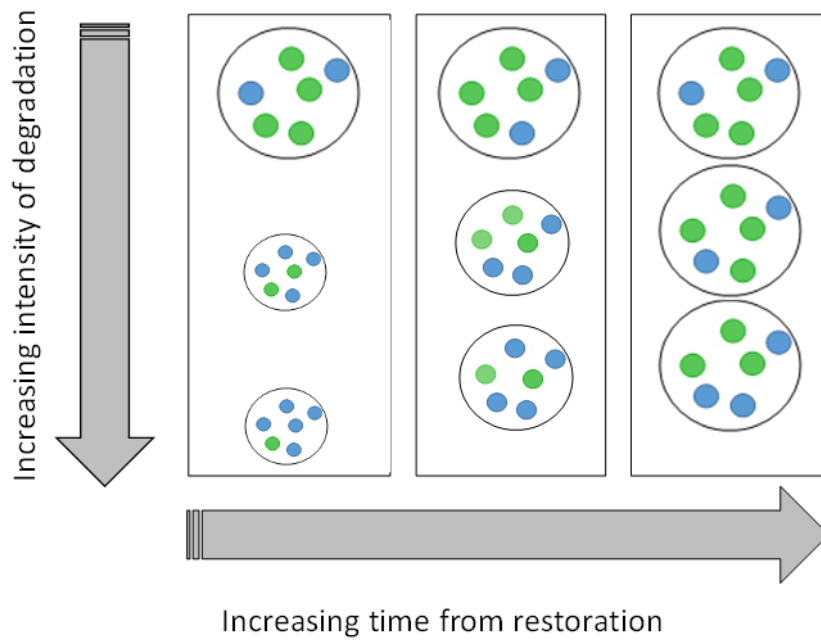
513

	S5	S11	S15
Spiders			
RF	0	9	1
MD	14	2	0
HD	4	1	0
Plants			
RF	0	0	0
MD	0	0	0
HD	0	0	0

514

515

516 Figure 1. Theoretical expectations regarding changes in assemblage heterogeneity (circle
517 diameter) and Indicator (green) vs generalist (bleu) species over time to restauration and along
518 a degradation intensity gradient. Figure made with GIMP 2.

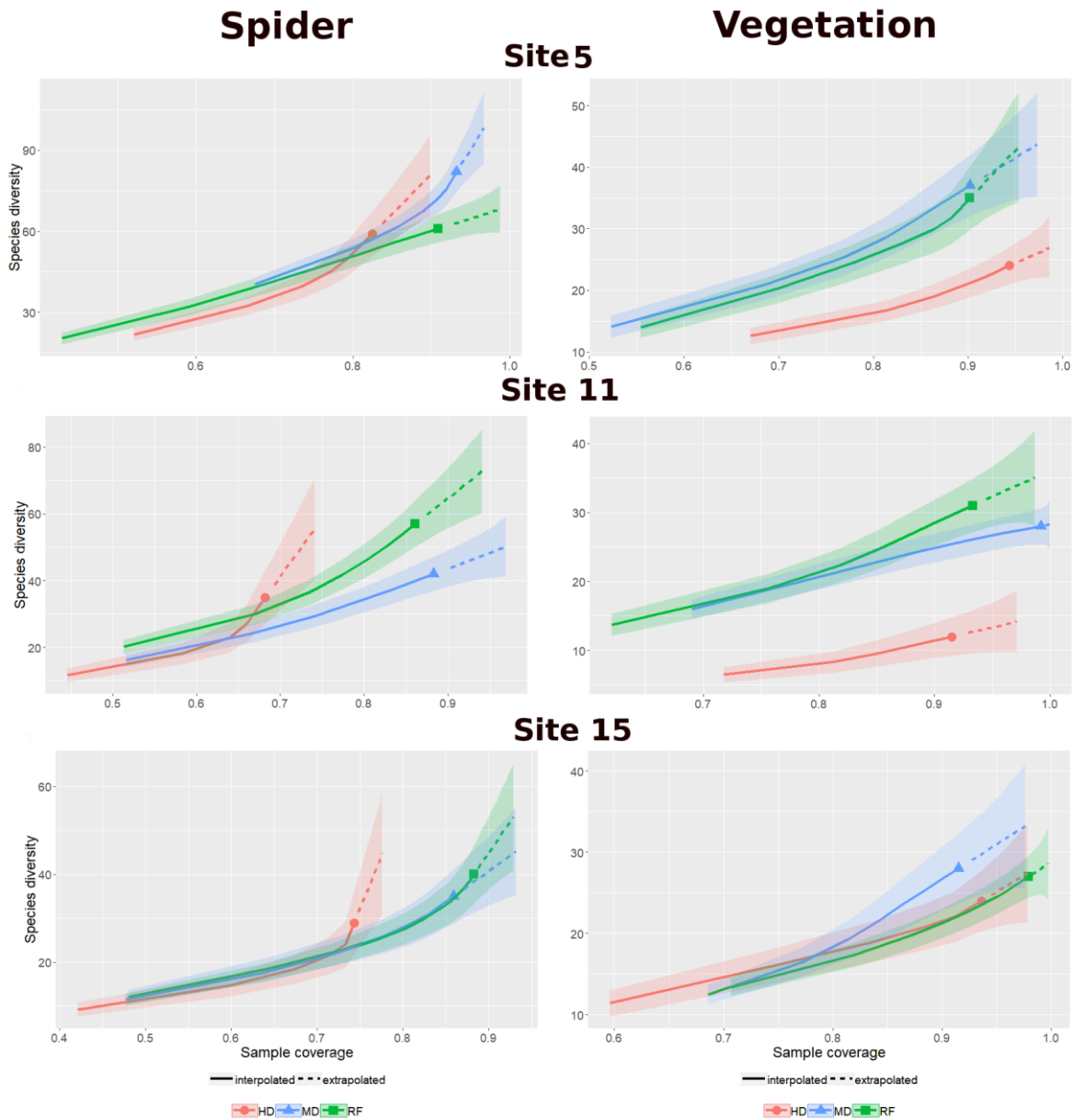


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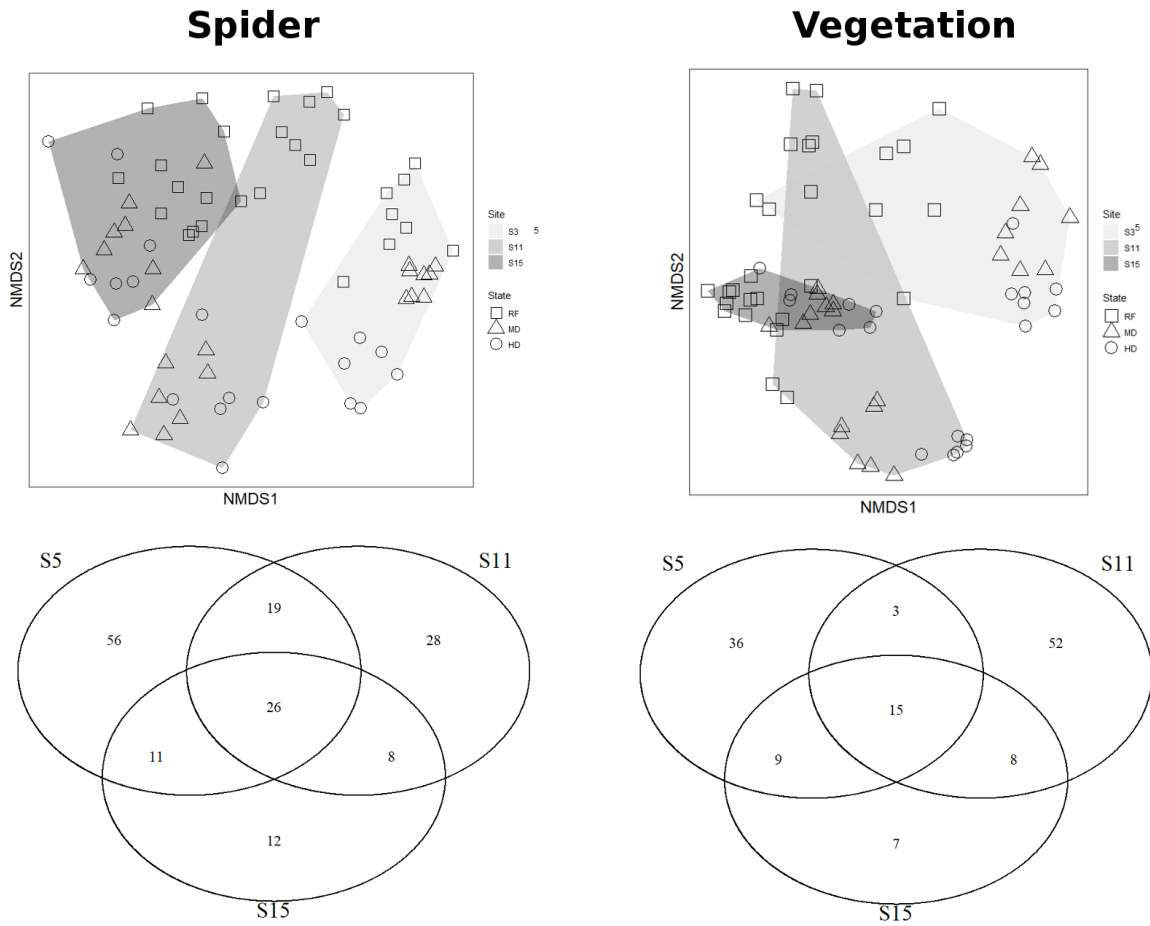
521 Figure 2. Estimated species richness for spiders and plants in each degradation state of the three
 522 sites (Highly degraded: red curve; Mildly degraded: blue curve; Reference: green curve). The
 523 coloured area around the curves represents the 95% confidence interval based on the bootstrap
 524 method. Figure made with R and iNext package (Chao et al. 2014)

525



526

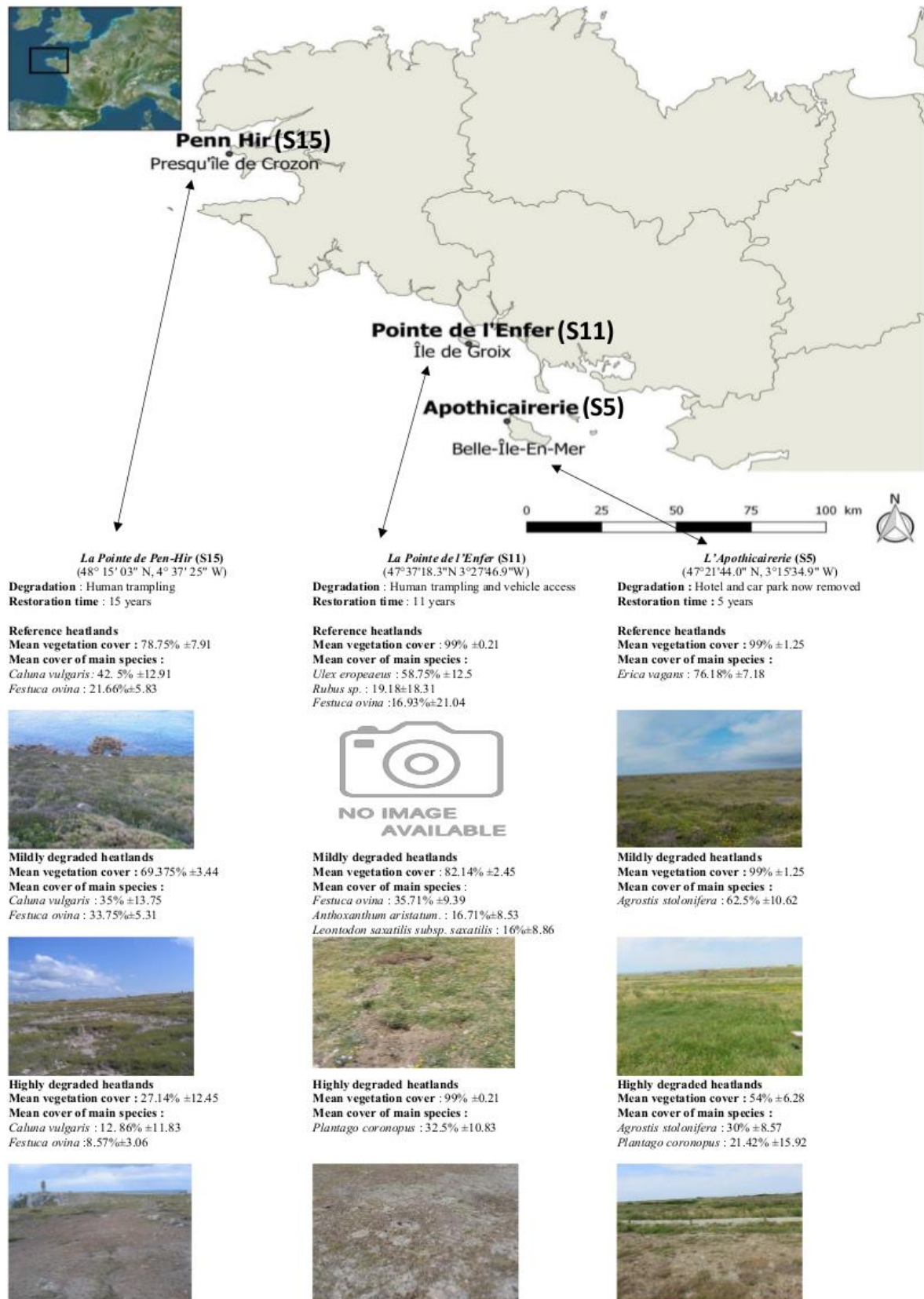
527 Figure 3. NMDS based on Sørensen dissimilarity matrix for spider and plant assemblages with
 528 the envelopes grouping sites. Venn diagrams with the number of species unique or shared by
 529 site for each taxa. Figure made with R with ggplot2 package (Wickham 2016).



530

531 Appendix 1. Localisation and characteristics of the three study sites (Brittany, Western France).

532 Figure made with GIMP 2.



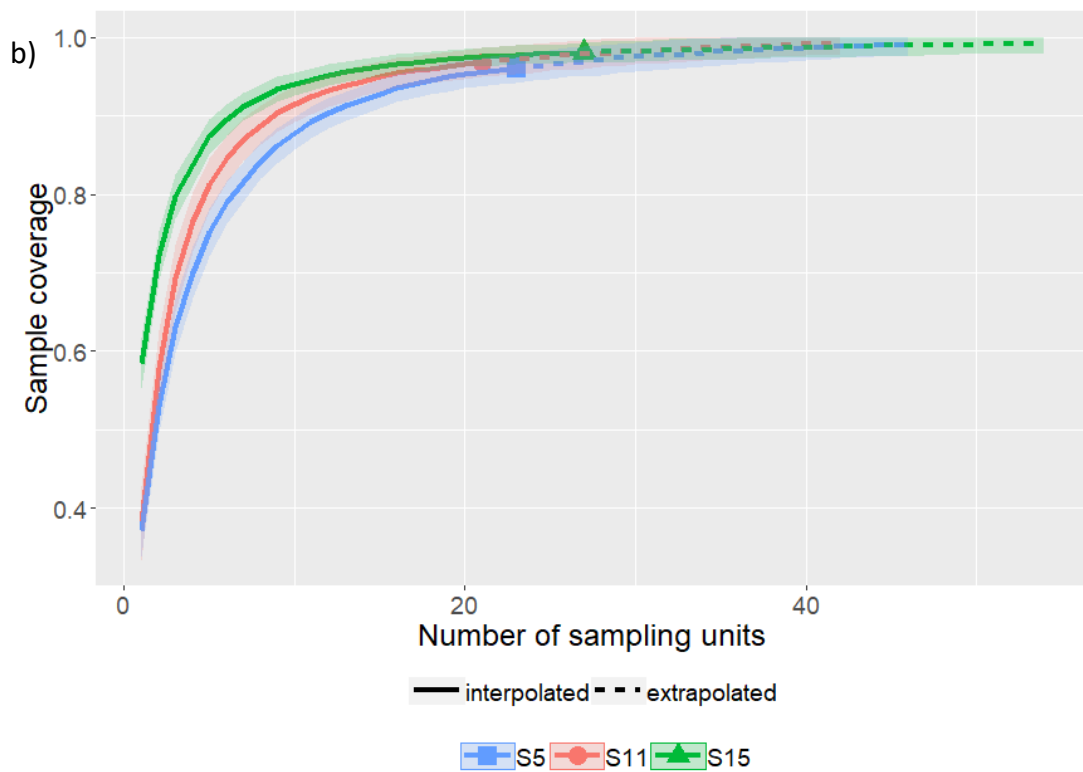
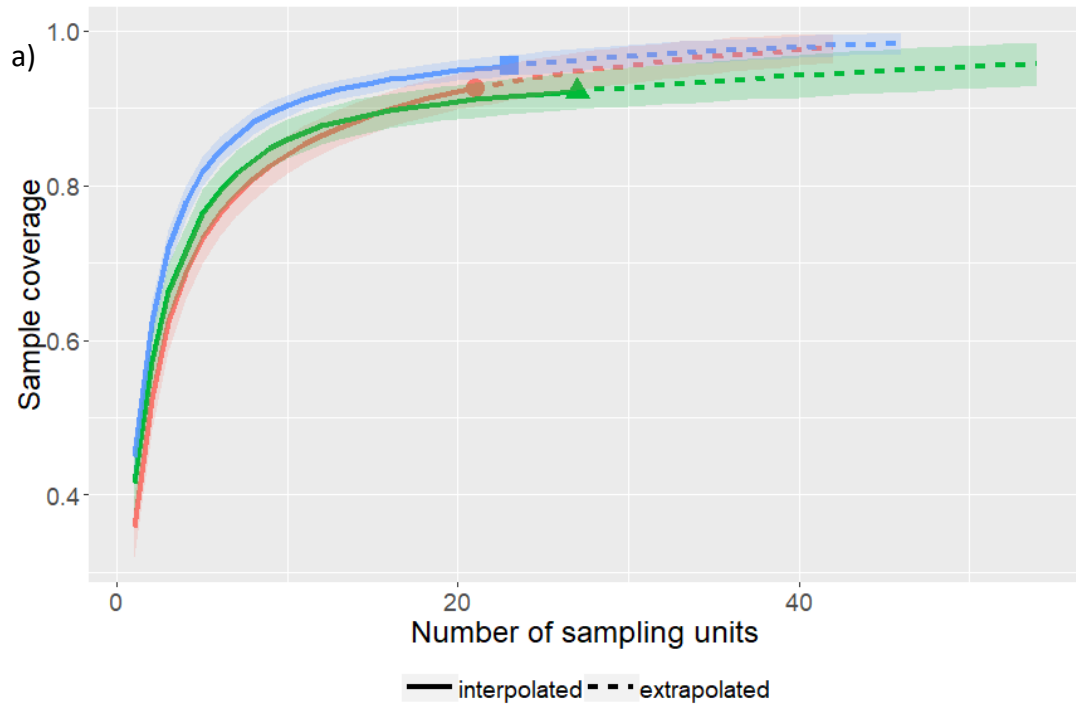
533

534 Appendix 2. Accumulation curves for a) spider and b) plant sampling coverage. Curve colours
535 correspond to different sampling sites (Blue: S5; Red: S11; Green: S15). The coloured area
536 around the curves is the 95% confidence interval based on bootstrapping (see Methods for more
537 details). Figure made with R and iNext package (Chao et al. 2014).

538

539

540



541 Appendix 3. Spider species presence/absence by site. Index letters indicate significant indicator
 542 species of a = Reference, b = Mildly degraded and c= Highly degraded states.

species	S5	S11	S15	species	S5	S11	S15
<i>Alopecosa barbipes</i>	0 ^b	0	1	<i>Micromata ligurina</i>	1	0	0
<i>Acartauchenius scurrilis</i>	0	1	0	<i>Micrommata virescens</i>	0	1	0
<i>Agroeca cuprea</i>	1	0	0	<i>Neon reticulatus</i>	0	0	1
<i>Agroeca brunnea</i>	1	0	0	<i>Neottiura suaveolens</i>	1	0	0
<i>Agroeca inopina</i>	1	1 ^a	1	<i>Neriere clathrata</i>	0	1	0
<i>Agroeca lusatica</i>	0	1	0	<i>Nomisia exornata</i>	0	1 ^b	0
<i>Agyneta rurestris</i>	1 ^c	1	1	<i>Oedothorax fuscus</i>	1	1	0
<i>Alopecosa farinosa</i>	1	0	1	<i>Oedothorax retusus</i>	0	1	1
<i>Alopecosa cuneata</i>	1	0	0	<i>Ostearius melanopygius</i>	0	1	0
<i>Alopecosa pulverulenta</i>	1 ^b	1	1	<i>Ozyptila atomaria</i>	0	1	1
<i>Amaurobius erberi</i>	0	1 ^a	1	<i>Ozyptila sanctuaria</i>	1 ^b	0	0
<i>Anelosimus pulchellus</i>	1 ^c	0	0	<i>Ozyptila scabricula</i>	0	1	1
<i>Antistea elegans</i>	1	0	0	<i>Ozyptila simplex</i>	1 ^b	0	1
<i>Arctosa cf. vilica</i>	0	1	0	<i>Palliduphantes ericaeus</i>	1 ^b	1	1
<i>Arctosa leopardus</i>	1	0	0	<i>Palliduphantes insignis</i>	1	1	0
<i>Arctosa perita</i>	1	0	0	<i>Palliduphantes pallidus</i>	1 ^b	0	0
<i>Argenna patula</i>	0	1	0	<i>Pardosa pullata</i>	1	0	1
<i>Argenna subnigra</i>	1	1	1	<i>Pardosa amentata</i>	0	1	0
<i>Asagena phalerata</i>	0	0	1	<i>Pardosa monticola</i>	1	1	1
<i>Atypus affinis</i>	0	1	0	<i>Pardosa nigriceps</i>	1	1 ^a	1
<i>Aulonia albimana</i>	1	1	1	<i>Pardosa palustris</i>	1	0	0
<i>Ballus rufipes</i>	1	0	0	<i>Pardosa prativaga</i>	1 ^b	0	1
<i>Bathyphantes gracilis</i>	0	1	0	<i>Pardosa proxima</i>	1	0	0
<i>Centromerita bicolor</i>	1	0	0	<i>Pardosa pullata</i>	1 ^b	1	1
<i>Centromerita concina</i>	0	0	1	<i>Pardosa saltans</i>	0	1	0
<i>Centromerus prudens</i>	1	0	0	<i>Peponocranium ludicrum</i>	1	0	0
<i>Cheiracanthium erraticum</i>	1	0 ^b	0	<i>Phaeoedus braccatus</i>	1	0	0
<i>Civizelotes civicus</i>	0	1	0	<i>Philodromus cf. rufus</i>	0	1	1
<i>Clubiona comta</i>	0	1	0	<i>Philodromus aureolus</i>	1	0	0
<i>Clubiona genevensis</i>	0	1	0	<i>Phlegra bresnieri</i>	0	1	0
<i>Clubiona phragmitis</i>	1	0	0	<i>Phlegra fasciata</i>	0	1	1
<i>Clubiona reclusa</i>	0	0	1	<i>Pholcomma gibbum</i>	1	0	1
<i>Clubiona terrestris</i>	0	0	1	<i>Phrurolithus festivus</i>	1	0	0
<i>Crustulina guttata</i>	1	1	1	<i>Phrurolithus minimus</i>	0	1	0
<i>Crustulina sticta</i>	1	1	0	<i>Phrurolithus nigrinus</i>	1	0	0
<i>Dictyna arundinacea</i>	0	1	0	<i>Pocadicnemis pumila</i>	1 ^b	0	0
<i>Diplostyla concolor</i>	1 ^b	0	0	<i>Poecilochroa variana</i>	1	1	1
<i>Dipoena erythropus</i>	1	0	0	<i>Robertus arundineti</i>	1	0	0
<i>Dipoena prona</i>	1	0	1	<i>Robertus lividus</i>	1	1	1
<i>Drassodes cf. lapidosus</i>	1	1	1	<i>Saaristoa abnormis</i>	1	1	0
<i>Drassodes pubescens</i>	1	0	0	<i>Segestria senoculata</i>	0	0	1
<i>Drassylus praefficus</i>	1	0	0	<i>Silometopus elegans</i>	1	0	0

<i>Drassylus pusillus</i>	1	0	0	<i>Steatoda phalerata</i>	1	0	0
<i>Drassylus villicus</i>	1	0	0	<i>Stemonyphantes lineatus</i>	1	1	0
<i>Dysdera crocata</i>	1	0	0	<i>Styloctetor compar</i>	1	0	0
<i>Dysdera erythrina</i>	1	1 ^a	1	<i>Talavera aequipes</i>	1	0	0
<i>Dysdera fuscipes</i>	0	1	0	<i>Tenuiphantes flavipes</i>	1	1	0
<i>Enoplognatha thoracica</i>	1	1	1	<i>Tenuiphantes tenuis</i>	1	1	1
<i>Enterlecara erythropus</i>	1	0	0	<i>Thanatus striatus</i>	1	0	1
<i>Episinus truncatus</i>	0	1	0	<i>Tiso vagans</i>	1	1 ^a	1
<i>Eratigena picta</i>	1	1	1	<i>Trachyzelotes pedestris</i>	1	1	0
<i>Erigone atra</i>	0	1	1	<i>Trichoncus saxicola</i>	1 ^b	0	0
<i>Erigone dentipalpis</i>	1 ^c	1 ^c	1	<i>Trochosa robusta</i>	0	1	0
<i>Ero furcata</i>	1	1	0	<i>Trochosa ruricola</i>	0	1	0
<i>Euophris semiglabrata</i>	1	0	0	<i>Trochosa terricola</i>	1 ^b	1	0
<i>Euophris frontalis</i>	0	1	0	<i>Walckenaeria acuminata</i>	0	0	1
<i>Euophris herbigrada</i>	1	1	0	<i>Walckenaeria alticeps</i>	1	0	0
<i>Gnaphosa lugubris</i>	1	1	0	<i>Walckenaeria capito</i>	0	1	0
<i>Gnaphosa occidentalis</i>	1	1	1	<i>Walckenaeria dysderoides</i>	0	0	1
<i>Gonatium rubens</i>	0	1	0	<i>walckenaeria clavicornis</i>	1	0	0
<i>Hahnia nava</i>	1 ^b	1	1	<i>Walckenaeria furcillata</i>	1	1	1
<i>Haplodrassus dalmatensis</i>	1 ^c	1	1	<i>Walckenaeria monoceros</i>	1	0	1
<i>Haplodrassus signifer</i>	1	1	1	<i>Walckenaeria nudipalpis</i>	1	1	0
<i>Haplodrassus umbratilis</i>	1	0	0	<i>Xysticus cristatus</i>	1	0	1
<i>Harpactea hombergi</i>	1	1	1	<i>Xysticus erraticus</i>	1	0	1 ^a
<i>Heliophanus auratus</i>	1	0	0	<i>Xysticus kempeleni</i>	1	1 ^a	0
<i>Heliophanus cupreus</i>	0	1	0	<i>Xysticus kochi</i>	1	1	1
<i>Hypsosinga albovittata</i>	1	1	0	<i>Xysticus lanio</i>	0	0	1
<i>Lasaeola coracina</i>	1	0	0	<i>Zelotes atrocaeruleus</i>	1	1 ^a	0
<i>Lasaeola prona</i>	0	0	1	<i>Zelotes latreillei</i>	1	0	0
<i>Lathys humilis</i>	0	0	1	<i>Zelotes pedestris</i>	0	1 ^a	0
<i>Mangora acalypha</i>	0	1	0	<i>Zelotes petrensis</i>	1	0	0
<i>Marpissa nivoyi</i>	0	1	0	<i>Zelotes praeficus</i>	0	1	0
<i>Mecopisthes peusi</i>	0	1	1	<i>Zelotes pusillus</i>	1	0	0
<i>Megalephyphantes nebulosus</i>	1	0	0	<i>Zelotes subterraneus</i>	1	0	0
<i>Meioneta innotabilis</i>	1	0	0	<i>Zodarion italicum</i>	1	1	1
<i>Mermessus trilobatus</i>	1 ^b	1	0	<i>Zora armillata</i>	1	0	0
<i>Metopobractus prominulus</i>	1	0	0	<i>Zora spinimana</i>	1	1 ^a	0
<i>Micaria albovittata</i>	1	0	0				
<i>Micaria formicaria</i>	1	0	0				
<i>Micaria pulicaria</i>	1	0	0				
<i>Microlinyphia pusilla</i>	0	1	0				

544 Appendix 4. Plant species presence/absence by site.

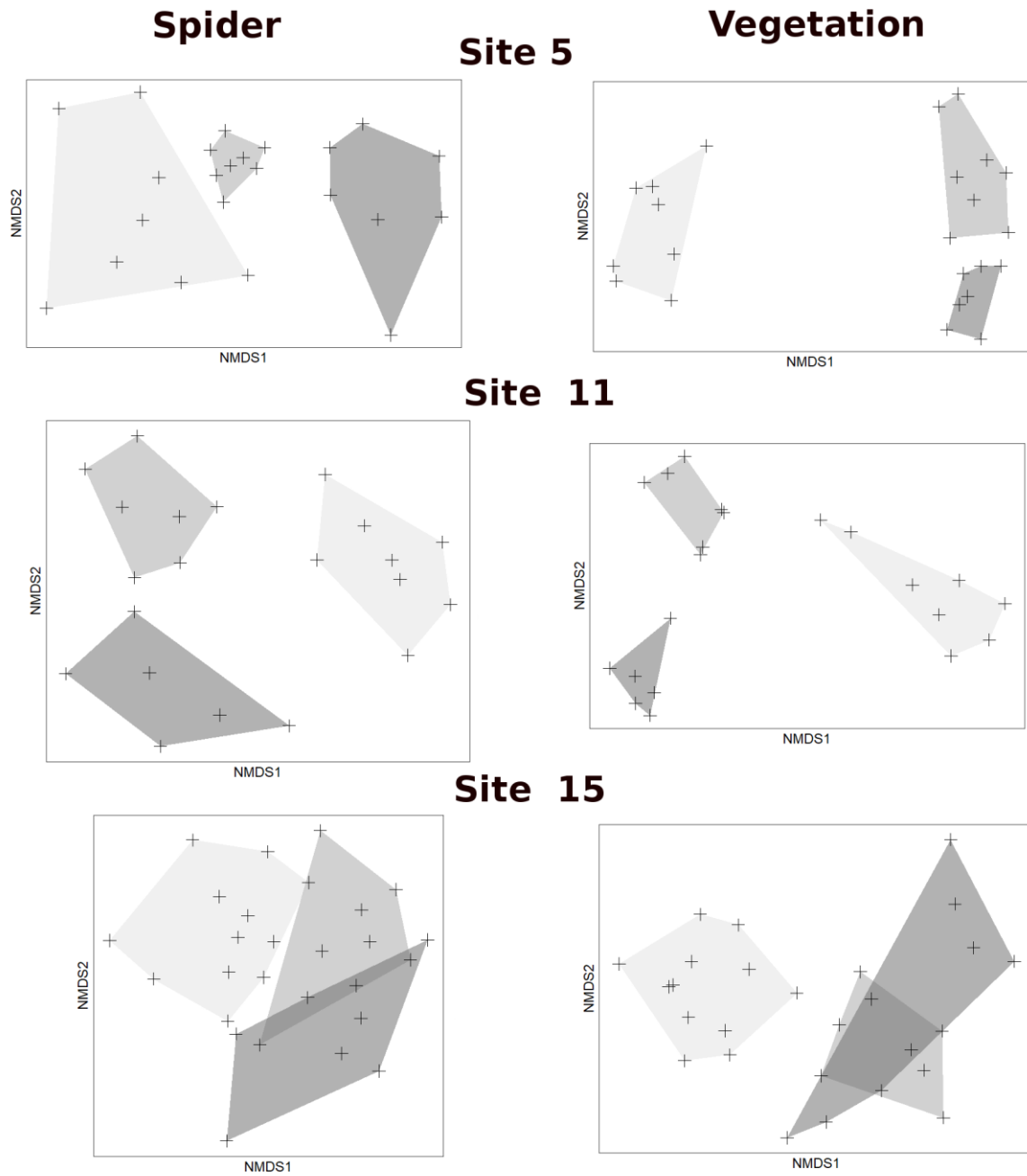
species	S5	S11	S15	species	S5	S11	S15
<i>Agrostis capillaris</i>	0	1	1	<i>Lonicera periclymenum</i>	1	1	0
<i>Agrostis stolonifera</i>	1	1	1	<i>Lotus corniculatus</i>	1	1	1
<i>Aira caryophylllea</i>	1	1	1	<i>Lotus subbiflorus</i>	0	1	1
<i>Aira praecox</i>	0	1	1	<i>Malva sylvestris</i>	0	1	0
<i>Anagallis arvensis</i>	1	1	1	<i>Medicago lupulina</i>	1	0	0
<i>Anthoxanthum aristatum</i>	0	1	0	<i>Mibora minima</i>	1	1	0
<i>Anthoxanthum odoratum</i>	0	1	0	<i>Moenchia erecta</i>	0	1	0
<i>Anthyllis vulneraria</i>	0	0	1	<i>Ononis repens</i>	1	1	0
<i>Armeria maritima</i>	1	1	1	<i>Parapholis incurva</i>	1	1	0
<i>Arrhenatherum elatius</i>	1	0	0	<i>Pedicularis sylvatica</i>	1	0	1
<i>Asparagus officinalis ssp. prostratus</i>	1	0	0	<i>Picris echioides</i>	1	0	0
<i>Atriplex hastata</i>	1	0	0	<i>Plantago coronopus</i>	1	1	1
<i>Atriplex sp.</i>	1	0	0	<i>Plantago holosteum var. littoralis</i>	0	1	0
<i>Avena fatua</i>	0	1	0	<i>Plantago lanceolata</i>	1	1	1
<i>Brachypodium sp.</i>	1	0	0	<i>Plantago major</i>	0	0	0
<i>Bromus hordeaceus ssp. ferronii</i>	1	1	1	<i>Polygala serpyllifolia</i>	1	0	1
<i>Calluna vulgaris</i>	0	0	1	<i>Potentilla erecta</i>	1	0	1
<i>Carex distans</i>	0	0	1	<i>Potentilla reptans</i>	1	0	0
<i>Carex sp.</i>	1	1	0	<i>Potentilla sp.</i>	0	1	0
<i>Centaurea nigra</i>	1	0	0	<i>Primula elatior</i>	0	0	1
<i>Centaurea sp.</i>	1	0	0	<i>Prunus spinosa</i>	1	0	1
<i>Centaureum erythraea</i>	1	0	1	<i>Puccinellia maritima</i>	1	0	0
<i>Centaureum maritimum</i>	0	1	0	<i>Pulicaria dysenterica</i>	1	0	0
<i>Centaureum sp.</i>	1	0	0	<i>Radiola linoidea</i>	0	1	0
<i>Cerastium diffusum</i>	0	1	1	<i>Romulea columnae</i>	0	1	0
<i>Cerastium fontanum</i>	1	0	0	<i>Rosa pimpinellifolia</i>	0	0	1
<i>Chamaemelum nobile</i>	0	0	1	<i>Rubia peregrina</i>	1	0	0
<i>Cirsium arvense</i>	1	1	0	<i>Rubus sp.</i>	1	1	0
<i>Cirsium filipendulum</i>	1	0	0	<i>Rumex acetosa</i>	1	1	0
<i>Cirsium vulgare</i>	1	0	0	<i>Rumex conglomeratus</i>	1	0	0
<i>Cochlearia danica</i>	1	1	1	<i>Rumex crispus</i>	1	0	0
<i>Convolvulus arvensis</i>	1	1	0	<i>Rumex sp.</i>	1	0	0
<i>Crepis sp.</i>	0	0	0	<i>Sagina maritima</i>	1	1	0
<i>Crepis capillaris</i>	1	1	1	<i>Sagina subulata</i>	0	0	1
<i>Crithmum maritimum</i>	1	1	1	<i>Salicornia ramosissima</i>	1	0	0
<i>Cuscuta epithymum</i>	0	1	1	<i>Scilla verna</i>	0	1	1
<i>Cynodon dactylon</i>	1	0	0	<i>Sedum acre</i>	0	1	0
<i>Cytisus scoparius</i>	0	1	0	<i>Sedum anglicum</i>	1	1	1
<i>Dactylis glomerata</i>	1	1	1	<i>Senecio jacobaea</i>	1	1	1
<i>Danthonia decumbens</i>	1	0	1	<i>Silene vulgaris ssp. maritima</i>	1	1	1
<i>Daucus carota</i>	1	1	1	<i>Solanum dulcamara</i>	1	0	0
<i>Desmazeria marina</i>	1	0	0	<i>Solidago virgaurea ssp. rupicola</i>	0	0	1
<i>Desmazeria sp.</i>	0	1	1	<i>Sonchus arvensis</i>	1	0	0

<i>Elymus repens</i>	1	0	0	<i>Sonchus asper</i>	1	1	0
<i>Erica ciliaris</i>	0	0	1	<i>Sonchus oleraceus</i>	0	1	1
<i>Erica cinerea</i>	1	1	1	<i>Spergularia rubra</i>	1	0	0
<i>Erica vagans</i>	1	0	0	<i>Spergularia rupicola</i>	1	1	1
<i>Eryngium campestre</i>	0	1	0	<i>Sueda sp.</i>	0	1	0
<i>Euphorbia portlandica</i>	0	1	1	<i>Tamarix sp.</i>	1	0	0
<i>Euphrasia sp.</i>	0	0	1	<i>Teucrium scorodonia</i>	1	1	0
<i>Festuca ovina</i>	1	1	1	<i>Thymus praecox</i>	0	0	1
<i>Festuca rubra ssp. pruinosa</i>	1	1	1	<i>Trifolium arvense</i>	0	1	1
<i>Frankenia laevis</i>	1	0	0	<i>Trifolium campestre</i>	0	0	1
<i>Galium aparine</i>	0	1	0	<i>Trifolium occidentale</i>	0	0	1
<i>Galium mollugo</i>	1	1	0	<i>Trifolium pratense</i>	1	0	0
<i>Galium sp.</i>	0	1	0	<i>Trifolium repens</i>	1	0	0
<i>Genista tinctoria</i>	1	0	0	<i>Ulex europaeus var. maritimus</i>	1	1	1
<i>Halimione portulacoides</i>	1	0	0	<i>Ulex gallii var. humilis</i>	0	0	1
<i>Hieracium umbellatum</i>	0	0	1	<i>Umbilicus rupestris</i>	1	1	0
<i>Holcus lanatus</i>	1	1	1	<i>Vicia hirsuta</i>	1	0	0
<i>Hyacinthoides non-scripta</i>	1	1	0	<i>Vicia sativa</i>	1	1	0
<i>Hypochaeris radicata</i>	1	1	1	<i>Viola riviniana</i>	1	0	1
<i>Inula crithmoides</i>	1	0	0	<i>Viola sp.</i>	1	0	1
<i>Jasione montana</i>	0	1	1	<i>Vulpia bromoides</i>	1	1	1
<i>Leontodon saxatilis ssp. saxatilis</i>	1	1	1				
<i>Limonium vulgare</i>	1	0	0				
<i>Linum bienne</i>	0	0	1				

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547 Appendix 5. NMDS per site for Spiders and Vegetation. Coloured area corresponding to
548 degradation state. Light grey: Reference; Grey: Mildly degraded; Dark grey: Highly degraded.
549 Figure made with R and ggplot2 package (Wickham 2016).



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