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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  $\beta$ -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'Apothicairerie (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 m<sup>2</sup> 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<sup>-1</sup>) 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 clifftop  
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

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326

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- 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

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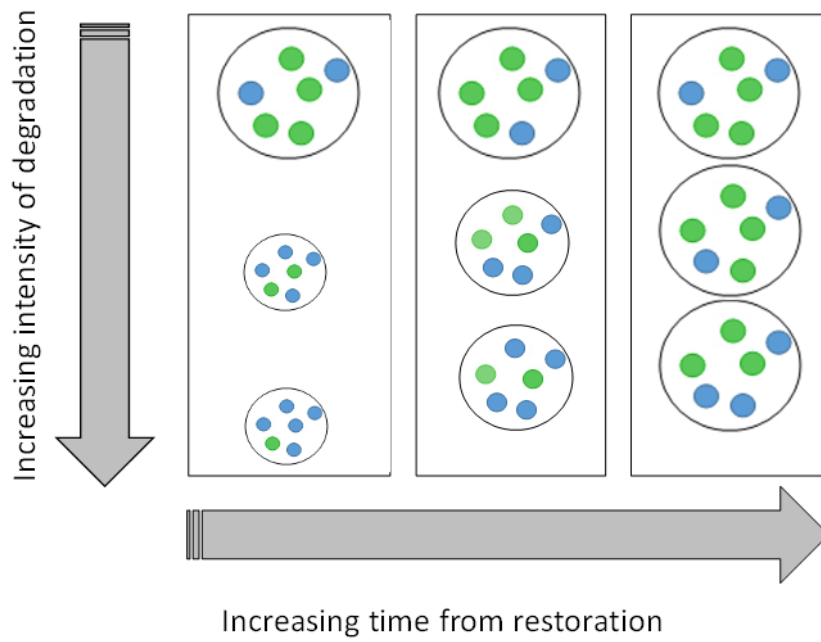
	S5	S11	S15
Spiders			
RF	0	9	1
MD	14	2	0
HD	4	1	0
Plants			
RF	0	0	0
MD	0	0	0
HD	0	0	0

---

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.

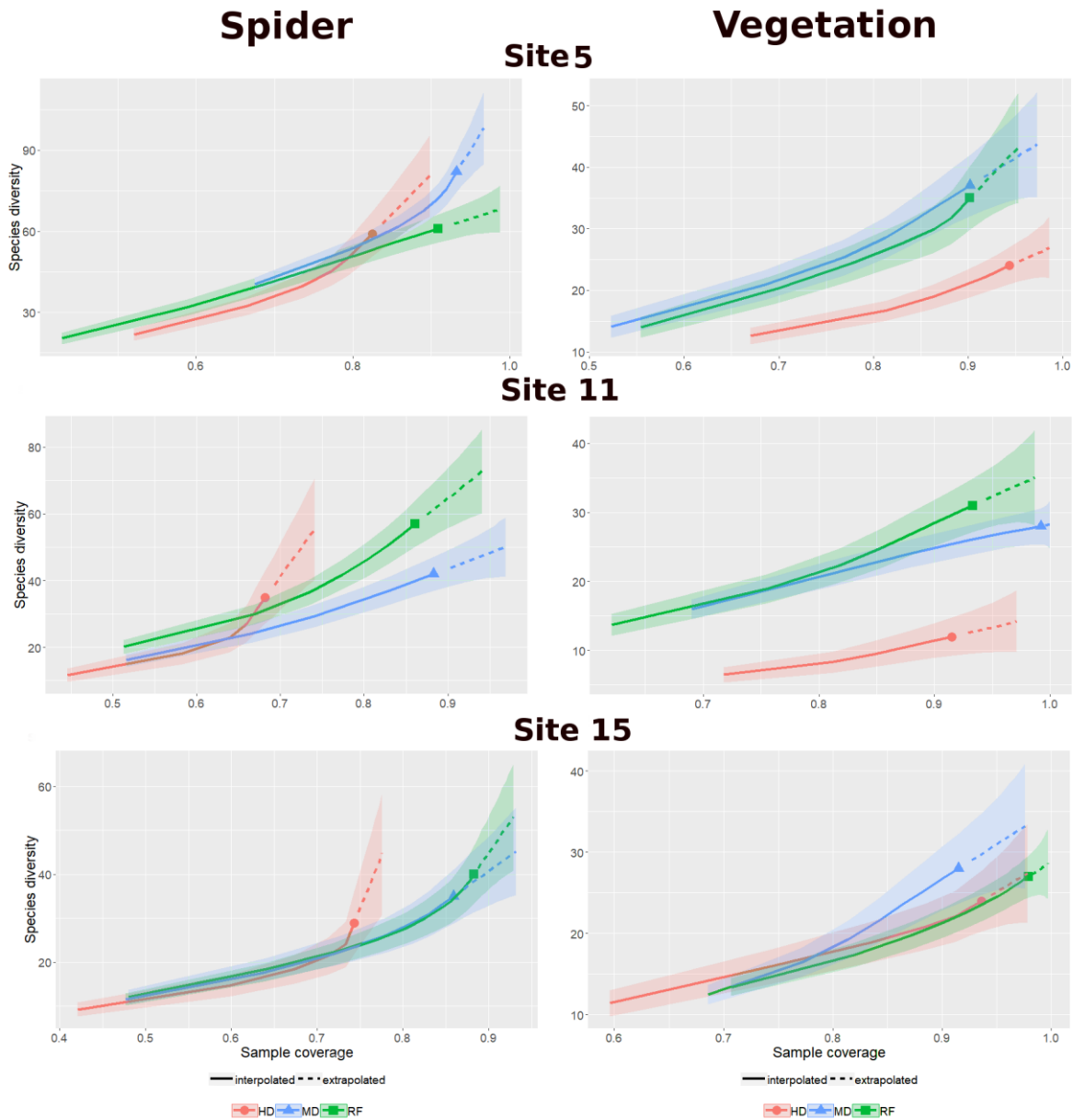


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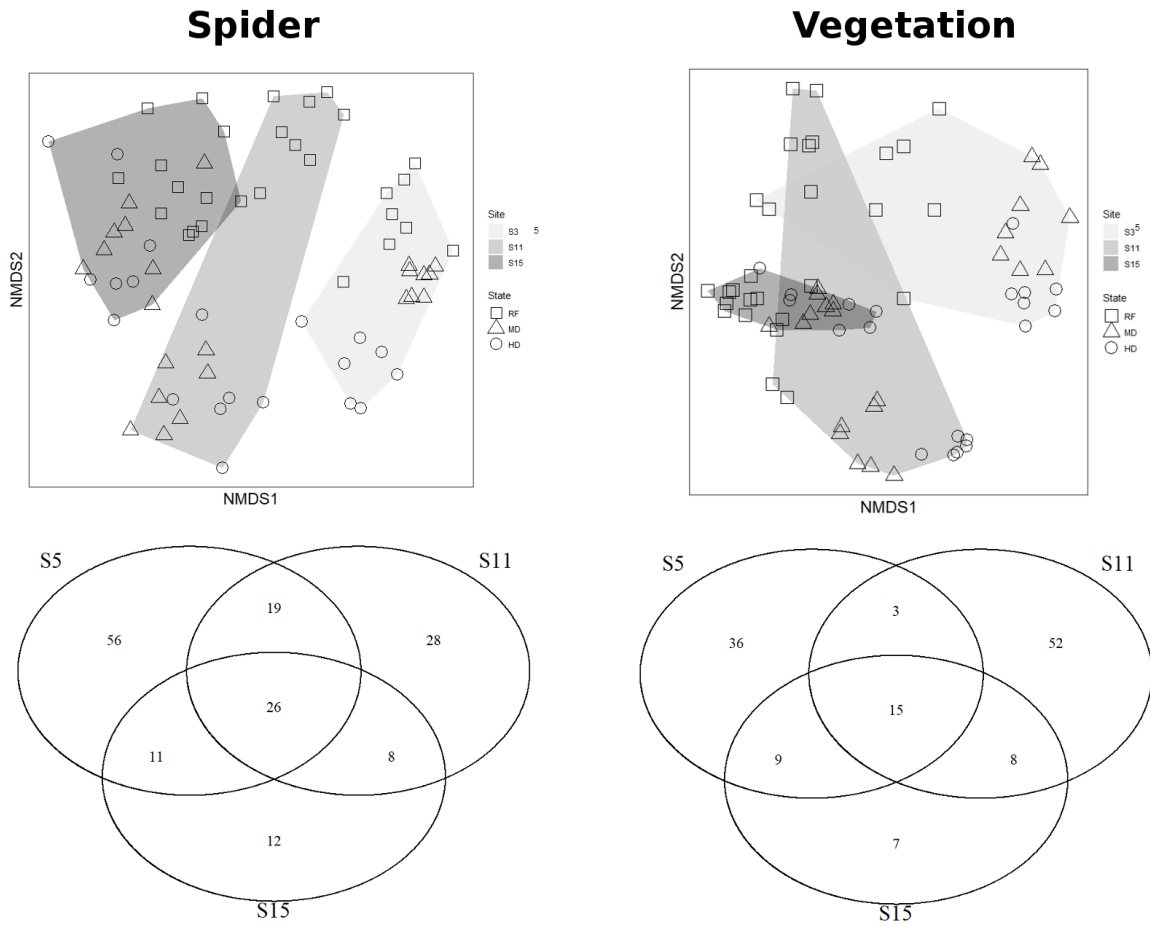
521 Figure 2. Estimated species richness for spiders and plants in each degradation state of the three  
 522 sites (Highly degraded: red curve; Mildly degraded: blue curve; Reference: green curve). The  
 523 coloured area around the curves represents the 95% confidence interval based on the bootstrap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

525



526

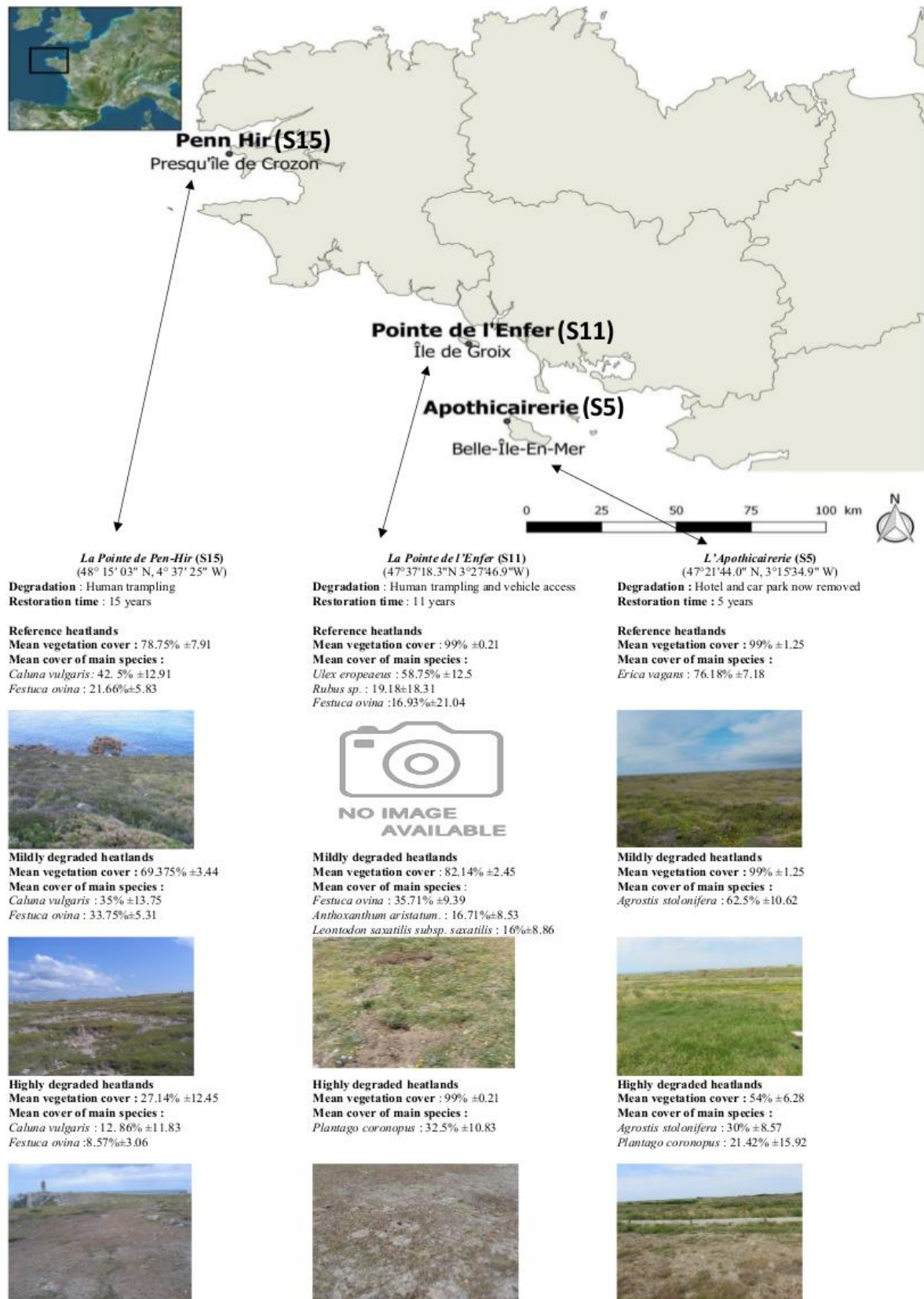
527 Figure 3. NMDS based on Sørensen dissimilarity matrix for spider and plant assemblages with  
 528 the envelopes grouping sites. Venn diagrams with the number of species unique or shared by  
 529 site for each taxa. Figure made with R with ggplot2 package (Wickham 2016).



530

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

532 Figure made with GIMP 2.



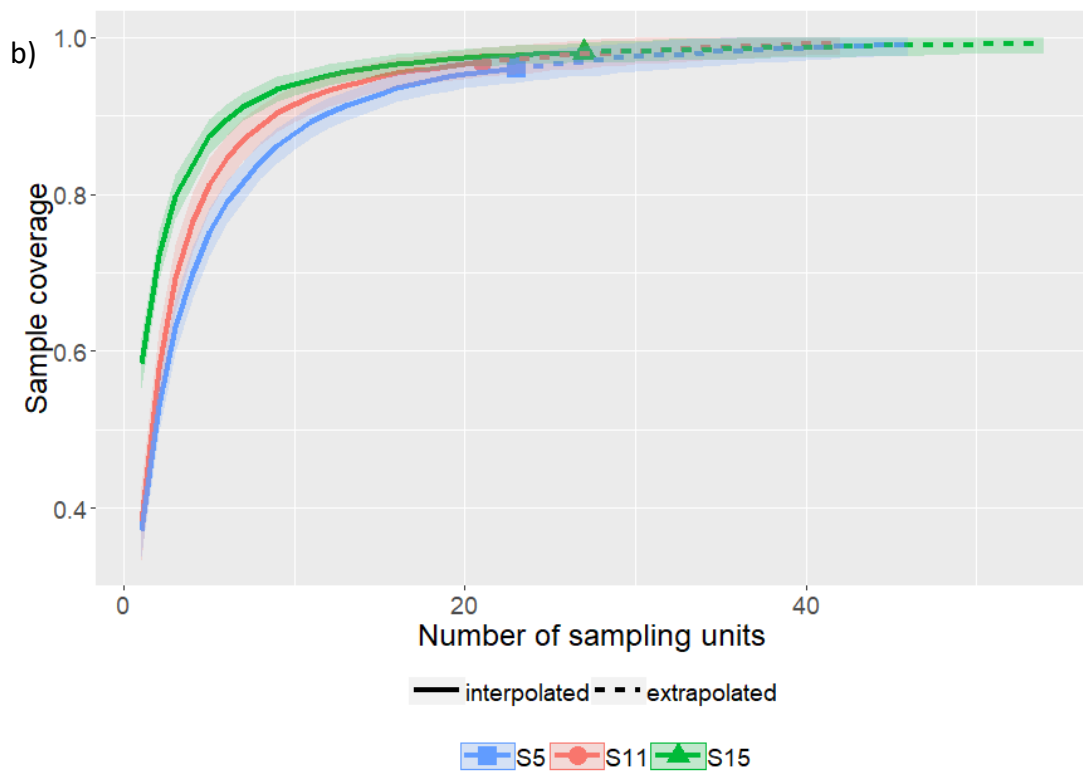
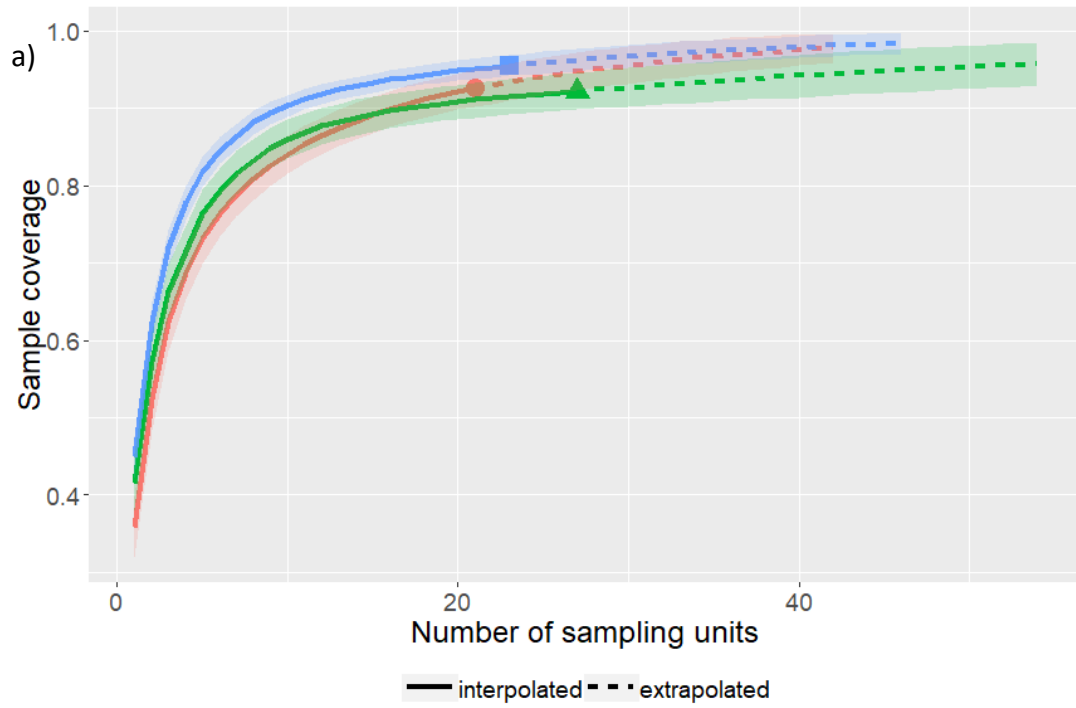
533

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 <sup>b</sup>	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 <sup>a</sup>	1	<i>Neriere clathrata</i>	0	1	0
<i>Agroeca lusatica</i>	0	1	0	<i>Nomisia exornata</i>	0	1 <sup>b</sup>	0
<i>Agyneta rurestris</i>	1 <sup>c</sup>	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 <sup>b</sup>	1	1	<i>Ozyptila atomaria</i>	0	1	1
<i>Amaurobius erberi</i>	0	1 <sup>a</sup>	1	<i>Ozyptila sanctuaria</i>	1 <sup>b</sup>	0	0
<i>Anelosimus pulchellus</i>	1 <sup>c</sup>	0	0	<i>Ozyptila scabricula</i>	0	1	1
<i>Antistea elegans</i>	1	0	0	<i>Ozyptila simplex</i>	1 <sup>b</sup>	0	1
<i>Arctosa cf. vilica</i>	0	1	0	<i>Palliduphantes ericaeus</i>	1 <sup>b</sup>	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 <sup>b</sup>	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 <sup>a</sup>	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 <sup>b</sup>	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 <sup>b</sup>	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 <sup>b</sup>	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 <sup>b</sup>	0	0
<i>Diplostyla concolor</i>	1 <sup>b</sup>	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 praeficus</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 <sup>a</sup>	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 <sup>a</sup>	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 <sup>b</sup>	0	0
<i>Erigone dentipalpis</i>	1 <sup>c</sup>	1 <sup>c</sup>	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 <sup>b</sup>	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 <sup>b</sup>	1	1	<i>Walckenaeria furcillata</i>	1	1	1
<i>Haplodrassus dalmatensis</i>	1 <sup>c</sup>	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 <sup>a</sup>
<i>Heliophanus auratus</i>	1	0	0	<i>Xysticus kempeleni</i>	1	1 <sup>a</sup>	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 <sup>a</sup>	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 <sup>a</sup>	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 <sup>b</sup>	1	0	<i>Zora armillata</i>	1	0	0
<i>Metopobractus prominulus</i>	1	0	0	<i>Zora spinimana</i>	1	1 <sup>a</sup>	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.

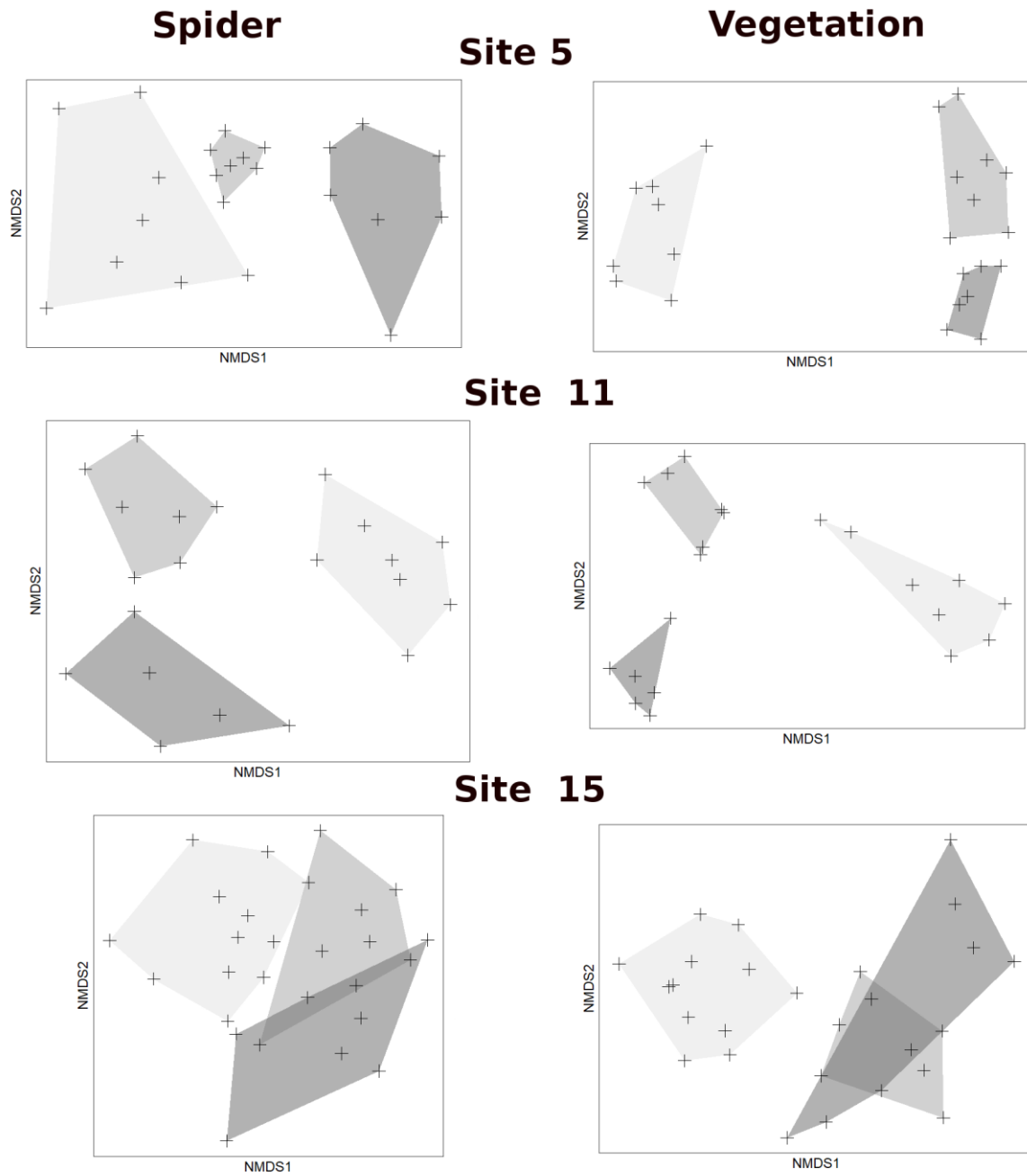
species	S5	S11	S15	species	S5	S11	S15
<i>Agrostis capillaris</i>	0	1	1	<i>Lonicera periclymenum</i>	1	1	0
<i>Agrostis stolonifera</i>	1	1	1	<i>Lotus corniculatus</i>	1	1	1
<i>Aira caryophylllea</i>	1	1	1	<i>Lotus subbiflorus</i>	0	1	1
<i>Aira praecox</i>	0	1	1	<i>Malva sylvestris</i>	0	1	0
<i>Anagallis 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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