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► To cite this version:

Boris Leroy, Isabelle Le Viol, Julien Pétilion. Complementarity of rarity, specialisation and functional diversity metrics to assess community responses to environmental changes, using an example of spider communities in salt marshes. *Ecological Indicators*, 2014, 46, pp.351-357. 10.1016/j.ecolind.2014.06.037 . hal-01101385

HAL Id: hal-01101385

<https://univ-rennes.hal.science/hal-01101385>

Submitted on 8 Jan 2015

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1 **Complementarity of rarity, specialisation and functional diversity**
2 **metrics to assess community responses to environmental changes, using**
3 **an example of spider communities in salt marshes**

4

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16

17 Number of words (abstract): 229

18 Number of words (full word file): 5180

19

20 **Abstract**

21 The study of community responses to environmental changes can be enhanced by the
22 recent development of new metrics useful in applied conservation: relative rarity,
23 ecological specialisation and functional diversity. These different metrics have been
24 critically assessed independently, but are rarely combined in applied conservation
25 studies, especially for less-studied taxa such as arthropods. Here we report how these
26 different metrics can complement each other by using the response of spider
27 communities to environmental changes in salt marshes as an example. Sampling took
28 place using pitfall traps in salt marshes of the Mont St Michel Bay (France) during
29 2004 and 2007. The sampling design was spatially replicated (3 plots per treatment
30 and 4 traps per plot) and encompassed four habitat treatments: control, sheep
31 grazing, cutting (annual, in summer) and invasion by the plant *Elymus athericus*. We
32 observed contrasting responses of spider communities to the different treatments:
33 grazing had a negative impact on both rarity and functional diversity but a positive
34 impact on specialisation; cutting had a negative impact on the three metrics; and
35 invasion only had a negative impact on rarity and specialisation. These contrasting
36 responses emphasise the necessity of using different complementary community
37 metrics in such conservation studies. Consequently, rarity-, specialization-, and
38 functional-based indices should be applied simultaneously more frequently, as they
39 potentially provide additional complementary information about communities. Such
40 complementary information is the key to better-informed conservation choices.

41 **Key-words:** Index of Relative Rarity; Community Specialisation Index; Functional
42 Divergence; Grazing; Cutting; Spiders.

44 **Abbreviations:**

45 CSI: Community Specialisation Index (Julliard et al., 2006)

46 FDiv: Functional Divergence Index (Villéger et al., 2008)

47 *I*_{RR}: Index of Relative Rarity (Leroy et al. 2013)

48 SSI: Species Specialisation Index (Julliard et al., 2006)

49

50 1. Introduction

51 Addressing responses of biodiversity to environmental changes at the
52 community rather than species level present the advantage of integrating the
53 responses of multiple species and their interactions. Responses of communities can
54 be assessed with different facets (taxonomic, phylogenetic or functional) for which
55 several new indices have been developed (*e.g.*, Devictor et al., 2010; Meynard et al.,
56 2011; Strecker et al., 2011). However, these different facets are still rarely used in
57 applied conservation studies, particularly for less-studied taxa such as arthropods.
58 The early methods used to assess communities in conservation studies were simple
59 taxonomic diversity metrics such as species richness or abundance (*e.g.*, Prieto-
60 Benítez and Méndez, 2011). However these simple metrics only reflect a fraction of
61 the biodiversity and do not take into account the identity of species and their
62 characteristics within and between communities, even though these aspects are
63 crucial to assess biodiversity distribution (α , β components), conservation concerns
64 (rarity), ecosystem functioning (functional traits) and importantly the processes
65 implied in the impact of environmental changes on this biodiversity (biotic and
66 functional homogenisation). Hence, species and communities were attributed values
67 with respect to the conservation goal, for example according to their rarity, or more
68 recently to their functional characteristics. In this study, we focus on recent
69 methodological advances regarding three aspects: rarity, ecological specialisation and
70 functional diversity.

71 Rarity primarily provides an insight into the facet of species biodiversity that is
72 most at risk of extinction (Gaston, 1994), also with respect to the maintenance of
73 vulnerable ecosystem functions (Mouillot et al., 2013). Different axes of rarity are
74 usually considered: restricted abundance, restricted geographic distribution and

75 narrow niche breadth. The study of rarity in arthropod communities has recently
76 been improved by the proposal of new indices based on species occurrence (Leroy et
77 al., 2012), which provide the possibility of integrating multiple spatial scales (Leroy et
78 al., 2013). Robust metrics have also been developed to assess the average niche width,
79 *i.e.* the specialisation of species communities (Devictor et al., 2010a). Using basic
80 predictions from the ecological niche theory, specialist species should indeed be
81 favoured in rather stable environments whereas generalists should be more able to
82 thrive in disturbed habitats (Levins, 1968). In the same way, species functional traits
83 are increasingly taken into account to provide a better assessment of the functional
84 responses of communities to environmental changes. The study of this facet of
85 biodiversity was improved thanks to the proposal of novel metrics which have been
86 developed and analysed critically (Devictor et al., 2010a; Villéger et al., 2008). The
87 loss of functional diversity was a criterion that had been overlooked initially, but is of
88 increasing concern in biological conservation (*e.g.*, Devictor et al., 2010b).

89 All these distinct approaches were successfully applied on arthropod
90 communities (*e.g.*, Leroy et al., 2013; Penone et al., 2013) to assess their responses to
91 environmental changes. They have each been critically assessed alone, but how they
92 complement each other in the case of applied conservation remained to be tested. In
93 this paper, we report a case study combining different recently developed metrics
94 (rarity, specialisation, functional diversity) to assess how they complement each other
95 to assess the response of arthropod communities to environmental changes, by using
96 the example of spider communities of salt marshes. The environmental changes are
97 here the replacement of natural vegetation of salt marshes by monospecific stands of
98 the species *Elymus athericus* (Bockelmann and Neuhaus, 1999), and two
99 management practices likely to limit the spread of this species: annual cutting and

100 sheep grazing. The impact of *E. athericus* will here be termed as an invasion in
101 accordance with previous work on this species (Pétillon et al., 2005).

102 Salt marshes are of important conservation value because they host stenotopic
103 species due to the constraining environmental conditions (Pétillon et al., 2011), and
104 geographically rare species because of the restricted distribution of salt marshes in
105 the western Palearctic (Leroy et al., 2013). In addition, salt marshes are subject to
106 environmental changes (invasion by *E. athericus* and management) which often
107 result in the replacement of the single dominant plant species by another (Veeneklaas
108 et al., 2012). These changes in vegetation in turn modify the structure and
109 composition of arthropod communities (Ford et al., 2012). The impacts of these
110 environmental changes on salt marsh arthropods are still poorly understood, and
111 results from scarce literature are often contradictory (*e.g.*, Rickert et al., 2012; van
112 Klink et al., 2013). Consequently, we expected the application of distinct community
113 metrics to provide new and complementary information, thus leading to a better
114 understanding of how environmental changes impact communities. For that purpose,
115 we compared the impacts of four treatments (control, invasion, cutting and grazing)
116 on spider communities of salt marshes using community-level indices. Spiders were
117 selected as a model group as they constitute one of the most abundant and diverse
118 groups of arthropods in salt marshes (Pétillon et al., 2008) and for their well-known
119 sensitivity to changes in habitat structure (*e.g.*, Marc et al., 1999).

120

121

122 2. Methods

123 2.1. Sampling design

124 The impacts of treatments on spider communities were investigated at two sites in
125 the Mont-Saint-Michel Bay (NW France, 48°37'N, 1°34'W), 1 kilometre apart. Four
126 treatments were investigated: control, invasion by *E. athericus*, vegetation cutting
127 (once a year, in July) and grazing by sheep (on average 50 sheep/ha) (Pétillon et al.,
128 2007). Treatments are representative of the main salt-marsh habitats of the Mont St-
129 Michel Bay (Pétillon et al., 2007), and covered all together 89% of the 4054 hectares
130 of salt marshes (*E. athericus*-invaded areas: 35%, cutting: 19%, sheep-grazing: 25%,
131 natural vegetation: 10%, data from 2007, Valéry and Radureau, personal
132 communication).

133 Spider communities were sampled between May and June in 2004 and 2007: the
134 former with control, invasion and cutting treatments, and the latter with control,
135 invasion and grazing treatments. The comparison between treatments was made in
136 similar salt-marsh zones within each site and the only apparent varying factors (at the
137 local and landscape scales) between plots were the presence/absence of management
138 practices (cutting and grazing) or invasion by *E. athericus*.

139 The sampling protocol was designed to be comparable among treatments: within
140 each site, each treatment was applied to three plots during the same sampling period.
141 Plots had a surface area of 100m² and were spaced 100m apart. Within each plot,
142 ground-dwelling spiders were sampled with four pitfall traps, set up regularly in a
143 square grid and placed 10m apart, as this is the minimum distance to avoid
144 interference between traps (Topping and Sunderland, 1992). Traps consisted of
145 polypropylene cups (10 cm diameter, 17 cm deep) containing ethylene-glycol as a
146 preservative. Traps were covered with a raised wooden roof to exclude the rain and

147 were visited weekly, tides permitting (i.e. three times per month during May and
148 June). To summarise, there were 36 traps per site (3 treatments * 3 plots * 4 traps)
149 and thus a total of 72 traps for the whole sampling protocol. To verify the impacts of
150 treatments on vegetation, percentage covers of all plant species were estimated once
151 within a radius of 1m around all traps.

152 2.2. *Spider community-level indices*

153 We calculated the average rarity, specialisation, and functional diversity of each
154 community (pitfall trap) using species characteristics obtained from spider datasets
155 (rarity, specialisation), and the literature (hunting strategy).

156 Data came from i) the western France spider database, and ii) the Catalogue of Spider
157 Species from Europe and the Mediterranean Basin (both datasets were detailed in
158 Leroy et al., 2013).

159 2.2.1. *Multiscale Index of Rarity*

160 For each spider species, we calculated rarity weights (w_{Mi}) according to the method
161 described in Leroy et al. (2013) (details in Appendix A). These rarity weights integrate
162 information on the occurrence of species at two spatial scales: the western France
163 scale and the western Palearctic scale. Weight values range from 0 to 2. The rarer the
164 species, the higher the weights, with species which are rare at both scales receiving
165 higher rarity weights than species which are rare at a single scale.

166 The Index of Relative Rarity (I_{RR}) of each pitfall community was then calculated as
167 the average weight of rarity of individuals of all the species of the considered
168 community, and was subsequently normalized to values between 0 (no rare species in
169 the community) and 1 (all individuals of the community belong to species with the

170 maximum rarity weight): $I_{RR} = ([\sum(a_i \times w_{Mi})/N] - w_{\min})/(w_{\max} - w_{\min})$ where a_i and
171 w_{Mi} respectively are the abundance and rarity weight of the i^{th} species of the
172 community; N is the total number of individuals in the community; and w_{\min} and
173 w_{\max} are the minimum and maximum possible weights, respectively.

174 *2.2.2. Community Specialisation Index*

175 Each species was characterised for habitat specialisation through using the
176 calculation of a Species Specialisation Index (SSI) according to Julliard et al. (2006).
177 To define habitat specialisation, the western France spider database was used. For
178 each species, the frequencies of occurrence in each habitat class were calculated (see
179 details in Appendix B). The coefficient of variation of these frequencies of occurrence
180 (standard deviation/average) as a measure of each Species Specialisation Index (SSI)
181 (Julliard et al., 2006) was then calculated. The SSI varied between 0.76 (most
182 generalist species) and 4.69 (most specialised species) (Table 1 and Appendix B). The
183 Community Specialisation Index (CSI) of each pitfall community was calculated as
184 the average SSI of the species detected, weighted by local species abundance, as
185 follows: $CSI = [\sum(a_i SSI_i)/N]$, where a_i and SSI_i respectively are the abundance and
186 species specialisation indices of species i ; and N is the total number of individuals in
187 the community (Devictor et al., 2008). The CSI was then standardised between 0 and
188 1 in a similar manner to the Index of Relative Rarity (Leroy et al., 2012); a CSI of 1
189 means that a community is composed of individuals of the most specialised species of
190 the database, whereas a CSI of 0 means that a community is composed of individuals
191 of the most generalist species.

192 *2.2.3. Functional diversity*

193 The functional diversity of spider communities was calculated on the basis of
194 functional traits related to hunting modes, because of the important impacts of
195 predator hunting modes in ecosystem functioning (Schmitz, 2009). We used
196 functional traits at the family level on the basis of the trait matrix of spider families of
197 Cardoso et al. (2011). The Functional Divergence (FDiv) index (Villéger et al., 2008)
198 was calculated in order to take into account both the occupation of functional space
199 by the different families and the relative abundance of families in communities.

200 *2.3. Analyses*

201 Because rarity weights and specialisation indices of species describe two axes of
202 rarity, we first analysed their correlation for the sampled species with Pearson's
203 correlation coefficient. Species richness and the three indices (I_{RR} , CSI and FDiv)
204 were then calculated for each community of spiders of the 72 traps. The FDiv index
205 was calculated for only 58 out of 72 communities, because functional divergence
206 cannot be estimated when communities contain less than three functionally singular
207 species. The effects of treatments on the calculated metrics were then analysed using
208 linear mixed-effects models because of the hierarchical nature of the sampling design.
209 We fitted linear mixed-effect models with the treatment as a fixed effect, and sites
210 nested in year as random effects. The significance of fixed effects was tested by
211 comparing models with vs. without fixed effects using likelihood ratio tests. We then
212 performed multiple comparisons between treatments with Tukey's post-hoc tests
213 with a correction on probability values by controlling the false discovery rate
214 (Benjamini and Hochberg, 1995). Welsh two sample t-tests were used to compare the
215 average abundance between treatments, of several species. Indices were calculated
216 with Rarity version 1.2-1 (Leroy, 2013) and FD version 1.0-11 (Laliberté and Shipley,
217 2011). Linear mixed effect models were performed in R 3.0.2 (R Core Team, 2013)

218 with the package lme4 version 1.0-5 (Bates et al., 2013), and post-hoc tests with the
219 package multcomp version 1.3-1 (Hothorn et al., 2008).

220

221 **3. Results**

222 *3.1. Samplings*

223 A total of 3826 spiders, representing 31 species, 10 families and 6 functional groups,
224 was collected (Table 1). The dominance of single plant species per treatment was
225 confirmed: *Atriplex portulacoides* in the control plots (mean±sd=66.8±11.5%,
226 range=[55%-88%], n=12), *Elymus athericus* in the invaded plots
227 (mean±sd=89.4±7.3%, range=[70%-93%], n=12), *Festuca rubra* in the cut plots
228 (mean±sd=62.9±5.4%, range=[55%-70%], n=12) and *Puccinellia maritima* in the
229 grazed plots (mean±sd=77.5±21.4%, range=[30%-90%], n=12).

230 *3.2. Correlation between rarity weights and specialisation indices of species*

231 We observed a positive correlation between rarity weights and specialisation indices
232 of species (Pearson's $R = 0.75$; $P < 0.001$; $N = 31$) (Fig. 1). Nevertheless, some species
233 had very high specialisation values but low rarity weights (*e.g.*, *Erigone longipalpis*),
234 or had very high rarity weights but intermediate specialisation values (*e.g.*, *Pardosa*
235 *purbeckensis*).

236 *3.3. Effects of treatments on communities*

237 We detected a significant treatment effect on all the measured metrics (see Figure 1
238 and details in Appendix B). The species richness was significantly lower in traps
239 located in invaded plots than in traps associated with other treatments ($\chi^2=13.5$,
240 $df=3$, $p=0.004$) (Fig. 2A). The relative rarity of communities was significantly higher
241 in control plot traps than in those located in managed or invaded plots ($\chi^2=24.1$,
242 $df=3$, $p<0.001$) (Fig. 2B). This increase in rarity was associated with a higher mean
243 abundance of the rare species *P. purbeckensis* in the control treatment than in other
244 treatments ($t=5.78$, $df=31.50$, $p<0.001$) (Table 1). Conversely, although the CSI was

245 significantly higher in the control treatment than under invasion or cutting
246 treatments, the highest CSI was observed in the grazed plots, and was significantly
247 higher than in control and in invaded or cut plots ($\chi^2=24.40$, $df=3$, $p<0.001$) (Fig.
248 2C). The higher specialisation under the control compared to invasion and cutting
249 treatments was associated with higher average abundance of specialised species such
250 as *P. purbeckensis* ($t=6.60$, $df=30.22$, $p<0.001$) and *Silometopus ambiguus* ($t=2.90$,
251 $df=33.08$, $p=0.007$) (Table 1). On the other hand, the very high specialisation value
252 observed under the grazing treatment was associated to the high abundance of the
253 specialised species *E. longipalpis*, with on average 13.83 ± 9.76 individuals per trap
254 versus 1.13 ± 2.05 individuals per trap (mean \pm sd) in other treatments ($t=4.49$,
255 $df=11.20$, $p<0.001$). However, grazing, and to a lesser extent cutting, appeared to
256 have a negative impact on the functional divergence of communities, with a
257 significantly lower FDiv in traps of grazed plots than in those of invaded or control
258 traps ($\chi^2=10.4$, $df=3$, $p=0.016$) (Fig. 2D). We compared this lower functional
259 diversity to the presence of functional groups under the grazing treatment, and we
260 observed only two dominant functional groups (“Ground hunters” and “Other
261 hunters”), while other treatments were more balanced, with an additional functional
262 group (“Orb web weavers”) (Table 1).

263

264 **4. Discussion**

265 In this paper, we combined different metrics (rarity, specialisation and functional
266 diversity) to analyse how spider communities of salt marshes respond to changes in
267 their environment, whether induced by a biological invasion (*Elymus athericus*) or by
268 management practices (grazing, cutting). As expected, environmental changes
269 generally had negative impacts on spider communities, which led to decreases in
270 rarity, specialisation and functional diversity of communities. While the general trend
271 was similar among metrics, we observed divergent responses to the relative impacts
272 of treatments between the three measured metrics.

273 *Influence of community composition on metrics*

274 In particular, the most interesting divergence was observed for the effect of grazing
275 treatment. Specialisation was higher in grazed plots than in control plots, whereas the
276 opposite was observed for rarity and functional diversity. This is surprising given the
277 observed positive relationship between rarity weights and specialisation indices at the
278 species level. However, this relationship has exceptions such as the widespread but
279 specialist species *E. longipalpis*. Incidentally, *E. longipalpis* was highly abundant in
280 the grazed plot, leading to a divergence between specialisation and rarity indices. This
281 pattern shows that metrics expected to vary conjointly can produce divergent
282 outcomes because of their sensitivity to the composition of communities. This
283 sensitivity is very important to highlight unexpected impacts of environmental
284 changes on communities.

285 Another important property of the metrics used here is that they are not biased by the
286 species richness or abundance: because the metrics are based on the average trait
287 (rarity, specialisation) of the species in the community, then a species-poor
288 community *can* have a higher value than a species-rich community (Julliard et al.,

289 2006; Leroy et al., 2012; Villéger et al., 2008). If we take the example of the CSI, a
290 community with only a few individuals from very specialised species will have a
291 higher CSI than a community with many individuals of generalist species. Because of
292 this averaging property, a decrease in CSI may result from a decrease of specialists
293 and/or from an increase of generalist species. Typically disturbances are expected to
294 negatively impact specialist species while fostering generalist species, as both
295 predicted by theory and empirically observed (see Devictor and Robert, 2009). As a
296 consequence it is expected that changes in community composition resulting from
297 environmental disturbances will generally result in lower CSI values. However, in
298 extreme cases, the reverse might be observed: for example a disturbance
299 corresponding to the extreme values of the abiotic gradient may have positive
300 impacts on only a few specialist species with particular adaptation to this disturbance
301 (*e.g.*, Doxa et al., 2010), which would thus result in a higher CSI value. Though this is
302 a particular case, it highlights the importance of verifying, as a second step, how
303 community composition changed. This impact is similar on the functional divergence
304 index: the loss of species occupying intermediate functions will increase the
305 functional value. However, this is not relevant in our case study since spider
306 functional groups are strongly divergent; thus, a decrease in abundance of any
307 functional group will decrease the functional value.

308 To summarise, the three applied metrics accurately synthesise how changes in
309 community composition affect different facets of biodiversity; such changes cannot
310 be detected by species richness alone. However, understanding these changes imply
311 to look at changes in community composition as a second step.

312 *Implications for salt marsh conservation*

313 The indices showed that grazing induced a decrease in the average rarity and
314 functional diversity of communities, but an increase in their specialisation. This

315 pattern is mainly due to the increase in widespread but specialist species such as *E.*
316 *longipalpis*. This positive impact of grazing on specialist species of salt marshes such
317 as *E. longipalpis* was reported by Ford et al. (2012), although they did not investigate
318 species rarity. The negative effect of grazing, and to a lesser extent cutting, on
319 functional diversity is clearly due to a reduction in the number of vegetation strata,
320 which negatively impacts spiders living in higher vegetation such as orb web weavers
321 (Uetz et al., 1999). On the other hand, no significant impact of grazing was detected
322 on species richness alone, unlike Rickert et al. (2012) and van Klink et al. (2013). In
323 fact, a negative impact on species richness was only observed for the invaded
324 treatment. We also found higher specialisation and rarity in control plots than in
325 invaded and cut plots, in accordance with a previous study that revealed more
326 continental, non-specialised, spider species in cut or invaded salt marshes (Pétillon et
327 al., 2005).

328 To summarise, our results suggest that undisturbed salt marshes generally support a
329 higher specialisation, rarity and functional diversity than disturbed salt marshes, with
330 the notable exception of the positive impact of grazing on specialised species. To
331 preserve all the facets of spider diversity, we would recommend maintaining the
332 grazing management in areas invaded by *E. athericus* rather than the cutting
333 treatment.

334 *Conclusion*

335 We therefore showed contrasting responses of spider communities to the different
336 environmental changes (invasion and management measures). These contrasts
337 emphasise the necessity of using different and complementary community metrics in
338 such conservation studies. As a consequence, rarity-, specialization- and functional-
339 based indices should be more frequently applied together, as they can potentially

340 contribute a wide range of complementary information about species communities.

341 Such complementary information is the key to better-informed conservation choices.

342 **Acknowledgements**

343 We thank Simon Potier, Alain Radureau and Vincent Schricke for fruitful discussion,

344 Damien Nougès and Mathieu de Flores for their contribution in field work and

345 spider identification. Aldyth Nys provided useful editing of the English of an earlier

346 draft. Loïc Valéry provided data on the spatial distribution of treatments. We thank

347 two anonymous reviewers for useful additions in an earlier draft.

348

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Table 1. Multiscale rarity weights, specialisation indices and functional groups of the sampled spider species, and their average \pm sd abundance in pitfall traps. The functional groups are based on Cardoso *et al.* (2011).

| Species | Multiscale rarity weights | Species specialisation indices | Functional groups | Abundance \pm sd | | | |
|------------------------------|---------------------------|--------------------------------|-------------------|--------------------|-----------------|-----------------|------------------|
| | | | | Control | Invasion | Cutting | Grazing |
| Family Araneidae | | | | | | | |
| <i>Argiope bruennichi</i> | 0.009 | 1.272 | Orb web weavers | 0.00 \pm 0.00 | 0.08 \pm 0.28 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| <i>Larinioides cornutus</i> | 0.004 | 1.225 | Orb web weavers | 0.04 \pm 0.20 | 0.08 \pm 0.28 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| <i>Neoscona adianta</i> | 0.002 | 1.271 | Orb web weavers | 0.00 \pm 0.00 | 0.04 \pm 0.20 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| Family Clubionidae | | | | | | | |
| <i>Clubiona stagnatilis</i> | 0.144 | 1.877 | Other hunters | 0.00 \pm 0.00 | 0.04 \pm 0.20 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| Family Dictynidae | | | | | | | |
| <i>Argenna patula</i> | 0.344 | 3.247 | Ground hunters | 0.71 \pm 1.16 | 3.29 \pm 4.22 | 0.83 \pm 0.83 | 0.92 \pm 1.00 |
| Family Gnaphosidae | | | | | | | |
| <i>Drassyllus pusillus</i> | 0.031 | 1.429 | Ground hunters | 0.04 \pm 0.20 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| <i>Silometopus ambiguus</i> | 0.697 | 3.164 | Other hunters | 3.29 \pm 3.38 | 1.58 \pm 2.21 | 0.08 \pm 0.29 | 2.33 \pm 1.97 |
| <i>Zelotes latreillei</i> | 0.026 | 1.749 | Ground hunters | 0.00 \pm 0.00 | 0.08 \pm 0.41 | 0.08 \pm 0.29 | 0.00 \pm 0.00 |
| Family Linyphiidae | | | | | | | |
| <i>Agyneta conigera</i> | 0.551 | 4.286 | Sheet web weavers | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.08 \pm 0.29 | 0.00 \pm 0.00 |
| <i>Bathyphantes gracilis</i> | 0.012 | 1.368 | Sheet web weavers | 0.21 \pm 0.51 | 0.08 \pm 0.28 | 0.17 \pm 0.39 | 0.08 \pm 0.29 |
| <i>Collinsia inerrans</i> | 0.525 | 2.222 | Other hunters | 0.04 \pm 0.20 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| <i>Erigone atra</i> | 0.010 | 1.346 | Other hunters | 0.46 \pm 0.78 | 0.04 \pm 0.20 | 1.50 \pm 1.62 | 0.67 \pm 0.89 |
| <i>Erigone dentipalpis</i> | 0.003 | 1.195 | Other hunters | 0.17 \pm 0.38 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| <i>Erigone longipalpis</i> | 0.234 | 4.690 | Other hunters | 2.50 \pm 2.69 | 0.25 \pm 0.53 | 0.17 \pm 0.39 | 13.83 \pm 9.76 |
| <i>Oedothorax fuscus</i> | 0.022 | 1.224 | Other hunters | 4.83 \pm 6.68 | 0.04 \pm 0.20 | 4.25 \pm 5.14 | 2.50 \pm 1.24 |
| <i>Oedothorax retusus</i> | 0.028 | 1.353 | Other hunters | 0.58 \pm 0.78 | 0.04 \pm 0.20 | 5.50 \pm 5.89 | 0.25 \pm 0.45 |
| <i>Pelecopsis parallela</i> | 0.051 | 1.830 | Other hunters | 0.00 \pm 0.00 | 0.33 \pm 0.82 | 0.42 \pm 0.67 | 0.00 \pm 0.00 |
| <i>Savignia frontata</i> | 0.325 | 3.720 | Other hunters | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.08 \pm 0.29 | 0.00 \pm 0.00 |

| | | | | | | | |
|--------------------------------|-------|-------|-------------------|-------------|-------------|-------------|-------------|
| <i>Stemonyphantes lineatus</i> | 0.031 | 1.424 | Other hunters | 0.04±0.20 | 0.13±0.34 | 0.00±0.00 | 0.00±0.00 |
| <i>Tenuiphantes tenuis</i> | 0.003 | 0.757 | Sheet web weavers | 0.75±1.03 | 0.75±1.11 | 0.50±0.67 | 1.33±0.78 |
| Family Liocranidae | | | | | | | |
| <i>Agroeca lusatica</i> | 0.555 | 2.442 | Ground hunters | 0.33±0.56 | 0.42±0.83 | 0.08±0.29 | 0.00±0.00 |
| Family Lycosidae | | | | | | | |
| <i>Alopecosa pulverulenta</i> | 0.007 | 1.464 | Ground hunters | 0.00±0.00 | 0.08±0.28 | 0.00±0.00 | 0.00±0.00 |
| <i>Arctosa fulvolineata</i> | 0.560 | 2.462 | Ground hunters | 3.13±2.42 | 2.17±1.97 | 4.00±3.49 | 2.00±1.28 |
| <i>Pardosa palustris</i> | 0.035 | 1.785 | Ground hunters | 0.04±0.20 | 0.00±0.00 | 0.08±0.29 | 0.08±0.29 |
| <i>Pardosa prativaga</i> | 0.023 | 2.046 | Ground hunters | 0.04±0.20 | 0.04±0.20 | 0.00±0.00 | 0.00±0.00 |
| <i>Pardosa proxima</i> | 0.019 | 1.507 | Ground hunters | 0.00±0.00 | 0.08±0.28 | 0.17±0.39 | 0.00±0.00 |
| <i>Pardosa purbeckensis</i> | 1.077 | 3.307 | Ground hunters | 21.13±10.11 | 6.17±5.26 | 7.17±4.13 | 13.17±6.67 |
| Family Tetragnathidae | | | | | | | |
| <i>Pachygnatha clercki</i> | 0.010 | 1.545 | Orb web weavers | 0.00±0.00 | 0.00±0.00 | 0.33±0.65 | 0.00±0.00 |
| <i>Pachygnatha degeeri</i> | 0.006 | 0.888 | Orb web weavers | 2.54±2.28 | 2.83±4.57 | 1.83±2.29 | 0.33±0.65 |
| Family Theridiidae | | | | | | | |
| <i>Enoplognatha mordax</i> | 0.214 | 2.375 | Space web weavers | 0.08±0.28 | 0.04±0.20 | 0.08±0.29 | 0.08±0.29 |
| Family Thomisidae | | | | | | | |
| <i>Ozyptila simplex</i> | 0.091 | 1.675 | Ambush hunters | 0.04±0.20 | 0.00±0.00 | 0.00±0.00 | 0.08±0.29 |
| Total abundances | | | | 41.00±14.63 | 18.71±11.96 | 27.42±11.77 | 37.67±10.53 |

Figure captions

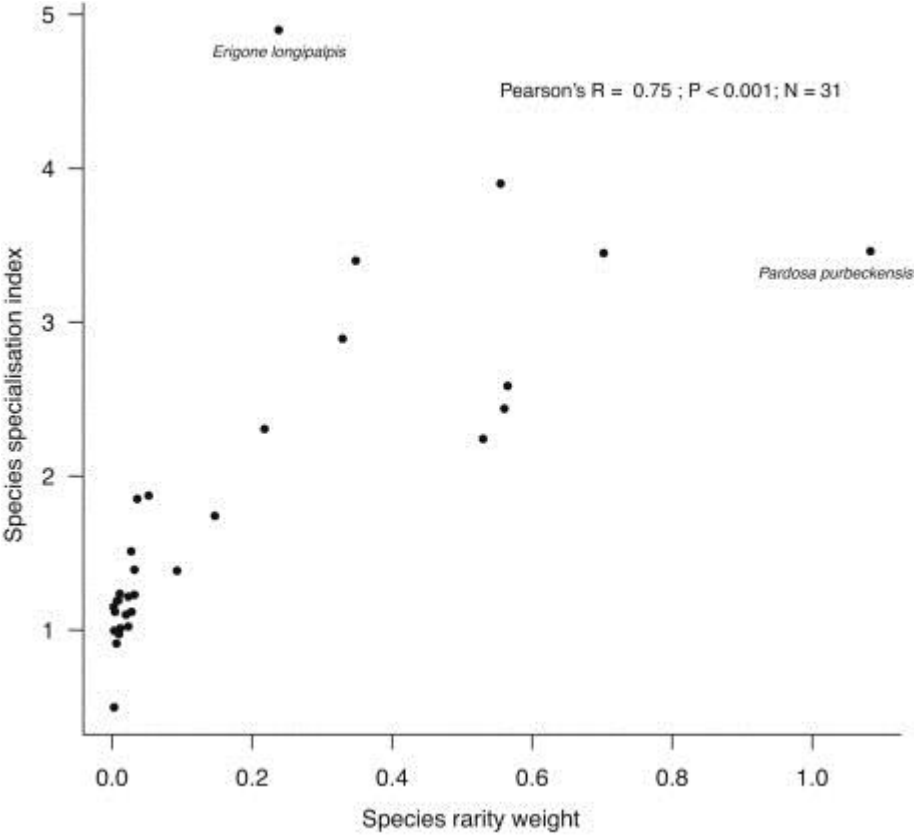


Figure 1. Correlation between specialisation indices and rarity weights of the sampled species. Two species highly abundant in some of the sampled sites and with high weight values are indicated: *Erigone longipalpis* and *Pardosa purbeckensis*.

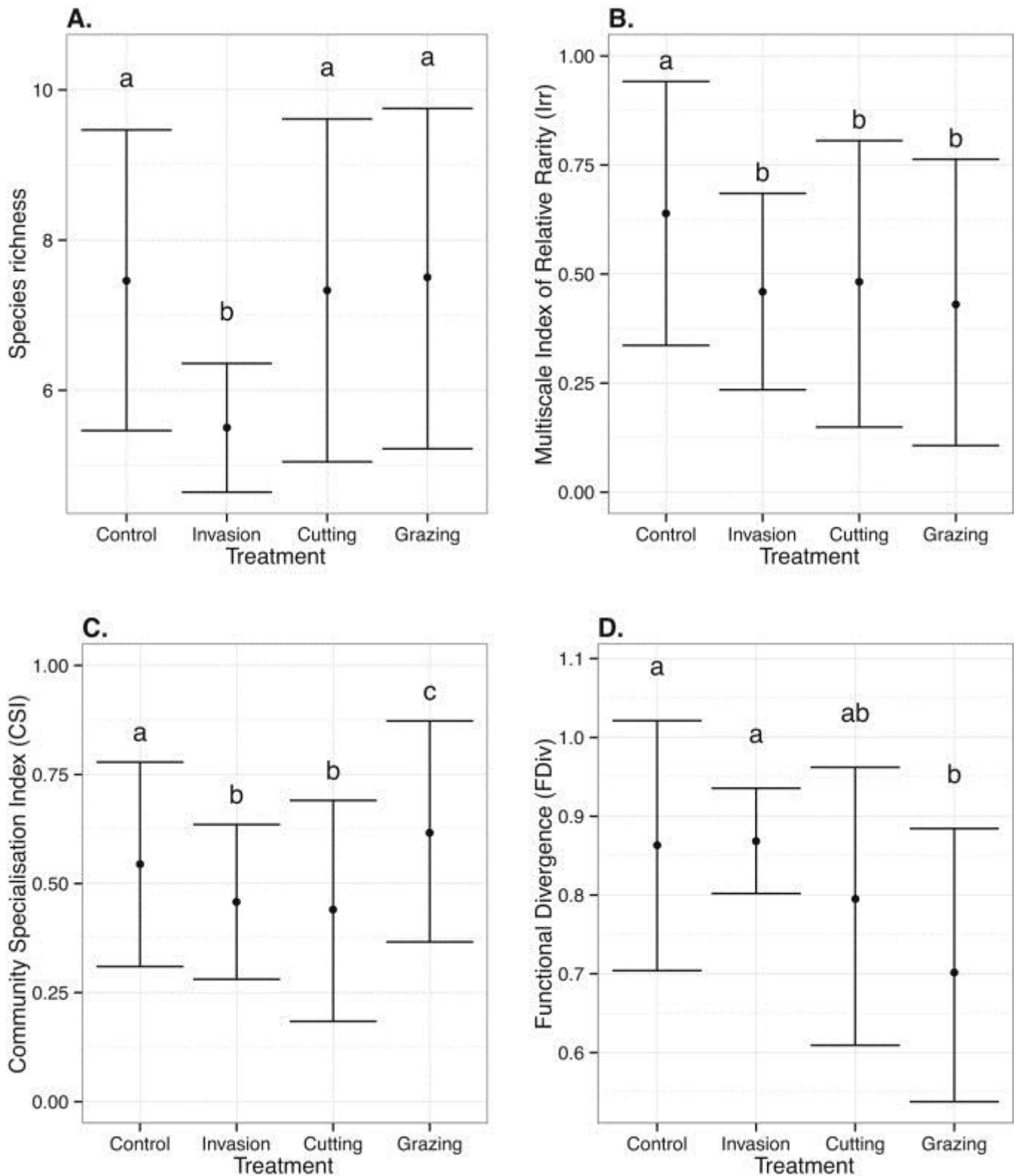


Figure 2. Average values of indices (A. Species richness, B. Multiscale Index of Relative Rarity, C. Community Specialisation Index, and D. Functional Divergence) and 95% confidence intervals (estimated by linear mixed-effects models (LMMs)) for the four treatments. Different successive letters indicate significant differences in means (revealed by corrected Tukey's post-hoc test on treatment effect following LMMs, with correction for the false discovery rate).