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

Boris Leroy<sup>a,b\*</sup>, Isabelle Le Viol<sup>c</sup> & Julien Pétillon<sup>a</sup>

<sup>a</sup> EA 7316 Biodiversité et Gestion des Territoires, Université de Rennes I, 263 Av. du Gal. Leclerc,  
35042 Rennes Cedex, France

<sup>b</sup> Ecologie, Systématique & Evolution, UMR CNRS 8079, Univ. Paris-Sud, Orsay Cedex FR-91405,  
France,

<sup>c</sup> Centre d'Ecologie et des Sciences de la Conservation (CESCO), UMR 7204 MNHN-CNRS-UPMC, 55  
rue Buffon, 75005 Paris, France

**\* Corresponding author:** Boris Leroy; Email: leroy.boris@gmail.com;

Tel.: +33 666 021 327.

**Present address:** Ecologie, Systématique & Evolution, UMR CNRS 8079, Univ. Paris-Sud,  
Orsay Cedex FR-91405, France

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## Abstract

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

**Key-words:** Index of Relative Rarity; Community Specialisation Index; Functional 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)

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## 1. Introduction

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

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

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

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

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## 2. Methods

### 2.1. Sampling design

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

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

The sampling protocol was designed to be comparable among treatments: within each site, each treatment was applied to three plots during the same sampling period. Plots had a surface area of 100m<sup>2</sup> and were spaced 100m apart. Within each plot, ground-dwelling spiders were sampled with four pitfall traps, set up regularly in a square grid and placed 10m apart, as this is the minimum distance to avoid interference between traps (Topping and Sunderland, 1992). Traps consisted of polypropylene cups (10 cm diameter, 17 cm deep) containing ethylene-glycol as a preservative. Traps were covered with a raised wooden roof to exclude the rain and



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

## 2.2. Spider community-level indices

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

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

### 2.2.1. Multiscale Index of Rarity

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

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

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

### 2.2.2. Community Specialisation Index

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

### 2.2.3. Functional diversity

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

### 2.3. Analyses

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

### 3. Results

#### 3.1. Samplings

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

#### 3.2. Correlation between rarity weights and specialisation indices of species

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

#### 3.3. Effects of treatments on communities

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

significantly higher in the control treatment than under invasion or cutting treatments, the highest CSI was observed in the grazed plots, and was significantly higher than in control and in invaded or cut plots ( $\chi^2=24.40$ ,  $df=3$ ,  $p<0.001$ ) (Fig. 2C). The higher specialisation under the control compared to invasion and cutting treatments was associated with higher average abundance of specialised species such as *P. purbeckensis* ( $t=6.60$ ,  $df=30.22$ ,  $p<0.001$ ) and *Silometopus ambiguus* ( $t=2.90$ ,  $df=33.08$ ,  $p=0.007$ ) (Table 1). On the other hand, the very high specialisation value observed under the grazing treatment was associated to the high abundance of the specialised species *E. longipalpis*, with on average  $13.83\pm9.76$  individuals per trap versus  $1.13\pm2.05$  individuals per trap (mean $\pm$ sd) in other treatments ( $t=4.49$ ,  $df=11.20$ ,  $p<0.001$ ). However, grazing, and to a lesser extent cutting, appeared to have a negative impact on the functional divergence of communities, with a significantly lower FDiv in traps of grazed plots than in those of invaded or control traps ( $\chi^2=10.4$ ,  $df=3$ ,  $p=0.016$ ) (Fig. 2D). We compared this lower functional diversity to the presence of functional groups under the grazing treatment, and we observed only two dominant functional groups (“Ground hunters” and “Other hunters”), while other treatments were more balanced, with an additional functional group (“Orb web weavers”) (Table 1).

#### 4. Discussion

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

##### *Influence of community composition on metrics*

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

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

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

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

#### *Implications for salt marsh conservation*

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



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

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

### *Conclusion*

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

contribute a wide range of complementary information about species communities.  
Such complementary information is the key to better-informed conservation choices.

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## References

- Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: Linear mixed-effect models using Eigen and S4. R package version 1.0-5. <http://CRAN.R-project.org/package=lme4>
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B. Methodol.* 57, 289–300.
- Bockelmann, A., Neuhaus, R., 1999. Competitive exclusion of *Elymus athericus* from a high-stress habitat in a European salt marsh. *J. Ecol.* 87, 503–513.
- Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS One* 6, e21710.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010a. Defining and measuring ecological specialization. *J. Appl. Ecol.* 47, 15–25.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Glob. Ecol. Biogeogr.* 17, 252–261.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010b. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–40.
- Devictor, V., Robert, A., 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Divers. Distrib.* 15, 122–130.
- Doxa, A., Bas, Y., Paracchini, M.L., Pointereau, P., Terres, J.-M., Jiguet, F., 2010. Low-intensity agriculture increases farmland bird abundances in France. *J. Appl. Ecol.* 47, 1348–1356.
- Ford, H., Garbutt, A., Jones, L., Jones, D.L., 2012. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conserv. Divers.* 6, 189–200.
- Gaston, K.J., 1994. *Rarity*. Chapman & Hall, London, UK.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. *Biometrical J.* 50, 346–363.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. *Ecol. Lett.* 9, 1237–44.
- Laliberté, E., Shipley, B., 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.
- Leroy, B., 2013. *Rarity*: Calculation of rarity indices for species and assemblages of species. R package version 1.2-1. <http://CRAN.R-project.org/package=Rarity>

385 Leroy, B., Canard, A., Ysnel, F., 2013. Integrating multiple scales in rarity assessments of  
386 invertebrate taxa. *Divers. Distrib.* 19, 794–803.

387 Leroy, B., Pétilion, J., Gallon, R., Canard, A., Ysnel, F., 2012. Improving occurrence-based  
388 rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect*  
389 *Conserv. Divers.* 5, 159–168.

390 Levins, R., 1968. *Evolution in Changing Environments: Some Theoretical Explorations.*  
391 Princeton University Press, Princeton, USA.

392 Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and  
393 bioindication. *Agric. Ecosyst. Environ.* 74, 229–273.

394 Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond  
395 taxonomic diversity patterns: how do  $\alpha$ ,  $\beta$  and  $\gamma$  components of bird functional and  
396 phylogenetic diversity respond to environmental gradients across France? *Glob. Ecol.*  
397 *Biogeogr.* 20, 893–903.

398 Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M.,  
399 Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., Thuiller,  
400 W., 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS*  
401 *Biol.* 11, e1001569.

402 Penone, C., Kerbiriou, C., Julien, J.-F., Julliard, R., Machon, N., Le Viol, I., 2013.  
403 Urbanisation effect on Orthoptera: which scale matters? *Insect Conserv. Divers.* 6, 319–  
404 327.

405 Pétilion, J., Georges, A., Canard, A., Lefeuvre, J.-C., Bakker, J.P., Ysnel, F., 2008. Influence of  
406 abiotic factors on spider and ground beetle communities in different salt-marsh systems.  
407 *Basic Appl. Ecol.* 9, 743–751.

408 Pétilion, J., Georges, A., Canard, A., Ysnel, F., 2007. Impact of cutting and sheep grazing on  
409 ground-active spiders and carabids in intertidal salt marshes (Western France). *Anim.*  
410 *Biodivers. Conserv.* 30, 201–209.

411 Pétilion, J., Lambeets, K., Ract-Madoux, B., Vernon, P., Renault, D., 2011. Saline stress  
412 tolerance partly matches with habitat preference in ground-living wolf spiders. *Physiol.*  
413 *Entomol.* 36, 165–172.

414 Pétilion, J., Ysnel, F., Canard, A., Lefeuvre, J.-C., 2005. Impact of an invasive plant (*Elymus*  
415 *athericus*) on the conservation value of tidal salt marshes in western France and  
416 implications for management: Responses of spider populations. *Biol. Conserv.* 126, 103–  
417 117.

418 Prieto-Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and  
419 richness of spiders (Araneae): A meta-analysis. *Biol. Conserv.* 144, 683–691.

420 R Core Team, 2014. R: A language and environment for statistical computing. R Foundation  
421 for Statistical Computing, Vienna, Austria.

422 Rickert, C., Fichtner, A., van Klink, R., Bakker, J.P., 2012.  $\alpha$ - and  $\beta$ -diversity in moth  
423 communities in salt marshes is driven by grazing management. *Biol. Conserv.* 146, 24–  
424 31.

425 Schmitz, O.J., 2009. Effects of predator functional diversity on grassland ecosystem function.  
426 Ecology 90, 2339–2345.

427 Strecker, A., Olden, J., Whittier, J.B., Paukert, C.P., 2011. Defining conservation priorities for  
428 freshwater fishes according to taxonomic, functional, and phylogenetic diversity. Ecol.  
429 Appl. 21, 3002–3013.

430 Topping, C.J., Sunderland, K.D., 1992. Limitations to the use of pitfall traps in ecological  
431 studies exemplified by a study of spiders in a field of winter wheat. J. Appl. Ecol. 29,  
432 485–491.

433 Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild structure of spiders in major crops. J. Arachnol.  
434 27, 270–280.

435 Van Klink, R., Rickert, C., Vermeulen, R., Vorst, O., WallisDeVries, M.F., Bakker, J.P., 2013.  
436 Grazed vegetation mosaics do not maximize arthropod diversity: Evidence from salt  
437 marshes. Biol. Conserv. 164, 150–157.

438 Veeneklaas, R.M., Dijkema, K.S., Hecker, N., Bakker, J.P., 2012. Spatio-temporal dynamics of  
439 the invasive plant species *Elytrigia atherica* on natural salt marshes. Appl. Veg. Sci. 16,  
440 205–216.

441 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity  
442 indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.

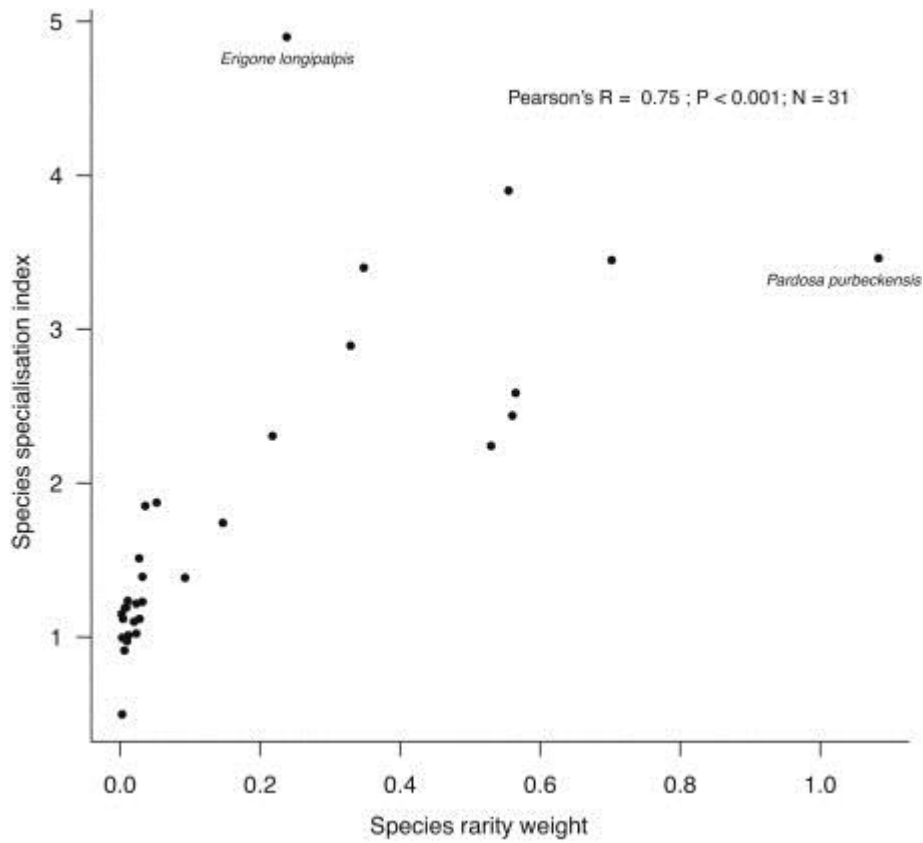
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**Table 1.** Multiscale rarity weights, specialisation indices and functional groups of the sampled spider species, and their average  $\pm$  sd abundance in pitfall traps. The functional groups are based on Cardoso *et al.* (2011).

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

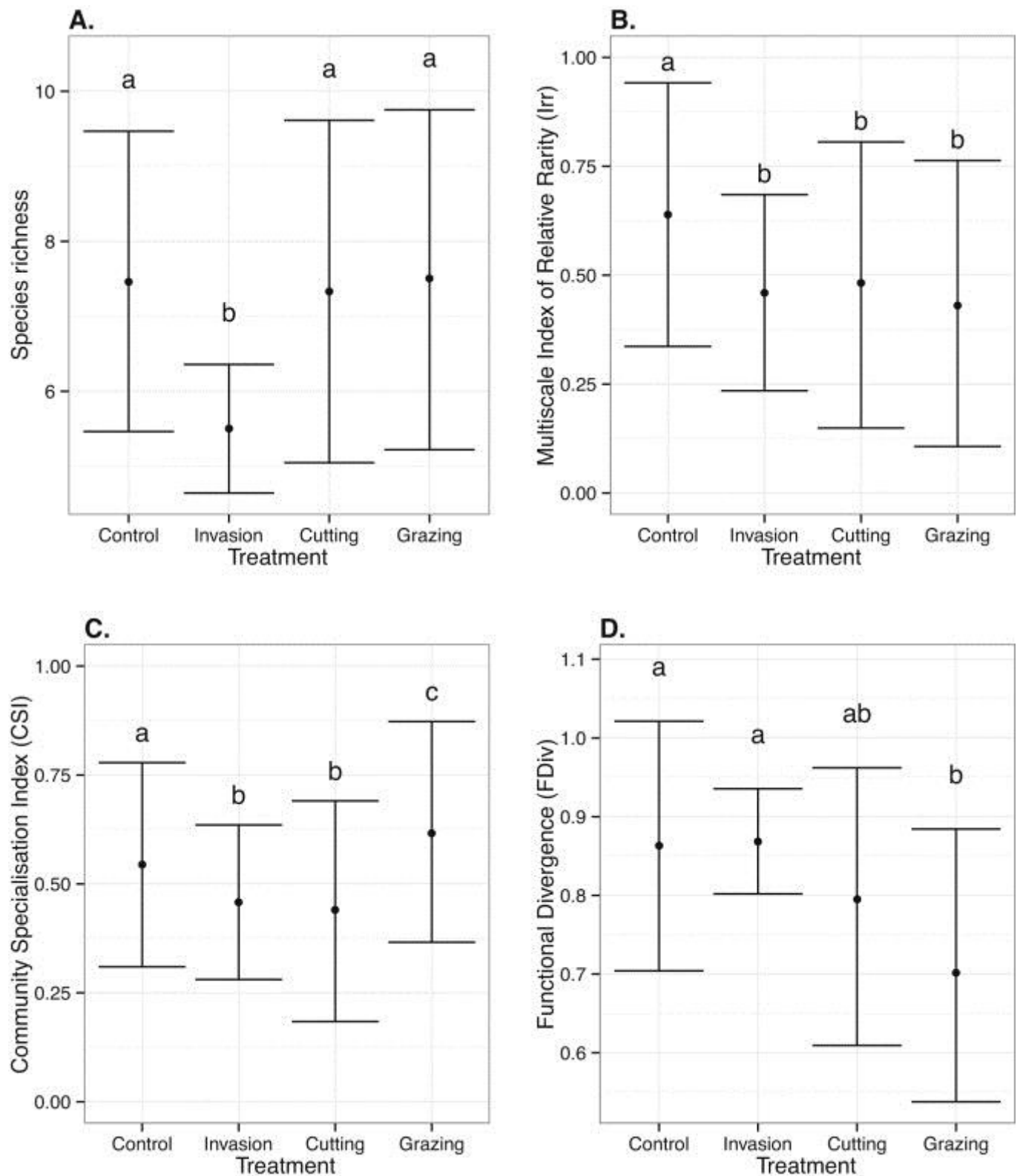
<i>Stemonyphantes lineatus</i>	0.031	1.424	Other hunters	0.04±0.20	0.13±0.34	0.00±0.00	0.00±0.00
<i>Tenuiphantes tenuis</i>	0.003	0.757	Sheet web weavers	0.75±1.03	0.75±1.11	0.50±0.67	1.33±0.78
Family Liocranidae							
<i>Agroeca lusatica</i>	0.555	2.442	Ground hunters	0.33±0.56	0.42±0.83	0.08±0.29	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).