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## **Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities**

Michalet, Richard ; Maalouf, Jean-Paul ; Choler, Philippe ; Clément, Bernard ; Rosebery, David ; Royer, Jean-Marie ; Schöb, Christian ; Lortie, Christopher

**Abstract:** Understanding the relative contribution of local and regional processes to local species richness is an important ecological question and a subject of controversy between macroecologists and community ecologists. We test the hypothesis that the contribution of local and regional processes is dependent on environmental conditions and that the effect of regional processes should be the highest in communities from intermediate positions along environmental severity gradients due to the importance of facilitation. We used the recently developed log-ratio method to analyze the relationship between Local Species Richness (LSR) and Regional Species Richness (RSR) for 13 plant communities from 4 habitat types of France (coastal sand dunes, oceanic heathlands, alpine grasslands, lowland calcareous grasslands). Each habitat type was split in 3-4 communities using multivariate analyses to identify the relative importance of stress, disturbance, competition, and facilitation functioning within the 13 communities. We found that the LSR/RSR relationship was highly dependent on environmental conditions with saturated communities occurring more frequently than unsaturated communities highlighting the relative importance of local drivers on species richness. We argued that competition was most likely the main source of community saturation whilst facilitation likely contributed to enhancing the importance of the regional species pool for all habitat types. However, the effect of facilitation might be stronger in the disturbed than in the stressed systems because unsaturated curves were only observed in the former conditions. In extreme conditions of disturbance LSR was only controlled by the intensity of disturbance. This effect was not observed in extreme stress conditions. Our study provides support for the emerging balance theory that both local and regional processes are important in nature with their relative contribution depending on environmental conditions. Additionally, this synthesis strongly suggests that facilitation contributes to an important process - the influence of regional species pool on local species richness.

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1 **Competition, facilitation and environmental severity shape the relationship**  
2 **between local and regional species richness in plant communities**

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27

## 28 **Abstract**

29 Understanding the relative contribution of local and regional processes to local species  
30 richness is an important ecological questions and a subject of controversy between  
31 macroecologists and community ecologists. We test the hypothesis that the contribution of  
32 local and regional processes is dependent on environmental conditions and that the effect of  
33 regional processes should be the highest in communities from intermediate positions along  
34 environmental severity gradients due to the importance of facilitation. We used the recently  
35 developed log-ratio method to analyze the relationship between Local Species Richness  
36 (LSR) and Regional Species Richness (RSR) for 13 plant communities from 4 habitat types of  
37 France (coastal sand dunes, oceanic heathlands, alpine grasslands, lowland calcareous  
38 grasslands). Each habitat type was split in 3-4 communities using multivariate analyses to  
39 identify the relative importance of stress, disturbance, competition, and facilitation  
40 functioning within the 13 communities. We found that the LSR/RSR relationship was highly  
41 dependent on environmental conditions with saturated communities occurring more  
42 frequently than unsaturated communities highlighting the relative importance of local drivers  
43 on species richness. We argued that competition was most likely the main source of  
44 community saturation whilst facilitation likely contributed to enhancing the importance of the  
45 regional species pool for all habitat types. However, the effect of facilitation might be  
46 stronger in the disturbed than in the stressed systems because unsaturated curves were only  
47 observed in the former conditions. In extreme conditions of disturbance LSR was only  
48 controlled by the intensity of disturbance. This effect was not observed in extreme stress  
49 conditions. Our study provides support for the emerging balance theory that both local and  
50 regional processes are important in nature with their relative contribution depending on  
51 environmental conditions. Additionally, this synthesis strongly suggests that facilitation

- 52 contributes to an important process - the influence of regional species pool on local species
- 53 richness.

## 54 **Introduction**

55 The contribution of different ecological filters or processes to local community composition  
56 and richness has been an important goal in ecology (Elton 1946, McArthur 1965, Ricklefs  
57 1987) and it is also a current topic of debate and controversy (Huston 1999, Lawton 1999,  
58 Loreau 2000, Lortie et al. 2004, Ricklefs 2008, Brooker et al. 2009, Vellend 2010, Cornell  
59 and Harrison 2013). After a long period of opposition between the two extreme views that  
60 community structure is primarily driven either by local more deterministic processes,  
61 competition and environmental conditions (Grime 1973, Tilman 1982), or by regional more  
62 stochastic processes related to dispersion, biogeography and species evolution (Ricklefs 1987,  
63 2008, Lawton 1999), a more balanced perspective is now emerging that both types of  
64 processes are important in all communities with their relative contribution depending on scale  
65 and environmental conditions (Huston 1999, Foster et al. 2004, Chase 2007, 2010, Brooker et  
66 al. 2009, Lepori and Malmqvist 2009, Michalet and Touzard 2010, Qian et al. 2013, Guo et al.  
67 2014). For example, the composition of experimental pond communities was found to be  
68 more influenced by deterministic than stochastic effects in severe compared to benign  
69 environmental conditions (Chase 2007). Similarly, stochastic priority effects increased with  
70 increasing productivity and diversity of the same communities (Chase 2010). Guo et al.  
71 (2014) also found in salt marsh communities that deterministic processes were more  
72 important in conditions of either high competition or high stress and that stochastic processes  
73 were important in more species-rich communities. In contrast, Lepori and Malmqvist (2009)  
74 found more deterministic macroinvertebrate stream communities at intermediate disturbance  
75 level. Consequently, current knowledge suggests that the relative importance of local more  
76 deterministic and regional more stochastic processes changes along environmental gradients.

77           The traditional approach to testing the relative importance of regional and local  
78 processes for local community richness consists of plotting local species richness (LSR)  
79 against regional species richness (RSR) (Terborgh and Faaborg 1980, Ricklefs 1987, Cornell  
80 and Lawton 1992, Pärtel et al. 1996, Srivastava 1999, Hillebrand and Blenckner 2002, Cornell  
81 et al. 2008, Cornell and Harrison 2013). When local richness is controlled by regional  
82 processes LSR linearly increases with increasing RSR because local communities are  
83 unsaturated with species. In contrast, when local richness is controlled by local processes LSR  
84 tends to an upper asymptote because local communities are saturated with species (Ricklefs  
85 1987). Most reviews of the literature demonstrate that unsaturated curves are much more  
86 common than saturated ones (Pärtel et al. 1996, Cornell et al. 2008, Harrison & Cornell 2008,  
87 Cornell and Harrison 2013), although several authors using other approaches concluded that  
88 local deterministic factors are sometimes more important (Casanovas et al. 2013, Richgels et  
89 al. 2013, Schils et al. 2013, Zhang et al. 2013). However, the use of this LSR/RSR  
90 relationship to infer the relative importance of local and regional community assembly  
91 processes has been strongly criticized for many reasons, including pseudoreplication and  
92 autocorrelation effects, the selection of communities, the species pool definition, the  
93 appropriate areas for richness measurements and the body size of organisms (Srivastava 1999,  
94 Loreau 2000, Shurin et al. 2000, Hillebrand and Blenckner 2002, Hillebrand 2005, Lessard et  
95 al. 2012, Wang et al. 2012, Szava-Kovats et al. 2012).

96           Szava-Kovats et al. (2012) proposed a new method based on log-ratio models that  
97 allow circumvent most statistical artefacts of the traditional method. In this method the  
98 unsaturated curve is a horizontal line (type 1 curve with zero slope in Fig. 1) resembling the  
99 relationship between LSR and RSR-LSR at the log-scale, whereas the saturated curve has a  
100 steep negative slope (type 2 curve, Fig. 1). Gonçalves-Souza et al. (2013) and Szava-Kovats  
101 et al. (2013) applied this new method and found via independent meta-analyses consistent

102 contradictions to the general consensus detected using the traditional approach. They both  
103 found that more than a third of the communities were misclassified in original studies and that  
104 saturated relationships were at least as common as unsaturated patterns, although Szava-  
105 Kovats et al. (2013) also found intermediate and indeterminate curves. The primary  
106 implication is that this new method should replace the traditional approach in subsequent  
107 contrasts of local versus regional drivers.

108         Although there is increasing evidence that the contribution of both local deterministic  
109 and regional stochastic processes to local community richness is dependent on environmental  
110 conditions, to the best of our knowledge there are only two studies that directly tested this  
111 hypothesis using the (traditional) LSR/RSR method (Huston 1999, Pärtel et al. 2000). Based  
112 on the humped-back model of species richness along net primary productivity gradient  
113 (Huston 1979) and the related model of Grime (1973), Huston (1999) proposed that  
114 communities should be saturated in conditions of low and high productivity due to local  
115 processes related to abiotic limitations (stress and disturbance) and competition, respectively,  
116 but that the size of the regional species pool should influence richness under conditions of  
117 intermediate productivity. The dataset of Pärtel et al. (1996) on Estonian plant communities  
118 was used to test this hypothesis splitting the LSR/RSR relationship into two curves, one for  
119 stressful species-rich communities (mostly calcareous grasslands and dry forests) and one for  
120 species-poor communities from benign environmental conditions. These findings supported  
121 this hypothesis with an unsaturated curve for the stressful communities and a saturated curve  
122 for the communities most likely to be structured by competition. Pärtel et al. (2000)  
123 confirmed the prediction of Huston (1999) using an enlarged dataset including 27  
124 communities instead of 14 in the Huston's (1999) study. However, these relationships have  
125 been criticized because of the inclusion of different habitats and communities within the same  
126 relationship (Srivastava 1999, Lawton 1999). The first objective of the study herein is to test

127 with the log-ratio method of Szava-Kovats et al. (2012) and Huston's (1999) hypothesis that  
128 competition and environmental severity (stress and disturbance) should enhance the saturation  
129 of LSR/RSR relationships. We also test the corollary that unsaturated communities are more  
130 likely to be observed at mid position along environmental severity gradients where species  
131 richness is known to be the highest because of intermediate level of competition, stress and  
132 disturbance (Grime 1973, Huston 1979). This would only be the third study to date on this  
133 topic and the first to use the new analytical method. We will also be careful not to mix broad  
134 habitat types as in the former test of this hypothesis.

135         Most predictions associated with the effect of local biotic processes on the regional  
136 and local species richness relationships are based on theoretical models primarily (and  
137 sometimes exclusively) including negative interactions (competition and predation) in  
138 ecological communities (Elton 1946, McArthur 1965, Grime 1973, Huston 1979, Tilman  
139 1982). However, positive interactions are now recognized as important driving forces of local  
140 communities, in particular in severe environmental conditions (Bertness and Callaway 1994,  
141 Callaway 1995) and facilitation has been included in mainstream ecological theory (Bruno et  
142 al. 2003, Schöb et al. 2012, McIntire and Fajardo 2014). Michalet et al. (2006) revisited the  
143 humped-back model of Grime (1973), including the role of facilitation for species richness  
144 (also see Xiao et al. 2009, Le Bagousse-Pinguet et al. 2014a). This body of emerging  
145 literature proposed that facilitation should peak at intermediate position along environmental  
146 severity gradient and thus contribute to the high species richness observed at this point of the  
147 humped-curve of Grime (1973). With increasing environmental severity beyond this point,  
148 facilitation should collapse and species richness decreases because the effects of nurse species  
149 are reduced by high stress and/or high disturbance, as demonstrated by several experimental  
150 studies (e.g. Le Bagousse-Pinguet et al. 2014b). Since facilitation is now considered as mainly  
151 occurring at intermediate position along environmental severity gradients (Michalet et al.

152 2006, Holmgren and Scheffer 2010, Verwijmeren et al. 2013, but see He et al. 2013) and as  
153 enhancing diversity in opposition to competition and environmental severity, we argue that  
154 facilitation might also contribute to shaping the regional vs local species richness relationship.  
155 Facilitation may act as an attractive force for species and increase the contribution of RSR to  
156 LSR in species-rich sink communities (*sensu* Mouquet and Loreau 2003) at intermediate  
157 position along the humped-back model of Grime (Fig. 1).

158 In order to test the competition/environmental severity effect hypothesis proposed by  
159 Huston (1999) and the facilitation hypothesis that we proposed herein, we chose to examine  
160 LSR/RSR relationships for communities located at different positions along the humped-back  
161 curve of Grime (1973). This test was conducted for four different habitat types located in four  
162 regions from France exhibiting contrasting regional species pools (coastal sand dunes, mesic  
163 heathlands and grasslands from acidic substrates, high-elevation grasslands and lowland  
164 calcareous grasslands). Disturbance and stress are the predominant drivers of species turnover  
165 within the first two, and the latter two habitat types, respectively (Forey et al. 2008, Clément  
166 1978, Choler and Michalet 2002, Royer 1987). We make the following predictions (Fig. 1):  
167 (i) with high competition or high physical stress or disturbance LSR/RSR relationship should  
168 show a saturated curve (type 2 curve, Huston's 1999 hypothesis), (ii) with high facilitation at  
169 mid-position along environmental severity gradients LSR/RSR relationship should show an  
170 unsaturated curve (type 1 curve, facilitation hypothesis).

171

## 172 **Materials and methods**

### 173 *Habitat types and preparation of data*

174 We selected four different habitat types located in four regions from France (Fig. 2). Each  
175 region has a regional species pool adapted to a particular set of environmental conditions.  
176 Coastal sand dunes communities are subjected to drought, nutrient stress, sand deposition and  
177 acidic soils (Forey et al. 2008). Nutrient stress is high and soils acidic in oceanic heathlands  
178 and grasslands but there is no physical stress (Clément 1978). Alpine communities are  
179 subjected to high cold and nutrient stress (Choler and Michalet 2002), and calcareous  
180 grasslands from the Jura range to drought and nutrient stress (Royer 1987). The geographical  
181 extent of each area is very similar, i.e. approximately 200 to 250 km-long and 100 to 150 km-  
182 wide, except the coastal sand dune region which has a very narrow width, i.e. less than 1 km  
183 (Fig. 2). All relevés were sampled using standardized phytosociological methodology (Braun-  
184 Blanquet 1932, Westhoff and van der Maarel 1978) with a relevé area of approximately 25-  
185 100 m<sup>2</sup>, depending on the minimum area of the target community.

186         The coastal sand dunes of Aquitaine include 2433 unpublished relevés sampled by the  
187 French National Forest Office in both 1997 and 1998. Relevés were located at sea level along  
188 94 W-E transects expanding every 20 km from the southern part of the Aquitaine dunes to its  
189 northern part. Differences in species composition across communities from this habitat type  
190 have been shown to be first driven by the level of disturbance induced by sand deposition  
191 (increasing towards the ocean), and second by the contrasted species pools of northern and  
192 southern dunes (Forey et al. 2008). This is a highly stressed ecological system due to water  
193 and nutrient limitations induced by the coarse texture of the sand (Forey et al. 2008). The  
194 oceanic heathlands and grasslands from Brittany include 666 relevés sampled throughout  
195 French Brittany by different authors between 1977 and 1995 (Forgeard 1977, Clément 1978,  
196 Clément et al. 1978, Gloaguen 1988, Wattez and Godeau 1986, de Foucault 1993, Wattez and  
197 Wattez 1995). Physical stress is low in this low elevation oceanic region (up to 387 m asl)  
198 characterized by heavy rainfall and low maximum summer temperatures, but nutrient stress is

199 high and soils are acidic (Aerts et al. 1990). The main ecological factor driving species  
200 composition in this ecological region is the level of human-induced disturbance generally  
201 related to the depth of the groundwater, with the least disturbed communities in the wettest  
202 and most anaerobic conditions (Clément 1978). For the French Alps region, we used a dataset  
203 of 2681 relevés assembled from a large survey of the grey literature (see Choler and Michalet  
204 2002 for details on this dataset) and completed in the recent period by the Conservatoire  
205 Botanique National Alpin. The vegetation relevés include subalpine grasslands and alpine  
206 meadows ranging from 1800 to 3000 m asl. The main ecological factors driving differences in  
207 species composition are mesotopography and elevation, with the most stressful communities  
208 located on convex topography at high elevation (Choler and Michalet 2002). The calcareous  
209 grasslands from the Jura region include 1250 relevés mostly sampled by Royer (1987)  
210 between 200 and 1600 m asl throughout the Jura massif. All relevés are located on calcareous  
211 substrates and overall characterized by moderate drought and nutrient stress due to the high  
212 porosity of the calcareous rocks. The main ecological factor driving differences in species  
213 composition in this region is the water availability related to soil depth itself depending on  
214 exposure, substrate type and topography (Royer 1987, Michalet et al. 2002).

215 We initially performed a Correspondence Analysis for each habitat type to identify the  
216 main axes of floristic variation. Rare species (frequency lower than 1% of the data set) were  
217 excluded before running the ordination. The underlying environmental factors driving floristic  
218 variations along the first ordination axis were easily identified since the four habitat types  
219 were each formerly studied for community types classifications using multivariate analyses  
220 and environmental measurements. The correspondence with those former studies was in  
221 particular made using the frequency and cover of dominant species along ordination axes, as  
222 well as information on community biomass (Table 1). We then plotted for each habitat type  
223 the species richness of the relevés against their scores on the CA axis 1 (Fig. 3). For the four

224 independent habitat types, we found a significant humped-back curve relating species richness  
225 and environmental severity, consistent with Grime (1973), but with different environmental  
226 severity factors depending on the habitat type. In both the coastal sand dunes and the oceanic  
227 heathlands and grasslands from Brittany the main source of variation in species composition  
228 (also structuring our relevés on the CA axes 1) is the level of disturbance (*sensu* Grime 1973),  
229 either induced by sand deposition in the former (Forey et al. 2008), or by human activities  
230 (mostly grazing or mowing) in the latter (Clément 1978). In alpine grasslands, the floristic  
231 turnover is associated with a gradient of low temperature stress that is mostly controlled by  
232 the snow cover duration, in relation with variation in mesotopography (Choler et al. 2001). In  
233 calcareous grasslands from Jura the main source of variation in species composition is the  
234 level of drought (and nutrient) stress induced by soil depth and topography (Royer 1987).

235         For each habitat type we split the relevés into three groups (four in the dunes) based on  
236 their CA axis 1 scores and positions on the humped-back curve (Fig. 3). Indeed, these three  
237 (or four) groups/community types correspond to three levels of environmental severity at  
238 three different positions along the humped-back curve, consistent to Grime (1973). In the  
239 benign part of the curves for all habitat types (left side of the curves), species richness  
240 increases with increasing environmental severity (Fig. 3). In the intermediate part of the  
241 curves occurs the maximum of species richness (intermediate environmental severity). In the  
242 severe part of the curves (right side of the curves), species richness decreases with increasing  
243 environmental severity (Fig. 3). In the dunes we separated the most severely disturbed dune  
244 communities in two subgroups due to good knowledge of the plant interactions occurring in  
245 this habitat type (Forey et al. 2010). We used the literature on plant interaction experiments in  
246 these four different habitat types to assign a dominant plant interaction characterizing each of  
247 the 3 (or 4) groups of each habitat type (see Table 1). For the coastal dunes, the experiment of  
248 Forey et al. (2010) conducted on four target species in four communities along the sand

249 deposition gradient clearly showed that facilitation occurs in the weakly disturbed community  
250 (the grey dune in Table 1) but collapses in the most disturbed communities (corresponding to  
251 the white dune and foredune in Table 1), due to extreme level of disturbance in these stressful  
252 conditions (see also Le Bagousse-Pinguet et al. 2013). Our dataset also includes grey dune  
253 shrub thickets for which we do not have information on the interactions occurring in this least  
254 disturbed community (Table 1). For the acidic heathlands and grasslands there is, to our  
255 knowledge, no specific information on plant interactions in French Brittany. However, the  
256 importance of competition in acidic and nutrient-poor heathlands has been shown by several  
257 studies conducted in very similar areas in the Netherland and UK (Aerts et al. 1990, Brooker  
258 et al. 2006, Bullock 2009). Additionally, Brooker et al. (2006) have shown that indirect  
259 facilitation due to protection against herbivores may occur in grazed heathlands and collapse  
260 in heavily grazed communities (Table 1). For the alpine grasslands, the experiment of Choler  
261 et al. (2001) conducted in six communities with five target species per community showed  
262 that competition was dominant in the most benign part of the curve and that facilitation was  
263 dominant at mid position along the gradient and in the most severe environmental conditions.  
264 However, for this habitat type facilitation may alternatively collapse in the most stressful  
265 conditions of the curve, in particular with the addition of disturbance, as shown by Le  
266 Bagousse-Pinguet (2014b) in the French Pyrenees. For the calcareous grasslands, the  
267 experiments of Corcket et al. (2003) and Liancourt et al. (2005a, b) on communities from  
268 contrasted water availabilities showed similar results than in the alpine grasslands, with  
269 competition in benign environmental conditions and facilitation at mid-position along the  
270 gradient. However, we do not have information on the possible interactions occurring in the  
271 driest conditions in this region and results of Maalouf et al. (2012a) from the Périgord Region,  
272 a drier southern region from France, indicate that facilitation may collapse in the most  
273 stressful conditions with the addition of high physical disturbance.

274

275 *Data analysis*

276 For three of the four habitat types, alpine grasslands, calcareous grasslands and coastal dunes,  
277 relevés were homogeneously distributed at the geographical scale. Each of those three regions  
278 was thus latitudinally divided into 9 subregions of approximately similar areas. The oceanic  
279 heathlands and grasslands habitat type had fewer relevés concentrated within 7 disparate  
280 subregions. Those 7 subregions thus determined regional divisions for further analyses in this  
281 habitat type. All community types related to a habitat type in particular were present in all the  
282 subregions delimited inside the region of the habitat type. For each habitat type, inside each  
283 subregion, and for each community type, we computed the Chao1 nonparametric estimation  
284 of species richness (Chao 1984) as recommended by Cornell et al. (2008) i) at the regional  
285 scale (RSR, cumulated Chao1 species richness across relevés) and ii) at the local scale (LSR,  
286 averaged Chao1 species richness across relevés). The Chao diversity estimates were all done  
287 using abundance, and not presence/absence matrices. For each community within each  
288 subregion, the chao species diversity was estimated per relevé, borrowing information  
289 provided by the other relevés in the pool. Then the Chao indices were averaged across relevés  
290 in each pool to provide values of LSR (one value per pool). Thus, there were a total of 111  
291 independent estimations of RSR and LSR (3 community types x 7 subregions in the oceanic  
292 heathlands) + (3 community types x 9 subregions in the alpine grasslands) + (3 community  
293 types x 9 subregions in the calcareous grasslands) + (4 community types x 9 subregions in the  
294 coastal dunes).

295 For each habitat type, the effects of RSR on LSR by community were assessed using  
296 an analysis of covariance (ANCOVA) model. We used the log-ratio method of Szava-Kovats  
297 et al. (2012):  $\ln(\text{LSR}/(\text{RSR}-\text{LSR}))$  was used as the dependent variable and  $\ln(\text{RSR})$  as the

298 covariate. Community type was introduced as a categorical independent variable (low,  
299 intermediate, high and very high disturbance levels for coastal dunes; low, intermediate and  
300 high disturbance levels for oceanic heathlands and grasslands; low, intermediate and high  
301 stress levels for Alpine and calcareous grasslands). A significant covariate/community type  
302 interaction indicates significant differences in saturation among communities. Furthermore,  
303 slope significance was tested inside each region and p-values were penalized using Holm's  
304 method (Holm 1979). We also checked slope departures from -1 examining if their 95%  
305 confidence intervals included the -1 value or not. Following Gonçalves-Souza et al. (2013)  
306 significant negative slopes represent saturated communities (i.e. mainly shaped by local  
307 processes), whereas insignificant slopes depict unsaturated communities (i.e. strongly  
308 dependent on the regional species pool). If the upper limits of confidence intervals associated  
309 to significant slopes were higher than -1, slopes were considered as "intermediate".  
310 Parametric model assumptions were met for all of the 4 ANCOVA models.

311         In order to assess how the arbitrary limits chosen along CA axes for partitioning our  
312 four habitats in discrete communities might have influenced our results we also calculated  
313 LSR/RSR slopes for communities captured by a sliding window (see Supplementary material  
314 1 for methods and results). Additionally, in order to assess how varying number of relevés  
315 among communities might have affected our results, the relationship between local and  
316 regional Chao1-approximated species richness was also made for the four different habitat  
317 types but considering 8 plots randomly sampled inside each community within each subregion  
318 of each habitat (see Supplementary material 2 for results). Both additional analyses produced  
319 very similar results (see Supplementary materials 1 and 2). All statistical analyses were done  
320 using R Software for Statistical computing (version 3.1.0, the R Core Team, 2014).

321

## 322 **Results**

323 For the coastal sand dunes there was a significant covariate/community type interaction with  
324 strong differences in slopes between the two least disturbed communities on the one hand and  
325 the two most disturbed ones on the other hand ( $p < 0.05$ , Fig. 4a and see Supplementary  
326 material 3 for p values). The two least disturbed communities, i.e. the grey dunes, had  
327 unsaturated curves (non significant slopes at  $p > 0.05$  and see Supplementary material 4 for p  
328 values), whereas the two most disturbed communities had saturated curves (significant  
329 negative slopes:  $p < 0.05$  for the high-disturbance community and  $p < 0.001$  for the very high-  
330 disturbance community). In contrast, for the oceanic heathlands and grasslands there was no  
331 significant covariate/community type interaction. However, the low- and high-disturbance  
332 communities had saturated curves ( $p < 0.001$  for both), whereas the intermediate disturbance  
333 community had an unsaturated curve (non significant slope, Fig. 4b).

334 For the alpine grasslands the covariate/community type interaction was significant ( $p$   
335  $< 0.05$ , Fig. 4c) because the low-stress community had a steeper negative slope than the  
336 intermediate- and high-stress communities. However, all three curves were highly  
337 significantly saturated ( $p < 0.001$ , Fig. 4c). Similar to the alpine grasslands, the calcareous  
338 grasslands had a highly significant covariate/community type interaction ( $p < 0.001$ , Fig. 4d)  
339 likewise due to a much steeper negative slope for the low-stress community than for the two  
340 other communities within this habitat type. The low- and high-disturbance curves were highly  
341 significantly saturated ( $p < 0.001$  for both), whereas the intermediate curve was only weakly  
342 significantly saturated ( $p < 0.05$ , Fig. 4d).

343

## 344 **Discussion**

345 Here, we tested the hypothesis that the contribution of local and regional processes is  
346 dependent on environmental conditions, and more specifically, that plant facilitation enhances  
347 the effect of regional processes at the intermediate positions along environmental severity  
348 gradients. A refined understanding of relative importance of these different drivers promotes  
349 more effective management and research in both macro and community ecology. We found a  
350 strong dependency of the LSR/RSR relationship on environmental conditions for the four  
351 habitat types with support for environmental condition dependency. In benign environmental  
352 conditions where competition is the dominant interaction (low disturbance in oceanic  
353 heathlands and low stress in both alpine grasslands and calcareous grasslands), communities  
354 were strongly saturated with steep curves and highly significant negative slopes. At  
355 intermediate positions along environmental severity gradients, where facilitation is the  
356 dominant interaction (low disturbance in coastal sand dunes, intermediate disturbance in  
357 oceanic heathlands and intermediate stress in both alpine grasslands and calcareous  
358 grasslands), communities were less saturated and even significantly unsaturated in the dunes  
359 and oceanic heathlands. In the most severe environmental conditions of the four habitat types,  
360 results were less homogenous with saturated communities only in the most disturbed  
361 conditions of both the coastal dunes and oceanic heathlands. However, we also detected  
362 patterns that did not support our first prediction. In the most stressful conditions of both the  
363 alpine and calcareous grasslands, communities did not become more saturated than at  
364 intermediate position along the stress gradients.

365 Most communities were saturated with only three cases of unsaturated communities of  
366 13 tested LSR/RSR relationships (i.e. 23%). Although our main goal was not to test the  
367 hypothesis that saturated curves are more common in plant communities than unsaturated  
368 curves, our study including contrasting habitat types from four different regions further  
369 divided in three to four community types of specific environmental conditions, clearly shows

370 the predominant role of local over regional processes for local species richness. The ubiquity  
371 of linear relationships between local and regional species richness has long been used to  
372 conclude that unsaturated communities are by far more common than saturated communities  
373 due to the prevalence in nature of regional over local processes for local species richness  
374 (Lawton 1999, Loreau 2000, Hillebrand 2005, Harrison and Cornell 2008, Cornell and  
375 Harrison 2013). However, this conclusion was in part influenced by the use of an  
376 inappropriate method. Thus, with the log-ratio method proposed by Szava-Kovats et al.  
377 (2012), Szava-Kovats et al. (2013) and Goncalves-Souza et al. (2013) found that saturated  
378 relationships were at least as common as unsaturated patterns. Szava-Kovats et al. (2013) also  
379 found that large proportion of studies produce no discernable patterns. Additionally,  
380 Gonçalves-Souza et al. (2013) argued that instead of focusing solely on local/regional  
381 richness plots to infer processes from patterns, additional approaches should be used to really  
382 understand the drivers of local community structure. In particular, they stressed the usefulness  
383 to add in the analyses observational information on local environmental and dispersal  
384 processes, as commonly used in meta-community studies (Cottenie 2005). In our study, we  
385 hypothesized that the saturation level of communities should be dependent on environmental  
386 conditions similar to the work of Huston (1999), and we thus indirectly controlled the effect  
387 of varying environmental conditions through our partition of the four habitat types along  
388 multivariate axes driven either by the level of stress or disturbance. It is likely that the large  
389 proportion of significantly saturated curves found in our study, as compared to the meta-  
390 analyses of Szava-Kovats et al. (2013) and Gonçalves-Souza et al. (2013) is related to the way  
391 we partitioned the data, i.e. along the main axis of floristic variation, and its ability to capture  
392 distinct environmental conditions. In other words, the mixing of different environmental  
393 conditions characterizing saturated and unsaturated communities within a single relationship  
394 certainly increases the probability of finding indeterminate curves. However, the high

395 proportion of saturated curves found in our study may also be due to the limitation of our  
396 analyses to terrestrial plant communities, as compared to meta-analyses including all  
397 organisms from both marine and terrestrial environments (Witman 2013, Cornell and  
398 Harrison 2013). Additionally, our results might have been influenced by the rather small  
399 spatial grain size used in this study. Most macroecological analyses use large grid cells (e.g.  
400 100 x 100 km size) whereas fine-grained analyses are rather rare.

401         In most macroecology studies assessing the importance of local vs. regional drivers of  
402 local species richness competition, predation and parasitism (i.e. negative interactions) are  
403 presented as the primary local factors likely to counteract the influence of regional processes  
404 for local richness (McArthur 1965, Lawton 1999, Loreau 2000, Foster et al. 2004, Cornell et  
405 al. 2008, Burgess et al. 2010, Cornell & Harrison 2013). The importance of plant-plant  
406 competition for local species richness is indeed one of the most important tenets of traditional  
407 community ecology (Grime 1973, Huston 1979, Huston 1999, Fridley et al. 2012) and several  
408 observational and experimental studies have shown the occurrence at local scale of a tight  
409 correlation between community biomass, the intensity of competition and species richness (Al  
410 Mufti et al. 1977, Keddy et al. 1997, Foster and Gross 1998, Michalet et al. 2002, Maalouf et  
411 al. 2012b, Maron et al. 2014). However, other authors have also observed that the occurrence  
412 of competition has no predictable consequences for plant community diversity (Lamb and  
413 Cahill 2008, Mitchell et al. 2009). In our study the first source of community saturation was  
414 the occurrence of competition. In three of the four studied habitat types (oceanic heathlands,  
415 alpine grasslands and calcareous grasslands) the steepest negative slope and thus strongest  
416 community saturation level was found in the most benign environmental conditions where  
417 community biomass is the highest and competition known to be the dominant interaction  
418 (Aerts et al. 1990, Choler et al. 2001, Liancourt et al. 2005a). In contrast, in the most benign  
419 environmental conditions of the fourth habitat type, the grey dune shrub thickets, we did not

420 find an increase in saturation as compared to the intermediately disturbed dunes. This result is  
421 likely due to the very harsh drought and nutrient stresses occurring in this sandy habitat type  
422 which impedes the occurrence of a competition strong enough to affect the LSR/RSR  
423 relationship, even in the absence of disturbance (Huston 1979). However, we do not have  
424 information from the literature on the type of interactions dominating in this specific  
425 community.

426         Although positive interactions such as mutualism have been early thought as local  
427 processes potentially contributing to local species richness (Ricklefs 1987), to our knowledge  
428 facilitation has been rarely proposed as a potential mechanism for shaping the LSR/RSR  
429 relationship (but see Szava-Kovats et al. 2013). This is quite surprising since facilitation has  
430 been included in mainstream ecological theory for two decades (Bertness and Callaway 1994,  
431 Callaway 1995, Bruno et al. 2003, Lortie et al. 2004, Brooker et al. 2008, 2009, Schöb et al.  
432 2012, McIntire and Fajardo 2014, Soliveres et al. 2014) and has even been proposed as an  
433 important mechanism enlarging species niches (or more accurately species' habitats),  
434 suggesting its important role for local species richness (Hacker and Gaines 1997, Bruno et al.  
435 2003, Michalet et al. 2006, Xiao et al. 2009, Le Bagousse-Pinguet et al. 2014a). Lortie et al.  
436 (2004) have proposed that positive interactions and mutualism act as local filters increasing  
437 the chance of inhabiting a local community for species from the regional species pool, in  
438 opposition to other filters deleting species such as negative interactions or environmental  
439 severity. Michalet et al. (2006) proposed a model where the positive effect of facilitation for  
440 diversity peaks at mid-position along the humped-back diversity-community biomass model  
441 (see also Xiao et al. 2009 and Le Bagousse-Pinguet et al. 2014a) and thus could contribute to  
442 shaping the relationship between local species richness and environmental severity proposed  
443 by Grime (1973) and Huston (1979). Thus, we made herein the hypothesis (2) that facilitation  
444 should contribute to shaping the regional vs. local species richness relationship, and in

445 particular to increase the contribution of RSR to LSR in species-rich sink communities (*sensu*  
446 Mouquet and Loreau 2003) at intermediate position along the humped-back model of Grime  
447 (1973). Our results supported this hypothesis; for the four habitat types the curves had the  
448 most gentle or even non-significant slopes at mid position along environmental severity  
449 gradients where facilitation has been shown to be the highest in several experimental studies  
450 conducted in the same ecological systems (Choler et al. 2001, Liancourt et al. 2005a, b,  
451 Brooker et al. 2006, Forey et al. 2010). Interestingly, the two most unsaturated communities  
452 with non-significant slopes were found for the two habitat types structured by disturbance  
453 (coastal dunes and oceanic heathlands and grasslands), whereas for the two other habitat types  
454 structured by stress (alpine and calcareous grasslands) the slopes were still significant and  
455 indicating saturated communities. This may be due to the contrasted functional strategies of  
456 the species involved along gradients of disturbance or stress, with more ruderal species with  
457 high dispersal abilities in the former and more stress-tolerant species with low dispersal  
458 abilities in the latter (Grime 1973). Pärtel and Zobel (2007) have shown that species  
459 functional composition may affect the productivity-diversity relationship through changes in  
460 dispersal ability. This effect is very likely to also influence community saturation. The strong  
461 regional effect observed in the grey dunes was maybe also due to the very linear geographic  
462 structure of the region of this habitat type (width < 1 km), enhancing dispersal effects on  
463 species richness (Forey et al. 2008). We have to design experiments allowing a  
464 straightforward assessment of the effect of facilitation on community saturation suggesting by  
465 our study, since we did not separate the facilitation hypothesis from a neutral model. We may  
466 compare LSR/RSR relationships of ecological regions with similar environmental conditions  
467 but contrasting importance of facilitation, due for example to the absence of potential nurse  
468 species in the region without facilitation.

469           Michalet et al. (2006) proposed that facilitation should collapse in extreme conditions  
470 of either stress or disturbance (*sensu* Grime 1973) because nurse plants might no more be able  
471 to ameliorate the physical conditions for their protégés, with local species richness mostly  
472 dependent on the environment in these extreme conditions consistent to Grime (1973) and  
473 Huston (1979). Interestingly, our results showed more saturated curves in extreme conditions  
474 of disturbance (foredunes and white dunes and oceanic grasslands) than at intermediate  
475 disturbance level, a result consistent with the collapse of facilitation and experimental  
476 evidence from the same habitat types (Brooker et al. 2006, Forey et al. 2010), but no  
477 important change in extreme conditions of stress (alpine and calcareous grasslands) as  
478 compared to conditions of intermediate stress. This suggests that facilitation can still  
479 contribute to enhancing local richness by adding species from the regional species pool in  
480 conditions of extreme stress as it does at intermediate stress level. Michalet et al. (2014)  
481 argued that the collapse of facilitation is due to a change in the effect of the nurse species  
482 which is more likely to occur along disturbance than stress gradients. Indeed, if the  
483 importance of either competition or facilitation is still discussed in extreme conditions of  
484 nutrient (Tilman 1982) or water stresses (Maestre and Cortina 2004), there is a consensus  
485 within the interactions literature dating back to McArthur and Wilson (1967) who also  
486 proposed that biotic interactions can vanish in conditions of extreme disturbance.

487

## 488 *Conclusions*

489 Our study analyzing 13 LSR/RSR relationships in contrasting environmental conditions from  
490 four habitat types of France showed that the relative contribution of local and regional drivers  
491 of local species richness is highly dependent on environmental conditions, as proposed by  
492 Huston (1999), Foster et al. (2004) and Chase (2007, 2010). In this set of regional contrasts,

493 saturated communities were much more common than unsaturated communities, highlighting  
494 the importance of local processes that are often neglected in macroecology studies.  
495 Competition was the main source of community saturation limiting the influence of the  
496 regional species pool, as proposed by Huston (1999) and Foster et al. (2004). However, the  
497 main novelty of our correlative study was to strongly suggest that facilitation may inversely  
498 enhance the influence of the regional species pool at intermediate position along  
499 environmental severity gradients, although further studies should separate the facilitation  
500 hypothesis from a neutral model. Finally, we showed, at least along disturbance gradients, that  
501 the collapse of facilitation in extreme conditions of environmental severity also counteracts  
502 the influence of the regional species pool as it does in competitive environments. Other tests  
503 of LSR/RSR relationships similarly controlling for environmental conditions may further  
504 assess the contrasting effect of stress and disturbance, as well as analyze the influence of  
505 species functional strategies (in particular their dispersal abilities) and regional geographical  
506 structure and size.

507

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513

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- 717

718 **Figures legend**

719 **Figure 1.** Predicted relationships between regional (RSR) and local (LSR) species richness at  
720 three positions along environmental severity gradients. The three upper panels show the  
721 relationship between Ln RSR and Ln (RSR/(LSR-RSR)) in communities structured by  
722 competition (left: saturated curve, i.e. type 2 curve *sensu* Gonçalves-Souza et al. 2013),  
723 facilitation (center: unsaturated curve, i.e. type 1 curve *sensu* Gonçalves-Souza et al. 2013)  
724 and environmental severity (right: saturated curve). The lower panel shows the unimodal  
725 pattern of plant-plant interactions along environmental severity gradients (Michalet et al.  
726 2006) together with the unimodal pattern of species richness proposed by Grime (1973). In  
727 the lower panel, the four parts of the gradient (A1, A2, B1 and B2) correspond to increasing  
728 environmental severity levels and contrasted functional compositions of the communities, i.e.  
729 only competitive species, dominant competitive species, dominant stress-tolerant species and  
730 only stress-tolerant species, respectively; and see Michalet et al. (2006) for the precise legend  
731 of the lower panel.

732

733 **Figure 2.** Location of the four regions of the four habitat types in France.

734

735 **Figure 3.** The relationship between local species richness and environmental severity  
736 gradients for four different habitat types (coastal dunes and oceanic heathlands and grasslands  
737 exposed to disturbance gradients; alpine grasslands and calcareous grasslands exposed to  
738 stress gradients). For each habitat type, the severity gradient is integrated by the first axis of a  
739 correspondence analysis performed on species composition data of the plots (environmental  
740 severity increases from left to right for the four habitat types). Four communities (for coastal

741 dunes) and three communities (for each of the three other ecological regions) were selected  
742 according to their CA axis 1 scores and based on expert knowledge. Communities were  
743 separated by vertical dashed lines and labelled by different symbols (for each habitat type,  
744 filled circles represented communities occurring in the most benign environmental conditions  
745 and empty circles represented those located in the most severe ones). Curves represent  
746 quadratic model predictions for each habitat type. The color of the curves (black or white)  
747 was modified according to visibility. All quadratic effects were highly significant ( $p < 0.001$ ).

748

749 **Figure 4.** The relationship between local and regional Chao1-approximated species richness  
750 based on the log-ratio method (Szava-Kovats et al. 2012) for the four different habitat types.  
751 For each habitat type, different regression lines represent communities submitted to contrasted  
752 levels of environmental severity (disturbance in coastal dunes and oceanic heathlands and  
753 grasslands; stress in alpine grasslands and calcareous grasslands). Filled diamonds, filled  
754 triangles, empty circles and empty triangles represent communities submitted to low,  
755 intermediate, high and very high levels of environmental severity, respectively. Holm-  
756 corrected slope significances (i.e. community saturation) are reported in the figure legends. \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

758

759

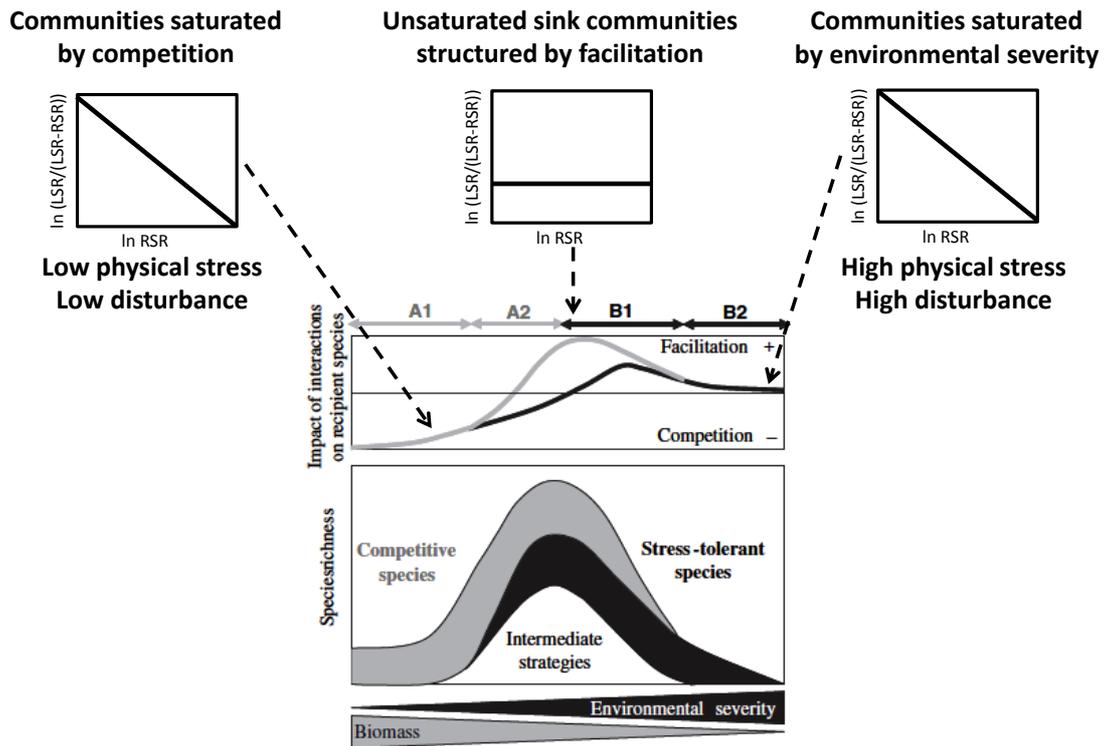
760 **Table 1.** Environmental severity level (either disturbance or stress *sensu* Grime 1973),  
 761 dominant species, aboveground biomass (with reference) and dominant interaction type (with  
 762 reference) of the 3-4 community types selected for each of the 4 habitat types.

Habitat type Communities	Environmental severity	Dominant species	Aboveground biomass g m <sup>-2</sup>	Reference	Interaction type	Reference
<b>Coastal dunes</b>						
<b>Disturbance</b>						
Grey dune thickets	Low	<i>Pinus pinaster</i>	> 300	Forey et al. 2008	?	
Grey dune	Intermediate	<i>Helichrysum stoechas</i>	200 + Lichens	Forey et al. 2008	facilitation	Forey et al. 2010
White dune	High	<i>Ammophila arenaria</i>	300	Forey et al. 2008	no interaction	Forey et al. 2010
Foredune	Very high	<i>Elymus farctus</i>	50	Forey et al. 2008	no interaction	Forey et al. 2010
<b>Heathlands</b>						
<b>Disturbance</b>						
Heathlands	Low	<i>Erica spp.</i> + <i>Calluna vulgaris</i>	> 1500	Clément 1978	Competition	Aerts et al. 1990
Intermediate	Intermediate	<i>Ulex spp.</i>	1000-1500	Clément 1978	Indirect facilitation	Brooker et al. 2006
Mesic grasslands	High	<i>Agrostis tenuis</i>	< 1000	Clément 1978	Weak indirect facilitation	Brooker et al. 2006
<b>Alpine grasslands</b>						
<b>Stress</b>						
Mesic grasslands	Low	<i>Nardus stricta</i>	> 600	Michalet et al. 2002	Competition	Choler et al. 2001
Intermediate	Intermediate	<i>Sesleria coerulea</i>	300-600	Michalet et al. 2002	Facilitation	Choler et al. 2001
Dry grasslands	High	<i>Carex myosuroides</i>	< 300	Michalet et al. 2002	Facilitation	Choler et al. 2001
<b>Calcareous grasslands</b>						
<b>Stress</b>						
Mesic grasslands	Low	<i>Brachypodium pinnatum</i>	> 600	Liancourt et al. 2005	Competition	Liancourt et al. 2005
Intermediate	Intermediate	<i>Bromus erectus</i>	300-600	Liancourt et al. 2005	Facilitation	Liancourt et al. 2005
Dry grasslands	High	<i>Festuca ovina</i>	< 300	Maalouf et al. 2012	?	

763

764

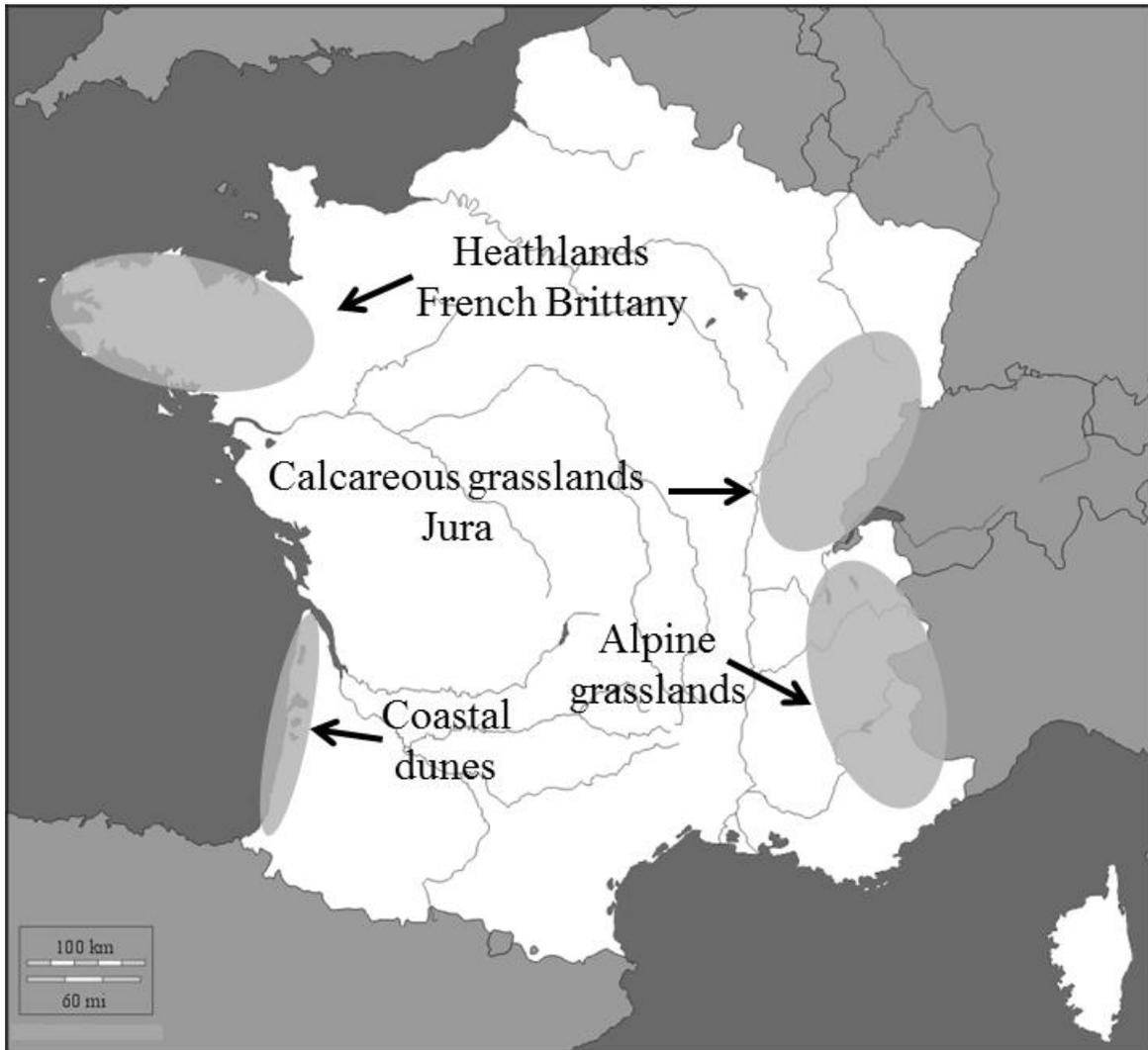
765 **Figure 1**



766

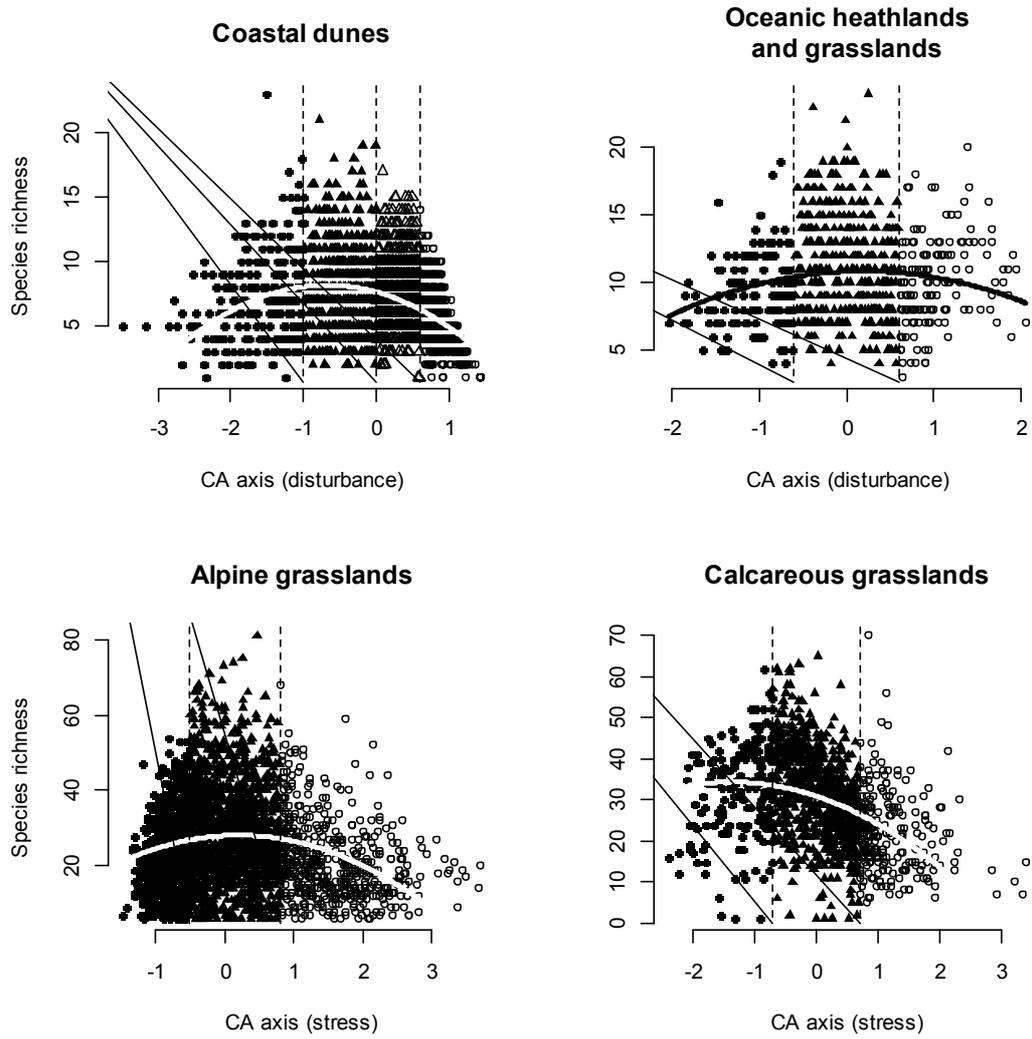
767

768 **Figure 2**



769

770 **Figure 3**

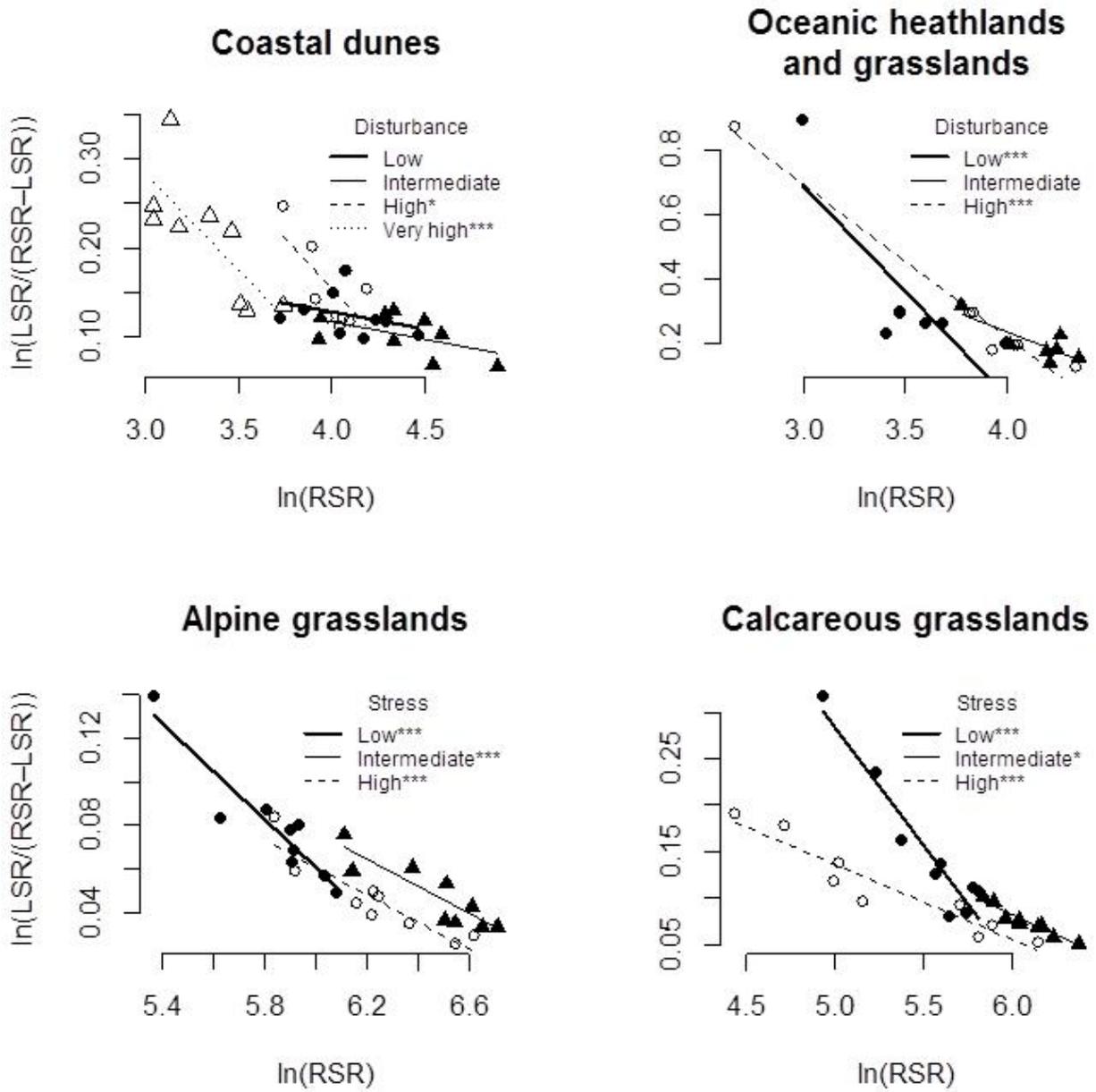


771

772

773 **Figure 4**

774



775

776

777 **Supplementary material 1:** LSR/RSR slopes for communities captured by a sliding window

778 defined as follows:

779 For each habitat:

780 1) Around fourteen communities were selected along an environmental severity gradient  
781 defined by the first axis of the correspondence analysis.

782 2) The number of plots for each habitat does not change (around 500 plots per community  
783 for all habitats, except oceanic heathlands: 300 plots per community, because we have  
784 fewer relevés for this habitat compared to the other ones).

785 3) For each habitat, 9 subregions are selected (except for heathlands: 7 subregions), a  
786 Goncalves-Souza slope is calculated and its significance is tested.

787 4) Slopes are plotted according to mean CA coordinates per habitat (severity gradient).

788 5) Significant Bonferroni-penalized p-values are represented by stars above the  
789 corresponding slopes (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .)

790 6) Two adjacent communities along the CA axis always partly overlap (sliding window)  
791 thus explaining the observed auto-correlations.

792 The sliding window analysis leads us to conclusions which are similar to those arising from  
793 the discrete split analysis reported in the paper, except for the oceanic heathlands and  
794 grasslands habitat. In the sliding window analysis, poorly disturbed communities in this  
795 habitat are associated with insignificant slopes. However, the most undisturbed community  
796 (first slope on the left) seems to be associated with a low slope, as expected, although  
797 insignificant.

798

799 **Supplementary material 2:** The relationship between local and regional Chao1-  
800 approximated species richness based on the log-ratio method (Szava-Kovats et al. 2012) for  
801 the four different habitat types as in Fig. 4 but considering 8 plots randomly sampled inside  
802 each community within each subregion of each habitat. Significant slope departures from zero  
803 were not strongly affected. The slope associated to the highly disturbed dune community was  
804 not significant anymore. Same legend as in Fig. 4.

805

806 **Supplementary material 3:** ANCOVA tables for the models testing the combinatory effects  
807 of community type (factor) and  $\ln(\text{RSR})$  (covariate) on  $\ln(\text{LSR}/(\text{RSR}-\text{LSR}))$  inside each of the  
808 four habitats.

809

810 **Supplementary material 4:** Holm-corrected p-values associated to slope significances inside  
811 each of the four habitats.