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► To cite this version:

Richard Michalet, Jean-Paul Maalouf, Philippe Choler, Bernard Clément, David Rosebery, et al.. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography*, 2014, 37, pp.1-11. 10.1111/ecog.01106 . hal-01118668

HAL Id: hal-01118668

<https://univ-rennes.hal.science/hal-01118668v1>

Submitted on 6 Jan 2025

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DOI: <https://doi.org/10.1111/ecog.01106>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-99659>

Journal Article

Accepted Version

Originally published at:

Michalet, Richard; Maalouf, Jean-Paul; Choler, Philippe; Clément, Bernard; Rosebery, David; Royer, Jean-Marie; Schöb, Christian; Lortie, Christopher (2015). Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography*, 38(4):335-345.

DOI: <https://doi.org/10.1111/ecog.01106>

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 m², 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

508 **Acknowledgements**

509 We thank the Nordic Ecological Society for organizing the Symposium in London and in
510 particular Jens-Christian Svenning for this Special Feature in Ecography. C.S. was supported
511 by the Swiss National Science Foundation (PA00P3_136474 and PZ00P3_148261). CJL was
512 supported by an NSERC DG.

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. *:
757 $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

758

759

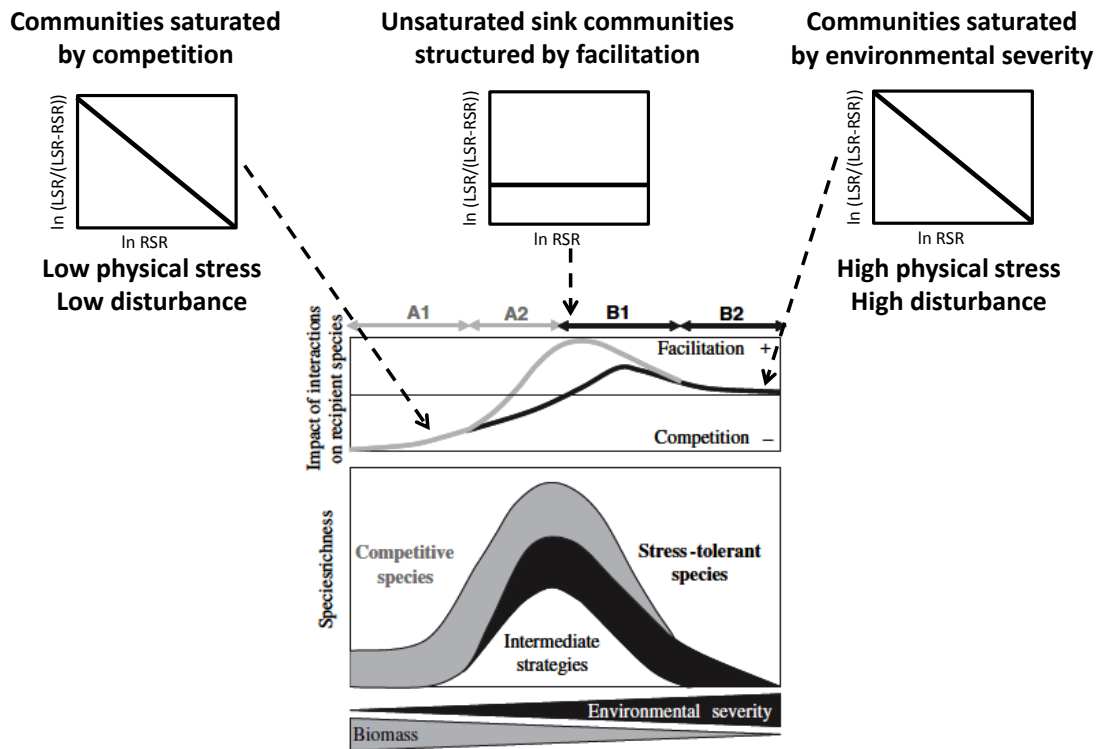
760 **Table 1.** Environmental severity level (either disturbance or stress *sensu* Grime 1973),
 761 dominant species, aboveground biomass (with reference) and dominant interaction type (with
 762 reference) of the 3-4 community types selected for each of the 4 habitat types.

Habitat type Communities	Environmental severity	Dominant species	Aboveground biomass g m ⁻²	Reference	Interaction type	Reference
Coastal dunes						
Disturbance						
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
Heathlands						
Disturbance						
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
Alpine grasslands						
Stress						
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
Calcareous grasslands						
Stress						
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	?	

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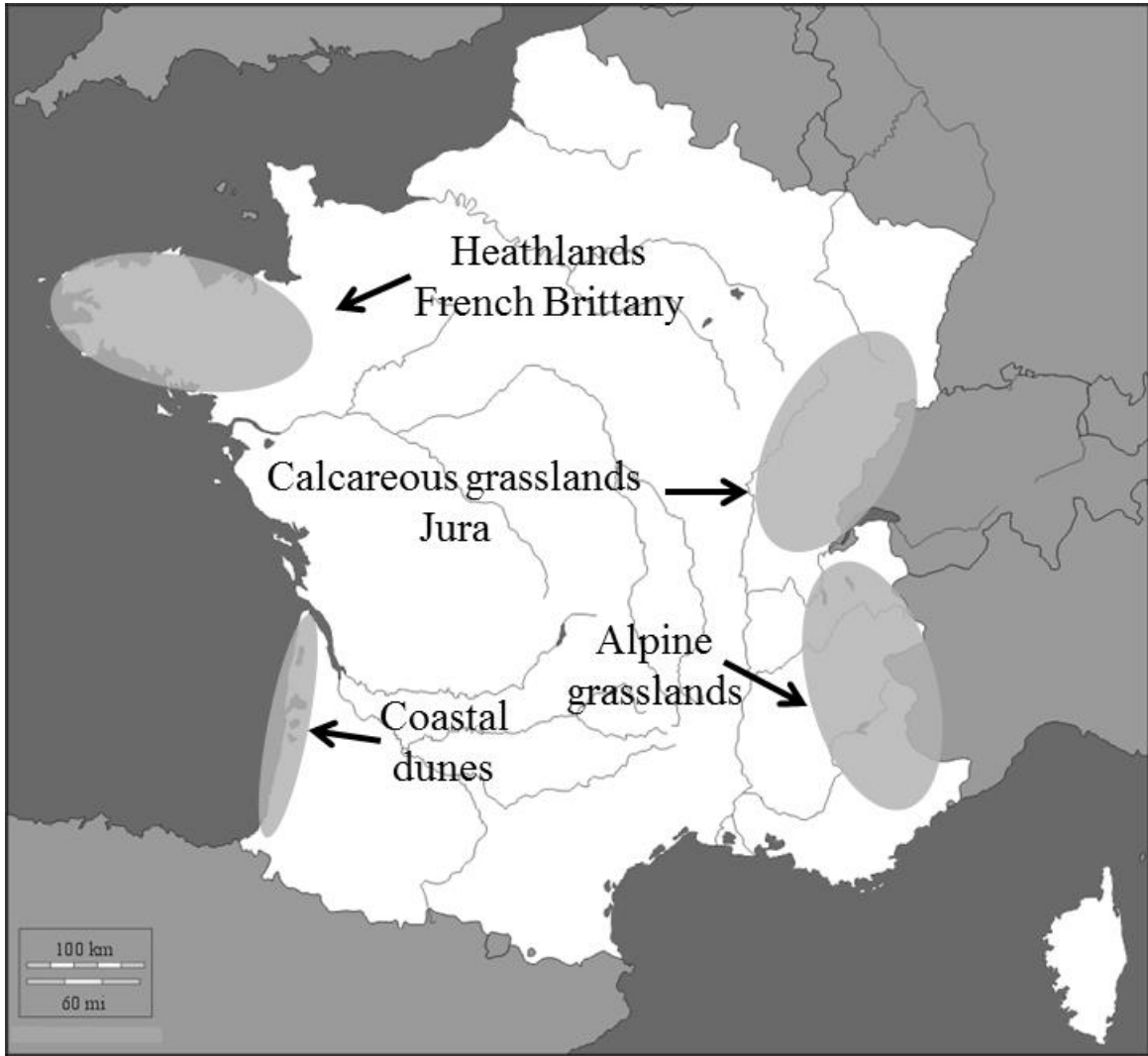
765 **Figure 1**



766

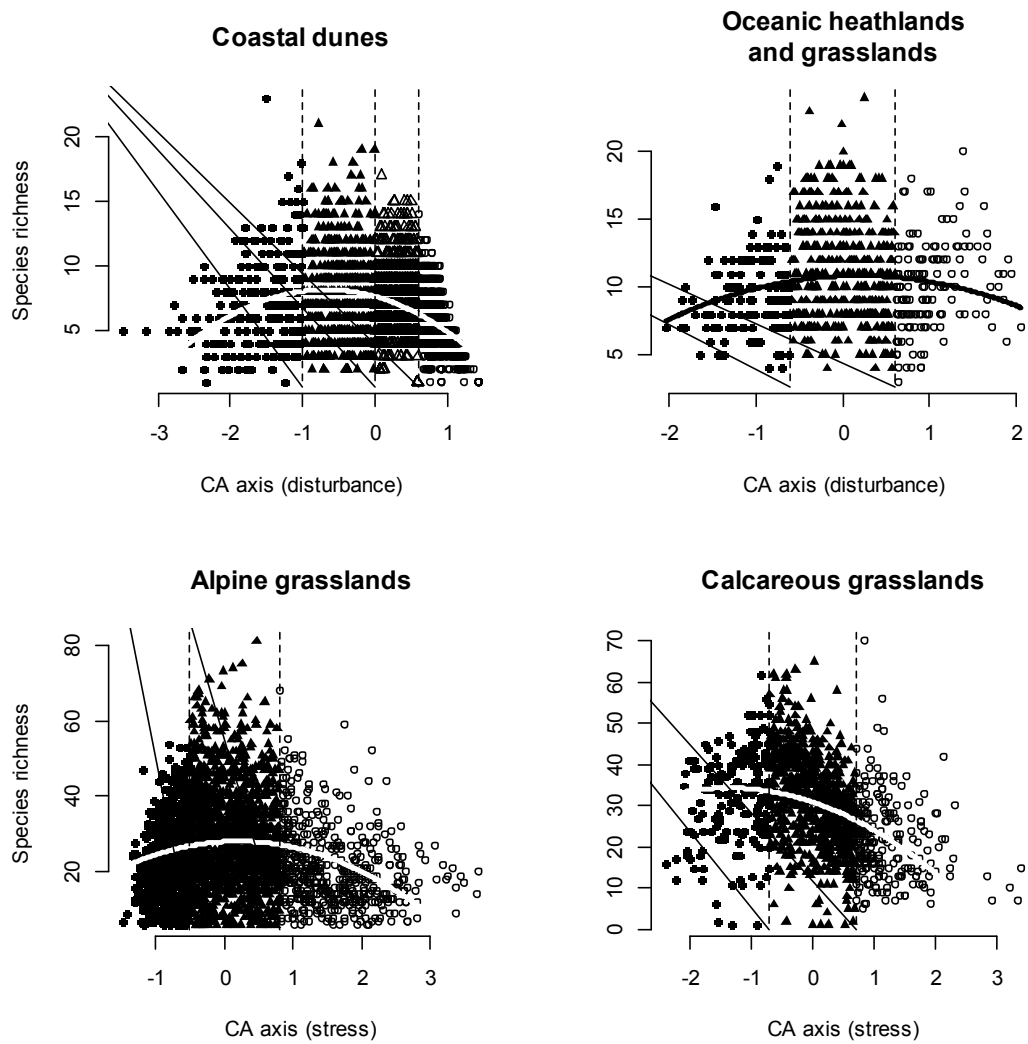
767

768 **Figure 2**



769

770 **Figure 3**

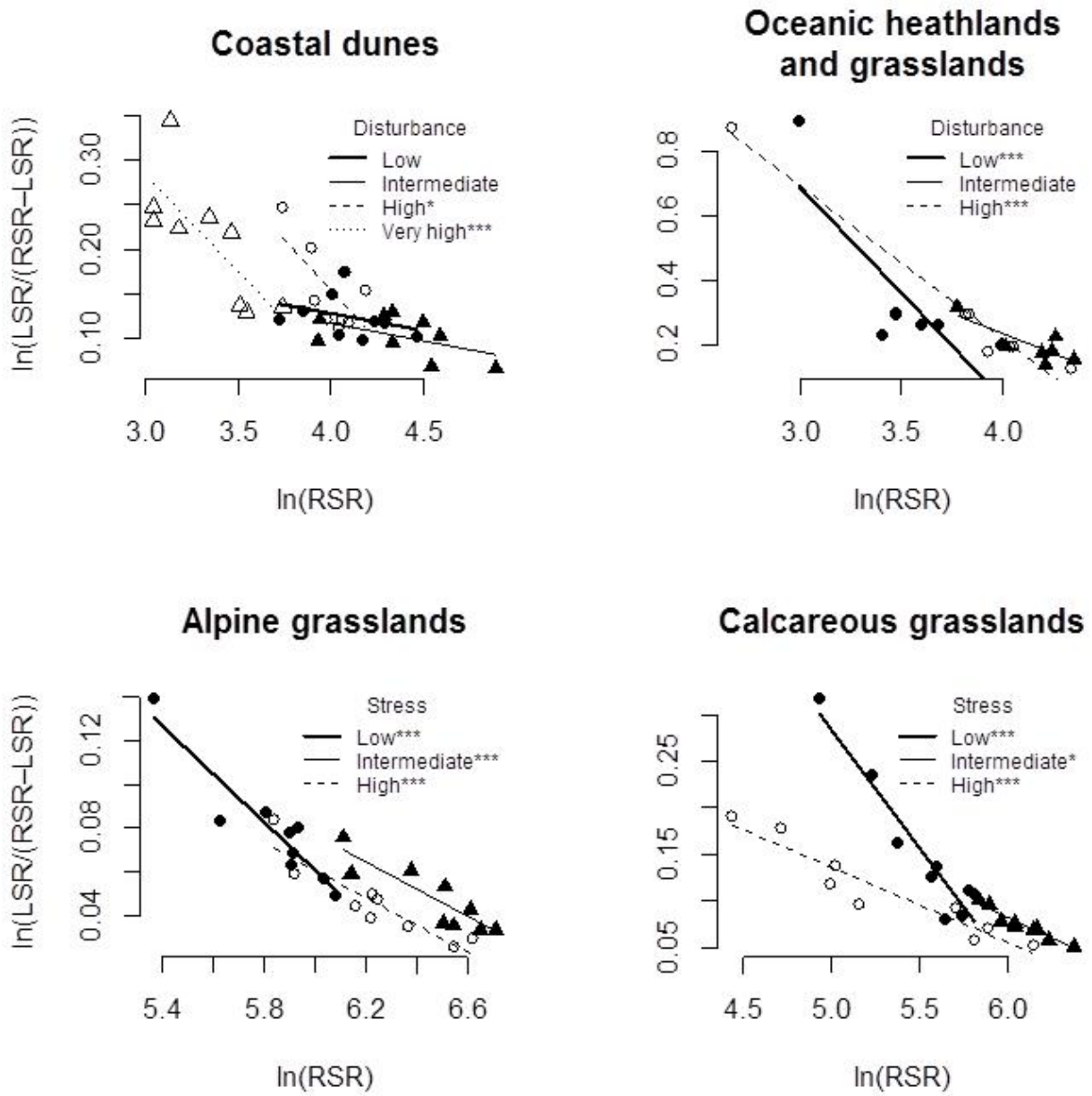


771

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.