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

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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.

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

that the relative importance of local more deterministic and regional more stochastic processes changes along environmental gradients.

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

Szava-Kovats et al. (2012) proposed a new method based on log-ratio models that allow circumvent most statistical artefacts of the traditional method. In this method the unsaturated curve is a horizontal line (type 1 curve with zero slope in Fig. 1) resembling the relationship between LSR and RSR-LSR at the log-scale, whereas the saturated curve has a steep negative slope (type 2 curve, Fig. 1). Gonçalves-Souza et al. (2013) and Szava-Kovats et al. (2013) applied this new method and found via independent meta-analyses consistent contradictions to the general consensus detected using the traditional approach. They both found that more than a third of the communities were misclassified in original studies and that saturated relationships were at least as common as unsaturated patterns, although Szava-Kovats et al. (2013) also found intermediate and indeterminate curves. The primary implication is that this new method should replace the traditional approach in subsequent contrasts of local versus regional drivers.

Although there is increasing evidence that the contribution of both local deterministic and regional stochastic processes to local community richness is dependent on environmental conditions, to the best of our knowledge there are only two studies that directly tested this hypothesis using the (traditional) LSR/RSR method (Huston 1999, Pärtel et al. 2000). Based on the humped-back model of species richness along net primary productivity gradient (Huston 1979) and the related model of Grime (1973), Huston (1999) proposed that communities should be saturated in conditions of low and high productivity due to local processes related to abiotic limitations (stress and disturbance) and competition, respectively, but that the size of the regional species pool should influence richness under conditions of intermediate productivity. The dataset of Pärtel et al. (1996) on Estonian plant communities was used to test this hypothesis splitting the LSR/RSR relationship into two curves, one for stressful species-rich communities (mostly calcareous grasslands and dry forests) and one for species-poor communities from benign environmental conditions. These findings supported this hypothesis with an unsaturated curve for the stressful communities and a saturated curve for the communities most likely to be structured by competition. Pärtel et al. (2000) confirmed the prediction of Huston (1999) using an enlarged dataset including 27 communities instead of 14 in the Huston's (1999) study. However, these relationships have been criticized because of the inclusion of different habitats and communities within the same relationship (Lawton 1999, Srivastava 1999). The first objective of the study herein is to test with the log-ratio method of Szava-Kovats et al. (2012) and Huston's (1999) hypothesis that competition and environmental severity (stress and disturbance) should enhance the saturation of LSR/RSR relationships. We also test the corollary that unsaturated communities are more likely to be observed at mid position along environmental severity gradients where species richness is known to be the highest because of intermediate level of competition, stress and disturbance (Grime 1973, Huston 1979). This would only be the third study to date on this topic and the first to use the new analytical method. We will also be careful not to mix broad habitat types as in the former test of this hypothesis.

Most predictions associated with the effect of local biotic processes on the regional and local species richness relationships are based on theoretical models primarily (and sometimes exclusively) including negative interactions (competition and predation) in ecological communities (Elton 1946, McArthur 1965, Grime 1973, Huston 1979, Tilman 1982). However, positive interactions are now recognized as important driving forces of local communities, in particular in severe environmental conditions (Bertness and Callaway 1994, Callaway 1995) and facilitation has been included in mainstream ecological theory (Bruno et al. 2003, Schöb et al. 2012, McIntire and Fajardo 2014). Michalet et al. (2006) revisited the humped-back model of Grime (1973), including the role of facilitation for species richness (also see Xiao et al. 2009, Le Bagousse-Pinguet et al. 2014a). This body of emerging literature proposed that facilitation should peak at intermediate position along environmental severity gradient and thus contribute to the high species richness observed at this point of the humped-curve of Grime (1973). With increasing environmental severity beyond this point, facilitation should collapse and species richness decreases because the effects of nurse species are reduced by high stress and/or high disturbance, as demonstrated by several experimental studies (Le Bagousse-Pinguet et al. 2014b). Since facilitation is now considered as mainly occurring at intermediate position along environmental severity gradients (Michalet et al. 2006, Holmgren and Scheffer 2010, Verwijmeren et al. 2013, but see He et al. 2013) and as enhancing diversity in opposition to competition and environmental severity, we argue that facilitation might also contribute to shaping the
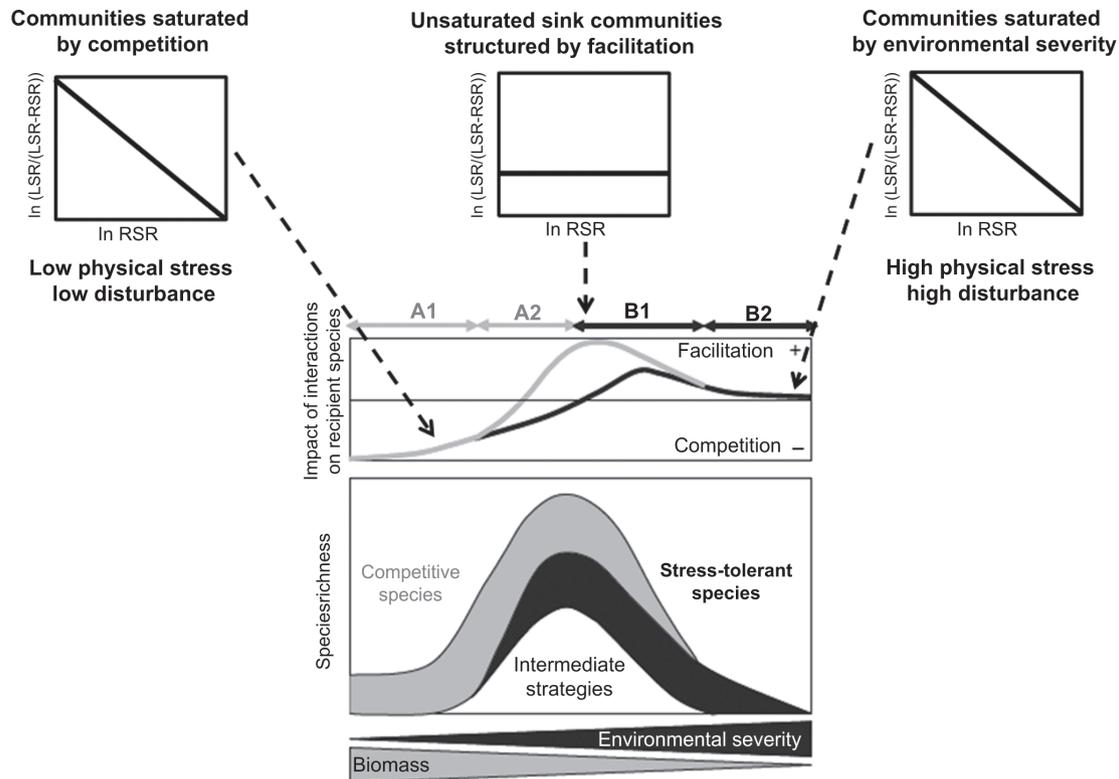
Figure 1. Predicted relationships between regional (RSR) and local (LSR) species richness at three positions along environmental severity gradients. The three upper panels show the relationship between Ln RSR and Ln (RSR/(LSR − RSR)) in communities structured by competition (left: saturated curve, i.e. type 2 curve sensu Gonçalves-Souza et al. 2013), facilitation (center: unsaturated curve, i.e. type 1 curve sensu Gonçalves-Souza et al. 2013) and environmental severity (right: saturated curve). The lower panel shows the unimodal pattern of plant–plant interactions along environmental severity gradients (Michalet et al. 2006) together with the unimodal pattern of species richness proposed by Grime (1973). In the lower panel, the four parts of the gradient (A1, A2, B1 and B2) correspond to increasing environmental severity levels and contrasted functional compositions of the communities, i.e. only competitive species, dominant competitive species, dominant stress-tolerant species and only stress-tolerant species, respectively; and see Michalet et al. (2006) for the precise legend of the lower panel.

regional vs local species richness relationship. Facilitation may act as an attractive force for species and increase the contribution of RSR to LSR in species-rich sink communities (sensu Mouquet and Loreau 2003) at intermediate position along the humped-back model of Grime (Fig. 1).

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

Material and methods

Habitat types and preparation of data

We selected four different habitat types located in four regions from France (Fig. 2). Each region has a regional species pool adapted to a particular set of environmental conditions. Coastal sand dunes communities are subjected to drought, nutrient stress, sand deposition and acidic soils (Forey et al. 2008). Nutrient stress is high and soils acidic in oceanic heathlands and grasslands but there is no physical stress (Clément 1978). Alpine communities are subjected to high cold and nutrient stress (Choler and Michalet 2002), and calcareous grasslands from the Jura range to drought and nutrient stress (Royer 1987). The geographical extent of each area is very similar, i.e. approximately 200 to 250 km-long and 100 to 150 km-wide, except the coastal sand dune region which has a very narrow width, i.e. less than 1 km (Fig. 2). All relevés were sampled using standardized phytosociological methodology (Braun-Blanquet 1932, Westhoff and van der Maarel 1978) with a relevé area of approximately 25–100 m², depending on the minimum area of the target community.

The coastal sand dunes of Aquitaine include 2433 unpublished relevés sampled by the French National Forest Office
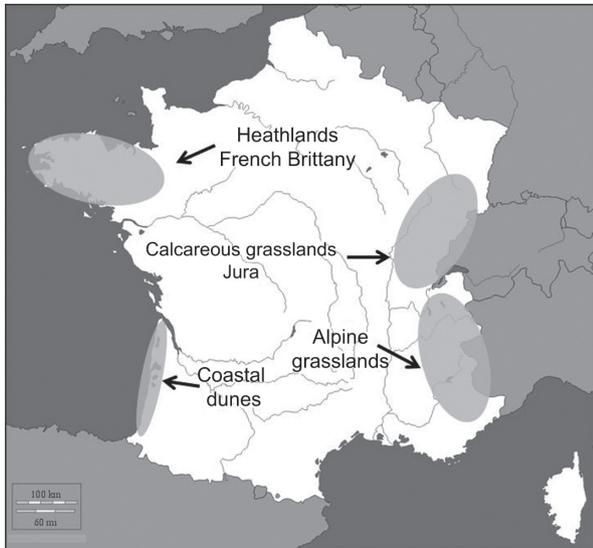
Figure 2. Location of the four regions of the four habitat types in France.

in both 1997 and 1998. Relevés were located at sea level along 94 W–E transects expanding every 20 km from the southern part of the Aquitaine dunes to its northern part. Differences in species composition across communities from this habitat type have been shown to be first driven by the level of disturbance induced by sand deposition (increasing towards the ocean), and second by the contrasted species pools of northern and southern dunes (Forey et al. 2008). This is a highly stressed ecological system due to water and nutrient limitations induced by the coarse texture of the sand (Forey et al. 2008). The oceanic heathlands and grasslands from Brittany include 666 relevés sampled throughout French Brittany by different authors between 1977 and 1995 (Forgeard 1977, Clément 1978, Clément et al. 1978, Wattez and Godeau 1986, Gloaguen 1988, de Foucault 1993, Wattez and Wattez 1995). Physical stress is low in this low elevation oceanic region (up to 387 m a.s.l.) characterized by heavy rainfall and low maximum summer temperatures, but nutrient stress is high and soils are acidic (Aerts et al. 1990). The main ecological factor driving species composition in this ecological region is the level of human-induced disturbance generally related to the depth of the groundwater, with the least disturbed communities in the wettest and most anaerobic conditions (Clément 1978). For the French Alps region, we used a dataset of 2681 relevés assembled from a large survey of the grey literature (see Choler and Michalet 2002 for details on this dataset) and completed in the recent period by the Conservatoire Botanique National Alpin. The vegetation relevés include subalpine grasslands and alpine meadows ranging from 1800 to 3000 m a.s.l. The main ecological factors driving differences in species composition are mesotopography and elevation, with the most stressful communities located on convex topography at high elevation (Choler and Michalet 2002). The calcareous grasslands from the Jura region include 1250 relevés mostly sampled by Royer (1987) between 200 and 1600 m a.s.l. throughout the Jura massif. All relevés are located on calcareous substrates and overall characterized by moderate drought and nutrient stress due to the high porosity of the calcareous rocks.

The main ecological factor driving differences in species composition in this region is the water availability related to soil depth itself depending on exposure, substrate type and topography (Royer 1987, Michalet et al. 2002).

We initially performed a correspondence analysis for each habitat type to identify the main axes of floristic variation. Rare species (frequency lower than 1% of the data set) were excluded before running the ordination. The underlying environmental factors driving floristic variations along the first ordination axis were easily identified since the four habitat types were each formerly studied for community types classifications using multivariate analyses and environmental measurements. The correspondence with those former studies was in particular made using the frequency and cover of dominant species along ordination axes, as well as information on community biomass (Table 1). We then plotted for each habitat type the species richness of the relevés against their scores on the CA axis 1 (Fig. 3). For the four independent habitat types, we found a significant humped-back curve relating species richness and environmental severity, consistent with Grime (1973), but with different environmental severity factors depending on the habitat type. In both the coastal sand dunes and the oceanic heathlands and grasslands from Brittany the main source of variation in species composition (also structuring our relevés on the CA axes 1) is the level of disturbance (sensu Grime 1973), either induced by sand deposition in the former (Forey et al. 2008), or by human activities (mostly grazing or mowing) in the latter (Clément 1978). In alpine grasslands, the floristic turnover is associated with a gradient of low temperature stress that is mostly controlled by the snow cover duration, in relation with variation in mesotopography (Choler et al. 2001). In calcareous grasslands from Jura the main source of variation in species composition is the level of drought (and nutrient) stress induced by soil depth and topography (Royer 1987).

For each habitat type we split the relevés into three groups (four in the dunes) based on their CA axis 1 scores and positions on the humped-back curve (Fig. 3). Indeed, these three (or four) groups/community types correspond to three levels of environmental severity at three different positions along the humped-back curve, consistent to Grime (1973). In the benign part of the curves for all habitat types (left side of the curves), species richness increases with increasing environmental severity (Fig. 3). In the intermediate part of the curves occurs the maximum of species richness (intermediate environmental severity). In the severe part of the curves (right side of the curves), species richness decreases with increasing environmental severity (Fig. 3). In the dunes we separated the most severely disturbed dune communities in two subgroups due to good knowledge of the plant interactions occurring in this habitat type (Forey et al. 2010). We used the literature on plant interaction experiments in these four different habitat types to assign a dominant plant interaction characterizing each of the 3 (or 4) groups of each habitat type (Table 1). For the coastal dunes, the experiment of Forey et al. (2010) conducted on four target species in four communities along the sand deposition gradient clearly showed that facilitation occurs in the weakly disturbed community (the grey dune in Table 1) but collapses in the most disturbed communities (corresponding to the white dune and foredune in Table 1), due to extreme level of disturbance

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

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

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

Data analysis

For three of the four habitat types, alpine grasslands, calcareous grasslands and coastal dunes, relevés were homogeneously distributed at the geographical scale. Each of those three regions was thus latitudinally divided into 9 subregions of approximately similar areas. The oceanic heathlands and grasslands habitat type had fewer relevés concentrated within 7 disparate subregions. Those 7 subregions thus determined regional divisions for further analyses in this habitat type. All community types related to a habitat type in particular were present in all the subregions delimited inside the region of the habitat type. For each habitat type, inside each subregion, and for each community type, we computed the Chao1 nonparametric estimation of species richness (Chao 1984) as recommended by Cornell et al. (2008) 1) at the regional scale (RSR, cumulated Chao1 species richness across relevés) and 2) at the local scale (LSR, averaged Chao1 species richness across relevés). The Chao diversity estimates were all done using abundance, and not presence/absence matrices. For each community within each subregion, the chao species diversity was estimated per relevé, borrowing information provided by the other relevés in the pool. Then the Chao indices were averaged across relevés in each pool to provide values of LSR (one value per pool). Thus, there were a total of 111 independent estimations of RSR and LSR (3 community types × 7 subregions in the oceanic heathlands) + (3 community types × 9 subregions in the alpine grasslands) + (3 community types × 9 subregions in the calcareous grasslands) + (4 community types × 9 subregions in the coastal dunes).

For each habitat type, the effects of RSR on LSR by community were assessed using an analysis of covariance (ANCOVA) model. We used the log-ratio method of Szava-Kovats et al. (2012): ln(LSR/(RSR – LSR)) was used as the
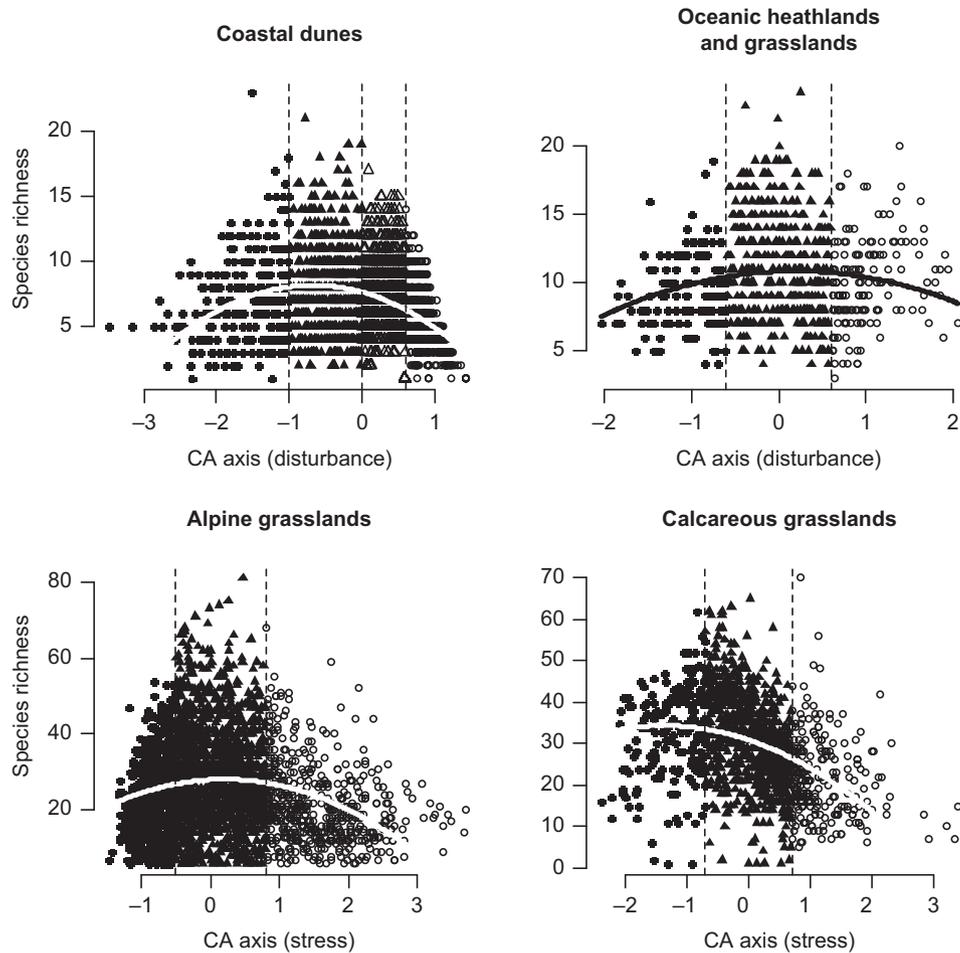
Figure 3. The relationship between local species richness and environmental severity gradients for four different habitat types (coastal dunes and oceanic heathlands and grasslands exposed to disturbance gradients; alpine grasslands and calcareous grasslands exposed to stress gradients). For each habitat type, the severity gradient is integrated by the first axis of a correspondence analysis performed on species composition data of the plots (environmental severity increases from left to right for the four habitat types). Four communities (for coastal dunes) and three communities (for each of the three other ecological regions) were selected according to their CA axis 1 scores and based on expert knowledge. Communities were separated by vertical dashed lines and labelled by different symbols (for each habitat type, filled circles represented communities occurring in the most benign environmental conditions and empty circles represented those located in the most severe ones). Curves represent quadratic model predictions for each habitat type. The color of the curves (black or white) was modified according to visibility. All quadratic effects were highly significant (p < 0.001).

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

as 'intermediate'. Parametric model assumptions were met for all of the 4 ANCOVA models.

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

Results

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

For the alpine grasslands the covariate/community type interaction was significant ($p < 0.05$, Fig. 4) because the low-stress community had a steeper negative slope than the intermediate- and high-stress communities. However, all three curves were highly significantly saturated ($p < 0.001$, Fig. 4). Similar to the alpine grasslands, the calcareous grasslands had a highly significant covariate/community type interaction ($p < 0.001$, Fig. 4) likewise due to a much steeper negative slope for the low-stress community than for the two

other communities within this habitat type. The low- and high-disturbance curves were highly significantly saturated ($p < 0.001$ for both), whereas the intermediate curve was only weakly significantly saturated ($p < 0.05$, Fig. 4).

Discussion

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

Most communities were saturated with only three cases of unsaturated communities of 13 tested LSR/RSR relationships (i.e. 23%). Although our main goal was not to test the hypothesis that saturated curves are more common in plant communities than unsaturated curves, our study including contrasting habitat types from four different regions further divided in three to four community types of specific environmental conditions, clearly shows the predominant role of local over regional processes for local species richness. The ubiquity of linear relationships between local and regional species richness has long been used to conclude that unsaturated communities are by far more common than saturated communities due to the prevalence in nature of regional over local processes for local species richness (Lawton 1999, Loreau 2000, Hillebrand 2005, Harrison and Cornell 2008, Cornell and Harrison 2013). However, this conclusion was in part influenced by the use of an inappropriate method. Thus, with the log-ratio method proposed by Szava-Kovats et al. (2012), Goncalves-Souza et al. (2013) and Szava-Kovats et al. (2013) found that saturated relationships were at least as common as unsaturated patterns. Szava-Kovats et al. (2013) also found that large proportion of studies produce no discernable patterns. Additionally,
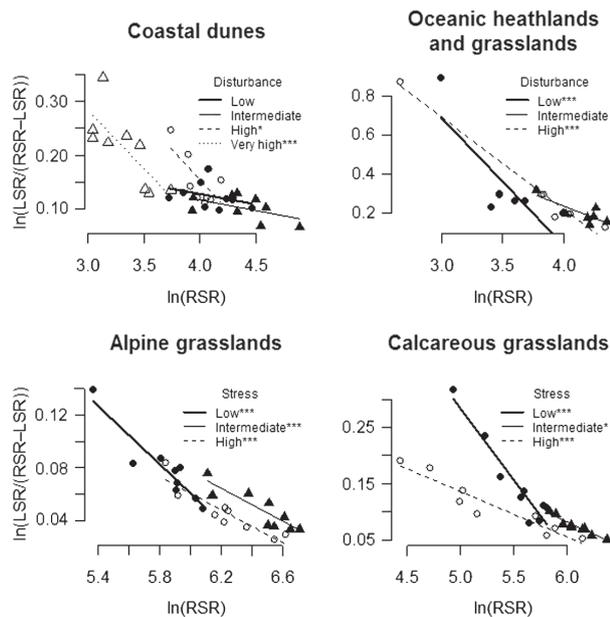

Figure 4. The relationship between local and regional Chao1-approximated species richness based on the log-ratio method (Szava-Kovats et al. 2012) for the four different habitat types. For each habitat type, different regression lines represent communities submitted to contrasted levels of environmental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

Gonçalves-Souza et al. (2013) argued that instead of focusing solely on local/regional richness plots to infer processes from patterns, additional approaches should be used to really understand the drivers of local community structure. In particular, they stressed the usefulness to add in the analyses observational information on local environmental and dispersal processes, as commonly used in meta-community studies (Cottenie 2005). In our study, we hypothesized that the saturation level of communities should be dependent on environmental conditions similar to the work of Huston (1999), and we thus indirectly controlled the effect of varying environmental conditions through our partition of the four habitat types along multivariate axes driven either by the level of stress or disturbance. It is likely that the large proportion of significantly saturated curves found in our study, as compared to the meta-analyses of Gonçalves-Souza et al. (2013) and Szava-Kovats et al. (2013) is related to the way we partitioned the data, i.e. along the main axis of floristic variation, and its ability to capture distinct environmental conditions. In other words, the mixing of different environmental conditions characterizing saturated and unsaturated communities within a single relationship certainly increases the probability of finding indeterminate curves. However, the high proportion of saturated curves found in our study may also be due to the limitation of our analyses to terrestrial plant communities, as compared to meta-analyses including all organisms from both marine and terrestrial environments (Cornell and Harrison 2013, Witman 2013). Additionally, our results might have been influenced by the rather small spatial grain size used in this study. Most macroecological analyses use large grid cells (e.g. 100×100 km size) whereas fine-grained analyses are rather rare.

In most macroecology studies assessing the importance of local vs regional drivers of local species richness competition, predation and parasitism (i.e. negative interactions) are presented as the primary local factors likely to counteract the influence of regional processes for local richness (McArthur 1965, Lawton 1999, Loreau 2000, Foster et al. 2004, Cornell et al. 2008, Burgess et al. 2010, Cornell and Harrison 2013). The importance of plant–plant competition for local species richness is indeed one of the most important tenets of traditional community ecology (Grime 1973, Huston 1979, 1999, Fridley et al. 2012) and several observational and experimental studies have shown the occurrence at local scale of a tight correlation between community biomass, the intensity of competition and species richness (Al Mufti et al. 1977, Keddy et al. 1997, Foster and Gross 1998, Michalet et al. 2002, Maalouf et al. 2012b, Maron et al. 2014). However, other authors have also observed that the occurrence of competition has no predictable consequences for plant community diversity (Lamb and Cahill 2008, Mitchell et al. 2009). In our study the first source of community saturation was the occurrence of competition. In three of the four studied habitat types (oceanic heathlands, alpine grasslands and calcareous grasslands) the steepest negative slope and thus strongest community saturation level was found in the most benign environmental conditions where community biomass is the highest and competition known to be the dominant interaction (Aerts et al. 1990, Choler et al. 2001, Liancourt et al. 2005a). In contrast, in the most benign environmental conditions of the fourth habitat type, the grey

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

Although positive interactions such as mutualism have been early thought as local processes potentially contributing to local species richness (Ricklefs 1987), to our knowledge facilitation has been rarely proposed as a potential mechanism for shaping the LSR/RSR relationship (but see Szava-Kovats et al. 2013). This is quite surprising since facilitation has been included in mainstream ecological theory for two decades (Bertness and Callaway 1994, Callaway 1995, Bruno et al. 2003, Lortie et al. 2004, Brooker et al. 2008, 2009, Schöb et al. 2012, McIntire and Fajardo 2014, Soliveres et al. 2014) and has even been proposed as an important mechanism enlarging species niches (or more accurately species' habitats), suggesting its important role for local species richness (Hacker and Gaines 1997, Bruno et al. 2003, Michalet et al. 2006, Xiao et al. 2009, Le Bagousse-Pinguet et al. 2014a). Lortie et al. (2004) have proposed that positive interactions and mutualism act as local filters increasing the chance of inhabiting a local community for species from the regional species pool, in opposition to other filters deleting species such as negative interactions or environmental severity. Michalet et al. (2006) proposed a model where the positive effect of facilitation for diversity peaks at mid-position along the humped-back diversity-community biomass model (see also Xiao et al. 2009 and Le Bagousse-Pinguet et al. 2014a) and thus could contribute to shaping the relationship between local species richness and environmental severity proposed by Grime (1973) and Huston (1979). Thus, we made herein the hypothesis 2) that facilitation should contribute to shaping the regional vs. local species richness relationship, and in particular to increase the contribution of RSR to LSR in species-rich sink communities (sensu Mouquet and Loreau 2003) at intermediate position along the humped-back model of Grime (1973). Our results supported this hypothesis; for the four habitat types the curves had the most gentle or even non-significant slopes at mid position along environmental severity gradients where facilitation has been shown to be the highest in several experimental studies conducted in the same ecological systems (Choler et al. 2001, Liancourt et al. 2005a, b, Brooker et al. 2006, Forey et al. 2010). Interestingly, the two most unsaturated communities with non-significant slopes were found for the two habitat types structured by disturbance (coastal dunes and oceanic heathlands and grasslands), whereas for the two other habitat types structured by stress (alpine and calcareous grasslands) the slopes were still significant and indicating saturated communities. This may be due to the contrasted functional strategies of the species involved along gradients of disturbance or stress, with more ruderal species with high dispersal abilities in the former and more stress-tolerant species with low dispersal abilities in the latter (Grime 1973). Pärtel and Zobel (2007) have shown that species functional composition may affect

the productivity–diversity relationship through changes in dispersal ability. This effect is very likely to also influence community saturation. The strong regional effect observed in the grey dunes was maybe also due to the very linear geographic structure of the region of this habitat type (width < 1 km), enhancing dispersal effects on species richness (Forey et al. 2008). We have to design experiments allowing a straightforward assessment of the effect of facilitation on community saturation suggesting by our study, since we did not separate the facilitation hypothesis from a neutral model. We may compare LSR/RSR relationships of ecological regions with similar environmental conditions but contrasting importance of facilitation, due for example to the absence of potential nurse species in the region without facilitation.

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

Conclusions

Our study analyzing 13 LSR/RSR relationships in contrasting environmental conditions from four habitat types of France showed that the relative contribution of local and regional drivers of local species richness is highly dependent on environmental conditions, as proposed by Huston (1999), Foster et al. (2004) and Chase (2007, 2010). In this set of regional contrasts, saturated communities were much more common than unsaturated communities, highlighting the importance of local processes that are often neglected in macroecology studies. Competition was the main source of community saturation limiting the influence of the regional species pool, as proposed by Huston (1999) and Foster et al. (2004). However, the main novelty of our correlative study was to strongly suggest that facilitation may inversely enhance the influence of the regional species pool

at intermediate position along environmental severity gradients, although further studies should separate the facilitation hypothesis from a neutral model. Finally, we showed, at least along disturbance gradients, that the collapse of facilitation in extreme conditions of environmental severity also counteracts the influence of the regional species pool as it does in competitive environments. Other tests of LSR/RSR relationships similarly controlling for environmental conditions may further assess the contrasting effect of stress and disturbance, as well as analyze the influence of species functional strategies (in particular their dispersal abilities) and regional geographical structure and size.

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Supplementary material (Appendix ECOG-01106 at <www.ecography.org/readers/appendix>). Appendix 1–4.