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Shrubs as foundation species in a high tropical alpine ecosystem: a multi-scale analysis of plant spatial interactions

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Background: Studies on plant–plant interactions in alpine ecosystems show a strong bias for temperate vs. tropical latitudes and pay limited attention to the implications of biophysical heterogeneity beyond the local plant scale.

Aims: To evaluate the effects of a dominant shrub (*Hypericum laricifolium*) on community organisation, integrating multiple scales of analysis, in a high Andean páramo in Venezuela.

Methods: We compared plant cover, species richness and Shannon diversity between plots placed under the shrub and outside (plant scale); quantified the spatial relations of *Hypericum* with its conspecifics, heterospecifics and rocks at different radial distances, using covariance functions (patch scale); analysed the effects of *Hypericum* shrubs on total species richness in the community (site scale); and evaluated the consistency of our results among four sites within the same region (between-site scale).

Results: Average species richness, Shannon diversity, and the abundance of common forbs and conspecific shrubs were consistently higher inside the *Hypericum* shrub, while the exotic *Rumex acetosella* was more abundant in open areas. However, the aggregated spatial distribution of conspecifics and other species extended beyond the local plant scale and there were no clear effects of *Hypericum* shrubs on community-level species richness.

Conclusions: Shrubs can function as foundation species in tropical alpine environments, modifying local community structure and alpha diversity, but not necessarily the species richness of the overall community. Our results stress the need of analysing multiple spatial scales to interpret the role of plant–plant interactions (facilitation/competition) in heterogeneous alpine ecosystems.

Keywords: competition; ecosystem engineering; facilitation; invader species; plant diversity; spatial structure

Introduction

Understanding the gamut of positive and negative interactions on community organisation is increasingly recognised as fundamental for the consolidation of modern plant community theory (Lortie et al. 2004; Callaway 2007). This has been linked with a re-evaluation of the importance of facilitation in many ecosystems (Callaway 1995; Bruno et al. 2003). A key driving idea for this paradigm shift has been that the relative importance of facilitation increases in unproductive environments where abiotic (stress) factors become important for plant performance, so that the benefits generated by the amelioration of environmental conditions induced by neighbours can outweigh their competitive effects (Bertness and Callaway 1994; Callaway 2007). The stress gradient hypothesis has been supported by empirical evidence gathered in a wide range of environments, including along elevation gradients in alpine areas (e.g. Choler et al. 2001; Callaway et al. 2002; Tirado and Pugnaire 2005). Even so, several conceptual and empirical questions regarding the analysis of the role of plant–plant interactions in unproductive or stressful ecosystems remain to be explored.

Dealing with the pervasive problem of scale (sensu Levins 1992) is one such question which still represents a major challenge in this field (Maestre et al. 2005, 2006; Malkinson and Tielbörger 2010). This is important because the scale (grain size and extent) at which environmental gradients and plant–plant interactions are studied determine the patterns and processes than can be detected (Leibold et al. 2004; Lortie and Callaway 2006; Badano et al. 2010).

Plant growth and survival are primarily determined by biotic and abiotic conditions in their immediate neighbourhood, and both theoretical and empirical research have shown a dynamic feed-back between local spatial structure and plant–plant interactions (Law and Dieckmann 2000; Stoll and Prati 2001; Llambí et al. 2004). A common approach to analyse the nature and importance of plant–plant interactions in extreme environments (e.g. water or temperature-limited regions) has been to study patterns in local spatial relationships, with spatial segregation suggesting net competitive effects, and spatial aggregation indicating net positive effects (e.g. Tirado and Pugnaire 2003; Kikvidze et al. 2005; Larrea-Alcázar and Soriano 2006; Dullinger et al. 2007; Llambí et al. 2013).

However, species can differ widely in the scales of their ecological neighbourhoods (Bruno et al. 2003; Lortie and Callaway 2006; Wiegand et al. 2006) and their local

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interactions are, in turn, embedded in heterogeneous bio-physical scenarios which can modulate the resulting relationships between species at different scales. For example, beyond the local plant scale, potential facilitators and their beneficiary species could show spatial aggregation within more favourable habitat patches, confounding the link between interspecific spatial association and direct facilitation effects. In addition, the nature and intensity of plant–plant interactions can change between apparently similar sites at larger scales as a result of processes such as: (a) random dispersal-colonisation and species-specific effects; (b) variations induced by architectural or ontogenetic differences between individuals of interacting species in different populations (e.g. Miriti 2006; Armas et al. 2013). Paraphrasing Levins (1969), the play of plant–plant interactions is performed on a heterogeneous stage, across scales.

Another limitation in our current understanding of plant–plant interactions in unproductive ecosystems is that the available evidence shows a strong bias for temperate vs. tropical latitudes (Anthelme et al. 2012; Anthelme and Dangles 2012). Tropical alpine ecosystems (TAE) represent ca. 10% of the alpine surface worldwide and constitute a global priority area for conservation by virtue of their outstanding levels of diversity and endemism (Armenteras et al. 2003; Körner et al. 2011). While some stress factors resulting from high elevation are similar between tropical and temperate alpine ecosystems (e.g. low temperatures, low nutrient availability, and high topographic heterogeneity), TAE are different in many aspects; they include higher levels of solar radiation, absence of persistent snow cover, and daily temperature oscillations that far exceed seasonal ones (and may induce daily freeze–thaw cycles). Consequently, there is year-round vegetative growth, and changes in precipitation become the most important seasonal pulse, especially in drier and/or higher-elevation regions, where there is marked seasonality (Sarmiento 1986; Nagy and Grabherr 2009; Anthelme and Dangles 2012). In addition, most TAEs in the Andes, East Africa and New Guinea attained present-day elevations much more recently than many of the alpine areas studied at mid-latitudes (e.g. the Alps or Rocky Mountains, Smith and Cleef 1988). This opens up interesting questions in terms of whether there has been sufficient time for the evolution of strong plant interdependences, such as those implied in many documented cases of alpine facilitation resulting in niche expansion of beneficiary species (Bruno et al. 2003; Callaway 2007).

The unique combination of environmental determinants characteristic of the cold tropics has influenced the evolution of remarkable landscapes in high-elevation sites (> 4000 m), where the sparse vegetation cover is characterised by the presence of large perennial life-forms, which could be expected to act as ecosystem engineers or foundation species (sensu Jones et al. 1997; Ellison et al. 2005). They include giant caulescent rosettes, sclerophyllous shrubs, tussock grasses and cushions (Hedberg and Hedberg 1979; Smith and Young 1987; Ramsay and Oxley 1997). The contrasting architectures of these diverse life-forms can result in differences in the mode and intensity of their effects on above-ground vs. below-ground abiotic drivers, and consequently, on their impact on community organisation (see Crooks 2002).

While previous studies in TAEs have shown that giant rosettes and cushions can increase soil organic matter, nutrient levels and soil stability in their neighbourhood (e.g. Young and van Arden Robe 1986; Pérez 1992; Rundel et al. 1994; Haussmann et al. 2009), only a few recent studies focusing cushions in the *páramos* (the TAEs of the northern Andes) have documented the local impact of foundation species on plant diversity and community structure (Sklenár 2009; Anthelme et al. 2012). However, the local effects of other life-forms such as shrubs and tussock grasses remain largely unexplored.

Our aim in this study was to analyse the role of a sclerophyllous shrub (*Hypericum laricifolium* Juss) on community organisation in a high páramo ecosystem in Venezuela (4250–4300 m a.s.l.). Given that *H. laricifolium* is one of the dominant species in the upper vegetation stratum and it is a long-lived perennial which forms compact crowns, we hypothesised that it would act as foundation species, increasing average alpha diversity and the abundance of conspecifics and heterospecifics under its crown (plant scale) as well as total species richness in the community (site scale). However, given the high spatial heterogeneity that characterises páramo environments, we hypothesised that environmental patchiness beyond the local plant scale would play a role in generating larger-scale patterns of spatial aggregation between plants (patch scale) and that the effects of *H. laricifolium* on community organisation could differ between apparently similar sites in the same region (between-sites scale, Figure 1).
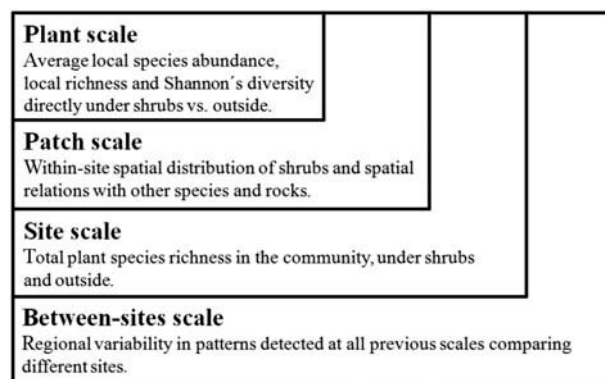

Figure 1. Conceptual framework used to analyse the role of a dominant shrub on community organisation and the implications of environmental heterogeneity at different scales in a high Andean páramo ecosystem.

Materials and methods

Study species

Hypericum laricifolium (Hypericaceae) is a widely distributed sclerophyllous shrub in the páramos from Ecuador to Venezuela (Luteyn 1999); in Venezuela its elevation distribution spans from 2200 to 4400 m (Briceño and Morillo 2002). It invests a high amount of resources to non-assimilating structural above-ground biomass, while only about 20% is allocated below ground (Berbesí 1990). Individuals present dense, rounded crowns with microphyllous leaves. Maximum abundances occur in sites with well-drained soils where the upper vegetation stratum attains less than 1.5 m in height (Fariñas et al. 2008) being also dominant in advanced stages of old-field succession (Sarmiento et al. 2003). Its architecture becomes more compact at higher altitudes (Robson 1990). The fact that *H. laricifolium* is at the upper limit of its distribution in our sites could be seen to imply it should play a minor role on community structuring; however, these shrubs can attain very high relative abundance in the high Andean páramo in Venezuela, dominating (together with giant rosettes) the upper vegetation stratum in many areas. Furthermore, its presence seems to have increased in the last 30 years at high elevations, something that might be related to climate change effects (F. Rada, pers. obs.).

Study area

The study was carried out in the high Andean páramo or superpáramo (Monasterio 1980) at Piedras Blancas, situated in the north-eastern sector of the Sierra de La Culata National Park, in the Venezuelan Andes (8° 52′ 1″ N; 70° 56′ 41″ E). Four similar study sites, southwest oriented and with slopes ranging between 20–35%, were selected at the upper limit of the Chama river watershed located between 4250 and 4300 m. Average distance between sites ranged between 0.5–2 km. All sites were covered by hillside deposits and colluvial material resulting from weathering and fragmentation of cirque walls and horns influenced by gelifraction processes (Monasterio 1979). Average annual rainfall in the area is 860 mm, showing a unimodal regime, with a dry season between December and March (Sarmiento 1986, 24 years of data). Mean annual temperature at 4118 m is ca. 3 °C, with a 2.7 °C difference between the coldest and warmest month. However, there are broad daily thermal fluctuations: air temperature near the soil surface during the dry season commonly rises to more than 40°C in clear days, and drops to less than -5 °C at night (Cáceres 2011). There are daily freeze–thaw cycles inducing repeated needle ice formation, which affect superficial soil layers (Pérez 1995). The landforms in this area were shaped by glacial and periglacial processes that created heterogeneous substrates consisting of gravel up to 20 cm and angular rock blocks of 20–50 cm in size. Most soils are shallow and acidic, with low organic matter and clay contents and a coarse texture

(entisols and inceptisols, see Malagón 1982; Pérez 1995).

Plant cover is sparse with a high proportion of bare soil (>40%) and with two vegetation strata: lower (close to soil surface) and upper (0.5–2.0 m). In our study sites, the upper vegetation stratum was dominated by *H. laricifolium* shrubs in association with smaller and less-abundant stem rosettes (*Espeletia schultzii* Wedd, *E. spicata* Sch. Bip.). Other present species in variable densities at the upper stratum included the forbs *Castilleja fissifolia* Lf. and *Senecio formosus* HBK. The lower stratum was dominated by the exotic forb *Rumex acetosella* L., non-caulescent rosettes (e.g. *Hypochoeris setosus* Wedd) and cushion plants (e.g. *Arenaria musciformis* Wall.). Human disturbance in the area is mainly associated with very extensive cattle and horse grazing (Molinillo and Monasterio 1997). Fires are not a common practice in the Venezuelan páramos (Sarmiento and Llambí 2011) and are not a source of disturbance in these high páramos.

Data collection and analysis

Plant scale. At each of the four study sites, we randomly selected 20 *H. laricifolium* individuals with crown diameter between 70 and 100 cm. A circular plot of 80 cm diameter was centred on every shrub delimiting the area underneath the crown.

We determined the total number of vascular plant species present. We also quantified the cover of conspecifics (generally much smaller individuals under the crown of sampled *H. laricifolium* individuals) and heterospecifics. Species cover was estimated by using the point-quadrat method (Greig-Smith 1983), vertically placing a 1-m long thin rod at random inside each plot, registering in each case the species that made contact with the rod (60 sampling points per plot). To compare community structure under the direct influence of the shrub with the local community not directly influenced by it (thus minimising the possible confounding effects of habitat patchiness at larger scales), the same measurements were taken in 20 circular plots of the same diameter established outside each selected shrub, 0.5 to 1.5 m from the canopy edge, in a random compass direction. The plant-scale data were obtained between November 2009 and February 2010. In total, 160 plots were studied. Plant names followed the nomenclature of The Plant List (2013).

We compared the average cover of conspecifics and of each of the other vascular plants under and outside shrub crowns using a paired *t*-test. This analysis was made independently at each site because of considerable differences in species composition and abundances between sites. The following attributes were also estimated in each plot under and outside crowns: species richness, Shannon's diversity (H') and total plant cover. These data were then analysed using a two-way permutational analysis of variance (Permanova+ for Primer 6.0, Anderson et al. 2008). We considered the local sampling

situation as a fixed factor with two levels (under crown vs. outside) and analysed the effect of heterogeneity between sites, including it as random factor with four levels (our four study sites).

Patch scale. One 20 m × 20 m grid, comprising 400 square cells of 1 m × 1 m, was randomly positioned in each of the four study sites, with one axis perpendicular to the main slope. Within every cell, we counted the number of individuals of *H. laricifolium* and other species that occupied the upper vegetation stratum (caulescent rosettes of *E. schultzii* and *E. spicata* and the forbs *Oxilobus glanduliferus* (Sch. Bip.), *Blackiella bartsiifolia* (S.F. Blake) Cuatrec., *Monticalia imbricatifolia* Sch. Bip. ex Wedd.*, C. fissifolia* and *Lupinus eremonomus* C. P. Sm.). Some of these species, such as the caulescent rosettes, could also have the potential to act as foundation species, so it was important to analyse their spatial relationships with *H. laricifolium*. Their abundances at our study sites were lower than those of our focal shrub. Counting the plants in the lower stratum in each cell proved too time-consuming, so they were not included at this scale. Sampling was carried out between September and October 2009. To obtain more detailed information about the structure and distribution of the populations of *H. laricifolium*, we classified individuals into two height classes: large (>30 cm above ground) and small (<30 cm). An individual was considered to lie within a cell if it contained the central point of the crown. It is important to note that the *H. laricifolium* individuals used for analyses at the plant scale were contained within these grids or immediately adjacent to them.

Superficial rock cover was visually scored in each cell, assigning values between 0 and 4 after dividing the cell in four smaller quadrats. Hence, if one quadrat was covered in more than 50% by rocks a value of 1 was assigned, and so on up to a maximum of 4 when all four quadrats showed more than 50% of rock cover.

Changes in the intensity and scale of spatial associations were analysed by using non-centralised radial covariance functions, which measure the co-variation of pairs of observations at a given radial distance. The expected value for these functions under complete spatial randomness is 1; values >1 indicate spatial aggregation at a given distance, while values <1 indicate segregation (see Purves and Law 2002 and Llambí et al. 2004). For analysing the spatial distribution of *H. laricifolium* (small and large individuals independently) we calculated auto-covariance functions. Using spatial cross-covariance functions we also analysed the spatial relationships between small and large shrubs; large shrubs and other species in the upper vegetation stratum; and large shrubs and superficial rock cover. To test for departures from randomness we used Monte Carlo procedures, independently randomising the data of each grid 1000 times to generate 95% confidence intervals for the covariance functions. All calculations

were made using *C*++ (see Llambí et al. 2004 for details). In the case of the analysis of the intraspecific spatial relationships, we calculated average covariance functions across the four sites, after verifying that at all sites there was a consistent spatial pattern (i.e. the intensity of conspecific spatial aggregation decreased monotonically with distance). For the cross-covariance analysis of the spatial relationships between *H. laricifolium* and heterospecifics, the functions were calculated independently in each site given the marked differences in heterospecific abundances between sites.

Site scale. We calculated total observed species richness for all 20 plots both under and outside the crown of the shrub, constructed species accumulation curves (using the Mao Tau rarefaction procedure) and estimated maximum species richness for each condition in each study site using the Chao 2 non-parametric estimator (EstimateS 8.2.0, Colwell 2009).

Finally, to obtain an integrated view of differences in community structure between areas located under *H. laricifolium* crowns and outside, we also constructed a matrix with the cover of all species found in the plots sampled in each site. These matrices were analysed by using non-metric multidimensional scaling ordination (NMDS), with Bray-Curtis as dissimilarity metric (Primer 6, Clarke and Gorley 2006; see also Clarke 1993). We tested for differences in community similarity between local conditions (under crown vs. outside, fixed factor) and between sites (four study areas, random factor) by using a multivariate two-way permanova on the integrated dissimilarity matrix for all sites (Permanova+ for Primer 6, Anderson et al. 2008). Hence, the between-site scale was explicitly incorporated here as a random factor in the analysis. To facilitate the interpretation of results the NMDS ordinations are presented separately for each site (the integrated NMDS for all sites was too complex to interpret visually).

Results

Plant scale

The cover of conspecific *H. laricifolium* individuals was significantly higher in the plots under the shrub than outside at all sites (Figure 2). The cover of some species was consistently higher under the shrub (*C. fissifolia*, *Lucilia venezuelensis* Steyerm. and *S. formosus*) than outside; others had a higher average cover outside (*R. acetosella* and *A. pulvinata*); and yet other species did not differ significantly between conditions (*H. setosus, O. epilobiifolia, Belloa longifolia* Cuatrec. & Aristeg. and *Geranium multiceps* Turcz.). In addition, there were species that showed variable patterns at different sites (Figure 2).
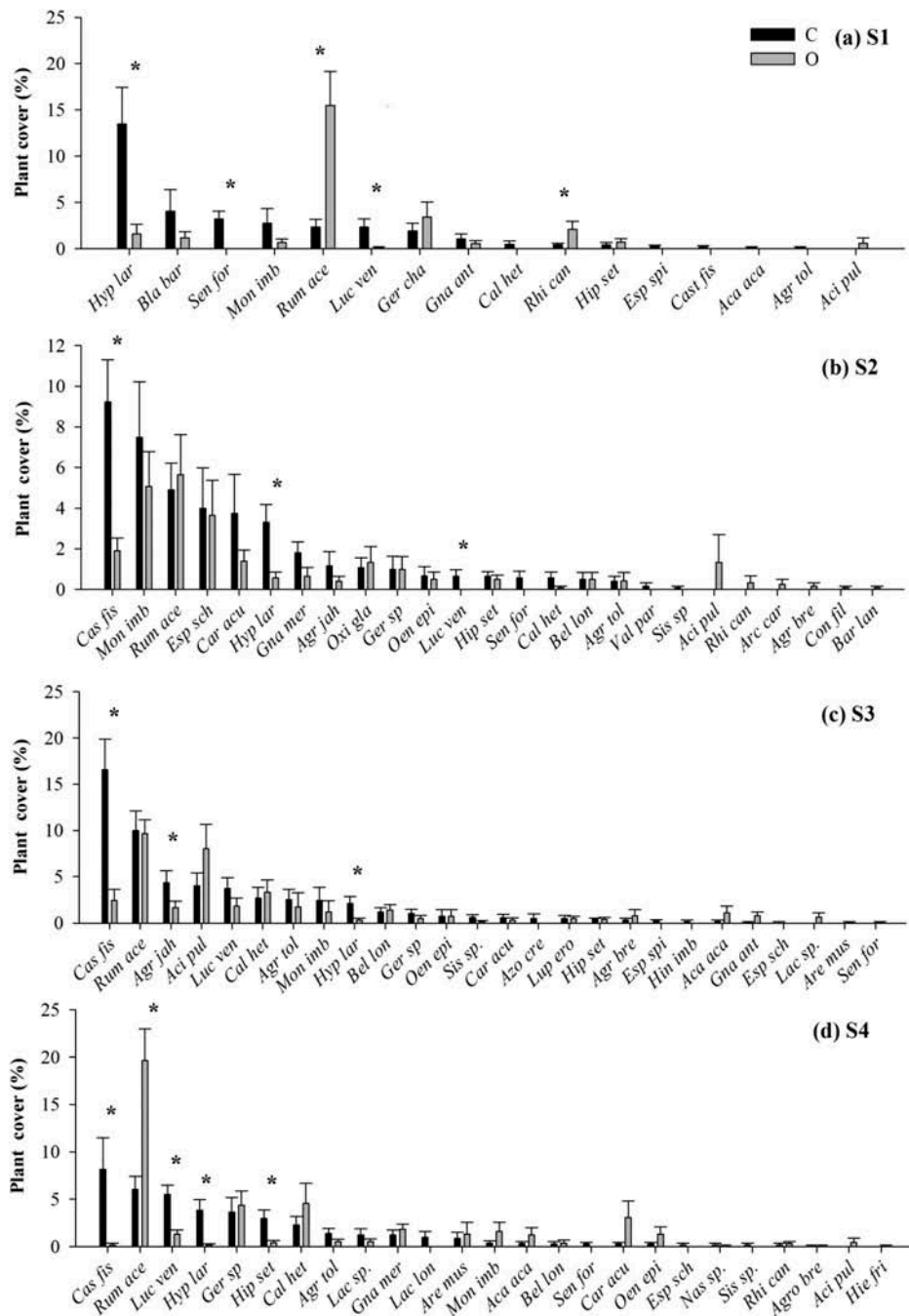
Figure 2. Rank abundance diagrams of each species found under *Hypericum laricifolium* (C, dark bars) and outside (O, light bars) in each of the four study sites (S1 to S4) in the Piedras Blancas páramo, Venezuela. Abundance is represented as mean percentage cover for each species ± standard error. * Indicate significant differences ($P < 0.05$) based on a paired *t*-test. Species are ordered according to their abundance under the shrub's crown. The complete names of all species are presented in Table 1.

Average local species richness and Shannon diversity were consistently higher under the shrub than outside (Figure 3; two-way permanova, $P < 0.001$). There were also significant differences in average richness and Shannon diversity among sites ($P < 0.05$), but no significant interaction between both factors (local condition and site). In the case of average plant cover, we only found statistically significant differences among the four study sites ($P = 0.0042$), but not between the plots under the shrub and those placed outside ($P = 0.159$).

Patch scale

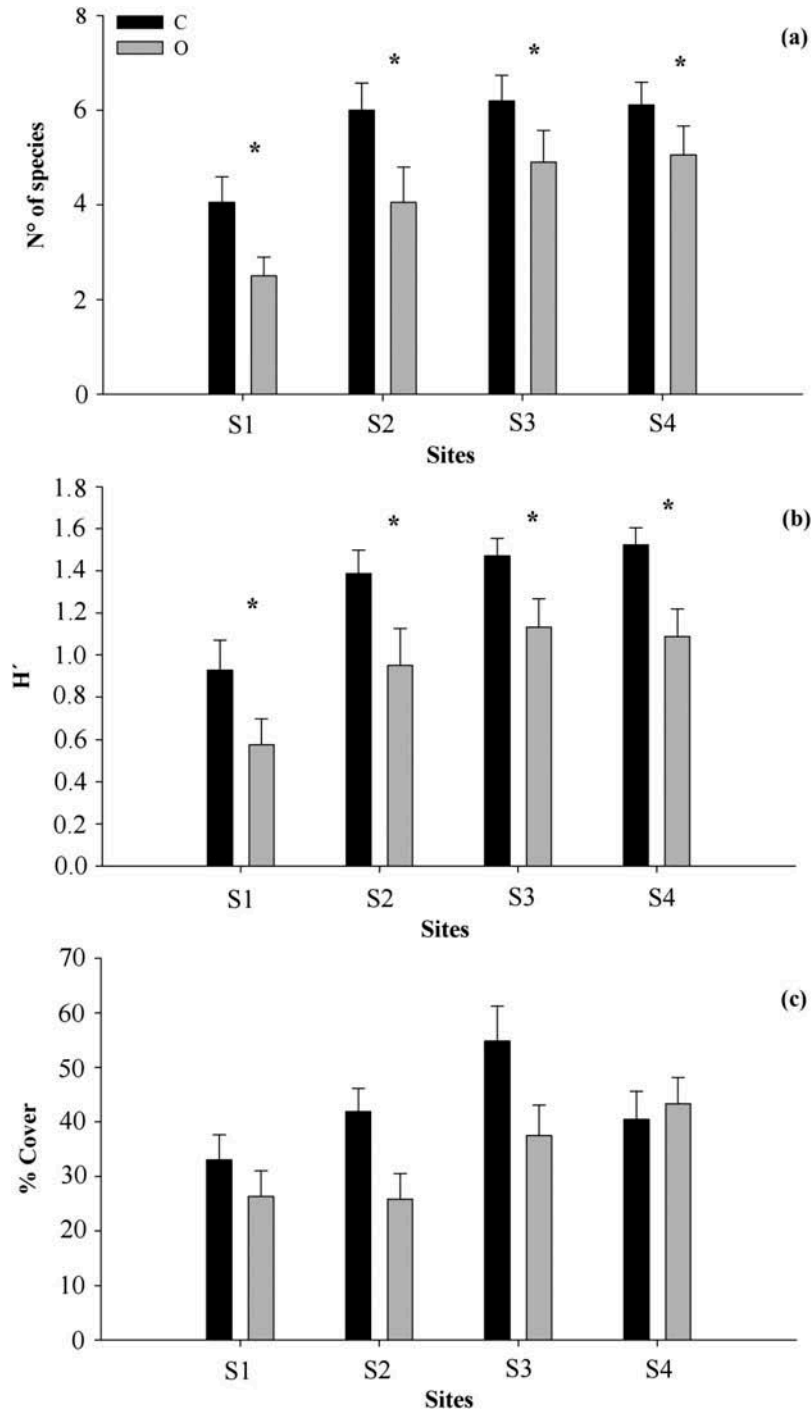The density of *H. laricifolium*, superficial rocks and co-dominant species in the upper stratum showed a

Figure 3.   Average (± standard error) of plant community attributes quantified under *Hypericum laricifolium* (C, dark bars) and outside (O, light bars) in each of the four sampling sites (S1 to S4) in the Piedras Blancas páramo, Venezuela. Species richness (a); Shannon´s species diversity (b); Total plant cover (c). For species richness and diversity there were statistically significant differences both between conditions (permanova, * $P < 0.001$) and between sites (permanova, $P < 0.05$), with no significant interaction. For total plant cover there were only significant differences between sites ($P = 0.0042$), but not between inside and outside shrub ($P = 0.159$), with no significant interaction ($P = 0.157$).

patchy spatial distribution within grids in all study sites (see examples in Figure 4). Total *H. laricifolium* densities ranged between 0.22 and 0.79 individuals m^{-2} (mean=0.50 ± 0.15) across sites. The composition and density of the other species in the upper

stratum were also variable between the grid plots analysed.

The average auto-covariance functions across grid plots indicated a significant spatial aggregation in both small and large individuals of *H. laricifolium*
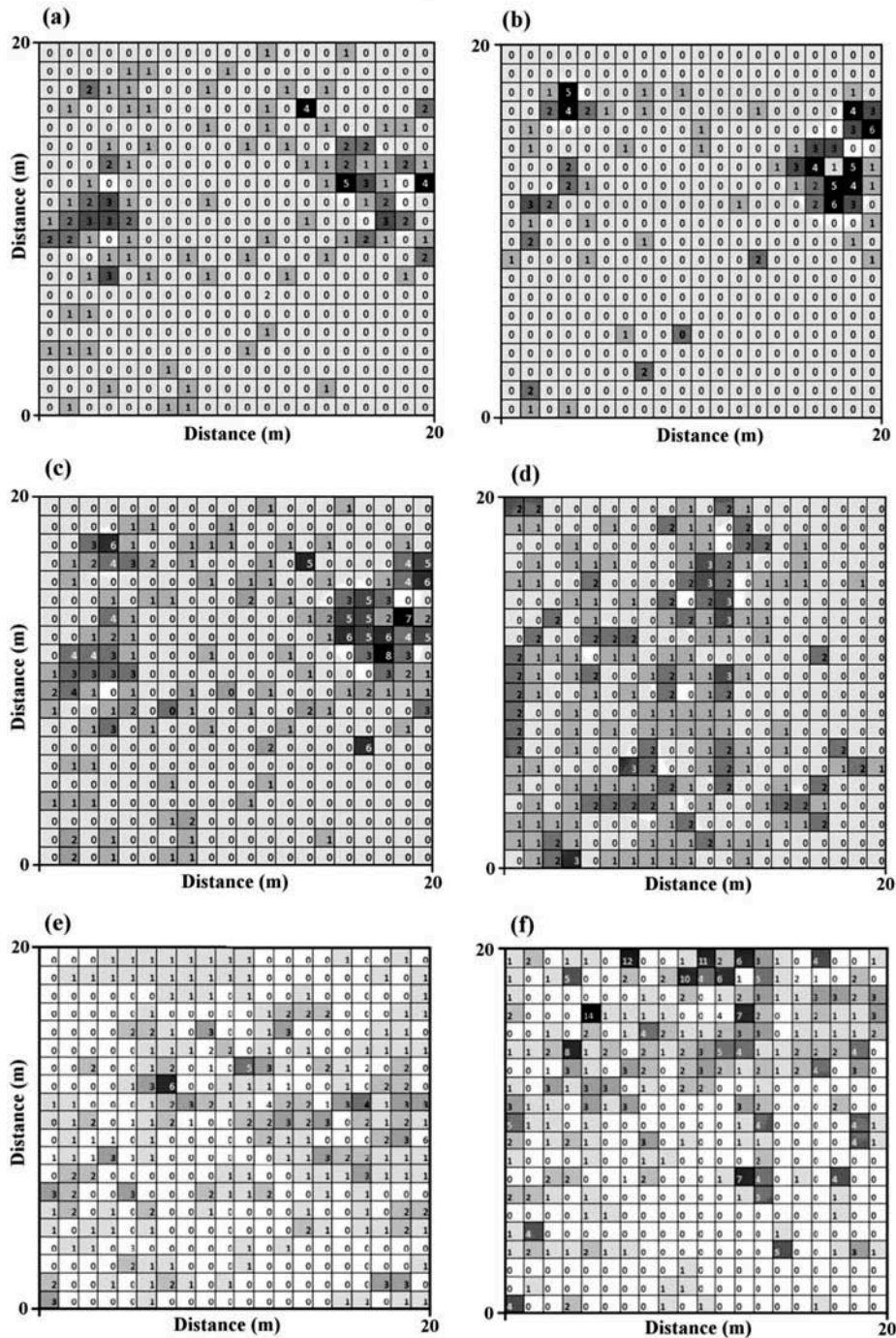
Figure 4.   Example for one of the study sites in the Piedras Blancas páramo, Venezuela of the spatial maps of: *Hypericum laricifolium* large shrubs (a), small shrubs (b), entire population (c), rocks as a micro topographic element (d), and co-dominant species in upper vegetation stratum; *Monticalia imbricatifolia* (e) and *Espeletia spicata* (f). Numbers and colours correspond with densities in each cell (except for rocks, in which a 0–4 scale was defined based on cover in the 1 m × 1 m cells).

(Figure 5(a) and (b)). In both cases, maximum aggregation intensity was found at the 1-m scale, with more intense aggregation for small individuals, densities being 2.5 times higher than the expected value under complete spatial randomness in neighbouring cells. The spatial scale of aggregation or average patch size (the radial distance where the covariance function crosses the upper 95% confidence interval) was similar for small and large individuals (extending to 4 and 5 m, respectively).

There was also spatial aggregation between large and small individuals (Figure 5(c)): the average cross-covariance was significantly higher than 1 up to 3 m in radial distance. Regarding rocks, the cross-covariance

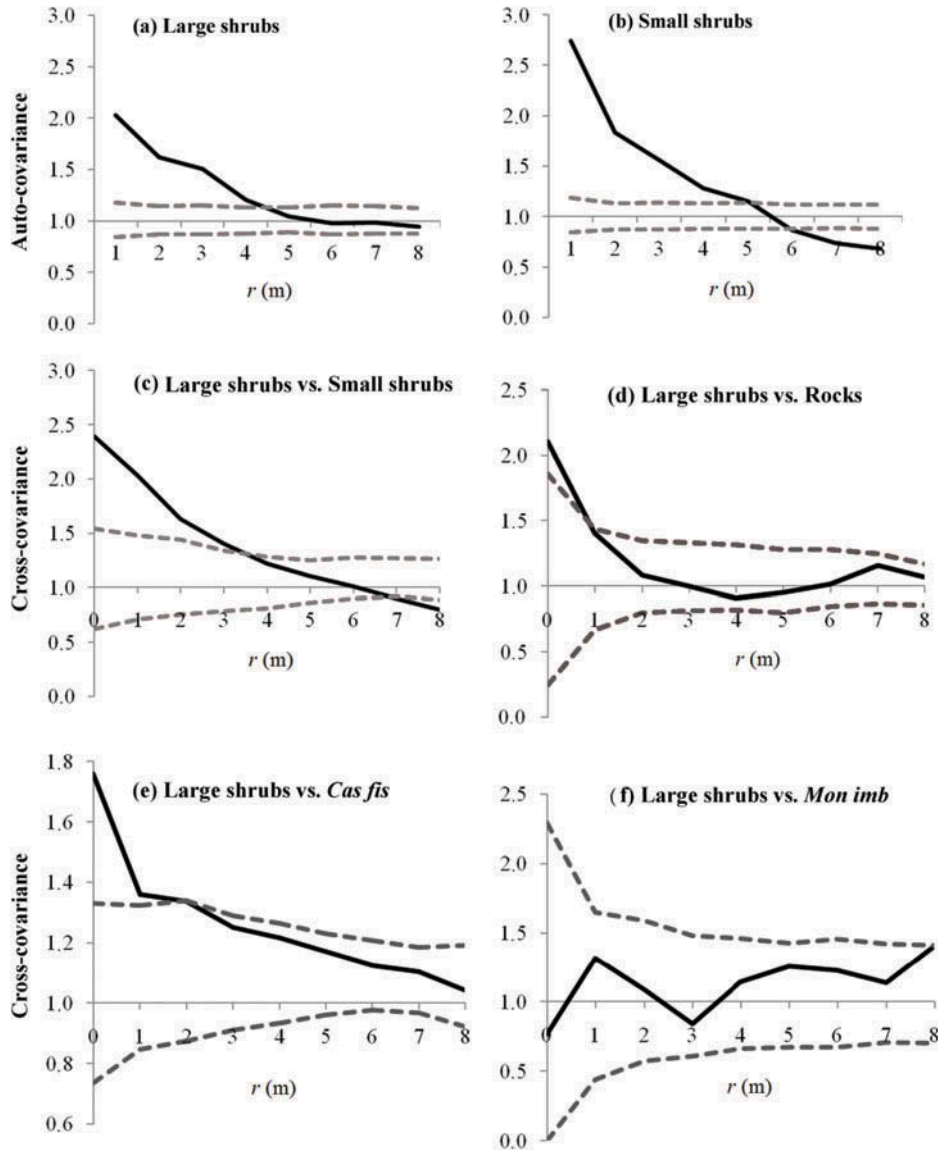Figure 5.   Across-site average auto-covariance functions (continuous line) for *Hypericum laricifolium (Hyp lar)* as a function of radial distance r, with 95% confidence limits based on Monte-Carlo simulations (dashed lines). Large shrubs (a); small shrubs (b); cross-covariance functions between large and small shrubs (c); large shrubs and rocks (d); large shrubs and other co-dominant species: *Castilleja fissifolia* (e); and *Monticalia imbricatifolia* (f).

functions showed an independent (random) spatial relationship with large shrubs in sites 1 and 4 (data not shown) and a positive spatial association in sites 2 and 3. In these cases, the spatial association was only significant at the within-cell scale (<1 m, see example in Figure 5(d)).

In relation to other species in the upper vegetation stratum, the resulting cross-covariance functions were consistent among the four sites for some species. *Castilleja fissifolia* always showed a positive association with shrubs (cross-covariance significantly higher than 1 up to 2 m), while *M. imbricatifolia* was in all cases spatially independent of shrubs (Figure 5(e) and (f)). For the other species, including large caulescent rosettes, results were variable across sites (ranging

between independence and spatial aggregation at scales between 1 and 6 m). However, no species in the upper stratum showed local intra- or inter-specific spatial segregation (i.e. regular or over-dispersed patterns) with respect to conspecifics or *H. laricifolium*.

Site scale

Species accumulation curves (Mao Tau rarefaction) for total observed species richness showed very similar values under the shrub and outside of it at three of the four study sites (ranging between 19 and 23 species). In all cases, except for site 2-outside, the observed number of species was only slightly below the estimated maximum richness based on the Chao 2 estimator (Figure 6). We found no
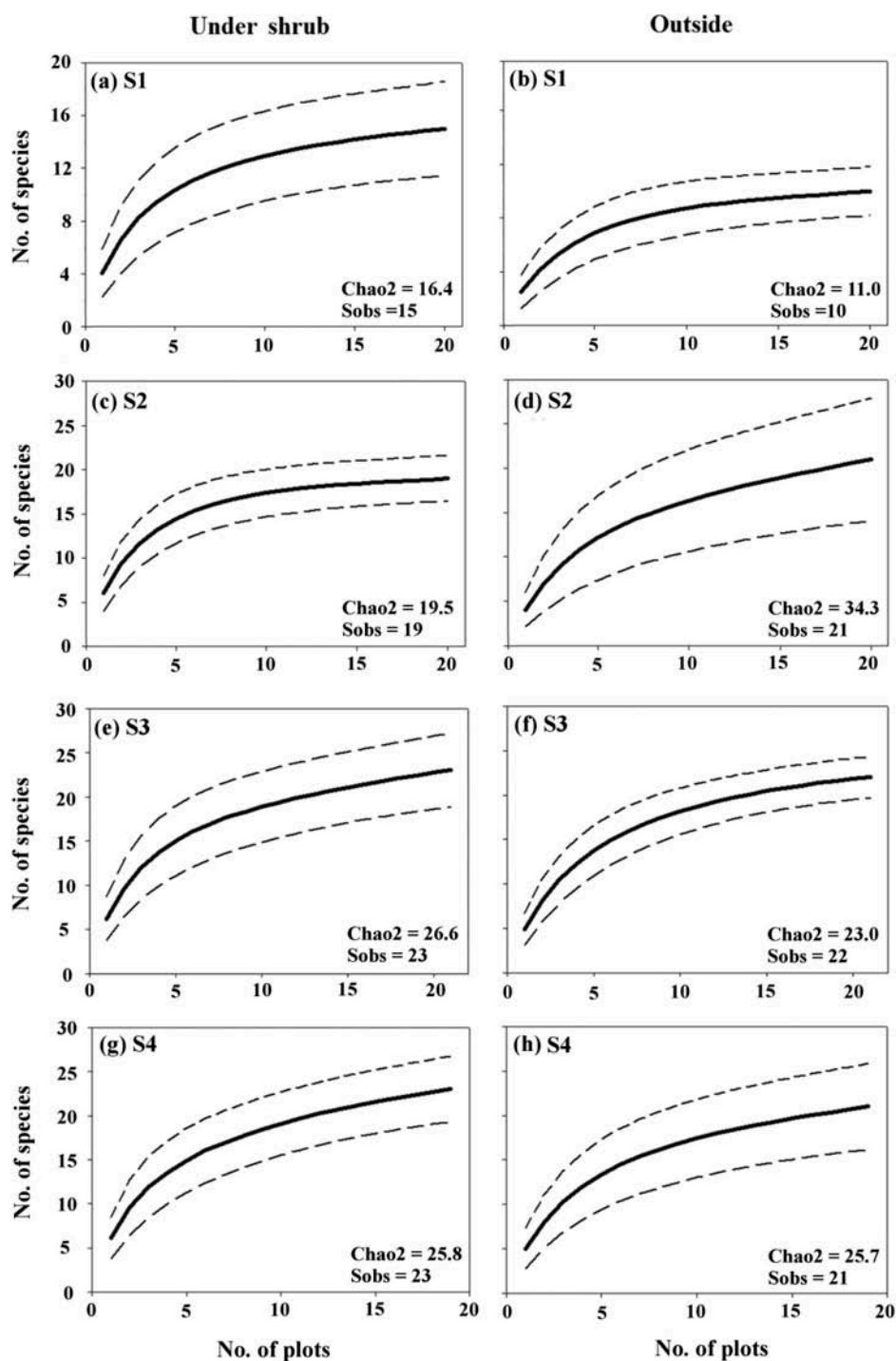
Figure 6.   Species accumulation curves (Mao Tau function) based on the sampling effort made in the two habitat conditions studied (under *Hypericum laricifolium* shrubs and outside) at the four sampling sites (S1 to S4) in the Piedras Blancas páramo, Venezuela. Solid lines, rarefaction curve; dashed lines, 95% confidence intervals. Sobs, observed species richness. Chao2, estimated species richness for 20 samples.

consistent evidence across sites of species being present exclusively outside or inside of the shrub (see Table 1).

The NMDS ordination analysis grouped the plots under and outside of the shrub in different sides or the diagrams, reflecting general differences in community structure between the two sampling conditions (this is

particularly evident in site 4, Figure 7). However, the dispersion of data points suggests some degree of overlap in the patterns of species abundances between plots under the shrubs and outside.

The permanova analysis on the integrated Bray-Curtis dissimilarity matrix across sites and local

Table 1. List of species sampled in the four study sites related to their presence (x) under the shrubs and in open areas (outside). Classification according to Briceño and Morillo (2006).

Name	Abbreviation	Family	Under shrub				Outside			
			S1	S2	S3	S4	S1	S2	S3	S4
Acaulimalva acaulis	*Aca aca*	Malvaceae	X		X	X			X	X
Aciachne pulvinata	*Aci pul*	Poaceae			X		X	X	X	X
Agrostis breviculmis	*Agr bre*	Poaceae			X	X		X	X	X
Agrostis jahnii	*Agr jah*	Poaceae		X	X			X	X	
Agrostis toluscensis	*Agr tol*	Poaceae	X	X	X	X		X	X	X
Arcytophyllum caracasanum	*Arc car*	Rubiaceae						X		
Arenaria musciformis	*Are mus*	Caryophyllaceae				X			X	X
Azorella crenata	*Azo cre*	Apiaceace		X						
Bartsia laniflora	*Bar lan*	Orobanchaceae						X		
Belloa longifolia	*Bell lon*	Asteraceae		X	X	X		X	X	X
Blackiella bartsiifolia	*Bla bar*	Asteraceae	X				X			
Calamagrostis heterophylla	*Cal het*	Poaceae	X	X	X	X		X	X	X
Carex acutata	*Car acu*	Cyperaceae		X	X	X		X	X	X
Castilleja fissifolia	*Cas fis*	Orobanchaceae	X	X	X	X		X	X	X
Conyza filaginoides	*Con fil*	Asteraceae						X		
Espeletia schultzii	*Esp sch*	Asteraceae		X	X	X		X		
Espeletia spicata	*Esp spi*	Asteraceae	X		X					
Geranium chamaense	*Ger cha*	Geraniaceae	X				X			
Geranium sp.	*Ger sp.*	Geraniaceae		X	X	X		X	X	X
Gnaphalium antennaroides	*Gna ant*	Asteraceae	X		X		X		X	
Gnaphalium meridensis	*Gna mer*	Asteraceae		X		X		X		X
Hieracium frigidum	*Hie fri*	Asteraceae								X
Hinterhubera imbricata	*Hin imb*	Asteraceae			X					
Hypochaeris setosa	*Hip set*	Asteraceae	X	X	X	X	X	X	X	X
Hypericum laricifolium	*Hyp lar*	Hypericaceae	X	X	X	X	X	X	X	X
Lachemilla sp.	*Lac sp.*	Rosaceae				X			X	X
Lasiocephalus longipenicillatus	*Lac lon*	Asteraceae				X				
Lucilia venezuelensis	*Luc mer*	Asteraceae	X	X	X	X	X		X	X
Lupinus eremonomus	*Lup ero*	Fabaceae			X			X		
Monticalia imbricatifolia	*Mon imb*	Asteraceae	X	X	X	X	X	X	X	X
Nassella sp.	*Nas sp.*	Poaceae			X					X
Oenothera epilobiifolia	*Oen epi*	Onagraceae		X	X	X		X	X	X
Oxilobus glanduliferus	*Oxi gla*	Asteraceae		X				X		
Rhizocephalum candollei	*Rhi can*	Campanullaceae	X			X	X	X		X
Rumex acetosella	*Rum ace*	Polygonaceae	X	X	X	X	X	X	X	X
Senecio formosus	*Sen for*	Asteraceae	X	X		X			X	
Sisyrinchium sp.	*Sis sp.*	Iridaceae		X	X	X			X	
Valeriana parviflora	*Val par*	Caprifoliaceae		X						

sampling conditions showed a significant interaction between local conditions and sites (two-way permanova, $P < 0.001$). This indicates that differences in community structure between conditions (under crown vs. outside) changed across sites. Subsequent pair-wise analyses showed that there was a significant difference in community structure under the shrubs vs. outside in sites 1, 3 and 4 ($P < 0.05$), but nor for site 2 ($P = 0.059$).

Discussion

Plant scale

Our results suggest that the sclerophyllous shrub *H. laricifolium* can be considered a foundation or keystone species in these high Andean páramos, significantly modifying the local abundance of native and introduced species as well as increasing local species richness and Shannon diversity under its crown.

These effects on community organisation could be linked with the capacity of the shrub to alter micro-environmental conditions, reducing incident radiation, dampening oscillations in air temperature and humidity and decreasing soil water loss under its compact foliage, as was shown by Cáceres (2011) in our study site and by Farji-Brener et al. (2009) for a dominant shrub of the same genus (*H. irazuence*) in Costa Rica.

Moreover, for the forbs *S. formosus* and *C. fissifolia* and the small herb *L. venezuelensis* (the species that were consistently overrepresented under the shrub), Cáceres (2011) found significantly higher midday leaf water potentials for individuals growing under the shrub compared
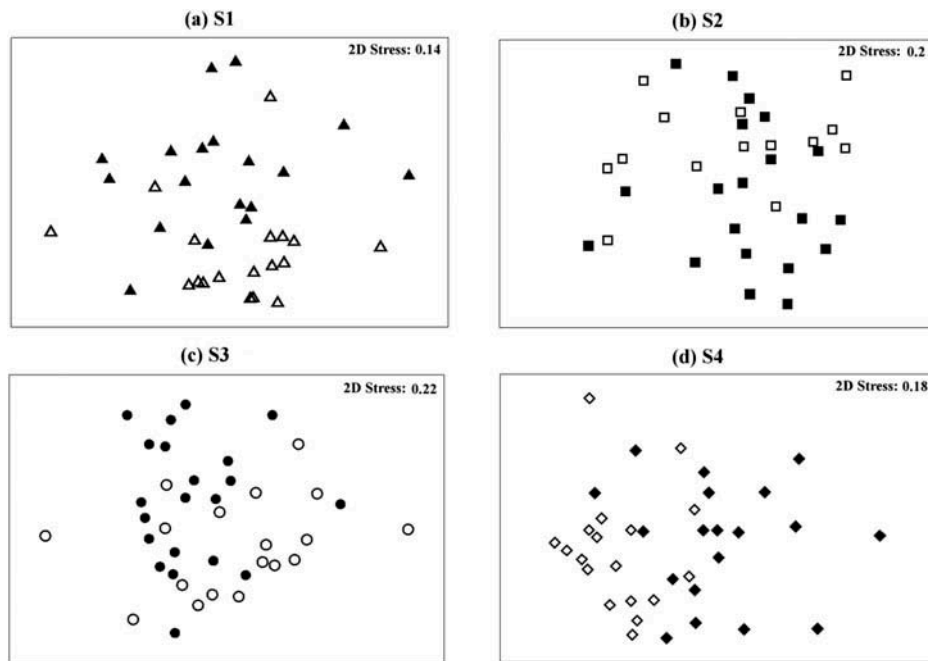
Figure 7.   Non-metric multi-dimensional scaling ordination (NMDS) based on Bray-Curtis dissimilarities in plant species cover within plots in each of the four study sites (S1 to S4) analysed separately at Piedras Blancas páramo, Venezuela. Under shrub conditions are represented with solid symbols, while outside shrubs conditions, centred on random points, are represented with an open symbol.

with those growing in nearby open areas. However, in the case of *C. fissifolia,* the positive association with the shrubs could be related to parasitic interactions instead of facilitative ones, as the *Castilleja* genus (Orobanchaceae) is widely known for its hemiparasitic character (Heckard 1962, Adler 2003).

In contrast, the exotic forb *R. acetosella* and the cushion *A. pulvinata* showed consistently higher cover outside the shrub. Interestingly, both species have been reported as indicators of páramo degradation by grazing (Molinillo and Monasterio 1997). *Rumex acetosella* has also been reported as a dominant ruderal species (sensu Grime 1977) in early successional fields after agricultural disturbance in the páramo (Sarmiento et al. 2003). Here, the negative spatial association between *R. acetosella* and *A. pulvinata* with *H. laricifolium* could result from: a) the protection from grazing induced by the crown, which could provide a refuge for other more palatable plants, increasing competition for these ruderal species; or b) the shading effect induced by the shrub's crown, which could negatively affect these heliophilous species. In fact, Cáceres (2011) showed that the light interception capacity of the crown of the shrub can be as high as 80% compared with the total amount of radiation that reaches soil surface in open areas.

The reduced abundance of the exotic *R. acetosella* under the shrub (the only introduced species found in our sites) contrasts with results from several studies in the high Andes of Chile, which indicate a facilitation effect by cushions for alien species, such as *Taraxacum officinale* F.H. Wigg. and *Cerastium arvense* L. (e.g.

Cavieres et al. 2005, 2007; Badano et al. 2007). Probably life-forms of contrasting architectures (i.e. shrubs vs. cushions) could have different effects on the invasion success of exotic species via differential effects on aboveground vs. below-ground resources. This hypothesis would need to be evaluated with experimental and ecophysiological research strategies.

We evidenced the role of *H. laricifolium* in favouring species richness and Shannon diversity at the plant scale, with a consistent and statistically significant pattern of higher average species numbers under shrubs across sites. However, we still need to explore the consistency of this result in response to temporal rather than spatial variability (e.g. between seasons or years, see Tielbörger and Kadmon 2000). Two other key aspects regarding spatio-temporal effects can also be explored: (a) variations in community structure under the shrub resulting from changes in its ontogenetic development (see Soliveres et al. 2010); and (b) changes in the spatial relationships of foundation species in the páramo in successional scenarios (e.g. Llambí et al. 2004).

Patch scale

Expanding the analysis from plant to patch scale allowed us to explore if the local association patterns detected could be linked with processes operating at larger scales (see Wiegand et al. 2006). Our results using spatial covariance functions showed that the aggregation of *H. laricifolium* conspecifics extended up to 4–5 m in distance. We also found aggregated interspecific spatial relationships

between our focal shrub and other species in the upper stratum extending beyond the plant scale. In particular, the forb *C. fissifolia,* which was consistently overrepresented inside the shrub, also showed a consistent aggregated spatial relation with adult shrubs up to 2 m distance.

This evidence suggests that *H. laricifolium* could co-occur in higher abundances with other species within more favourable habitat patches (e.g. in terms of water or nutrient availability). Hence, we could confound positive spatial association patterns induced by abiotic heterogeneity, with those directly attributable to local biotic interactions, such as facilitation. Here, this led to paring the plots used for analysing plant-scale effects of the shrubs (within a maximum of 1.5 m), so that those placed outside the crowns could be interpreted as areas within the same patch.

Small surface rocks could be one of the factors responsible for generating within-site abiotic heterogeneity. We found a positive association between large shrubs and rock cover in two of the four sites (but only at a within-cell – 1 m × 1 m scale). Positive spatial associations between tropical alpine plants and surface rocks seem to be a common phenomenon reported in other studies (e.g. Pérez 1992; Kleier and Lambirinos 2005; Llambí et al. 2013). Rocks have been shown to increase minimum temperatures and affect water availability in tropical high mountains, influencing local species distribution patterns (Pfitsch 1988; Goldstein et al. 1994; Pérez 2009).

In the case of the spatial aggregation found between large and small *H. laricifolium* shrubs, another key underlying process could be clonal-vegetative reproduction, given that many of the small individuals recorded in our study originated from plant rhizomes emerging under the crown of a nearby adult.

We did not find evidence of intraspecific spatial segregation for large individuals of *H. laricifolium*, which have been commonly reported for other dominant shrubs in unproductive environments, such as tundra and deserts (e.g. Fonteyn and Mahall 1981; Chapin et al. 1989). Regular patterns in severe environments have generally been attributed to neighbourhood-dependent mortality due to intense competition for edaphic resources. We did not find evidence either for interspecific spatial segregation between dominant species in the upper stratum, a process known as 'heteromyopia' which can result from intense competition (see Murrell and Law 2003). Hence, our results at a patch scale suggest that both intraspecific and interspecific competition could be overridden in these high páramos (in terms of the net outcome of the interactions) by positive plant–plant interactions and/or abiotic heterogeneity, which could generate favourable habitats at plant to patch scales, promoting positive spatial relations of conspecifics and heterospecifics.

Site scale

An integrated analysis of the communities present under *H. laricifolium* shrubs vs. those present outside (using NMDS ordination) support the idea that shrubs can modify patterns of species abundance at the site scale. However, while at the plant scale the areas under the shrub crowns contained, on average, more species than equivalent open areas, this did not seem to result in a clear increase in total species richness at the site/community scale (at least when comparing the areas under the shrub with nearby areas outside). These apparently contradictory results can be explained by considering that the higher average richness in plots under the shrubs seems to be compensated by a significantly higher variability in species richness among plots in open areas vs. those inside shrubs (*P*=0.015, '*perm-disp*' homogeneity of variance permutation test, Anderson et al. 2008); while many plots in open areas had zero species present, a few showed species numbers as high as those found inside of the shrub (with a maximum of 10 species), accounting for the similar site-scale species richness found in both conditions. This suggests that shrubs could have a stabilising effect on the spatial variability of species richness in the community.

Further, we did not find compelling evidence for species being present exclusively under or outside of the shrub (see Table 1). Hence, there is no evidence of specialist species in terms of local habitat preferences. However, a higher number of replicate plots may be necessary to achieve complete saturation of the species accumulation curves, so that site-scale effects of shrubs can be determined with more certainty.

Our results contrast with those reported in the high páramos in Ecuador (Sklenár 2009) and the high Andes in Chile (e.g. Badano and Cavieres 2006; Cavieres and Badano 2009). They have shown that dominant cushions increased species richness at the site scale even in cases where they did not have a significant local effect on average species richness and diversity (Badano et al. 2006).

Three hypotheses may be further explored to explain the divergence between our results and those of other studies with cushions along the Andes. First, a possible recent increase in the abundance of *H. laricifolium* in these high-elevation sites could help to explain why we still do not have clear evidence for processes of niche expansion and evolution linking the presence of particular plant species exclusively to the presence of the shrub (which was studied at the upper end of its elevation range). Second, the different modes in which contrasting life-forms modify their local micro-environment (e.g. shrubs vs. cushions) could be important in explaining the way in which they, in turn, alter plant community organisation. Third, it is possible that the Mediterranean climate characteristic of most sites studied in Chile (with low summer precipitations, Cavieres and Badano 2009) could impose more stressful conditions than those experienced in our páramo sites, which could, in turn, promote a stronger facilitation effect of foundation species on community species richness.

Between-sites scale

We interpreted the between-site scale as a transversal axis, evaluating the consistency of our results at all previous

scales (i.e. plant, patch and site scales). Many results were consistent between sites: e.g. differences in average species richness and Shannon diversity between areas under the shrub and outside. However, other patterns detected showed different responses among sites. For example, shrubs were positively associated with surface rocks in two out of four sites and community structure between areas under the shrub and areas outside was significantly different in three out of our four study sites. This supports the idea that spatial heterogeneity at a regional scale can modulate the spatial outcome of plant community assembly (see Badano et al. 2005; Medina et al. 2006).

Conclusions

Although we are aware that the approach presented here can only be considered as a starting point to fully explore scale implications on the study of plant–plant interactions, our results illustrate the importance of integrating multiple spatial scales in the analysis (see Badano et al. 2010). In particular, these findings suggest caution when interpreting results based on single scales or single sites (ignoring the problems implicit in spatial pseudo-replication, see Hurlbert 1984), especially if we consider the marked heterogeneity that characterises alpine ecosystems (Körner 1999; Sarmiento and Llambí 2004). First, we showed how conclusions can differ not only when analysing the role of foundation species on plant richness at plant vs. site scales but also when comparing nearby sites in the same region. Second, we showed the usefulness of combining spatial analyses at plant and patch scales to explore the possible importance of processes that operate beyond the immediate plant neighbourhood domain. In particular, our results indicate that within-site abiotic/biotic patchiness (which can result in spatial aggregation beyond the plant scale), needs to be acknowledged to avoid confounding the net effects of direct plant–plant interactions with those attributable to other factors, such as shared habitat preferences between species or clonal reproductive strategies. This requires knowledge of the spatial extent of patchiness, so that appropriate paired observational or experimental designs can be applied.

This study also shed some light on the application of alpine facilitation theory (mostly based on mid-latitude research with cushion plants as facilitators) to the diverse vegetation of high tropical ecosystems, where other large and long-lived perennial life-forms (e.g. sclerophyllous shrubs, giant rosettes) have the potential to act as foundation species. In particular, our results with shrubs do not support the hypothesis of a positive/facilitation effect of foundation species on community diversity. Our findings also suggest that shrubs could differ from cushions in their effects on ruderal exotic species (e.g. via shading or grazing exclusion effects). In addition, in these young and relatively mesic páramo ecosystems (which attained present-day altitudes in the last 3–5 million years, Smith and Cleef 1988), there could have been less scope for the evolution of strong facilitative interactions, which would link increases in diversity with the presence of foundation species.

Finally, we consider that further research is needed to bridge the gap between the study of patterns of spatial plant interactions and the processes that underpin community organisation in tropical alpine environments (see also Anthelme and Dangles 2012). Particular emphasis should be placed on comparing the effects of foundation species of contrasting life-forms on resource and non-resource abiotic drivers along severity gradients (Maestre et al. 2009), and on studying their effects on plant abundance and performance integrating different research strategies (e.g. ecophysiology, population dynamics, experimental manipulations).

Notes on contributors

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