

1 **Linking patterns and processes through ecosystem engineering: effects of shrubs on microhabitat**
2 **and water status of associated plants in the high tropical Andes**

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5 Plant Ecology.

6 DOI: 10.1007/s11258-014-0429-5

7 Received: 1 July 2014/ Accepted: 10 November 2014. Published online: 20 November 2014.

8 <http://link.springer.com/article/10.1007/s11258-014-0429-5>

9 *Abstract*

10 Studies on alpine and semi-arid environments indicate that plants that act as ecosystem engineers improve
11 microhabitat conditions and modify local plant abundance and diversity. However, few studies have linked these
12 patterns with the physiological responses of associated species. We analyze the role of a dominant shrub (*Hypericum*
13 *laricifolium*) as an ecosystem engineer in páramo ecosystems at two altitudes (3715 m and 4300 m) in the
14 Venezuelan Andes. Superficial soil temperatures, soil water content and organic matter were compared under the
15 crown and outside. We selected species with positive and negative spatial relations with the shrub and compared
16 their midday leaf water potentials and turgor loss points in individuals growing under shrubs and outside. Results
17 show that *H. laricifolium* dampened temperature oscillations and increased soil water and organic matter contents,
18 the effect being more pronounced at the drier, lower elevation site. While positively associated forbs showed an
19 improvement in their water status when growing under the crown, the species with the lowest water potentials and
20 higher water-stress tolerance were grasses with a negative spatial relation with the shrub; this was consistent at both
21 elevations. Moreover, the effect of the shrub on the water status and abundance of the exotic herb *Rumex acetosella*
22 changed from positive in the drier site to negative in the more mesic site. Our results provide mechanistic evidence
23 for interpreting spatial association patterns between nurse plants and other species in the alpine tropics. We propose
24 that stress resistance strategies (tolerance vs. avoidance) and origin (native vs. exotic) influence interactions with
25 ecosystem engineers.

26 *Key words:* drought resistance; facilitation; invasive species; plant-plant interactions; soil resources.

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2

1 *Introduction*

2 A dominant paradigm on the role of positive interactions in nature is that they prevail under intense consumer
3 pressure or under severe environmental conditions, when one or more plants reduce the physical stress affecting
4 associated species (Bertness and Callaway 1994). This facilitation may be direct (e.g. abiotic stress amelioration) or
5 indirect (e.g. competition intransitivity) (McIntire and Fajardo 2014). However, direct modification of the
6 microhabitat is the most common form for a species to facilitate establishment, growth and survival of others
7 (Callaway 2007). In many cases, studies on facilitation have focused on the analysis of the effects of so-called
8 ‘ecosystem engineers’ (EE), organisms that directly or indirectly control the available resources, generating changes
9 in both abiotic and biotic conditions; these species are able to create, maintain or destroy the habitat for other species
10 as they modulate the environment (Jones et al. 1997; Badano and Cavieres 2006).

11 Many studies on EE analyze plant spatial association patterns and microhabitat effects as a strategy for inferring the
12 net balance of facilitation and competition in the field (e.g. Valiente-Banuet et al. 1991; Cavieres et al. 2002;
13 Callaway et al. 2002; Sklenář 2009; Anthelme et al. 2011; Schöb et al. 2012). For arid environments, there is
14 evidence of increases in the availability of resources such as water and soil nutrients under EE (Callaway &
15 Pugnaire 1999). In this case, the most common mechanism proposed for the generation of positive interspecific
16 spatial associations is reduced incident radiation under the shade of nurse plants (typically shrubs), which in turn
17 reduces temperature amplitudes and evaporative demands and increases soil water availability (Holmgren et al.
18 1997; Holzapfel and Mahall 1999; Pugnaire et al. 2004). In alpine ecosystems, most studies on EE have focused on
19 cushion plants in mid-latitude areas (e.g. Badano et al. 2006; Cavieres et al. 2007) and the evidence suggests that
20 habitat enhancement typically occurs through the mitigation of non-resource type stressors (e.g. temperature, wind;
21 Körner 2003; Cavieres et al. 2006; Schöb et al. 2012).

22 However, remarkably fewer studies have analyzed the physiological mechanisms underlying these patterns, and
23 those available have mostly been carried out in mid-latitude Mediterranean environments. In a lowland semi-arid
24 ecosystem, Maestre et al. (2003) showed that a dominant tussock grass had a positive effect on photosynthetic
25 efficiency (measured through chlorophyll fluorescence) and survival of an associated native shrub. The same was
26 found by Cavieres et al. (2008) analyzing the effect of a dominant cushion plant on an exotic herb in an alpine
27 Mediterranean environment. Other studies in these ecosystems have also evaluated the physiological status of the
28 EE itself; Pugnaire et al. (2004) analyzed stomatal conductance, predawn leaf water potential, relative water content

1 and photosynthetic efficiency in several shrub species that act as EE, finding that the physiological status of the
2 nurse plant produces no apparent effect on the type of interaction with herbaceous beneficiaries. More recently,
3 Schöb et al. (2014) measured the water status of three herb species associated with a cushion; they showed that
4 while herbs are favored physiologically and reproductively when growing inside the cushion, the water status and
5 flower density of the nurse was negatively correlated with the abundance of the beneficiaries, revealing the existence
6 of feedback effects of beneficiaries on nurse plants.

7 Regarding tropical alpine ecosystems (TAE), the limited available evidence suggests that under these scenarios, a
8 diverse set of life forms of large size and longevity can act as EE (e.g. giant rosettes, cushion plants, trees)
9 modifying both the levels of available resources (water and nutrients) and non-resource stress factors (Anthelme and
10 Dangles 2012). Evidence on the role of EE in TAE comes mainly from páramos, a biome extending for over 2,150
11 km along the northern Andes, generally occurring above 3000 m (Monasterio 1980a). The páramos are ecosystems
12 with very particular characteristics associated to their tropical distribution combined with high elevations, including
13 high levels of incoming solar radiation and constant average temperatures throughout the year, but with marked
14 daily oscillations. Additionally, these environments show a wide range of rainfall and moisture patterns from hyper-
15 humid páramos with precipitation exceeding 4000 mm (especially in external flanks of the Andean Cordillera
16 exposed to the influence of the Amazon) to páramos with markedly seasonal precipitation (< 1000 mm) in
17 intermountain valleys (Monasterio 1980a; Sarmiento 1986; Azócar and Rada 2006). Hence, in the less humid
18 páramos, seasonal changes in precipitation may be the most important environmental pulse.

19 For the high Andean páramos or ‘super páramos’ (above 4000 m, Monasterio 1980a), several authors have
20 documented the effect of giant rosettes and cushion plants on the microenvironment associated with their local
21 neighborhood, reporting: a) increases in air and soil temperatures induced by *Coespeletia* and *Espeletia* stem
22 rosettes (Smith 1981; Pérez 1989) and changes in soil physico-chemical properties, increasing soil water holding
23 capacity, nitrogen and phosphorus content, cation exchange capacity and soil organic matter in areas under their
24 influence (Pérez 1992); and b) reductions in wind speed and increased levels of nutrients and water in *Azorella*
25 *aretioides* cushions (Anthelme et al. 2011). Similarly, *Polylepis sericea* forests have been described as thermal
26 refuges where freezing temperatures are much less frequent compared to open high páramo areas (Goldstein et al.
27 1994; Rada et al. 2011).

1 Regarding the effect of EE on the structure of high Andean páramo communities, Sklenář (2009) reported an
2 increase in richness and diversity of species establishing on cushion plants in the Ecuadorian Andes. Also in
3 Ecuador, Anthelme et al. (2011) reported changes in the type of interactions between the cushion *A. aretioides* and
4 its associated communities, supporting the stress gradient hypothesis (Bertness and Callaway 1994); they
5 documented a predominance of negative to neutral local spatial relations at 4400 and 4550 m and mostly positive
6 relationships at 4700 m. More recently, Cáceres et al. (2014) showed, through a multiple spatial-scales analysis, that
7 a widely distributed shrub (*Hypericum laricifolium*) can be described as a foundation species (*sensu* Ellison et al.
8 2005), significantly changing abundance patterns of other native and exotic species and generating a local increase
9 in plant diversity. Summing up, these studies suggest that the presence of several keystone species of different life
10 forms result in changes in micro-environmental conditions and community structure in the high Andean páramo.
11 However, to our knowledge, there are no previous studies in TAE which link local changes in limiting factors
12 induced by EE, with changes in the physiological responses of species that show different patterns of spatial
13 association with them. Consequently, our general aim in this study was to analyze some of the ecophysiological
14 mechanisms that could mediate the role of the widely distributed shrub *Hypericum laricifolium* as an EE on two
15 páramos at different altitudes (3715 and 4300 m) in an intermountain valley of the Venezuelan Andes.
16 Given that water availability is the most important annual pulse in these páramos and that *H. laricifolium* is a
17 dominant species in the upper vegetation stratum, which presents a thick and compact crown, we evaluate the
18 following hypotheses: 1) the areas under the crown of the shrub will present more favorable microenvironmental
19 conditions reducing temperature amplitudes and increasing water availability compared to adjacent exposed areas;
20 2) individuals of other plant species that have a positive spatial association with the shrub will show a more
21 favorable water status when growing under its crown compared to individuals growing in adjacent open areas; and
22 3) the effects induced on microenvironmental conditions and the water status of species positively associated with
23 the shrub will be more pronounced in areas with more limiting water conditions. Through this approach we attempt
24 to link the patterns of plant-plant associations with some of the underlying mechanisms, in order to contribute to the
25 understanding of the role that EE play in alpine community assembly.

26

1 *Methods*

2

3 *Study Area*

4 This work was carried out at two localities in the northeastern portion of the Sierra La Culata National Park, in the
5 Piedras Blancas páramo; one located in the Andean páramo belt at 3715 m a.s.l and the other in the High Andean
6 páramo belt at 4300 m a.s.l. Zoning of these ecosystems follows the system proposed by Monasterio (1980b) which
7 sets 4000 m as the approximate boundary between both belts, considering traces of Quaternary glacial events,
8 periglacial morphogenesis, and high cover of bare soil ($\geq 50\%$) as defining elements of the high Andean belt. This
9 region, influenced by the dry climate of the high Chama river basin, corresponds to the area with the lowest
10 precipitation in the high mountains of Venezuela. Total annual precipitation in the region varies from 860 mm (*Pico*
11 *El Águila* weather station, 4118 m) to 688 mm (*Mucuchíes* station, 2980 m). Less than 5% of this precipitation falls
12 during the dry season, which extends from December to March (Sarmiento 1986).

13 Both study sites were established on mountain slopes ranging between 15-25° in inclination, with a southeast
14 orientation and characterized by a high dominance of *H. laricifolium*, a widespread sclerophyllous shrub in the
15 Cordillera de Mérida and one of the most abundant species of the Venezuelan páramos. This species presents dense
16 rounded crowns with microphyllous, opposite, decussate and sessile leaves. In the Venezuelan Andes, it extends
17 from 2200 to 4300 m (Briceño and Morillo 2002), although we have recorded its presence up to 4500 m. Sampled
18 *H. laricifolium* individuals had crown sizes between 60 and 100 cm in diameter.

19

20 *Microenvironmental characterization*

21 Two sampling conditions were established at both altitudes: a) outside of the shrub, in open areas 1-2 m away from
22 the influence of *H. laricifolium*'s crowns; and b) under the shrub, in areas below the direct influence of *H.*
23 *laricifolium*'s crowns. Three replicate temperature sensors (TidbiTv2, HOBO Onset) were installed just below the
24 soil surface (-2 cm) for both sampling conditions at both altitudes, for a total of 12 sensors. Measurements were
25 carried out every hour for 13 consecutive days, seven corresponding to the end of the dry season and the remaining
26 six to the beginning of the wet season in March 2014. Measurements of soil relative water content (SWC) and
27 organic matter (SOM) were performed by taking soil samples from 5 to 10 cm below the surface at each altitude and
28 sampling condition. In each case, five paired replicates were used, randomly choosing the shrub and the area outside

1 of its crown. SWC measurements were carried out using the gravimetric method, calculating the percentage of water
2 in the sample through differences between wet and dry weights. SOM content determinations were obtained using
3 the weight difference between a sample of dry soil and the incinerated ashes of the sample. SWC and SOM
4 measurements were done during the dry season in February 2012.

5

6 *Local spatial relations*

7 In order to determine the type of spatial association (positive, negative or neutral) between *H. laricifolium* and other
8 species in each plant community at the two studied altitudes, 60 circular microplots (1 m diameter) were randomly
9 positioned, 30 placed outside the shrub and 30 under the shrub.

10 For each microplot, biovolume for each species (an estimate of above-ground biomass, see Sarmiento 2006) was
11 determined using a modified version of the point-quadrat method (Greig-Smith 1983). For this, a two-meter long rod
12 marked every 5 cm was used to count the number of sub-sections touched by each species at each sampling point.
13 This rod was placed vertically in 25 random sampling points inside each circular microplot. The biovolume of those
14 species within the microplot touched by the rod was calculated as the total number of contacts with all 5 cm vertical
15 sections divided by the total number of sampling points (25).

16 From the biovolume of each species, the Relative Interaction Index (RII) was calculated using the following
17 equation (modified from Armas et al. 2004):

18

$$RII_{BV} = \frac{BV_{US} - BV_{OS}}{BV_{US} + BV_{OS}}$$

19

20

21 Where BV_{US} corresponds to the biovolume of the species under the influence of the shrub and BV_{OS} to the biovolume
22 of the species in open areas. The values for RII range from -1 to +1, values below 0 indicating a negative spatial
23 relation and those above 0 a positive spatial association.

24 Based on this information, we selected species that satisfied two criteria: a) having a clear pattern of positive or
25 negative spatial association with our focal shrub in terms of the RII; b) being among the most abundant species in
26 the communities under the shrub or outside. At 3715 m the species selected were *Noticastrum marginatum* (rosette
27 forb), *Stevia lucida* (shrub), *Rumex acetosella* (erect forb) and *Vulpia myuros* (grass); At 4300 m they were
28 *Castilleja fissifolia* (erect forb), *Pentacalia imbricatifolia* (shrub), *Rumex acetosella* (erect forb) and *Acciachne*

1 *acicularis* (matt forming grass). For all of them we present the results of the RII with our focal shrub. These species
2 were then used for subsequent analysis of changes in their water status under the shrub vs. open areas at both study
3 sites.

4

5 *Water status of associated species*

6 For each selected species, five individuals were randomly chosen for each sampling condition to measure minimum
7 leaf water potential (Ψ_1^{\min}) in the field (between 10:00 and 12:00 h). These measurements were obtained on two
8 clear days during the dry season in February 2012. Similarly, five individuals from under the shrub and from open
9 areas were excavated with intact roots and soil and taken to the laboratory for the determination of leaf water
10 potential components via pressure-volume curves (Percy et al. 1989). Measurements were carried out after
11 rehydrating for 12 h in darkness.

12 Cell turgor pressure is essential for processes such as cellular growth and leaf gas exchange. When leaf water
13 potentials reach this threshold, i.e. the leaf water potential at turgor loss, key physiological processes for
14 maintenance and survival may be at risk. Consequently, comparisons between leaf water potential at turgor loss
15 (Ψ_1^{TLP}) and Ψ_1^{\min} measured in the field allowed us to make inferences on the effect of *H. laricifolium* on the water
16 status and level of stress induced by water limitations on the associated species. All field and laboratory leaf water
17 potential measurements were carried out using a pressure bomb.

18

19 *Data analysis*

20 The mean and standard deviation of temperatures measured hourly from the three replicate sensors, under both
21 sampling conditions and for both altitudes were calculated. A two-way permutational analysis of variance
22 (PERMANOVA+ for Primer 6.0, Anderson et al. 2008) was used to compare average SWC and SOM for each
23 situation, defining altitude (3715 vs. 4300 m) and sampling condition (outside the shrub vs. under the shrub) as fixed
24 factors. In addition, one-way PERMANOVA were performed using the sampling condition as a fixed factor to
25 compare average Ψ_1^{\min} obtained from individuals established under and outside the influence of the shrub for each
26 species; the same was done for the Ψ^{TLP} to determine if species showed osmotic adjustments.

1 A one-way PERMANOVA was also used to compare Ψ^{TLP} vs. Ψ_1^{min} values for a given species within each sampling
 2 condition, to evaluate the effect of the shrub on the water status of each species. In all PERMANOVA tests the
 3 number of permutations was set to 9999 and the probability of type I error was established at 95% ($\alpha=0.05$).

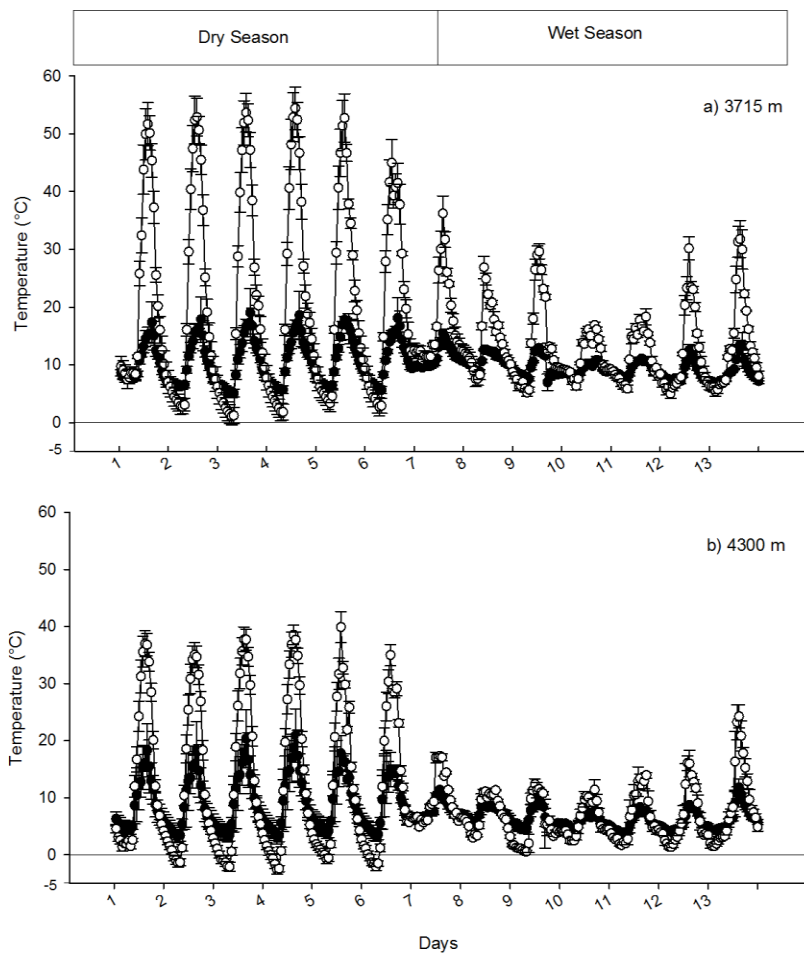
4 *Results*

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6 *Effects on microhabitat*

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Fig. 1 Daily courses of soil surface temperature (-2 cm) during the end of the dry season and start of the wet season in the two studied sites: (a) Andean páramo (3715 m); (b) High Andean páramo (4300 m). Average temperature \pm one standard deviation (n=3) measured hourly during thirteen continuous days. Under the shrub (●) and outside the shrub (○)

1 At 3715 m, the soil temperature range was considerably broader in open areas compared to beneath the shrub
 2 (Figure 1a). This trend was maintained during both dry and wet seasons although the difference was more evident
 3 during the dry period. Mean temperature for open areas was 17.2°C while under the shrub it was 10.1°C. Absolute
 4 maximum and minimum temperatures were registered in open areas, 58.7°C and -0.6°C, respectively, while under
 5 the crown, maximum and minimum values were 23.9°C and 4.4°C. Soil temperatures at 4300 m followed the same
 6 trends presented for the lower altitude (Figure 1b). However, temperature amplitudes were narrower in open areas.
 7 Mean temperatures were 9.8°C in open areas and 7.7°C under the crown of the focal species, while maximum and
 8 minimum soil temperatures were 42.4°C and -3.4°C outside the shrub compared with 27.4°C and 1.7°C,
 9 respectively, under the influence of *H. laricifolium*.

10 A significant decrease in average SOM was observed with increasing altitude ($p=0.0001$) (Figure 2). Similarly, a
 11 significant effect of the presence of the shrub on SOM content was observed, values being consistently higher under
 12 the shrub for both altitudes ($p=0.0455$). The relative change in SOM contents between both situations was 35.3% at
 13 3715 m and 38.6% at 4300 m. Moreover, the two-way PERMANOVA indicated there was no significant interaction
 14 between both factors (altitude and local condition, $p=0,108$)

15 Average SWC was higher at 4300 than at 3715 m ($p=0.015$, Figure 3). The presence of our focal species also had a
 16 significant effect, increasing the amount of soil water under the shrub's crown at both altitudes ($p=0.005$), with no
 17 significant interaction between both factors ($p=0.0928$). In this case, the relative change in SWC contents between
 18 both situations was 202.3 % at 3715 m and 28.8% at 4300 m.

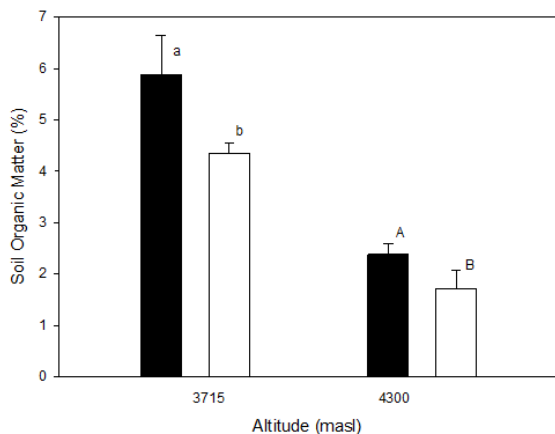
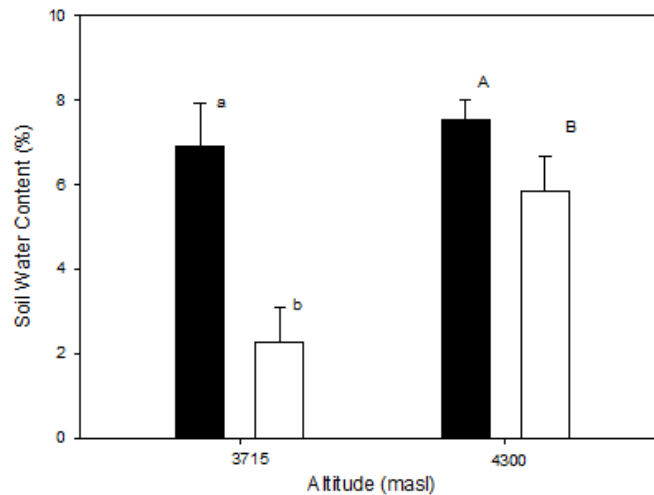


Fig. 2 Soil organic matter content (%) between 5-10 cm for two local sampling conditions (under shrub ■; outside shrubs □) in an Andean (3715 m) and High Andean (4300 m) páramo. Average ± one standard error. Uppercase vs. lowercase letters indicate significant differences for the altitude factor. Different letters indicate significant differences for the local sampling condition factor. The interaction between altitude and local sampling condition was not statistically significant



1

2 **Fig. 3** Relative soil water content (%) between 5 and 10 cm for two local sampling conditions (under shrub ■;
 3 outside shrubs □) in an Andean (3715 m) and High Andean (4300 m) páramo. Average \pm one standard error.
 4 Uppercase vs. lowercase letters indicate significant differences for the altitude factor. Different letters indicate
 5 significant differences for the local condition factor. The interaction between altitude and local condition was not
 6 statistically significant

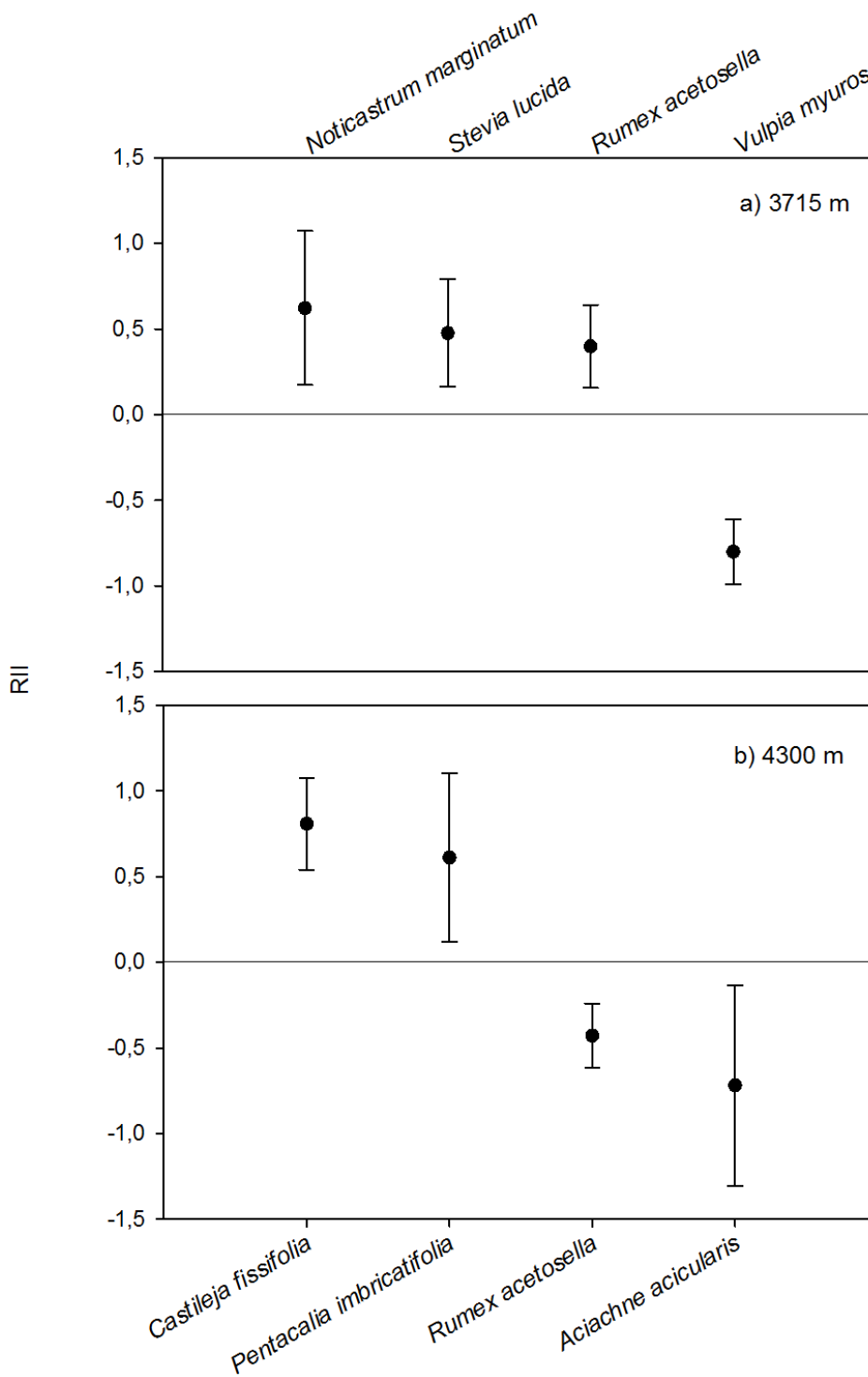
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8 *Local spatial relations*

9 For the Andean páramo (3715 m), the forbs *Noticastrum marginatum* and *Rumex acetosella*, and the shrub *Stevia*
 10 *lucida* showed a positive average RII, indicating a positive spatial association with our focal shrub. On the contrary,
 11 the grass *Vulpia myuros* showed a negative interaction index (Fig. 4a). For the high Andean páramo, at 4300 m, the
 12 forb *Castilleja fissifolia* and the shrub *Pentacalia imbricatifolia* exhibited positive interaction indexes, while *Rumex*
 13 *acetosella* and the grass *Aciachne acicularis* presented a negative RII (Fig. 4b). For none of these species did the
 14 95% confidence interval of the RII include zero, indicating that all of them showed a significant and consistent
 15 positive or negative pattern of spatial association with the shrub. Moreover, it is worth noting that the introduced
 16 invader *R. acetosella* presented a marked change in the direction of its spatial association with the shrub between
 17 altitudes and was consistently among the dominant species in the community.

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1

2 **Fig. 4** Average Relative Interaction Index (RII) based on the changes in biovolume of dominant species in 30
 3 circular plots (1 m diameter) inside and 30 plots outside the crown of *Hypericum laricifolium* shrubs at two sites: (a)
 4 Andean páramo (3715 m); (b) High Andean páramo (4300 m). Error bars indicate the 95% confidence interval

1 *Water status of associated species*

2 Minimum leaf water potentials were higher under the crown of the shrub compared to open areas for *N. marginatum*,
 3 *S. lucida* and *R. acetosella*, all positively associated to the focal shrub at 3715 m (Figure 5a), although statistically
 4 significant differences were recorded only for *N. marginatum* ($p = 0.0089$) and *R. acetosella* ($p = 0.007$). The grass
 5 *V. myuros*, negatively associated to the shrub, was found exclusively in open areas (during the dry season, when this
 6 analysis was carried out), and presented the lowest average Ψ_1^{\min} (-3.8 MPa). On the other hand, *S. lucida* showed
 7 significant differences in Ψ_1^{TLP} between individuals established in open areas compared to the ones beneath the
 8 shrub's crown ($p=0.0081$, Figure 5a), while no differences were observed for *N. marginatum* and *R. acetosella*
 9 between individuals under the crown and in open areas. When Ψ_1^{\min} and Ψ_1^{TLP} were compared, we found that *N.*
 10 *marginatum* and *R. acetosella* had similar average values both for individuals under and outside the shrub, while *S.*
 11 *lucida* showed significantly lower Ψ_1^{\min} compared to Ψ_1^{TLP} under ($p=0.012$) the shrub. The same was true outside the
 12 shrub ($p=0.007$). This same response (Ψ_1^{\min} below Ψ_1^{TLP}) was recorded for *V. myuros* established in open areas
 13 ($p=0.0001$).

14 In the case of the High Andean páramo at 4300 m (Figure 5b), *C. fissifolia* was the only species with a significantly
 15 higher Ψ_1^{\min} in individuals beneath *H. laricifolium*'s crown compared to open areas ($p=0.0166$). *P. imbricatifolia* also
 16 showed more positive Ψ_1^{\min} in individuals underneath the focal species, although the differences were not
 17 statistically significant. On the contrary, in the case of *R. acetosella*, Ψ_1^{\min} was more positive in open areas, but the
 18 differences were not statistically significant. *A. acicularis* showed similar Ψ_1^{\min} under both sampling conditions and
 19 also the lowest values reported at this altitude. When Ψ_1^{TLP} was compared between sampling conditions, no
 20 significant differences were found among the studied species at this altitude. However, when comparing Ψ_1^{\min} and
 21 Ψ_1^{TLP} , most of the species showed Ψ_1^{\min} below the Ψ_1^{TLP} , with statistically significant differences for *P.*
 22 *imbricatifolia*, both for individuals under the shrub ($p=0.007$) and outside ($p=0.028$) and for *A. acicularis*, both for
 23 individuals under the shrub ($p=0.035$) and outside ($p=0.017$).

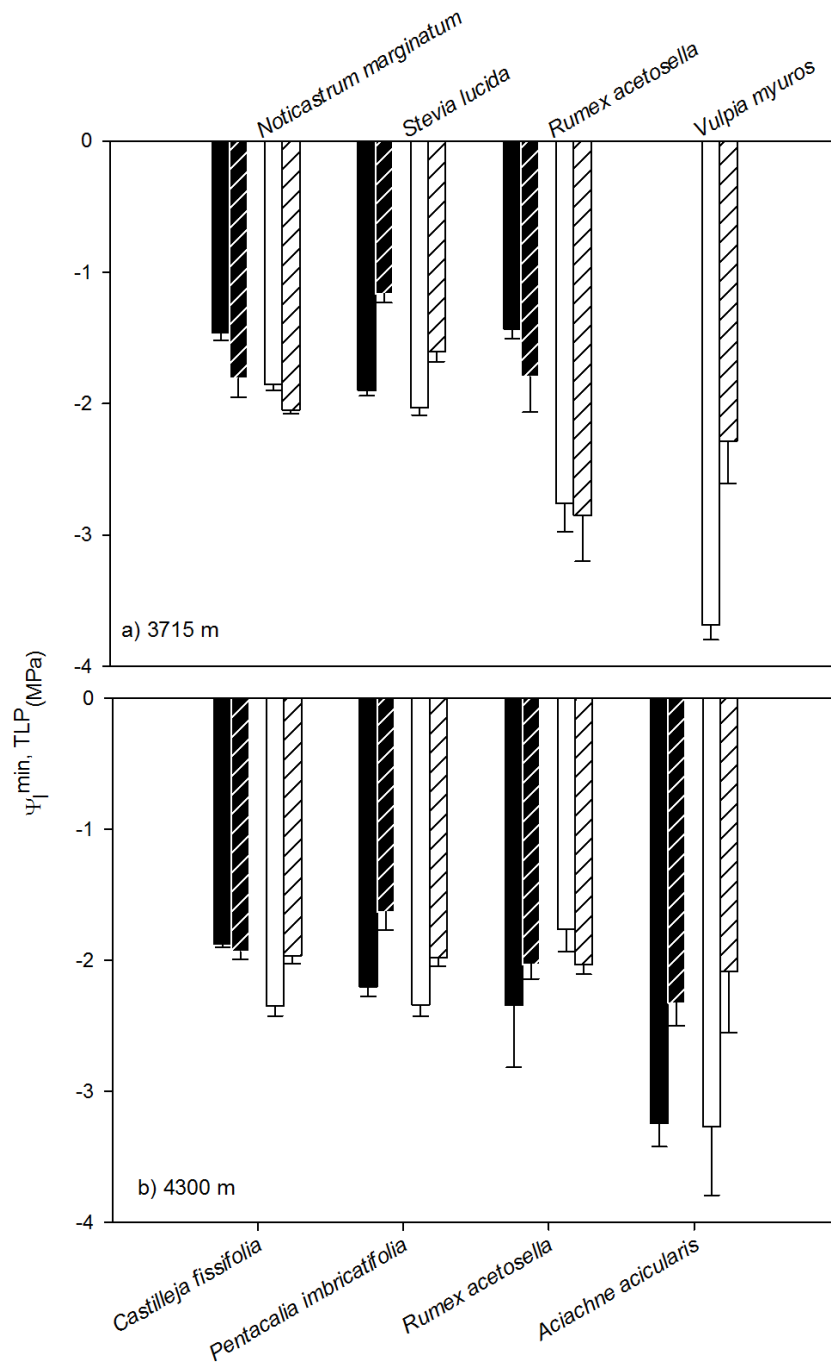
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2 **Fig. 5** Minimum leaf water potential (Ψ_L^{\min}) and leaf water potential at turgor loss (Ψ_L^{TLP}) for species with different
 3 patterns of spatial association with the shrub *Hypericum laricifolium* in the (a) Andean páramo (3715 m) and (b)
 4 High Andean páramo (4300 m). Average \pm one standard deviation for Ψ_L^{\min} under the shrub (■) and outside the
 5 shrub (□), and Ψ_L^{TLP} under the shrub (▨) and outside the shrub (▩). Species are ordered in terms of their
 6 Relative Interaction Index with the shrub, going from most positive to most negative from left to right

7

1 *Discussion*

2 The results presented here support the first two hypotheses we set out to evaluate, indicating that *H. laricifolium* acts
3 as an EE in the high tropical Andes by: 1) inducing more favorable environmental conditions under the shrub's
4 crown (reducing temperature fluctuations and increasing SOM and SWC); and 2) improving the water status of
5 those species that show a clear positive spatial association with the shrub. Hence, tropical alpine shrubs seem
6 capable of modifying levels of available resources (water) and stress factors of the non-resource type (temperature),
7 playing a similar role to shrubs in arid ecosystems, and to giant rosettes and cushions in TAE (Perez 1989, 1992;
8 Anthelme et al. 2011).

9 On the other hand, our results partially support our third hypothesis that the role of the shrub as an EE should be
10 more important under more limiting environmental conditions (see also Farji-Brener et al. 2009). The shrub's crown
11 generated a more marked increase in SWC and a clearer attenuation of temperature variability in the driest site
12 (3715 m) compared to the more mesic site (4300 m). However, the shrub seemed to have similar positive effects on
13 the water status of species positively associated with it at both altitudes. Still, when the exotic herb *R. acetosella*
14 changed its spatial association with the shrub from positive to negative, this was linked to a change in the effect of
15 the shrub on the water status of the species from positive (in the most xeric site) to negative (in the most mesic site).

16

17 *Effects on microhabitat*

18 In arid environments shrubs modify the microhabitat under their crown, inducing lower soil temperatures, higher
19 soil moisture contents, reduced evaporative demands and improved soil organic matter contents (Aguiar and Sala
20 1994; Franco-Pizaña et al. 1996; Holmgren et al. 1997; Pariente 2000). However, little is known about the role of
21 shrubs as microhabitat modifiers in TAE.

22 Under the shrub's crown the temperature range was narrower than in open areas, with the most extreme maximum
23 and minimum temperatures found in the environment outside the shrub influence (see also Alvizu 2004 and Cáceres
24 2011 for the high Andean belt). The largest temperature oscillations both under and outside the crown were found
25 during the dry season and in the drier/ lower elevation site (3750 m), where the maximum temperature was recorded.

26 In addition, at the 4300 m site, below zero temperatures were not recorded under the shrub while they did occur in
27 open areas. These differences in temperature regimes under the crown are associated to changes in the radiation
28 balance induced by the shrub. In our study site, Ramírez (2013) reported an attenuation of the average daily

1 accumulated radiation comparing environments under *H. laricifolium* vs open areas of 76.6% and 70.5% at 3715 m
2 and 4300 m respectively (during the dry season).

3 Temperature buffering has been proposed as a contributing factor in positive interactions among species in mid
4 latitude alpine environments (Callaway and Pugnaire 1999; Maestre et al. 2009; Cavieres et al. 2006; Anthelme et al.
5 2011). Heat loss by re-irradiation at night and high daytime radiation inputs result in more pronounced oscillations at
6 the soil surface, a phenomenon documented by several authors in the páramo (Pfitsch 1988; Monasterio and Lamotte
7 1989; Meinzer et al. 1994). Consequently, life forms that grow closer to the ground in high tropical mountains (e.g.
8 rosettes forbs, small erect or prostrate forbs and grasses) and the juveniles of most species are more exposed to the
9 physiological effects of frequent high daytime and low nighttime temperatures, including freezing (Larcher 1995;
10 Azócar and Rada 2006). Hence, the environment under the shrub could constitute a refuge where other smaller
11 plants could experience less temperature related stress induced both by high or low temperatures, particularly near
12 the soil surface.

13 Regarding soils, SOM contents were significantly higher in areas under the shrub compared to open areas at both
14 elevations. The increase in SOM under these shrubs growing on young soils (entisols or inceptisols, Malagón 1982)
15 clearly suggests an effect of ecosystem engineering, in which the shrub's necromass production could contribute to
16 generate resource islands. An increase in SOM could, in turn, be linked to an increase in the soil's water and nutrient
17 holding capacity (see Körner 2003). Other TAE studies that have documented increases in SOM mediated by giant
18 rosettes and cushions, have also described higher nutrient levels in the vicinity of the EE (Pérez 1992; Anthelme et
19 al. 2011). The formation of resource or fertility islands by necromass accumulation induced by vegetation patches in
20 unproductive environments has also been reported for other systems outside of the highland tropics (e.g. Jackson
21 and Caldwell 1996; Kelly et al. 1996; Schlesinger et al. 1996).

22 Moreover, we found that the SWC in areas under the influence of *H. laricifolium* was higher, something that could
23 also be linked to a higher water retention capacity under the crown. Shrubs could also increase soil water through
24 increased fog interception and decreased evaporative demands under the canopy, as has been documented in semi-
25 arid environments (Callaway 1995; Callaway and Pugnaire 1999).

26 Differences in SWC were larger at the Andean Belt site (3715 m), where maximum soil temperatures occurred and
27 soil moisture was much lower in exposed areas. This suggests that plants are exposed to more severe water
28 limitations at the lower elevation site, although it would be important to compare the measured SWC with the soil

1 wilting point and field capacity at both altitudes. A key factor that may explain lower SWC at the lower elevation
2 site could be its higher proximity to the center of the Chama River's intermountain valley (Mucuchíes), where the
3 lowest precipitations in the region have been recorded (Sarmiento 1986).

4

5 *Spatial relations and water status of associated species*

6 Overall, our results suggest that species with a strong positive spatial association with *H. laricifolium*, tend to have
7 an improved water status when growing under its crown. In contrast, the two species with a negative spatial
8 association with our focal species at 4300 m showed similar leaf water potentials under both situations. In addition,
9 there seemed to be an inverse relationship between the Ψ_L^{\min} that species were able to tolerate in open environments
10 and their RII with our focal shrub. However, we would need to analyze a higher number of species to evaluate this
11 hypothesis with enough statistical power.

12 Other studies at higher latitudes in arid and alpine ecosystems have reported that the water status of associated
13 species can be improved by nurse plants (Callaway and Pugnaire 1999; Holzapfel et al. 2006; Schöb et al. 2014). A
14 reduction in transpiration demands due to lower temperatures and lower vapor pressure deficits, and an increase in
15 soil water availability due to a lower evaporation or an increase in water retention capacity of the soil, could all
16 contribute to a reduced water stress in plants established under the crown of shrubs (Holmgren et al. 1997).

17 However, in the case of *C. fissifolia*, an improved water status under the shrub's crown could also be related to a
18 hemiparasitic relation, given that the genus *Castilleja* is known to establish these types of interactions (Adler 2003).

19 As for the relationship between Ψ_L^{\min} and Ψ_L^{TLP} , species responses varied not only in terms of their RII but also to
20 the life-form they belong to. The forbs *N. marginatum* and *C. fissifolia* (positive RII) showed similar average Ψ_L^{\min}
21 and Ψ_L^{TLP} values (both under and outside the shrub). This, together with their relatively high Ψ_L^{\min} values compared
22 to the other species, suggests these two species depend on drought avoidance strategies for survival. However, the
23 shrubs *S. lucida* (3715 m) and *P. imbricatifolia* (4300 m), which also showed a positive RII, presented Ψ_L^{\min} below
24 their respective Ψ_L^{TLP} (both under and outside the shrub), suggesting they tolerate water stress to a greater degree
25 and that their association to the shrub could be determined by other non-drought related factors. Finally, the grasses
26 *V. myurus* and *A. acicularis*, negatively associated with the shrub, showed the most negative Ψ_L^{\min} , which was
27 significantly below their Ψ_L^{TLP} , suggesting an even larger tolerance to drought.

1 For drought tolerant grasses, the maintenance of very negative water potentials could be linked to an increased
2 ability to extract water from dry soils. Additionally, other factors such as reduced light availability under the shrub
3 could have a net negative effect on their growth and performance, which could explain the antagonistic relationship
4 with the shrub. In addition, *A. acicularis*, a matt forming grass, may be modifying its own environment as suggested
5 for TAE cushions (Anthelme et al. 2011). Overall, these results seem to support the hypothesis that drought tolerant
6 species are less dependent on nurse plants for survival or growth than species with stress avoiding strategies. In fact,
7 other studies have shown that stress-tolerant and light demanding species, such as grasses, tend to compete with
8 nurse plants, while stress-intolerant shade species interact positively with benefactor species (Pagés and Michalet
9 2006; Michalet 2007).

10 Finally, the behavior of the exotic forb *R. acetosella* is particularly interesting, being the only dominant species in
11 our study area that clearly reversed its spatial relationship with our focal shrub from positive at lower elevations to
12 negative at higher elevations. This was paralleled by a change in the effect of the shrub on its water status from
13 positive in the lower, more xeric site to negative in the higher, more mesic site. Holmgren et al (1997) developed a
14 competition-facilitation model based on the effect of canopies of nurse plants on light and soil moisture availability
15 for other species. They argued that in more mesic environments, light limitations under the canopy should be more
16 important compared to soil water limitations, so net interactions tend to be negative, while the opposite would be
17 true in drier environments. Sarmiento et al (2003) and Llambí et al (2003) report *R. acetosella* as a ruderal, fast
18 growing heliophile species in the páramos, which dominates early stages of secondary succession. This could then
19 support the hypothesis that the reduced light availability under the canopy of the shrub could become limiting for
20 this ruderal species, an effect that could be more evident under less demanding hydric conditions. In this context, it
21 could be interesting to compare the distribution and physiological optima for *R. acetosella*, defined as *strain* by
22 Gross et al. (2010). These authors suggest that when a species is under increasing strain levels, the direction of its
23 interaction with a nurse plant may shift from negative to positive (as long as there is an improvement of the abiotic
24 conditions by the facilitator).

25 In the Chilean central Andes, Badano et al. (2007) also reported that cushions that act as EE have more positive
26 effects on the performance of invasive exotic species (*Taraxacum officinale*) under more limiting environments.
27 However, in their study the most severe environments corresponded to those at higher elevations, whereas here, the
28 most limiting water conditions occurred at the lower site (see also Cavieres et al 2005). More generally, it has been

1 suggested that species origin (native vs. exotic) can influence its interaction with potential benefactors, with exotic
2 species tending to show antagonistic interactions with nurse plants (Vilá and Weiner 2004; He et al 2013). However,
3 as discussed above, the net effect of an EE on exotic species could be modulated by environmental severity and the
4 strain to which the invader is subjected.

5 In conclusion, the results presented here provide physiological evidence for interpreting spatial association patterns
6 between potential nurse plants and other species in the alpine tropics. In particular, they suggest that positive spatial
7 relations with EE can be mediated by an improvement in the water status of associated plants (at least in ecosystems
8 with marked rainfall seasonality). Our results also support the idea that both a species stress resistance strategy (i.e.
9 tolerance vs. avoidance) and origin (native vs. exotic) can influence the net balance of its interactions with EE and
10 that this is in turn modulated by environmental severity. We suggest that this mechanistic approach should help
11 bridge the gap between patterns and processes in alpine community ecology.

12 Among the aspects that could be further explored are: a) the detailed mechanisms involved in the changes in the
13 water status of plants with different spatial relations with EE (e.g. changes in stomatal control); b) the effects of
14 shrubs on soil nutrients, and the importance of nutrient limitations in driving local plant-plant interactions in TAE;
15 and c) the way in which changes in the ontogenetic relations between EE and beneficiary species affect the outcome
16 of plant-plant interactions (Callaway and Walker 1997). Even though the patterns we described in this study are
17 based on adult plants, the study of these responses may be essential in seedlings and saplings, the most vulnerable
18 stages in páramo plants (Goldstein et al. 1985; Estrada and Monasterio 1991; Fagua and González 2007).

19

20

21 *Acknowledgments*

22 We wish to thank C. García, T. Schwarzkopf, M. Fariñas and two anonymous referees for their insightful comments
23 and suggestions and the technical staff at ICAE for their help during field and laboratory work (N. Marquez, W.
24 Dugarte, Z. Méndez). This work was financed by the CDCHTA at Universidad de Los Andes (project E-1769-12-
25 01-EM).

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