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**RESEARCH ARTICLE**

**Journal of Vegetation Science**

**Patch-level facilitation fosters high-Andean plant diversity at regional scales**

**Sabrina S. Gavini**| **Cecilia Ezcurra**| **Marcelo A. Aizen**

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| INIBIOMA, CONICET-Universidad Nacional |  |  |  |  |
|  | **Abstract** |  |
| del Comahue, Rio Negro, Argentina |  |  |  |
| **Correspondence** |  |  | **Aim:** Local effects of ecosystem engineers on biodiversity can scale up to the land- |  |
|  |  | scape level, stressing the importance of ecological processes as determinants of spe- |  |
| Sabrina S. Gavini, INIBIOMA, CONICET- |  |  |  |
| Universidad Nacional del Comahue, Quintral |  |  | cies richness at larger spatial scales. In harsh environments, cushion plants often act |  |
| 1250, 8400 San Carlos de Bariloche, Rio |  |  | as ecosystem engineers given their ability to buffer extreme abiotic conditions, thus |  |
| Negro, Argentina. |  |  |  |
| Email: [sabrinagavini@comahue-conicet.](mailto:sabrinagavini@comahue-conicet.gob.ar) |  |  | providing unique and more favorable niches for the establishment of less stress-tol- |  |
| [gob.ar](mailto:sabrinagavini@comahue-conicet.gob.ar) |  |  | erant plant species. We assessed if facilitation by cushion plants influences patterns |  |
|  |  |  |  |
| **Co-ordinating Editor:** Francisco Pugnaire |  |  | of plant diversity at increasing spatial scales. |  |
|  |  |  | **Location:** Northern Patagonian Andes, Argentina. |  |
|  |  |  | **Methods:** Based on plant species records within and outside cushions, we compared |  |
|  |  |  | plant diversity in the presence and absence of cushions at the community, mountain |  |
|  |  |  | and regional scale. Specifically, observed and estimated numbers of species occurring |  |
|  |  |  | in either cushion plants or in the surrounding open areas were compared with the |  |
|  |  |  | species numbers of the open areas. |  |
|  |  |  | **Results:** The presence of cushion plants significantly increased species richness at all |  |
|  |  |  | spatial levels analyzed. At the patch level, a higher number of species was recorded |  |
|  |  |  | growing within cushion plants than in open area plots of similar size. Consistently, |  |
|  |  |  | hypothetical communities lacking cushion plants showed significantly lower spe- |  |
|  |  |  | cies richness than observed communities with cushion plants. These differences in |  |
|  |  |  | species richness at patch and community scales increased with altitude, hence fa- |  |
|  |  |  | cilitation by cushion plants became more important at higher elevations. Moreover, |  |
|  |  |  | according to asymptotic non-parametric estimators, cushion plants could increase |  |
|  |  |  | overall regional species richness up to 40%. |  |
|  |  |  | **Conclusions:** Our findings suggest that about one third of the high-Andean flora of |  |
|  |  |  | the region owes its presence to the existence of nursing plants, defying the view that |  |
|  |  |  | abiotic factors alone are enough to fully determine species occurrences at large spa- |  |
|  |  |  | tial scales. This study provides evidence that local-scale ecological processes can be |  |
|  |  |  | crucial in promoting and maintaining biodiversity at any spatial scale. |  |
|  |  |  | **KEYWORDS** |  |
|  |  |  | alpine, cushion plants, ecosystem engineers, Patagonian Andes, plant–plant interactions, |  |
|  |  |  | positive interactions, species richness |  |
|  |  |  |  |  |



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|  | **2  |** |  |  | GAVINI et al. |  |
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|  | **1** | **INTRODUCTION** | | | Cavieres *et al*., 2007). This type of biotic interaction, in which associ- |  |
|  |  |  |  | ated organisms benefit from the lessening of physical stresses by other |  |
|  | Multiple ecological, evolutionary and biogeographical processes can | | | coexisting organisms, is known as facilitation (Bertness and Callaway, |  |
|  | promote species diversity, yet understanding the mechanisms that | | | 1994). In particular, cushion plants can act as effective facilitators. |  |
|  | drive patterns of local and regional diversity remains challenging. In | | | Plants adopting this compact growth form usually facilitate the estab- |  |
|  | fact, the relative importance of these processes and the link between | | | lishment of other species by ameliorating nutrient, water and tempera- |  |
|  | diversity at different spatial scales have been central subjects of de- | | | ture stresses that characterize alpine regions, where this type of plants |  |
|  | bate in ecological and evolutionary research (e.g., Ricklefs and Schluter, | | | commonly occurs (Bertness and Callaway, 1994; Callaway *et al*., 2002; |  |
|  | 1993; Godfray and Lawton, 2001; Noda, 2004). One view sustains that | | | Cavieres *et al*., 2014, 2016). Given the capability of cushion plants to |  |
|  | large-scale, evolutionary and biogeographical processes are overriding | | | nurse less stress-tolerant species, they are considered as foundation |  |
|  | in determining species richness at any scale, with the number of species | | | species in community succession of alpine ecosystems (Reid and Lortie, |  |
|  | present in local communities reflecting the richness of regional species | | | 2012; Schöb *et al*., 2012) and as keystone species in sustaining and |  |
|  | pools (Ricklefs, 1987; Cornell and Lawton, 1992; Ricklefs and Schluter, | | | promoting alpine plant diversity (Nuñez *et al*., 1999; Butterfield *et al*., |  |
|  | 1993; Cornell and Karlson, 1997; Cornell, 1999; Cornell *et al*., 2008). | | | 2013; Cavieres *et al*., 2016; Gavini *et al*., 2019). However, most stud- |  |
|  | The broad-scale processes determining regional species richness in- | | | ies on the facilitating role of cushion plants have been conducted at |  |
|  | clude long-distance dispersal, speciation, and extinction (Ricklefs, | | | the scale of individuals, making extrapolations at larger spatial scales a |  |
|  | 1987; Wiens and Donoghue, 2004; Harrison and Cornell, 2007, 2008). | | | matter of speculation (but see Cavieres and Badano, 2009; Chen *et al*., |  |
|  | A less explored, non-exclusive alternative to the top-down par- | | | 2015; Cavieres *et al*., 2016). More specifically, this scale-up extrapo- |  |
|  | adigm is a bottom-up perspective in which locally-acting ecological | | | lation is not guaranteed due to the fact that many plant species that |  |
|  | factors are important determinants of species richness at any spatial | | | are typically nursed by cushion plants can sometimes establish in the |  |
|  | scale (Huston, 1999; Michalet *et al*., 2006). Assessment of an ecolog- | | | open under less stressful conditions (e.g., Cavieres *et al*., 2002; Arroyo |  |
| ical-driven bottom-up perspective on the determinants of regional | | | | *et al*., 2003; Cavieres *et al*., 2006; Badano *et al*., 2007). Therefore, be- |  |
| species diversity has been hindered, in part, by the complexity of eval- | | | | cause facilitation by cushion plants can be a facultative interaction, the |  |
| uating biotic interactions among multiple coexisting species (Ricklefs, | | | | consequence of this local interaction in promoting species diversity at |  |
| 2004, 2008; Harrison and Cornell, 2007). Progress in assessing this | | | | larger scales is uncertain and merits research. |  |
| view has also been hampered by the assumption that competition | | | | Here, we assessed the hypothesis that local-scale biotic in- |  |
| for limiting resources is the ultimate ecological force determining the | | | | teractions determine regional-scale patterns of species diversity. |  |
| maximum number of species that can coexist locally (Shurin and Allen, | | | | Specifically, we tested if facilitation by cushion plants, which behave |  |
| 2001; Herzog and Kessler, 2006). However, this bottom-up perspec- | | | | as alpine ecosystem engineers, influences patterns of species diversity |  |
| tive may be relevant to explain patterns of species richness in biomes | | | | at both local and regional scales. Following this proposal, we expect |  |
| characterized by local communities structured by facilitative interac- | | | | that: (a) cushion plants would harbor higher species numbers than |  |
| tions, where diversity begets diversity (Cavieres *et al*., 2016). | | | | neighboring patches without cushion plants; and (b) regional species |  |
|  | Biotic interactions can play an essential role as determinants of | | | richness would decrease in the hypothetical absence of cushion plants. |  |
| community structure and dynamics. In particular, the presence of | | | | Implicit in this hypothesis is the assumption that many alpine plants |  |
| ecosystem engineers can greatly affect local biodiversity patterns | | | | can be found only growing associated with cushion plants, despite the |  |
| that can scale up to the landscape level (Crooks*,* 2002; Wright *et al*., | | | | strong environmental gradients that characterize alpine regions. To |  |
| 2002; Romero *et al*., 2015). Ecosystem engineers are organisms that | | | | evaluate this hypothesis, we compared the number of plant species |  |
| create, modify and maintain habitat patches not present elsewhere in | | | | in the landscape with the expected richness under the hypothetical |  |
| the landscape (Jones *et al*., 1994, 1997; Wright and Jones, 2006). If | | | | removal of cushion plants, which results in a landscape without engi- |  |
| the novel niches associated with these engineered habitats allow the | | | | neering species. We carried out this comparison at scales larger than |  |
| establishment of species not found elsewhere, then engineers could | | | | individual patches (i.e., community, mountain, and regional) and differ- |  |
| allow more species to coexist locally. To the extent that these species | | | | ent elevations (i.e., 1,600, 1,800, and 2,000 m) based on plant surveys |  |
| cannot persist outside the habitats created by the engineering spe- | | | | conducted in 21 alpine plant communities in the northern Patagonian |  |
| cies, this increase in local diversity would scale up at the landscape | | | | Andes. In this way, we evaluated to what extent facilitation is crucial in |  |
| and even regional scales (Wright *et al*., 2002; Badano and Cavieres, | | | | promoting and maintaining biodiversity at any spatial scale. |  |
| 2006a, 2006b; Wright, 2009; Cavieres and Badano, 2009; Romero | | | |  |  |
| *et al*., 2015). This simple proposal defies the view that broad- rather | | | | **2** | **METHODS** |  |
| than small-scale processes are the main factors determining local-scale | | | |  |
| species richness (Harrison and Cornell, 2007, 2008). | | | | **2.1**|**Study area** |  |
|  | Plants with cushion life forms often act as ecosystem engineers | | |  |
| in stressful environments due to their ability to buffer extreme envi- | | | |  |  |
| ronmental conditions, favoring the establishment and survival of other | | | | This study was conducted in high-Andean communities occurring |  |
| species growing inside them (Badano *et al*., 2007; Callaway, 2007; | | | | mostly within Nahuel Huapi National Park (Argentina), which is |  |



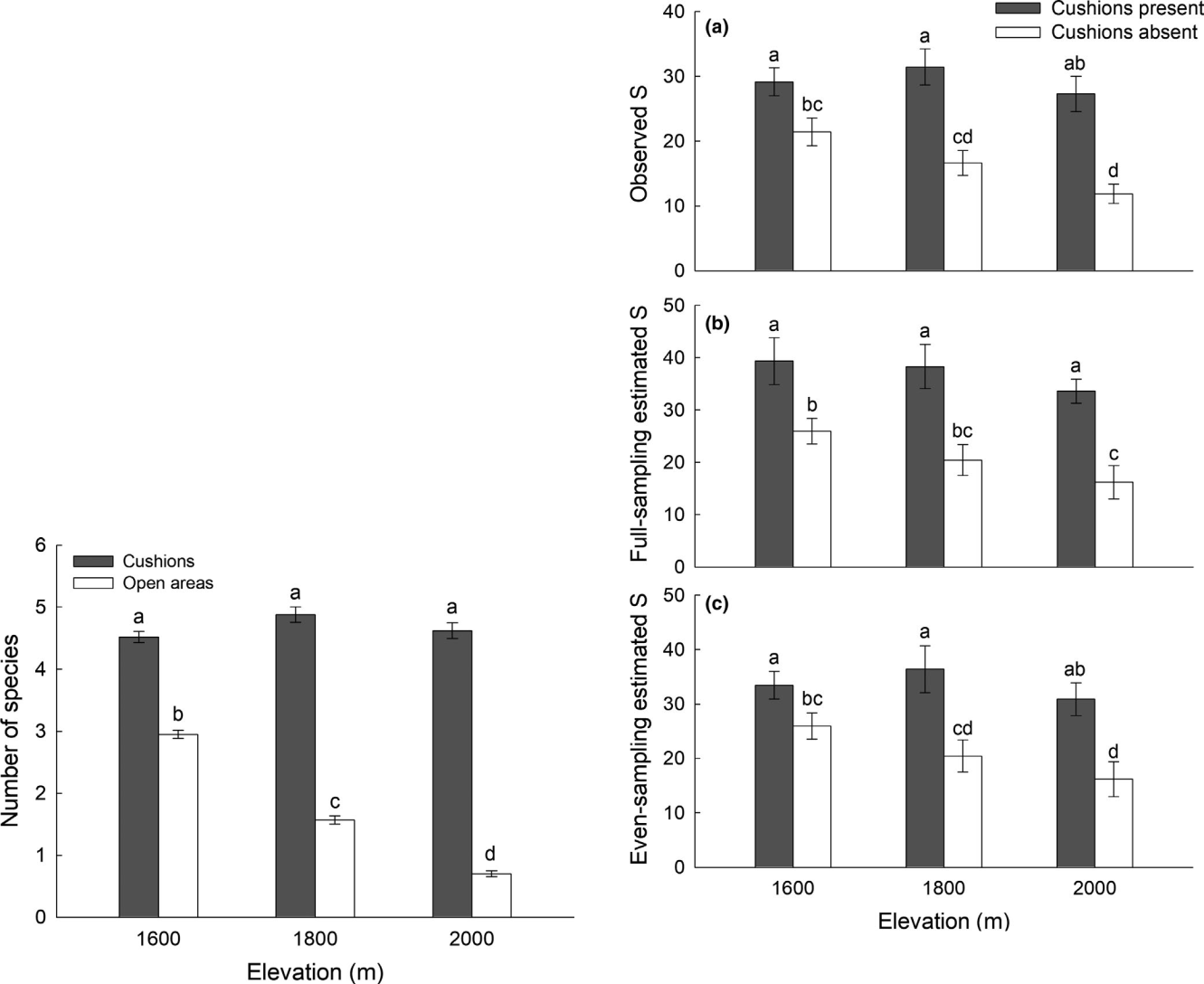
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| situated at ~41° S in northwestern Patagonia, Argentina, border- | of its area. In total, we sampled 2,100 plots (1,050 cushion plants and | | | |  |
| ing with Chile to the west. The region is characterized by a steep | 1,050 open area plots). | |  |  |  |
| precipitation gradient from about 4,000 mm at the western side of |  |  |  |  |  |
| the Andes in Chile to about 500 mm at the drier eastern side of the | **2.3**|**Effect of cushions on species richness at** | |  |  |  |
| Andes in Argentina, and at ~800 m (Wardle *et al*., 2001; Daniels and |  |  |  |
| Veblen, 2004). Deciduous forests of *Nothofagus pumilio* occur from | **different spatial scales** | |  |  |  |
| ~1,000 m to the treeline, at ~1,600 m, where this species grows pros- |  |  |  |  |  |
| trated and forms a low 'krummholz' (Wardle *et al*., 2001). The alpine | Based on the species sampled within and outside individual cushion | | | |  |
| high-Andean zone lies above this treeline (Ferreyra *et al*., 1998), with | plants, we assessed how plant diversity, estimated here as species | | | |  |
| most mountain peaks ranging between 2,000 and 2,700 m and a few | richness, depended on facilitation by cushion plants at the commu- | | | |  |
| peaks above 3,000 m (Daniels and Veblen, 2004). Mean annual tem- | nity, mountain, and regional scales. Specifically, for each of these | | | |  |
| perature (across the 21 sampled communities, see below) is approx. | scales we estimated the number of species recorded in either of the | | | |  |
| 3.7°C, with short, mild, dry summers and cold, wet winters (mean | two sampled habitat types (i.e., cushion plant or open area) and com- | | | |  |
| temperature of the coldest quarter −1.5°C, mean temperature of the | pared it with the number of species recorded in the open area only | | | |  |
| warmest quarter 8.9°C); and average annual precipitation is approx. | (Badano and Cavieres, 2006a, 2006b). These estimates were based | | | |  |
| 860 mm, most of which falls in the form of snow between May and | on the number of plant species recorded in the 50, 150, and 1,050 | | | |  |
| October (precipitation of the coldest quarter approx. 395 mm, pre- | paired cushion and open area plots, and in the open area plots only, | | | |  |
| cipitation of the warmest quarter approx. 93 mm) (Worldclim, Fick | that were sampled in each of the 21 communities, each of the seven | | | |  |
| and Hijmans, 2017; see Appendix S1: Table S1). In these high-Andean | mountains, and the whole region, respectively. | |  |  |  |
| communities, plant cover is extremely low (ranging from 5% to 20%) | Since counts of species richness are highly sensitive to the num- | | | |  |
| due to severe climatic conditions that create a patchy landscape | ber, size, and spatial arrangement of the sample units (Gotelli and | | | |  |
| represented by a bare ground matrix and isolated cushion-plant | Colwell, 2011), we also estimated asymptotic species richness using | | | |  |
| patches. Despite low plant cover, more than 230 species of vascu- | non-parametric estimators. Non-parametric estimators of species | | | |  |
| lar plants have been recorded in the high-Andean zones of Nahuel | richness, which use information of the rare species in an assemblage | | | |  |
| Huapi National Park in the Patagonian Andes, with Asteraceae, | to calculate the number of species present but not detected, are | | | |  |
| Poaceae, and Apiaceae as the best-represented angiosperm fami- | the most adequate to estimate number of species in an assemblage | | | |  |
| lies (Ferreyra *et al*., 1998). Overall, predominant life forms comprise | (Gotelli and Colwell, 2011), Chao2 being the most proper estimator | | | |  |
| perennial herbs and shrubs, which commonly are of dwarf stature | of species richness for incidence data (Chao, 1987; Colwell, 2013). | | | |  |
| or adopt a cushion-like form. Although more than 15 cushion-plant | Using the software EstimateS (V.9.1.0; Colwell, 2013), we calcu- | | | |  |
| species occur in the region, the most frequent are *Oreopolus glacialis* | lated Chao2 values of species richness at different spatial scales for | | | |  |
| and *Mulinum leptacanthum* (Nuñez *et al*., 1999). | both scenarios, i.e., with and without cushion plants, based on the | | | |  |
|  | respective total number of sampled plots. Because estimates of spe- | | | |  |
| **2.2**|**Study sites and vegetation sampling** | cies richness in the absence of cushion plants was based on halved | | | |  |
| sample sizes (i.e., number of plots), we also calculated expected rich- | | | |  |
|  | ness in the presence of cushion plants for sample sizes equivalent to | | | |  |
| We conducted a survey of the alpine vegetation on seven mountains | the scenario lacking them. This was done to verify possible down- | | | |  |
| of the Patagonian Andes from January to March in 2017 and 2018 | ward-biased estimations owed to a lower sampling effort and not to | | | |  |
| (Appendix S1: Figure S1). On each mountain, we established one | the absence of cushions. In all species-richness estimates, cushion | | | |  |
| study site at each of three elevations (ca. 1,600, 1,800 and 2,000 m). | plant species were excluded from species counts and taken into ac- | | | |  |
| These sites were chosen based on accessibility and availability of | count only if they were nursed by others. However, in no community | | | |  |
| cushion plants. Accordingly, we sampled a total of 21 alpine plant | a cushion species was considered as both nurse and nursed, so that | | | |  |
| communities (i.e., seven mountains × three elevations) dominated | comparisons between overall plant species richness vs. plant species | | | |  |
| by cushion plants (Appendix S1: Table S1). At each community, 50 | richness in open area only, at the community and larger spatial scales | | | |  |
| individual cushion plants were haphazardly selected within an area | are not biased by the inclusion of cushion plants into species counts. | | | |  |
| of approx. 0.5 ha, pairing each cushion with an adjacent non-cushion |  |  |  |  |  |
| or open area 50 cm away in a random direction. In order to sample a | **2.4**|**Trends in beta-diversity** | |  |  |  |
| similar surface in the surrounding open area, a wire hoop was shaped |  |  |  |
| to match the size of the sampled cushion that was then placed on |  |  |  |  |  |
| the ground. The number and identity of all plant species (follow- | We calculated species dissimilarity (i.e., beta diversity; Whittaker, | | | |  |
| ing Zuloaga *et al*., 2008) were recorded at both cushion and open | 1960) to evaluate to what extent plant species composition differs | | | |  |
| area plots. Given that cushion plants are roughly elliptical, micro- | between cushion and open area plots. If cushion plants increase re- | | | |  |
| sites were defined as elliptical plots, and thus, the longer and shorter | gional diversity, they should harbor species not present elsewhere in | | | |  |
| axes of each cushion were measured as an approximate estimation | the landscape. Beta diversity may reflect two additive and antithetic | | | |  |



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| **4  |** |  |  |  | GAVINI et al. |  |
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| phenomena: species turnover and nestedness (Baselga, 2010). | | | cushion plant species by including altitude as a fixed effect, and | |  |
| Species turnover is caused by the replacement of some species by | | | cushion species and community nested within mountain as crossed | |  |
| others from site to site (Gaston and Blackburn, 2000) as a conse- | | | random effects. We tested whether the inclusion of cushion spe- | |  |
| quence of niche specialization (Qian *et al*., 2005). Instead, nested- | | | cies as a random effect improved the model fit significantly. Models | |  |
| ness characterizes differences in species richness, where the poorer | | | were run with and without size of the cushion plant as a covariate | |  |
| assemblages are non-random subsets of the species present in richer | | | to test whether the quality of a nurse plant depended on its size. | |  |
| assemblages (Ulrich and Gotelli, 2007). | | | Using a GLMM, we also compared observed and Chao2 expected | |  |
| Here, we estimated overall beta diversity, and its two respective | | | estimates of species richness with and without cushion plants at | |  |
| components, comparing the species assemblages associated with | | | the community and mountain levels. At the community level, we in- | |  |
| cushion plants and those surveyed in the surrounding areas. These | | | cluded cushion plant (present vs. absent), altitude (1,600, 1,800, and | |  |
| analyses involve the use of species incidence (i.e., presence/absence) | | | 2,000 m), and the interaction between these two effects as fixed | |  |
| matrices. We used the tools provided by Baselga (2010) as imple- | | | factors, considering community nested within mountain as a random | |  |
| mented in the betapart package (V1.4; Baselga, 2010, 2012) of the R | | | effect. At the mountain level, we considered cushion plant (present | |  |
| software (R Development Core Team, 2017) to estimate overall inci- | | | vs. absent) as a fixed factor and mountain as a random effect. We | |  |
| dence-based beta diversity (measured as the Sorensen dissimilarity | | | considered GLMMs with a Poisson distribution (as no overdispersion | |  |
| index, βSOR). In turn, βSOR was decomposed into a component due to | | | was detected) and a log-link function (Zuur *et al*., 2009) to analyze | |  |
| species replacement (spatial turnover or Simpson dissimilarity index, | | | observed number of species, whereas a Gaussian distribution and an | |  |
| βSIM) and nestedness (nestedness-resultant dissimilarity, βNES). | | | identity link function for expected species richness. Pairwise dissim- | |  |
| Accordingly, we first assessed intra-community beta diversity | | | ilarities indices, including total dissimilarity (Sorensen index), species | |  |
| indices by calculating the overall dissimilarity between species as- | | | replacement (turnover) and species loss (nestedness), were analyzed | |  |
| semblages of the two microsite types, i.e., the pool of all species | | | with GLMMs with a beta distribution with the function *glmmadmb* of | |  |
| found in the 50 cushion plants with respect to the 50 open area | | | the package glmmADMB (V.0.8.3.3, Skaug *et al*., 2016), using eleva- | |  |
| plots. This pairwise comparison allowed us to estimate to what ex- | | | tion as a fixed factor and mountain as random effect. | |  |
| tent cushion plants harbor unique species not present growing in | | |  |  |  |
| the surrounding open area. Hence, using the “beta.pair” function | | | **3** | **RESULTS** | |  |
| of the betapart package we calculated the beta diversity between | | |  |
| microsites, with its respective components, for each of the 21 com- | | |  |  |  |
| munities. The same additive partition can be conducted for multiple | | | Across the 21 high-Andean communities, we identified and sam- | |  |
| comparisons by using the function “beta.multi”. Therefore, we also | | | pled a total of fifteen angiosperm cushion species acting as nurse | |  |
| calculated estimates of beta diversity, and their turnover and nest- | | | plants (Appendix S1: Table S1). *Mulinum leptacanthum* (Apiaceae) | |  |
| edness components, among: (i) communities; (ii) elevations, pool- | | | and *Oreopolus glacialis* (Rubiaceae) were the most frequent cushion | |  |
| ing data across mountains; and (iii) mountains, pooling data across | | | plants, accounting for 34 and 17% of all sampled cushions, respec- | |  |
| elevations. This was done for species assemblages associated with | | | tively. Furthermore, at some sites, typical herbaceous and sub- | |  |
| cushion plants and growing in the open area, separately. We also | | | shrub species belonging to the genera *Acaena* (Rosaceae), *Gaultheria* | |  |
| conducted a beta-diversity analysis among the different nurse-plant | | | (Ericaceae), *Nassauvia* (Asteraceae) and *Baccharis* (Asteraceae) | |  |
| species, by pooling data across all sampled cushions from the same | | | adopted a cushion growth form, harboring other plant species within | |  |
| species within each mountain and overall, to assess the importance | | | (Appendix S1: Table S1, Figure S2). | |  |
| of different cushion species in the composition of plant assemblages. | | | Cushion plants favor the establishment of many plant species, | |  |
|  |  |  | given that a higher number of species were found associated with | |  |
| **2.5**|**Statistical analyses** | | | individual cushion plants than in nearby open areas of similar size | |  |
| (*X*microsite2 | = 1,034, *df* = 1, *p* < 0.0001). The number of plant species |  |
|  |  |  | growing within individual cushions ranged between 0 and 12 (me- | |  |
| We tested for statistical effects of the importance of cushion plants | | | dian = 4), whereas in paired open area plots of similar size it var- | |  |
| on plant richness at different spatial scales using generalized linear | | | ied between 0 and 7 (median = 2). These microhabitat differences | |  |
| mixed-model analysis (GLMM) programmed in the R software (R | | | in species richness persisted even when an increasing number of | |  |
| Development Core Team, 2017). To compare species richness be- | | | sampling units were considered within a community (Appendix S1: | |  |
| tween microhabitats, we used a GLMM (*glmer* function of the lme4 | | | Figure S3). Only 1.7% of the cushions did not harbor species growing | |  |
| package; Bates *et al*., 2015) where we included habitat type (cushion | | | inside, whereas this percent increased to 27% in open area plots. On | |  |
| plant vs. open area), altitude (1,600, 1,800, and 2,000 m), and the | | | average, the number of species decreased with increasing elevation | |  |
| interaction between these two effects as fixed factors, consider- | | | (*X*elevation2 | = 21.4, *df* = 2, *p* < 0.0001). However, this was due to a strong |  |
| ing also plot area as a covariable and the community nested within | | | decrease in the number of species occurring outside cushion plants, | |  |
| mountain as a random effect. Additionally, using data from cushion | | | as the number of species occurring within cushions remained rela- | |  |
| plants only, we compared variation in plant species richness across | | | tively constant throughout the elevation gradient (Figure 1). Hence, | |  |



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| differences in species richness between cushion and open area plots | | cushion plants increased the observed number of species by an av- | | | | |  |
| increased with elevation (*X*microsite2 | × elevation = 370, *df* = 2, *p* < 0.0001). | erage of 57% (*X*observed2 | = 30.3, *df* = 1, *p* < 0.0001; Figure 3a), and the | | | |  |
| Finally, the number of species increased with plot size (*X*area2 = 124.4, | | expected number of species by 50 and 35% according to the full- and | | | | |  |
| *df* =1, *p* <0.0001). Therefore, the relevance of the nurse effect in- | | even-sampling schemes, respectively (*X*full2 − sampling = 19.1, *df* = 1, | | | | |  |
| creased with altitude, being also dependent on the size of the nurse | | *p* <0.0001; *X*even2−sampling=14.6, *df* =1, *p* =0.0001; Figure 3b,c), | | | | |  |
| plants. Consideration of nurse plant species as a random effect | | at the mountain scale. In turn, by pooling surveys from all sampled | | | | |  |
| into the model slightly improved its fit (*X*2 = 4.2, *p* = 0.04) but not | | mountains, our results revealed that cushion plants increased plant | | | | |  |
| when the size of the cushion plant was also included as a covariate | | diversity by 33% at the regional scale (Figure 3a). However, Chao | | | | |  |
| (*X*2 = 1.92, *p* = 0.16). This indicated that individuals of different nurse | | estimations indicated that cushion plants could even increase re- | | | | |  |
| plant species host a similar number of species, once differences in | | gional richness up to 40% according to the full-sampling scheme | | | | |  |
| size were accounted for (Appendix S1: Figure S4). | | (Figure 3b), and by about 26% according to the even-sampling | | | | |  |
| The presence of cushions greatly increased species richness at | | scheme (Figure 3c). Therefore, positive effects of cushion plants on | | | | |  |
| the community level. Hypothetical communities lacking cushion | | local species richness persisted at larger spatial scales. | | |  |  |  |
| plants exhibited lower richness, both observed and expected, than | | Beta diversity analysis confirmed that cushion plants host spe- | | | | |  |
| communities with cushion plants (Figure 2, Table 1), even when | | cies not found growing in the open area. According to pairwise | | | | |  |
| sampling effort was controlled for (Figure 2c). Differences in spe- | |  |  |  |  |  |  |
| cies richness due to the presence of cushion plants increased with | |  |  |  |  |  |  |
| altitude (Figure 2), which was reflected by a significant cushion | |  |  |  |  |  |  |
| plant × elevation interaction (Table 1). Thereby, the presence of | |  |  |  |  |  |  |
| cushion plants increased observed community species richness, on | |  |  |  |  |  |  |
| average, by 36% at the lowest elevations and by 128% at the high- | |  |  |  |  |  |  |
| est elevations (Figure 2a), averaging 86% across all the 21 sampled | |  |  |  |  |  |  |
| communities. Likewise, when accounting for differences in sample | |  |  |  |  |  |  |
| sizes, the presence of cushion plants increased expected community | |  |  |  |  |  |  |
| species richness by 54% at the lowest elevations and by 113% at | |  |  |  |  |  |  |
| the highest elevations (Figure 2b), averaging 89% across all the 21 | |  |  |  |  |  |  |
| sampled communities. Therefore, asymptotic estimations of species | |  |  |  |  |  |  |
| richness indicated that cushion plants sustain a large proportion of | |  |  |  |  |  |  |
| total species richness at the community scale. | |  |  |  |  |  |  |
| The increase in species richness attributed to the presence | |  |  |  |  |  |  |
| of cushion plants persisted at the mountain and regional scales. | |  |  |  |  |  |  |
| By pooling data within mountains, we found that the presence of | |  |  |  |  |  |  |



**FI G U R E 1** Pattern of plant species richness at the local scale.Number of species (mean ± 1*SE*) within cushion plants and in open area plots along the elevation gradient. Different letters indicate significant differences (*p* < 0.05) according to a Tukey's HSD post-hoc test

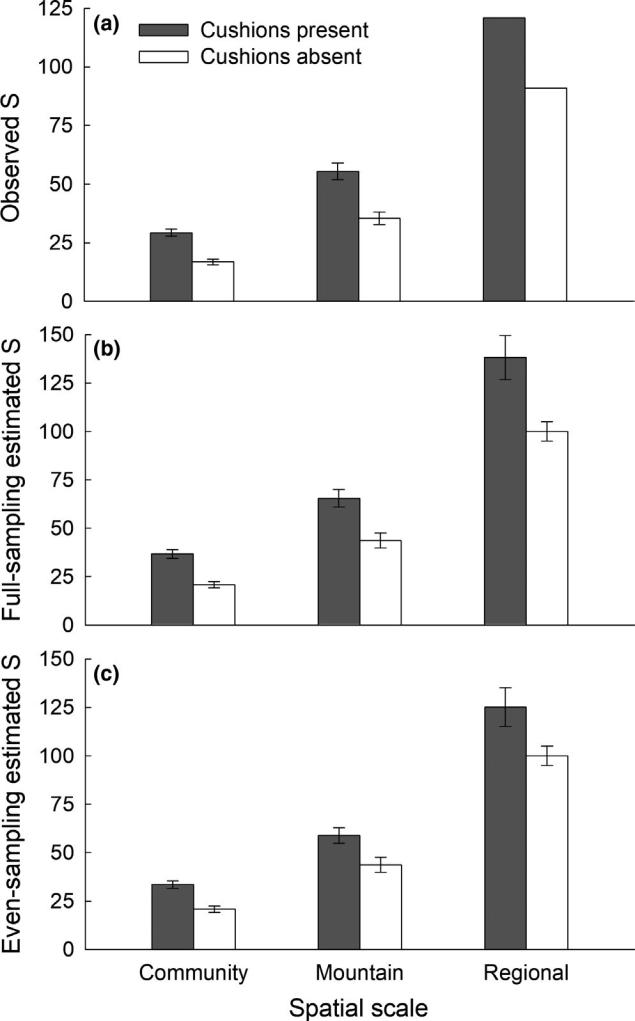
**FI G U R E 2** Pattern of plant species richness at the communityscale along the elevation gradient. Number of species or “*S*” (mean ± 1*SE*) that was (a) observed, and estimated considering

1. full- and (c) even-sampling efforts when cushion plants are present and absent (i.e. hypothetical communities lacking cushion plants). Different letters indicate significant differences (*p* < 0.05) according to a Tukey's HSD post-hoc test

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|  |  |  |  | **No. spp. Expected** | |  |  |  |  | **TA B L E 1** Generalized linear mixed- |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  | effect model testing the effect of cushion |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  | **No. spp. observed** | | |  | **Full-sampling** | |  | **Even-sampling** | | | plant presence and altitude on the number |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  | of species at the community level |  |
|  |  | ***df*** | **X2** | ***p*** | | **X2** | | ***p*** |  | **X2** | ***p*** | |  |
|  |  |  |  |  |
| Cushion | | 1 | 67.7 | <0.0001 | | 80.2 | | <0.0001 | 101.7 | | <0.0001 |  |  |  |
| Elevation | | 2 | 6.6 | 0.036 | | 4.4 | | 0.11 | 3.9 | | 0.14 |  |  |  |
| Cushion × Elevation | | 2 | 9.8 | 0.007 | | 1.1 | | 0.57 | 8.7 | | 0.013 |  |  |  |



**FI G U R E 3** Pattern of plant species richness at different scales.Number of species or “*S*” (a) observed, and estimated considering



1. full- and (c) even-sampling efforts in the actual landscape with cushion plants present and hypothetical scenarios lacking cushion plants. For the community and mountain scales, the mean ± 1 *SE* are shown, whereas for the overall regional scale the error bars represent the analytical standard deviations associated with the Chao estimates

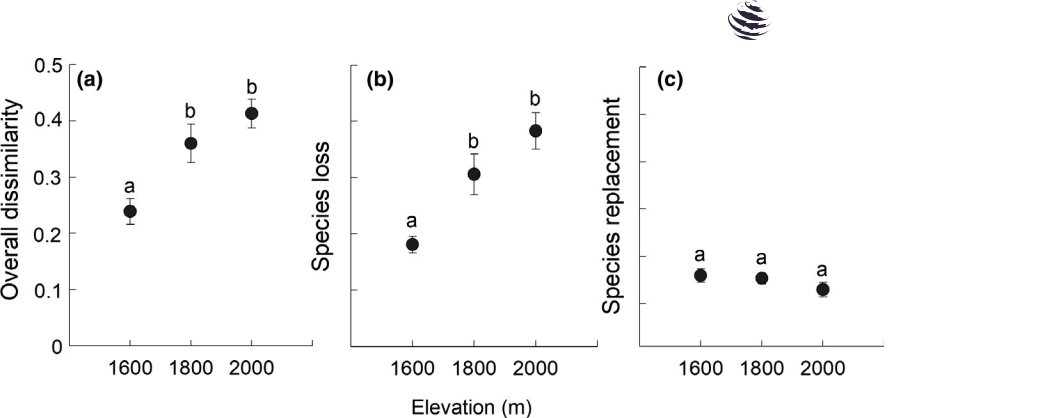
estimations of beta diversity within communities, overall dissimi-larity between cushion plants and open area plots increased with elevation (*X*2 = 31, *df* = 2, *p* < 0.0001; Figure 4a). This change in beta diversity was caused by non-random species loss (*X*2 = 34, *df* = 2,

*p* <0.0001), rather than species turnover (*X*2=3.5, *df* =2, *p* =0.17).Particularly, species loss explained 75% of the dissimilarity between cushion plants and open areas plots at the lowest elevation, rising up to 92% at the highest communities (Figure 4b). Instead, species turnover contributed very little to between-microsite dissimilarity, remaining relatively constant throughout the elevation gradient (Figure 4c). The non-random species loss observed in open area plots indicated that many species are found exclusively associated with cushion plants, whereas few or none species exclusively grow in the open. Regarding the multiple-site comparisons, overall beta diversity was always higher outside than inside cushion plants either among communities, altitudes or mountains (Appendix S1: Table S2). These differences in beta diversity could be mostly attributed to dif-ferences in species turnover, with plant assemblages associated with cushion plants consistently exhibiting lower species turnover than those associated with open areas, whereas nestedness did not con-tribute much to shape beta diversity patterns at these large spatial scales (Appendix S1: Table S2). Finally, according to beta diversity values, there were relatively large differences among plant assem-blages associated with different cushion plant species (Appendix S1: Table S3). Mean (± SE) beta diversity among cushion species within mountains was 0.65 ± 0.02 (βSIM = 0.42 ± 0.06, βNES = 0.23 ± 0.04), whereas overall beta-diversity (i.e., pooling data from all mountains) was 0.852 (βSIM = 0.693, βNES = 0.159). Therefore, species turnover, rather than differential species loss, was the most important deter-minant of differences in the plant assemblages associated with dif-ferent cushion plant species.

**4** | **DISCUSSION**

Locally occurring facilitation can be a key determinant of spe-cies richness at larger spatial scales (Cavieres and Badano, 2009; Cavieres *et al*., 2014, 2016; Chen *et al*., 2015). Our results indi-cate that the presence of cushion plants increases species rich-ness at all spatial levels analyzed, with the magnitude of this effect depending on the specific spatial scale and environmental conditions. Overall, this study strengthens the growing body of evidence showing that cushion plants can act as ecosystem en-gineers with remarkable positive effects on species richness at local and community scales. Furthermore, this study also reveals for the first time that patch-level facilitation can also increase re-gional diversity.

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**FI G U R E 4** Pairwise dissimilarity in plant species assembly between cushion plants and open areas along the elevation gradient. Thevalues depicted are means ± 1*SE* for (a) overall dissimilarity measured as the Sorensen index, and its two components, (b) non-random species loss or nestedness, and (c) species replacement or turnover measured as the Simpson index. Different letters indicate significant differences (*p* < 0.05) according to a Tukey's HSD post-hoc test

**4.1**|**Facilitation effects on species richness:**

**from the patch to the community scale**

Cushion plants harbored more than twice as many plant species than equivalent sized open areas, findings that agree with previ-ous studies assessing the effect of cushion plants at local scales (e.g., Nuñez *et al*., 1999; Cavieres *et al*., 2002, 2008; Arroyo *et al*., 2003; Kikvidze *et al*., 2015). This positive effect is largely owed to the patch-level modification of the abiotic environment by plants with cushion life-forms (e.g., Nuñez *et al*., 1999; Badano *et al*., 2006; Cavieres *et al*., 2007, 2008), facilitating the recruitment, growth and survival of many plant species (Badano *et al*., 2007; Cavieres *et al*., 2007, 2008). Here, cushion plants from different species were similarly effective in terms of the number of species they can host, once differences in size were taken into account. Therefore, independent of species, cushion plants in the studied Andean communities indeed act as ecosystem engineers (Badano and Cavieres, 2006a, 2006b).

Local effects of engineering organisms can influence biodi-versity at the landscape scale (Crooks, 2002; Wright *et al*., 2002; Wright and Jones, 2004; Romero *et al*., 2015). To the extent that ecosystem engineers create new habitats that are occupied by species that would not be able to persist outside them, patch-level effects will scale up enriching the species assemblages of entire communities occurring over a landscape (Jones *et al*., 1997; Wright *et al*., 2002; Cavieres and Badano, 2009). Here, we revealed thatcushion plants have an important influence on plant diversity in alpine landscapes of the Northern Patagonian Andes. In particular, the presence of cushions increased plant species richness of the entire community, as it has been reported for other alpine areas or other biomes (e.g., Valiente-Banuet and Verdu, 2007; Cavieres and Badano, 2009; Cavieres *et al*., 2016). For instance, studies conducted on the western side of the Southern Andes reported that cushion plants increased the number of plant species within communities between 10% and 144% (Badano and Cavieres, 2006a; Cavieres and Badano, 2009). Our study, conducted on the eastern side of the Andes, showed relatively similar increases in

community species richness with the presence of cushion plants, ranging between 25% and 175%.

Environmental factors can greatly determine the strength of cushion plants’ facilitative effect at the community scale (Wright and Jones, 2004; Wright *et al*., 2006). Because ecosystem en-gineers affect communities by modifying local environmental conditions, their impact and importance are likely to shift along gradients of environmental stress (Brooker and Callaghan, 1998; Callaway *et al*., 2002; Wright *et al*., 2006), with facilitative inter-actions becoming more frequent with increasing environmental stress (Bertness and Callaway, 1994). In our study area, the impor-tance of the nurse effect exerted by cushion plants at both patch and community levels increased greatly with altitude, probably associated with gradients of decreasing temperature, increasing temperature oscillations, and decreasing soil-water retention ca-pacity (Körner, 2003). Therefore, the ability of cushion plants to buffer environmental stresses resulted in no observable changes in the species number occurring within cushions along the altitu-dinal gradient, whereas there was a strong decrease in the number of species growing in open areas of similar size (Figure 1). The in-creasing importance of the nurse effect with altitude (Figure 2) is an indication that many Andean species will not be able to survive without the presence of cushion plants as environmental condi-tions become more stringent. However, the strength of facilita-tion through the nurse effect in alpine communities not always increases or changes monotonically with elevation (Cavieres *et al*., 2006; De Bello *et al*., 2011). For instance, a recent global study reported that cushion plants increased total community diversity by an average of 7% at higher elevations, whereas this effect rose up to 27% at lower elevations (Cavieres *et al*., 2016), because en-vironmental severity can be very high at lower elevations due to summer drought (Cavieres *et al*., 2006). The contrast between this global study and ours suggests that the importance of the nurse effect is context-dependent. In particular, its change in strength along altitudinal gradients will depend on the altitudinal range, the magnitude of the associated temperature and water-stress gradi-ents, and the capacity of cushion plants to buffer those stresses.

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| **4.2**|**Facilitation effects on species richness at** | | | species are restricted to the buffered microhabitat provided by cush- |  |
| **larger spatial scales** | | | ion plants, whereas very few species occur exclusively in the open. In |  |
|  |  |  | fact, the almost absence of species turnover in explaining microsite |  |
| Studies examining the importance of facilitation beyond the patch | | | differences indicates that open area habitat-specialist species are |  |
| scale are not only scarce, but also have not evaluated its influence | | | certainly rare in these Andean communities. This finding supports |  |
| on biodiversity beyond the community scale (Cavieres and Badano, | | | the assumption underlying our scaling-up hypothesis that even at |  |
| 2009; Cavieres *et al*., 2014, 2016; Chen *et al*., 2015). Here, the posi- | | | very large spatial scales there is a substantial proportion of species |  |
| tive effect of cushion plants on patch-level species richness scaled | | | that will not survive outside the cushion engineered habitats. The |  |
| up to the mountain and even regional scales. Considering all the | | | fact that some species are exclusively present, or more frequently |  |
| scales studied, the presence of cushion plants increased the number | | | found, in engineered patches is possibly related to a much higher |  |
| of plant species by >100%, 70%-80%, 50%-60%, and 30%-40% at | | | rate of local extinction than colonization of those species in the sur- |  |
| the patch, community, mountain, and regional levels, respectively. | | | rounding matrix (Ulrich *et al*., 2009). These are presumably the least |  |
| This decreasing trend in the cushion-plant effect on species rich- | | | stress-tolerant species that would be potentially excluded from the |  |
| ness reflects that, as the spatial scale increases, some plant species | | | community in the absence of cushions (Cavieres *et al*., 2016). Even |  |
| exclusively associated with cushion plants in one community could | | | species growing in the open might not be able to persist without |  |
| be found growing in the open in others. In fact, biotic interactions | | | the propagule subsidy from conspecific individuals thriving within |  |
| determining whether a species thrives or withers in a given envi- | | | cushions. Accordingly, cushion plants and the surrounding matrix |  |
| ronment could be neutral in another (Araújo and Rozenfeld, 2014). | | | could represent source and sink habitats, respectively (Eriksson, |  |
| Consequently, the overall importance of these interactions in de- | | | 1996; Kadmon and Tielborger, 1999). Furthermore, the increase in |  |
| termining local species persistence can be lost at broader scales | | | nestedness towards higher elevations implies a decrease of habitat- |  |
| (Whittaker *et al*., 2001; Pearson and Dawson, 2003; McGill, 2010). | | | generalist species. Consequently, the role of cushions as biodiversity |  |
| Despite this dilution effect, our results suggest that still about | | | refuges strongly increased with environmental severity given that an |  |
| one third of the high-Andean flora of this region owes its presence to | | | increasing number of plant species become completely dependent |  |
| the existence of nursing cushion plants, defying the widely accepted | | | on these engineered patches for their survival. |  |
| view that climate alone is enough to fully determine species occur- | | | Even though different nurse plant species tended to support |  |
| rences at larger scales (Whittaker *et al*., 2001; Pearson and Dawson, | | | different plant assemblages, we found consistently lower plant di- |  |
| 2003). Therefore, and as suggested by some modeling studies, bi- | | | versity and higher species turnover in the matrix (e.g. Kikvidze *et al*., |  |
| otic interactions may leave a broad-scale imprinting on species co- | | | 2015) that could be driven by abiotic factors (Shurin, 2007). Shurin's |  |
| existence and, hence, on species presence and distribution (Meier | | | model demonstrated that a negative relationship between patch- |  |
| *et al*., 2010; Bateman *et al*., 2012; Madon *et al*., 2013; Araújo and | | | level diversity and turnover arises because species turnover is gov- |  |
| Rozenfeld, 2014); yet empirical evidence for these broad-scale ef- | | | erned by the degree of environmental heterogeneity and the range |  |
| fects of biotic interactions is still fragmentary (e.g., Valiente-Banuet | | | of species’ tolerances. In particular, higher environmental variation |  |
| *et al*., 2006; Chalcoff *et al*., 2012). Nevertheless, a theoretical study | | | promotes greater species turnover through space and time (Stegen |  |
| has provided insights into whether the geographical imprinting of bi- | | | *et al*., 2013; Stein *et al*., 2014; Stein and Kreft, 2015). Therefore, high |  |
| otic interactions persists across spatial scales (Araújo and Rozenfeld, | | | variability in snow cover, soil moisture and temperature in the open |  |
| 2014). Specifically, local signatures of negative interactions like com- | | | (Löffler and Finch, 2005; Löffler, 2007), compared to the buffered |  |
| petition do not tend to scale up, whereas those of positive interac- | | | microhabitat provided by cushion plants, have possibly contributed |  |
| tions are more likely to manifest across all spatial scales (Araújo and | | | to the observed higher turnover values (Appendix S1: Table S2). |  |
| Rozenfeld, 2014). This could explain why the effect of ecosystem | | | This is so given that most species tend to thrive in different habi- |  |
| engineers, although local, can be still detected at broader spatial | | | tats rather than occur along entire gradients; a key factor that could |  |
| scales. Ultimately, this study is one of the first in demonstrating the | | | explain why the effect of cushion plants, even if still strong, dilutes |  |
| potential of positive biotic interactions in promoting diversity at mul- | | | somewhat at increasing spatial scales. |  |
| tiple spatial scales. | | |  |  |



**4.3**|**Turnover and species loss**

Exploring variation in species assemblage composition can provide insights into the causality of processes underlying biodiversity pat-terns. Interestingly, plant assemblage dissimilarities within commu-nities, i.e., between cushion plants and those growing in open area, were almost completely caused by species loss (nestedness) rather than species replacement (turnover). This result confirms that many

**5** | **CONCLUDING REMARKS AND CONSERVATION IMPLICATIONS**

The presence of cushion plants influences positively regional plant diversity in the Northern Patagonian Andes. Our findings strongly support the comparatively less explored bottom-up paradigm where widespread local-scale phenomena, particularly biotic interactions, can have consequences for large-scale biodi-versity patterns. Moreover, the extent to which nestedness and

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| turnover contribute to biodiversity patterns may provide insights | | generalized or idiosyncratic effects on species diversity? *Journal of* | | | | | | | | |  |
| into alpine plant conservation strategies. The facts that different | | *Biogeography*, *33*, 304–313. | | |  |  |  |  |  |  |  |
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| cushion plant species host different plant species assemblages, | |  |
| impacts of ecosystem engineers on community organization: a gen- | | | | | | | | |  |
| and of a differential species loss between cushion and open area | |  |
| eral approach illustrated by effects of a high-Andean cushion plant. | | | | | | | | |  |
| habitats indicate that conservation strategies should mainly focus | | *Oikos*, *115*, 369–385. |  |  |  |  |  |  |  |  |  |
| on detecting and protecting spots with high diversity of cushion | | Badano, E.I., Villarroel, | E., Bustamente, | | | R.O., | Marquet, P.A. and | | | |  |
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| plants (Gianuca *et al*., 2017). Cushion plants should be further con- | |  |
| by exotic plants in high-Andean ecosystems. *Journal of Ecology*, *95*, | | | | | | | | |  |
| sidered in conservation biology or restoration strategies of alpine | |  |
| 682–688. |  |  |  |  |  |  |  |  |  |
| landscapes as they provide refuges that prevent biodiversity loss, | | Baselga, A. (2010) Partitioning the turnover and nestedness com- | | | | | | | | |  |
| especially important in the face of an undergoing climate change | | ponents of beta diversity. *Global Ecology and Biogeography*, | | | | | | | *19*, |  |  |
| 134–143. |  |  |  |  |  |  |  |  |  |
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| similarity derived from nestedness, and nestedness. *Global Ecology* | | | | | | | | |  |
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| long-lived growth form and the more favorable habitat they create | | Bateman, B.L., VanDerWal, J., Williams, S.E. and Johnson, C.N. (2012) | | | | | | | | |  |
| could contribute to their persistence, as well as of nursed species | | Biotic interactions influence the projected distribution of a special- | | | | | | | | |  |
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| both small and large scales. | | mixed-effects models using lme4. *Journal of Statistical Software*, *67*, | | | | | | | | |  |
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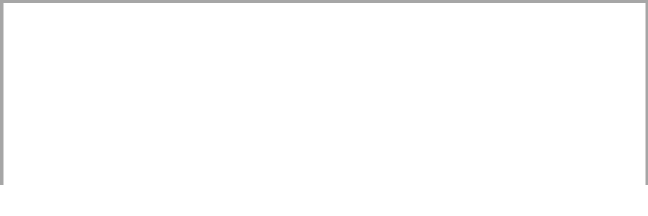
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