Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes

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ABSTRACT

Ecosystem engineers are organisms able to modulate environmental forces and, hence, may change the habitat conditions for other species. In so doing, ecosystem engineers may affect both species richness and evenness of communities and, in consequence, change species diversity. If these changes in community attributes are related to the magnitude of the habitat changes induced by the engineers, it seems likely that engineer species will have greater effects on diversity in sites where they cause larger habitat changes. We addressed this issue by evaluating the effects of three alpine cushion plants on species richness, evenness, and diversity of high-Andean plant communities. Given that the difference in microclimatic conditions between cushions and the external environment increases with elevation, we proposed that these organisms should have greater effects on community attributes at higher than at lower elevation sites. Results showed that the three cushion species had positive effects on species richness, diversity, and evenness of plant communities. It was also observed that the magnitude of these effects changed with elevation: positive effects on species richness and diversity increased towards upper sites for the three cushions species, whereas positive effects on evenness increased with elevation for one cushion species but decreased with elevation for other two cushion species. These results suggest that the presence of cushions is important to maintain plant diversity in high-Andean communities, but this positive effect on diversity seems to increase as the difference in environmental conditions between cushions and the external environment increases with elevation.

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INTRODUCTION

Environmental abiotic conditions and species interactions have been traditionally proposed to determine species diversity patterns in natural communities (Connell & Orias, 1964; Connell, 1978; Grime, 1979; Tilman *et al.*, 1997; Tilman, 1999). However, although all organisms interact with their physical environment, it has been appreciated that some of them substantially change the environmental conditions and resource availability via non-trophic interactions, hence affecting other species and, consequently, altering community attributes of natural species assemblages (Flecker, 1996; Aho *et al.*, 1998; Berkenbusch & Rowden, 2003; Lill & Marquis, 2003; McCabe & Gotelli, 2003; Perelman *et al.*, 2003; Flecker & Taylor, 2004; Casas-Crivillé & Varela, 2005). Jones *et al.* (1994, 1997) coined the term 'physical ecosystem engineering' to refer to this biotic process of habitat transformation,

and 'physical ecosystem engineers' to enclose those organisms responsible of such habitat changes. Furthermore, Jones *et al.* (1994, 1997) defined that there are two types of ecosystem engineers: 'allogenic engineers', which change the environment by transforming living or non-living materials from one state to other but not necessarily remaining as part of the engineered habitat, and 'autogenic engineers', which modify the environment via their own physical structures, remaining as a part of the engineered habitat.

In recent years, it has been shown that both, allogenic and autogenic engineers, may affect either the incidence or the abundance of other species in natural communities (Flecker, 1996; Thomas *et al.*, 1998; Crooks & Khim, 1999; Wright *et al.*, 2002; McCabe & Gotelli, 2003; Castilla *et al.*, 2004). However, studies indicating how engineer species might influence community diversity by altering species richness and/or evenness are conspicuously lacking. Furthermore, although it would be useful to

know what engineers and in which sites will have greater effects on communities (Jones *et al.*, 1997), only a few studies have addressed this issue (e.g. Wright & Jones, 2004; Crain & Bertness, 2005). In a pioneer article on ecosystem engineering, Jones *et al.* (1997) proposed that the impacts of ecosystem engineers on community attributes would depend, on one hand, on the magnitude of the environmental changes exerted by the engineers and, on the other hand, on the number of species in the regional pool that respond to such changes. Thus, if an engineer species modulates environmental conditions that are critical for persistence of other species, it seems likely that such an engineer would have greater effects on species richness and evenness, and hence on diversity, in those sites where it causes larger environmental changes.

Alpine cushion plants are well known for their ability to modify their physical environment (Hager & Faggi, 1990; Cavieres *et al.*, 1998; Núñez *et al.*, 1999; Arroyo *et al.*, 2003; Körner, 2003; Molina-Montenegro *et al.*, 2005). For instance, cushions can reduce wind speed up to 98% when compared with their surrounding exposed areas (Hager & Faggi, 1990), which in turn may decrease the heat loss by convection. This decouple of temperatures might allow cushions to maintain temperatures up to 15 °C higher than the external environment (Körner, 2003), providing suitable habitat patches for plant species close to their limits of tolerance to low temperatures (Arroyo *et al.*, 2003). Furthermore, soils below high-Andean cushions can retain up to 50–70% more water (Cavieres *et al.*, 1998, 2006), and provide microsites with 45–90% more nitrogen (Núñez *et al.*, 1999; Cavieres *et al.*, 2006), than soil of surrounding exposed open areas. Recent studies have indicated that these microclimatic modifications by cushions may enhance the survival of other non-cushion plant species. For instance, in a series of transplant experiments conducted in the high-Andes of central Chile, Cavieres *et al.* (2006) observed that seedling survival of *Cerastium arvense* (Caryophyllaceae) and *Hordeum comosum* (Poaceae) within cushion plants were *c.* 30% and 80%, respectively, whereas survival in exposed open areas was lower than 10% for both species. On the other hand, cushions create large habitat patches, which can reach up more than 3 m in diameter, persisting over decades (Benedict, 1989; McCarthy, 1992; Le Roux & McGeoch, 2004; Mark & Wilson, 2005) and even centuries (Ralph, 1978; Kleier & Rundel, 2004). Therefore, the ability of cushions to transform the habitat, together with the fact that they create large and persistent structures, suggests that these growth-forms can be acting as physical ecosystem engineers in the high-Andes (*sensu* Jones *et al.*, 1994, 1997). Furthermore, given that habitat modification occurs because of the interaction of the physical structures of cushions (branches, leaves, etc.) with the environment, and given that cushions remain as a part of the modified environment, they can be considered as autogenic engineers (*sensu* Jones *et al.*, 1994, 1997).

High-mountain environments are well known for their low air and soil temperatures (Körner, 2003). However, while these temperatures decrease with elevation (Körner, 2003), cushion plants can maintain similar substrate temperatures at different elevations (Arroyo *et al.*, 2003). This indicates that the decoupling of

temperature between cushions and the surrounding environment increases with altitude. Moreover, it has been suggested that these decoupling of temperature between cushions and the external habitat would be more important in increasing the incidence of other non-cushion species at higher than at lower elevation sites (Cavieres *et al.*, 2002; Arroyo *et al.*, 2003). Thus, considering the importance of temperature on the physiological and reproductive performance of alpine plants (Körner, 2003), it could be proposed that cushion plants should have larger effects on community diversity at higher elevations than at lower ones.

In this study, we evaluate the impacts of three alpine cushion species on species richness, evenness, and diversity of plant communities located at different elevations in high-Andean ecosystems. Given the ability of cushions to modify the habitat to other species, we propose that these growth forms have positive effects on community diversity by increasing either species richness or evenness. On this vein, since the importance of the mitigation of extreme low temperatures within cushions increases with elevation, we propose that these positive effects on community attributes should be greater at higher than at lower elevation sites.

METHODS

Study sites

This study was conducted in two high-Andean areas of central Chile: (1) slopes of Mt. Franciscano (33° S), in the Río Molina basin, 50 km east of the city of Santiago; and (2) slopes of Mt. Colorado (30° S), in the Río Elqui basin, 85 km east of the city of La Serena. In both areas, climate has been classified as alpine with influence from the Mediterranean-type climate that prevails in the lowlands (di Castri & Hajek, 1976). Precipitations and temperatures show a sharp seasonality in both sites, although the Río Elqui basin is drier than the Río Molina basin (di Castri & Hajek, 1976). In the Río Molina basin, precipitations mainly occur as snow during winter months, with an estimated annual precipitation of 400–900 mm above the tree line (Santibañez & Uribe, 1990); estimated mean annual temperature of the air at 3150 m is 3 °C, and the estimated annual lapse rate for this site is 6.1 °C km⁻¹ (Cavieres & Arroyo, 1999). In the Río Elqui basin, mean annual precipitation at 3750 m is 242 mm, where 96% of precipitation falls in winter as snow (Squeo *et al.*, 1994); estimated mean air temperature at 3700 m is 4.6 °C and decreases with a lapse rate of 6.5 °C km⁻¹ (Squeo *et al.*, 1994). In both study sites, cushion plants form spatially discrete habitat patches isolated from similar units by large open areas, mainly comprised by rocks and bare ground, hence, there are no other large and persistent structures created by organisms that could potentially bias the engineering effects of cushions.

In Mt. Franciscano, we sampled two plant communities dominated by cushions of *Azorella monantha* Clos (Apiaceae), one at 3200 m and other at 3600 m. At both elevations, most *A. monantha* cushions had diameters between 40 cm and 60 cm, but a few individuals were larger than 80 cm diameter. In this site, cover of cushions was *c.* 10% at both elevations (see below).

In Mt. Colorado, we sampled two plant communities dominated by cushions of both *Azorella madreporica* Clos (Apiaceae) and *Adesmia subterranea* Clos (Fabaceae), one at 3700 m and the other at 4000 m. At both elevations, most of the cushions had diameters between 30 cm and 50 cm, being no cushions larger than 90 cm diameter. Cover of these cushion was similar (*c.* 10%, see below), both between cushion species and between elevations.

Effects on community attributes

To estimate the effect of an ecosystem engineer on community attributes, Wright *et al.* (2002) proposed that one must first estimate community attributes in areas not affected by the engineer species (i.e. unmodified habitat patches) and then compare these attributes with those observed in an equally sized area that incorporates the habitat patches modified by the engineer (i.e. the engineered landscape = unmodified + modified habitat patches). For this, at each elevation, we selected 100 points in open areas away from cushions, which represented the unmodified habitat, and 100 cushion individuals larger than 40-cm diameter, which represented the modified habitat patches. Both, points in open areas and cushions, were selected by using datasheets with points defined by random directions and distances from the centre of a 1-ha plot previously delimited at each elevation. To record species richness and abundances in each habitat type, we placed a 30-cm diameter circular plot at each selected point in open areas and on each selected cushion; all plant species growing within these plots were identified and the number of individuals of each species was counted. Although we randomly sampled open areas, we carefully controlled to put down these sampling plots at a minimum distance of 1 m away from any cushion in order to avoid biases due to interferences between habitat types. On the other hand, for the cushion samples, plots were placed at the centre of cushions; we did it because the microenvironment at the cushion edges could correspond to a mixture of conditions between open areas and cushions and, then, the real effect of cushions on species richness and abundances could be masked by edge effects. Furthermore, in the cushion samples, we did not include the cushion-forming plant as another species into the sampling.

Data from open areas were used to estimate species richness, diversity, and evenness that communities would have had in unengineered situations, while data from open areas and cushions were pooled in a single data set to estimate these attributes in engineered situations. In Mt. Colorado, where cushions of *A. madreporica* and *A. subterranea* are growing together at both elevations, data of each cushion species were pooled separately with data from open areas. We included all plots from open areas and cushions to estimate these community attributes, irrespectively if plots had or not plants other than cushions. Despite the intensive sampling, some rare (infrequent) species might have not been detected within samples, which could cause biased estimations of the effects of cushions on community attributes. To deal with this limitation, community attributes in both engineered and unengineered situations were estimated with sample-based rarefactions (Gotelli & Colwell, 2001). We also measured cover of

cushions and open areas in each site to control the estimation of community attributes in engineered situations for the difference in habitat availability as suggested by Wright *et al.* (2002). Cover of cushions and open areas at each sampling site were recorded on 10 parallel line transects (50-m-long each, and distanced 10 m). Furthermore, along these line transects, we also determine the frequency of occurrence of each cushion species at each elevation. In all cases, average cover of cushions was *c.* 10%, thus, a proportion 1 : 9 was used to construct those data sets in which data from cushion patches were included (engineered situations); that is, while cushion data set was included only once, data from open areas were replicated nine times. On the other hand, frequencies of occurrence (i.e. incidence) of each cushion species were similar between elevations. Average incidence (individuals per transect ± 1 s.e.) of *A. monantha* in Mt. Franciscano was 8.6 (± 0.9) and 8.4 (± 1.3) at 3200 m and 3600 m, respectively. In Mt. Colorado, average incidences of *A. madreporica* and *A. subterranea* at the lower elevation site were 5.1 (± 0.5) and 5.7 (± 1.0), respectively, and 4.2 (± 1.3) and 4.7 (± 1.5) at the upper site.

Rarefactions were carried out with the software ESTIMATES 6.0 (Colwell, 2000), and included from 1 to 100 samples (the maximum number of samples taken at each habitat type) in all cases. One hundred with-replacement rarefaction runs (i.e. random permutations) were performed at each sampling size with data sets from unengineered (open areas only) and engineered (open areas plus cushion patches) situations. At each rarefaction run, species richness (S) and diversity (H') were estimated with the Coleman's algorithm (Coleman *et al.*, 1982) and the Shannon–Wiener's formula (Magurran, 1988), respectively. Values of the Coleman estimator and the Shannon–Wiener index were averaged to obtain the maximum likelihood estimators of S and H' at each sampling size (Colwell, 2000). Thus, these values represent the average species richness and the average species diversity that might be detected in communities if 1, 2, 3, … 100 random samples are sequentially taken only in open areas or in areas that include cushion patches. Maximum likelihood estimators of S and H' were plotted against sample sizes to construct rarefaction curves in which it can be observed how S and H' vary with sampling size (Colwell, 2000). Furthermore, we also calculated 95% confidence intervals for these estimators of H' and S to assess statistical differences between open areas and open areas plus cushions. Significant effects of cushions on these community attributes were assumed if confidence intervals did not overlap at the asymptote of rarefaction curves. Maximum likelihood estimators of S and H' were used to compute species evenness (J) at each sampling size in both open areas and communities including cushions; J was computed as $Jn = H'n/\ln(Sn)$, where $\ln(Sn)$ indicates the maximum diversity that communities could attain if all species were equally abundant (Magurran, 1988), and n indicates the number of samples pooled at each sampling size. Values of J from open areas and communities including cushions were plotted against sampling sizes to visually evaluate effects of cushions on this community attribute.

To assess whether effects of cushions on community attributes change with elevation, we used maximum likelihood estimators of S, H', and J at 100 samples to estimate the relative contribution
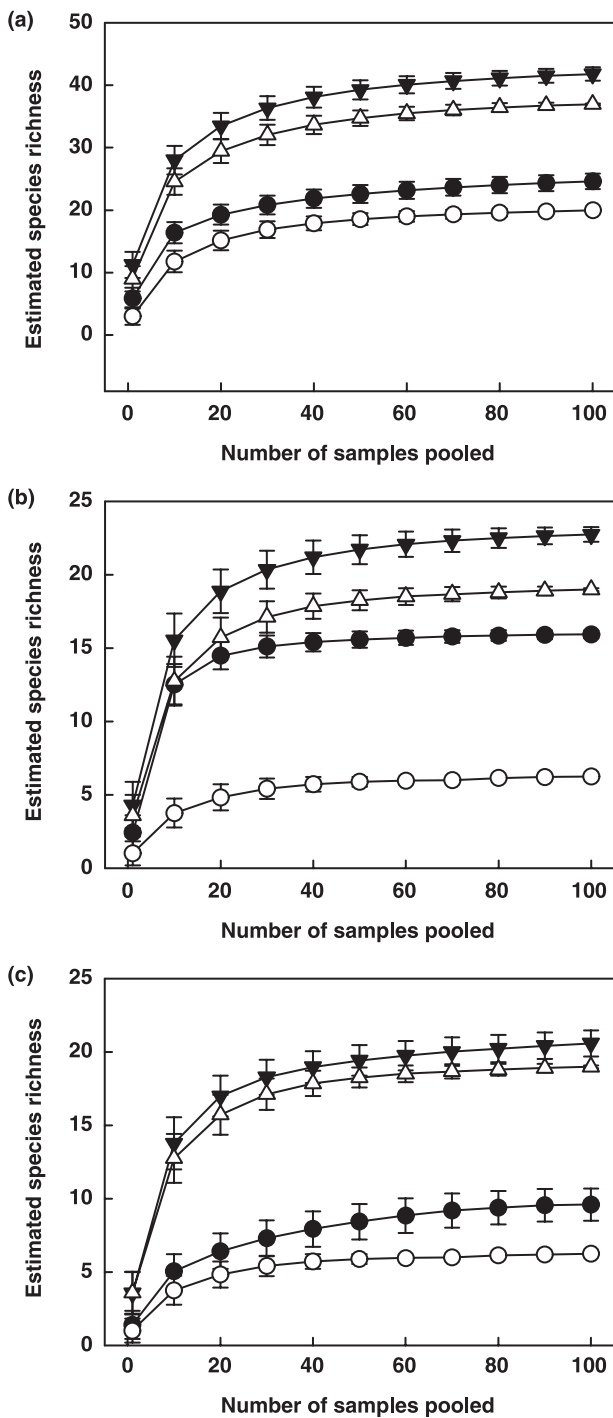
Figure 1 Rarefied values of species richness (± 95% confidence intervals) in open areas (empty symbols) and when cushions are included (solid symbols) at the upper (circles) and the lower (triangles) elevation. (a) *Azorella monantha*, (b) *Azorella madreporica*, and (c) *Adesmia subterranea*.

that the presence of cushion patches made to community attributes at each altitude. Hence, for species richness (*S*) we computed: $[(SL–Su)/Su]$, where *SL* and *Su* are the estimated values of species richness at 100 samples for the community with

and without cushions, respectively, and the difference (*SL–Su*) estimates the net effect of cushions on species richness. For species diversity (*H′*) we computed $[(H'L–H'u)/H'u]$, where *H'L* and *H'u* are the estimated diversity at 100 samples for the community with and without cushions, respectively, and the difference (*H'L–H'u*) estimates the net effect of cushions on diversity. Finally, for species evenness (*J*), we computed $[(JL–Ju)/Ju]$, where *JL* and *Ju* are values of evenness estimated from *H′* and *S* at 100 samples for the community with and without cushions, respectively, and the difference (*JL–Ju*) estimates the net effect of cushions on evenness.

RESULTS

In both Mt. Franciscano and Mt. Colorado, and at both elevation sites, more than 96% of sampling plots within cushions had at least one species. In Mt. Franciscano, 94% of sampling plots in open areas at the lower elevation (3200 m) had at least on species, whereas this proportion decreased to 83% at the upper elevation site (3600 m). In Mt. Colorado, 86% and 79% of sampling plots in open areas had at least one species at the lower (3700 m) and the upper (4000 m) elevation site, respectively.

In both study sites, the number of species decreased with elevation. In Mt. Franciscano, regardless *A. monantha*, 44 and 28 species were detected at 3200 m and 3600 m, respectively. Here, at the lower elevation, seven species were detected exclusively inhabiting *A. monantha* cushions and 21 species were exclusively detected in open areas. At the upper elevation site, eight species were detected exclusively within cushions and other eight species were only detected in open areas (see Appendix S1 in Supplementary Material). In Mt. Colorado, where cushions of *A. madreporica* and *A. subterranea* dominate plant communities, 22 and 16 species were detected at 3700 m and 4000 m, respectively. At the lower elevation, three species were only detected within cushions and three species were only recorded in open areas; in contrast, at the upper elevation, 10 species were exclusively detected within cushions and only one species was exclusively detected in open areas (see Appendix S2 in Supplementary Material). In all sampling sites, rarefaction curves of species richness (Fig. 1) and species diversity (Fig. 2) reached the asymptote before 100 samples, both for open areas only and communities including cushions, indicating that the sampling effort was enough to fully capture composition and diversity of plant species assemblages.

In all study sites, species richness in open areas always showed significantly lower values than when cushions were included (Fig. 1), indicating that cushions had positive effects on this community attribute. In Mt. Franciscano, at 3200 m, rarefactions estimated *c.* 37 species for open areas and *c.* 42 species when *A. monantha* cushions were included, whereas at 3600 m these values were *c.* 20 and 25 species for open areas and open areas plus cushions, respectively (Fig. 1a). In this site, estimated values of species richness for communities including cushions indicated that the relative contribution of the presence of *A. monantha* to species richness was 13% and 21% at 3200 m and 3600 m, respectively. In Mt. Colorado, at 3700 m, estimated species richness in open areas was *c.* 19 species, whereas *c.* 23 species
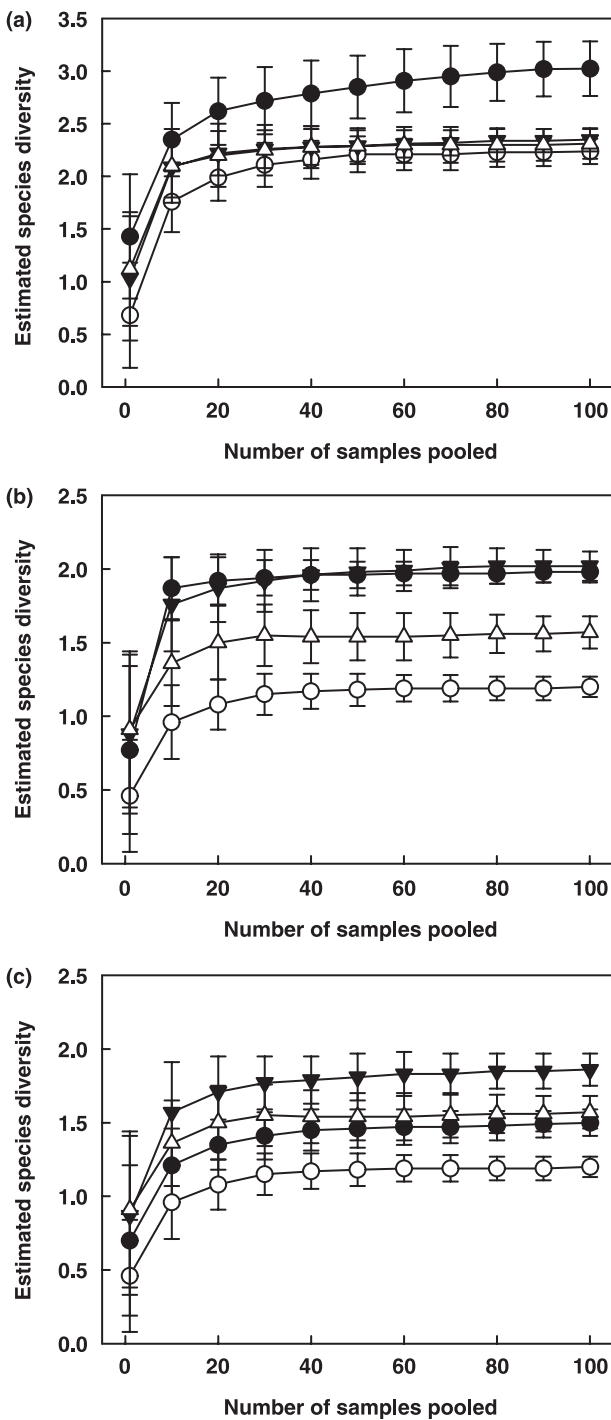
Figure 2 Rarefied values of species diversity (± 95% confidence intervals) in open areas (empty symbols) and when cushions are included (solid symbols) at the upper (circles) and the lower (triangles) elevation. (a) *Azorella monantha*, (b) *Azorella madreporica*, and (c) *Adesmia subterranea*.

were estimated when *A. madreporica* cushions were included (Fig. 1b) and *c*. 21 species for the inclusion of *A. subterranea* cushions (Fig. 1c). At 4000 m, estimated species richness in open areas was *c*. six species, whereas *c*. 16 and *c*. 10 species were estim-

ated for the communities including cushions of *A. madreporica* (Fig. 1b) and *A. subterranea* (Fig. 1c), respectively. The presence of *A. madreporica* cushions increased 20% and 144% of community species richness at 3700 m and 4000 m, respectively, whereas *A. subterranea* cushions increased species richness by 10% at the lower site and by 53% at upper site. Therefore, in all cushion species studied here, their relative contribution to species richness at the community level increased with elevation.

In Mt. Franciscano, the presence of *A. monantha* did not increase community diversity at 3200 m (Fig. 2a). In contrast, at 3600 m, the inclusion of *A. monantha* cushions produced significantly higher species diversity than open areas (Fig. 2a), increasing community diversity by 35%. At both elevations of Mt. Colorado, estimated values of the Shannon–Wiener diversity index were significantly lower in open areas than when either *A. madreporica* (Fig. 2b) or *A. subterranea* (Fig. 2c) was included, indicating that both cushion species increased community diversity. These positive effects of both cushion species on community diversity increased with elevation: *A. madreporica* increased species diversity by 20% at 3200 m and by 77% at 4000 m, whereas increases in species diversity due to *A. subterranea* were 10% and 53% at the lower and upper elevation, respectively.

In Mt. Franciscano, open areas and the community including *A. monantha* cushions at 3200 m showed similar values of species evenness, whereas the presence of *A. monantha* at 3600 m increased community species evenness by 26% (Fig. 3a). At both elevations of Mt. Colorado, species evenness in open areas was lower than in communities including either *A. madreporica* (Fig. 3b) or *A. subterranea* (Fig. 3c), but the magnitude of these positive effects on species evenness decreased with elevation. At 3700 m, *A. madreporica* and *A. subterranea* increased community evenness by 17% and 15%, respectively, whereas these positive effects of cushions at 4000 m were 8% for *A. madreporica* and 6% for *A. subterranea*.

DISCUSSION

In general, our results suggest that the presence of cushion plants positively affects diversity attributes of high-Andean plant communities. Thus, a relatively low cover of cushion plants (*c*. 10% when compared with open areas) in the studied communities provides enough 'engineered habitat' to cause an increase in species richness up to 144%, and increase species diversity and evenness by 77% and 26%, respectively. In a recent study, Badano and Cavieres (2006) showed that a 10% of cushion cover is a commonly expected situation in the high-Andes of Chile and Argentina, although these authors indicated that these organisms may increase community diversity between 20% and 111%, depending on the cushion species. Despite the overall large positive effects of cushion plants on community attributes, our results partially support the initial proposal that such positive effects would increase with elevation. While in both study sites positive effects of cushions on species richness and diversity consistently increased with elevation, positive effects of cushions on community evenness increased with elevation in Mt. Franciscano but decreased in Mt. Colorado.
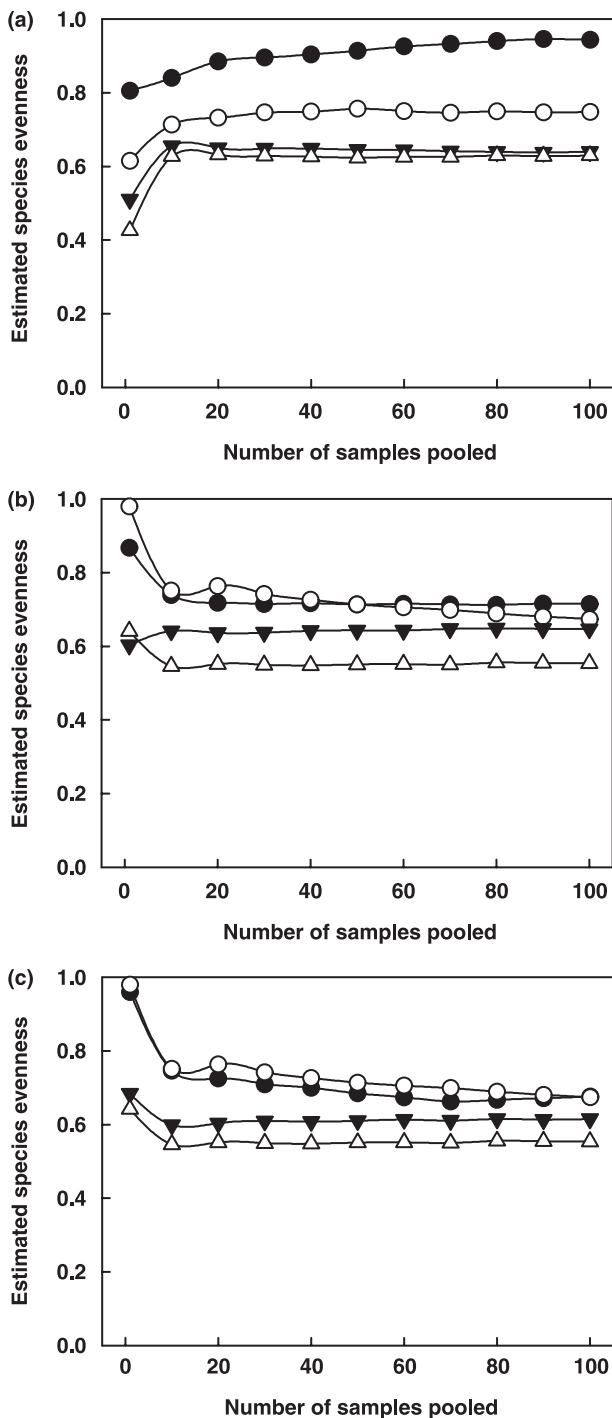
Figure 3 Values of evenness estimated from rarefied values of species richness and diversity in open areas (empty symbols) and when cushions are included (solid symbols) at the upper (circles) and the lower (triangles) elevation. (a) *Azorella monantha*, (b) *Azorella madreporica*, and (c) *Adesmia subterranea*.

Although community species richness decreased with altitude, positive effects of cushion plants on community species richness increased towards higher elevations, and these effects could be attributed to the large proportion of species that were detected inhabiting exclusively within cushion patches at the upper elevation

sites. For instance, at the lower elevation of Mt. Franciscano, *C. arvense* (Caryophyllaceae) and *Erigeron andicola* (Asteraceae) were detected in both open areas and *A. monantha* cushions, but these species were exclusively recorded within *A. monantha* cushions at the upper elevation site (see Appendix S1 in Supplementary Material). On the other hand, while several species were detected in both open areas and cushions of either *A. madreporica* or *A. subterranea* at the lower elevation of Mt. Colorado, some of them were only detected within cushions at the upper elevation site (e.g. *Calandrinia* spp., *C. arvense*, *E. andicola*, *Gayophytum micranthum*; see Appendix S2 in Supplementary Material). These results suggest that, despite the altitudinal loss of species, the presence of cushions at upper sites may extend the altitudinal distribution range of some species from lower sites, hence causing the observed increase in species richness at upper elevation plant communities. Furthermore, although our study was purely correlational and more experimental evidence is needed, these results concur with the suggestion that mitigation of extreme low temperatures by cushions could be more critical for the persistence of other high-Andean plant species as elevation increases (Cavieres *et al.*, 2002; Arroyo *et al.*, 2003).

Cushions were also observed to increase species evenness in most of the studied communities. Given that evenness is related to patterns of species dominance within communities (Magurran, 1988), such positive effects of cushions on the evenness could be explained in two ways. First, some subordinate, rare species from open areas may increase their abundances within cushion patches, reaching similar abundances than dominant species in open areas and becoming codominant species when cushion patches and open areas are considered together as a whole 'engineered landscape'. Second, some of the species that inhabit exclusively within cushions could have similar abundances to that of dominant species in surrounding open areas, and cause codominance when cushion patches and open areas are considered together. These two explanations are not mutually exclusive and both would lead to higher community evenness. However, irrespective of the manner by which cushions increase community evenness, results showed a contrasting pattern between sites: the positive effect of *A. monantha* on evenness increased with elevation in Mt. Franciscano, whereas these effects of *A. madreporica* and *A. subterranea* decreased with elevation in Mt. Colorado. These differences between sites could be due to differential responses, in terms of abundances, of species constituting the regional species pool from each site. For instance, in Mt. Franciscano, abundances of subdominant species at the lower elevations may be dramatically enhanced by the presence of cushions at the upper elevation, hence causing the observed increase in community evenness. In contrast, in Mt. Colorado, abundances of species at the upper elevation seem to be less affected by the presence of cushions than at the lower elevation, then causing the smaller increase in evenness observed at the upper elevation.

Such effects on species richness and evenness could be related to the greater effects of cushions on species diversity at the upper elevation sites. A series of theoretical and empirical studies indicates that higher values of species diversity could be reached by increasing either species richness or evenness within communities

(Peet, 1975; Stirling & Wilsey, 2001). Thus, the higher positive effect of cushions on species diversity at upper than at lower elevation sites could be a consequence, at least in part, of the greater positive effects of cushions on community species richness. Regarding species evenness, the increasing positive effect of *A. monantha* towards the upper elevation in Mt. Franciscano suggests that such an effect could contribute to increase diversity at that site. However, in Mt. Colorado, the decreasing positive effect of *A. madreporica* and *A. subterranea* on species evenness with increasing elevation suggests that the higher diversity observed at upper elevation sites would to be mainly due to positive effects of cushions on species richness only.

Since Jones *et al.* (1994) coined the term 'ecosystem engineers' to include those organism able to transform habitat by modulating environmental forces, several studies have shown the effects that engineering activities may have on species richness and evenness. For example, meadows resulting from the construction of dams by beavers (*Castor canadensis*) add new herbaceous plant species into riparian communities of north-east USA and increase species richness by 33% (Wright *et al.*, 2002); creation of new substrata by ascidians (*Pyura praeputialis*) in intertidal habitats of the Pacific Coast of northern Chile provides habitat for marine macroinvertebrates and algae, increasing community species richness by *c.* 55% (Castilla *et al.*, 2004); bulldozing activities of fishes (*Prochilodus mariae*) in tropical piedmont streams of Venezuelan Andes can either increase or decrease the abundance of freshwater macroinvertebrates, diatoms, and cyanobacteria (Flecker, 1996); soil mounds created by kangaroo rats (*Dipodomys spectabilis*) in the Chihuahuan Desert increase abundance of some ant species whereas decrease the abundance of others (Schooley *et al.*, 2000); and the list of studies showing effects of ecosystem engineers on these diversity components continues rising (e.g. Thomas *et al.*, 1998; Crooks & Khim, 1999; Lill & Marquis, 2003; McCabe & Gotelli, 2003; Wright *et al.*, 2003; Fritz *et al.*, 2004). However, to date, there are no studies integrating the effects that engineer species may have on both species richness and evenness in order to evaluate what effect is more important to affect community diversity. Furthermore, only a few studies evaluated how the effects of engineers on other species may vary with changes in the environmental context (Crain & Bertness, 2005).

In this study, we used the Shannon–Wiener diversity index to integrate the effects different engineer species sharing the same archetype (all of them are alpine cushion plants) on species richness and evenness, and such integration would allow us to assess how the presence of cushions may affect species diversity of high-Andean plant communities. In general, our results suggest that cushions may affect community diversity by affecting species richness, evenness, or both community attributes, but the relative importance of these effects seems to change with elevation. Given that the decoupling of temperature between cushions and the surrounding environment increases at higher altitudes (Arroyo *et al.*, 2003), the effects of cushions on community attributes could be linked with the magnitude with which those organisms control temperature, and other related environmental conditions (nutrient availability, soil moisture, etc.), at different elevations. Despite the currently accepted view that both regional and local processes are acting together in structuring local diversity (Ricklefs, 1987), environmental engineering by organisms is seldom recognized as another structuring process at local scales (Jones *et al.*, 1997; Wright *et al.*, 2003). As our results suggest, ecosystem engineering could be very important in shaping local diversity by affecting species richness, evenness, or both, particularly in habitats where the environmental changes exerted by the engineer species are crucial for the survival of several other species.

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SUPPLEMENTARY MATERIAL

The following material is available online at
http://www.blackwell-synergy.com/loi/ddi

Appendix S1 Species list from communities dominated by cushions of *Azorella monantha* on slopes of Mt. Franciscano (33° S) at 3200 m and 3600 m.

Appendix S2 Species list from communities dominated by cushions of *Azorella madreporica* and *Adesmia subterranea* on slopes of Mt. Colorado (30° S) at 3700 m and 4000 m.