ORIGINAL
ARTICLE

Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity?

Ernesto I. Badano* and Lohengrin A. Cavieres

ECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales & Oceanográficas, Universidad de Concepción, Casilla, Concepción, Chile

ABSTRACT

Aim To integrate the effects of ecosystem engineers (organisms that create, maintain or destroy habitat for other species) sharing the same archetype on species diversity, and assess whether different engineer species have generalized or idiosyncratic effects across environmentally similar ecosystems.

Location High-Andean habitats of Chile and Argentina, from 23° S to 41° S.

Methods We measured and compared the effects of eight alpine plants with cushion growth-form on species richness, species diversity (measured as the Shannon–Wiener index) and evenness of vascular plant assemblages across four high-Andean ecosystems of Chile and Argentina.

Results The presence of cushion plants always increased the species richness, diversity (measured as the Shannon–Wiener index) and evenness of high-Andean plant assemblages. However, while the presence of different cushion species within the same ecosystem controlled species diversity in the same way, these effects varied between cushion species from different ecosystems.

Main conclusions Results consistently supported the idea that increases in habitat complexity due to the presence of ecosystem engineers, in this case cushion plants, would lead to higher community diversity. Results also indicate that effects of the presence of different cushion species within the same ecosystem could be generalized, while the effects of cushion species from different ecosystems should be considered idiosyncratic.

Keywords
Andes, community ecology, cushion plants, ecosystem engineers, species evenness, species diversity, species richness.

*Correspondence: Ernesto I. Badano, ECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales & Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile.
E-mail: ebadano@udec.cl

INTRODUCTION

Species diversity is a key feature linked with the stability, invasiveness, functioning and several other properties of natural ecosystems (Chapin *et al.*, 1997, 1998; Shea & Chesson, 2002; Díaz *et al.*, 2003; Naeem & Wright, 2003). In community ecology, species diversity is basically defined as a function of its components, i.e. species richness and evenness (Margalef, 1957; MacArthur & MacArthur, 1961; Dickman, 1968; Tramer, 1969; Hurlbert, 1971; Peet, 1974, 1975; Cuba, 1981). The first of these components, species richness, is simply the number of

species within a community, while evenness refers to the relative importance of each species (Peet, 1974, 1975). Both the physical environment and biotic interactions have been traditionally invoked as determinants of these community attributes, and consequently of species diversity across natural ecosystems (Grime, 1979; Sousa, 1984; Tilman, 1984, 1987; O'Brien, 1993). However, the control of community diversity by organisms able to modulate environmental forces has received considerably less attention.

Since Jones *et al.* (1994, 1997) coined the term 'ecosystem engineers' for those organisms able to create, maintain or

destroy habitat for other species by modulating environmental forces, a wide variety of animal and plant species has been shown to affect community attributes through their engineering activities (e.g. Flecker, 1996; Crooks & Khim, 1999; Wright *et al.*, 2002; Perelman *et al.*, 2003; Castilla *et al.*, 2004; Fritz *et al.*, 2004; Zhang *et al.*, 2004). Ecosystem engineers create habitat patches where environmental conditions and resource availability substantially differ from the surrounding unmodified environment (Jones *et al.*, 1994, 1997). Then, the presence of such habitat patches may affect species diversity in two ways: (1) by providing suitable habitat for species that cannot survive in the unmodified habitat, and hence increase species richness by adding new species into communities (e.g. Wright *et al.*, 2002; Lill & Marquis, 2003; Castilla *et al.*, 2004); or (2) affecting the abundance of species already present within communities (e.g. Flecker, 1996; Thomas *et al.*, 1998; Crooks & Khim, 1999), and hence changing the evenness of species assemblages. However, in spite of the large amount of evidence pointing to the effects of ecosystem engineers on either species richness or species abundance, studies integrating the impacts of these effects on species diversity across engineer species and ecosystems are lacking. In this paper we address this issue and evaluate the effects of different ecosystem engineers on species diversity through their effects on species richness and evenness.

As well as the lack of studies integrating the effects of ecosystem engineers on species diversity, another important question that remains unanswered within the conceptual framework surrounding the concept of ecosystem engineers is whether engineer species sharing common features have generalized or idiosyncratic effects on communities (Jones *et al.*, 1997). Here we have also addressed this issue, and conjecture that ecosystem engineers belonging to different species, but sharing common features, may perform parallel environmental modifications when they are present in environmentally similar ecosystems. If so, these different engineer species would have parallel effects on species diversity across ecosystems.

Looking for such generalities, we assessed and compared the effects on species richness, diversity and evenness of eight ecosystem engineers sharing the same archetype, alpine plants with cushion growth-form, being present in four high-elevation habitats of the Andes. We chose this archetype because the compact architecture and low stature of cushion plants allows them to mitigate extreme low and high temperatures (Cavieres *et al.*, 1998; Arroyo *et al.*, 2003; Molina-Montenegro *et al.*, 2005), increase soil moisture and nutrient availability (Cavieres *et al.*, 1998; Núñez *et al.*, 1999; Molina-Montenegro *et al.*, 2005) and decrease the abrasive effects of wind (Hager & Faggi, 1990). Recent studies have shown that the microclimatic modifications performed by cushion plants increases the survival of several high-Andean plant species (Cavieres *et al.*, in press), suggesting that such processes enhance both the incidence and abundance of other vascular plants in these environments (Núñez *et al.*, 1999; Molina-Montenegro *et al.*, 2000; Badano *et al.*, 2002; Cavieres *et al.*, 2002; Arroyo *et al.*, 2003). Furthermore, cushion plants create large habitat patches, which can reach over 3 m in diameter and persist over decades (Benedict, 1989; McCarthy, 1992; Le Roux & McGeoch, 2004) or even centuries (Ralph, 1978; Kleier & Rundel, 2004). Thus, the ability of cushion plants to transform the habitat, together with the fact that they create large and persistent structures, suggest that such plants can act as ecosystem engineers (*sensu* Jones *et al.*, 1994, 1997). Given that cushion plants modify the habitat via their own physical structures (branches, leaves, etc.) and remain as a part of the engineered environment, constituting engineered habitat patches by themselves, they can be considered as 'autogenic ecosystem engineers' (*sensu* Jones *et al.*, 1994, 1997). Here, we hypothesize that the presence of cushion plants in high-Andean communities should lead to increased species diversity through their effects on species richness and evenness. Further, we also propose that these community-level effects should be a generalized phenomenon across high-Andean ecosystems.

METHODS

Study system

We studied eight cushion plant species across four high-elevation sites in the Andes of Chile and Argentina: (1) *Pycnophyllum bryoides* Rohrb. (Caryophyllaceae) in the high-Andean Atacama plateau, northern Chile (23° S, 68° W; 4400 m); (2) *Azorella madreporica* Clos (Apiaceae) and *Adesmia subterranea* Clos (Fabaceae) in the Valley of Elqui, northern-central Chile (30° S, 70° W; 3700–4000 m); (3) *Azorella monantha* Clos (Apiaceae) and *Laretia acaulis* (Cav.) Gill et Hook. (Apiaceae) in the basin of Rio Molina, central Chile (33° S, 70° W; 3200–3600 m); (4) *Mulinum leptacanthum* Phil. (Apiaceae), *Oreopolus glacialis* (Poepp. & Endl.) Ricardi (Rubiaceae) and *Discaria nana* (Gay) Weberb. (Rhamnaceae) on Mount Chalhuaco, southern Argentina (41° S, 71° W; 1600–1700 m). At all these sites, cushion plants generate spatially discrete patches isolated from similar units by large open areas mainly composed of rocks and bare ground. Thus, in this study, cushion patches were considered 'engineered habitat patches' and surrounding open areas as 'unmodified habitat'.

Effects of cushion plants on community diversity

To assess the magnitude of the effect of ecosystem engineers on species richness, diversity and evenness, one must first measure these attributes in a landscape without the engineer species (i.e. open areas) and then in an equally sized area including engineered patches (Wright *et al.*, 2002). Hence, the difference between community attributes in the landscape with a mix of unmodified and engineered patches (i.e. open areas plus cushion plants) and the landscape composed only of unmodified habitat (i.e. open areas only) estimates the magnitude of the community-level effects of ecosystem engineers (Wright *et al.*, 2002). To assess such effects, we chose a plant community dominated by each cushion species. In each

Table 1 Average percentage cover (± 2 SE) of cushion patches and open areas in the different communities considered in this study. Cover in each community was estimated from 10 parallel line-transects (50 m long, distanced 10 m apart). The table also shows the results of ANOVA goodness of fit tests performed to assess whether species abundances followed a broken-stick distribution

Location	Cushion species	Cushion cover (%)	Open areas cover (%)	Results of ANOVA
Atacama plateau, northern Chile	Pycnophyllum bryoides	5.3 (± 2)	94.7 (± 2)	$F_{3,8} = 15.17$, $P < 0.01$, $r^2 = 0.73$
Valley of Elqui, northern-central Chile	Azorella madreporica	9.9 (± 1)	91.1 (± 1)	$F_{3,13} = 99.24$, $P < 0.01$, $r^2 = 0.91$
	Adesmia subterranea	10.4 (± 2)	89.6 (± 2)	$F_{3,11} = 32.81$, $P < 0.01$, $r^2 = 0.86$
Basin of Rio Molina, central Chile	Azorella monantha	12.2 (± 2)	87.8 (± 2)	$F_{3,17} = 36.50$, $P < 0.01$, $r^2 = 0.81$
	Laretia acaulis	31.1 (± 1)	68.9 (± 1)	$F_{3,38} = 23.90$, $P < 0.01$, $r^2 = 0.62$
Mount Chalhuaco, southern Argentina	Mulinum leptacanthum	6.0 (± 2)	94.0 (± 2)	$F_{3,22} = 221.32$, $P < 0.01$, $r^2 = 0.95$
	Oreopolus glacialis	4.8 (± 1)	96.2 (± 1)	$F_{3,21} = 121.31$, $P < 0.01$, $r^2 = 0.92$
	Discaria nana	13.0 (± 2)	87 (± 2)	$F_{3,22} = 34.16$, $P < 0.01$, $r^2 = 0.74$

community, we delimited a 1-ha plot, and randomly selected 100 individual cushions within these plots. All plant species growing within selected cushions were identified and the number of individuals of each species was counted. To obtain comparable samples of species richness and abundances in surrounding open areas, the shape and area of each sampled cushion were emulated with wire rings. The rings were randomly placed in open areas away from cushions and species within rings were identified and the number of individuals counted. Data from open areas were used to estimate species richness, diversity and evenness of landscapes without cushion plants, and data from cushions and open areas were pooled to estimate community attributes of landscapes where cushion plants are present (hereafter 'engineered landscape').

Species richness and species diversity (hereafter S and H', respectively) in open areas and in the engineered landscape were estimated through sample-based rarefactions to account for differences in sampled area, as suggested by Gotelli & Colwell (2001). Further, since cushion patches represent only a small fraction of the habitat compared with open areas, we measured the cover of both habitats to correct estimations of community attributes in engineered landscapes, as suggested Wright et al. (2002). That is, if cushion cover was 10% then cushion data were transposed only once in the data set for the engineered landscape while data from open areas were transposed nine times. The average cover of cushions and open areas in each studied community is shown in Table 1. Randomizations in rarefactions were carried out with replacement (Colwell, 2000), and S and H' at each rarefaction run were estimated using Coleman's species richness estimator (Coleman et al., 1982) and the Shannon–Wiener diversity index (Magurran, 1988), respectively. Since species abundances in all studied communities followed a broken-stick distribution (Table 1), Shannon–Wiener diversity indices were computed by using natural logarithms (ln) (May, 1975). One hundred rarefaction runs were conducted, and these values of S and H' were averaged per sampling size. Hence, these rarefied values estimate the average species richness and the average species diversity that might be detected in communities if 1, 2,

3,…, 100 random samples were subsequently taken in open areas or in the engineered landscape. For each sampling size, evenness (hereafter J) was computed as $J_n = H'_n/\ln(S_n)$ (Magurran, 1988), where n indicates the sampling size from which values of H' and S were taken to compute evenness.

Rarefied values of S and H' estimated for open areas and the engineered landscape were plotted against sampling sizes, and values estimated at the asymptote of these 'rarefaction' curves were considered maximum-likelihood estimators of species richness and species diversity (Gotelli & Colwell, 2001). To assess statistical differences between open areas and the engineered landscape, 95% confidence intervals were estimated for these values of S and H' and significant differences were assumed when confidence intervals did not overlap. Further, values of S and H' at the asymptote of rarefaction curves were used to compute maximum-likelihood estimators of species evenness (J) for open areas and the engineered landscape of each community.

To estimate the magnitude of the change in community attributes brought about by cushion plants, maximum-likelihood estimators of S, H' and J were used to calculate the relative contribution that the presence of each cushion species made to these attributes in its respective community. Hence, for species richness we computed $[(SL - Su)/Su] \times 100$, where SL and Su are estimated values of species richness at the asymptote of rarefaction curves for the engineered landscape and open areas, respectively. For species diversity we computed $[(H'L - H'u)/H'u] \times 100$, where $H'L$ is the estimated species diversity at the asymptote of rarefaction curves for the engineered landscape and $H'u$ is its equivalent value in open areas. Finally, for evenness, we computed $[(JL - Ju)/Ju] \times 100$, where JL and Ju are values of species evenness estimated from values of H' and S at the asymptote of rarefaction curves for the engineered landscape and open areas, respectively.

To evaluate whether changes in the community values of H' were mainly due to effects of cushions on S or J, and hence infer the generalized or idiosyncratic effects of cushions, we used linear multiple regression analyses with categorical variables (Neter et al., 1996). Theoretically, positive relationships should exist between H' and S and H' and J (De

Benedictis, 1973; but see Stirling & Wilsey, 2001), thus, differences in these relationships between open areas and engineered landscapes could shed light on the effects of cushions on community diversity. Given that changes in species diversity could be due to changes in both species richness and evenness (Peet, 1975; Stirling & Wilsey, 2001), we propose that cushions would have generalized effects if all cushion species controlled community diversity through their effects on species richness, evenness or both. Otherwise, if some cushions species affect species diversity through their effects on species richness while others affect diversity through their effects on evenness, the effects of cushions on species diversity would be idiosyncratic.

Regression analyses were performed with rarefied values of H', S and J estimated from 1 to 100 samples in open areas and the engineered landscape. S values were ln-transformed so as to scale with values of H'. We used H' as the dependent continuous variable, either $\ln(S)$ or J as the continuous predictive variable, and 'open areas' vs. 'engineered landscape' as the two levels of the categorical predictive variable. We also included an interaction term between continuous and qualitative predictive variables to account for differences in the slopes of regression functions obtained for the different levels of the qualitative variable (Neter et al., 1996). Then, a linear regression function is obtained for each level of the categorical variable, and relationships between continuous variables are indicated to differ between levels of the categorical variable if significant differences are detected between estimated parameters (intercepts or slopes) of linear regression functions (Neter et al., 1996). We assessed differences between these regression parameters with t-tests (Neter et al., 1996). Although it could be argued that the relationships between H' with J may be improper because J is a function of both H' and S (De Benedictis, 1973), our aim with these analyses was to determine what component of diversity (species richness or evenness) is more affected by the presence of cushions. In the relationships between H' and S, if open areas and engineered landscapes show different values of H' for a given S value, then, it can be inferred that community diversity is mainly affected by changes in J. On the other hand, in the relationships between H' and J, if open areas and engineered landscapes show different values of H' for a given J value, then it can be inferred that community diversity is mainly affected by changes in S.

RESULTS

Both species richness and species composition varied across study sites (see Appendices S1, S2, S3 and S4 in Supplementary Material). The number of species detected in samples increased from north to central Chile, with a peak in the community dominated by *L. acaulis* cushions (40 species), and decreased again towards southern latitudes (see Appendices S1, S2, S3 and S4 in Supplementary Material). In all communities, and for both open areas and the engineered landscape, rarefaction curves of S and H' reached the asymptote before
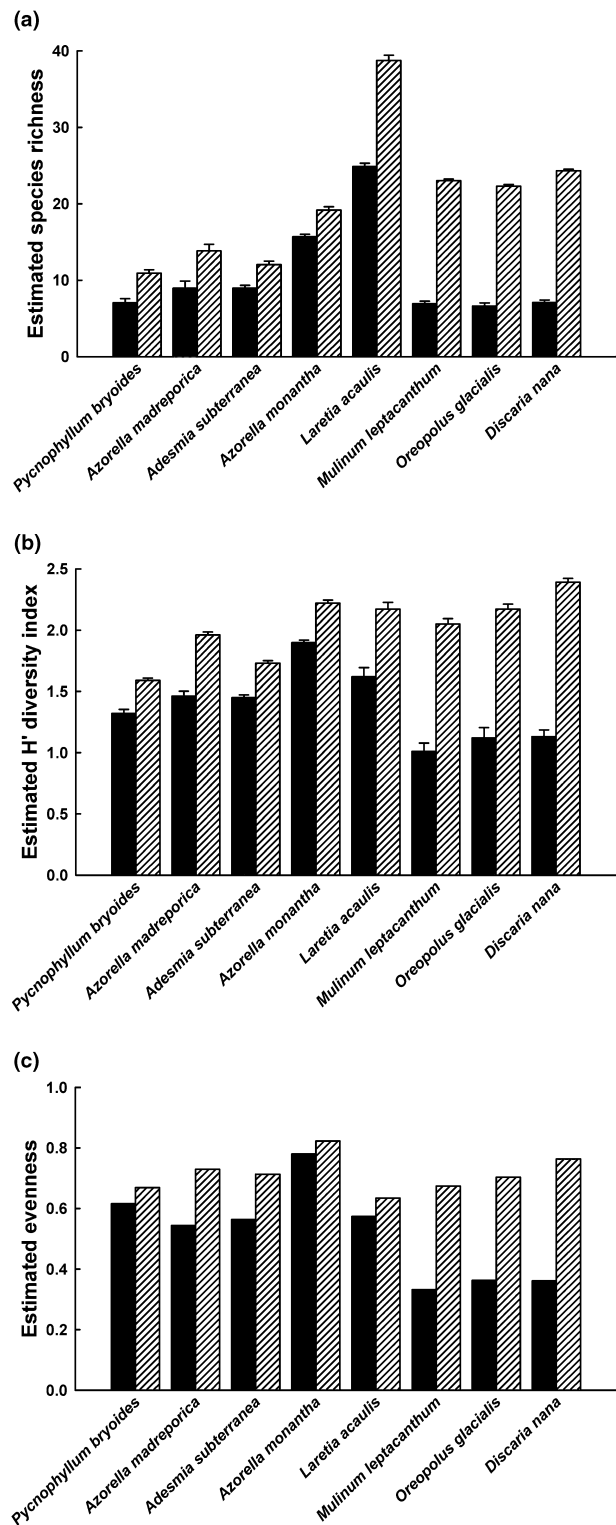

Figure 1 Estimated values (± 95% confidence intervals) of species richness (a) and Shannon–Wiener diversity indices (b) at the asymptote of the rarefaction curves, with their respective values of species evenness (c), for open areas (solid bars) and the landscape (dashed bars) in the different high-Andean communities where each cushion plant species is present.

Location	Cushion species	S (%)	H' (%)	J (%)
Atacama plateau, northern Chile	*Pycnophyllum bryoides*	54.8	20.5	8.6
Valley of Elqui, northern-central Chile	*Azorella madreporica*	54.6	34.2	34.2
	Adesmia subterranea	34.1	19.3	26.6
Basin of Rio Molina, central Chile	*Azorella monantha*	22.3	17.0	5.5
	Laretia acaulis	55.7	34.0	10.6
Mount Chalhuaco, southern Argentina	*Mulinum leptacanthum*	232.3	103.0	100.3
	Oreopolus glacialis	236.7	93.8	93.8
	Discaria nana	243.0	111.5	101.5

Table 2 Proportional increases in species richness (S), species diversity (H') and evenness (J) due to the presence of cushion plants in the different locations considered in this study

100 samples (data not shown), indicating that sampling effort was enough to fully capture the species composition of plant assemblages.

The presence of cushion plants had positive effects on all the three community attributes measured in this study. Estimated values of S (Fig. 1a) and H' (Fig. 1b) at the asymptote of rarefaction curves were significantly higher for the engineered landscape than for open areas in all studied communities. Values of J, estimated from rarefied values of S and H', were also higher for the engineered landscape than for open areas (Fig. 1c). Relative increases in S, H' and J due to the presence of cushion plants varied between cushions species and across study sites (Table 2). All cushion species had greater effects on S than either on H' or J, *A. monantha* in central Chile being the cushion species with the smallest effects on the evaluated community attributes and *D. nana* in southern Argentina the species with the largest effects (Table 2).

In all communities, and in both open areas and the engineered landscape, positive relationships were found between H' and S (Fig. 2). Comparison of the regression functions of H' on S between open areas and engineered landscapes indicated that the effects of cushions on J varied across study sites but not between cushion species within the same site. Effects of the presence of cushion plants on H' through its effects on J were detected for *P. bryoides* in northern Chile (intercepts $t_{1,196} = 0.65$, $P = 0.52$; slopes $t_{1,196} = 2.01$, $P < 0.05$; Fig. 2a); *A. monantha* (intercepts $t_{1,196} = 3.86$, $P < 0.01$; slopes $t_{1,196} = 5.82$, $P < 0.01$; Fig. 2d) and *L. acaulis* (intercepts $t_{1,196} = 6.19$, $P < 0.01$; slopes $t_{1,196} = 10.10$, $P < 0.01$; Fig. 2e) in central Chile; *M. leptacanthum* (intercepts $t_{1,196} = 24.69$, $P < 0.01$; slopes $t_{1,196} = 31.92$, $P < 0.01$; Fig. 2f), *O. glacialis* (intercepts $t_{1,196} = 24.45$, $P < 0.01$; slopes $t_{1,196} = 28.50$, $P < 0.01$; Fig. 2g) and *D. nana* (intercepts $t_{1,196} = 38.93$, $P < 0.01$; slopes $t_{1,196} = 48.03$, $P < 0.01$; Fig. 2h) in southern Argentina. In contrast, no effects on H' due to changes in J were detected for either *A. madreporica* (intercepts $t_{1,196} = 0.45$, $P = 0.65$; slopes $t_{1,196} = 1.55$, $P = 0.11$; Fig. 2b) or *A. subterranea* (intercepts $t_{1,196} = 0.55$, $P = 0.58$; slopes $t_{1,196} = 0.10$, $P = 0.96$; Fig. 2c) in northern-central Chile.

Relationships between H' and J were positive in both open areas and the engineered landscape in most of the studied communities, with the exception of communities dominated by cushions of *P. bryoides*, *A. madreporica* and *A. subterranea*

(Fig. 3). Comparisons of these regression functions of H' on J between open areas and engineered landscapes indicated that cushions mainly had effects on S in northern-central Chile, where *A. madreporica* (intercepts $t_{1,196} = 3.00$, $P < 0.01$; slopes $t_{1,196} = 1.99$, $P < 0.05$; Fig. 3b) and *A. subterranea* (intercepts $t_{1,196} = 2.22$, $P < 0.05$; slopes $t_{1,196} = 2.18$, $P < 0.05$; Fig. 3c) are present, and in southern Argentina, where communities are dominated by *M. leptacanthum* (intercepts $t_{1,196} = 2.35$, $P < 0.05$; slopes $t_{1,196} = 6.59$, $P < 0.01$; Fig. 3f), *O. glacialis* (intercepts $t_{1,196} = 2.11$, $P < 0.05$; slopes $t_{1,196} = 6.64$, $P < 0.01$; Fig. 3g) and *D. nana* (intercepts $t_{1,196} = 7.25$, $P < 0.01$; slopes $t_{1,196} = 9.93$, $P < 0.01$; Fig. 3h). No effects on H' due to changes in S were detected for *P. bryoides* in northern Chile (intercepts $t_{1,196} = 0.59$, $P = 0.56$; slopes $t_{1,196} = 0.48$, $P = 0.63$; Fig. 3a) or for *A. monantha* (intercepts $t_{1,196} = 0.86$, $P = 0.39$; slopes $t_{1,196} = 0.81$, $P = 0.42$; Fig. 3d) or *L. acaulis* (intercepts $t_{1,196} = 0.72$, $P = 0.47$; slopes $t_{1,196} = 0.23$, $P = 0.82$; Fig. 3e) in central Chile.

DISCUSSION

Our results indicate two broad generalities for the effects of cushion plants on the diversity of vascular plants in high-Andean communities. Firstly, the presence of this growth-form leads to higher species richness, diversity and evenness of plant communities, and these positive effects on community attributes seem to be a generalized phenomenon across high-Andean environments (see Fig. 1 and Table 2). Secondly, although regression analyses indicated that the effects of cushion plants on species diversity are idiosyncratic across study sites (see Figs 2 & 3), these analyses also consistently indicated that the presence of those cushion species in the same site would control species diversity in the same way (i.e. by increasing species richness, evenness or both).

Increases in species richness have been proposed to be an inevitable consequence of the presence of ecosystem engineers in natural communities (Jones *et al.*, 1997). This is because the creation of engineered patches usually increases habitat diversity in the landscape and, hence, the number of available niches for other species (Jones *et al.*, 1997). This has been supported by several studies conducted in different ecosystems (e.g. Wright *et al.*, 2002; Lill & Marquis, 2003; Castilla *et al.*, 2004), and our results concur with the expectation of higher
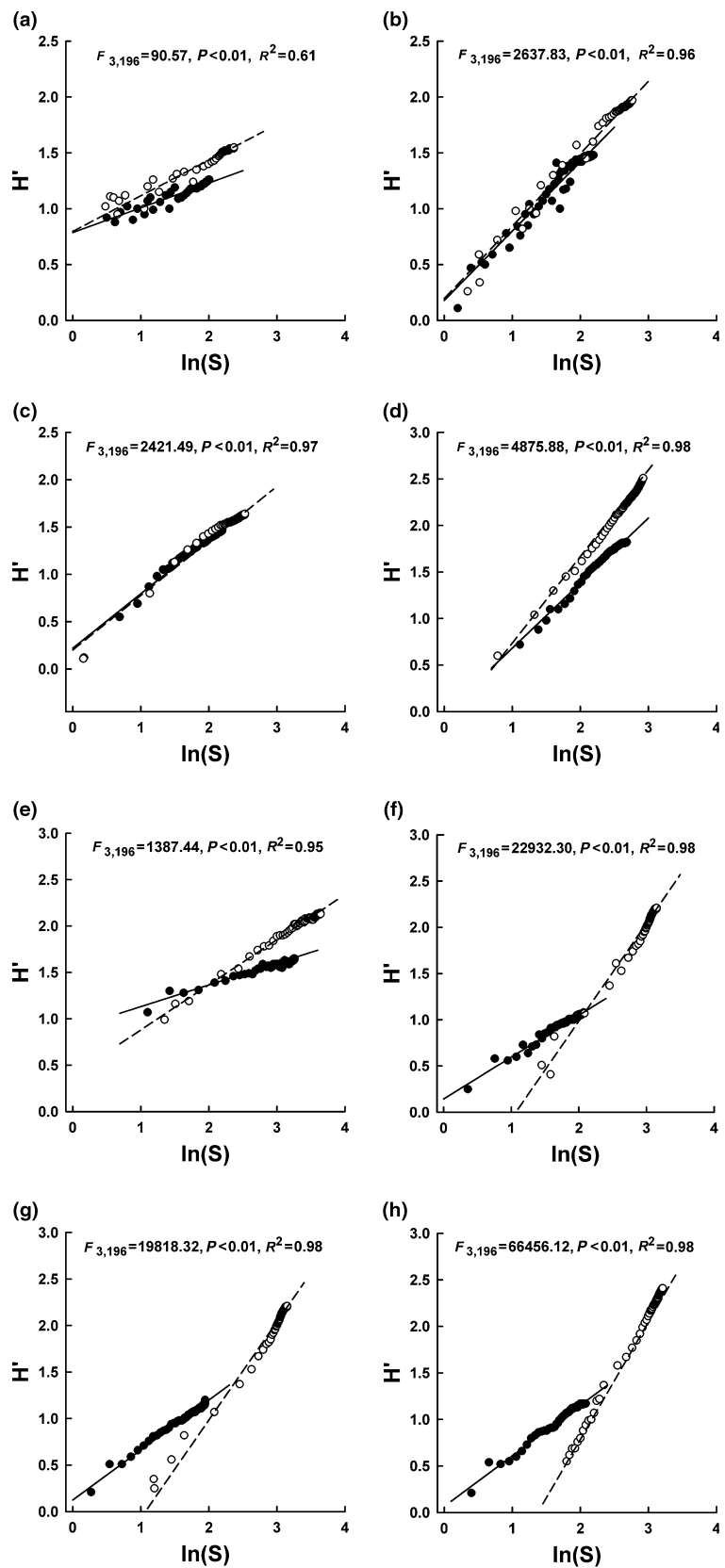
Figure 2 Relationships between rarefied values of species diversity (H') and species richness (S) in open areas (solid symbols, solid line) and the engineered landscape (empty symbols, dashed line) of communities dominated by *Pycnophyllum bryoides* from the Atacama plateau in northern Chile (a), *Azorella madreporica* (b) and *Adesmia subterranea* (c) from the Valley of Elqui in northern-central Chile, *Azorella monantha* (d) and *Laretia acaulis* (e) from the basin of Rio Molina in central Chile, and *Mulinum leptacanthum* (f), *Oreopolus glacialis* (g) and *Discaria nana* (h) from Mount Chalhuaco in southern Argentina. Results of goodness of fit ANOVA for the multiple regression analysis conducted in each community are shown in the respective figures.

species richness when engineer species are present. We observed that habitat patches created by cushion plants always increased the number of vascular plant species in high-Andean communities, with increases in local species richness due to the presence of this growth-form ranging from 22% to 243%, depending on the cushion species and the study site. Several
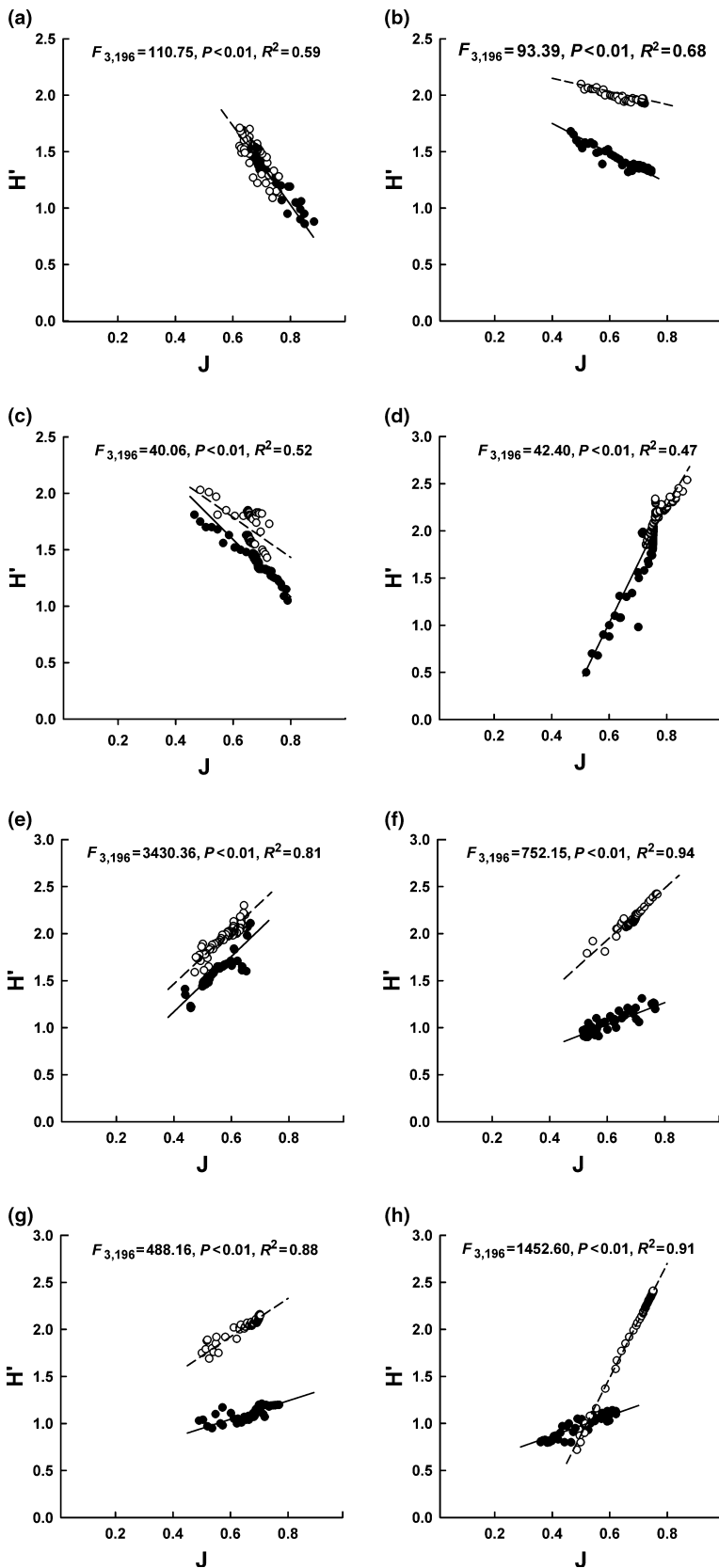
Figure 3 Relationships between rarefied values of species diversity (H') and evenness (J) in open areas (solid symbols, solid line) and the engineered landscape (empty symbols, dashed line) of communities dominated by *Pycnophyllum bryoides* from the Atacama plateau in northern Chile (a), *Azorella madreporica* (b) and *Adesmia subterranea* (c) from the Valley of Elqui in northern-central Chile, *Azorella monantha* (d) and *Laretia acaulis* (e) from the basin of Rio Molina in central Chile, and *Mulinum leptacanthum* (f), *Oreopolus glacialis* (g) and *Discaria nana* (h) from Mount Chalhuaco in southern Argentina. Results of goodness of fit ANOVA for the multiple regression analysis conducted in each community are shown in the respective figures.

other studies conducted in the in high Andes of Chile and Argentina have previously shown that the presence of cushion plants increases the species richness of plant communities

(Núñez *et al.*, 1999; Molina-Montenegro *et al.*, 2000; Badano *et al.*, 2002; Cavieres *et al.*, 2002; Arroyo *et al.*, 2003). However, few of these studies have evaluated the effects of the

cushion growth-form on species diversity and its components (but see Badano *et al.*, 2002; Cavieres *et al.*, 2002). Indeed, in spite of the large number of studies that have reported changes in species richness and species abundances where engineer species are present in natural communities (e.g. Flecker, 1996; Thomas *et al.*, 1998; Crooks & Khim, 1999; Wright *et al.*, 2002; Lill & Marquis, 2003; Castilla *et al.*, 2004), no studies have integrated these effects on species diversity.

In this study we found that besides increasing species richness, the presence of cushion plants also positively affected community diversity and evenness. However, our results also indicated that the magnitude of these effects varied between cushion species (see Table 2), and these differences could occur for a number of reasons. For instance, differences in species richness and species composition observed across study sites (see Appendices S1, S2, S3 and S4 in Supplementary Material) suggest that regional species pools providing species to the studied communities are of different sizes and comprise different species. This may cause a 'size effect', in which the number of species depending on the environmental modulation performed by cushion plants could be a function of the size of the regional pool, so that larger species pools are more likely to contain species that require cushions to persist within communities. On the other hand, cushion plants may perform similar environmental modulations in different high-Andean environments (i.e. all of them modulate temperature, moisture or nutrient availability), but the intensity with which each cushion species modulates the environment may not necessarily be equivalent across sites. Then, although all regional species pools providing species to studied communities were similar in size or species composition, differences in the intensity with which cushion plants modulate the environment may cause differences in the magnitude with which this growth-form increases diversity.

Irrespective of these differences in magnitude, cushion plants always had positive effects on species diversity, and such changes could be due to the positive effects of cushions on species richness, evenness or both. Here, we suggested that different cushion species would have generalized effects on species diversity across high-Andean communities if all of them controlled species richness or evenness in a similar way. However, this suggestion was only partially supported. For example, in the high-Andean community from northern Chile (see Figs 2a & 3a), as well as in communities from central Chile (see Figs 2d,e & 3d,e), increases in species diversity mainly depended on the effect of cushion plants on evenness rather than on species richness. In contrast, in both studied communities from central-northern Chile (see Figs 2b,c & 3b,c), the effects on species diversity were related to the effect of cushions on species richness. Furthermore, in southern Argentina (see Figs 2f–h & 3f–h), the three cushion species affected species diversity through their effects on both species richness and evenness. Therefore we suggest that the effects of different cushion species being present within the same site may be considered generalized, while the effects of

cushion species from different sites should be considered idiosyncratic.

As far as we are aware, no previous studies have provided empirical evidence indicating that a group of ecosystem engineers sharing common features may have generalized or idiosyncratic effects on species diversity. However, in recent years several authors have reviewed the potential effects that ecosystem engineers may have on different components of species diversity. Aquatic shell-producing molluscs (Gutiérrez *et al.*, 2003) and suspension feeders (Wotton, 2003), invasive plant and animal species (Crooks, 2002), marine bioturbator fishes (Coleman & Williams, 2002), pocket gophers (Reichman & Seabloom, 2002), leaf shelter-building insects (Fukui, 2001) and ants (Folgarait, 1998) are some examples of groups of engineers that have been reviewed. A common conclusion of most of these reviews is that those ecosystem engineers that increase the habitat complexity of a landscape (i.e. introduce new habitats into the landscape) would lead to higher species diversity, while engineers that decrease habitat complexity (i.e. destroy available habitat) would diminish the diversity of species assemblages (Crooks, 2002). In the particular case of high-Andean cushion plants, previous studies have indicated that this growth-form increases landscape habitat complexity by creating habitats with a different microclimate from the surrounding open areas (Cavieres *et al.*, 1998, in press; Núñez *et al.*, 1999; Arroyo *et al.*, 2003), and our results consistently support the idea that these increases in habitat complexity would lead to a higher diversity of vascular plants. Further, in spite of a lack of data indicating the exact intensity with which environmental conditions are modulated by each cushion species in its respective community, we suggest that our approach provides a valuable insight into the degree of generalization that could be achieved by integrating and comparing the effects of different engineer species across communities. We suggest that by applying such an approach to different groups of engineer species sharing common features we could gain a more complete idea about the mechanisms controlling species diversity in natural communities. We hope that there will be more studies addressing this issue, which in turn will help to construct general predictive models for the effects of ecosystem engineers on species diversity and its components.

ACKNOWLEDGEMENTS

REFERENCES

Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A. & Arroyo-Kalin, M.A. (2003) Positive interactions between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, **169**, 121–129.

Badano, E.I., Molina-Montenegro, M.A., Quiroz, C.L. & Cavieres, L.A. (2002) Efectos de la planta en cojín *Oreopolus glacialis* (Rubiaceae) sobre la riqueza y diversidad de especies en una comunidad alto-andina de Chile central. *Revista Chilena de Historia Natural*, **75**, 757–765.

Benedict, J.B. (1989) Use of *Silene acaulis* for dating: the relationship of cushion diameter to age. *Arctic and Alpine Research*, **21**, 91–96.

Castilla, J.C., Lagos, N.A. & Cerda, M. (2004) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series*, **268**, 119–130.

Cavieres, L.A., Peñaloza, A., Papic, C. & Tambutti, M. (1998) Efecto nodriza del cojín *Laretia acaulis* (Umbelliferae) en la zona alto-andina de Chile Central. *Revista Chilena de Historia Natural*, **71**, 337–347.

Cavieres, L.A., Arroyo, M.T.K., Peñaloza, A., Molina-Montenegro, M.A. & Torres, C. (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, **13**, 547–554.

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez-González, S. & Molina-Montenegro, M.A. (in press) Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*.

Chapin, F.S., III, Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. (1997) Biotic control over the functioning of ecosystems. *Science*, **227**, 500–504.

Chapin, F.S., III, Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenorth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L. & Tilman, D. (1998) Ecosystem consequences of changing biodiversity. *BioScience*, **48**, 45–52.

Coleman, F.C. & Williams, S.L. (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution*, **17**, 40–44.

Coleman, B.D., Mares, M.A. & Willig, M.R. (1982) Randomness, area and species richness. *Ecology*, **63**, 1121–1133.

Colwell, R.K. (2000) *EstimateS: statistical estimation of species richness and shared species from samples*. University of Connecticut, Storrs, CT.

Crooks, J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, **97**, 153–166.

Crooks, J.A. & Khim, H.S. (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology*, **240**, 53–75.

Cuba, T.R. (1981) Diversity: a two level approach. *Ecology*, **62**, 278–279.

Díaz, S., Symstad, A.J., Chapin, F.S., III, Wardle, D.A. & Huenneke, L.F. (2003) Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution*, **18**, 140–146.

De Benedictis, P.A. (1973) On the correlations between certain diversity indices. *The American Naturalist*, **107**, 295–302.

Dickman, M. (1968) Some indices of diversity. *Ecology*, **49**, 1191–1193.

Flecker, A.S. (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, **77**, 1845–1854.

Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221–1244.

Fritz, K.M., Gangloff, M.M. & Feminella, J.W. (2004) Habitat modification by the stream macrophyte *Justicia americana* and its effects on biota. *Oecologia*, **140**, 388–397.

Fukui, A. (2001) Indirect interactions mediated by leaf shelters in animal-plant communities. *Population Ecology*, **43**, 31–40.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley & Sons, London.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, **101**, 79–90.

Hager, J. & Faggi, A.M. (1990) Observaciones sobre distribución y microclima de cojines enanos de la isla de Creta y del noroeste de la Patagonia. *Parodiana*, **6**, 109–127.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.

Kleier, C. & Rundel, P.W. (2004) Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral Ecology*, **29**, 461–470.

Le Roux, P.C. & McGeoch, M.A. (2004) The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Artic, Antarctic and Alpine Research*, **36**, 509–517.

Lill, J.T. & Marquis, R.J. (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, **84**, 682–690.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.

Margalef, R. (1957) La teoría de la información en ecología. *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, **32**, 373–449.

May, R.M. (1975) Patterns of species abundance and diversity. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 81–120. Belknap Press, Cambridge, MA.

McCarthy, D.P. (1992) Dating with cushion plants: establishment of a *Silene acaulis* growth curve in the Canadian Rockies. *Arctic and Alpine Research*, **24**, 50–55.

Molina-Montenegro, M.A., Torres, C., Parra, M.J. & Cavieres, L.A. (2000) Asociación de especies al cojín *Azorella trifurcata* (Gaertn.) Hook. (Apiaceae) en la zona andina de Chile central (37°S). *Gayana Botanica*, **57**, 161–168.

Molina-Montenegro, M.A., Badano, E.I., Hinostroza, P. & Cavieres, L.A. (2005) Intercambio gaseoso en dos especies de plantas alto andinas de Chile central: efecto de la asociación a plantas en cojín. *Ecología Austral*, **15**, 49–58.

Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567–579.

Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied linear statistical models*, 4th edn. WBC/McGraw-Hill, Boston, MA.

Núñez, C., Aizen, M. & Ezcurra, C. (1999) Species associations and nurse plant effect in patches of high-Andean vegetation. *Journal of Vegetation Science*, **10**, 357–364.

O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, **20**, 181–198.

Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285–307.

Peet, R.K. (1975) Relative diversity indices. *Ecology*, **56**, 496–498.

Perelman, S.B., Burkart, S.E. & Leon, R.J.C. (2003) The role of a native tussock grass (*Paspalum quadrifarium* Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. *Biodiversity and Conservation*, **12**, 225–238.

Ralph, C.P. (1978) Observations on *Azorella compacta* (Umbelliferae), a tropical Andean cushion plant. *Biotropica*, **10**, 62–67.

Reichman, O.J. & Seabloom, E.W. (2002) The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology and Evolution*, **17**, 44–49.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.

Stirling, G. & Wilsey, B. (2001) Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist*, **158**, 286–299.

Thomas, F., Renaurd, F., de Meeûs, T. & Poulin, R. (1998) Manipulation of host behavior by parasites: ecosystem engineering in the intertidal zone? *Proceedings of the Royal Society of London Series B, Biological Sciences*, **265**, 1091–1096.

Tilman, G.D. (1984) Plant dominance along an experimental nutrient gradient. *Ecology*, **65**, 1445–1453.

Tilman, G.D. (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.

Tramer, E.J. (1969) Bird species diversity: components of Shannon's formula. *Ecology*, **50**, 927–929.

Wotton, R.S. (2003) Expanding traditional views on suspension feeders – quantifying their role as ecosystem engineers. *Oikos*, **101**, 441–443.

Wright, J.P., Jones, C.G. & Flecker, A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Zhang, Y., Richardson, J.S. & Negishi, J.N. (2004) Detritus processing, ecosystem engineering and benthic diversity: a test of predator-omnivore interference. *Journal of Animal Ecology*, **73**, 756–766.

BIOSKETCHES

Ernesto I. Badano graduated from the Universidad Nacional de Salta (Argentina) and is currently a PhD candidate at the Departamento de Botánica, Universidad de Cocepción (Chile). His current research interests are ecosystem engineering and community structure in high-mountain environments.

Lohengrin A. Cavieres is an Associate Professor at the Departamento de Botánica, Universidad de Cocepción, Chile. His main research activities are the ecology and ecophysiology of plants in high-mountain environments and the distribution of native and alien species in Chile.

Editor: John Lambshead

SUPPLEMENTARY MATERIAL

The following supplementary material is available from http://www.Blackwell-Synergy.com

Appendix S1 Species list from the community dominated by *Pycnophyllum bryoides* in the high-Andean Atacama plateau, northern Chile (23° S, 68° W; 4400 m).

Appendix S2 Species list from communities dominated by *Azorella madreporica* (AM) and *Adesmia subterranea* (AS) in the high Andes of the Valley of Elqui, northern-central Chile (30° S, 70° W; 3700–4000 m).

Appendix S3 Species list from communities dominated by *Azorella monantha* (AM) and *Laretia acaulis* (LA) in the high Andes of the basin of Rio Molina, central Chile (33° S, 70° W; 3200–3600 m).

Appendix S4 Species list from communities dominated by *Mulinum leptacanthum* (ML), *Oreopolus glacialis* (OG) and *Discaria nana* (DN) on Mount Chalhuaco, southern Argentina (41° S, 71° W; 1600–1700 m).