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Predicting effects of ecosystem engineering on species richness along primary productivity gradients

Ernesto Iván Badano [a,*], Pablo Angel Marquet [b,c,d], Lohengrin Alexis Cavieres [c,e]

[a] División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica, Camino a la Presa San José 2055, Colonia Lomas 4ta Sección C.P., 78216 San Luis Potosí, Mexico
[b] Center for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile
[c] Institute of Ecology and Biodiversity (IEB), Facultad de Ciencias Universidad de Chile, Casilla 653, Santiago, Chile
[d] The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA
[e] Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Chile

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ABSTRACT

Physical ecosystem engineering is the process by which some species change the distribution of materials and energy in ecosystems. Although several studies have shown that this process is a driver of local species diversity, the current challenge is predicting when and where ecosystem engineering will have large or small impacts on communities, while also explaining why impacts vary in magnitude across engineer species and environments. This study addresses this issue and proposes a series of predictions for these effects at the three spatial scales (the patch, the habitat and the landscape) along environmental gradients of physical stress. The integrative prediction of this study was that the difference in species diversity between engineered and unmodified situations (patches, habitats or landscapes) will increase as the difference in physical stress between engineered and unmodified patches becomes larger. To test the prediction, the effects of two well known high-Andean ecosystem engineers, the cushion plants *Azorella madreporica* and *Laretia acaulis*, were assessed on plant species richness in central Chile. The results support the main prediction, showing that ecosystem engineers have negative effects on species diversity at sites when the environmental modifications they perform increase physical stress for other species, while they have positive effects at sites where these habitat changes mitigate physical stress. Then, the effects of the ecosystem engineers on species diversity seem to depend on the environmental context, where larger environmental modifications are reflected in greater impacts, either positive or negative, on species diversity.

1. Introduction

Physical ecosystem engineering is the process by which some species, the ecosystem engineers, change the distribution of materials and energy in natural landscapes via non-trophic interactions with their abiotic environment (Jones et al., 1994, 1997). This concept has received much attention in the last ten years and generated strong controversies (Wright and Jones, 2006). On the one hand, detractors of the concept argue that most species, if not all, modify the environment at some extent, suggesting that the ubiquity of this process in the nature makes the concept too broad to be useful in ecology (Power, 1997; Reichman and Seablom, 2002a,b). On the other hand, several authors propose that such a ubiquity makes this concept suitable for developing general ecological principles and predictive models on the impacts of ecosystem engineers on species diversity and ecosystem functions (Moore, 2006; Crain and Bertness, 2006; Badano and Cavieres, 2006a; Badano et al., 2006; Badano and Marquet, 2008; Badano and Marquet, 2009). Therefore, instead of determining whether an organism is an ecosystem engineer or not, the current challenge is predicting when and where ecosystem engineering will have large or small impacts on natural communities (Wright and Jones, 2006; Badano et al., 2006).

In one of the pioneer articles on the concept, Jones et al. (1997) proposed that the impacts of ecosystem engineering on species diversity would depend, among other factors, on the magnitude of the environmental changes performed by the engineers and the number of species in the regional species pool that respond to

* Corresponding author. Tel.: +52 444 8342000; fax: +52 444 8342010.
E-mail address: ernesto.badano@ipicyt.edu.mx (E.I. Badano).

these changes. Following this argument, Wright and Jones (2004) developed a simple conceptual model to predict patch-scale effects of ecosystem engineering on species richness. Their theoretical model predicts larger differences in species richness, either positive or negative, between patches created by ecosystem engineers and patches without engineers as the differences in the environmental conditions between patch types become greater. This kind of patch-scale comparisons of species richness has a long tradition in ecology [reviewed in Wright and Jones, 2004], but ecosystem engineers can also affect species richness at larger spatial scales, such as the habitat and the landscape (Jones et al., 1994; Badano and Cavieres, 2006a; Badano et al., 2006; Wright et al., 2002). Considering that ecosystem engineers usually create spatially discrete and distinctive patches immersed in a matrix of unmodified habitat, the "engineered habitat" is defined by the sum of all patches created by a focal engineer species (Badano et al., 2006; Wright et al., 2002). The contrast situation, the unmodified habitat, is then comprised by the background matrix (Badano et al., 2006; Wright et al., 2002). In this context, the landscape scale is defined as the spatial extent containing both, the engineered and the unmodified habitat (Badano et al., 2006; Badano and Marquet, 2008; Wright et al., 2002; Badano and Cavieres, 2006b). Although some studies have evaluated the effects of ecosystem engineers on species diversity at these three spatial scales (Badano and Cavieres, 2006a; Badano et al., 2006; Wright et al., 2002, 2006; Borthagaray and Carranza, 2007), general cross-scale predictions for the effects of ecosystem engineers on species richness along spatial environmental gradients are still lacking. In this article, we focus on this issue and propose a series of predictions for these effects of ecosystem engineers on species richness along physical stress gradients.

Predicting the effects of ecosystem engineering on species richness along physical stress gradients would require knowing: (1) how much an engineer species modify stress at each point of the gradient, and (2) how many species in the regional species pool respond to such a change. To fully satisfy these conditions, one should measure a number of environmental variables (e.g., temperature, moisture, nutrient content in soil, among others) within and outside engineered patches, and further assessing how the changes in these variables affect each component of the regional species pool. However, evaluating the relative importance of each stress factor that may affect a community, and determining the response of each species in natural, uncontrolled systems is often complex and difficult. Under this scenario, the widely accepted assumption that productivity and/or biomass of plant communities decrease with increasing physical stress may be helpful to estimate the levels of stress that affect a community (Grime, 1979). Evidences supporting this assumption come from both observational and experimental studies. For instance, a series of correlative analysis conducted on communities of the Santa Catalina Mountains (Arizona, USA) indicated that the biomass of plant communities decreases with elevation because of decreasing temperatures (Whittaker and Niering, 1975). On the other hand, a number of greenhouse and field studies performed with experimental plant communities have indicated that increases in environmental harshness and/or reductions in nutrient contents lead to reduced primary productivity (Austin and Austin, 1980; Baer et al., 2003; Fay et al., 2003). Following this approach, the differences in stress between contrasting environmental situations – engineered vs. unmodified patches – are likely to be reflected by differences in the productivity of their plant assemblages (Wright and Jones, 2004). This approach has been used in several other studies, both for estimating changes in physical stress and predicting responses of plants to changes in physical stress (Wright and Jones, 2004; Callaway et al., 2002; Austin, 1980; Greenlee and Callaway, 1996).

In our case, ecosystem engineers can be assumed to ameliorate physical stress if plant assemblages growing within the habitat patches they create, are more productive than those established in equivalent areas of unmodified habitat. Conversely, engineered patches would be more stressful if plant productivity inside them is lower than that in the unmodified patches. Then, the magnitude and the direction (positive or negative) with which engineers alter physical stress could be estimated from the difference in plant productivity between engineered and unmodified patches at each point of the gradient. It is important to note that, here, plant productivity is used as a *proxy* to the magnitude of physical stress modulation by ecosystem engineers, but it is not a direct measure of physical stress.

Concerning the species that may inhabit each patch type, it can be assumed that increasing physical stress will reduce species richness because of the physiological limitations of plants in the regional species pool, so as just a few species can survive at higher stress levels (Grime, 1979). Thus, if ecosystem engineers are able to ameliorate physical stress – i.e. primary productivity within engineered patches is higher than that in equivalent areas of unmodified habitat – the engineered patches can be expected to contain more species than unmodified patches because they provide habitats with ecological conditions within the physiological thresholds of species. Conversely, plants would grow more frequently in the unmodified habitat if ecosystem engineers increase physical stress.

Taking into account these assumptions, a simple cross-scale prediction can be proposed for the effects of ecosystem engineers on species richness along stress gradients: "the difference in species richness between engineered and unmodified situations (patches, habitats or landscapes) will increase as the difference in plant productivity between engineered and unmodified patches becomes larger". However, before proceeding with the particular predictions for each spatial scale of interest (the patch, the habitat and the landscape), it is important to introduce a note of caution about the assumptions behind this general prediction. Several studies have indicated that productivity of plant communities increases with increased biodiversity (Tilman and Downing, 1997; Tilman et al., 1996; Wilsey and Potvin, 2000). Thus, the differences in productivity between engineered and unmodified patches could be a consequence of the effects of ecosystem engineering on species richness at this spatial scale (Badano and Marquet, 2009). However, these effects of ecosystem engineers on species richness at the patch scale are usually related with the intensity with which they modulate physical stress (Wright et al., 2002; Badano and Cavieres, 2006b; Borthagaray and Carranza, 2007; Callaway et al., 2002). Therefore, the difference in primary productivity between engineered and unmodified patches would provide an easy and quick way for assessing of the magnitude of stress modulation by ecosystem engineers along environmental gradients in order to perform predictions on their effects on species diversity at larger spatial scales, such as the habitat and the landscape. With this conceptual framework in mind, the predictions at each particular spatial scale of interest can be performed.

1.1. Patch-scale predictions

Here the focus is determining whether a single engineered patch has, in average, more or less species than an equally sized area of unmodified habitat (Wright and Jones, 2004). If ecosystem engineers decrease physical stress, the engineered patches are predicted to be more species rich than unmodified patches. Along stress gradients, the magnitude of these positive effects on species richness will increase as the unmodified habitat becomes more stressful. In contrast, if ecosystem engineers increase physical

stress, the engineered patches are predicted to contain less species than the equivalent areas of unmodified habitat.

1.2. Habitat-scale predictions

The effects of ecosystem engineers on species richness at this spatial scale rely in assessing whether the engineered habitat of a landscape has more or less species than an equally sized area of unmodified habitat (Badano et al., 2006). Although these habitat-scale effects seem similar to the patch-scale effects, there is a fundamental difference. The patch-scale effects just consider the average number of species in a single patch, without considering that the different patches belonging to a given habitat type may differ in species composition. Thus, if species composition differs among the patches comprising the engineered (or unmodified) habitat, the species richness at this spatial scale can be higher than that at any single patch. Taking into account these considerations, we can predict that the engineered habitat will have more species than the unmodified one if ecosystem engineers decrease physical stress and along stress gradients, and that the magnitude of these positive effects will increase as the unmodified habitat becomes more stressful. On the contrary, the engineered habitat will have fewer species if engineers increase stress.

1.3. Landscape-scale predictions

Ecosystem engineers may introduce new species into communities if the environmental changes they perform provide suitable habitat for species that cannot survive in the unmodified habitat (Wright et al., 2002; Badano et al., 2007). Therefore, when the engineered and the unmodified habitats are combined at the landscape scale, the local species richness may be higher than that expected in absence of ecosystem engineers (Badano and Cavieres, 2006b; Wright et al., 2006). The magnitude of these effects will be close to zero if species within engineered patches are the same that those inhabiting the unmodified habitat or if engineered patches have no species. However, these effects will be largely positive as the number of species depending on the environmental modifications performed by the engineers increase. Variations in the magnitude of these effects along physical stress gradients would then indicate what sites are more susceptible to lose species because of the local extinction of an ecosystem engineer. Under these assumptions, we predict that ecosystem engineers that decrease stress will have larger landscape-scale effects on species richness as stress in the unmodified habitat increases. On the other hand, the magnitude of this landscape-scale effect will be irrelevant, close to zero, if ecosystem engineers increase stress as compared to the unmodified habitat.

2. Materials and methods

2.1. Study system

We tested our predictions by evaluating the impacts of two well-know engineer species from the high-Andes of central Chile, the cushion plants *Azorella madreporica* Clos. (Apiaceae) and *Laretia acaulis* (Cav.) Gill. et Hook (Apiaceae). High-mountain environments are well known for their low air and soil temperatures, which decrease with elevation (Körner, 2003). On the other hand, in arid mountains like the northern and central Andes of Chile, equatorial-facing slopes are usually drier than polar-facing ones (Rozzi et al., 1989). Then, in these ecosystems, physical stress gradients affecting primary productivity and plant species performances may result from the combined effect of elevation and slope aspect.

In the high-Andes of Chile, both *L. acaulis* and *A. madreporica* cushions create discrete and distinctive habitat patches that are in marked contrast with their surrounding matrix habitat, or open areas, mainly composed by bare rocky soil that has limited vegetation cover (Fig. 1). Furthermore, these cushion species have been reported to modulate both temperature and soil moisture, but the magnitude of such environmental changes seems to depend on the environmental context. For instance, *A. madreporica* modulates substrate and air temperatures maintaining higher minimum temperatures than the surrounding open areas (Badano et al., 2006; Molina-Montenegro et al., 2006; Cavieres et al., 2007), and this decoupling of temperatures increases towards upper, colder elevations (Arroyo et al., 2003). In contrast, *L. acaulis* usually maintains lower substrate temperatures than open areas (Molina-Montenegro et al., 2006, 2005; Cavieres et al., 2007), and the magnitude of such a temperature modulation increases in lower, warmer elevations (Cavieres et al., 2006). These cushion species have also been reported to improve soil water retention. Soil beneath both cushion plants is usually wetter than soil of open areas (Badano et al., 2006; Molina-Montenegro et al., 2006; Cavieres et al., 2007), but such an environmental change is greater at drier sites (Cavieres et al., 2006). These effects of *A. madreporica* and *L. acaulis* on abiotic conditions have been shown to affect the performance (photosynthetic performance, biomass and survival) of plant species able to inhabit cushion-dominated patches as compared to conspecific individuals growing in open areas, where these effects were reported to be positive, neutral or negative depending on the plant species and the environmental context (Badano and Marquet, 2008; Badano et al., 2007; Cavieres et al., 2007, 2005).

2.2. Study sites

This study was conducted in the Rio Molina basin, high-Andes of Central Chile (33°S, 71°W), 50 km to the East of the city of Santiago. The alpine zone extends from just above the treeline of *Kageneckia angustifolia* D. Don (Rosaceae) at 2200 m, to the upper distribution limit of plants at 3800 m (Cavieres et al., 2000). Climate in the study area is alpine, but it is strongly influenced by the Mediterranean-type climate predominating at lower elevations (Cavieres and Arroyo, 1999). At 2600 m, the mean temperature of the air during summer months (December–March) varies between 7 °C and 12 °C but decreases in 7 °C per 1000 m of increase in elevation (Cavieres and Arroyo, 1999). Main precipitation events occur during winter

Fig. 1. A typical high-Andean landscape of Central Chile where cushion plants (*Azorella madreporica* in this case) grow immersed in a matrix habitat of open areas composed by rocks, bare soil and other small plants species (picture by E.I. Badano).

months (June–August) as snow. Estimated annual precipitation just above the treeline is 400 mm, but surpasses 900 mm at 3200 m (Santibáñez and Uribe, 1990). Rainfall events may occur during summer months, but are more frequent at higher than lower elevations (Cavieres et al., 2007). The length of the snow-free growing season at lower elevations (2600–2700 m) is 5–6 months, usually starting in November, but it is reduced to 3–4 months at upper sites (3400–3600 m) (E.I. Badano, personal observation).

In January 2006, 10 sampling sites at different elevations and on different slope aspects were selected in the study area. Plant communities were dominated by *A. madreporica* cushions at four of the sites, while the remaining sites were dominated by *L. acaulis* cushions. Details on elevation and slope aspect of each sampling site are given in Table 1.

2.3. Vegetation sampling

At each site, in order to control for area effects during sampling, we first determined the amount of cushion habitat and surrounding matrix habitat (open areas hereafter) by measuring the cover of both habitat types. Cover was measured along 10 parallel 50-m long line-transects, spaced by 10 m each. The percent cover of cushions at each site is shown in Table 1. Later, 40 cushions larger than 60 cm in diameter (the most common cushion size) were randomly selected at each site. On each cushion we randomly dropped a 0.2 m^2 circular plot and all species within it were identified. Species richness in open areas was sampled in a similar way, but the number of samples in this habitat was proportional to the difference in cover between habitat types. In other words, if cushion cover in the landscape was 10%, then 10 samples in open areas were taken per each cushion sampled (the number of samples taken in the open areas at each site is shown in Table 1). Aerial parts of each species detected within cushions and in open areas were collected and stored in individual paper bags (one bag per species per sample). We only collected the aboveground parts of plants because complete belowground structures are difficult to obtain. This is because cushion plants are compact structures, literally attached to the soil, and obtaining roots of plants growing within them would imply their complete destruction. Paper bags were placed in a ventilated stove at 75 °C within 3–4 h after collection to avoid tissue degradation. Bags were dried for 72 h and weighed to determine the aboveground dry biomass of each species within each sample. We then calculated the standing crop aboveground biomass of each sample (i.e., the ratio between the dry biomass and the sampled area) and these values were used as surrogate of plant productivity. Cushions themselves were not included in samplings because we were interested in measuring their effects on standing crop and plant species richness. In our study system, standing crop is a very good surrogate of primary productivity because high-Andean plants well known for their ability to accumulate biomass

during the growing season (Körner, 2003). Further, since plants just dispose of a limited time span for developing their aerial structures each year, the interannual variation in aboveground standing crop is minimal.

2.4. Effects of cushion plants standing crop and species richness

To assess the effects of cushion plants on standing crop and species richness at each study site we used the *effect size*, a meta-analytic metric proposed by Glass (1976) and modified by Hedges (1981). We chose this metric because it summarizes differences between treatment (cushions) and control groups (open areas) using the average response to each situation, together with their associated standard deviations and sample sizes.

At each sampling site, the effect size of cushions on standing crop was calculated as:

$$g = \frac{(X^E - X^C)}{S}, \tag{1}$$

where g is the effect size of cushions on standing crop, X^E and X^C are the average standing crop of samples taken within cushions and in open areas, respectively, and S is the pooled standard deviation of both averages. Here, S was calculated as:

$$S = \sqrt{\frac{(N^E - 1)(s^E)^2 + (N^C - 1)(s^C)^2}{N^E + N^C - 2}}, \tag{2}$$

where N^E and N^C are the number of samples taken within cushions and open areas, respectively, and s^C and s^E the standard deviation of X^E and X^C, respectively.

Positive values of effect sizes indicate that cushions increase standing crop compared to open areas whilst negative values indicate the converse situation. Following this procedure, the size of the patch-scale effect of cushions on species richness was calculated by averaging the number of species in samples taken within cushions (X^E) and in open areas (X^C), and calculating their respective standard deviations (s^C and s^E, see equation (2)).

Before assessing the habitat-scale effect size of cushions on species richness, we determined whether our sampling effort fully captured species composition of the cushion-engineered habitat at each study site. For this, we constructed a species × sample matrix for the cushion habitat from each site and estimated species-area accumulation curves using sample-based rarefactions (Gotelli and Colwell, 2002). Rarefactions were run in EstimateS v. 8 (Colwell, 2006) and included sampling sizes from 1 to 40 samples (the maximum number of samples taken within cushions). For each sampling size, 100 Monte-Carlo random permutations were run without-replacement, and the estimated values of species richness were averaged and standard deviation calculated. These averages values of species richness were plotted against their respective

Table 1
Study sites selected in the Rio Molina basin, high-Andes of central Chile, for this study. The table indicates longitude and latitude, elevation, slope aspect, cushion species that dominates the landscape, percent cover of cushion (average ± 2SE) and number of samples taken in open areas study. Sites were numbered according to decreasing elevation.

	Latitude	Longitude	Elevation	Slope aspect	Cushion species	Cushion cover	Open areas samples
Site 1	33°19′09″ S	70°15′35″ W	3600 m	SE	*Azorella madreporica*	10.2 (±1.1)	400
Site 2	33°18′58″ S	70°14′09″ W	3600 m	NW	*Azorella madreporica*	9.6 (±0.8)	400
Site 3	33°19′33″ S	70°15′19″ W	3400 m	SE	*Azorella madreporica*	14.8 (±1.1)	280
Site 4	33°20′02″ S	70°14′48″ W	3200 m	SE	*Azorella madreporica*	21.5 (±1.7)	200
Site 5	33°20′02″ S	70°14′50″ W	3200 m	SE	*Laretia acaulis*	13.5 (±0.9)	280
Site 6	33°19′35″ S	70°16′42″ W	3200 m	NW	*Laretia acaulis*	32.1 (±1.6)	120
Site 7	33°19′48″ S	70°17′10″ W	3000 m	S	*Laretia acaulis*	43.2 (±1.7)	80
Site 8	33°19′34″ S	70°17′00″ W	3000 m	N	*Laretia acaulis*	12.1 (±1.9)	320
Site 9	33°21′22″ S	70°15′34″ W	2700 m	SE	*Laretia acaulis*	23.1 (±1.3)	160
Site 10	33°21′23″ S	70°15′31″ W	2700 m	NE	*Laretia acaulis*	17.3 (±1.9)	240

sampling sizes to construct the curves. All curves reached the asymptote before 40 samples (see Appendix A in the electronic Supplementary material), indicating that our sampling effort was adequate to fully capture the species composition in the cushion habitat at all sites. The average number of species estimated at 40 cushion samples then estimates X^E, and its associated standard deviation estimates s^E (see equations (1) and (2)). Since estimation of habitat-scale effects of ecosystem engineers requires equally sized areas of engineered and unmodified habitats for comparisons (Badano et al., 2006), species richness of open areas should also be estimated at 40 samples. For this, we constructed a species × sample matrix for the open areas of each site, performed sample-based rarefactions, and constructed species-area accumulation curves using the same protocol described above. However, since in most of the study sites we took more samples in open areas than within cushions because of differences in cover between these habitat types, these curves included from 1 sample to the maximum number of samples taken in this habitat type (the number of samples taken in open areas at each site is shown in Table 1). The number of species estimated at 40 samples in these curves and its associated standard deviation then estimate X^C and s^C, respectively. These values were then used to calculate the effect size of cushion on the habitat-scale species richness following the g's formula (equation (1)).

Ideally, the magnitude of the landscape-scale effects of ecosystem engineers should be assessed by comparing species richness between equal sized, naturally occurring landscapes with and without engineers (Badano et al., 2006; Wright et al., 2002). However, this approach has a series of limitations. Firstly, most natural landscapes are likely to be engineered by some species, and natural occurring landscapes differing only in the presence of a focal engineer species would be extremely hard to find. Secondly, experimental manipulations implying species removal from engineered patches and the later assessment of patch recolonization are not feasible within our life span if recruitment of these species requires several years. Finally, experimental removal of ecosystem engineers may have strong ethical implications if the focal engineer species is supporting a great part of the landscape species diversity, as in our case [see Badano and Cavieres, 2006a,b; Badano et al., 2006]. This later implication would be even more critical if that engineer is a long-living species with slow growth, so, natural recovery of the manipulated system to its original state could take several years. Assessing the landscape-scale effects of ecosystem engineers then relies in comparing the current species richness that a landscape has due to the presence of a focal engineer species against the expected species richness that the same landscape would be expected to have in absence of the engineer species (Badano et al., 2006; Badano and Marquet, 2008; Wright et al., 2002).

Given these limitations, to assess the landscape-scale effect size of cushion plants on species richness, we first estimated the number of species that the landscape of each study site has due to the presence of cushions. For this, we generated a synthetic dataset for each site by combining samples from cushions and open areas but, since cushions always represented a smaller fraction of the landscape than open areas (see Table 1), the proportional difference in cover between habitat types was used to control for area effects. Synthetic datasets were then generated by randomly replacing 40 samples in the species × sample matrix constructed for the unmodified landscape by the 40 samples taken within cushions. Thus, these "engineered landscapes" had the same size (i.e., included the same number of samples) than the "unmodified landscapes" only composed by open areas, but maintained the proportional difference in cover between habitat types. To avoid biases due to differences in the samples that were replaced, we simulated 100 engineered landscapes for each site, and a species-area curve was performed for each one using the same rarefaction protocol described above. We further averaged the 100 values of species richness estimated at each sampling size and constructed a unique species-area curve for the engineered landscape of each site. The average species richness estimated at the maximum sampling size (see Appendix A in the electronic Supplementary material) and its associated standard deviation then estimate X^E and s^E, respectively. On the other hand, the average species richness estimated at the maximum sampling size in the previously performed species-area curves for open areas (see Appendix A in the electronic Supplementary material) and its standard deviation were used as estimates of X^C and s^C, respectively. The landscape-scale effect size of cushions on species richness was then calculated with the g's formula (equation (1)). Since the sampling size in open areas defined the landscape size (i.e., the number of samples included) at all study sites, N^E and N^C was equal to the maximum sampling size in open areas (see Table 1).

We then performed simple linear regression analyses to assess whether the effect sizes of cushions on species richness at the patch, the habitat and the landscape scales (g_P, g_H, and g_L hereafter) were related with their effect sizes on standing crop (g_{SC} hereafter). If $g_{(P, H\ or\ L)} = f(g_{SC})$, then we could be able to make predictions on the effects of cushion plants on species richness at the three spatial scales from the difference productivity between patch types. As a first approximation, all regression analyses were conducted separately for the effects of A. madreporica and L. acaulis. Later, we pooled the effects of both cushion species to assess whether these relationships could be generalized across the engineer species from the same region. All regression analyses were performed using the software R v. 2.3 (R Development Core Team, 2005).

3. Results

A total of 83 species were recorded across the 10 sampling sites included in this study (Appendix B in the electronic Supplementary material). Aboveground standing crop was higher within cushion patches than in open areas at three of the four sites dominated by A. madreporica (Table 2). Across the sites dominated by L. acaulis, cushion patches showed higher standing crop values than open areas at four sites and lower values at two sites (Table 2).

A the patch scale, the effect sizes of A. madreporica cushions on species richness were positively related (g_P) with its effects on standing crop (g_{SC}) (Goodness of fit ANOVA: $F_{1,2} = 144.00$, $p = 0.006$, $R^2 = 0.99$, Fig. 2A). Negative effects of A. madreporica on species richness at this spatial scale were only detected at the site where cushions decreased standing crop as compared to open areas (Site 4), being species richness in open areas 4% higher than within cushions (Table 2). A. madreporica cushions were indicated to contain up to 60% more species than open areas at the remaining three sites (Table 2). Similarly, g_P and g_{SC} were positively related across sites dominated by L. acaulis (Goodness of fit ANOVA: $F_{1,4} = 72.23$, $p = 0.001$, $R^2 = 0.95$, Fig. 2B). Negative effects of L. acaulis on patch-scale species richness were detected at the two sites where cushions negatively affected standing crop (Sites 5 and 7), being open areas indicated to contain 11–19% more species than cushions (Table 2). In contrast, species richness within L. acaulis was up to 49% higher than in open areas at the site where these cushions had the greatest positive effect of on standing crop (Site 8 in Table 2).

For both cushion species, the habitat-scale effect sizes on species richness (g_H) increased with their effects on standing crop (g_{SC}) (Goodness of fit ANOVA A. madreporica: $F_{(1,2)} = 26.39$, $p = 0.036$, $R^2 = 0.93$, Fig. 3A; Goodness of fit ANOVA L. acaulis: $F_{(1,4)} = 162.57$, $p < 0.001$, $R^2 = 0.97$, Fig. 3B). Across sites dominated

Table 2
Average aboveground standing crop of plants within cushion patches and in open areas at each study site, and estimated values of species richness at the patch, the habitat and the landscape scale for engineered and unmodified situations (details on methods used in these estimations are given in the text). References for sites are given in Table 1.

	Standing crop biomass (g/m^2)		Patch-scale richness		Habitat-scale richness		Landscape-scale richness	
	Cushions	Open areas	Engineered	Unmodified	Engineered	Unmodified	Engineered	Unmodified
Site 1	86.4	13.4	5	2	24	20	33	24
Site 2	43.2	2.7	4	1	16	11	24	14
Site 3	50.9	8.3	5	2	28	21	40	27
Site 4	49.5	60.9	7	7	37	38	49	42
Site 5	23.9	55.2	4	7	23	38	45	42
Site 6	70.6	10.7	6	2	30	18	34	20
Site 7	47.8	79.6	5	6	32	37	43	39
Site 8	95.6	22.1	6	2	28	19	31	21
Site 9	63.5	48.4	8	5	33	26	38	31
Site 10	62.8	16.9	6	3	22	15	28	19

by *A. madreporica*, the habitat created by this cushion species showed a slightly lower (2%) species richness than the matrix habitat only composed by open areas at the site where cushions negatively affected standing crop (Site 4), but the *A. madreporica* habitat contained 10–17% more species than open areas at sites where cushions increased standing crop (Table 2). Across sites dominated by *L. acaulis*, the surrounding open areas were more species rich (7–23%) than the cushion habitat at the two sites where cushions negatively affected standing crop (Sites 5 and 7), but the cushion habitat had 9–24% more species at the sites where the effects of *L. acaulis* on standing crop were positive (Table 2).

Effect sizes of *A. madreporica* and *L. acaulis* on the landscape-scale species richness (g_L) also increased linearly with their effects on standing crop (g_{SC}) (Goodness of fit ANOVA *A. madreporica*: $F_{1,2} = 10.20$, $p = 0.048$, $R^2 = 0.91$, Fig. 4A; Goodness of fit ANOVA *L. acaulis*: $F_{(1,4)} = 358.06$, $p < 0.001$, $R^2 = 0.99$; Fig. 4B). Values of g_L were larger than zero at all sites, indicating that *A. madreporica* and

L. acaulis added new plant species into landscapes even when their effects on patch standing crop were negative. For landscapes dominated by *A. madreporica*, the presence of cushions increased species richness by 7% at the site where this cushion species had negative effects on standing crop (Site 4), but increased species richness of plant communities up to 26% at sites where *A. madreporica* positively affected the standing crop (Table 2). *L. acaulis* just increased plant species richness by 3–5% at sites where cushions negatively affected standing crop (Sites 5 and 7), but species richness of plant communities increased up to 26% due to the presence of *L. acaulis* at sites where cushions increased standing crop as compared to open areas (Table 2).

When data of both cushions species were pooled, the relationships between their effects on species richness and standing crop showed the same patterns that were previously recorded for each cushion species separately. The effect sizes of cushions on species richness at the patch (Fig. 5A), the habitat (Fig. 5B), and the
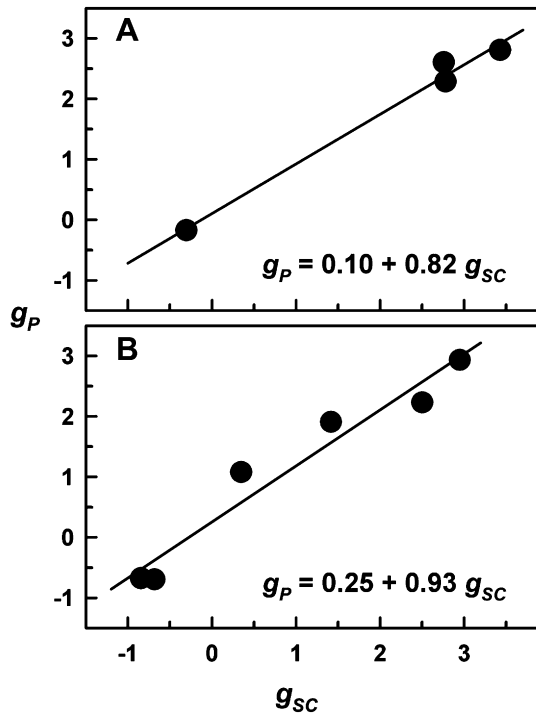

Fig. 2. Relationships between patch-scale effect sizes of cushion plants on species richness (g_P) and standing crop biomass of plants (g_{SC}) across sites dominated by *Azorella madreporica* (A) and *Laretia acaulis* (B). Regression functions relating g_P and g_{SC} are shown within each figure.
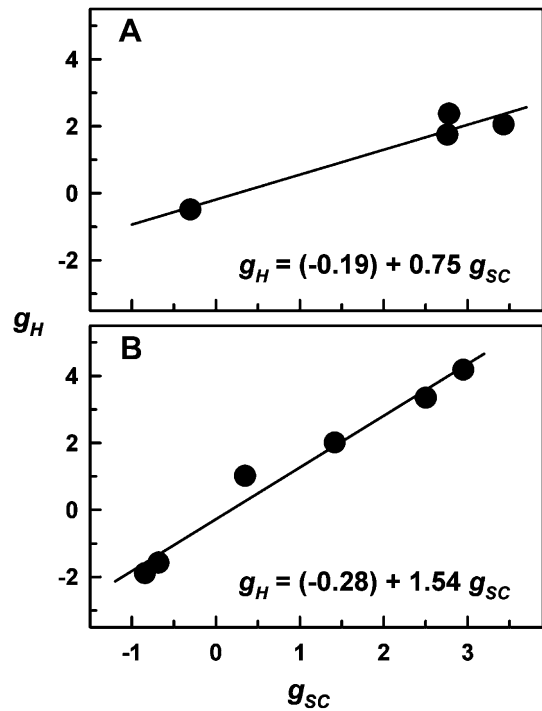
Fig. 3. Relationships between habitat-scale effect sizes of cushion plants on species richness (g_H) and standing crop biomass of plants (g_{SC}) across sites dominated by *Azorella madreporica* (A) and *Laretia acaulis* (B). Regression functions relating g_H and g_{SC} are shown within each figure.
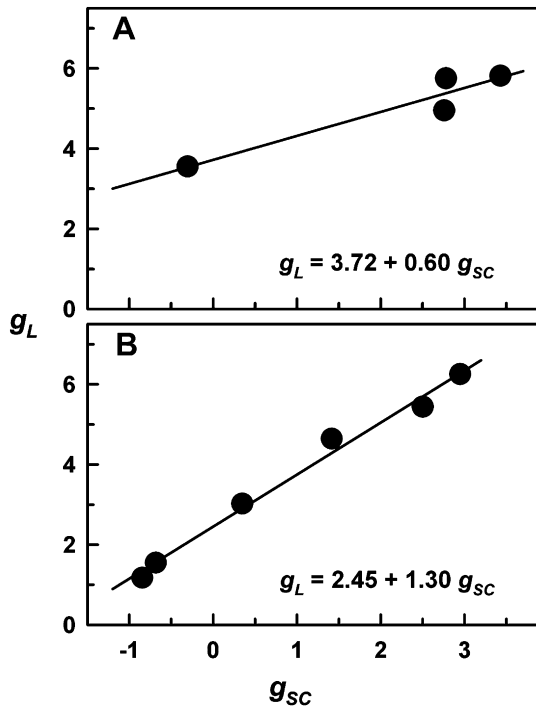
Fig. 4. Relationships between landscape-scale effect sizes of cushion plants on species richness (g_L) and standing crop biomass of plants (g_{SC}) across sites dominated by *Azorella madreporica* (A) and *Laretia acaulis* (B). Regression functions relating g_L and g_{SC} are shown within each figure.

landscape (Fig. 5C) scale increased linearly with larger positive effects of cushions on standing crop (Goodness of fit ANOVA patch scale: $F_{(1,8)} = 147.52$, $p < 0.001$, $R^2 = 0.96$; Goodness of fit ANOVA habitat scale: $F_{(1,8)} = 30.41$, $p < 0.001$, $R^2 = 0.79$; Goodness of fit ANOVA landscape: $F_{(1,8)} = 69.13$, $p < 0.001$, $R^2 = 0.90$).

4. Discussion

Predicting when and where ecosystem engineers will have strong or feeble effects on natural communities is a key issue within the current conceptual framework of ecosystem engineering (Wright and Jones, 2006, 2004; Moore, 2006; Crain and Bertness, 2006; Badano and Cavieres, 2006a; Badano et al., 2006; Wright et al., 2006). The results of this study support the proposal that the magnitude of the effects of ecosystem engineers on species diversity vary along environmental gradients, and indicate that these effects can be predicted by estimating the magnitude of the effects of ecosystem engineers on habitat conditions. In our particular case, we used the aboveground standing crop of plant assemblages as surrogate of physical stress and showed that the two engineer species studied here had larger effects on the diversity of high-Andean vascular plant assemblages as the magnitude of their effects on standing crop increase. Indeed, these effects were consistent across the three spatial scales included in this study: the patch, the habitat and the landscape. Furthermore, the effects of *A. madreporica* and *L. acaulis* on species richness and standing crop were consistently related each other even when data of both cushion species were pooled in single regression analyses, suggesting that predictions of the magnitude with which these engineer species affect species diversity with increasing physical stress could be generalized across engineer species.

The increasing positive effects of *A. madreporica* and *L. acaulis* on standing crop and species richness could be linked with the widely
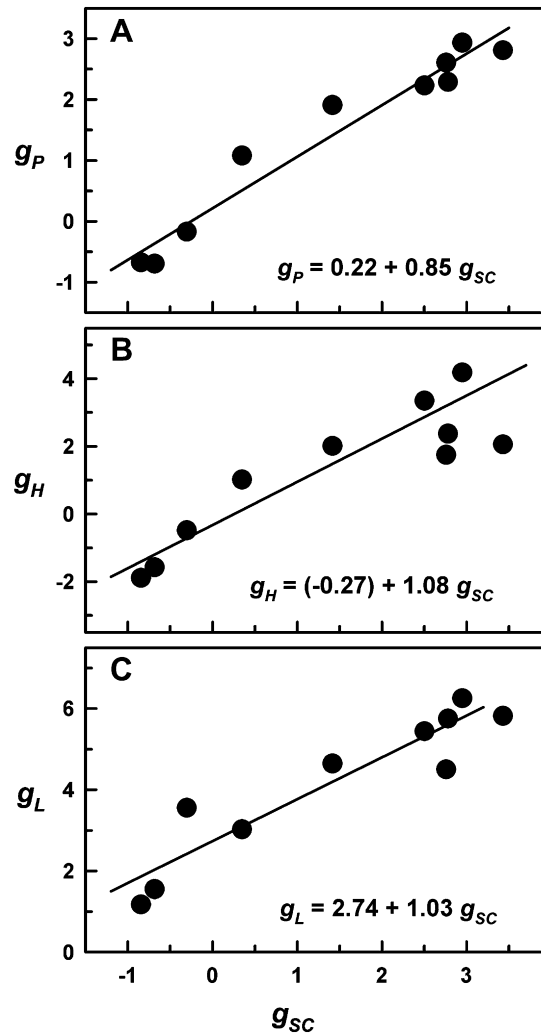

Fig. 5. Relationships for the combined effects of *Azorella madreporica* (empty circles) and *Laretia acaulis* (solid circles) on species richness and standing crop at the patch (A), the habitat (B) and the landscape (C) scales. Regression functions relating effects on cushions on species richness ($g_{P,\ H\ or\ L}$) and g_{SC} are shown within each figure.

reported ability of cushion plants to mitigate extreme low temperatures and water shortage conditions, which have been suggested to be more important for other species in extremely cold or dry sites in the high-Andes of Chile (Cavieres et al., 2007; Arroyo et al., 2003; Molina-Montenegro et al., 2005). On the other hand, the negative patch- and habitat-scale effects of cushions on species richness at some sites may rise from increases in physical stress within cushion patches as compared to open areas.

Our results on the effects of cushion plants on species richness at the patch and habitat scales concur with the predictions of the model proposed by Wright and Jones (2004) for the single-patch-scale effects of ecosystem engineers. Nevertheless, that model performs separate predictions for the effects of engineers that increase primary productivity and engineers that decrease primary productivity, making no integrative predictions for the effects of engineer species that may either increase or decrease productivity along environmental gradients. In this study, we show that the effects of *A. madreporica* and *L. acaulis* cushions on plant species richness at these two spatial scales seems to depend on the environmental context, being positive when cushions increase stranding crop as compared to open areas, but negative when cushions decreased standing crop. Further, we also show that the

magnitude, positive or negative, of these effects on species richness could be predicted as a function of the effects of cushions on standing crop through simple linear models.

Interestingly, the magnitude of the landscape-scale effects of *A. madreporica* and *L. acaulis* on species richness was always larger than zero, even at those sites where species assemblages within cushion patches had lower standing crop biomass than plant assemblages growing in the surrounding open areas. These results suggest that the presence of cushion plants in the studied high-Andean landscapes increases species richness of plant communities by adding species that would not survive in the unmodified matrix habitat surrounding cushions (Badano et al., 2006; Badano and Cavieres, 2006b). Jones et al. (1997) early proposed that such an increase in the species richness at spatial scales larger than the habitat – i.e., the landscape – is almost an inevitable consequence of ecosystem engineering because of the increased habitat diversity at these spatial scales. However, the addition of new species at sites where standing crop biomass of plants was lower within cushions seem somehow counterintuitive with our predictions because this suggests that cushions plants increase physical stress. If so, the addition of plant species by *A. madreporica* and *L. acaulis* at these sites may be mediated by effects of cushions on habitat variables other than those causing physical stress, such as mitigation of the negative effects of disturbances caused by wind erosion and snowmelt runoff. Alternatively, more complex mechanisms, such species-specific positive interactions between cushions and other plant species, may be occurring at these sites. Nevertheless, irrespectively of the mechanisms involved, the magnitude of these landscape-scale effects on plant species richness increased with larger differences in standing crop biomass between cushions and open areas, suggesting that the effects of cushions on diversity of high-Andean plant communities could be predicted. Here, the positive relationship between the magnitude of the landscape effects of cushions on species richness and standing crop indicate that plant assemblages in the high-Andes of central Chile are more susceptible to lose species because of the local extinction of cushion plants in more stressful, less productive sites.

In this study, the relationships between the effects of cushion plants on species richness and standing crop were linear at the patch, habitat and landscape scale. However, the shape of these relationships may vary across ecosystems and across engineer species. Factors likely influencing the shape of these relationships may include: (1) the physiological tolerance thresholds to physical stress of species in the regional species pool; (2) the magnitude and direction in which engineers modulate stress factors at each point of an environmental gradient; and (3) the magnitude with which stress factors vary across sites of a gradient. For example, if increasing physical stress limits the survival of most species from the regional species pool and it increases dramatically from low to high-stress levels, then engineers that ameliorate stress conditions will have positive effects on species richness. However, these effects on species richness would increase linearly, as in our case, if engineered patches from high-stress sites reproduce the habitat conditions of the unmodified habitat of those sites immediately below in the stress gradient. Alternatively, these effects may increase exponentially if habitat conditions within engineered patches at high-stress sites are those of the unmodified habitat from several stress levels below. On the other hand, if variations in physical stress along a gradient are within the physiological tolerance thresholds of species, ecosystem engineers will have no effects on species richness at any site irrespectively of the magnitude and direction in which they modulate stress. Nevertheless, ecosystem engineers may cause other community-level changes besides of affecting species richness, such as changes in the species dominance

patterns within a community (Badano and Cavieres, 2006a,b; Badano et al., 2006).

Finally, it is important to note that, in this study, we linked only the effects of ecosystem engineering on standing crop and plant species richness. However, other interesting phenomena may be masked by this relationship. For instance, it is widely accepted that output of ecosystem functions increase with increasing species diversity (Tilman and Downing, 1997; Tilman et al., 1996; Wilsey and Potvin, 2000; Hector et al., 1999; Hooper et al., 2005). Thus, at the patch scale, the higher standing crop observed within cushion plants at some sites may be a consequence of their higher species richness. This may occur because an increasing number of species leads to higher efficiency and/or complementarity in the use of resources (Hooper, 1998; Naeem, 1998) or an increased importance of positive interactions (Mulder et al., 2001; Cardinale et al., 2002). Some recent studies have shown that biomass of high-Andean plant communities increases with species richness, and indicated that presence of cushion plants enhance the output these relationships because they add new species into communities (Badano and Marquet, 2008; Badano and Marquet, 2009). Therefore, if cushion plants affect the number of species, they are also likely to affect the fluxes of matter and energy between the abiotic and biotic compartments of the ecosystems at the patch, the habitat and the landscape scales. However, more refined experiments and observations would be required to determine these effects.

5. Conclusions

This study indicates that the effects of ecosystem engineering on species richness depend on the environmental context. Moreover, the results clearly show that these effects can be predicted from knowing the magnitude of the environmental modifications performed by the engineer species. Then, we suggest that future research may use approaches similar to those used here for modelling the impact of ecosystem engineering processes along environmental gradients.

Acknowledgments

Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.actao.2009.09.008.

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