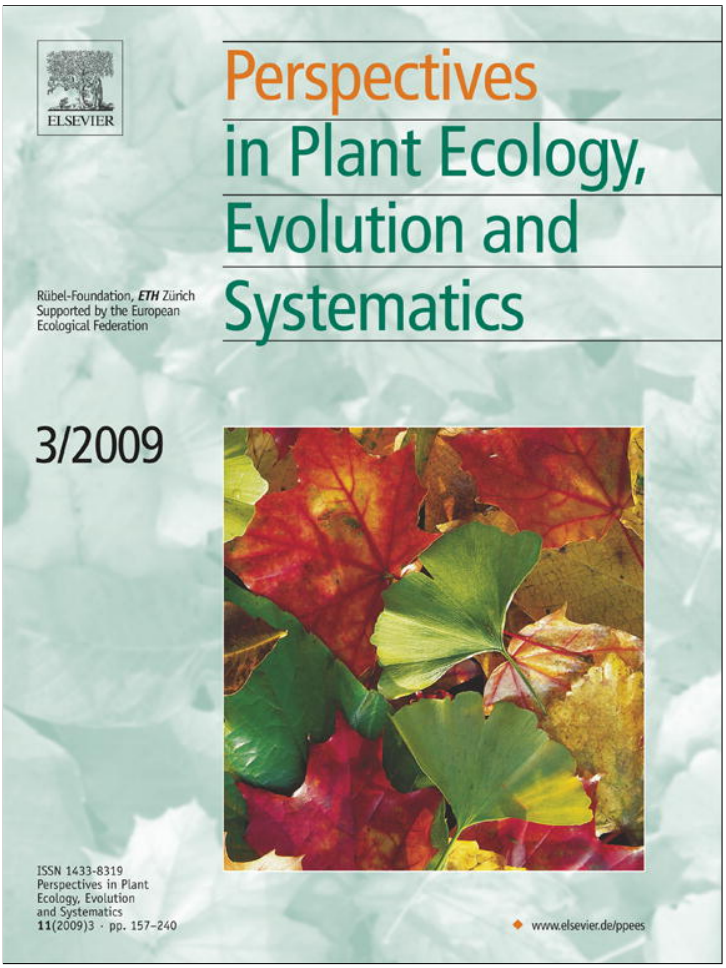

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Biogenic habitat creation affects biomass–diversity relationships in plant communities

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Abstract

Biogenic habitat creation refers to the ability of some organisms to create, maintain or destroy habitats. These habitat changes affect species diversity of natural communities, but it remains to be elucidated if this process also affects the link between ecosystem functions and species diversity. Based on the widely accepted positive relationships between ecosystem functions and species diversity, we hypothesize that these relationships should be different in biogenically created habitat patches as compared to unmodified habitat patches. We tested this hypothesis by assessing the effects of a high-Andean cushion plant, *Azorella madreporica*, which creates habitat patches with different environmental conditions than in the surrounding open areas with reduced vegetation cover. We used observational and experimental approaches to compare the plant biomass–species richness relationships between habitat patches created by *A. madreporica* cushions and the surrounding habitat without cushion plants. The observational assessment of these relationships was conducted by counting and collecting plant species within and outside cushion patches. In the experiment, species richness was manipulated within and outside cushion patches. The cushion plant itself was not included in these approaches because we were interested in measuring its effects. Results of both approaches indicated that, for a given level of species richness, plant biomass within cushions was higher than in the surrounding open areas. Furthermore, both approaches indicated that the shape of plant biomass–species richness curves differed between these habitat types. These findings suggest that habitat modifications performed by *A. madreporica* cushions would be positively affecting the relationships between ecosystem functions and species diversity.

Keywords: Alpine ecology; Ecosystem functioning; Ecosystem engineering; Facilitation; Nurse effect; Positive interactions

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Introduction

Most species, if not all, interact in non-trophic ways with their abiotic environment causing physicochemical changes within their area of influence. Nevertheless, while the non-trophic effects of most species are of little relevance for others, a few species strongly interact with the environment and create suitable micro-habitats, or safe sites (*sensu* Harper, 1977), for the establishment and development of other organisms (McAuliffe, 1984; Callaway, 1992; Bertness and Callaway, 1994; Jones et al., 1994, 1997; Bruno et al., 2003). This process of biogenic habitat creation has been called *facilitation* (see Callaway, 1995; Callaway and Pugnaire, 1999; Kikvidze, 2002), *nurse effect* (see Turner et al., 1966; McAuliffe, 1984; Cavieres et al., 2002) or *ecosystem engineering* (see Jones et al., 1994, 1997).

Irrespective of the given name, it has been widely demonstrated that the biogenic habitat creation affects community organization (Bertness and Callaway, 1994; Jones et al., 1994, 1997; Brooker and Callaghan, 1998; Lortie et al., 2004; Wright and Jones, 2006; Badano and Cavieres, 2006a). In riparian forests of northeast USA, for example, plant assemblages within meadows created by beavers differ from those in the surrounding riparian forest, and this is because some species can only persist within beaver-modified patches (Wright et al., 2002). Environmental differences between biogenically modified habitats and unmodified habitats can also affect the performance of species able to inhabit both habitat types (Aho et al., 1998; Crooks and Khim, 1999; Schooley et al., 2000; Fritz et al., 2004; Badano et al., 2007), but the direction (positive or negative) of these effects seems to depend on the species involved. For instance, in Venezuelan Andean streams, bulldozing activities of detritivorous fishes on bottom sediments positively impact densities of cyanobacteria, but negatively affect densities of diatoms in comparison to surrounding undisturbed sites (Flecker, 1996). Moreover, several studies have shown that the magnitude of the biotic effects of species able to modify habitat conditions varies with physical stress, having larger positive effects with increasing environmental harshness (Tewksbury and Lloyd, 2001; Callaway et al., 2002; Badano and Cavieres, 2006b). However, although the empirical evidences indicate that the biogenic habitat creation may drive biodiversity, its repercussion on ecosystems functions remains to be elucidated.

Several studies have shown that the relationship between ecosystem functioning and species diversity is positive (Tilman and Downing, 1994; Naeem et al., 1995; Tilman et al., 1997a; Chapin et al., 1998; Hector et al., 1999; Wilsey and Potvin, 2000; Hooper et al., 2005). These positive effects of species diversity have been ascribed, in part, to increased complementarity in the use of resources and/or increased frequency of positive interactions among species (Loreau, 1998; Mulder et al., 2001; Loreau and Hector, 2001; Cardinale et al., 2002). Alternatively, these relationships have also been explained through "sampling effects" (Tilman et al., 1997b). Sampling effects imply that higher ecosystem functioning at higher levels of species diversity is merely a stochastic effect due to an increased likelihood of including species with a specific property (e.g., high productivity) as more species are included in the community (Huston, 1997; Aarssen et al., 2003; Petchey, 2004). Although the mechanisms behind these relationships are still matter of discussion, it can be proposed that changes in community diversity due to biogenic habitat creation would affect ecosystem functions.

The experiments dealing with the relationships between ecosystem functioning and species diversity have been mainly performed in lowland grasslands (Naeem and Wright, 2003), but little is known on these relationships in less productive environments, such as alpine habitats (see Rixen and Mulder, 2005; Rixen et al., 2008). Indeed, just a few studies have evaluated the effects of the biogenic habitat creation on ecosystem functioning. For instance, Levine (2000) reported that increased cover of native species within habitat patches created by the tussock-forming sedge *Carex nudata* may help to prevent biological invasions. On the other hand, Badano and Marquet (2008) indicated that enhancements in ecosystem functioning occur when the habitat modification leads to the addition of new species into communities. Nevertheless, this later study was only focused on the large-scale consequences of the biogenic habitat creation, including modified and unmodified habitats all together as parts of the same landscape (see Badano and Marquet, 2008).

In this study, we propose that the shape of the ecosystem functioning–species diversity relationships should differ between habitat types if species respond differentially to modified and unmodified habitat patches. To test this hypothesis, we used observational and experimental approaches to assess the relationships between plant biomass (the most widely used surrogate of ecosystem function) and species richness (the most commonly used measure of species diversity) in modified and unmodified habitat patches of a high-Andean landscape. We focused on the effects of the high-Andean cushion plant *Azorella madreporica* Clos (Apiaceae). This cushion plant creates discrete and distinctive habitat patches immersed in a habitat matrix of rocks and bare soil, or open areas, with scarce vegetation cover (Fig. 1). Previous studies reported that high-Andean cushion plants can modulate substrate temperatures, reducing daily thermal fluctuation in comparison to open areas (Arroyo et al., 2003; Badano et al., 2006; Molina-Montenegro et al., 2006; Cavieres et al., 2006, 2007). On the other hand, cushion plants also modify water availability, where soil beneath

Fig. 1. Landscape of the study site showing *Azorella madreporica* cushions growing surrounded by the habitat matrix of open areas composed by rocks, bare soil and other plants species.

cushions retains more water than soil from open areas (Badano et al., 2006; Molina-Montenegro et al., 2006; Cavieres et al., 2007). Given the positive effects that these environmental modifications have on other high-Andean plant species (Cavieres et al., 2005, 2006, 2007; Badano et al., 2006, 2007), we suggest that plant biomass should increase strongly with increasing species richness within cushions than in the surrounding open areas.

Materials and Methods

Study site

This study was conducted in the high-Andes of central Chile, on a polar-facing slope at 3400 m elevation (33°19′S, 70°15′W). At this site, the length of the snow-free growing season is 4–5 months, starting in November and finishing in March (E. I. Badano, pers. obs.). During the growing season, the estimated mean temperature of the air at 3400 m is ca. 6 °C (Cavieres and Arroyo, 1999), but temperatures below 0 °C can be reached at night (Badano et al., 2006, 2007). Precipitation usually exceeds 900 mm (Santibáñez and Uribe, 1990), mainly occurring as snow during winter months. Thus, water shortage conditions are likely to occur during the growing season (Cavieres et al., 1998, 2006). Soil is mainly a clay-type mixed with some sedimentary and volcanic rocks (Cavieres et al., 2000). Although *A. madreporica* cushions dominate the plant community, a number of small perennial and annual herbs as well as some prostrate shrubs grow both within and outside cushions.

Environmental modifications performed by cushions

To assess whether *A. madreporica* cushions modify environmental conditions in comparison to open areas, we performed a quick assessment of the relative water content of soil and substrate temperatures in both habitat types. The relative water content of soil was measured *in situ* with a time-domain reflectometer probe (ThetaProbe ML2x, Delta-T Services, Cambridge, UK) connected to a moisture meter (HH2, Delta-T Services, Cambridge, UK). These measures were performed during a clear sunny day in January 2006 between 12:00 and 15:00 h. Twenty cushions were randomly selected at the study site and a small hole (10 cm diameter) was drilled at the center of each selected cushion to reach the soil beneath them, where the reflectometer probe was dug at 10-cm deep. Each measure beneath cushions had a paired measure performed in the soil of the adjacent open areas using the same methodology. Soil moisture was compared between habitat types using *t*-tests for paired comparisons.

Substrate temperatures were recorded during 3 consecutive days in February 2007 using soil temperature probes (TMCx-HD, Onset Computer Corporation, MA, USA) connected to dataloggers (HOBO H8, Onset Computer Corporation, MA, USA) programmed to record the temperature every 30 min. For this, two cushions were randomly selected at the study site, and a temperature probe was placed 2 cm below the cushion surface. Each cushion had a paired probe 2 cm below the soil surface in an adjacent open area. Temperature data from cushions and open areas were averaged at each hour across the 3 days of measurement.

Observational relationships between plant biomass and species richness

In January 2006, 40 cushions (larger than 50 cm diameter; smaller sizes were not used to avoid unnecessary damage on developing cushions) and 40 points in open areas were selected by using points located at random directions and distances from the center of a previously delimited 1-ha plot randomly centered in the study site. On each selected cushion and at each point in open areas we randomly dropped a 0.2 m^2 circular plot. All adult plants within each plot were identified and counted. We did not detect seedlings of any species within these plots. *A. madreporica* itself was not included in this sampling because we were interested in measuring the effects of this species. Aerial parts of species within plots were collected and stored in individual paper bags

(one bag per species per sample), and placed in a ventilated stove at 75 °C within 3–4 h of collection to avoid metabolic tissue degradation. Bags were dried for 72 h and weighed to determine the aboveground dry biomass of each species within each sample. It is important to note that *A. madreporica* cushions were not taken into account because it is part of the treatment. Since many species were shared between cushions and open areas, *t*-tests were used to determine whether biomass of these species varied between habitat types.

To assess whether plant biomass increased with the number of species in samples, and to determine whether these relationships differed between cushions and open areas, we performed regression analyses with categorical variables (Neter et al., 1996). To perform these analyses, samples from cushions and open areas were sorted according to their species richness and plant biomass was averaged across samples within each richness level (Tilman et al., 1996). Then, in regression analyses, the average biomass at each richness level (B hereafter) was the response variable, species richness (S hereafter) was the continuous predictive variable and the habitat types (cushions or open areas) were the two levels of the categorical predictive variable. We also included an interaction term between continuous and categorical predictive variables to account for differences in the estimated parameters (β values hereafter) of regression functions obtained for the two levels of the categorical variable (Neter et al., 1996). Regression functions obtained for each level of the categorical variable were compared by assessing differences in β values with *t*-tests (Neter et al., 1996). Given that we could not predict *a priori* the shape of these relationships, regression analyses were conducted using a linear regression model ($B = \beta_0 + \beta_1 \times S$) and a logarithmic model [$B = \beta_0 + \beta_1 \times \ln(S)$]. We chose the model that, after meeting assumption of regression analyses, explained a higher proportion of the variance in data (i.e., the higher R^2 value).

Table 1. Plant species (family name is given in brackets) included in the experiment performed to assess plant biomass–species richness relationships.

Species	Cushions	Open areas
Acaena pinnatifida (Rosaceae)	1	0
Bromus setifoluis (Poaceae)	1	0
Bromus catharticus (Poaceae)	1	0
Calandrinia caespitosa (Portulacaceae)	1	0
Carex sp. 1 (Cyperaceae)	1	1
Carex sp. 2 (Cyperaceae)	1	0
Cerastium arvense (Caryophyllacea)	1	1
Chaetanthera euphrasioides (Asteraceae)	0	1
Erigeron andicola (Asteraceae)	1	1
Festuca magellanica (Poaceae)	1	0
Hordeum comosum (Poaceae)	1	1
Hypochaeris tenuifolia (Asteraceae)	1	0
Loasa sigmoidea (Loasaceae)	1	1
Montiopsis andicola (Portulacaceae)	1	0
Montiopsis potentilloides (Portulacaceae)	1	1
Nassauvia uniflora (Asteraceae)	0	1
Nastanthus agglomeratus (Calyceraceae)	1	0
Olsynium scirpoideum (Iridaceae)	1	1
Perezia carthamoides (Asteraceae)	0	1
Perezia pilifera (Asteraceae)	1	0
Phacelia secunda (Hydrophyllaceae)	0	1
Plantago barbata (Plantaginaceae)	1	0
Poa alopecurus (Poaceae)	1	1
Poa pratensis (Poaceae)	1	1
Pozoa coriacea (Apiaceae)	0	1
Rytidosperma violaceum (Poaceae)	1	1
Senecio looseri (Asteraceae)	1	0
Taraxacum officinale (Asteraceae)	1	1
Thlaspi magellanicum (Brassicaceae)	1	0
Trisetum preslei (Poaceae)	1	0
Viola atropurpurea (Violaceae)	0	1
Total number of species	25	17

"1" denotes the habitat type where the seeds of the species were collected (within *A. madreporica* cushions or in open areas), while "0" indicates that the species was not detected in that habitat type. Authorities of species can be found in Marticorena and Quezada (1985).

Experimental relationships between plant biomass and species richness

To experimentally assess whether plant biomass increased with species richness, we conducted a field experiment by manipulating the number of species within cushions and in open areas. For this, seeds of 25 species growing within cushions and 17 species growing in open areas were collected during February–March 2006 (see Table 1). Seeds from cushions and open areas were stored separately. Soil from open areas was also collected in the study site and meshed to remove small rocks and organic matter. After that, soil was sterilized in a ventilated stove at 200 °C to eliminate any biological activity. In October 2006, 240 plastic cups (10 cm diameter, 15 cm depth) were filled with this soil, and 120 of these plots were assigned to cushions and 120 to open areas. We then generated 5 species richness treatments by randomly drawing 1, 2, 4, 6 and 8 species from each habitat type (24 replicates per treatment). These richness treatments were performed separately for cushions and open areas with the seeds collected at the respective habitat type. We used this experimental design because there are species that only grow in cushions, but not in the open areas and vice versa. On the other hand, only soil from the open areas was used for filling the experimental plots because the soil beneath

cushion plants has been reported to concentrate more mineral nutrients than soil from open areas (Núñez et al., 1999; Cavieres et al., 2006). Thus, we preferred to control potential effects due to different initial concentration of nutrients by using the same soil type across all experimental plots.

Forty-eight seeds were initially sowed at each experimental plot and species were evenly represented within each plot – i.e., each plot of the richness treatment "1" contained 48 seeds of a single species, each plot of the richness treatment "2" contained 24 seeds of each species, and so on until 8 species combinations. Because seed germination is hard to obtain in field, seeds were germinated in growth chambers under controlled temperature conditions (20/10 °C day/night) during November and December 2006. The reason to use such a high sow density in plots (ca. 6111 seeds/m^2) was because we did not know the germination rate of each species in advance, but previous experiences indicated that germination for some Andean species is low even in growth chambers. Then, we assumed that high sow densities would ensure the development of seedlings of some species. Despite our efforts, not all seeds germinated prior to transplanting plots in the field and the number of seedlings varied across plots. Then, to avoid confounding effects due to differences in germination rates, we removed part of the seedlings and left 24 seedlings per plot, so that species were evenly represented (plots of the richness treatment "1" contained 24 seedling of a single species, plots of the richness treatment "2" contained 12 seedling of each species, plots of the richness treatment "4" contained 6 seedling of each species and plots of the richness treatment "8" contained 3 seedling of each species).

The plots with seedlings were taken to the study site at the beginning of January 2007, at the middle of the growing season, when the natural seed germination of most species finishes (E.I. Badano, pers. obs.). Plots were planted, after removing the plastic cup container, within 120 randomly selected cushions and 120 randomly selected points in open areas. We recorded the number of surviving species within each plot in March 2007, at the end of the growing season, after all the natural factors driving growth and mortality had acted on the seedlings. Shoots and roots of each of these species were then collected in individual paper bags (one bag per species per experimental plot). These bags were dried following the same protocol described above and weighed to determine the dry biomass of shoots and roots, and the total biomass of each species within each plot. Samples from cushions and open areas were sorted according to their species richness. Species biomasses were averaged across samples within each richness level. With these data, we performed regression analyses with categorical variables following the same methodology described above to assess whether shoot, root and total plant biomass increased with species richness, and to assess whether these relationships differed between cushions and open areas. However, the numbers of survivors in plots within cushions and plots on open areas were compared with a *t*-test before performing these regression analyses. This was because plant mortality has been shown to differentially affect seedlings in cushions and open areas (Cavieres et al., 2006, 2007; Badano et al., 2007), and these differences may also influence the relationships between plant biomass and species richness. All statistical analyses described above were conducted using the software R v. 2.3 (R Development Core Team, 2005).

Results

Environmental modifications performed by cushions

The relative water content of the soil was higher beneath *A. madreporica* cushions than in open areas ($27.60\% \pm 1.37$ vs. $14.55\% \pm 0.9113$; $t_{(1,19)} = 15.95$, $p < 0.01$). Cushions also modified extreme substrate temperatures as compared to open areas. The lower substrate temperatures in both habitat types were recorded between 4:00 and 8:00 h and, while open areas reached freezing temperatures during this extreme cold period, *A. madreporica* cushions always maintained temperatures above 0 °C. Open areas showed a peak of maximum temperatures between 11:00 and 15:00 h, with substrate temperatures up to 35 °C, but temperatures within cushion were 6–24 °C lower than in open areas during this period (data not shown).

Observational relationships between plant biomass and species richness

A total of 41 species were detected in the study site. Fourteen of these species were detected exclusively within cushion patches, 13 species were exclusively detected in open areas and 14 species were detected in both habitat types (Table 2). Species richness in the 0.2 m^2 samples taken within cushions varied between 2 and 11 species, and the average aboveground plant biomass varied between 21.13 and 84.45 g m^{-2} across these richness levels. In the surrounding open areas, the number of species in samples varied between 1 and 5 species, and the average aboveground plant biomass varied between 9.33 and 18.06 g m^{-2}. In average, species detected within cushions showed higher biomass values than species from open areas (Table 2). Four of the species shared between cushions and open areas (*Antennaria chilensis*, *Cerastium arvense*, *Erigeron andicola* and *Taraxacum officinale*) showed biomass values significantly higher within cushions, but any of the

Table 2. Plant species (family name is given in brackets) detected in the 0.2 m^2 samples taken to assess observational plant biomass–species richness relationships.

Species	Cushions	Open areas	*p*-value
Acaena patagonica (Rosaceae)	1.95±0.78	0	NA
Adesmia sp. (Fabaceae)	0.05±0.09	1.11±1.01	0.063
Antennaria chilensis (Asteraceae)	0.75±0.27	0.25±0.16	0.022*
Barneoudia major (Ranunculaceae)	0.05±0.08	0.20±0.29	0.432
Bromus setifoluis (Poaceae)	0.10±0.17	0	NA
Caiophora coronata (Loasaceae)	0	1.00±0.39	NA
Calandrinia affinis (Portulacaceae)	0.15±0.23	0	NA
Calandrinia caespitosa (Portulacaceae)	0.10±0.18	0	NA
Calandrinia sp. (Portulacaceae)	0	0.05±0.02	NA
Carex sp. 1 (Cyperaceae)	0.45±0.48	0.75±0.57	0.568
Carex sp. 2 (Cyperaceae)	0	0.95±0.36	NA
Carex sp. 3 (Cyperaceae)	0.85±0.74	0	NA
Cerastium arvense(Caryophyllacea)	8.45±3.52	0.15±0.13	<0.001*
Chaetanthera euphrasioides (Asteraceae)	0	0.05±0.07	NA
Erigeron andicola (Asteraceae)	1.40±0.63	0.10±0.09	<0.001*
Festuca magellanica (Poaceae)	1.10±0.60	0	NA
Hordeum comosum (Poaceae)	1.95±0.22	1.50±0.79	0.375
Hypochaeris tenuifolia (Asteraceae)	0.20±0.12	0	NA
Loasa sigmoidea (Loasaceae)	0.45±0.35	0.55±0.28	0.751
Montiopsis andicola (Portulacaceae)	2.85±0.91	0	NA
Montiopsis potentilloides (Portulacaceae)	0.20±0.17	0.82±0.63	0.138
Nassauvia lagascae (Asteraceae)	0	0.10±0.14	NA
Nassauvia pyramidalis (Asteraceae)	0	0.99±0.42	NA
Nastanthus agglomeratus (Calyceraceae)	15.75±1.94	0	NA
Olsynium scirpoideum (Iridaceae)	0.06±0.03	0.05±0.07	0.846
Oxalis compacta (Oxalidaceae)	0	0.25±0.22	NA
Perezia carthamoides (Asteraceae)	0	1.35±0.64	NA
Perezia pilifera (Asteraceae)	0.45±0.51	0	NA
Phacelia secunda (Hydrophyllaceae)	0	0.45±0.36	NA
Plantago barbata (Plantaginaceae)	2.75±0.56	0	NA
Poa alopecurus (Poaceae)	0	0.10±0.14	NA
Pozoa coriacea (Apiaceae)	0	0.40±0.17	NA
Rytidosperma pictum (Poaceae)	0.51±0.11	0.21±0.16	0.031
Rytidosperma violaceum (Poaceae)	0.33±0.18	0.19±0.17	0.423
Senecio looseri (Asteraceae)	0.75±0.49	0	NA
Taraxacum officinale (Asteraceae)	5.02±1.53	2.40±0.96	0.038*
Thlaspi magellanicum (Brassicaceae)	2.45±0.86	0	NA
Trisetum preslei (Poaceae)	3.05±1.07	0	NA
Tropaeolum polyphyllum (Tropaeolaceae)	0	0.25±0.10	NA
Viola atropurpurea (Violaceae)	0	0.80±0.31	NA
Viola philippii (Violaceae)	0.05±0.09	0.09±0.11	0.620
Average biomass across species	1.86±1.02	0.56±0.21	

Values are the average aboveground biomass ($g\,m^{-2}$±2 s.e.) of each species across samples taken within *A. madreporica* cushions or in the surrounding open areas; zero values indicate that the species was not detected in that habitat type. The *p*-value of *t*-test conducted to compare the abundance of species shared between habitat types is indicated in the last column (critical $\alpha = 0.05$; * = significant differences; NA = comparison not allowed). Authorities of species can be found in Marticorena and Quezada (1985).

species shared between these habitat types displayed significantly higher values of biomass in open areas (Table 2).

Aboveground plant biomass increased with species richness both within and outside cushions (Fig. 2). Multiple regression analyses indicated that the logarithmic model explained a higher proportion of the variance in biomass than the linear model (goodness of fit ANOVA: $F_{(4,11)} = 96.9$, $p<0.01$, $R^2 = 0.90$). While regression functions characterizing cushions and open areas did not differ in their intercepts ($t_{(1,11)} = 1.12$, $p = 0.29$), the magnitude with which biomass increases as new species were detected in samples was significantly higher within cushions ($t_{(1,11)} = 4.34$, $p<0.01$).

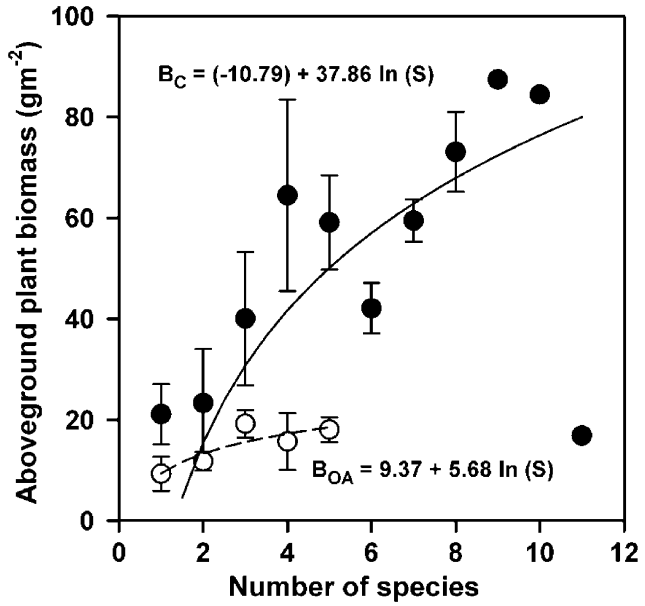


Fig. 2. Observational relationships between the average aboveground plant biomass of species assemblages ($g\,m^{-2} \pm 2$ s.e.) and species richness within *A. madreporica* cushions (solid symbols, solid line) and in open areas (empty symbols, dashed line). Regression functions estimated for each habitat type are shown in the figure (B_C = biomass within cushions; B_{OA} = biomass in open areas; S = species richness).

Experimental relationships between plant biomass and species richness

When experimental plots were recovered from field in March 2007, of the 120 plots originally planted in each habitat type, only 22 plots from *A. madreporica* cushions and 13 plots from open areas contained at least one species; all species at the remaining experimental plots died during the experiment. Although plant mortality affected the number of seedlings on both habitat types, the number of surviving seedlings was significantly higher ($t_{(1,33)} = 2.49$; $p > 0.01$) for plots within cushions than for plots on open areas (6.76 ± 1.66 vs. 3.77 ± 1.18; values are averages ± 2 SE). Plant mortality affected the number of species within the recovered plots, leading to different species richness treatments than those originally performed in the laboratory. For instance, no plot with 8 species was recovered in the field, but some of these plots persisted until the end of the experiment with fewer species numbers. Thus, the species richness of plots that were included in the analyses was not the original seed species richness. The actual species richness in plots recovered from cushions varied between 1 and 6 species, and varied between 1 and 4 species in plots recovered from open areas.

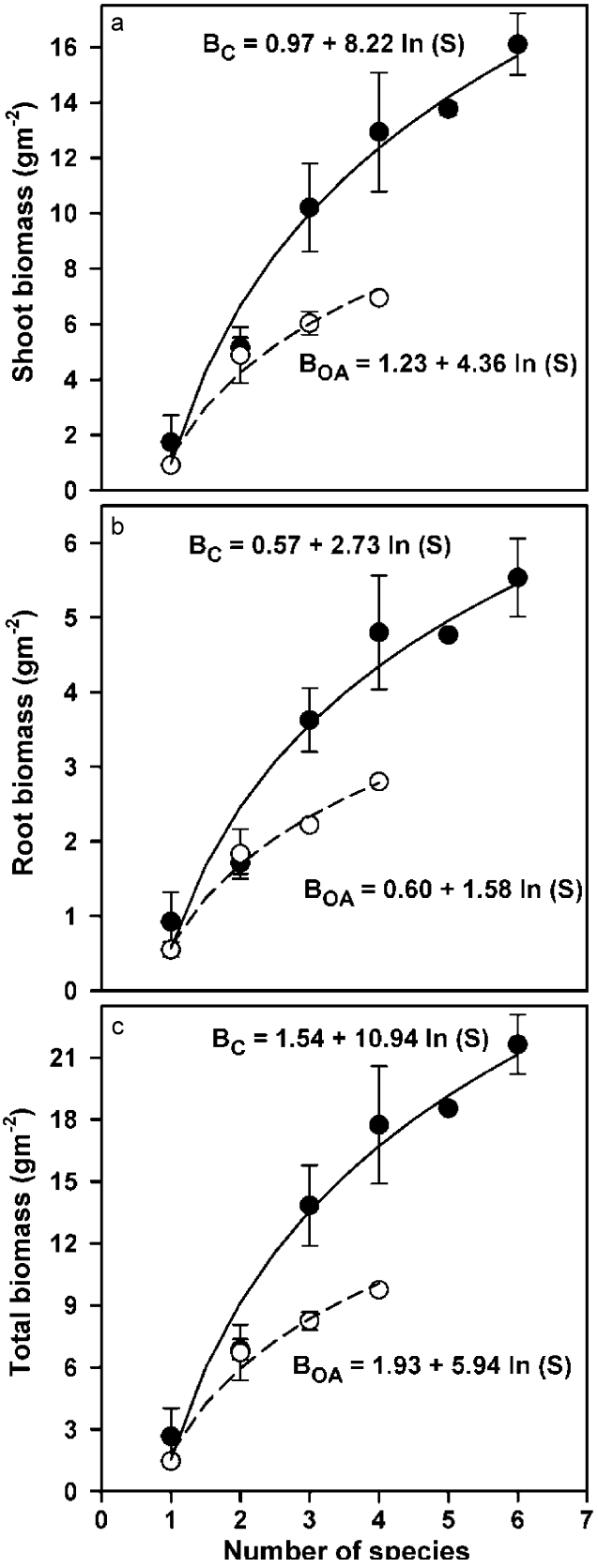
Shoot, root and the total plant biomass of seedlings within experimental plots increased with species richness both within cushions and in open areas (Fig. 3). In all cases the logarithmic model explained a higher proportion of the variance in biomass than the linear model (goodness of fit $ANOVA_{shoot\ biomass}$: $F_{(4,6)} = 304.39$, $p < 0.01$, $R^2 = 0.90$; goodness of fit $ANOVA_{root\ biomass}$: $F_{(4,6)} = 167.78$, $p < 0.01$, $R^2 = 0.96$; goodness of fit $ANOVA_{total\ biomass}$: $F_{(4,6)} = 263.06$, $p < 0.01$, $R^2 = 0.98$). Estimated regression functions for cushions and open areas did not differ in their intercepts ($p > 0.05$ in all cases), but the magnitude with which biomass values increased with species richness was significantly higher within cushions than in open areas ($p < 0.05$ in all cases).

Discussion

Our results indicate that *A. madreporica* cushions modify both soil moisture and temperature conditions compared to open areas, generating more benign microhabitats for other plant species. This process of biogenic habitat creation might cause the higher number of surviving seedlings detected at the experimental plots located within cushions and, consequently, it could be responsible for the higher species richness of plots located in this habitat type. Moreover, these positive effects of cushions could be linked with the observed differences in plant biomass–species richness relationships when cushions and open areas were compared. Both the observational and experimental results obtained in this study indicate that plant biomass accumulates faster within cushions than in open areas as the number of species increases. Thus, our study suggests that the biogenic habitat creation mediated by *A. madreporica* has positive impacts on ecosystem functions through its effects on plant species diversity.

Several manipulative experiments have shown positive relationships between ecosystem functions and species diversity (Tilman and Downing, 1994; Naeem et al., 1995; Hector et al., 1999; Cardinale et al., 2002). However, most of these experiments have been conducted in homogenous landscapes, maximizing the environmental control across experimental units in order to compare these relationships among ecosystems (see Hector et al., 1999). In this study, the manipulative experiment was designed to compare ecosystem functioning–species diversity relationships between two habitat types within the same landscape, cushion-modified patches and unmodified open areas, and the experimental results indicated differences in these relationships between habitat types. Indeed, the relationships assessed with observational data show a similar pattern. Thus, the environmental heterogeneity within a landscape may induce local differences in the relationships between ecosystem functions and species diversity, and we

suggest that future studies should address this issue instead of looking for homogeneous micro-environments for performing the experiments.



The amelioration of extreme environmental conditions may be responsible, in part, for the stronger increase in plant biomass with increasing species richness within cushion patches. This hypothesis is reinforced by a series of recent studies that have shown that such a mitigation of physical stress by cushion plants enhances the survival, abundances and photosynthetic performances of several other high-Andean species when compared to conspecific individuals growing in surrounding open areas (Cavieres et al., 2005, 2006, 2007; Badano et al., 2006, 2007; Badano and Marquet, 2008). Our experimental and observational results concur with those of other studies focused in evaluating changes in ecosystem functioning–species diversity relationships under different physical stress conditions. For instance, Rixen et al. (2008) showed that increased physical stress due to human activities in subalpine grassland communities may potentially decrease species richness and, consequently, the outcome of ecosystem functions. On the other hand, Rixen and Mulder (2005) used simulated communities of tundra mosses to assess the effects of physical stress on ecosystem functions; they reported that community biomass increased with moss richness under low physical stress conditions, but not under harsh physical situations. In spite of this recent interest in assessing the effects of changing environmental conditions on ecosystem functioning–species diversity relationships, few studies have addressed this issue in view of the process of biogenic habitat creation (see Levine, 2000). Taking into the growing number of studies indicating positive effects of some species (called *nurses*, *facilitators* or *ecosystem engineers*) on community diversity, and considering that the magnitude of these effects varies with environmental harshness (see Callaway et al., 2002), more studies are required in order to determine the importance and ubiquity of this process in the nature.

The observed differences in plant biomass–species richness relationships between cushions and open areas could also be related to the identity of species inhabiting each habitat type. In particular, the degree of specialization of some species to the cushion habitat could be a potential factor driving the observed trends. For instance, 14 species found within *A. madreporica* patches were not detected in the open areas, and the average

Fig. 3. Experimental effects of species richness on average ($g\,m^{-2} \pm$ s.e.) shoot biomass (a), root biomass (b) and total plant biomass (c) of species assemblages within *A. madreporica* cushions (solid symbols, solid lines) and in open areas (empty symbols, dashed lines). Regression functions estimated for each habitat type are showed in the respective figure (B_C = biomass within cushions; B_{OA} = biomass in open areas; S = species richness).

aboveground biomass of 5 of these species was greater than the biomass of any species able to grow in open areas. On the other hand, most of the species shared between habitat types showed higher biomasses within cushions than in open areas. Then, for a given level of species richness, differences in species composition and/or differences in the performance of the shared species might also lead to the observed differences in the plant biomass–species richness relationships between cushions and in open areas.

Plant biomass increased with species richness both within and outside *A. madreporica* cushions following a logarithmic model. However, plant assemblages within cushions reached higher richness levels and greater biomass values than open areas. These results could be a consequence of a higher efficiency and/or complementarity in the use of resources, or an increased importance of positive interactions as the number of species increases (Hooper, 1998; Naeem, 1998; Dukes, 2001; Mulder et al., 2001; Cardinale et al., 2002). Although our results do not allow us to test for the relative importance of these hypotheses in explaining the observed relationships, the higher numbers of coexisting species detected within cushions, with their associated greater biomasses, may be linked to an increased availability and heterogeneity of resources as a consequence of the habitat modification by cushions. Indeed, all the mechanisms proposed above are likely to be acting together. However, more complex experiments would be required to discern what mechanisms are more important.

Irrespective of the mechanisms involved, our results clearly indicate that the biogenic habitat creation mediated by *A. madreporica* affects the relationships between ecosystem functions and species diversity. In this particular case, such effects seem to be positive. Ecosystem functions performed by species assemblages directly or indirectly provide a range of benefits to humans, or ecosystem services (Costanza et al., 1997). Thus, we suggest that by including the effects of biogenic habitat creation processes in predictive models of biotic global change we would increase our understanding of the future behavior of ecosystems in a world dominated by ecosystem degradation.

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