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Ecosystem engineering affects ecosystem functioning in high-Andean landscapes

Ernesto I. Badano · Pablo A. Marquet

Abstract Ecosystem engineers are organisms that change the distribution of materials and energy in the abiotic environment, usually creating and maintaining new habitat patches in the landscape. Such changes in habitat conditions have been widely documented to affect the distributions and performances of other species but up to now no studies have addressed how such effects can impact the biotically driven physicochemical processes associated with these landscapes, or ecosystem functions. Based on the widely accepted positive relationship between species diversity and ecosystem functions, we propose that the effects of ecosystem engineers on other species could have an impact on ecosystem functions via two mutually inclusive mechanisms: (1) by adding new species into landscapes, hence increasing species diversity; and (2) by improving the performances of species already present in the landscape. To test these hypotheses, we focused on the effects of a high-Andean ecosystem engineer, the cushion plant *Azorella monantha*, by comparing the accumulation of plant biomass and nitrogen fixed in plant tissues as species richness increases in landscapes with and without the engineer species. Our results show that both ecosystem functions increased with species richness in both landscape types, but landscapes including *A. monantha* cushions reached higher outcomes of plant biomass and nitrogen fixed in plant tissues than landscapes without cushions. Moreover, our results indicate that such positive effects on ecosystem functions could be mediated by the two mechanisms proposed above. Then, given the conspicuousness of ecosystem engineering in nature and its strong influence on species diversity, and given the well-known relationship between species diversity and ecosystem function, we suggest that the application of the conceptual framework proposed herein to other ecosystems would help to advance our understanding of the forces driving ecosystem functioning.

Keywords Alpine ecology · Cushion plants · Ecosystem engineers · Plant communities · Plant ecology

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E. I. Badano · P. A. Marquet
Departamento de Ecología, Facultad de Ciencias Biológicas,
Center for Advanced Studies in Ecology and Biodiversity
(CASEB), Pontificia Universidad Católica de Chile,
Casilla 114-D, Santiago, Chile

E. I. Badano · P. A. Marquet
Institute of Ecology and Biodiversity (IEB),
Casilla 653, Santiago, Chile

P. A. Marquet
National Center for Ecological Analysis and Synthesis (NCEAS),
735 State Street, Suite 300, Santa Barbara, CA 93101-5504, USA

E. I. Badano (✉)
Departamento de Ciencias Químico Biológicas,
Escuela de Ingeniería y Ciencias, Universidad de las Américas
Puebla, Santa Catarina Martir, Cholula 72820, Puebla, Mexico
e-mail: ernesto.badano@udlap.mx

Introduction

Ecosystem engineering is the process by which some organisms, or ecosystem engineers, change the distribution of materials and energy in a landscape by means of non-trophic interactions with their abiotic environment (Jones et al. 1994, 1997). This process usually leads to the creation and maintenance of new habitat patches in the landscape,

with quite different physicochemical conditions compared to the surrounding unmodified habitat matrix (Lill and Marquis 2004; Badano et al. 2006; Gutierrez and Jones 2006; Moore 2006).

Such a change in habitat conditions may directly affect the distributions of other species (Jones et al. 1997). For instance, Wright et al. (2002) and Badano and Cavieres (2006a) have shown that the presence of engineered patches in natural landscapes provides habitats for species that cannot survive in the surrounding unmodified habitat matrix, hence enhancing the landscape species diversity by adding new species into the community. On the other hand, several studies have indicated that the performances and abundances of those species able to inhabit both engineered and unmodified patches may strongly differ between these habitat types (Flecker 1996; Crooks and Khim 1999; Schooley et al. 2000; Fritz et al. 2004; Badano et al. 2007). For example, Badano et al. (2006) have shown that numerically subordinate plant species inhabiting the unmodified habitat can become dominant species within the engineered habitat. However, despite the large amount of evidence indicating that the presence of ecosystem engineers affects species diversity and the performances of other species in natural landscapes, few studies have addressed how such effects can impact the biotically driven physicochemical processes associated with biodiversity, or ecosystem functions (but see Neira et al. 2005, 2006).

Ecosystem-level consequences of engineer organisms could be of crucial importance for ecosystem ecology. Understanding the relationship between biodiversity and ecosystem functions has become a scientific imperative given the extent and intensity of human-induced changes in the biosphere (Millennium Ecosystem Assessment 2005). There is ample evidence indicating that higher species diversity leads to higher ecosystem functioning (Tilman et al. 1997; Chapin et al. 1997; Naeem et al. 1995; Loreau 1998; Hector et al. 1999; Fonseca and Ganade 2001), and several mechanisms have been proposed to explain these relationships.

Positive relationships between the outcome of ecosystem processes and species diversity may occur because of increased complementarity in the use of resources (Loreau 1998; Loreau and Hector 2001) or increased intensity of positive interspecific interactions (Mulder et al. 2001; Cardinale et al. 2002) as species diversity increases. Alternatively, some of these relationships have been explained through "sampling effects," where higher outcomes of ecosystem processes with increasing species diversity are merely due to an increased likelihood of including species with a specific property, highly relevant to the processes under study, as species diversity rises (Huston 1997; Aarssen et al. 2003; Petchey 2004).

The shapes of these relationships, and the mechanisms behind them, are still a matter for discussion (see Giller and

O'Donovan 2002). However, the widely accepted positive relationship between ecosystem functions and species diversity leads us to hypothesize that the effects of ecosystem engineers on other species could positively impact ecosystem functions via two mutually inclusive mechanisms. Firstly, ecosystem engineers may add new species to landscapes, enhancing local species diversity and, consequently, leading to higher outcomes of ecosystem processes by increasing complementarity in the use of resources or increasing the likelihood of positive interactions among species. Alternatively, engineers may improve the performances of species that are able to inhabit more than one habitat type, increasing their contributions to local ecosystem processes. Both mechanisms can lead to higher outcomes of ecosystem processes at the landscape scale than those expected in the absence of engineers.

To test these hypotheses, we focused on the effects of a high-Andean ecosystem engineer, the cushion plant *Azorella monantha* Clos. (Apiaceae). This cushion species usually grows in cold high-mountain environments, immersed in a matrix habitat of open areas dominated by rocks and bare soil (Fig. 1). In the high Andes of Chile, the engineer-
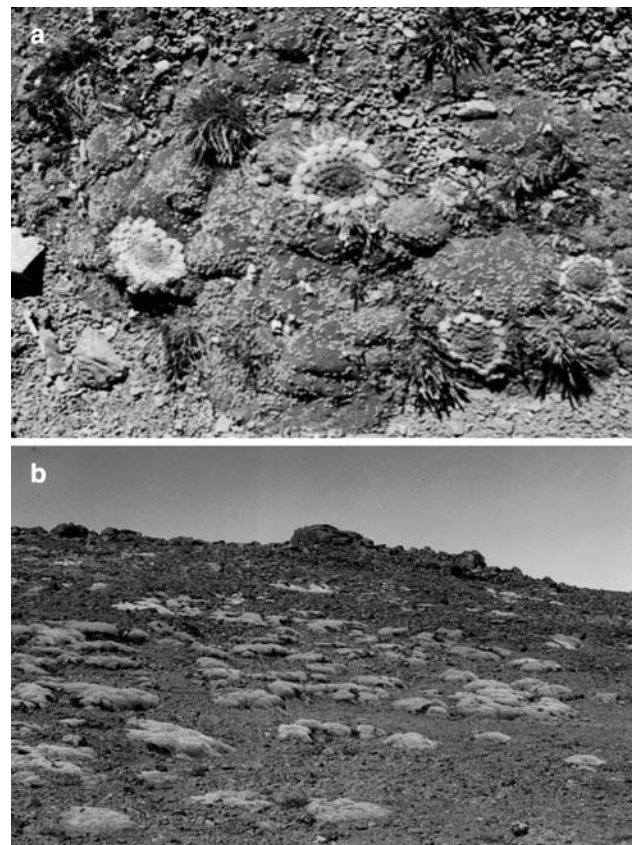
Fig. 1a–b An *Azorella monantha* cushion with forbs and grasses growing on it (**a**) and the landscape of the study sites (**b**), showing *A. monantha* surrounded by a habitat matrix of open areas composed of rocks, bare soil and other plants species (photos by E. I. Badano)

ing effects of *A. monantha* on the abiotic environment have been well established and include: (1) modulation of substrate temperatures, where cushions maintain lower maximum temperatures and higher minimum temperatures than open areas, reducing daily thermal fluctuations (Arroyo et al. 2003; Badano et al. 2006; Molina-Montenegro et al. 2006; Cavieres et al. 2007); (2) improvement of water availability, where the soil beneath *A. monantha* cushions retains up to 33% more water than open areas (Badano et al. 2006; Molina-Montenegro et al. 2006; Cavieres et al. 2007); (3) increased stability of substrate, making cushions more stable habitats, less susceptible to wind or snowmelt runoff disturbances than open areas (Cavieres et al. 2005; Badano et al. 2006); and (4) higher concentrations of available mineral nitrogen beneath cushions (Badano et al. 2006). Furthermore, a series of studies have shown that the presence of cushion plants in high-Andean landscapes positively affects species diversity of plant communities, allowing the persistence of species that cannot survive in the surrounding unmodified habitat matrix (Núñez et al. 1999; Cavieres et al. 2002; Arroyo et al. 2003; Badano and Cavieres 2006a, 2006b). Additionally, other studies comparing survivals, abundances and photosynthetic efficiencies of conspecific plants growing within and outside cushions have documented that cushion plants improve the performances of several species that also inhabit the surrounding open areas (Badano et al. 2002, 2006, 2007; Molina-Montenegro et al. 2005; Cavieres et al. 2005, 2006, 2007).

In this study, we assessed the effects of *A. monantha* cushions on two ecosystem processes: plant biomass and the amount of nitrogen fixed in plant tissues. These two response variables are indicative of the amount of energy and materials that are transferred from the abiotic environment to plant species assemblages inhabiting landscapes with and without cushions (hereafter engineered and unmodified landscapes, respectively). Specifically, we determined whether plant biomass and nitrogen fixed in plant tissues increase with species richness in both engineered and unmodified landscapes, and compared these relationships in order to assess the effects of *A. monantha* cushions. Further, after assessing these effects, we evaluated whether differences between landscape types occur because of the addition of new species to landscapes by *A. monantha* cushions (species diversity effects), through changes in the performances of species that are able to inhabit both cushions and open areas (performance effects), or both.

Materials and methods

The effects of *A. monantha* on ecosystem processes were assessed in two mountaintop landscapes in the high Andes of central Chile, Mt. Franciscano (33°19′S 70°15′W, 3,580 m.a.s.l.) and Mt. Tres Puntas (33°19S 70°14W, 3,630 m.a.s.l.). These mountaintop landscapes were considered as independent replicates to assess the consistency of the effects of *A. monantha* on ecosystem processes. Both mountaintops are located 50 km to the east of Santiago and are similar in species composition and environmental conditions (Badano et al. 2006). Estimated mean summer temperature at 3,600 m is ca. 4°C (Cavieres and Arroyo 1999), but temperatures of below 0°C can be reached at night (Badano et al. 2006). Annual precipitation exceeds 900 mm (Santibáñez and Uribe 1990), and mainly occurs as snow during winter months. A detailed description of these study sites is given in Badano et al. (2006).

Ideally, according to Wright et al. (2002), to assess the effects of ecosystem engineers on a natural system one should compare the variables under study between equally sized, naturally occurring landscapes with and without engineers. However, naturally occurring landscapes differing only in terms of the presence of a focal engineer species do not exist. Further, experimental manipulations are not feasible given the temporal and spatial scales of the processes under study. Thus, the effects must be assessed by comparing the response variable in the natural landscape with the focal engineer species against that of the same landscape after the effect of the engineer species has been statistically removed, and controlling for area effects (see Badano et al. 2006 for a detailed discussion). To do this, we first controlled for area effects by determining the amount of *A. monantha* engineered habitat and surrounding matrix habitat at each mountaintop by measuring the cover of both habitat types in January 2006 (mid-growing season in the southern Andes). Cover was measured along ten parallel line transects (each 50 m long with 10-m sample intervals). The average cover of cushions was 10% on both mountaintops, concurring with the cover values reported by Badano et al. (2006) for these sites. This means that, on average, one of ten random samples taken in each landscape should correspond to the cushion habitat. Then, to assess the effects of the cushion on ecosystem functions, our sampling was designed so as to reflect these differences in habitat availability between engineered and unmodified habitats. At each mountaintop, 40 cushions (50–70 cm in diameter) were selected by using points in random directions and at random distances from the center of a previously delimited 1-ha plot. If these random points did not coincide with a cushion, we considered the closest cushion to each point. Samples in open areas were distributed by using the same protocol used for cushions, but we selected ten points in open areas per selected cushion (i.e., a total of 400 samples in open areas).

On each selected cushion and at each point in open areas, a 0.2-m^2 circular plot was randomly dropped, and all

species within these plots were identified. Aerial parts of species within plots were collected and stored in individual paper bags (one bag per species per sample). Bags with collected material were 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. After weighing, the percentage nitrogen in plant tissue was determined for each species in each sample (Laboratory of Soil Analyses, Faculty of Agronomy, Universidad de Concepción, Chile), and the total amount of nitrogen per species was estimated by multiplying the percentage nitrogen by the biomass of the respective species in the respective sample. We only collected the aboveground parts of plants because complete belowground structures are difficult to obtain in this study system. Indeed, since *A. monantha* cushions are compact structures, literally attached to the soil (see Fig. 1), obtaining roots of plants growing within them would imply their complete destruction, an unacceptable action since they are subject to long-term monitoring.

To compare ecosystem functions between landscapes with and without engineers, we first defined the size (area) of the target landscape. At each mountaintop, the unmodified landscape without cushions was defined by the 400 samples of 0.2 m^2 taken in open areas, which represent 80 m^2 of unmodified landscape. For this landscape, we generated a species × samples matrix where each cell (*i*, *j*) contained the biomass or the total nitrogen of the *i* species in the *j* sample. Given that equally sized landscapes with engineers must include 10% cushion patches, we generated engineered landscapes for each mountaintop by randomly replacing 40 samples in the species × samples matrix constructed for the unmodified landscape by the 40 samples taken within cushions. Thus, engineered landscapes also had an area of 80 m^2, but included 10% cushion samples. To avoid biases due to differences in the samples that were replaced, we generated 20 engineered landscapes for each mountaintop and generated a species × samples matrix for each of these landscapes (see Badano et al. 2006).

To assess how ecosystem functions varied as the number of species in the landscape increased, we estimated the total biomass and total nitrogen fixed in plant tissues that an engineered or unmodified landscape would be expected to have for different species richness levels (from 1 to *S* species, where *S* is the maximum number of species in the landscape). To do this, we calculated the marginal vectors of total biomass and total nitrogen per species for each species × samples matrix. The expected plant biomass (or nitrogen) in a landscape with one species is estimated by randomly drawing 500 times the biomass (or nitrogen) of one species from the marginal vector and then averaging

these 500 biomass (or nitrogen) values. To estimate the plant biomass or nitrogen fixed in plant tissues in landscapes with two species, three species, ..., *S* species, we just increased the number of randomly selected species at each resampling event. Then, the expected plant biomass or nitrogen in a landscape composed of *S* species corresponds to the average of 500 draws of size *S*. At each resampling event, the probability of a species being included in the resample was proportional to its relative incidence in the respective species × samples matrix, so that the more common species were more likely to be included in samples than less common species. This analysis was performed using the module "Sampling with Probability Proportional to Size" included in the software PopTools v. 2.5.7 (Hood 2006).

To assess how ecosystem functions vary with species richness in the unmodified landscape of each mountaintop (i.e., landscapes only composed of matrix habitat), plant biomass and nitrogen values estimated for each richness level were plotted against their respective number of species. To assess these relationships in engineered landscapes, values of plant biomass and nitrogen estimated for each richness level were averaged across the 20 engineered landscapes generated for each mountaintop. These averages were then plotted against their respective number of species. To compare unmodified vs. engineered landscapes, we calculated the 95% confidence intervals for each of these averages. Hence, for a given richness level, landscape types were assumed to differ if confidence intervals obtained for engineered landscapes did not contain the values of plant biomass or nitrogen estimated for the unmodified ones.

Our next step was to assess whether the effects of *A. monantha* on ecosystem functions were mediated by the addition of new species into landscapes or by changing the performances of species found both in cushions and open areas. To do this, we compared the relationships between ecosystem functions and species richness obtained for the unmodified landscape of each mountaintop with two relationships drawn from engineered landscapes: (1) a relationship that included species from open areas plus species inhabiting cushions, but excluding from cushions those species that also grew in open areas; and (2) a relationship that included species from open areas plus species inhabiting cushions, but excluding from cushions those species that only grew within cushions. The first relationship accounted for the effects of the new species added by cushions (i.e., species diversity effects), and the second relationship accounted for the effects of cushions on species that can also inhabit open areas (i.e., species performance effects). For simplicity, throughout the rest of the text, those species that were only detected within cushions will be called "cushion habitat specialist species," and those species detected on both habitat types as "habitat general-

ist species," as suggested by Badano et al. (2006). To construct these relationships, we used the same methodology as described above. We generated 20 engineered landscapes for each situation and calculated the marginal vectors of plant biomass and nitrogen; for each of these landscapes, we randomly resampled the plant biomass or nitrogen at each richness level 500 times and averaged these values; these estimated values of biomass and nitrogen were averaged across the 20 landscapes, and 95% confidence intervals were calculated to assess differences with the unmodified landscape.

Results

Effects of cushions on ecosystem processes

A total of 34 species were detected on Mt. Franciscano; 10 were restricted to the *A. monantha* cushion, 10 were restricted to surrounding open areas, and 14 species were detected in both habitat types (see Appendix S1 in the "Electronic supplementary material"). On Mt. Tres Puntas we detected 24 species, with 10 being detected only within cushions, 8 only in open areas, and the remaining 6 were

shared between habitat types (see Appendix S1 in the "Electronic supplementary material"). These results indicate that the habitat engineered by *A. monantha* cushions affects the distribution of species in both mountaintops studied, adding new species to landscapes.

On both mountaintops, plant biomass and nitrogen showed different trends when engineered and unmodified landscapes were compared. On Mt. Franciscano, landscape types differed in plant biomass after 14 species were added to landscapes (Fig. 2a), while differences in nitrogen were observed after 12 species were added (Fig. 2b). On Mt. Tres Puntas, the engineered and the unmodified landscape substantially differed in terms of biomass (Fig. 2c) and nitrogen (Fig. 2d) after two species were added to the landscapes. In all cases, the rates of biomass and nitrogen accumulation with increasing species richness were higher in engineered than in unmodified landscapes (see Fig. 2).

Species diversity effects of cushions

On both mountaintops, engineered landscapes that included cushion habitat specialist species reached higher values of plant biomass and nitrogen than unmodified landscapes (Fig. 3). On Mt. Franciscano, significant

Fig. 2a–d Estimated values of accumulated biomass (*left*) and nitrogen content in plant tissues (*right*) as species richness increased in simulated landscapes with and without *Azorella monantha* cushions on Mt. Franciscano (**a**, **b**) and Mt. Tres Puntas (**c**, **d**). *Solid symbols* are values of biomass and nitrogen (±95% confidence intervals) estimated by pooling species detected in both open areas and *A. monantha* cushions (i.e., engineered landscapes), and *empty symbols* are values of biomass and nitrogen estimated by only including species growing in open areas (i.e., unmodified landscapes).
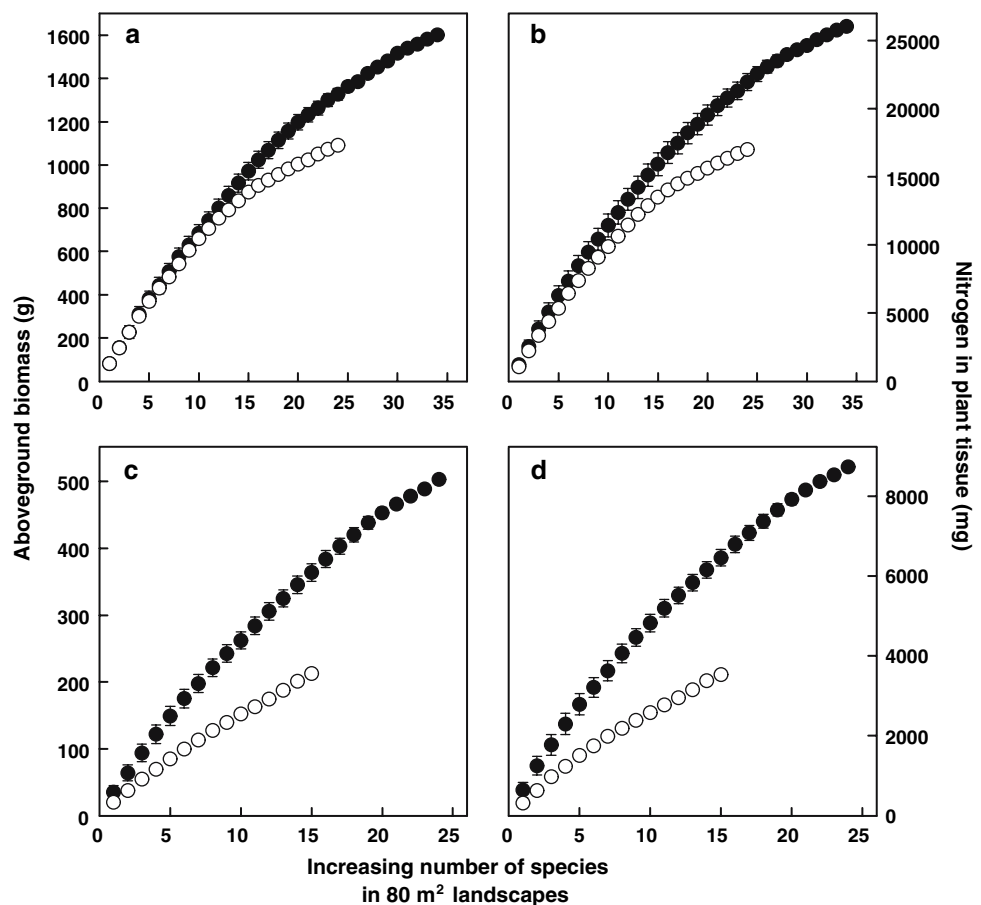
Fig. 3a–d Species diversity effects of cushions on Mt. Franciscano (**a**, **b**) and Mt. Tres Puntas (**c**, **d**). Figures show the estimated values of accumulated biomass (*left*) and nitrogen content in plant tissues (*right*) as species richness increases. *Solid symbols* are the values of biomass and nitrogen (±95% confidence intervals) estimated by pooling species from open areas plus those species that were only detected within *Azorella monantha* cushions (i.e., engineered landscapes that only include the effect of cushions on habitat specialist species), and *empty symbols* are values of biomass and nitrogen estimated by only including species growing in open areas (i.e., unmodified landscapes)
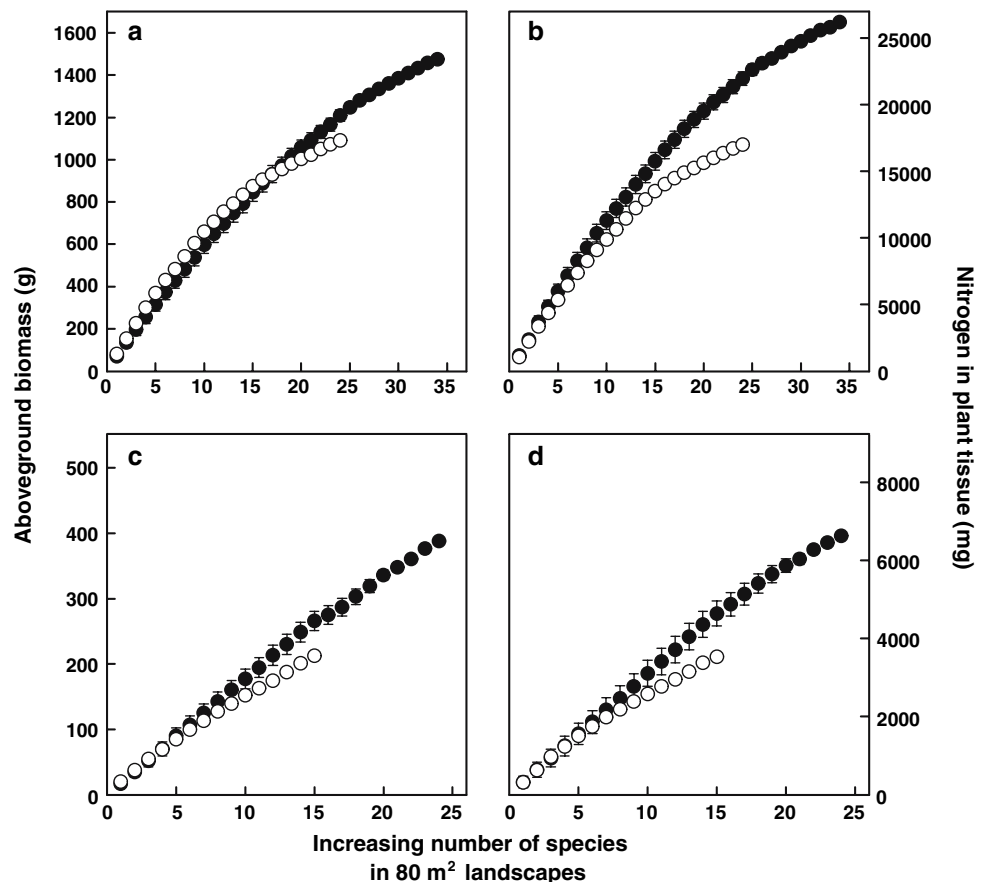
differences in biomass were detected after 23 species were added to the landscapes (Fig. 3a), and significant differences in nitrogen were indicated after adding 12 species (Fig. 3b). On Mt. Tres Puntas, biomass values differed between landscape types after 11 species were added (Fig. 3c), and nitrogen values differed after adding 10 species (Fig. 3d). In all cases, the rates of biomass and nitrogen accumulation with increasing species richness were higher in engineered landscapes than in unmodified ones.
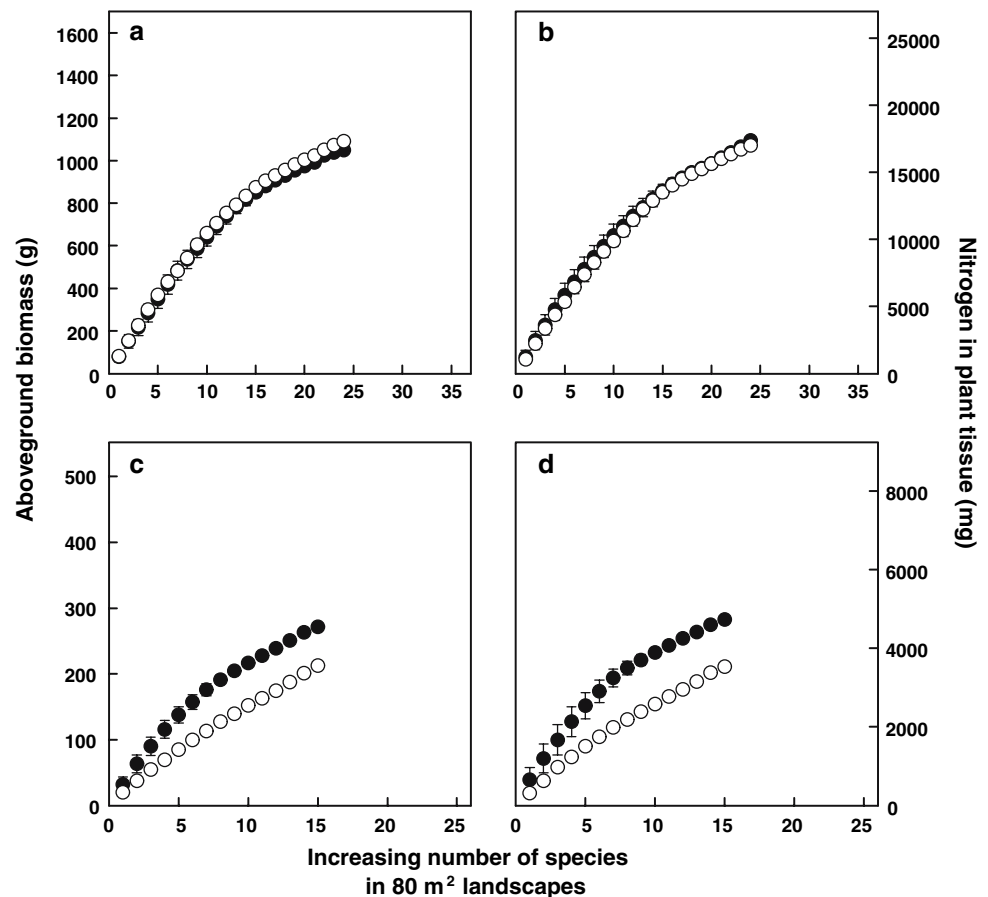
Species performance effects of cushions

Relationships between ecosystem functions and species richness estimated for engineered landscapes that only included habitat generalist species within cushions showed different patterns between mountaintops. On Mt. Franciscano, the engineered and the unmodified landscapes did not differ in terms of biomass or nitrogen as species richness increased (Fig. 4a, b). However, on Mt. Tres Puntas, the engineered landscape showed higher values of biomass and higher nitrogen than the unmodified landscape after two species were added (Fig. 4c, d). These results indicate that the effects of the engineer species are spatially variable with regards to habitat generalist species.

Discussion

Positive effects on species diversity and the performances of other species have been shown for a wide variety of engineer species, including mammals (Aho et al. 1998; Wright et al. 2002), freshwater fishes (Flecker 1996), marine macroinvertebrates (Thomas et al. 1998; Castilla et al. 2004; Borthagaray and Carranza 2007), tussock grasses (Perelman et al. 2003), and even high-Andean cushion plants (Badano and Cavieres 2006a, 2006b; Badano et al. 2006). However, no study had yet explored how the effects of ecosystem engineers could impact ecosystem functions performed by species inhabiting a natural landscape. Overall, our results indicated that the existence of just 10% of *A. monantha* cushion habitat positively impacts on ecosystem processes on mountaintop landscapes (see Fig. 2). Moreover, our results clearly establish that cushions may drive such positive effects either by adding new species to the landscapes (species diversity effects) or by affecting the performances of species able to inhabit both cushion-engineered and unmodified habitats (species performance effects).

Although both proposed mechanisms were found to affect plant biomass and nitrogen on Mt. Tres Puntas, only species diversity effects seem to affect ecosystem processes

Fig. 4a–b Species performance effects of cushions on Mt. Franciscano (**a**, **b**) and Mt. Tres Puntas (**c**, **d**). Figures show the estimated values of accumulated biomass (*left*) and nitrogen content in plant tissues (*right*) as species richness increases. *Solid symbols* are the values of biomass and nitrogen (±95% confidence intervals) estimated by pooling species from open areas plus habitat generalist species detected within *Azorella monantha* cushions (i.e., engineered landscapes that only include the effect of cushions on habitat generalist species), and *empty symbols* are values of biomass and nitrogen estimated by only including species growing in open areas (i.e., unmodified landscapes)

on Mt. Franciscano. This suggests that species diversity effects would be more consistent than species performance effects at explaining the positive impact of *A. monantha* on ecosystem processes across these high-Andean landscapes. Nevertheless, further experimental studies are required to determine whether these positive effects of cushions on ecosystem functions are mediated by increased complementarity in the use of resources, a higher intensity of positive interactions within cushion habitat patches, or simply because of sampling effects.

It is important to highlight that determining which one of the effects of ecosystem engineers (species diversity or performance effects) is more relevant in affecting ecosystem functions strongly relies on identifying which species are *specialists* for engineered and unmodified patches and which species are habitat *generalists* at each study site (see Badano et al. 2006 for a detailed discussion). In our study, four habitat generalist species from Mt. Franciscano switched to cushion habitat specialists on Mt. Tres Puntas (see Appendix S1 in the "Electronic supplementary material"), and such switches may be intensifying the diversity effects of cushions on Mt. Tres Puntas (see Fig. 3a, b). On the other hand, three species identified as open areas specialists on Mt. Tres Puntas switched to the habitat generalist category on Mt. Franciscano (see Appendix S1 in the

"Electronic supplementary material"), but such a switch did not enhance the species performance effects of cushions at the latter site (see Fig. 4a, b). Therefore, the local effects of ecosystem engineers on ecosystem functions may vary idiosyncratically across sites within a region, where the magnitude of these effects would depend on the impact of the ecosystems engineers on each species group at each particular location. Indeed, although our results showed that species diversity effects of *A. monantha* are important in both sites, increases in the spatial scale may dilute such an effect. This would occur because increases in the spatial scale would result in an increased probability of finding a given species in more than one habitat type; in other words, specialist species for the engineered habitat at some particular location would be more likely to be detected in the unmodified habitat as more locations are added. Therefore, species diversity effects of ecosystem engineers are more likely to occur at local spatial scales, while species performance effects would be more important in affecting ecosystem functions at regional scales.

But should we always expect relevant effects of ecosystem engineers on ecosystem functions despite the mechanisms involved (i.e., species diversity or performance effects)? To answer this question, we must consider that such effects of engineer species would probably prove to be

relevant when the habitats they create are sufficiently different from the unmodified habitat, so that it can have an effect on the performance of resident species, and such an effect is persistent enough to enable the new species to become part of the modified landscape (Jones et al. 1997). In the particular case of cushion plants, their ability to modulate extreme substrate and air temperatures (Cavieres et al. 1998; Arroyo et al. 2003; Badano et al. 2006) and improve soil water retention (Molina-Montenegro et al. 2005, 2006; Badano et al. 2006; Cavieres et al. 2007) have been indicated as putative causes of their positive effects on the performances of other plant species in the arid high Andes of Chile and Argentina (Núñez et al. 1999; Cavieres et al. 2002, 2006; Arroyo et al. 2003; Badano et al. 2006; Badano and Cavieres 2006b). On the other hand, cushion plants are structures that remain part of the engineered habitat and can persist over decades (Le Roux and McGeoch 2004; Mark and Wilson 2005) and even centuries (Ralph 1978; Kleier and Rundel 2004), so that their effects on other species, and hence on ecosystem processes, are likely to be sustained over time. Another factor that must be included in order to assess the importance of the effects of a given engineer species is the ratio of engineered to unmodified habitat (Wright et al. 2002; Badano et al. 2006). In our case, *A. monantha* cushions added just 10% of engineered habitat to landscapes, and we showed that this amount of engineered habitat is enough to produce a substantial effect on the ecosystem functions of interest. Hence, if the conditions mentioned above are met (relevance of environmental modifications and persistence in time), it is feasible to expect that increases in the amount of modified habitat provided by engineer species lead to higher rates of ecosystem functioning.

As a final remark, given the conspicuousness of ecosystem engineering in nature and its strong influence on the diversities and compositions of natural communities (Wright and Jones 2006), and given the well-known relationships between these community attributes and ecosystem functioning (Tilman et al. 1997; Chapin et al. 1997; Naeem et al. 1995; Loreau 1998; Hector et al. 1999; Fonseca and Ganade 2001), we claim that the conceptual framework proposed herein can be applied to other ecosystems. We suggest that such an approach would improve our understanding of the forces driving ecosystem functioning and contribute to the development of simple ways to assess the current state of ecosystem functions in a world dominated by human-induced species extinctions and ecosystem degradation.

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