Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant

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Comparative and integrative tools are of fundamental value in ecology for understanding outcomes of biological processes, and making generalizations and predictions. Although ecosystem engineering has been shown to play a fundamental role in community organization, there are no standardized methods to measure such effects. We present a framework and methodology for assessing the impact of physical ecosystem engineers on three general features of community organization: (1) species richness and composition, (2) stability of richness over time, and (3) dominance patterns of species assemblages. We then apply the framework and methodology to assess the effects of the cushion plant *Azorella monantha* on high-Andean plant communities on two mountaintops. Substrate temperatures, soil moisture and the availability of mineral nutrient resources were compared between *A. monantha* and surrounding open areas to ascertain whether cushions altered abiotic environmental conditions, while community analysis assessed changes in species richness, composition and abundances at patch and landscape levels. Cushions thermally buffered temperature extremes and increased soil moisture, but had no detectable effect on soil mineral nutrients. Cushion habitat was not more species rich than surrounding areas, but cushions added new species into the community, altering species composition and markedly enhancing landscape-level richness. Cushions also showed potential for stabilizing species richness over time, and changed patterns of species dominance. Findings were consistent across mountaintops. We evaluate the general utility of the framework and call for its application in other systems as a means to generate comparative data sets for assessing the general effects of ecosystem engineers on community organization.

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Physical ecosystem engineers are organisms that non-trophically change the distribution, amount or composition of energy and materials in the abiotic environment via their own physical structures (e.g. tree canopies and trunks) or artifacts they create (e.g. beaver dams) (Jones et al. 1994). In so doing, they create, modify, maintain or

destroy habitats for species and can affect community organization (Jones et al. 1997, Wright et al. 2002, Wright and Jones 2004). Although all organisms can change the physical environment to some degree, some species have larger ecological impacts than others (Jones et al. 1994, 1997, Reichman and Seablom 2002, Wilby 2002, Wright and Jones 2004). A current challenge is to predict when ecosystem engineers will have large or small impacts on communities while also explaining why impacts vary in magnitude (Jones et al. 1997, Wright and Jones 2006).

Interest in general predictive models that quantify the community impacts of ecosystem engineers is growing (Fukui 2001, Wright et al. 2002, Lill and Marquis 2003, Castilla et al. 2004, Fogel et al. 2004, Wright and Jones 2004, Badano and Cavieres 2006a, Crain and Bertness 2006). In particular, predicting the effects of ecosystem engineers on species richness at higher levels of organization – communities in landscapes comprised of both engineered and unmodified patches (Wright et al. 2002, Badano and Cavieres 2006b) – is one central goal of research on ecosystem engineering. By increasing landscape-level habitat diversity, engineers should increase species diversity if species that cannot persist in unmodified habitats can do so within engineered habitats (Jones et al. 1997). A number of recent studies quantitatively support this generalization (Wright et al. 2002, Lill and Marquis 2003, Castilla et al. 2004, Badano and Cavieres 2006b) although there were considerable differences in the way these effects were quantified. Further, although some species may be able to persist in both habitat types, altered environmental conditions within engineered patches might be expected to lead to changes in abundances of those species, as demonstrated by a large number of studies (Flecker 1996, Thomas et al. 1998, Ceballos et al. 1999, Crooks and Khim 1999, Schooley et al. 2000, Raspopov et al. 2002, McCabe and Gotelli 2003, Clarke et al. 2004, Fritz et al. 2004, Flecker and Taylor 2004), albeit using different approaches and metrics. Thus, the development of comparative and integrative tools is fundamental for understanding the outcomes of this type of biological processes, enabling the emergence of generalizations and predictions.

In order to develop general models and test them and to conduct quantitative comparative analyses, we need simple, readily measurable metrics integrating engineer effects across levels of organization (i.e. populations and communities) and spatial extent (i.e. habitat patches and landscapes). Indeed, robust tests of general models require metrics that can compare effects across disparate ecosystems and engineer species. Lastly, since ecosystem engineers can create or destroy habitats of other species, quantitative metrics of their community impacts could be useful tools in conservation biology, helping us assess which native species are important engineers or which exotic engineers are having the largest impacts.

Here we present an integrative framework for understanding and quantifying the effects of ecosystem engineers on three general features of community organization: (1) species richness and composition; (2) stability of species richness over time; and (3) species dominance patterns. We develop simple metrics that quantify these effects, and then apply the framework and metrics to assess the ecosystem engineering effects of the cushion plant *Azorella monantha* Clos. (Apiaceae) in two high-Andean plant communities from central Chile. We end by examining the caveats, assumptions and limitations of the approach and its general utility as a means of assessing and understanding impacts of ecosystem engineers on community organization.

Conceptual framework and quantification of engineering effects

A simple way to assess engineer impacts on community organization is to compare and integrate features of species assemblages in engineered and unmodified patches. Here, unmodified refers to patches where the abiotic environment is not altered by the particular engineering species of interest, but does not imply that such patches are not also engineered by other species. Although this approach cannot be applied to situations where engineered patches are not clearly distinguishable from unmodified patches, many ecosystem engineers do create discrete, distinctive patches (Wright et al. 2002: beaver; Cavieres et al. 2002: cushions plants; Lill and Marquis 2003: leaf-tying caterpillars; Machicote et al. 2004: burrowing mammals; Castilla et al. 2004: marine macroinvertebrates; Fritz et al. 2004: freshwater macrophytes; Wright et al. 2006: shrub mounds): this is a common situation in nature (see Jones et al. 1994, 1997, Crooks 2002 for a detailed list of examples).

Consider then an area comprised only of unmodified habitat of one type. If an ecosystem engineer now appears in this area and creates spatially discrete, distinctive patches, then, provided that the entire area is not modified (Wright et al. 2002), the resulting landscape will now consist of two patch types: engineered and unmodified. Further, if these habitat patches are suitable to other species, the resulting community is likely to be affected by the presence of the engineer. Thus, given sufficient time for species from the regional pool or the unmodified patches to occupy the new habitat type, we can ask: in what ways could the engineer have changed the distributions and abundances of species within the community in new this landscape? Given the means to measure such potential changes and assuming that sufficient time has passed to avoid transient dynamics due to colonization, an observer could make an assessment of engineer impact from a post-facto (i.e. post-engineer arrival) snapshot of this

landscape. While individual species within the community will very likely undergo changes in distribution and abundance due to stochastic variation and deterministic factors (e.g. climate, competition, predation, etc.), the average community-level pattern should nevertheless reflect impacts of the engineer.

Within this landscape, we can find three kinds of species present in the community: (1) species found only in engineered patches, i.e. engineered habitat specialists; (2) species found only in unmodified patches, i.e. unmodified habitat specialists; and (3) species found in both patch types, i.e. habitat generalists. The questions about potential engineer effects on community organization that we pose, and the different metrics we develop to assess such effects pertain to these habitat specialists and generalists.

Species richness

In such a landscape, we can ask about effects of ecosystem engineers on species richness at both the patch (habitat) level and the landscape level.

Patch-level

Do engineers make habitats that are more or less rich in species than unmodified habitats? Here we are assessing whether or not the control and modulation of abiotic environmental factors results in engineered patches having more, less or the same number of species compared to unmodified patches. Such a patch-level question has a long tradition in ecology (reviewed by Wright and Jones 2004); there are specific predictions about expected general patterns (Jones et al. 1997), and a recent model for predicting the direction and magnitude of such effects as a function of engineer-induced changes in primary productivity (Wright and Jones 2004). We will call this the relative habitat richness (RHR) effect of the engineer. The magnitude of this effect can be estimated as a ratio – the number of all species found in engineered patches divided by the number of all species found in unmodified patches (i.e. [engineered habitat specialists + generalists]/[unmodified habitat specialists + generalists]; Table 1). Thus, ecosystem engineers will have no RHR effect (RHR $\cong$ 1) if both habitat types have similar numbers of species, RHR >1 if engineered patches have more species, and RHR <1 if they have fewer.

Since this effect integrates across all types of species in the landscape, differences in RHR will collectively arise from: the addition of new specialist species into engineered habitat (via the regional pool or local speciation); the degree to which habitat-independent specialization by species differs between engineered and unmodified habitats (i.e. more, same or less specialist species; reflecting differences in the tendency for specialization in different abiotic environments); and the extent

to which species found in unmodified habitat are also found in the engineered habitat (i.e. engineered habitat may accumulate generalist species at higher or lower rates than unmodified habitat, causing RHR effects irrespective of the presence of habitat specialist species).

Landscape-level

If there is at least one species that occurs solely in engineered habitat, then the addition of engineered patches will cause the richness of both habitats combined – landscape-level species richness – to increase (Jones et al. 1997, Wright et al. 2002). However, to what degree do engineers increase species richness of the landscapes they occupy via addition of specialists? As noted above, there is growing interest in quantifying such an effect and understanding what determines its effect magnitude (Wright et al. 2002, 2006, Lill and Marquis 2003, Castilla et al. 2004, Badano and Cavieres 2006a). This landscape richness enhancement (LRE) effect, as we have called it (Wright et al. 2006), therefore reflects the degree to which the ecosystem engineer has introduced new species into the community. We can estimate the magnitude of this effect as a ratio of the number of engineered habitat specialists to the number of species that the landscape would be expected to have if the ecosystem engineer were not present (i.e. the number of species in unmodified patches; LRE = engineered habitat specialists/[unmodified habitat specialists + generalists]; Table 1). Thus LRE will be zero if there are no engineered habitat specialists, but will increase as more species become dependent upon the environmental changes caused by the ecosystem engineer. Such new species could come from the regional species pool or from local speciation of unmodified habitat specialists or generalists, but we cannot know the origin of these species from a post-facto snapshot.

Stability of species richness over time

Ecosystem engineers may affect the abundances of habitat generalists, potentially stabilizing temporal variation in species richness at both the patch and the landscape levels.

Patch-level

The species richness of generalists in an unmodified habitat patch may be stabilized if they are prone to local extinction (e.g. are rare) but can be reestablished from conspecific populations in nearby engineered patches. While such effects could occur in the converse direction (i.e. unmodified rescues engineered) and rescue could also occur from the regional pool, we will ignore these influences because our framework focuses on the possible effects of the engineer, not the unmodified habitat or

Table 1. Effects of *Azorella monantha* cushions on community organization. RHR: relative habitat richness; LRE: landscape richness enhancement; HRP: habitat rescue potential; LIP: landscape insurance potential; HSO: habitat species organization. Se and Su: species richness in engineered and unmodified patches, respectively; $Se_{(eng)}$: number of engineered habitat specialist species; Sg: number of habitat generalists in the landscape; $Sg_{(>eng)}$: number of habitat generalists at greater abundance in engineered habitat; SL: total number of species in the landscape; $k_{i(eng)}$: abundance category that the ith habitat generalist species occupies in the engineered habitat; $k_{i(unm)}$: Abundance category of the same species in the unmodified habitat. Table shows values obtained in Mt. Franciscano and Mt. Tres Puntas estimated from species lists and Chao 2. For statistical comparisons see Fig. 3 and 4 and Results.

Metric	Derivation	From species lists		From Chao 2	
		Franciscano	Tres Puntas	Franciscano	Tres Puntas
RHR	Se/Su	1.00	0.94	1.00	0.94
LRE	$Se_{(eng)}$/Su	0.40	0.25	0.21	0.22
HRP	$Sg_{(>eng)}$/Sg	0.42	0.54	0.31	0.52
LIP	Sg/SL	0.43	0.55	0.65	0.61
HSO	$\dfrac{\Sigma_{i=1}^{Sg}(\lvert k_{i(eng)} - k_{i(unm)}\rvert/Sg)}{Sg}$	0.47	0.38	0.28	0.35

the region. Hence, we will call this effect the habitat rescue potential (HRP) of ecosystem engineers on the unmodified habitat. Since rescue effects are more likely to occur as the difference in species abundances between habitat patches increases (Wells and Richmond 1995), the magnitude of this effect can be assessed as the proportion of habitat generalists with higher abundances within engineered patches relative to all generalists (i.e. generalists at greater abundance in engineered habitat/all generalists [at higher, equal or lower abundance] in both habitat types; Table 1). Thus, ecosystem engineers will have small HRP effects (HRP $\cong$ 0) if there are few habitat generalists with higher abundance within engineered patches, with the value tending towards unity when most generalist species are at greater abundance in engineered habitat. Although this simple metric allows some assessment of engineering effects on the stability of species richness, it is important to note that HRP estimates 'potential', not actual habitat rescue effects of ecosystem engineers. Furthermore, HRP ignores the increased risk of extinction of generalists at higher densities in engineered (or unmodified) habitat that could arise from increased density-dependent mortality.

Landscape-level

An analogous process to HRP could also occur at the landscape level. By definition, ecosystem engineers create a different abiotic environment from that of unmodified habitat (Jones et al. 1994, 1997). Thus, environmental conditions in these two habitat types could fluctuate somewhat differently when external abiotic forcing changes through time. Given that generalists can live in either habitat type, there is then the potential for such species to persist in one habitat (i.e. that with lower environmental fluctuation or stress) if they go extinct in the other. Thus, the habitat diversity

created by the engineer may function as insurance, again stabilizing species richness in the landscape by decreasing the risk of species loss under periodically unfavorable conditions. We will call this effect the landscape insurance potential (LIP), which can be simply expressed as the proportion of habitat generalists relative to all species in the landscape (i.e. generalists/[generalists + engineered habitat specialists + unmodified habitat specialists]; Table 1). Thus, ecosystem engineers will have the greatest LIP when the majority of species are habitat generalists. As with HRP, LIP does not assess actual landscape persistence, but only evaluates the 'potential' for such effects to occur.

Species dominance patterns

While some habitat generalists may have higher abundance within engineered patches, others may occur at the same or lower densities in engineered patches as in unmodified habitat (Flecker 1996, Crooks and Khim 1999). Such differences may arise because species show different individualistic responses to abiotic environmental change (Grime 1979, Tilman 1987), or because different abiotic environmental conditions alter the strength and nature (positive or negative) of species interactions (Bertness and Callaway 1994, Brooker and Callaghan 1998). Irrespective of which of these two general mechanisms underlies differences in generalist abundance between habitat types, the end result may be a different pattern of species dominance when the abundance distributions of generalist species are compared between engineered and unmodified patches (since, by definition, the occurrence and abundances of specialist species are the result of habitat-independent specialization, comparison of their abundances between habitat types is not meaningful in the context of our framework). We will call this the habitat species organization (HSO) effect of the engineer. It can be estimated from the differences in the relative rank abundances of

generalists in engineered vs unmodified habitat types. We can sort species inhabiting both habitat types based on their abundances and then calculate the distance between the abundance category (i.e. rank abundance) that each generalist species occupies in one habitat type vs the other ($|k_{i(eng)} - k_{i(unm)}|$ in Table 1). Absolute values of $|k_{i(eng)} - k_{i(unm)}|$ are of primary interest here, because they reflect changes in rank abundances irrespective of the direction of that change (positive or negative). Although interesting to know, without an a priori knowledge on the response of each species to the environmental changes exerted by the engineer we cannot predict the direction of such changes in abundance. Furthermore, because we are interested in comparing the HSO effect between different communities affected by the same or a different engineer, the absolute difference can then be relativized by the number of habitat generalists present in each community ($|k_{i(eng)} - k_{i(unm)}|/Sg$ in Table 1), to give values that are independent of the total number of habitat generalists found in different communities. The relative differences can also be averaged across all habitat generalists within each community (see HSO in Table 1) to arrive at a mean deviation of abundance distributions within engineered patches with respect to unmodified ones. Thus, HSO $\cong 0$ will be observed when ecosystem engineers do not change abundance distributions, with the value tending to unity as more generalist species have altered abundances within engineered patches.

Quantifying metrics
The simplest way to compute the above five metrics in a landscape where ecosystem engineers have created discrete, distinctive habitat patches is to determine the number and abundances of all species inhabiting engineered and unmodified patches, which can be summarized in a species list for each habitat type. However, classifying species as habitat specialists or generalists requires that the sampling effort be sufficient to fully capture species richness and composition of both patch types (i.e. the number of engineered and unmodified habitat specialists and habitat generalists in the landscape should have reached an asymptote with increasing patches sampled). Such an approach finds the rare species and reduces the risk of misclassification of a generalist as a specialist. A straightforward approach to this sampling-effort dependency is to generate species-area curves in which the number of species in engineered and unmodified habitats, as well as the entire landscape, are accumulated as the number of sampled patches increases (also called species accumulation curves; Gotelli and Colwell 2001). Using such curves, we can assess whether the sampling effort was sufficient to fully capture species richness and composition in the different habitat types (Colwell and Coddington 1994). There are two further important considerations in

applying this species–area approach. First, species–area curves may asymptote at a different number of patches sampled in engineered vs unmodified habitats, requiring the use of rarefaction techniques (Gotelli and Colwell 2001) to reduce bias from unequal sample sizes (Wright et al. 2002, Badano and Cavieres 2006b). Second, estimating landscape-level metrics requires that the relative proportion of engineered to unmodified habitat within the landscape be taken into account.

Another way to address sampling-effort dependency is to use extrapolative species richness estimators, which use the observed values of species richness in samples to estimate the value of community richness as if they had been fully sampled (Colwell and Coddington 1994). The species richness parameters required to calculate the proposed metrics can then be derived from these estimated values (Material and methods).

Finally, as an adjunct to all the above, differences in community organization between engineered and unmodified habitat can be summarily visualized using ordination techniques (Green et al. 1999, Wright et al. 2002, Lill and Marquis 2003, Perelman et al. 2003, Castilla et al. 2004), compared using similarity indices (Wright et al. 2002, Castilla et al. 2004), and described by summation from species lists. Ordinations are particularly useful because they allow us to assess whether the effects of ecosystem engineers on community organization are largely due to a few engineered patches containing rare species, or whether these effects occur because most of engineered patches across the landscape contain species that are either not present or at different abundances in unmodified habitat samples.

Material and methods

Study system

To apply and evaluate the proposed framework and metrics, we measured effects of the cushion plant *Azorella monantha* in mountaintop plant communities. The cushion growth form – recumbent plants with short internodes, closed canopies and a subsurface accumulation of tightly packed living non-photosynthetic and dead plant tissues that insulate the soil – is very common in alpine environments (Körner 2003). This growth habit occurs in about 338 species around the world, belonging to 78 genera and 34 plant families, and ca the half of these species grow in the South American Andes (Hauri and Schröter 1914). In the southern Andes, the most commonly reported cushion plants belong to the family Apiaceae, but there are also some species of Asteraceae, Rubiaceae, Caryophyllaceae, Rhamnaceae and Fabaceae showing this growth habit (Marticorena and Quezada 1985). Cushions create large, circular habitat patches, which can be more than 3 m in diameter and persist for decades (Benedict 1989, McCarthy 1992, Le Roux and
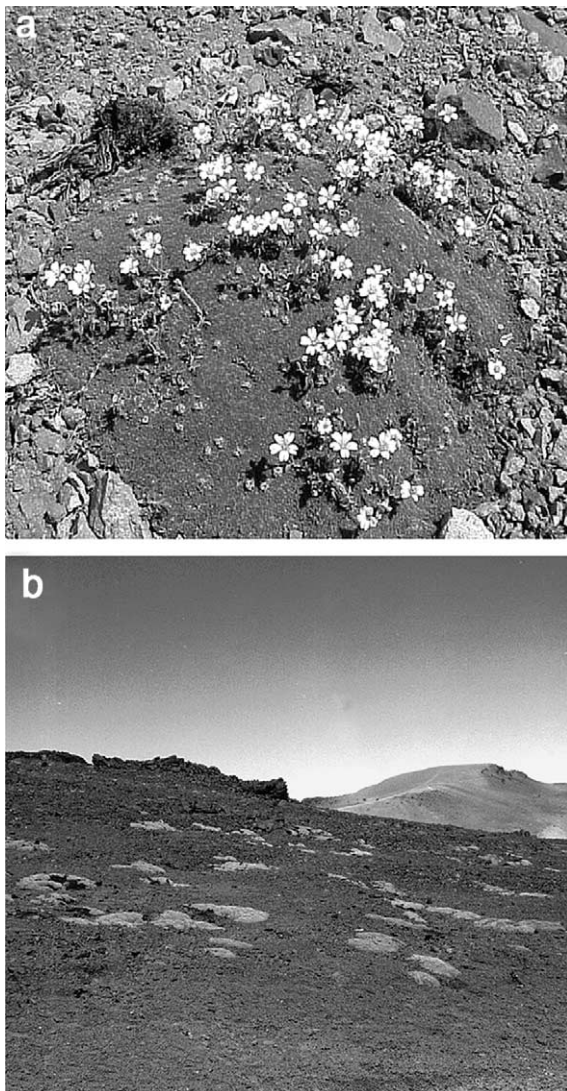
Fig. 1. An *Azorella monantha* cushion (a), showing its approximately circular growth form (this cushion is ca 40 cm diameter), and part of a mountaintop community (b) dominated by *A. monantha* cushions interspersed by bare ground. In this study, cushion patches comprise engineered habitat and surrounding open areas were considered unmodified habitat. The landscape comprises both cushions and open areas.

McGeoch 2004, Mark and Wilson 2005), and even centuries (Ralph 1978, Kleier and Rundel 2004). These discrete, distinctive habitat patches (Fig. 1a) are often in marked contrast to the more or less bare surrounding rocky soil (Fig. 1b) that has limited vegetation cover, particularly at the highest elevations that are close to the distributional limits of other plant species. Cushion species in cold alpine ecosystems have been reported to substantially modify soil temperature by as much as 15°C, reducing the maximum and increasing the minimum temperatures compared to adjacent soil outside cushions (Arroyo et al. 2003, Körner 2003, Cavieres et al.

2006). Cushions also substantially increase soil moisture retention, potentially important in more arid alpine regions (Cavieres et al. 1998, 2006), and can also enhance the availability of some mineral nutrients such as nitrogen, phosphorus and potassium (Núñez et al. 1999, Cavieres et al. 2006). This improvement of environmental conditions has been suggested to be responsible of the observed increased survival of several species within cushions (Cavieres et al. 2005, 2006). Therefore, cushions can influence plant community organization by differentially affecting plant species (Badano et al. 2002, Cavieres et al. 2002, Arroyo et al. 2003).

Although *A. monantha* has a broad distributional range in South America (Hoffmann et al. 1998), we selected mountaintop communities to assess engineering effects because these landscapes contain a relatively limited number of other plants (ca 30 species), so that fully sampling the plant communities is relatively easy. *A. monantha* cushions in these landscapes are surrounded by open areas that are almost entirely composed of rocks and bare ground with isolated individual plants of other species (Fig. 1b). Thus, since there are no other above ground macro structures created by organisms, estimates of the effects of cushion engineering on community organization therefore represent a relatively clear comparison of engineered vs unmodified habitat.

Study site

To assess the consistency of metrics, we considered two mountaintop plant communities in the high-Andes of central Chile as independent replicates: Mt. Franciscano (33°19′ S, 70°15′ W, 3580 m) and Mt. Tres Puntas (33°19′ S, 70°14′ W, 3630 m). These mountaintops are located 50 km to the east of the city of Santiago and they are similar in terms of species composition and environmental conditions. Estimated mean summer temperature at 3600 m is ca 4°C (Cavieres and Arroyo 1999) with precipitation exceeding 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). The length of the snow-free growing season is 4-5 month usually starting in November (E. I. Badano, pers. obs.). Soil in both mountaintops is mainly a clay-type (Cavieres et al. 2000) mixed with sedimentary and volcanic rock. Although *A. monantha* is the most conspicuous species in both communities, a number of small perennial and annual herbs as well as prostrate shrubs grow both within and outside cushions. Since the majority of these plant species are perennial (ca 95%), single event sampling reflects temporal integration of the community, reducing the

potential for misclassification of species as habitat specialists or generalists.

Abiotic environmental modification

Substrate temperature, soil moisture and soil macro-nutrients (N, P, K) were measured and compared between cushions and adjacent open areas to illustrate the magnitude of the differences in some abiotic conditions between engineered and unmodified habitats. Soil moisture was measured at both sites. Temperature and macronutrients were measured at Mt. Franciscano.

Substrate temperatures were recorded between 29 November 2003 and 17 January 2004 (in the mid-growing season) using soil probes (TMCx-HD, Onset Computer Corporation, MA, USA) connected to data-loggers (HOBO H8, Onset Computer Corporation, MA, USA) programmed to record temperature every hour. Four cushions were randomly selected and a temperature probe was placed at the center of each cushion 2 cm below the surface. Each cushion had a paired probe placed 2 cm below the soil surface in an adjacent open area 3 m away in a random direction that was also at least 3 m from any other cushion. Data from the four cushions and the four open areas were averaged at each hour, and the difference in average temperature between cushions and open areas (cushion $-$ open area $=$ $\Delta_{temperature}$) was calculated at each hour. These values were then compared with the respective open area average temperature using linear regression. An effect was deemed to have occurred when the slope of the regression line significantly differed (critical $\alpha = 0.05$) from 0 (warmer when values were >0; colder when values were <0).

To assess differences in soil moisture, we measured the soil matric potential in mid-growing season 2004, using tensiometers (Jet Fill 2725 Series, Soilmoisture, CO, USA) placed beneath 20 randomly selected cushions and 20 randomly selected points in open areas. In both habitat types, tensiometers were inserted to 20 cm soil depth by digging a small hole (2.18 cm diameter) with the appropriate insertion tool (7/8 in, Soilmoisture, CO, USA), and matric potentials were registered after 30 min stabilization. All measures were carried out on clear sunny days (24 and 25 January at Mt. Franciscano and 26 and 27 January at Mt. Tres Puntas) between 12:00 and 15:00 h. Matric potentials from each mountaintop were compared between habitat types using t-tests for paired comparisons (critical $\alpha = 0.05$), where higher matric potentials (closer to zero) indicate higher soil moisture.

To estimate macronutrient (N, P, K) availability, soil cores (10 cm depth) were taken below five randomly selected cushions and five randomly selected points in open areas on 10 January 2004. Soil cores were placed in hermetic plastic bags at 5°C and analyzed (Laboratory of Soil Analyses, Faculty of Agronomy, Univ. of Concepción, Chile) within the next 12 days. Available nitrogen was estimated separately as nitrate (NO_3^-) and ammonium (NH_4^+), using the colorimetric techniques of Robarge et al. (1983) and Longeri et al. (1979), respectively. Available phosphorus was estimated as (PO_4^{-3}) by extraction with sodium bicarbonate ($NaHCO_3$, solution 0.5 N, pH 8.5) followed by colorimetry (Olsen and Sommers 1982). Available potassium was estimated as exchangeable potassium (K^+) by extraction with ammonium acetate (CH_3COONH_4, solution 1 N, pH 7.0) followed by atomic absorption and emission spectrophotometry (Sadzawka et al. 2000). Concentrations of each macronutrient were compared between cushions and open areas using t-tests for paired comparisons (critical $\alpha = 0.05$).

Community effects

Vegetation sampling

One hundred cushions with a range of diameters (min. 20 cm, max. 155 cm) were selected at each mountaintop using points at random directions and distances from the center of a previously delimited 1 ha plot at each site. If these random points did not coincide with a cushion, we sampled the closest cushion to each point. The identity and abundance of each plant species growing within each cushion was recorded. The area of each cushion (m^2) was estimated from the length of the major and minor axes as $[(\pi \times major\ axis\ length \times minor\ axis\ length)/4]$, a reasonable approximation based on the generally circular growth form (Fig. 1a). To obtain comparable samples of species richness and abundances in open areas, the shape and area of each cushion was emulated with wire-rings. Rings were placed in open areas in a random direction and distance from the respective cushion, while maintaining a minimum distance of 50 cm from any other cushion. Plants within rings were identified and the number of individuals of each species recorded.

Species-area curves and species richness estimation

As noted above, metric values based solely on species lists are potentially subject to bias if the communities are not fully sampled. We therefore evaluated the degree to which the sampling regime sampled the community by first plotting the mean number of species observed against sampling effort for cushions, open areas and the landscape (i.e. cushions + open area plots) at each mountaintop. A species-accumulation curve that has largely reached an asymptote is indicative of a well-sampled community. We also calculated the Chao 2 estimate for the total number of species likely to be

observed in each habitat at each site at 100 samples. The Chao 2 richness estimator uses the ratio of the number of species observed only once in a dataset to the number of species observed twice to estimate the actual number of species present in a habitat type (Colwell and Coddington 1994). The degree to which the Chao 2 estimator exceeds the total observed species provides an indication of how thoroughly the assemblage has been sampled.

Our regime sampled only cushions or open areas. In order to generate a species accumulation curve for the landscape as a whole, i.e. the expected curve if samples were placed at random with respect to habitat type, we generated synthetic datasets combining plots from both cushions and open areas for each site. Since cushions occupy a smaller fraction of the landscape than open areas, the percent cover of each habitat type was used to weight the landscape dataset. We recorded the cover of cushions and open areas on ten parallel line-transects (each 50 m long with 10 m sample intervals) at each mountain top. The average cover of cushions was 10% in both sites; therefore the landscape datasets were compiled using 10 randomly selected plots from cushions and 90 randomly selected plots from open areas in each simulation. We synthesized 20 landscape datasets and computed the mean of the number of species observed at each level of sampling intensity and the Chao 2 species richness estimator across the 20 runs. To test for differences between patch types in species accumulation, we estimated the 95% confidence intervals for each value of species richness, assuming statistically significant differences between habitat types (cushions vs open areas) and levels of organization (habitats vs landscape) when confidence intervals did not overlap. All species richness estimates were calculated using EstimateS 7.5 (Colwell 2005).

Metric estimation from species lists

We compiled a species list for each mountaintop (Appendix A), classifying all recorded species as 'habitat specialists' or 'habitat generalists' depending on the habitat types in which they were found (cushions, open areas or both habitats). We then estimated RHR, LRE and LIP as described in Table 1. To calculate HRP, absolute abundances (individuals m^{-2}) of habitat generalist species at each mountaintop were first compared between habitat types within a mountaintop using t-tests for paired comparisons (critical $\alpha = 0.05$) in order to ascertain the number of species with higher abundances within cushions. To calculate HSO, habitat generalists were ranked in decreasing order according to their absolute abundances within a given habitat type and then computed as in Table 1. The distributions of rank abundances for habitat generalists were then compared

between cushions and open areas using χ^2 goodness of fit tests (critical $\alpha = 0.05$).

Metric estimation from Chao 2

Since the number of species estimated by Chao 2 constitutes a maximum likelihood estimator of species richness in a habitat (Colwell and Coddington 1994), these values were also used to derive parameters for calculating metrics in order to compare values with metrics derived from species lists. The estimated number of species for cushions, open areas and the landscape were considered estimators of species richness within engineered patches (Se), unmodified patches (Su) and the landscape (SL), respectively (Table 1). From these values, the number of habitat specialists within cushion patches, $Se_{(eng)}$, was estimated from $(SL - Su)$, and the number of habitat generalists in the landscape, Sg, was estimated from $(Se + Su - SL)$. Using these values, we then calculated RHR, LRE and LIP as described in Table 1. To compute HRP and HSO we replaced the term Sg by $(Se + Su - SL)$ in the respective formulas, and combined them with data on species abundances $(Sg_{(>eng)}$ and $|k_{i(eng)} - k_{i(unm)}|)$ from the field data. Since the sampling regime fully sampled the community (Results), the abundance values used in HRP and HSO were assumed to be unbiased estimates.

Ordination

In addition to metric computation, we performed non-metric multidimensional scaling ordinations (NMS; McCune and Mefford 1999) to assess the degree of community overlap between cushions and open areas at each mountaintop. Ordinations were performed using the absolute abundance of each species in each sample (individuals m^{-2}) to account for differences in the areas sampled for each habitat type. In these analyses, the Sørensen coefficient was used as measure of distance between samples in the ordination space (McCune and Mefford 1999).

Results

Abiotic environmental modification

Maximum average hourly substrate temperatures in both habitat types were recorded between 14:00 and 15:00 h, with minimum temperatures around 7:00 h (Fig. 2a). After midday, when both habitats had higher temperatures, *Azorella monantha* maintained temperatures 12–18°C lower than open areas (Fig. 2a). Values of $\Delta_{temperature}$ had a negative relationship to average temperatures in open areas ($F_{1,1210} = 6415.45$, $p < 0.01$, $r^2 = 0.84$; Fig. 2b). Most values of $\Delta_{temperature}$ were negative; cushions maintained lower temperatures than open areas much of the time (Fig. 2b). However, positive values of $\Delta_{temperature}$ were observed when
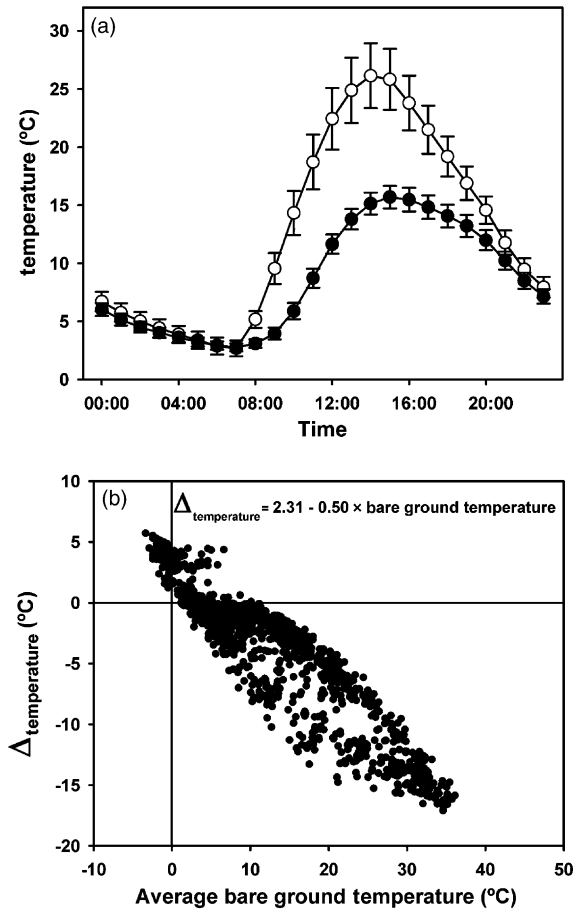
Fig. 2. (a) Average (± 2 SE) temperatures within cushions (solid symbols) and adjacent open areas (empty symbols) at each hour. (b) Relationship between the difference in average substrate temperatures between habitat types (cushion-open areas $= \Delta_{temperature}$) and average temperature in open areas. The equation above the scatterplot shows regression parameters; the vertical line is 0°C in open areas, and the horizontal line indicates the trend if cushions do not affect temperature ($\Delta_{temperature} = 0$).

open areas were below 5°C and close to freezing (Fig. 2b), with cushions being 5–9°C higher than open areas.

Soil beneath cushions had significantly higher matric potentials than open areas at both sites (mean kPa± 2 SE, inside vs outside: Franciscano: -16.01 ± 1.22 vs -19.35 ± 0.88, $t_{1,38} = 4.23$, $p < 0.01$; Tres Puntas: -14.11 ± 1.44 vs -18.60 ± 1.16, $t_{1,38} = 4.99$, $p < 0.01$), indicating higher soil moisture beneath cushions. No significant differences between cushions and open areas were found for the four macronutrients (mean mg kg$^{-1} \pm 2$ SE, inside vs outside: NO$_3^-$: 3.48 ± 2.55 vs 1.32 ± 1.04, $p = 0.16$; NH$_4^+$: 0.16 ± 0.08 vs 0.22 ± 0.04, $p = 0.22$; PO$_4^{-3}$: 11.68 ± 3.92 vs 8.54 ± 2.07, $p = 0.19$; K$^+$: 360.62 ± 46.53 vs 538.54 ± 378.19, $p = 0.38$).

Community effects of *Azorella monantha*

A total of 28 plant species were found in Mt. Franciscano and 20 in Mt. Tres Puntas. In Mt. Franciscano, cushions and open areas had 8 habitat specialists each, with 12 generalist species inhabiting both patch types (Appendix A). In Mt. Tres Puntas, there were 4 cushion specialists, 5 specialists in open areas and 11 habitat generalists.

Species–area curves for cushions, open areas and the landscape reached an asymptote before 100 samples in both mountaintops (Fig. 3), indicating that the sampling effort was sufficient to fully capture the richness and composition of assemblages. The values of Chao 2 estimate did not differ from the observed species richness in each habitat type (95% confidence intervals of the observed species richness and the estimate overlapping at 100 samples; Fig. 3), indicating that all species in the communities were found in the sampling.

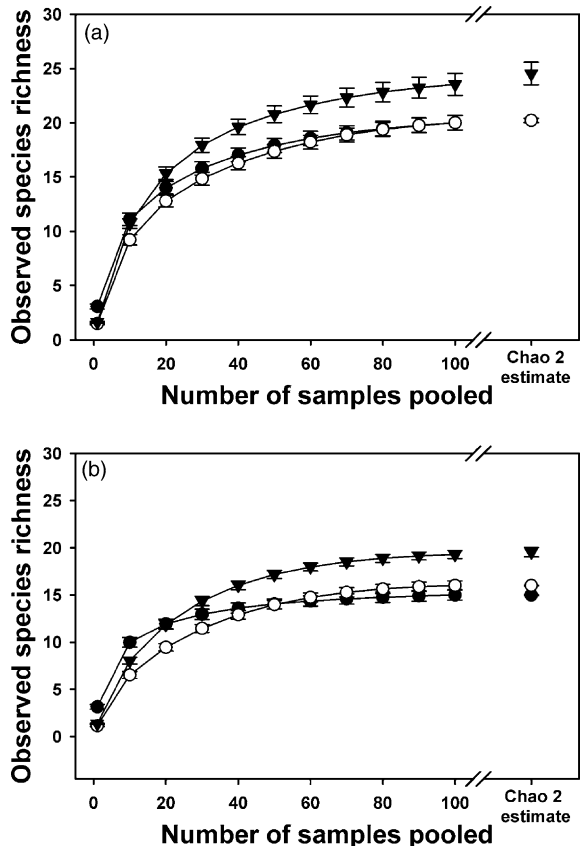**RHR.** Values of RHR estimated from both species lists and Chao 2 were close to unity at both Mt.

Fig. 3. Species accumulation curves (± 95% confidence intervals) within *Azorella monantha* cushions (solid circles), open areas (empty circles) and the landscape (solid triangles) in Mt. Franciscano (a) and Mt. Tres Puntas (b). Separate symbols at the right of the curves are the values of the Chao 2 estimate at 100 samples.

Franciscano and Mt. Tres Puntas (Table 1). Cushions and open areas therefore had similar species richness. The overlapping 95% confidence intervals of the species-area curves for cushions and open areas at virtually all cumulative sample sizes, including the asymptote, indicated that there was no statistically significant difference in species richness between the two habitat types (Fig. 3).

LRE. Data from species lists showed that cushions enhanced landscape-level species richness at Mt. Franciscano and Mt. Tres Puntas by 40% and 25%, respectively (Table 1). LRE values calculated from Chao 2 gave somewhat lower, but similar estimated enhancement values of 21% in Mt. Franciscano and 22% in Mt. Tres Puntas (Table 1). The non-overlapping 95% confidence intervals of species–area curves for the landscape relative to both habitat types at cumulative sample sizes >20, including the asymptote, indicated that cushions significantly increased species richness in both landscapes (Fig. 3).

HRP. In Mt. Franciscano, 5 habitat generalist species (of 12 generalist species) had significantly higher abundances within cushions (Fig. 4a). Thus HRP calculated from species lists indicated that 42% of habitat generalists could potentially benefit from conspecific rescue from cushions into open areas. Data from Chao 2 estimated HRP at a similar value of 31% (Table 1). In Mt. Tres Puntas, 6 habitat generalists (of 11 generalist species) had significantly higher abundances within cushions (Fig. 4b) with an HRP effect of 54% from species lists, and a similar 52% when estimated from Chao 2 (Table 1).

LIP. Values of LIP estimated from species lists indicated that 43% of species in Mt. Franciscano (12 of 28 species in total) and 55% of species in Mt. Tres Puntas (11 of 20 species in total) could potentially benefit from having more than one habitat type due to the presence of cushions (Table 1). LIP estimates based on Chao 2 gave similar, but somewhat higher values of 60% for both mountaintops (Table 1).

HSO. In Mt. Franciscano, habitat generalists dominant in open areas were recorded as subordinate species within *A. monantha*, while subordinate species from open areas were recorded as dominant or co-dominant species in cushions (Fig. 4a). In Mt. Tres Puntas, the same species (*Hordeum comosum*) was dominant in both cushions and open areas, but most (6 of 11 generalist species) subordinate species in open areas had higher abundances within cushions (Fig. 4b). The HSO effect of cushions estimated from species lists was higher in Mt. Franciscano than in Mt. Tres Puntas, but the converse was observed when HSO was calculated using Chao 2, although values were in the same general range in all cases (0.28–0.47, Table 1). There was a significant difference in the distribution of rank abundances of habitat generalists between cushions and open areas at both mountain tops (Franciscano: $\chi^2_{(1,11)} = 130.65$, p < 0.01; Tres Puntas: $\chi^2_{(1,10)} = 72.35$, p < 0.01).

NMS ordinations. Ordination analyses grouped samples from cushions and open areas separately at both mountaintops (Fig. 5), indicating differences in species composition between habitat types. However, the percent variance explained by all ordination axes was relatively low (< 50%) and there was a considerable dispersion of data points, indicating a relatively high degree of overlap between species assemblages in cushions and open areas.
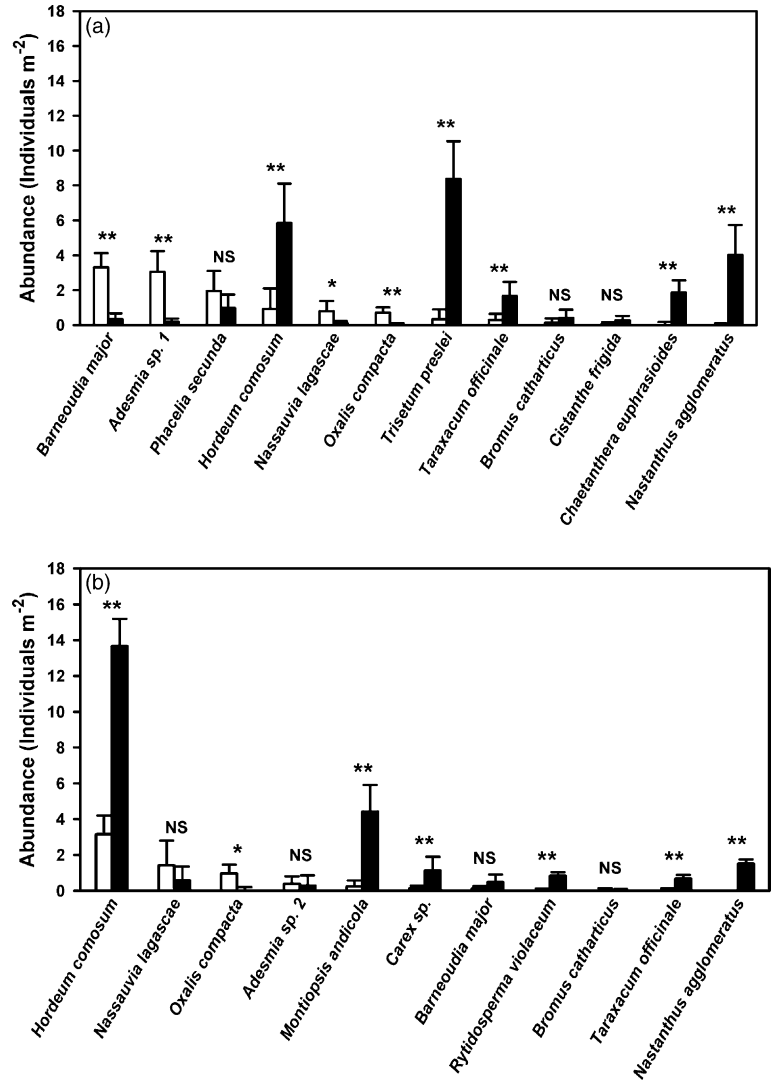
Discussion

Abiotic environmental modification

In these high-Andean ecosystems, *Azorella monantha* creates thermally-buffered habitat patches with higher soil moisture than surrounding open areas, but does not detectably affect N, K and P macronutrient concentrations in the soil beneath. The marked effects on temperature and soil moisture are clear evidence that this cushion species is an ecosystem engineer from the perspective of abiotic environmental modification alone. In addition, since temperature and soil moisture are key factors influencing plant growth survival and reproduction in alpine environments (see below), it is reasonable to argue that these engineering affects, via their differential influence on growth and survival of species in cushions *vs.* the outside environment, may account for many of the effects of cushions on plant community organization.

Temperatures within *A. monantha* were never lower than 0°C even when open areas were close to or below freezing; cushions maintained a substantially warmer environment (5–9°C higher) under such chilling conditions. Similar mitigation at low temperature has been reported for *A. monantha* in the Patagonian Andes of Chile, with cushions being 6–10°C higher than surrounding open areas (Arroyo et al. 2003), and *Silene acaulis* in the central European Alps where cushion temperatures are 5–15°C higher at air temperatures below 10°C (Körner 2003). Such increases in temperature would be crucial for plant species living close to their thermal minima (Arroyo et al. 2003).

Azorella monantha can also maintain lower temperatures when the surrounding environment has high temperatures. This finding is in accord with that reported by Cavieres et al. (1998, 2006) for *Laretia acaulis* cushions in the Andes of central Chile that maintained temperatures 11–17°C lower than surrounding open areas when they exceeded 35°C. In our study, *A. monantha* maintained temperatures close to 15–17°C when open areas reached temperatures higher than 40°C (Fig. 2b). This marked thermal buffering would reduce direct heat shock and mortality of plants living in cushions (Cavieres et al. 2006), while simultaneously

Fig. 4. Mean abundances (individuals m^{-2} ±2 SE) of habitat generalist species within *Azorella monantha* cushions (solid bars) and in open areas (empty bars) in Mt. Franciscano (a) and Mt. Tres Puntas (b). Results of t-tests comparing abundances of habitat generalists between habitat types are shown in the figures (t-test a =0.05; * p <0.05; ** p <0.01; NS =no significant difference).

reducing soil moisture evaporation. This should lead to higher water availability below the cushion surface, and may contribute to the higher soil matric water potential measured beneath *A. monantha* compared to open areas. The thermal buffering at low and high temperatures is most likely due to the insulation properties of the thick, dense layer of non-photosynthetic and dead plant material beneath the cushion surface (up to 20 cm deep), while the tightly packed, resin-coated surface of the cushion (Hauri 1912) may also reduce evaporation compared to open areas.

Water limitation during the growing season is likely common in the Andes of central Chile because summer precipitation is scarce (<30 mm average; Santibáñez and Uribe 1990) and stored soil moisture is largely derived from snow melt (Cavieres et al. 1998). Drought is considered one of the most important factors influencing plant growth and survival in arid alpine environments

(Forbis 2003). Thus, thermal mitigation and amelioration of water limitation may well account for the positive influence of cushions on many of the plant species. For example, Molina-Montenegro et al. (2005) showed that modulation of substrate temperature and soil moisture was related to higher photosynthesis for some plant species growing within cushions, and recent studies experimentally increasing soil moisture have shown that this increases seedling survival (L.A. Cavieres, unpubl.).

In contrast to some other cushions species, such as *Mulinum leptacanthum* and *Oreopolus glacialis* (Núñez et al. 1999), *A. monantha* appears to have no detectable effects on macronutrient concentrations in the soil beneath the cushion. However, the absence of detectable effects on soil macronutrient concentrations does not preclude potential differences in nutrient availability, nor influences on nutrient availability via thermal and
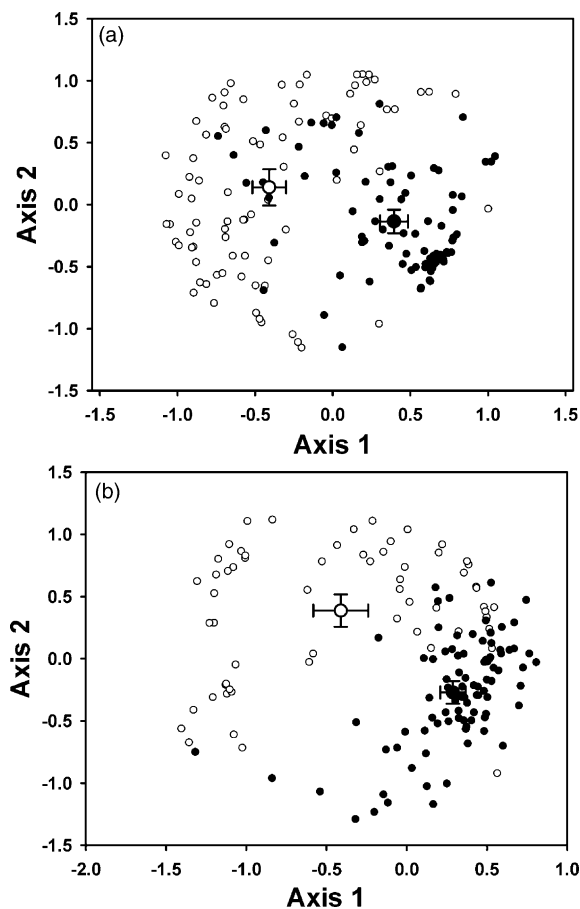
Fig. 5. NMS ordinations comparing species composition between *Azorella monantha* (solid symbols) and open areas (empty symbols) in Franciscano (a) and Tres Puntas (b). Larger symbols are the centroids (± 2 SE) for each habitat type.

moisture effects (Chapin 1980, Lambers et al. 1998). For example, there could be available nutrients in the deep layer of plant material beneath the cushion surface and above the soil surface through which the roots of other plants grow, and nutrient recycling rates may differ under cushions compared to the outside – variables that we did not measure.

Community effects

Cushion habitat does not contain more species than open areas, but cushions add new species into the community, resulting in habitats with different, but somewhat overlapping composition, and an increase in species richness of the landscape. Cushion habitat has the potential to increase the temporal stability of species richness both at the habitat and the landscape levels, and cushion habitat has substantially different dominance patterns compared to open areas.

Since the RHR metric approximated unity, *A. monantha* cushion habitat is neither more nor less species-rich than open areas. This finding contrasts with that found for some other cushion species; *Mulinum leptacanthum* (Núñez et al. 1999), *Azorella trifurcata* (Molina-Montenegro et al. 2000), *Oreopolus glacialis* (Badano et al. 2002) and *Bolax gummifera* (Cavieres et al. 2002) all had higher species richness within cushions compared to open areas. However, Cavieres et al. (1998) reported lower species richness in *Laretia acaulis* cushions compared to open areas. These varied patterns are in accord with the postulate that effects of ecosystem engineers on patch level species richness will be idiosyncratic, and will depend upon the degree to which the ecosystem engineer modulates the abiotic environment and the number of species that respond to such modulation (Jones et al. 1997, Wright and Jones 2004).

In contrast to the patch level, the LRE metric indicated that *A. monantha* increased landscape-level species richness by 21–40%. This finding is in accord with: 1) the suggestion that abiotic modulation by cushion plants increases species diversity in Andean plant communities by adding species that cannot survive in open areas (Núñez et al. 1999, Badano et al. 2002, Cavieres et al. 2002, Arroyo et al. 2003); and 2) the postulate of Jones et al. (1997), that the addition of engineered patches should almost invariably increase landscape-level species richness via a net increase in habitat diversity.

In both mountain tops, the HRP and LIP metrics suggest that *A. monantha* cushions have the potential to increase the stability of species richness over time for habitat generalist species at both the habitat and landscape levels. Many generalist species were at higher abundance in cushions (31–54%), and 43–65% of all species had more than one habitat to live (other than open areas) because of the presence of cushion habitat patches. In high-alpine habitats, plant mortality during the growing season is mainly due to unpredictable abiotic events generated by the combination of fluctuating soil temperatures, drought, and soil disturbance from snowmelt runoff erosion, wind and land slips (Chambers 1995, Forbis 2003). The thermal buffering and increased soil moisture effects, along with the compact, deep-rooted cushion architecture suggest that such events may be less likely to occur in cushions than in the open, and the relatively high values for the HRP and LIP metrics justify research into whether such rescue potential and insurance is actually realized.

The HSO metric indicated that this cushion species also has strong effects on dominance patterns of habitat generalists, with 28–47% of generalists showing altered dominance rankings inside vs outside cushions. Changes in species dominance patterns have been reported by Badano et al. (2002) for *Oreopolus glacialis* cushions in

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southern Chile, with the authors suggesting that such changes may be due to differences in establishment and/ or survival rates within cushions compared to outside. Such individualistic abundance responses have been reported in many other plant communities, where dominant species may become either co-dominant or subordinate with changes in the availability of resources or abiotic conditions (Tilman 1987). On the other hand, several authors have argued that different physical environments alter the strength of plant–plant interactions to the extent that, in some cases, outcomes can change from negative to positive or vice versa (Bertness and Callaway 1994, Brooker and Callaghan 1998). Abiotic environmental modulation by *A. monantha* could affect species abundances via their individualistic responses to altered conditions and/or enhanced competitive or facilitative interactions among species. In addition, other biotic processes, such as plant–microbial interactions, may be different within cushions. Which of the above underlying mechanisms contribute to observed changes in dominance patterns remains to be seen, but the large values for the HSO metric would justify such investigations.

Overall, all metrics other than RHR were statistically significant and often large in magnitude. Metric values estimated by different methods (species lists and Chao 2) were similar within a site and there was high congruity for metric values between mountaintops. All of which, in combination with the ordination results and species lists, justify the conclusion that *A. monantha* cushions have marked effects on the structure and dynamics of high-Andean plant communities at patch and landscape levels. Given the marked effects of cushions on local thermal regimes and soil moisture, as well as other possible influences such as soil stabilization and wind protection, it is plausible that ecosystem engineering by *A. monantha* is at least partially and perhaps largely responsible for these community effects.

Utility of the proposed framework and metrics

Our approach rests upon a number of important caveats and assumptions, and has limitations. While many of these issues were briefly articulated in the framework, some deserve reiteration and further comment. First, the analysis of community impacts presupposes that the focal ecosystem engineer species is the primary cause of altered abiotic environmental conditions, and that these abiotic changes are, in turn, responsible for altered community patterns. These two assumptions can be tested by experimentally removing or adding the engineer, and/or by manipulating abiotic conditions and simulating the influences of the engineer (McCabe and Gotelli 2003, Lill and Marquis 2003, 2004, Fogel et al. 2004). In some situations, such as beaver creation of

ponds (Wright et al. 2002), these assumptions may be obviously valid. In yet other circumstances, as is the case in this cushion plant study, experimental studies demonstrating engineer effects may provide sufficient precedent for conducting community analyses (Cavieres et al. 2005, 2006). However, if there is insufficient evidence supporting the above two assumptions, experimental manipulation will be required as a part of any research program focused on the community-level effects of an ecosystem engineer. While our approach is based upon a focal engineering species, we do not assume that there is only one ecosystem engineer in the engineered habitat, nor do we preclude the influence of other types of interactions (e.g. predation, direct resource competition, parasitism or mutualisms) on community organization within this habitat. The degree to which other engineers and/or other interactions affect community structure and dynamics is also amenable to experimental parsing.

Second, the engineer must create discrete, distinctive patches. While often the case, this is certainly not invariably so. For example, different trees species may well create different local light, water and thermal environments (Suzán et al. 1996, Barnes and Archer 1999, Pugnaire and Lázaro 2000), but in a forest such environments likely overlap. Analyzing community effects on understory vegetation, for example, would require substantial modification of our approach to encompass non-discrete neighborhood influences of multiple tree engineer species.

Third, other habitats in the landscape are assumed to be unmodified by the focal engineer, requiring spatially limited abiotic influence of the engineer species. Clearly there will be circumstances in which this will not be true – for example downstream effects on hydrology of upstream beaver impoundments. Such cases would require spatial delimitation of engineering influence, which may be accomplished by combining the community analyses with spatial sampling of the relevant abiotic environmental variables (Flecker and Taylor 2004). However, since our framework and metrics are based on habitat comparisons with subsequent integration of habitat types into landscape influence, a judicious choice of what constitutes unmodified habitat is required.

Fourth, the requirement that the entire landscape not be entirely modified by the engineer (i.e. becomes a single habitat type) is clearly paramount. If this is the case there can be no community comparisons. However, the degree to which a landscape can be engineered before community comparison becomes invalid is a more difficult issue. Logically, this should depend on the degree to which a sufficient area of unmodified habitat remains in a given landscape for reliable estimation of richness (Wright et al. 2002). The same principle should apply to the converse situation – there will be some minimum required area of engineered habitat for valid sampling.

Fifth, our approach makes a number of assumptions about the temporal stability of observed community patterns. When applied as a single "post-facto snapshot", the approach assumes that sufficient time has elapsed since the engineer arrived for species to establish, and that current patterns reflect long-term averages – particularly with respect to our local classification of species as habitat specialists and generalists. This time dependency can be evaluated by repeated sampling over time (something that we did not do in this short-term study). In the absence of long-term data, the misclassification risk will be less when communities are largely comprised of longer-lived perennial species (as is the case with our cushion plant system), and/or when colonization from the regional species pool is not periodically limiting (i.e. regionally abundant species with high propagule dispersal capacity). Some assessment of the veracity of the classification of species can be obtained by spatio-temporal substitution of multiple, independent landscapes of the same type, as was done here using two mountaintops.

Sixth, LIP and HRP metrics assess only the potential for insurance and habitat rescue; and the HRP ignores the possibility of inverse rescue (i.e. unmodified rescues engineered), and the risk of increased density-dependent mortality when abundances are greater in the engineered habitat. These metrics can only be used to indicate likelihood (higher values indicate higher probability), and clearly, independent studies would be required to ascertain if the potential is realized. In a similar vein, while HSO indicates engineer-induced altered rank abundances of generalists, no inference can be made from this finding with respect to underlying mechanisms.

Lastly, full community area-based sampling, species richness estimation, and habitat area-based landscape resampling are all very important parts of the approach. Full community sampling may prove difficult to do in some circumstances (e.g. many rare species that accumulate very slowly with area), but approximations based on extrapolative estimators (Chao and bootstrap; Colwell and Coddington 1994) can be used, as was done here. Thus, the choice of the method used to estimate the proposed metrics (species list or extrapolative estimators) would depend on the features of the target community (total number of species, abundances of species, number of specialists and generalist species) and the degree to which they can be readily quantified. For example, in fully sampled communities (censed communities), extrapolative estimation will be not necessary. Conversely, in highly rich communities with large numbers of rare species, extrapolative estimations would be required to reduce the risk of misclassification of a generalist as a specialist species. Regarding this point, is important to note that the reduction of complex community patterns into simple metrics, while usefully distilling complexity into numbers, can also lead us

astray if they are not derived with good assurance of reliability and accuracy.

If we wish to develop and test predictive and explanatory models of variation in the diversity of community impacts of different engineer species, we first need to be able to compare effects across systems. As noted in the introduction, there is growing evidence that ecosystem engineering can be an important force influencing communities and their dynamics. However, the types of effects, their magnitudes, and ways in which they were estimated vary, making comparison difficult or impossible (Wright and Jones 2004). Therefore, we think that developing a sound basis for quantitative comparison is an eminently worthwhile precursor to the predictive and explanatory goals. The framework, general methodology and metrics we have proposed and evaluated in the *A. monantha* system are a way to move forward. However, while our findings reveal large, important effects of this cushion on community organization, it is just one example. To achieve the general goals will require some degree of agreement among ecologists about what should be measured, why it is worth measuring, and how to measure it.

We do not suggest that the exact metric derivations and methodology we used should be applied "carte blanche". However, we do think that the framework addresses many of the key questions ecologists might ask about engineering effects on community organization, and the metrics capture many of these effects in a relatively direct, easy to measure manner. Despite the many caveats above, we consider that the requirements can be met in many situations, the assumptions are transparent and amenable to testing, and the creativity of community ecologists can help address some of the obvious limitations. We therefore hope that use of the framework and metrics will spur the generation of comparative data sets that can be used in the development and testing of general predictive and explanatory models of the effects of ecosystem engineers on community organization.

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Appendix A. Species lists from Mt. Franciscano and Mt. Tres Puntas and summarization. Species were classified according to the habitat type in which they were found at asymptotic sampling (see Material and methods). Cushions: engineered habitat specialists in *azorella monantha cushions*; open: unmodified habitat specialists in open areas; both: habitat generalists in both cushions and open areas); Absent indicates species not detected at a given mountaintop. Authorities of species were assigned following Marticorena and Quezada (1985).

Species	Mt. Franciscano	Mt. Tres Puntas
Adesmia **sp. 1 (Fabaceae)**	Both	Open
Adesmia **sp. 2 (Fabaceae)**	Open	Both
Barneoudia major **Phil. (Ranunculaceae)**	Both	Both
Bromus catharticus **Vhal (Poaceae)**	Both	Both
Carex **sp. (Cyperaceae)**	Absent	Both
Cerastium arvense **L. (Caryophyllaceae)**	Cushions	Absent
Chaetanthera euphrasioides **Meigen (Asteraceae)**	Both	Open
Chaetanthera lycopodioides **Cabr. (Asteraceae)**	Open	Absent
Chaetanthera pusilla **Hook. (Asteraceae)**	Absent	Open
Cistanthe frigida **Barn. (Portulacaceae)**	Both	Absent
Erigeron andicola **DC. (Asteraceae)**	Cushions	Cushions
Galium gilliesii **H. et A. (Rubiaceae)**	Cushions	Absent
Hordeum comosum **(J. Presl.) Love (Poaceae)**	Both	Both
Junellia uniflora **(Phil.) Mold. (Verbenaceae)**	Open	Absent
Montiopsis andicola **Gill. ex H. et A. (Portulacaceae)**	Absent	Both
Montiopsis potentilloides **(Barn.) D.I. Ford (Portulacaceae)**	Cushions	Absent
Nassauvia lagascae **(D. Don) Meigen (Asteraceae)**	Both	Both
Nassauvia pyramidalis **Meyen (Asteraceae)**	Open	Open
Nastanthus agglomeratus **Miers (Calyceraceae)**	Both	Both
Olsynium scirpoideum **(Poepp.) Goldbl. (Iridaceae)**	Cushions	Absent
Oxalis compacta **Gill. ex H. et A. (Oxalidaceae)**	Both	Both
Perezia carthamoides **(D. Don) H. et A. (Asteraceae)**	Open	Absent
Phacelia secunda **J.F. Gmel. (Hydrophillaceae)**	Both	Absent
Pozoa coriacea **Lag. (Apiaceae)**	Open	Open
Rytidosperma violaceum **(Desv.) Nicora (Poaceae)**	Cushions	Both
Senecio looseri **Cabr. (Asteraceae)**	Cushions	Cushions
Taraxacum officinale **(L.) Weber (Asteraceae)**	Both	Both
Thlaspi magellanicum **Comm. ex Poir. (Brassicaceae)**	Cushions	Cushions
Trisetum preslei **(Kunth) Desv. (Poaceae)**	Both	Cushions
Viola atropurpurea **Leyb. (Violaceae)**	Open	Absent
Viola philippii **Leyb. (Violaceae)**	Open	Absent
Total number of species	28	20
Number of engineered habitat specialists	8	4
Number of unmodified habitat specialists	8	5
Number of habitat generalists	12	11