Reciprocal interactions between a facilitator, natives, and exotics in tropical alpine plant communities

Luis D. Llambí[a,*], Nicole Hupp[b], Agustin Saez[c], Ragan Callaway[d]

[a] Instituto de Ciencias Ambientales y Ecológicas, Universidad de Los Andes, Mérida 5101, Venezuela
[b] Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, MT, 59812, USA
[c] Universidad Nacional del Comahue and INIBIOMA-CONICET, 8400 San Carlos de Bariloche, Río Negro, Argentina
[d] Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, MT, 59812, USA

A R T I C L E   I N F O

A B S T R A C T

Facilitation by nurse plants has received considerable attention, but the feedback effects of beneficiaries on the benefactor fitness remain comparatively unexplored. In particular, to our knowledge there have been no studies of feedback effects of exotic species on nurse plants. Furthermore, there have been few studies of how exotic plants interact with native beneficiaries, potentially generating indirect effects on the nurse. Here, through spatial association analyses, we estimate the reciprocal interactions between the cushion nurse-plant *Arenaria musciformis,* native beneficiaries, and the dominant exotic *Rumex acetosella* (a fast growing heliophile species) in a tropical alpine ecosystem of the Venezuelan Andes, locally known as *páramos*. We recorded the density of natives and the exotic within *Arenaria* cushions and in paired open areas at three sites and calculated Relative Interaction Indices (RII) to explore the effects of the cushion. Then, we analyzed the feedback effects of *Rumex* and the natives on the density of flowers produced by *Arenaria*. Finally, we analyzed how *Rumex* abundance is related to the abundance of native species inside and outside cushions. RIIs indicated a facilitative effect of cushions on the abundance of native plants, but no effect on *Rumex*. We found a negative relationship between the density of natives and cushion flower density, but no such relationship for *Rumex*. However, at high densities, *Rumex* was negatively correlated with the abundance of the natives both inside and outside of cushions. Our results suggest the possibility of complex reciprocal interactions between nurses, natives and exotics, and that native and exotic plants can differ in their feedback effects on nurse cushions. Native plants appeared to be facilitated by cushions and then develop a parasitic relationship with their nurses. In contrast, the exotic *Rumex* had a neutral interaction with the nurse, but competitive effects on the native beneficiary community, which could indirectly modulate the feedback effects of natives on the nurse. These results highlight the importance of analyzing direct and indirect reciprocal interactions and the impacts of exotic invaders for understanding alpine community assembly.

1. Introduction

Facilitative interactions are important processes in plant community assembly (Lortie et al., 2004; Brooker et al., 2008). In particular, there is a large body of evidence for positive interactions driving increases in species abundance and diversity in low-productivity environments (Callaway 2007; Cavieres et al., 2014). We know much about the effects of facilitators on other species, but we know little about the reciprocal feedback effects (RFE) of the beneficiaries on the fitness or performance of the facilitator, or "nurse" species (Schöb et al., 2014a, 2014b; García et al., 2016). Understanding the nature of the bi-directional interaction between nurses and beneficiaries (i.e. parasitism, commensalism or

mutualism) has implications for the evolution of these interactions (Bronstein 2009; Brooker and Callaway 2009). For example, if beneficiaries have negative feedback effects on the fitness of benefactors, this could select for mechanisms employed by the nurse plant to reduce the abundance of beneficiaries or to tolerate their negative effects (Schöb et al., 2014b).

A few studies in semi-arid ecosystems have shown that the RFEs of beneficiaries on benefactors can be positive (e.g. Pugnaire et al., 1996; Holzapfel and Mahall 1999). However, most research in desert and alpine communities has reported negative effects of beneficiaries on the growth or reproduction of the nurse (Valiente-Banuet et al., 1991; Flores-Martínez et al., 1994; Michalet et al., 2011; Cranston et al., 2012;

* Corresponding author.
  E-mail addresses: ldllambi@gmail.com (L.D. Llambí), nicole.hupp@umontana.edu (N. Hupp), agustinsaezmail@gmail.com (A. Saez), ray.callaway@mso.umt.edu (R. Callaway).

Schöb et al., 2014a). In alpine ecosystems, where cushion plants commonly facilitate other species (e.g. Arroyo et al., 2003; Cavieres and Badano 2009; Yang et al., 2010; Cavieres et al., 2014), research at a global scale showed that beneficiary species predominantly have negative effects on the flower production and seed set of the cushions that host them (Schöb et al., 2014b). These RFEs were variable in their directionality and intensity depending on the environmental context, with high-productivity sites showing weaker negative effects of beneficiaries on the benefactor (Schöb et al., 2014c).

However, to our knowledge, there have been no studies of the RFEs of exotic species on nurse plants. These interactions may be particularly important in ecosystems where exotic species have become invasive. Exotic species are generally uncommon in alpine ecosystems and global research indicates that their richness decreases with altitude in mountains regions (Pauchard et al., 2009; Alexander et al., 2011; Seipel et al., 2012). This may be due to more frequent introductions at low elevations, strong environmental filtering, and low disturbance at higher elevations. However, close to two hundred exotic plant species have been reported in alpine areas worldwide and their impacts on native alpine plant communities remain largely unexplored (Alexander et al., 2016). Although many of these species are not considered invasive, this may change with increasing effects of climate and land use change in alpine areas, which are expected to promote invasion (Theurillat and Guisan, 2001; Alexander et al., 2016).

Natives and exotics could differ in their direct impact on nurse species due to differences in resource use strategies, and thus the intensity of their competitive effects on the benefactor (Callaway, 2007). For example, if exotics grow faster and have higher resource demand than natives in general, they could have a stronger negative feedback effect on the benefactor. This is reasonable to expect for introduced species with ruderal strategies in unproductive environments where stress tolerant strategies are likely to be favored in the natives (Tilman 1982). However, having evolved in environments with different selective pressures, there could be lower temporal or spatial niche overlap in resource use between exotic species and the nurse, which would reduce their impact on the benefactor fitness relative to natives. Differences in the effects of natives and exotics on the reproductive output of the nurse could also occur if they have different interactions with pollinators. This would depend on the degree to which natives and exotics share the same pollinators with the nurse, and whether exotics, natives and the nurse compete for pollinators (e.g. Muñoz and Cavieres, 2008Muñoz and Cavieres 2008; Morales and Traveset 2009) or alternatively, there are net facilitative effects through mutual attraction of pollinators (e.g. Moragues and Traveset, 2005).

Exotic species could also have important RFEs on nurse plants indirectly through their interactions with the native beneficiary community. In many invaded systems exotic plants suppress native species (Vilà et al., 2011; Besaw et al., 2011; Shah et al., 2014), and thus create scenarios in which indirect effects might be strong. In the temperate Chilean Andes, cushion nurses positively affect the abundance and performance of abundant invaders (Cavieres et al., 2005; Badano et al., 2007; Cavieres et al., 2008). In turn, this facilitation of invaders could ultimately suppress native species within cushion plants, and indirectly dampen the negative feedback effects of natives on the nurse (i.e. "a competitor's enemy is a friend", Levine, 1999; Callaway and Pennings, 2000). These types of indirect facilitation effects between nurses, natives and exotics have not been explored, especially in the context of studies on RFEs. More generally, indirect facilitation and non-transitive plant-plant interactions have received limited empirical attention, although they can be an important mechanisms for promoting species coexistence (particularly in species rich communities), and considerably expand our understanding of community assembly rules and species interdependence (Callaway 2007; Brooker et al., 2008; Filazzola and Lortie 2014; Aschehoug et al., 2016).

Here, we analyze the RFEs of native species and a dominant exotic (*Rumex acetosella* L.) on the flowering of a cushion nurse plant, *Arenaria*

musciformis Triana & Planch, in a tropical alpine ecosystem in the high Andes of Venezuela. There has been little previous research on the role of facilitation and nurse plants on community structure in the tropical alpine of the Andes (see review by Anthelme and Dangles 2012). This represents an important knowledge gap since these systems, known as *páramos* in the Andes, comprise more than 90% of the global tropical alpine biome (Jacobsen, 2008). They also host a very diverse flora with outstanding levels of endemism (Simpson and Toddzia, 1990). In the páramos of Ecuador and Venezuela, cushion plants can increase local species richness and facilitate other species in the community, with facilitation increasing in importance at higher elevations (Sklenář, 2009; Anthelme et al., 2011; Hupp et al., 2017). In the high Venezuelan páramos, nurse shrubs also increase local species diversity, modify community structure and improve the performance of other associated species (Cáceres et al., 2015; Ramírez et al., 2015).

To our knowledge, RFEs of beneficiaries on nurses have only been studied at two sites in the páramo, in Ecuador and Venezuela, in the broader context of a global study on RFEs (Schöb et al., 2014c). In these tropical alpine sites, no feedback effect of beneficiaries on the flower production of cushions was found. However, this study did not distinguish between the effects of natives vs. exotic beneficiaries. In Venezuela, the exotic forb *Rumex acetosella* (called *Rumex* hereafter) has become a dominant herbaceous species both in cushions and in open spaces. *Rumex* is also one of the most widespread exotic species in the high tropical Andes. Consequently, this is an ideal study system to explore potential direct and indirect interactions among nurse cushions, native beneficiaries, and exotic beneficiaries. Here we investigate how native and exotic beneficiaries may differ in their feedback effect on nurses. We asked the following questions: 1) Does the cushion species *A. musciformis* facilitate the abundance of other native plants and the exotic *Rumex*? 2) Do the feedback effects of native beneficiaries on flower production of *A. musciformis* differ than those of *Rumex*? 3) What is the relationship between *Rumex* abundance and the density of native plants? And 4) Do these effects differ inside vs. outside of the cushions? We investigated these questions by comparing the abundance of native species and *Rumex* inside and outside of cushions. Then we reanalyzed data from Venezuela included in Schöb et al. (2014c) on the relationship between the number of flowers produced by *Arenaria* cushions and the density of beneficiaries inside cushions, but separating the effects of *Rumex* and the natives. Finally, we analyzed the relationship between the abundance of *Rumex* and the abundance of the natives inside and outside the nurse, to evaluate the possibility of indirect effects of the exotic on the nurse.

2. Methods

2.1. Study site

The study was conducted in the northern tropical Andes, in the Piedras Blancas páramo, Sierra de La Culata National Park, Venezuela, during January 2014, the dry season. Sites were located between 4250–4350 m, on northeast facing slopes with inclinations ranging between 15 and 25°. We sampled at three similar sites within a 5 km² area: Rio Azul (Lat 8.8866,Long −70.8685), Avenida (8.8847, −70.8666), and Gloria (8.8928, −70.8714). Mean annual temperature is 3 °C ± 2.7 and relatively constant throughout the year, but daily topsoil temperature can range from 40 °C during the day to less than −5 °C at night (Ramirez et al., 2015). This region has an average annual precipitation of 860 mm with a dry season between December and March (*Pico El Águila* weather station, 4118 m). The soils at the study sites are entisols, shallow, with a coarse sandy texture, acid and with low soil organic matter levels, and subject to constant disturbance by needle-ice formation due to daily freeze-thaw cycles (Pérez, 1987).

The plant community in these high páramo areas generally attains less than 40% cover and the vegetation is highly clustered. Cover is partitioned to some degree into two strata, one dominated by giant

rosettes and shrubs, and the other consisting of cushions, grasses, forbs, and acaulescent rosettes (Cáceres et al., 2015). Our focal nurse plant, *Arenaria musciformis* (Caryophyllaceae, called *Arenaria* hereafter), is one of the most abundant cushion species in the region. It is endemic to the northern páramos of Colombia and Venezuela (3500 and 4500 m, Briceño and Morillo, 2002). The exotic invader forb *Rumex acetosella* has become the dominant species in terms of cover and density within the lower vegetation stratum in our study region, and it is the only exotic species present at our study sites (Cáceres et al., 2015). *Rumex* was introduced into the Venezuelan páramos from Europe with wheat cultivation during the 1800's (Salgado-Labouriau and Schubert, 1977). Sarmiento et al. (2003) and Llambí et al. (2003) described *Rumex* as a ruderal, fast growing heliophile species in páramos at lower elevations (between 3300 and 3800 m), which strongly dominates early stages of secondary succession in agricultural old-fields, being almost completely displaced by the natives after about 10 years. However, *Rumex* has expanded its distribution from the agricultural belt into high sub-nival environments, probably taking advantage of the increase in bare soil cover with elevation and reduced competition with tall native plants at high altitudes.

2.2. Sampling design

At each of the three study sites we haphazardly selected 35 individual *Arenaria* cushions within a 200×200 m area. We only sampled individuals with their maximum length measuring at least 20 cm. We placed a wire ring 20 cm in diameter on each cushion plant and recorded the identity and abundance (number of individuals) of all vascular plant species within. We defined individuals as ramets, as some species in the páramo, including the exotic *Rumex*, are interconnected underground. Then, we randomly sampled open substrate 1 m from each cushion (in 35 paired samples at each site) and measured the abundance of all plant species within the rings in the same way we did inside the cushion. Hence, a total of 105 samples were collected inside and 105 outside of cushions across the three sites. The average maximum length and width of the 105 *Arenaria* individuals included in the sample across the three sites was 51.6×29.3 cm. At each of the three sites we also quantified the cover of our focal cushion species using the line-intercept method (Greig-Smith, 1983).

To estimate the density of flowers within *Arenaria* cushions, we haphazardly placed five 10×2.5 cm micro-quadrats within each of the 105 cushion plants sampled, and counted all the flowers present within each micro-quadrat. The majority of the cushions in the research sites were in flower during our study.

2.3. Data analysis

We first calculated the total number of individuals (density) of all native vascular plant species found inside and outside of *Arenaria* cushions. We also calculated the density of *Rumex*. Then, to analyze the relationship of the cushion with the abundance of natives and *Rumex*, we calculated the Relative Interaction Index (*RII*, Armas et al., 2004) for each replicate pair using the formula $RII = N_{cushion} - N_{open} / N_{cushion} + N_{open}$, where N represents the density of the natives or invader species. We then averaged these values and calculated the 95% confidence interval across all replicate pairs combining the three sites and for each site separately. RII values range from 1 to -1, where positive values suggest a net facilitative effect (with the 95% confidence interval not including zero) and negative values indicate a net antagonistic effect of cushions on native/exotic densities. The average density of both natives and *Rumex* inside vs. outside of the cushions was also compared using a two-way permutational analysis of variance (PERMANOVA) using the Permanova + for Primer 6.0 software (Anderson et al., 2008). Here, we defined the local sampling situation as a fixed factor with two levels (inside vs. outside *Arenaria*) and the sampling site as a random factor with three levels (the three study

sites).

To evaluate the feedback effect of both the density of natives and invaders on the number of flowers produced by *Arenaria,* we used a generalized linear mixed-effect model. Data were analyzed with the *glmmadmb* function from the *glmmADMB* package (Bolker et al., 2012) of the R software (version 2.15.1). Given that the response variable (i.e. number of flowers) corresponds to counts, we assumed a negative binomial error distribution with a log-link function. Density of native plants and the invader *Rumex* were included as additive fixed effects, and the sampling site as a random effect, allowing the intercept to vary among sites. Since we had five replicate flower density measurements *per* cushion plant, we defined the individual cushion identity as a random factor nested within the sites.

Finally, to analyze the effect of the density of the exotic *Rumex* on the total density of native plants, both inside and outside the cushions, we used linear mixed-effects models. Data analysis was carried out using the *lme* function from the *nlme* package (Pinheiro et al., 2015) of the R software (version 2.15.1), assuming a Gaussian error distribution, and a quadratic relationship between predicted and response variables. The density of *Rumex* and type of habitat (i.e. inside *vs* outside cushions) were included as interactive fixed effects, to evaluate if the quadratic relation between *Rumex* and Native densities depends on whether the plants are inside or outside cushions; the sampling site was included as a random effect. We log transformed the response variable (i.e. density of native pants) as $ln + 1$ to fulfil the normality assumption (Shapiro-Wilk test).

3. Results

At the *Rio Azul* and *Avenida* sites, *Arenaria musciformis* comprised 2% of the total landscape cover, while at the *Gloria* site the cover of the cushion was 5%. The average size of each of the 105 cushions of *Arenaria* included in our sample was 0.49 ± 0.04 m^2 (with no differences between the three replicate sites).

3.1. Effect of cushions on native and invader densities

The Relative Interaction Index (RII) indicated a positive effect of *Arenaria* cushions on the density of native plants, but no effect on *Rumex* (Fig. 1). The average ($\pm$ SE) density of native plants inside *Arenaria* was 75.8 ± 9.1 individuals m^{-2} *versus* 37.3 ± 6.2 per m^{-2} in open areas around cushions (*pseudoF* = 25.32; $p = 0.0384$). There was no significant site effect ($p = 0.3251$) and no interaction between site and microhabitat ($p = 0.6244$; i.e. the positive effect of cushions on
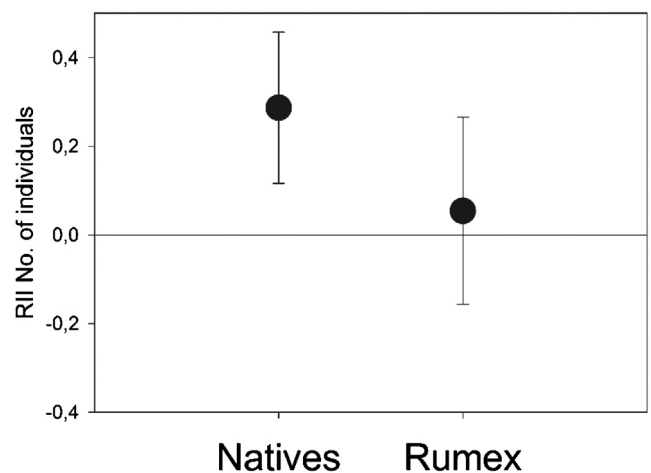

Fig. 1. Mean relative interaction index (RII) and $\pm$ 95% confidence levels for local total density of natives plants and the exotic invader *Rumex acetosella* sampled in rings placed inside and outside *Arenaria muscuformis* cushion plants at three sites in the Venezuelan high páramo.
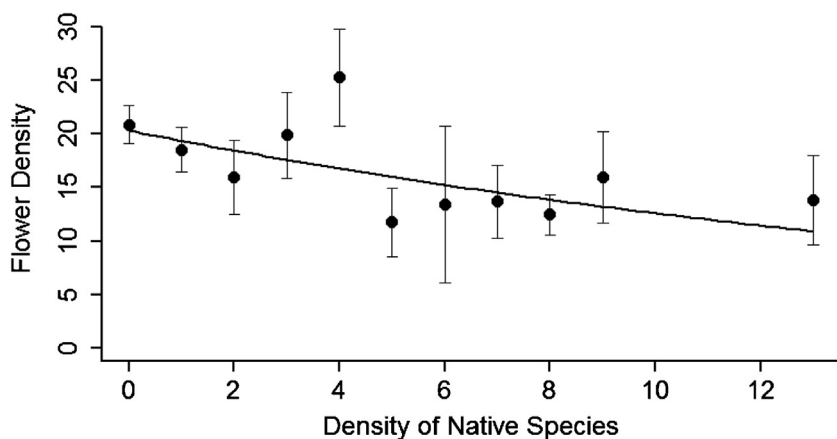
Fig. 2. Relationship between *Arenaria musciformis* flower density (flowers per micro-quadrat) as a function of the total density of native plants within the sampling rings. Symbols represent mean ± SE, while the solid curve the regression equation estimated from the negative binomial model.

native plants was consistent across the three sites). For *Rumex*, the average density inside the cushions was 27.6 ± 4.4 per m^2 versus 30.9 ± 5.1 per m^2 in the open areas, and this difference was not statistically significant (*pseudoF* = 1.33; *p* = 0.3608). There was a significant difference in the exotics abundance between the study sites (*pseudoF* = 15.90; *p* = 0.001), and no interaction between site and microhabitat (i.e., *Rumex* densities did not differ inside vs. outside of *Arenaria* in any of the three sites).

Both inside and outside of the cushions, species accumulation curves approached asymptotes indicating that our sampling represented most of the local species pool (see Hupp et al., 2017). Across the three sampling sites, more vascular plant species accumulated inside *Arenaria* cushions (30 spp.) than in the associated open samples (23 spp.).

3.2. Effects of native and invader densities on cushion flower density

The mixed-effects model for flower production by *Arenaria* as a function of the density of natives and invaders, showed a significant negative relationship between the density of natives and flower produced by the cushion (Fig. 2, $\beta_1 = -0.047$, *SE* = 0.023, *p* = 0.038), but not for the density of *Rumex* ($\beta_2 = 0.075$, *SE* = 0.055, *p* = 0.137). The estimated mean number of flowers produced by the cushions decreased 53%, from 20.3 flowers per micro-quadrat^{-1} when native plants were absent to 10.9 flowers per micro-quadrat^{-1} at the maximum native plant density observed within the cushions.

3.3. Effect of invader densities on native densities

Across our three study sites, *Rumex* represented in average 26.7% of the total plant density within *Arenaria* cushions and 45.3% of the total density in open areas. This made *Rumex* the dominant species in open areas, and co-dominant with the grass *Agrostis breviculmis* within cushions. There was a complex density-dependent relationship between the exotic *Rumex* and the density of native plants, both inside and outside the cushions. In both cases, the abundance of native species showed a hump-shaped relationship with the abundance of *Rumex* (Fig. 3). This was explained by a quadratic function, with parameters $\beta_1 = 0.676$, *SE* = 0.084, *p* < 0.001, $\beta_2 = 0.650$, *SE* = 0.154, *p* < 0.001, $\beta_3 = -0.142$, *SE* = 0.037, *p* < 0.001, inside the cushions, and $\beta_1 = 0.297$, *SE* = 0.084, *p* < 0.001, $\beta_2 = 0.599$, *SE* = 0.154, *p* < 0.001, $\beta_3 = -0.099$, *SE* = 0.037, *p* = 0.001, outside the cushions (Fig. 3). The only parameter of the quadratic function that was different between the two fitted curves was the intercept (i.e. β_1) (estimated ± SE = −0.37 ± 0.11, *p* = 0.001), which was higher inside the cushions. This indicates that when *Rumex* was not present, the density of native plants is higher inside cushions than outside. Aside from this, the linear (i.e. β_2) and quadratic (i.e. β_3) parameters of the polynomial function were not statistically different inside *vs* outside the cushions (estimated ± SE = −0.51 ± 0.203, *p* = 0.802, and

0.043 ± 0.045, *p* = 0.345, respectively).

4. Discussion

The general aim of this study was to evaluate if the feedback effects on the reproductive output of nurse cushions differed between native plants and a common exotic invader (*Rumex acetosella*) in tropical alpine communities. We found that native beneficiaries had a direct negative effect on the cushion flower production, but the exotic did not. However, because at high densities the exotics show a negative effect on the abundance of natives within cushions, they could indirectly modulate the native's effect on the cushion fitness. Hence, our results highlight the need to consider both direct and indirect interactions for interpreting the complex reciprocal relations that can develop between nurses and beneficiaries of contrasting adaptive strategies and/or origins (i.e. natives *vs* exotics). Moreover, it offers an original way to explore indirect non-trophic interactions between plants, and their importance for community organization.

4.1. Cushion effects on the abundance of natives and exotics

To evaluate the RFEs of natives and exotics on the nurse, we first needed to analyze their relationship with *Arenaria*. Our results indicated that *Arenaria* cushions had a positive effect on the density of native plant species, but no effect on the exotic *Rumex*. At these same study sites Hupp et al., 2017 found a positive effect of *Arenaria* cushions on local plant species richness, a significant increase in soil organic matter, and a decrease in temperature amplitudes within these cushions. Interestingly, the other abundant cushion species at these sites, *Azorella julianii*, had a positive association with *Rumex*, and a positive effect on soil water, while *Arenaria* did not (Hupp et al., 2017). *Rumex* has a lower water use efficiency than many native páramo species (Llambí et al., 2003), and this may explain its positive association with *Azorella* but not with *Arenaria*. More generally, these results suggest that interactions between the exotic and cushions can be species-specific, which in turn might drive different kinds of reciprocal interactions than those we report here. Other studies in the high páramos of Ecuador reported positive effects of *Arenaria* and *Azorella* cushions on plant abundance and local richness, but only at sites above 4600 m (Sklenár, 2009; Anthelme et al., 2011).

4.2. Feedback effects of natives and the exotic Rumex on cushion reproduction

Previous results from the high tropical Andes of Ecuador and Venezuela indicated a neutral effect of benefactor densities within cushions on the nurse reproductive output (Schöb et al., 2014c). However, when we separated the RFE of natives and exotics, our results indicated a significant negative effect of native abundance on the flower
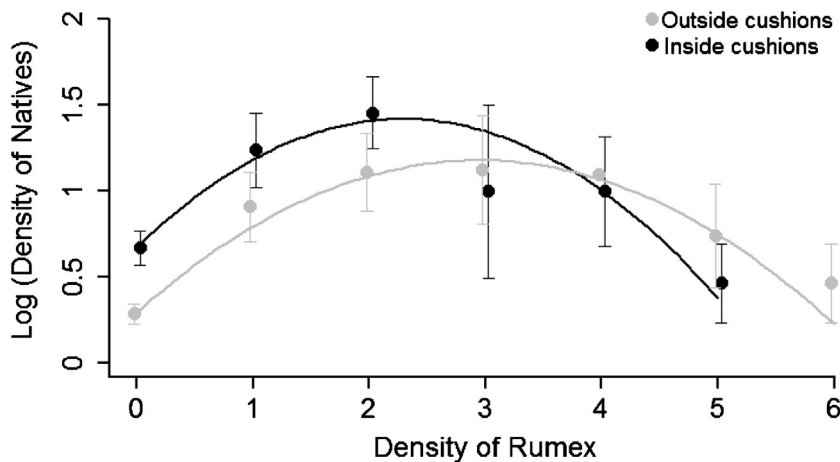
Fig. 3. Relationship between the density of native plants as a function of the density of the invader *Rumex acetosella,* both inside and outside the cushions. Symbols represent mean ± SE, while the solid curves the quadratic equations estimated from the mixed effect model for inside (gray) and outside (black) cushions.

density of *Arenaria*. We observed 53% fewer flowers in cushions where the maximum native density was observed, compared to cushions with no natives. In contrast, *Rumex* density had no significant correlation with flower density. This suggests that the native community has a 'parasitić relationship with nurse cushions in our systems, as has been recently reported across many temperate alpine sites (Schöb et al., 2014b, 2014c). However, we evaluated RFE using flower density, and further research is needed to explore how this relates to fruit and seed set and seed quality. Even so, previous research on feedback effects of beneficiaries on cushion reproduction indicates that a reduction in flower densities is consistently associated with a reduction in seed production (but not seed quality or fruit set), in both experimental and observational contexts (Schöb et al., 2014b; but see García et al., 2016). This would be compatible with the reproductive feedback effects being induced by resource competition between the natives and the cushion (Schöb et al., 2014a). Negative feedback effects mediated by pollinator competition seem less likely, as many of the dominant species in the native community growing within the nurse in our system are wind-pollinated grasses (Hupp et al., 2017), whereas *Arenaria* cushions are pollinated by insects (Wyat, 1986).

The lack of a significant effect of *Rumex* on *Arenaria* flower densities may have been due to an indirect positive effect derived from the substantial decrease in abundance of natives at high densities of *Rumex* (see below). This may also explain why Schöb et al. (2014c) did not find significant feedback effects from beneficiaries on the flower density of other cushion species. To explore this would require experimental manipulation of the densities of natives and exotics. Interestingly, interactions with native species mediated by pollinators are also unlikely in the case of *Rumex*, as it is wind pollinated (Friedman and Barret 2009). This contrasts with the case of the alien *T. officinalis* in Chile, which competes with native species for insect pollinators (Muñoz and Cavieres 2008).

4.3. Effects of Rumex on native plant densities

Rumex was the dominant species outside cushions, and co-dominant with the grass *Agrostis breviculmis* inside cushions. Moreover, *Rumex* seemed to have a density-dependent effect on the abundance of natives. We found a quadratic relationship between the density of *Rumex* and native plants species as a group both inside and outside the cushions. Both natives and *Rumex* increased in abundance at low densities, but at high densities of the exotic, the natives showed a marked decrease in abundance, indicating a competitive effect of *Rumex* (and the possibility of an indirect facilitation effect on the nurse). Interestingly, the same quadratic relationship was found between *Rumex* density and native species richness (results not shown). We did not find a significant reciprocal effect of native abundance on the density of *Rumex*. We suspect that at low densities of *Rumex*, both native species and the

exotic increase in abundance in response to microhabitat quality, inside and outside of cushions. Inside cushions, this could be due to observed differences in the cover of dead-tissue patches within different *Arenaria* individuals, which could have influenced the quality of cushions as facilitators, modifying how other plant species occupy them (e.g. Anthelme et al., 2017).

The contrasting behavior of *Rumex* and the natives could be linked both with its exotic character (offering an advantage through mechanisms such as the scape from natural enemies) and several adaptive traits which could make it a strong competitor in high tropical alpine ecosystems. *Rumex* has been found to behave as a ruderal in páramo old-fields at lower elevations and to have a higher SLA, higher leaf N, CO_2 assimilation and growth rates than other native páramo species (Llambí et al., 2003). It is also very effective in expanding both clonally (thorough rhizomes and an extensive root system) and via seeds (Escarre and Houssard, 1989). This could explain why *Rumex* is able to displace the natives when it can attain high densities in favorable microsites, such as in open subnival environments dominated by low-stature, slow growing, stress-tolerant plants, and where soil disturbance by solifluction is common (i.e. outside cushions, where it is the dominant species).

Though our research provides evidence that high exotic densities can have a negative effect on native species, this does not always seem to be the case. For example, in the Australian Alps *Rumex* has been common in the alpine zone for at least 60 years, but there is no evidence of negative effects on native species richness (Alexander et al., 2016). Furthermore, in a Mediterranean ecosystem in the central Andes of Chile, Cavieres et al. (2005) found a positive correlation between the exotic *Taraxacum officinale* and the density and species richness of natives within cushions. In open areas, there were no differences in overall native density or richness with or without the exotic, but several species showed negative associations with *T. officinale*.

5. Conclusions

Our results indicate the potential existence of complex reciprocal effects between nurses, natives and exotic plants in the high tropical Andes, and that natives and exotics differ in their feedback effects on the nurses (Fig. 4). Native plant species were facilitated by *Arenaria* cushions, and the native community growing within *Arenaria* had a negative feedback effect on this nurse plantś flower production, suggesting a parasitic relationship. In turn, we found no significant relationships between the exotic *Rumex* and *Arenaria*. But at high densities, the invader was associated with much lower densities of native species both inside and outside cushions. This may have an indirect positive effect on the cushionś reproduction through the reduction of the density of natives within them. These conclusions are based on spatial associations and correlative patterns, and need to be further
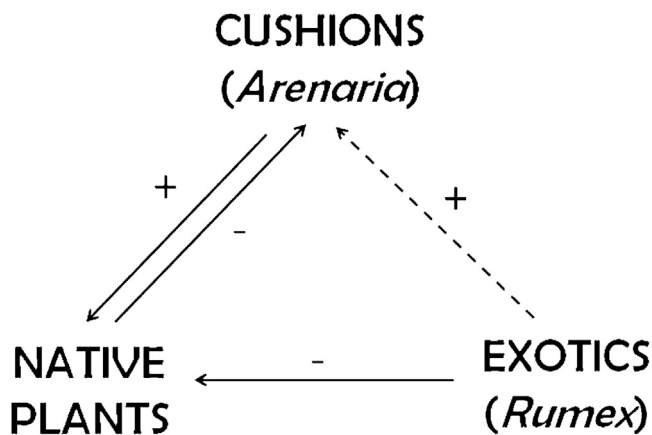
Fig. 4. Schematic diagram representing the potential nature of the interactions between our focal cushion plant (*Arenaria musciformis*), the other native species in the community and the exotic *Rumex acetosella*. Solid arrows indicate direct positive (+) or negative effects (−), while the dotted arrow indicates the possibility of an indirect positive effect of *Rumex* on the cushions reproduction mediated by the exotics negative effect on native beneficiaries.

explored through manipulative experiments. Even so, our results suggest the possibility of complex direct and indirect reciprocal interactions between facilitators and beneficiaries and emphasize the importance of documenting the impacts of exotic invaders on alpine plant communities.

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