RESEARCH ARTICLE

Effects of indirect facilitation on functional diversity, dominance and niche differentiation in tropical alpine communities

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Abstract

Question: Positive interactions between plants have well-known effects on community species richness and biomass via micro-environment improvements. However, the effects of indirect facilitation performed by a nurse on an associated plant community, occurring e.g., through protection against grazing, have not attracted much attention in the literature so far, in particular regarding the functional traits of the associated plant communities. Because characteristics of trait distributions can reveal selective pressures at play, they offer valuable information for the study of grazing pressure. Here, we tested the extent to which indirect facilitation affects the amount of distinct trait combinations (H1), trait dominance (H2) and niche differentiation between species (H3) of associated plant communities living under nurse plants.

Location: Tropical alpine peatlands, Cordillera Real, Bolivia.

Methods: We set up a grazing exclusion experiment over two dominant nurse cushion species: one providing indirect facilitation under grazing pressure and the other not. We measured three functional traits in the associated communities, which are known to vary depending on the grazing level: LDMC, leaf thickness and maximum height. We assessed the amount of distinct trait combinations by computing the volume of the phenotypic space (H1). The variation in trait dominance was quantified with kurtosis and skewness of the trait distributions (H2). The variation in niche differentiation was evaluated using mean intra-population trait variance relative to intra-community trait variance (H3).

Results: We did not find a significant effect of grazing and indirect facilitation on the volume of the phenotypic space (H1). However, our study revealed a significant effect of indirect facilitation on dominance in the associated communities by maintaining the evenness of the trait distributions (maximum height and leaf thickness) in grazed compared to ungrazed plots (H2), and on niche differentiation by maintaining trait overlaps (LDMC and maximum height) between species in grazed compared to ungrazed contexts (H3).

Conclusion: Our results suggest that indirect facilitation promotes the co-existence of contrasting functional strategies (H2) and species niches (H3) in associated plant communities subject to grazing. These results reflect the buffering effect of indirect

facilitation on the grazing selective pressures exerted on associated plant communities living under the protection of nurses.

1 | INTRODUCTION

Interactions between organisms are fundamental drivers of community composition, which in turn determines ecosystem properties such as productivity and resilience. Abiotic constraints (i.e., stress and disturbance) and negative interactions (i.e., competition and predation) have traditionally been considered to be the main processes structuring ecological communities (Vellend, 2010), although numerous studies have also outlined the importance of facilitative interactions (Bertness & Callaway, 1994; Callaway, 2007; Cardinale, Palmer, & Collins, 2002; Wright, Wardle, Callaway, & Gaxiola, 2017). Direct facilitation from a facilitator to an associated species arises from improvement of the surrounding abiotic environment, such as water retention, decrease in evapotranspiration and shading (Filazzola & Lortie, 2014). Indirect facilitation between two species occurs via a third species, most commonly arising from niche specialization (Levine, Bascompte, Adler, & Allesina, 2017), shared competitors (Wootton, 1994) or grazing (Danet, Kéfi, Meneses, & Anthelme, 2017b; Milchunas & Noy-Meir, 2002). For example, an unpalatable plant (hereafter referred to as a "nurse") can reduce the feeding rate of a grazer on palatable plants growing in the neighbourhood of the nurse (the so-called associated community), resulting in indirect facilitation from the nurse to the associated community.

Empirical and theoretical studies have shown that direct and indirect facilitation could contribute to locally increase species richness, productivity and biomass (Callaway, 2007; Graff, Aguiar, & Chaneton, 2007; Michalet et al., 2006, 2015). Those previous studies have, however, rarely investigated the associated changes in functional traits (Butterfield & Callaway, 2013), apart from a few pioneering studies (Gross et al., 2009, 2013; Schöb, Armas, Guler, Prieto, & Pugnaire, 2013; Schöb, Butterfield, & Pugnaire, 2012; Soliveres et al., 2014). Investigating the variations in plant morphological traits is one way to better understand the underlying processes leading to facilitation (Pawar, 2015; Violle et al., 2007). For instance, the Leaf Dry Matter Content (LDMC) is closely related to a plant's relative growth rate (Garnier, Navas, & Grigulis, 2016) and to the species susceptibility to herbivory (Gross, Liancourt, Butters, Duncan, & Hulme, 2015). In the context of grazing, it is predicted that low LDMC species will benefit more from the shelter of a nurse than less palatable, high LDMC species (Liancourt, Callaway, & Michalet, 2005). Schöb et al. (2012) also showed that the plant communities associated with alpine cushions had different trait value ranges from those found in open areas. While previous studies have shown that using a trait-based approach may help to understand

the outcomes of competitive and facilitative interactions between species, very few have examined how direct and indirect facilitative interactions impact the community structure as a whole (Gross et al., 2009). Thus, how facilitation shapes plant functional diversity and community structure constitutes a substantial research gap in community ecology (Enquist et al., 2015; Violle et al., 2012).

Facilitation has been hypothesized to increase functional diversity (Butterfield & Callaway, 2013; Gross et al., 2009; Schöb et al., 2012). However, there are multiple ways through which facilitation may impact community structure (Gross et al., 2009). (i) Previous studies have suggested that facilitation is especially beneficial to maladapted species that can persist at low abundance under the shelter of nurse species (Bruno, Stachowicz, & Bertness, 2003; Liancourt et al., 2005; Soliveres, Maestre, Berdugo, & Allan, 2015). By maintaining rare species with contrasted trait syndromes compared to the well-adapted nurse plant species, facilitation may therefore increase functional diversity by increasing the phenotypic space occupied by species in a community (phenotypic space hypothesis, H1). (ii) Studies have also shown that facilitation could benefit dominant species in some cases. Schöb et al. (2012) notably showed that, in response to increasing elevation, alpine cushions could either move, relax environmental pressures on associated communities or both, resulting in changes in the trait distributions observed in the associated communities. By modifying the environmental pressures, facilitation may impact the dominant status of species in communities and thus modify the trait abundance distribution of the whole community, possibly leading to flat or even bimodal trait distributions (Gross et al., 2009, 2017; trait abundance distribution hypothesis, H2). (iii) Moreover, facilitated species often co-occur under nurse species with other beneficiaries. Bulleri, Bruno, Silliman, and Stachowicz (2016) proposed that the facilitation of co-occurring beneficiaries could lead to a decrease in niche difference between beneficiaries via niche expansion of each beneficiary and thus to an increase in competition between them. In such a case, facilitation should result in more niche overlap between the species of associated communities. An alternative hypothesis could be that facilitation, by decreasing environmental pressure, enables beneficiary species to develop a larger range of traits and thus lead to an increase of the niche differences between beneficiaries (the niche differentiation hypothesis, H3). We tested these three alternative hypotheses (i–iii) on the role of indirect facilitation on the functional structure of plant communities.

Our study took place in tropical alpine peatland ecosystems of the Cordillera Real, Bolivia. As in most alpine environments (Callaway

et al., 2002), plant communities of tropical alpine environments are strongly driven by positive interactions among plants (Hupp, Llambí, Ramírez, & Callaway, 2017; Malatesta, Tardella, Piermarteri, & Catorci, 2016), but the mechanisms underlying those interactions differ (reviewed in Anthelme & Dangles, 2012).

In our study sites, cushion species are a source of direct facilitation and host specific plant communities that are not found outside the cushions (Loza Herrera, Meneses, & Anthelme, 2015; Ruthsatz, 2012). These ecosystems are used as rangelands (Buttolph & Coppock, 2004). Two cushion-forming species dominate the ecosystems: *Distichia muscoides* Nees & Meyen and *Oxychloe andina* Phil. (Loza Herrera et al., 2015; Raevel, Anthelme, Meneses, & Munoz, 2018). *D. muscoides* forms a compact cushion, which decreases the possibilities for a grazer to harvest their leaves. *O. andina* develops very sharp and long leaves which repel grazers. The two cushion species differ in other characteristics such as their compaction and height (see also Loza Herrera et al., 2015 for more details). Previous studies showed that *D. muscoides* is among the preferred food for camelid livestock (López López, 2004; Reiner & Bryant, 1986) but that *O. andina* is also consumed (Meneses, Beck, & Anthelme, 2015). As far as we know, there is no evidence for other types of protection against herbivores, such as chemical compounds, in either cushion species. Two recent studies suggested that the protection of *O. andina* against grazing extends to its associated community (indirect facilitation), whereas that of *D. muscoides* does not (Danet et al., 2017b; Raevel et al., 2018). We performed a grazing exclusion experiment and evaluated the response of the functional diversity of the associated communities in these two dominant nurse plants. Differences in the traits of the associated plant communities found in *D. muscoides* with and without grazing were expected to reveal the direct effects of grazing on the associated plant communities in the absence of indirect facilitation. In turn, comparison of the traits of the associated plant communities observed in *O. andina* with and without grazing was expected to reveal both direct and indirect effects. Therefore, comparing the effects exerted by these two nurse plants was expected to reveal the effect of indirect facilitation on the traits of the associated plant communities.

2 | METHODS

2.1 | Study site

Our study took place in the tropical alpine peatlands of the Palcoco Valley (16°08′50″ S, 68°17′08″ W) at an elevation of 4,500 m a.s.l. to the north of La Paz, Bolivia (Figure 1 and Supporting information Figure S1 in Appendix S1). The site has a dry tropical climate characterized by a short humid season (Dec to Mar, rainfall reaches 410 mm and average temperature is 6.4°C) and a long dry season (rest of the year, rainfall reaches 184 mm and average temperature is 4.5°C; Loza Herrera et al., 2015). Those peatlands, dominated by the two cushion species *D. muscoides* and *O. andina*, generate a specific wetland plant community that is absent outside the cushions (Loza Herrera et al., 2015; Ruthsatz, 2012). The cushion species are thus
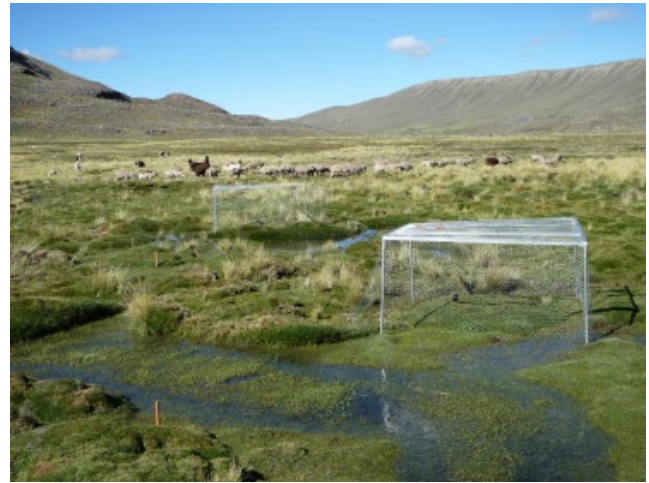

FIGURE 1 A peatland of the Palcoco valley showing two plots (front, right), one exclusion cage and one control (bottom; visible thanks to the wooden post). The structuring vegetation is composed of two cushion-forming plants: *Oxychloe andina* and *Distichia muscoides*. In the background, the cushions are increasingly colonized by the tussock grass *Festuca dolichophylla* spreading from the borders of the peatland [Colour figure can be viewed at wileyonlinelibrary.com]

considered obligate nurses through direct facilitation for a number of associated species.

2.2 | Experimental design

We set up a grazing exclusion experiment in two peatlands of the Palcoco valley 1.5 km distant from each other and taken as repetitions. Those peatlands are extensively grazed by a domestic herd of about 300 individuals, mainly llama (*Llama glama* L.), alpaca (*Llama pacos* L.) and a few sheep (*Ovis aries* L.). The metal fences (1.5 m × 1.5 m × 0.5 m; Figure 1) excluding grazers were established in Feb 2014 over *D. muscoides* and *O. andina* cushions. The fences were covered with chicken wire to also exclude medium to large herbivores naturally present, such as viscacha (*Lagidium* sp). The studied plots had an area of 1 m², with a 25-cm border on each side inside the cage to avoid side effects. The fenced plots displaying unexpected signs of grazing were excluded from the analysis. Note that the fences were not made to exclude small grazers, such as caterpillars, and it would be an interesting follow-up to estimate the importance of the effects of other grazers, such as caterpillars, which can also have an important effect on functional community structure (Deraison, Badenhausser, Loeuille, Scherber, & Gross, 2015). However, there is no reason to think that smaller grazers could create confounding effects. The control plots were paired to the fenced plots (1–2 m away) to increase the statistical power of the analysis of grazing effects. We sampled 40 plots in total: ten ungrazed over *O. andina*, ten ungrazed over *D. muscoides*, ten control plots over *O. andina* and ten control plots over *D. muscoides*. See Danet et al. (2017b) for a more extensive description of the experimental design.
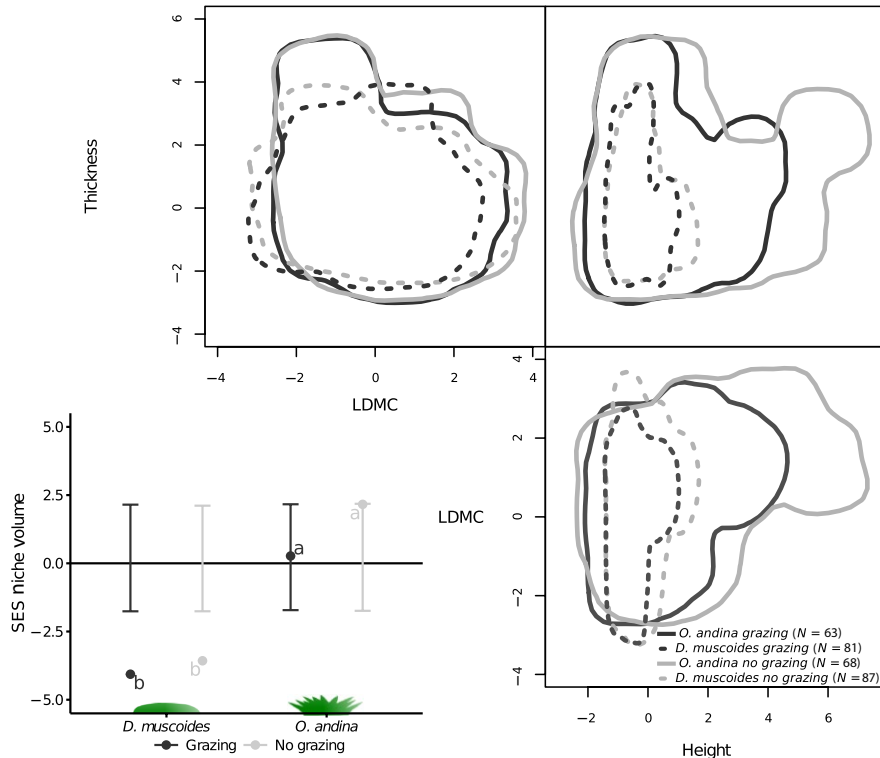
FIGURE 2 Main panel: hypervolume of the associated communities (N: number of individuals). Bottom left panel: Standardized effect sizes (SES) of phenotypic space of the associated communities inside the nurse cushion species for control (i.e., grazed; dark grey) and grazing exclusion (light grey). Error bars represent the limits at 95% of the distribution of the sizes of the null hypervolumes. Different letters represent significantly different groups according to post-hoc contrasts (Supporting information Table S3 in Appendix S1) [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Data collection

Plot sampling occurred 22 months after the start of the grazing exclusion, in December 2015. We collected relative cover, maximum height and leaves of all the associated species present in each of the plots. To assess the response of the associated plant communities to grazing, we measured three functional traits relevant in the context of grazing, which represent different dimensions of plant strategies (see Danet et al., 2017b; Raevel et al., 2018 for details on the variations of those traits in the same system under different grazing conditions). LDMC characterizes plant resource acquisition strategies and is negatively correlated with maximum relative growth rate because of a trade-off between resource acquisition speed and nutrient conservation (Westoby, Falster, Moles, Vesk, & Wright, 2002). LDMC has also been linked to palatability (Louault, Pillar, Aufrere, Garnier, & Soussana, 2005); high values of LDMC being correlated with low palatability. Together, those covariations reflect the growth–defence trade-off (Lind et al., 2013). There is also strong evidence that leaf mechanical properties play a role in deterring herbivores (Read & Stokes, 2006), notably leaf toughness (Ibanez, Lavorel, Puijalon, & Moretti, 2013). The physical resistance of the leaves is largely linked to their thickness (Pérez-Harguindeguy et al., 2013). Leaf thickness was thus used to assess variations in the physical resistance of the leaves. Although often measured as a major trait accounting for above-ground competition (Westoby, 1998), we also considered maximum height as the closest proxy for grazing effects (see Díaz, Noy-Meir, & Cabido, 2001) and as an indicator of above-ground biomass (Catchpole & Wheeler, 1992).

In each plot and for each species, we sampled three leaves on four individuals and measured the maximum height of those individuals.

For species with tiny leaves, we collected the whole individual (Danet et al., 2017b). The trait collection followed standardized guidelines (Pérez-Harguindeguy et al., 2013). In total, 357 individuals were sampled for the 30 associated species found in the whole data set. The data set can be found online (see Appendix 1; Danet, Kéfi, Meneses, & Anthelme, 2017a).

2.4 | Data analysis

The trait measurements were averaged to give a single observation per species and per plot for each functional trait. Trait values were standardized (i.e., centred and scaled) across the whole data set to make their variations comparable, in particular for comparisons of the phenotypic space.

Since the plots contained only a few data points and since the species abundances were highly variable because of the extreme environmental conditions, we pooled all the replicates (plots) of a given treatment combination for the subsequent analysis; this means that we had one community per treatment combination, i.e., four different communities in total (see Figure 2). Statistical inference was obtained by permutations and

$$SES = \frac{x_{obs} - \bar{x}_{null}}{s_{null}} \quad (1)$$

resampling methods. In simple terms, we randomized trait values in the communities and compared the observed communities to the randomized ones. This method is common for analysis of the phenotypic space and of the species niche differentiation; the details of null community computation are given in the following parts. The null communities provided a null distribution of parameters from

which Standardized Effect Sizes (SES) were derived as the difference between the observed value of a parameter (x_{obs}) and the mean value of the null parameter distribution ($\bar{x}_{null}$), divided by the SD of the null parameter distribution (s_{null}) (Equation 1).

We used the null distributions to define the confidence intervals with α = 0.05, by reporting the positions of the quantiles at 0.025 and 0.975. We derived *p*-values by computing the proportion of the N null communities ($x_{i,\ null}$) showing an absolute difference superior or equal to the observed one (Equation 2). We considered the difference as significant when this proportion was inferior to 5%.

$$p = \frac{\sum_{i=1}^{N} (|x_{i,null}| \geq |x_{obs}|)}{N} \qquad (2)$$

2.5 | Hypotheses

In the absence of plant communities outside the cushion species (see Section 2.1), the comparison between the two cushion species in both grazed and ungrazed conditions is the only way to assess the effect of indirect facilitation on the associated plant communities. For a given variable, (a) if the ungrazed plots are not different from the grazed plots in both cushions that would suggest that grazing had no significant effect; (b) if grazed and ungrazed plots are different for both cushion species it would be difficult to reach conclusions about indirect facilitation; (c) if there are differences between ungrazed and grazed plots in *D. muscoides* and not in *O. andina*, that would suggest that *O. andina* protects its associated communities against grazing, providing evidence of indirect facilitation; finally, (d) if the ungrazed plots are different from the control plots only in *O. andina*, that would contradict our expectation that the protection against grazing provided by *O. andina* was better than that of *D. muscoides*. The comparison between the grazed and ungrazed treatments in each of the cushion species allows us to isolate the effect of large mammal herbivores from potential differences in facilitation mechanisms between the two cushion species. Previous studies have documented the difference in protection between *D. muscoides* and *O. andina*, and shown that the protection of *O. andina* against grazing extends to its associated community, whereas that of *D. muscoides* does not (Danet et al., 2017b; Raevel et al., 2018), suggesting that our design is well suited to evaluate the effects of indirect facilitation on associated communities.

2.5.1 | H1: Phenotypic space

To characterize the amount of distinct trait combinations found in the associated communities, we evaluated functional diversity by computing the phenotypic space occupied by the associated communities, which is the multidimensional space occupied by all trait combinations. This measures the range of life strategies present in a given community. The phenotypic space is a representation of the functional richness; a lower volume has been suggested to lead to a lower productivity, lower resistance to invasions and lower buffering of environmental conditions (Mason, Mouillot, Lee, & Wilson, 2005).

Hypervolume computation

The phenotypic space was obtained by computing a hypervolume containing all the trait combinations of the associated communities. Here, the hypervolume was restricted to a volume since only three traits were considered (maximum height, leaf thickness and LDMC). The unit of the volumes is expressed in numbers of *SD* of the centred and scaled trait values (SD^3). Hypervolumes were computed with the R package hypervolume (Blonder, Lamanna, Violle, & Enquist, 2014) with the recommended parameters of the package. The hypervolume is computed with a multidimensional kernel density estimation. More details on the methods can be found in Blonder et al. (2014), and some applications can be found in the literature (Loranger et al., 2016). Other approaches to analyse functional diversity in a multidimensional phenotypic space have been proposed (Carmona, de Bello, Mason, & Lepš, 2016), but have, as far as we know, not yet been implemented. Each of the traits made a different contribution to the phenotypic space, but the hypervolume building was not highly unbalanced toward any one variable (Supporting information Table S1 in Appendix S1), suggesting that the trait combinations were not driven by one variable.

Null model

To test if the volume of the phenotypic space occupied by the associated communities was different from that of a random mix of individuals coming from all the data set, we computed a null phenotypic space. Therefore, we simulated 5,000 null communities for each of the observed communities. Each null community was built by sampling individuals in the regional pool (the whole data set) assuming that it has the same number of individuals as the observed one. Indeed, keeping the number of individuals identical in the observed communities and in their null counterparts is important, since size of the phenotypic space is expected to increase with the number of individuals (Blonder et al., 2014).

Hypothesis testing

To test if the differences in phenotypic space between treatments were significant, we compared the observed differences to the expected differences drawn from the null communities simulated as described above (Equation 2).

2.5.2 | H2: Abundance trait distribution

To characterize the distribution of abundances of traits values, we computed their kurtosis and skewness, two parameters describing the shape of a distribution (respectively the "tailedness" and "asymmetry" of a distribution). High values of kurtosis mean that the distribution is peaked and that the abundance of traits is unevenly distributed, indicating the dominance of a few trait values. In contrast, low values of kurtosis mean that the distribution of traits is flat and that the abundance of traits is evenly distributed, indicating low dominance (Enquist

et al., 2015; Le Bagousse-Pinguet et al., 2017). High values of skewness mean that the distribution is asymmetric and that the abundance of traits is biased towards one direction (low or high trait values), indicating the presence of extreme trait values (Enquist et al., 2015; Le Bagousse-Pinguet et al., 2017).

Subsampling

To estimate the community trait distributions, we subsampled individuals (i.e., observations) in species trait distributions (Enquist et al., 2015). We assumed that the distribution X_{ijk} of trait i of species j in a particular community k follows a normal distribution of mean μ_{ijk} and SD σ_{ijk} (Equation 3).

$$X_{ijk} \sim N(\mu_{ijk}, \sigma_{ijk}) \tag{3}$$

Based on the values of μ_{ijk} and σ_{ijk} estimated from the data in each community, trait values were sampled in this distribution for n individuals per species, where the number of individuals was determined by the total number of individuals observed in the community (N) weighted by the relative cover of the species in the community. The advantages of this approach are that it allows more realistic trait distributions by using most of the information contained in the trait measurements and takes into account intra-specific trait variations (Enquist et al., 2015).

We only kept species that had at least five measurements for a given trait in a community to compute relevant estimates of SD. The relative biomass of each species was approximated using their cover. The total cover of each species in the community was determined by summing their cover values across the plots. The relative cover of each species in the community was obtained by scaling the sum of their cover to 1. Since there was an average of 6.5 species in each community, considering an average of ten individuals per species and plot, we proposed $N = 650$ as a realistic number of individuals in each community.

Parameter estimation

We computed the skewness and kurtosis of the simulated trait distributions X_{ijk}. Since we did not have community replicates per treatment, we used the jackknife method to evaluate the standard error of our parameter estimation (Chernick & LaBudde, 2011). Jackknife computes parameters by removing one data point at a time and repeating the procedure as many times as the number of data points in the data set. To see if the parameters of the trait distributions were sensitive to one particular species, we computed the trait distribution parameters with one species of the community removed, as many times as the number of species present in the community. To decrease variability due to the subsampling procedure, we ran three simulations for each species removal. We then averaged the parameter outputs of those three simulations.

Hypothesis testing

We used the variability created by the jackknife procedure to compute 95% confidence interval (CI) of the parameters and to compare the treatments with each other. We performed Mann–Whitney rank tests to compare the treatments, and used the Benjamini and Hochberg (1995) correction method to control for inflation of the type I error due to multiple comparisons.

As skewness and kurtosis are mathematically linked (Gross et al., 2017), we also tested if the link between kurtosis and skewness changed across treatments. Details of the analysis and of the results can be found in Supporting information Appendix S1 (Figures S2 and S3); we did not find differences in the link between kurtosis and skewness, meaning that the variations in skewness and kurtosis were constrained by their mathematical relationship, thus could not be interpreted independently.

2.5.3 | H3: Species niche differentiation

Niche differentiation is defined as the degree of separation between the traits of the species in a community. Niche theory predicts that the more the species traits overlap with each other, the more those species compete with each other because they harvest the same resources. A corollary is that species that have a perfect niche overlap should not be able to co-exist (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Macarthur & Levins, 1967). We tested here how grazing and indirect facilitation affected the niche overlap between species.

To determine the niche differentiation of the species in the communities, we used the $T_{IP/IC}$, which is part of the T-statistics developed in Violle et al. (2012). The $T_{IP/IC}$ is the mean intra-population variance relative to the intra-community variance; it is computed as:

$$T_{\frac{IP}{IC}} = \frac{\frac{1}{N} \sum_{i=1}^{N} \sigma_{IP,i}^2}{\sigma_{IC}^2} \tag{4}$$

with $\sigma_{IP,i}^2$ the trait variance of species i, σ_{IC}^2 the trait variance of the community and N the number of species.

If the distributions of traits of the populations in a community completely overlap with each other, $T_{IP/IC}$ is equal to 1. In contrast, if species traits are perfectly separated inside the community, $T_{IP/IC}$ tends toward 0. The index was computed with the R package cati (Taudiere & Violle, 2016). We obtained one value per community and per trait.

We used a permutation procedure to determine if the differences between communities were significant. We compared the differences between treatments observed in the data to those expected under the null hypothesis. The null hypothesis assumed that the species traits are derived from a random sample of the community traits, meaning that the traits are shuffled between species. We simulated 5,000 null communities per treatment and per trait. We then computed the p-values as defined in Equation 2.

3 | RESULTS

3.1 | H1: Phenotypic space

Grazing did not significantly decrease the phenotypic space of the associated communities in the two cushion species (Figure 2; *O. andina*:
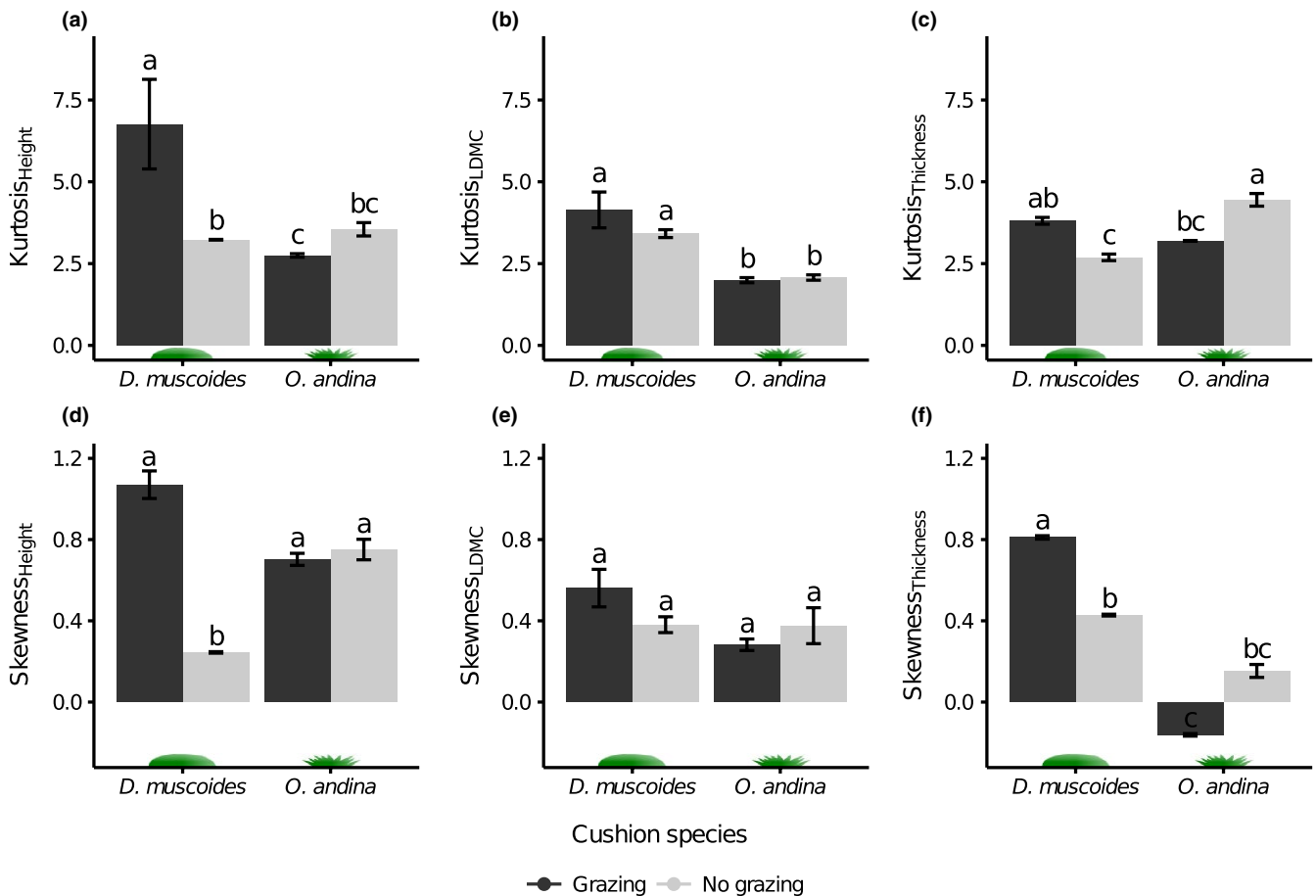
FIGURE 3 Kurtosis and skewness of the trait distributions of the associated communities inside the nurse cushion species for control (i.e., grazed; dark grey) and grazing exclusion (light grey). Error bars represent 95% CI built from the jackknife. Different letters represent significantly different groups according to post-hoc contrasts (Supporting information Table S4 in Appendix S1) [Colour figure can be viewed at wileyonlinelibrary.com]

−34.7 SD^3, p = 0.22; *D. muscoides*: −10.8 SD^3, p = 0.64; Supporting information Table S3). The cushion type, however, significantly affected the phenotypic space of the associated communities, which was overall larger in *O. andina* than in *D. muscoides*, independent of the grazing status (Figure 2 left panel; grazed: 71.5 SD^3, p = 0.008; ungrazed: 95.4 SD^3, p = 0.002). This suggests that the panel of life strategies developed by the associated communities was larger in *O. andina* than in *D. muscoides*.

The trait contribution to the hypervolume (Supporting information Table S1 in Appendix S1) showed that, in *O. andina* maximum height contributed most to the hypervolume in ungrazed plots, while leaf thickness was the largest contributor in grazed plots (Supporting information Table S1, contribution to hypervolume; thickness: 4.21, height: 3.39, LDMC: 3.08). In *D. muscoides*, however, maximum height contributed relatively less to the hypervolume than the other traits (contribution of maximum height to hypervolume: 1.07 in grazed communities and 1.41 in ungrazed communities).

3.2 | H2: The abundance trait distribution

The shape of the trait distributions was clearly more affected by grazing in *D. muscoides* than in *O. andina* cushions (Figure 3),

which is consistent with previous findings that the protection provided by *O. andina* extends to its associated community (Danet et al., 2017b). In *D. muscoides* cushions, grazing significantly increased the kurtosis of the maximum height and leaf thickness distributions (height: −2.98, t_6 = −4.02, p = 0.02; thickness: −1.12, t_6 = −3.20, p = 0.02; Figure 3a,c) as well as their skewness (height: −0.71, t_6 = −3.79, p = 0.04; thickness: −0.35, t_6 = −3.57, p = 0.01; Figure 3d,f). The kurtosis and skewness of LDMC distributions were, however, not affected by grazing in *D. muscoides* cushions (kurtosis: −0.41, t_6 = −0.72, p = 0.58; skewness: −0.18, t_6 = −0.72, p = 0.88; Figure 3b,e). In contrast, grazing did not affect the trait distributions of the associated communities in *O. andina* (Figure 3; Supporting information Table S4), except for the kurtosis of leaf thickness distribution, which significantly increased in grazing exclusion plots (1.36, t_6 = 4.04, p = 0.02).

The associated communities were also compared across cushions to see if and how cushion type affected the associated communities. Overall, the trait distributions of the associated communities situated in *O. andina* cushions were similar or significantly less skewed and peaked than those in *D. muscoides* (Supporting information Table S4; ten comparisons with 12), except for the kurtosis of leaf
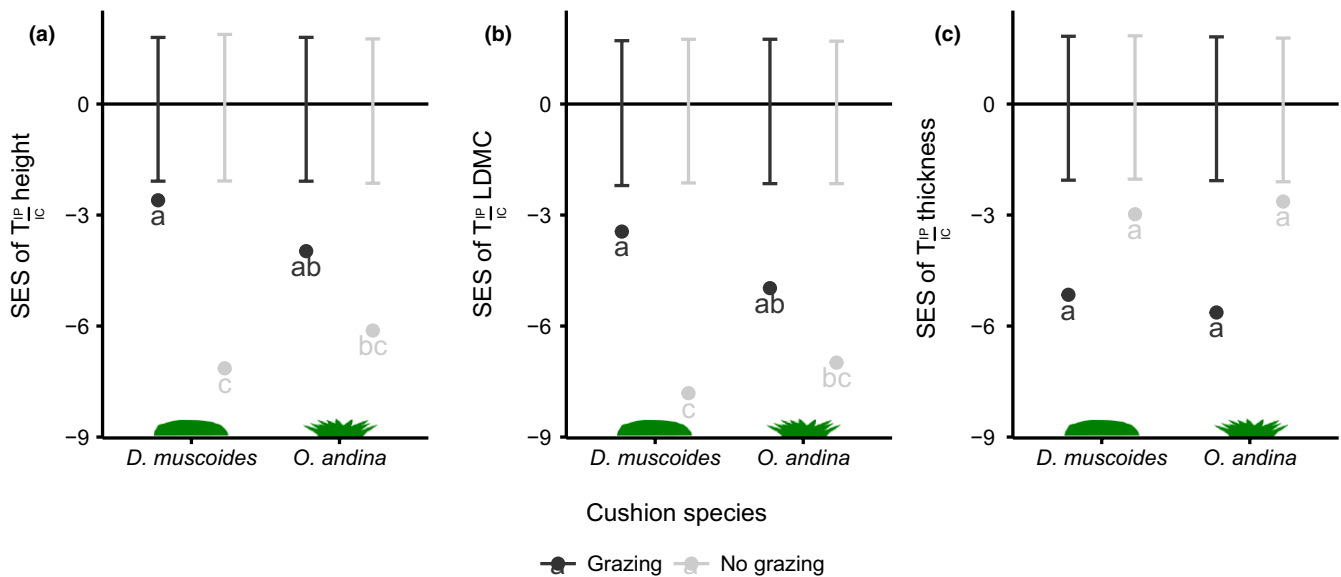
FIGURE 4 Standardized effect sizes (SES) of the T-statistic $T_{IP/IC}$ (intra-population variance relative to intra-community variance) of plant communities associated with the nurse cushion species for control (dark grey) and grazing exclusion (light grey). Different letters represent significantly different groups according to post-hoc contrasts (Supporting information Table S6 in Appendix S1). The lower the value, the lower the species overlap [Colour figure can be viewed at wileyonlinelibrary.com]

thickness and skewness of maximum height in ungrazed conditions, which were larger (respectively: 1.83, t_6 = 4.90, p = 0.01; 0.48, t_6 = 2.68, p = 0.08).

3.3 | H3: Species niche differentiation

The interspecific niche differentiation was more affected by grazing in *D. muscoides* than in *O. andina* (Figure 4). Yet, it was not significantly affected by the grazing status in either of the two cushion species for the leaf thickness (Supporting information Table S6). Grazing exclusion significantly decreased the mean species trait overlap ($T_{IP/IC}$) of maximum height and LDMC in *D. muscoides* cushions (height: −0.51, p < 0.05; LDMC: −0.44, p < 0.05), indicating that grazing increased species niche overlap in the associated community. In *O. andina* cushions, however, grazing exclusion did not significantly affect the $T_{IP/IC}$ of the associated communities (height: 0.36, p = 0.07; LDMC: 0.31, p = 0.07), indicating that indirect facilitation in *O. andina* was able to promote niche differentiation between associated species when grazing was present.

However, when comparing the cushions within the same grazing treatment, the niche overlap of the associated species was not significantly different between the associated communities situated in *O. andina* or in *D. muscoides* cushions, for each of the traits considered (Figure 4, Supporting information Table S6).

4 | DISCUSSION

We investigated the effects of indirect facilitation on contrasted facets of functional diversity in Bolivian tropical alpine peatlands using a grazing exclusion experiment. We did not find a significant effect of grazing exclusion on the phenotypic space of the community (H1). This suggests that grazing does not influence the presence of the trait syndromes in those communities. However, our results also show that, in grazed conditions, indirect facilitation can maintain higher evenness in the trait abundance distribution (H2) and higher niche differentiation between beneficiary species (H3) than in the absence of indirect facilitation. Therefore, indirect facilitation can favour the co-existence of contrasted functional strategies and species in cushion plant species.

Previous studies have suggested that facilitation could allow mal-adapted phenotypes to be maintained in unfavourable environments (Bruno et al., 2003; Soliveres, Smit, & Maestre, 2015). Such an effect of facilitation should translate into higher phenotypic space through the maintenance of contrasted trait syndromes. We found no significant effect of grazing on phenotypic space in the control cushion species (i.e., *D. muscoides*). Therefore, we could not draw any conclusions about the effect of indirect facilitation through grazing on the amount of distinct trait combinations (H1). This is congruent with previous work of Rota, Manzano, Carmona, Malo, and Peco (2017), suggesting that grazing affected more functional redundancy than functional originality (i.e., redundancy of trait combinations found in the associated communities), meaning that grazing did not lead to trait exclusions.

In agreement with our hypothesis H2, we found that indirect facilitation impacted the abundance structure of trait distributions in the associated communities, thereby affecting the dominance status in the community (see similar evidence for facilitation in Gross et al., 2009, 2015). In *D. muscoides*, we found that the trait distributions of the associated communities in the grazed treatment were significantly more peaked and skewed for maximum height and more

skewed for leaf thickness than in the ungrazed treatment. This was not the case in the spiny *O. andina*, suggesting that indirect facilitation had an effect on the maintenance of lower trait dominance in the associated plant communities (H2) for maximum height and leaf thickness. We did not find any effect of grazing exclusion on the kurtosis and skewness of the LDMC distribution in the associated communities. This result is quite surprising because grazing is known to affect LDMC (Cruz et al., 2010; Danet et al., 2017b; Louault et al., 2005; Peco, de Pablos, Traba, & Levassor, 2005). Overall, our results show that indirect facilitation can modify trait abundance distribution (H2) but not the presence of contrasted trait combinations (H1).

An important result of our study was to show that the beneficiary species had lower niche overlap (i.e., a larger niche differentiation) than expected by chance, and that the level of this overlap was mediated by indirect facilitation. We found that, in *D. muscoides* (where there is no protection against grazing), the $T_{IP/IC}$ of the associated communities was significantly lower in the grazed than in the ungrazed treatment for maximum height and LDMC, indicating more trait overlap and therefore more competition between beneficiaries in the grazed compared to the ungrazed treatment. Liancourt et al. (2005) proposed that when considering pair-wise interactions, the species that better tolerate competitive interactions also benefit more from being facilitated by a nurse. Our study extends their proposition to the case of multiple co-occurring beneficiary species. The fact that in *O. andina* (in which there is protection against grazing), the $T_{IP/IC}$ of the associated communities was not significantly different in the grazed compared to the ungrazed treatment for maximum height and LDMC indicates that indirect facilitation maintained the niche differentiation between species of the associated communities for maximum height and LDMC (H3), meaning weaker competition between beneficiary species. Thus, indirect facilitation could increase the benefit of direct facilitation of the cushions toward the beneficiary species by maintaining weaker competition between the beneficiary species.

Niche differentiation between species has been shown to be a key mechanism promoting stable co-existence between species pairs in experiments (HilleRisLambers et al., 2012; Levine et al., 2017). Our work on niche differentiation complements the approaches developed by Bruno et al. (2003) and Bulleri et al. (2016). Bulleri et al. (2016) focused on the consequences of the broadening of the niche of all beneficiary species caused by facilitation. They hypothesized that the consequences of the broadening of all beneficiary species niche could lead to a dramatic decrease in niche differentiation resulting in a loss of stable co-existence between species. In contrast, we showed that indirect facilitation could maintain species co-existence in the communities benefiting from this facilitation. One interpretation is that indirect facilitation through grazing, stemming from the decrease in the negative effect of grazing on the associated communities, relaxes the selective pressure imposed by grazing, reducing trait convergence, and thereby allowing populations of different species to develop different sets of traits through niche differentiation processes (Violle et al., 2012).

As argued in a previous study (Danet et al., 2017b), comparing the associated communities living under two different cushion species to infer indirect facilitation is less definitive than a cushion/ no cushion treatment, but this approach was constrained by the ecosystem in which we set up the experiment, where almost no plant species are found growing outside the cushions.

Our study opens stimulating perspectives regarding understanding of co-existence between facilitated species. It does not provide conclusions about whether the observed niche convergence of the associated species found in *D. muscoides* is due to changes in species composition or intra-specific variations of the same species. At the community level, is the positive effect received by the facilitated species from the nurses strengthened by a concomitant decrease in negative interactions with other facilitated species? Addressing this question would extend the results of Liancourt et al. (2005), which suggest that the most facilitated species are also those that have the highest competitive response ability, indicating that they increase the benefit of the environmental improvement by the nurse.

5 | CONCLUSION

There have been numerous calls in the literature on the need to introduce facilitative interactions into ecological theory (Bruno et al., 2003; Bulleri et al., 2016; Michalet et al., 2006; Wright et al., 2017). Indeed, facilitative interactions have been shown to affect community composition (Callaway, 2007) and ecosystem functioning (Cardinale et al., 2002). We tested how indirect facilitation may simultaneously impact contrasted facets of plant functional diversity in harsh tropical alpine environments, where the constraints generating positive plant interactions are distinct from those of other environments (low seasonality, absence of snow cover, long history of livestock grazing, different interacting life forms; Michalet et al., 2016). Our results suggest that indirect facilitation can release the selective pressures of grazing on associated plant communities by maintaining lower dominance and niche differences between the beneficiary species, but that indirect facilitation does not alter the functional strategies able to persist in these harsh conditions. Hence, our study implies that positive interactions can alter predictions about the effect of a selective pressure on the structure of communities by maintaining low dominance and strong niche differentiation between species.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Location of the data

Figure S1 Experimental design representation

Figure S2 Relationship between kurtosis and squared skewness

Figure S3 Relationship between kurtosis and squared skewness

Figure S4 Hypervolumes with one community by plot

Figure S5 Moment sampling with one community by plot

Table S1 Importance of the variables in building of the hypervolume

Table S2 Contribution of the different scales to the variance of traits

Table S3 Contrasts comparison for the volume of the hypervolume

Table S4 Contrasts comparison for the skewness and kurtosis of the trait distributions

Table S5 $T_{IP/IC}$ values by treatment

Table S6 Contrasts comparison for the $T_{IP/IC}$