



## Plant–plant interactions promote alpine diversification

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### Abstract

Plant–plant interactions can promote diversification in harsh environments through (1) natural selection producing divergent adaptations to extreme and varying abiotic conditions in plants that grow in the open, or (2) genetic drift involving little niche differentiation in plants that grow associated with others. We assessed whether alpine plant genera characterized by competitively-excluded or facilitated species are more diverse than genera characterized by habitat-generalist species at both global and local scales. Based on literature data, we characterized plant–plant interactions for 642 alpine species in 254 genera worldwide, using the relative interaction index (RII) that indicates the extent to which a plant species is competitively-excluded or facilitated by others. We tested whether the RII can be considered as a plant trait relatively well-preserved at the generic level and, within a phylogenetic framework, assessed how the number of alpine species per genus varies along the entire gradient of plant–plant interactions at both global and local scales. Species belonging to the same genus tended to be more similar in the RII-values than species from different genera, with ca. 20% of the variation in RII accounted by differences among genera. The relation between the total number of alpine species per genus and mean RII showed two comparable peaks, with genera in the competitive-exclusion or facilitation categories having, on average, more than twice as many species as genera in the neutral category. However, we found that more congeneric species from the competitive-exclusion category coexist locally than congeneric species from the facilitation category. This pattern of plant species richness at the community level was consistent with predictions from the hypotheses that competition promotes adaptive niche divergence at local scales, whereas facilitation promotes divergence with little niche differentiation. We conclude that both negative and positive ecological interactions play an important role as evolutionary drivers of alpine plant diversity.

**Keywords** Alpine plants · Diversification · Plant–plant interactions · Nurse effect · Facilitation · Competitive-exclusion · Niche differentiation

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## Introduction

Although different abiotic factors can be key in shaping biological diversity through space and time (Benton 2009), biotic interactions can also play a significant role in determining patterns of species diversity at different spatial scales and in promoting diversification of lineages through time (Valiente-Banuet and Verdú 2007; Liow et al. 2015; Voje et al. 2015). In particular, interspecific interactions can be crucial in promoting diversification by posing novel ecological opportunities and evolutionary challenges (Thompson 2004; McPeek 2008), which in turn can increase speciation and decrease extinction rates (Thompson 2004; Ricklefs 2010). In this context, much attention has been placed on the role of interspecific antagonistic interactions such as herbivory, parasitism, predation, and competition on lineage diversification (Thompson 2004, 2005; Ricklefs 2010; Yoder and Nuismer 2010). However, positive interspecific interactions, e.g. mutualism, can also fuel important diversification processes, as the radiation of flowering plants driven by specialized pollinators and seed dispersers (Hu et al. 2008; Crepet and Niklas 2009; Lengyel et al. 2009; Van der Niet et al. 2014; Eriksson 2016). Even though both negative and positive interactions can be determinant in promoting lineage diversification (Valiente-Banuet and Verdú 2007; Kikvidze and Callaway 2009), their comparative importance is difficult to unravel because most studies focus on either organisms from different trophic levels, taxonomic groups or environments.

Negative and positive interactions, however, can occur between species from the same trophic level and taxonomic group. For instance, among plants two or more species can compete with each other for abiotic resources such as space, light, water, different nutrients, and even biotic resources such as pollinators and seed dispersers (Goldberg 1990), or facilitate each other's growth and survivorship by increasing the local availability of different abiotic and biotic resources (Cavieres et al. 2007). Facilitative interactions among plants are particularly common in harsh environments (Callaway et al. 2002), where several factors limit the establishment of many species that can only survive in the relatively benign micro-habitat conditions created by established individuals of the same or other species, which are termed “nurse plants”. These are organisms that facilitate the establishment of other species by offering microhabitats more favourable for seed germination and/or seedling survival than the surrounding environment (Callaway 1995). Ultimately, in these environments plant strategies encompass the entire competition-facilitation gradient, ranging from species that will never or rarely be found growing associated with others (competitively-excluded species) to species that will never or rarely be found growing alone (facilitated species). Occupying the middle range of this gradient, there are species that are neither excluded nor facilitated by others (neutral species) and, thus, may be considered as habitat generalists as they can occur indistinctively associated or not with other plants (Badano et al. 2006).

The alpine regions of the world, which occupy ca. 3% of the emerged lands (excepting Antarctica), host a rich flora that includes between 8000 and 10,000 species. This flora occurs in regions characterized by extreme abiotic conditions such as very low temperatures and wide temperature oscillations, high radiation, limited water and nutrient availability, and short growing seasons that determine a low plant cover (Körner 2003). Frequent plant adaptations to these extreme alpine conditions include the production of frost-resistant tissues, the placement of photosynthetic organs within a few centimeters just above ground, and the positioning of buds and meristems at or below ground level (Körner 2003). These plant traits characterize typical alpine growth forms such as graminoid tussocks,

dwarf shrubs, rosettes and cushion plants (Körner 2003). Despite evolution of these adaptive growth forms, it is puzzling why such high plant diversity occurs in the bare alpine environments of the world.

Here we assessed the role of plant–plant interactions in promoting lineage diversification in alpine regions. In these environments, plant individuals of species that are competitively-excluded and recruit in the open are subject to strong and varying selection pressures that occur along abrupt temperature, radiation, and soil-moisture gradients, which unfold at spatial scales as short as a few hundred meters (Löffler and Finch 2005; Löffler 2007; Bertel et al. 2016). Thus, these rapidly changing abiotic conditions might define a multiplicity of different ecological niches occurring in relatively small areas. These abrupt gradients could favour diversification via parapatric or even sympatric speciation in plant lineages that do not grow associated with other plants and are specialized to the different micro-habitats occurring on bare ground. On the other hand, plants that nurse others provide less water-stressed and more nutrient-rich stable micro-habitats that buffer seedlings growing within from extreme temperatures, wind, and high radiation. In alpine environments greatly devoid of vegetation, most plant populations of facilitated species persist thanks to the presence of their patchy nurse plants (Cavieres et al. 2007, 2014, 2016). However, the fragmented nature of their populations could promote diversification via genetic drift involving little niche divergence (Boucher et al. 2016). According to this conceptual framework, it is then expected that lineages of either competitively-excluded or facilitated species should be more diverse than lineages of habitat-generalist (i.e. neutral) species.

We compiled a global data base of 254 alpine plant genera to explore the relation between diversification and plant–plant interactions. Several alpine plant genera have experienced extraordinary radiations (Hughes and Atchison 2015; Nürk et al. 2017) associated with the recent geological origin of major orographic systems (Andes, Alps, Himalayas, etc.). Therefore, the number of species per genus should provide an adequate taxonomic estimation of diversification in alpine regions. We first tested the underlying assumption that the type of plant–plant interaction is relatively well-preserved at the generic level. Within a phylogenetic framework, we then assessed how the number of alpine (and non-alpine) species per genus varies along the entire gradient of plant–plant interactions at both the global and local community scales. Our results strongly support the view that both competitive and facilitative plant–plant interactions have played an important role in the diversification of the alpine floras of the world, also providing insights into the mechanisms involved.

## Methods

### Data collection and phylogeny reconstruction

We conducted a survey of published articles about competition/facilitation in alpine communities searching Google Scholar in April 2017. The completeness of this survey was rechecked with a similar article search in Scopus. We considered articles that provided the Relative Interaction Index, RII (Armas et al. 2004), or information on the abundance of species inside and outside nurse plants that allowed us to calculate this index (Supporting Information Appendix S1, Data collection). This index varies from –1, for species that are never found associated with nurses (i.e. competitively-excluded), to +1, for species that are never found growing alone (i.e. facilitated). Values close to 0 indicate habitat-generalist

species that are equally found growing in both micro-habitats (inside and outside nurses). The RII is probably the most commonly used index to describe plant–plant interactions because it has defined limits, it is symmetrical around zero with an identical range of absolute values to estimate competition and facilitation, and it is practical to use in statistical operations because it does not have discontinuities in its range (Armas et al. 2004). From 30 articles, we retrieved 1499 records for 642 species in 254 genera. For each species, we characterized the dependency on nurse plants using the RII, averaging RII values when a given species occurred in more than one community. For comparative purposes and based on results from other authors, genera were classified into three commonly used categories; genera characterized by competitively-excluded species had average RII's  $\leq -0.2$  (i.e. competitive-exclusion category), those characterized by facilitated species RII's  $\geq +0.2$  (i.e. facilitation), whereas those by neutral species  $-0.2 < \text{RII's} < +0.2$  (i.e. neutral) (Supporting Information Appendix S1, Plant–plant interactions). As a measure of recent lineage diversification, we considered the total number of species per genus reported in Mabberley (2008) (Supporting Information Appendix S2). For each genus, we also estimated the number of alpine and non-alpine species based on a review of species distributions (Supporting Information Appendix S1, Lineage diversification). We assessed the habitat distribution of 17,282 species out of 38,013 species (45%) in March of 2018. The fraction of species classified as alpine allowed us to estimate the number of alpine (and non-alpine) species per genus (Supporting Information Appendix S2 and Appendix S3). To assess and account for phylogenetic effects we constructed a template phylogenetic tree including all 254 genera using Phyloomatic in Phylocom 4.2 (Webb et al. 2008) with node dates updated according to the well-supported mega phylogeny of Zanne et al. (2014) and polytomies below family-level solved through recent articles (Supporting Information Appendix S1, Phylogeny reconstruction).

## Statistical analyses

### Variation in RII values

An implicit assumption of our study is that plant–plant interactions (i.e. preference to grow in the open or associated with nurses) are relatively well-preserved within genera (i.e. niche conservatism, Wiens et al. 2010), so that RII's from species from the same genus will tend to be more similar than RII's from species from different genera. To test this assumption, we estimated variance components in RII among and within genera by means of a random effect model performed with the lmer function implemented in the package lme4 (Bates et al. 2011) for R (v 3.4). This model also estimated mean RII's for each genus adjusted by differences in sample sizes.

### Phylogenetic signal

In addition to testing for similarity in habitat preference among species within genera, we assessed the magnitude and significance of phylogenetic signal in plant–plant interactions and diversification at the generic level. Using the reconstructed phylogeny (Supporting Information Appendix S1, Fig. S1), we estimated the amount of phylogenetic signal in the RII by means of Blomberg's K-statistic (Blomberg et al. 2003). Also, using the same statistic, we estimated the phylogenetic signal in the number of species (i.e. alpine, non-alpine, and total) per genus. Since the suitability of any model fit considering

phylogenetically-structured data should be diagnosed by estimating phylogenetic signal in the residuals of the response variable given suggested predictors (Revell 2010), we also estimated the K-statistic of the residuals of generalized additive models' describing the relation between number of species (alpine, non-alpine, and total) per genus and RII (see below). The K-statistic measures the amount of phylogenetic signal of the real data relative to that predicted by a Brownian model of trait evolution and varies from 0 to  $+\infty$ . Therefore,  $K=0$  when there is no phylogenetic conditioning of the evolution of the trait,  $K=1$  when the trait has evolved in agreement with a Brownian motion model of evolution, and  $K>1$  when the trait is more similar between close relatives than expected under a Brownian motion model of trait evolution (Blomberg et al. 2003). For accurate model testing, number of species was log-transformed to comply with the assumption of normality of the model residuals. We estimated Blomberg's K using the function `phylosig` from the R `phytools` package version 0.6 (Revell 2012).

We also evaluated the extent of phylogenetic clumpiness of the genera in terms of the different interaction categories. This was assessed using the D-statistic (Fritz and Purvis 2010), which allows computation of phylogenetic signal for binary variables. Unlike the K-statistics,  $D=0$  indicates Brownian motion-like evolution, whereas  $D=1$  indicates no phylogenetic conditioning. By coding, alternatively, each of the three categories as 1 and the other two as 0, we were able to evaluate whether genera in the competitive-exclusion, neutral, or facilitation category were more phylogenetically related than random expectations. We estimated the D-statistic using the `phylo.d` function from the R package `caper` version 0.5-2 (Orme et al. 2012).

## Global pattern of diversification

We explored the shape of the association between diversification and plant–plant interactions using a smoothing fit. We fitted generalized additive models (GAM) considering the mean RII as the smooth predictor and the number of species (alpine, non-alpine, and total) per genus as the response variable. GAMs are semi-parametric extensions of GLMs (Hastie and Tibshirani 1990) and provide a better tool for data exploration than other smoothing-fit models owed to its ability to find and deal with highly non-linear and non-constant relationships (Hastie and Tibshirani 1990). Hence, features such as pronounced asymmetry and presence of several maxima in the data can be easily detected. We tested for a lack of phylogenetic signal in the GAMs residuals to judge the appropriateness of these non-phylogenetically informative fits (see above). In all cases, we used a quasipoisson GAM because of overdispersion in number of species per genus. This model was implemented with the `gam` function of the R `gam` package version 1.14-4 (Hastie 2006). Lastly, we explored, by means of a null model, the possibility that the observed relation between number of species per genus and the RII can be an artifact resulting from the uneven number of species per genus available in the literature to estimate those RIIs (Supporting Information Appendix S1, Null-model analysis).

This statistical analysis was complemented with a phylogenetically-informed analysis, where RII's are discretized into the three plant–plant association categories defined above. To assess the effect of plant–plant interaction category (competitive-exclusion, neutral, and facilitation) on the number of species (alpine, non-alpine and total) per genus, we conducted a single-factor analysis using generalized least-squares models that accounted for phylogenetic relations. Number of species was log-10 transformed to satisfy model assumptions of normality and homoscedasticity. Analyses were conducted

considering four different models of trait evolution (Independence, Brownian motion, Ornstein–Uhlenbeck’s and Grafen’s) that predict different expected correlation matrices between the 254 genera based on the phylogenetic tree (Supporting Information Appendix S1, Models of trait evolution). The use of these different models allowed us to assess how robust our results were in the face of different hypotheses on trait evolution. These models were performed with the corBrownian, corMartins and corGrafen functions, respectively, using the R package ape version 4.1 (Paradis et al. 2004). Predicted means of number of species per genus for each interaction category were compared pairwise with a Tukey test. Using a binomial test with a parameter  $p = 0.5$ , we also tested whether genera in the competitive-exclusion and facilitation categories tend to have more alpine than non-alpine species, whereas no trend would be expected in genera belonging to the neutral category. Because the total number of alpine species was smaller than the number of non-alpine species overall, for this test the number of alpine and non-alpine species were relativized to the maximum observed in the genus *Astragalus* (~700 alpine and ~1800 non-alpine species).

### Effects of co-variables on the alpine diversification pattern

We evaluated the effect of other potentially confounding factors in the phylogenetically-controlled analyses that might affect the relation between type of plant–plant interaction and alpine diversification. Specifically, we assessed whether alpine diversification was influenced by plant life-form, geographical distribution, or lineage age by means of generalized least squares models. These models had as a backbone model the best fitted previous evolutionary model based on AIC (i.e. Grafen’s; see Results), considering as predictors the plant–plant interaction categorical variable with three levels (i.e. competitive-exclusion, neutral, and facilitation) and one of the three previously mentioned covariables. In terms of growth form, genera were classified according to the dominant life-form as shrub, cushion and herb. We considered three categories of geographical distribution, America, Eurasia, and Cosmopolitan, excluding six genera from Oceania because of a lack of at least one genus in the competitive-exclusion category among them. Phylogenetic distance to the nearest node, which was retrieved from the distance matrix obtained with the cophenetic.phylo function of the ape package (Paradis et al. 2004), was used as a comparative proxy of lineage age.

### Local pattern of congeneric species coexistence

We assessed whether the number of alpine species/genus present in each local community was also related to the prevalent plant–plant interaction of the genera they belong to. To this aim, we considered the list of species of each of the 66 communities reported in the 30 studies reviewed. Given that at local community scale most genera were represented by just one species, we analyzed the mean number of species per genus, averaged over all the genera occurring in each plant–plant interaction category in each community, rather than the raw data. Data were analyzed with an ANOVA model that considered plant–plant interaction category as a fixed factor and community as a blocking factor. Additionally, we compared the relative frequency of genera represented by more than one species in each plant–plant interaction category using a Chi square test.

## Results

### Variation in RII values

Plant–plant interactions varied extensively among and within genera. However, species within genera tended to be more similar in the type and magnitude of their dependence on nurse plants than species from different genera, with the factor “genus” accounting for 18.1% of the variation in RII ( $X^2=33.6$ ,  $df=1$ ,  $P<10^{-9}$ ). In consequence, plant–plant interactions can be seen, at least in part, as a genus characteristic. The RII’s estimated at the generic level were distributed over the entire competition-facilitation gradient, ranging from –1 to +1.

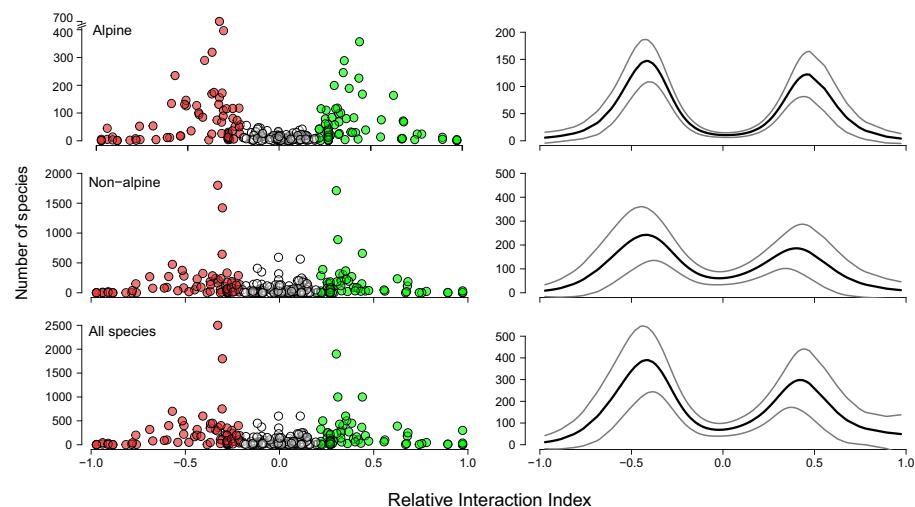
### Phylogenetic signal

Phylogenetic effects of the generic RII’s were extremely weak ( $K=0.18$ ,  $P=0.1$ ), and there was no evidence of phylogenetic clumpiness of genera in the competition-exclusion ( $D=0.90$ ,  $P=0.14$ ), neutral ( $D=0.99$ ,  $P=0.48$ ), or facilitation ( $D=0.92$ ,  $P=0.18$ ) categories. Phylogenetic effects were not detected in neither the number of species per genus characterized as alpine nor non-alpine, or in the total number of species ( $K\sim0.17$  for all three response variables,  $P>0.20$ ). Consistently, we did not find phylogenetic signal for the GAM residuals assessing the effect of the RII upon alpine, non-alpine, or total diversification ( $K=0.15$ ,  $P=0.65$ ;  $K=0.20$ ,  $P=0.13$ ; and  $K=0.17$ ,  $P=0.27$ , respectively). Therefore, there was little evidence that both plant–plant interactions and species diversification were phylogenetically structured above the generic level.

### Global pattern of diversification

Plant–plant interactions were predictive of global diversification patterns at the generic level. Generalized additive models showed a relation between number of species per genus and RII characterized by a depression at a RII value close to 0 and two symmetric peaks at values close to -0.5 and +0.5. Therefore, genera characterized by RII’s nearby zero presented relatively low diversification, whereas those with higher absolute RII’s, either in the competitive-exclusion or facilitation regions of the competition-facilitation gradient, had, on average, much higher number of species (Fig. 1). This relation was much stronger for the number of alpine species than for the number of non-alpine species or total number of species per genus (Supporting Information Appendix S1, Table S1). The null-model analysis (Supporting Information Appendix S1, Null-model analysis) revealed that the reduced number of species per genus associated with genera with extreme RIIs (i.e. around –1 or +1) could actually reflect the limited number of species available to estimate those RIIs. This analysis, however, predicts a one- rather than a two-peak relation between number of species per genus available for RII estimation and the estimated RII (Supporting Information Appendix S1, Figs. S2 and S3). Therefore, the low diversification exhibited by genera with RIIs around 0 cannot be interpreted as an artifact of the uneven number of species available to estimate the RIIs.

Overall, the number of alpine species differed between plant–plant association categories, with genera in the competitive-exclusion and facilitation categories diversifying to a similar extent, but having, on average, two to three times as many species as genera in the neutral category (Supporting Information Appendix S1, Fig. S1). This was a



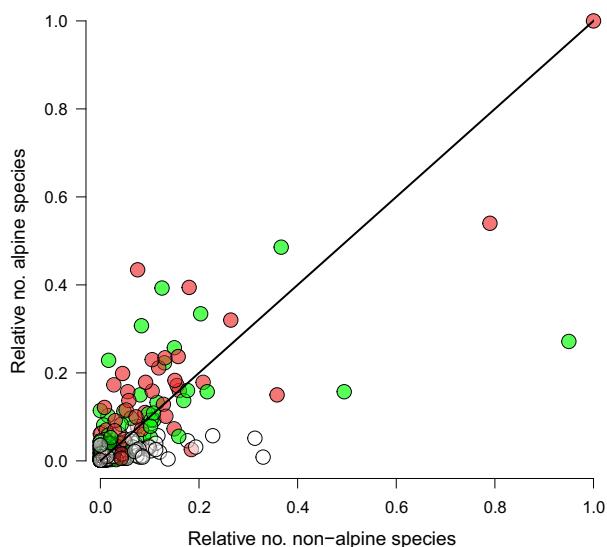
**Fig. 1** Global patterns of diversification in relation to plant–plant interactions. Number of alpine, non-alpine and total number of species per genus are depicted according to the Relative Interaction Index (RII) characterizing each genus. The left panels depict the raw data (red, white, and green symbols represent genera assigned to the competitive-exclusion, neutral, and facilitation categories, respectively). The right panels depict the GAMs' fit (black lines) and the boundaries of the 95% confidence intervals (grey lines). (Color figure online)

consistent pattern regardless of whether phylogenetic relations between genera were taken into account and, if so, of the evolutionary model used (Supporting Information Appendix S1, Table S2). Despite showing a similar trend, the number of non-alpine and total species per genus did not differ significantly among plant–plant interaction categories (Supporting Information Appendix S1, Table S3). Relative to the maximum number of alpine and non-alpine species found for any genera, more than half of the genera in the competitive-exclusion (76%) and facilitation (70%) categories diversified to a larger extent in the alpine than non-alpine regions (binomial test,  $P < 0.001$  and  $P = 0.001$  respectively, Fig. 2), whereas no differences were found for genera in the neutral category (i.e., 46%,  $P = 0.45$ ). All these results support a relation between plant–plant interactions and lineage diversification in the alpine regions of the world.

### Effects of co-variables on the alpine diversification pattern

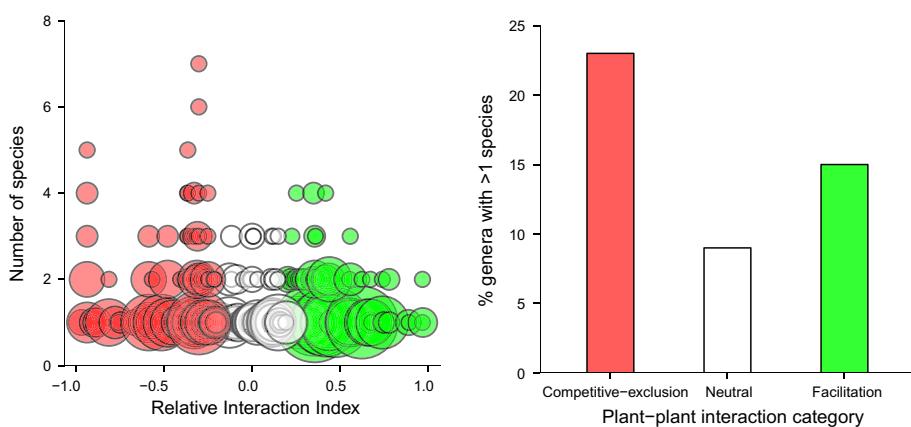
The relation between diversification and plant–plant interaction was not unduly influenced by any other factor. Neither plant life-form nor lineage age was significantly associated with alpine diversification. The number of alpine species did differ among categories of geographical distribution, with cosmopolitan genera being more speciose than American or Eurasian genera (back-transformed least-square mean [95% CI] = 26.0 [20–32], 10.0 [6–14], 7.5 [5–10], respectively). However, the relation between alpine diversification and plant–plant interactions was independent of geographical distribution as revealed by a non-significant plant–plant association\*geographical distribution interaction (Supporting Information Appendix S1, Table S4).

**Fig. 2** Relative number of alpine versus non-alpine species per genus. Number of alpine and non-alpine species for each of 247 genera was relativized to the maximum observed in the genus *Astragalus* (i.e. the right- and upper-most point). Red, white, and green symbols represent genera assigned to the competitive-exclusion, neutral, and facilitation categories, respectively. The line  $x = y$  is provided as reference. Those genera represented by circular dots above the line have a relatively higher number of alpine than non-alpine species, whereas those below, a relatively lower number of alpine than non-alpine species. (Color figure online)



### Local pattern of congeneric species coexistence

Patterns of species diversity at the community level reflected to some extent the global pattern. At this more local scale, most genera (84%) were represented by just one species. However, 23 and 15% of the genera in the competitive-exclusion and facilitation categories had more than one species coexisting locally, whereas this fraction was of only 9% in the case of genera in the neutral category (Chi square test,  $X^2 = 18.9$ ,  $df = 1$ ,  $P < 0.001$ , Fig. 3). This was also reflected in differences in the mean number of species per genus between the



**Fig. 3** Coexistence of congeneric species in local communities in relation to plant–plant interactions. The left panel depicts the number of congeneric species in local communities as a function of the Relative Interaction Index (RII), with symbol size proportional to sample size due to data overlapping. The right panel depicts the percentage of genera in local communities represented by  $> 1$  species. Red, white, and green symbols and bars represent genera assigned to the competitive-exclusion, neutral, and facilitation categories, respectively. (Color figure online)

interactive and neutral categories (Supporting Information Appendix S1, Table S5). Unlike the global pattern, there were differences between the two plant–plant interactive categories, with a larger number of genera with two or more species ( $X^2 = 7.7$ ,  $df = 1$ ,  $P = 0.006$ ) and larger mean number of species/genus for genera in the competitive-exclusion than in the facilitation category (Fig. 3; Supporting Information Appendix S1, Table S5).

## Discussion

Although alpine plant diversity is assumed to be mainly regulated by large-scale abiotic filters such as climate, geomorphology and historical processes (Körner 2003), this study suggests that plant–plant interactions in alpine environments play an important role as evolutionary drivers of plant diversity. Specifically, we showed that plant genera characterized by either competitively-excluded or facilitated species display higher species numbers than genera characterized by neutral species. The effect of plant–plant interactions on genus diversification was independent of growth form, lineage age, or geographic distribution. These findings indicate that habitat specialization resulting from plant–plant interactions promotes diversification in alpine environments worldwide, whereas lack of habitat specialization relates to a decrease in diversification potential.

Because our analysis was conducted assessing species diversity at the generic level, it rests on the underlying assumption that congeneric species are more similar in their tendency to grow or not associated with other plants, particularly nurse plants, than species belonging to different genera. We tested this assumption showing that a highly significant fraction (about 20%) of the variation in the RII, the index that estimates this tendency, could be accounted by variation among genera. Although this might not seem to represent a very high fraction of the total variation in how plants interact with others, it has to be considered that data used to estimate RIIs come from different studies, which applied different methodologies and used different abundance estimates. These uncontrolled sources of variability undoubtedly increase the sampling error in RII estimates (Michalet et al. 2014), thus inflating the component of variation attributed to species within genera. This niche conservatism (Wiens and Graham 2005) at the generic level also indicates that even though plant–plant interactions can be seen as facultative interactions (e.g. species that are only nursed by others under harsh conditions; Butterfield 2009), they can also be considered as a species trait. This species-specific characteristic, perhaps associated with growth form and physiology (Hacker and Bertness 1995; Herben 2004; Giron et al. 2013), can thus be seen, at least in part, as inherited by descent. Above the genus level, our phylogenetic analysis provides no evidence that closely related genera are more similar in the prevalent type of plant–plant association, indicating relatively little niche conservatism (Wiens and Graham 2005) in recruitment microhabitat over long periods of time. These results strengthen the view that genus is the proper taxonomic level to analyze patterns of diversification in alpine environments in relation to plant–plant interactions.

Alpine ecosystems develop under harsh and highly variable climatic conditions that determine low productivity (Körner 2003). These conditions are assumed to limit biodiversity, in general, and lineage diversification, in particular (McCain and Grytnes 2010). However, mountain uplifts have created highly fragmented environments with considerable diversity of microhabitats and niches along steep temperature, rainfall, wind, and sun-exposure gradients that have promoted extraordinary speciation rates in several plant genera (Coyne and Orr 2004; Hughes and Atchison 2015; Nürk et al. 2017).

Although our findings do not fully elucidate the entire processes driving speciation in alpine plants, they do provide insights into plausible mechanisms involving plant–plant interactions in which the position along the competition-facilitation gradient plays a critical role.

Species at the competitive side of the gradient occur preferentially on bare ground, possibly because they are outcompeted by either the nurse plants themselves or other plants facilitated by them (Holmgren et al. 1997). These competitively-excluded species are subject to strong and varying small-scaled selection pressures that unfold along the abrupt environmental gradients that characterize alpine ecosystems, conditions that might boost diversification through local adaptation (Körner 2003; Buehler et al. 2013; Bertel et al. 2016). In fact, there is evidence suggesting that the multiplicity of niches associated with this high environmental heterogeneity (Kikvidze et al. 2015) can promote population divergence in alpine ecosystems (Voelckel et al. 2008). In particular, substrate type has been shown to be a major driver of population genetic structure in these environments (Alvarez et al. 2009), whereas temperature and precipitation can be major selection factors driving phenotypic change (Chaves et al. 2003; Manel et al. 2012). Additionally, steep variation in these factors can further limit gene flow via phenological segregation (Kudo and Hirao 2006), promoting reproductive isolation at small spatial scales. Therefore, conditions exist for parapatric or even sympatric speciation for those alpine genera with species that specialize in different microhabitats (Dieckmann et al. 2004; Bolnick and Fitzpatrick 2007; Nosil 2008; Bird et al. 2012; Bertel et al. 2016), which might in turn favour coexistence of multiple congeneric species in local communities.

Species at the facilitative side of the gradient occur preferentially associated with others because they exhibit poor recruitment under the harsh environmental conditions existing on the bare ground (Cavieres et al. 2007; Valiente-Banuet and Verdú 2007). Instead, facilitated species thrive under the less water-stressed and more nutrient-rich microenvironment provided by their nurse plants (Callaway 2007). However, species growing under the ameliorated and buffered conditions provided by nurse plants should exhibit more fragmented populations due to their dependence on pre-existing vegetation patches, which shall result in smaller and more isolated populations (e.g., Badano and Cavieres 2006; Cavieres and Badano 2009; Namazi 2015; Catorci et al. 2016). Accordingly, drift can also be an important speciation driver in alpine lineages characterized by species with small populations, which can even undergo stronger genetic bottlenecks during glacial periods (Verboom et al. 2015). Allopatric speciation with little ecological niche divergence has been suggested to be the main speciation mechanism of many groups of alpine plants (Boucher et al. 2016). Therefore, facilitative plant–plant interactions can promote non-adaptive diversification (Gittenberger 1991; Liancourt et al. 2012) via allopatric speciation involving relatively low niche differentiation (Vargas 2003; Kadereit et al. 2004; Gehrke and Linder 2011; Kikvidze et al. 2015; Verboom et al. 2015; Boucher et al. 2016), which might in turn reduce the chance of coexistence of congeneric species in local communities.

Although we lack direct evidence on the different diversification mechanisms involved, the contrast between the global pattern of diversification and the local pattern of congeneric species coexistence lends support to the proposed conceptual framework. Both the global and local pattern of number of species per genus in relation to RII depicts a relation between species number per genus with two peaks. However, whereas the global pattern suggests similar rates of diversification between genera in the competitive-exclusion and facilitation categories, the congeneric coexistence patterns suggest a higher chance that species coexist locally in the former category. This pattern agrees with the idea that specialization to the different niches available at small spatial scales promotes diversification

in genera characterized by competitively-excluded species (Kikvidze et al. 2015), whereas a lack of niche differentiation underlies the diversification mode of facilitated plants.

Finally, we explored the possibility that the two-humped pattern of diversification along the competition-facilitation gradient could be, alternatively, an artifact of the uneven number of species per genus available for RII estimation. Indeed, the more speciose plant lineages (i.e. the ones with RII values around  $-0.5$  or  $+0.5$ ) were also genera with more available information at the species level to estimate their RIIs, whereas genera with few records (i.e. less than two species) were found throughout the entire gradient (Fig. S2a). Nevertheless, our null-model analysis discarded the possibility that the two-peak pattern of diversification could be an artifact of the uneven distribution of number of species per genus available to estimate the RIIs, accentuating the biological connection between plant–plant interactions and lineage diversification. On the other hand, the null-model analysis revealed that the low diversification exhibited by genera with extreme RIIs (i.e. approaching  $-1$  or  $+1$ ) might indeed reflect the limited number of species available to estimate those genera's RIIs. However, a biological alternative to this null-model explanation could also account for a decrease in diversification as the RII approaches  $-1$  or  $+1$ . This could happen if extreme specialization to a very narrow niche outside nurse plants, in one case, or complete confinement to nurse plants, on the other, not only fostered speciation but also extinction, thus lowering diversification rates (Walker and Preston 2006).

Beyond these unresolved aspects of the pattern reported here and the need of more exploration of the mechanisms involved, our findings indicate that both negative and positive interactions can be equally important ecological forces in a lineage diversification. Certainly, assessing macro evolutionary consequences of biotic interactions represents one of the major challenges to understand patterns of species diversity (Jablonski 2008; Kikvidze and Callaway 2009; Liancourt et al. 2012). Meeting this challenge, the reported two-humped pattern of diversification along the competition-facilitation gradient provides strong evidence that habitat specialization and/or fragmentation driven by plant–plant interactions can represent strong diversification forces in alpine environments. The plant–plant version of these opposing interaction types seems to be key to understand the high plant species diversity existing in the harsh alpine environments of the world.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Data availability statement** All data generated or analyzed during this study are included in this published article [and its supplementary information files].

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