

Research

Plant–plant facilitation increases with reduced phylogenetic relatedness along an elevation gradient

Milen Duarte, Miguel Verdú, Lohengrin A. Cavieres and Ramiro O. Bustamante

M. Duarte (<https://orcid.org/0000-0003-4784-9880>) ✉ (milenduartem@gmail.com) and *R. O. Bustamante* (<https://orcid.org/0000-0001-6441-7006>), *Dept de Ciencias Ecológicas, Facultad de Ciencias, Univ. de Chile, Santiago, Chile.* – *MD, ROB and L. A. Cavieres* (<https://orcid.org/0000-0001-9122-3020>), *Inst. de Ecología y Biodiversidad, Santiago, Chile.* *LAC also at: Dept de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Univ. de Concepción, Chile.* – *M. Verdú, Centro de Investigaciones sobre Desertificación (CIDE CSIC-UV-GV), Apartado Oficial, Moncada, Valencia, Spain.*

Oikos

00: 1–12, 2020

doi: 10.1111/oik.07680

Subject Editor: Yanjie Liu

Editor-in-Chief: Dries Bonte

Accepted 26 October 2020

Environmental conditions can modify the intensity and sign of ecological interactions. The stress gradient hypothesis (SGH) predicts that facilitation becomes more important than competition under stressful conditions. To properly test this hypothesis, it is necessary to account for all (not a subset of) interactions occurring in the communities and consider that species do not interact at random but following a specific pattern. We aim to assess elevational changes in facilitation, in terms of species richness, frequency and intensity of the interaction as a function of the evolutionary relatedness between nurses and their associated species. We sampled nurse and their facilitated plant species in two 1000–2000 m. elevation gradients in Mediterranean Chile where low temperature imposes a mortality filter on seedlings. We first estimated the relative importance of facilitation as a mechanism adding new species to communities distributed along these gradients. We then tested whether the frequency and intensity of facilitation increases with elevation, taking into account the evolutionary relatedness of the nurse species and the facilitated species.

We found that nurses increase the species richness of the community by up to 35%. Facilitative interactions are more frequent than competitive interactions (56% versus 44%) and facilitation intensity increased with elevation for interactions involving distantly related lineages.

Our results highlight the importance of including an evolutionary dimension in the study of facilitation to have a clearer picture of the mechanisms enabling species to coexist and survive under stressful conditions. This knowledge is especially relevant to conserve vulnerable and threatened communities facing new climate scenarios, such as those located in Mediterranean-type ecosystems.

Keywords: Chilean Mediterranean ecosystem, nurse species, phylogenetic specificity, positive interactions, relative interaction index

Introduction

Competition and facilitation are ecological interactions of opposite sign that mainly modulate the structure of plant communities (Bertness and Callaway 1994, Callaway 1995, Lortie et al. 2004). While competition has traditionally been the most studied interaction, in the last two decades facilitation is receiving increasing attention, with theoretical models and experiments demonstrating its importance to plant diversity in terms of functional traits diversity (Spasojevic and Suding 2012, Schöb et al. 2013, Madrigal-González et al. 2020), taxonomic richness (Cavieres et al. 2002a, 2014, Cavieres and Badano 2009, Sklenář 2009) as well as phylogenetic diversity (Bruno et al. 2003, Valiente-Banuet and Verdú 2007, Butterfield et al. 2013, Pistón et al. 2015, Vega-Álvarez et al. 2019). Facilitation, by assembling phylogenetically and functionally diverse communities, ultimately promotes diverse ecosystem functions (Navarro-Cano et al. 2014, 2016).

Current environmental conditions can modify the intensity and sign of ecological interactions. According to the stress gradient hypothesis (SGH) facilitative interactions are expected to be more frequent in either biotic (i.e. high herbivory) or abiotic stressful environments such as desert or alpine habitats, while competitive interactions dominate under more benign environmental conditions (Bertness and Callaway 1994). Most of the studies addressing the SGH have examined how facilitative interactions change with the abiotic stress by using a subset of plant species in the community (Callaway et al. 2002) or studying communities containing just a single (or a few) nurse species (Armas et al. 2011). Few studies have accounted for the whole network of facilitative interactions occurring in communities where many nurses are present. When the community is assembled by one or a few nurses, such as in some alpine plant communities where cushions are key nurses, facilitation is important in determining species diversity at the community level (Cavieres and Badano 2009, López et al. 2016, Liancourt et al. 2017). Nevertheless, at what extent facilitative interactions play a role in communities comprising many potential nurses and how this change along an environment severity gradient remains elusive (but see Pistón et al. 2016).

As nurses modify microhabitat temperature (Breshears et al. 1998, Drezner 2006, Cavieres et al. 2007), moisture (Maher et al. 2005, Cavieres et al. 2007) and nutrients (Pugnaire et al. 1996, Zabinski et al. 2002, Gómez-Aparicio et al. 2005), most studies have focused on comparing the species richness beneath the canopy of nurses versus that of adjacent open sites. Studies using this approach have found that species richness beneath nurses is higher (Raffaele and Veblen 1998, Badano et al. 2005, Koorem and Moora 2010), similar or lower (Gutiérrez et al. 1993, Pugnaire et al. 1996, Madrigal-González et al. 2016) or results dependent on species-specific relationships (Soliveres et al. 2012a, Pistón et al. 2016, Farzam and Ejtehadi 2017). However, as both microhabitats (within or beneath nurse and open areas) belong to the same community, it is important to

evaluate whether there are species added to the community due to the presence of nurses (Cavieres and Badano 2009, Cavieres et al. 2016). This perspective has started to be incorporated in recent years, showing that the presence of nurses increases the richness of communities (Badano and Cavieres 2006, Cavieres and Badano 2009, Cavieres et al. 2014) especially under stressful conditions, as predicted by the SGH (Armas et al. 2011, Kleinhesselink et al. 2014, Cavieres et al. 2016).

Plant species are not easily interchangeable units in facilitative interactions (Callaway 2007, Valiente-Banuet and Verdú 2008). Therefore, a proper SGH test should account for the specificity of the facilitative interactions (Soliveres et al. 2015). Evolutionary relatedness between species can be used to account for such specificity of facilitative interactions (Valiente-Banuet and Verdú 2007, Montesinos-Navarro et al. 2012, Sortibrán et al. 2014, Pistón et al. 2015). This is because nurse species tend to facilitate phylogenetically distant species (Valiente-Banuet and Verdú 2008, Verdú et al. 2009). Given trait conservatism, closely related species tend to have similar requirements and therefore competition between them can be intense and facilitation weak (Verdú et al. 2009, Burns and Strauss 2011, Soliveres et al. 2012b). On the contrary, more distantly related species tend to have different requirements and consequently competition will be low (Butterfield et al. 2013) and facilitation intense (Valiente-Banuet et al. 2006). This relationship between distant species can be translated into phylogenetic patterns, where the association between nurses and their associated species occurs between distant lineages, thereby resulting in over-dispersed community structures (Valiente-Banuet and Verdú 2007). It should be noted that phylogenetically clustered communities could be produced when competitive ability is evolutionarily conserved and therefore fitness differences instead of niche differences are the main community assembly mechanism (Mayfield and Levine 2010). However, facilitative interactions have been shown to be mainly mediated by niche differences (Valiente-Banuet and Verdú 2007, Butterfield and Briggs 2011, Alcántara et al. 2019a, Navarro-Cano et al. 2019). Including the phylogenetic specificity between interacting plants at the community level could thus shed light on SGH in natural communities.

According to SGH, it is expected that the frequency and intensity of facilitative interactions increase with environmental severity in many systems and over many gradients (He et al. 2013). Elevation gradients have been widely used to test the SGH (Choler et al. 2001, Cavieres et al. 2002b, Zabinski et al. 2002, le Roux and McGeoch 2010) because several environmental features such as temperature and growing season length decrease with elevation, while wind speed and light intensity increase, ultimately generating conspicuous gradients of environmental severity. Thus, communities having nurses that mitigate these environmental constraints, such as cushion plants (Cavieres et al. 2002b, Schöb et al. 2013) or shrubs (Pistón et al. 2016, Chen et al. 2019) tend to harbor a greater number of species as elevation increases (but see Cavieres et al. 2006). However, these studies have

been conducted above the treeline, so the study of facilitation requires further elevation gradients on other systems below the treeline (Ramírez et al. 2006) to draw more general pictures. By considering the phylogenetic specificity between nurses and their associated species according to the SGH, it can be hypothesized that, at community level, the increase of facilitation with elevation should be more marked for distantly related clades.

The sclerophyllous Chilean matorral occurs in the Mediterranean type-climate zone of the country, spanning from the sea-level up to 2200 m a.s.l. Although facilitative interaction has been widely studied in the Chilean matorral (Fuentes et al. 1984, 1986, Holmgren et al. 2000) there are no studies including the whole network of interactions at the community level (but see Badano et al. 2005), and never along a severity gradient.

In this study, we examine plant–plant interactions in the montane Mediterranean sclerophyllous forest of central Chile using two perspectives: first, we assessed whether nurses increase species richness at the community level along elevation gradients and, second, we tested whether the intensity of interactions along elevation gradients depended on the evolutionary relatedness between nurses and their associated species.

Material and methods

Study sites and sampling procedure

The sampling sites were located in the montane sclerophyllous forest of the Mediterranean-type climate zone of central Chile. This type of vegetation occurs between 32°–37°S and 73°–70°W (Arroyo et al. 1999) and ranges from 1000 to 2100 m a.s.l. (Cavieres et al. 2000). We sampled two similar elevation gradients, Farellones in Lo Barnechea and Lagunillas in San José de Maipo at four elevations (~ 1000, ~ 1400, ~ 1600 and ~ 2000 m a.s.l.; the exact coordinates and elevations are listed in Supplementary information). Although we did not evaluate environmental differences between the two gradients, they belong to the same mountain range, about 30 km away from each other, and for the analyses they were considered part of the total variation of the system and included as blocks, not as treatments, in the statistical design.

The sampled elevation gradient reflects an environmental severity gradient. In the central Chilean Andes mountain range, elevational gradients are characterized by increases in solar radiation and snow cover (from 0–10% to 50–60% of snow cover at 1000 and 2000 m a.s.l. on some days during winter, respectively, Saavedra et al. 2017). In Lo Barnechea site, a smooth increase in precipitation (from 531 mm at 986 m a.s.l. to 545 mm at 2370 m a.s.l.) has been described (data from 1979 to 2016 CR2MET, Alvarez-Garretón et al. 2018). According to elevation decrease in air temperature (lapse rate) for this zone (6°C km⁻¹, Cavieres and Arroyo 1999) there is a difference of 6°C in the average temperature between our gradient's extremes.

Vegetation is mainly composed by evergreen woody species such as *Quillaja saponaria* (Quillajaceae), *Lithrea caustica* (Anacardiaceae), *Acacia caven* (Fabaceae), *Colliguaja odorifera* (Euphorbiaceae), *Cryptocarya alba* (Lauraceae), *Azara dentata* (Salicaceae), *Baccharis linearis* (Asteraceae) and *Kageneckia oblonga* (Rosaceae), but summer deciduous plants are also abundant at elevations around to 1000 m a.s.l. (Parsons 1976). The treeline is located at 2200 m a.s.l., where only one tree species, *Kageneckia angustifolia* (Rosaceae), is abundant (Rundel 1981, Piper et al. 2006). Vegetation is assembled in multispecific patches of woody species surrounded by a matrix of annual forbs and grasses, dominated by exotic species (Fuentes et al. 1984). This patchy structure could be the result of facilitation and competition as key mechanisms shaping community assemblages (Aguilar and Sala 1999).

Despite elevational variations in temperature and precipitation, the vegetation is relatively homogeneous along the studied gradients, consisting of pre-montane sclerophyllous scrubland. We did not consider elevations above 2200 m. a.s.l. because abiotic variables such as radiation, chemical characteristics of the soil and winter snow accumulation are very different from those at the lower part of the gradient (Cavieres et al. 2000). In addition, vegetation is typically alpine (> 2600 m a.s.l.) with prostrate shrubs and rosette plants (Cavieres et al. 2000) and with cushion plants such as *Laretia acaulis* (Apiaceae) and *Azorella a. madreporica* (Apiaceae) setting up a different facilitation scenario.

For each elevation we measured the cover of all the potential nurse within four 150-m² plots (25 × 6 m) separated approximately by 15 m each other. We consider as potential nurses all the individuals of woody species taller than 1.5 m, with this we tried to ensure that nurse individuals were adults (i.e. have produced flowers and fruits), and therefore established before than the associated, facilitated, individuals. It should be noted that low stature nurse species like cushion plants do not inhabit in our study area; they occur in the Andes way above the treeline (2800–3600 m at this latitude). Plots were divided into 5 × 2 quadrats, with a total of 15 quadrats per plot. Within each quadrat, we recorded the presence and abundance (as number of individuals) of every vascular species beneath the canopy of potential nurses as well as on the adjacent open ground (ca 0.5 m) (Alcántara et al. 2019b). We also measured the nurse canopy size as the projected area of the shrub canopy.

Facilitation effects on species richness

To estimate the effects of facilitation on species richness at the community level, we followed the approach of Cavieres and Badano 2009, who compared the number of species between a community with nurses and a community without nurses. We constructed species accumulation curves (Heck Jr et al. 1975) for two conditions: 1) the entire community (both beneath nurses and on open ground) and 2) only on open ground. These curves show the sampling effort necessary to increase an asymptotic estimate of species richness (Gotelli and Colwell 2001). Because the area beneath nurses was not

always similar to open ground, rarefaction and extrapolation techniques were used to construct these curves (Colwell and Coddington 1994). To construct the curves, incidence matrices of $i \times j$ dimensions were generated, with i representing the species and j the sites. The dimension of each matrix depends on the number of samples obtained, and this reflects the coverage by nurses at each site. The potential differences given by nurse coverage area in relation to open site area were treated by extrapolating the rarefaction curves to 150 samples. Five hundred samples were randomly taken without replacement for each sample size (from one sample to the maximum number of samples), and these species richness values were averaged. The rarefaction curves for each site (entire community versus open sites) showed the average richness for each sample and its 95% confidence interval. Two curves were considered significantly different when their confidence intervals did not overlap once the asymptotes were reached (Gotelli and Colwell 2001). Richness and rarefaction curves were calculated with EstimateS ver. 9.1.0 (Colwell 2013).

The contribution of nurses to total diversity was also estimated with the proportion of increase in species richness as $S_{\text{total}} - S_{\text{open}} / S_{\text{total}}$; S_{total} being the total species richness, including the nurse effects, and S_{open} being the species richness in open areas not influenced by nurses (Cavieres and Badano 2009).

Interactions intensity and phylogenetic distances

To assess sign and the intensity of plant–plant interactions experienced by each species, we calculated the relative interaction index (RII) (Armas et al. 2004) based on the species abundance as $\text{RII} = (\text{abundance beneath nurse} - \text{abundance outside nurse}) / (\text{abundance beneath nurse} + \text{abundance outside nurse})$. The abundance estimations were corrected by the canopy area of nurse plants or the area outside the nurse by dividing the number of individuals of each species by the respective area. Thus, $\text{RII} = 1$ if the 100% of species abundance occurs beneath the nurse, i.e. facilitation; 0 if the abundance is equally distributed between the nurse and outside the nurse; and -1 when 100% of species abundance occurs outside the nurse, i.e. competition. We only calculated the RII values between the nurse and those species that were observed associated with it at least once. By doing this, we discarded all the RII values of -1 , a value indicating that two species do not interact. The number of such non-interacting pairs is usually very high ($> 75\%$) not only in facilitation networks but also in other ecological networks involving positive interactions (Olesen and Jordano 2002, Valiente-Banuet and Verdú 2008).

We first tested whether the intensity of interactions (RII) differed from zero using a one sample t-test in the *stats* ver. 4.0 for R (www.r-project.org). Then we tested whether positive interactions were more frequent than negative ones at each elevation through χ^2 tests.

The phylogenetic distance (PD) between a nurse and its associated species was calculated as the sum of the branch lengths separating the two species in a phylogenetic tree.

The phylogenetic tree containing the 96 species recorded in the community was constructed with the *S.phylomaker* R function using the *PhytoPhylo* megaphylogeny containing more than 31 000 plant species as a backbone (Qian and Jin 2016). This function constructs a community phylogeny by 1) retaining the species included in the megaphylogeny that were observed in the community, 2) pruning the species in the megaphylogeny not observed in the community and 3) grafting the observed species in the community that were absent in the megaphylogeny. We used the scenario in which missing genera or species were added as basal polytomies within their families or genera. The resulting community phylogeny was well resolved, with just nine polytomic nodes out of the 95 possible nodes of a fully resolved tree containing 96 species. Phylogenetic distances were obtained with the *cophenetic.phylo* function in the *ape* package for R (Paradis and Schliep 2018).

We used a linear mixed effects model to test for the effect of elevation on RII, with elevation as a proxy of severity (le Roux and McGeoch 2010, Pistón et al. 2016). The model included the factor nurse (14 nurse species) within site (Farellones and Lagunillas) as a random effect to account for statistical non-independence of associated plant species sharing the same nurse species and site. As elevation was represented by four discrete elevations (1000, 1400, 1600 and 2000 m a.s.l.), we considered it as a four categorical ordered factor. In addition to the linear trend, we also tested for non-linear quadratic or cubic trends of facilitation intensity with elevation.

We subsequently added the phylogenetic distance (log-transformed) between nurse and facilitated species to the model to test whether the intensity of the interaction between facilitation and elevation was different between closely and distantly related species. Statistical models were fitted using the *lme4* package for R (Bates et al. 2015).

Results

Facilitation effects on species richness

The rarefaction curves reached an asymptote in most of the sampled sites (Fig. 1), indicating that the sampling effort was large enough to capture the richness of the community at different elevations. Facilitation by nurse species increased species richness at the community, but there was not a greater increase of species richness due to the nurses toward higher elevations. Comparisons of rarefaction richness at the maximum number of samples, indicated that nurses contained more species than open areas at 1000, 1600 and 2000 m a.s.l. (Fig. 1). The magnitude of these positive effects varied between elevations, with an increase in species richness of 0.395, 0.192, 0.219 and 0.204 at 1000, 1400, 1600 and 2000 m a.s.l., respectively (Table 1). Nurses' contributions to the total richness of the community were 35% (14 species), 17.2% (5 species), 19.6% (10 species) and 17.5% (10 species) at 1000, 1400, 1600–2000 m a.s.l., respectively.

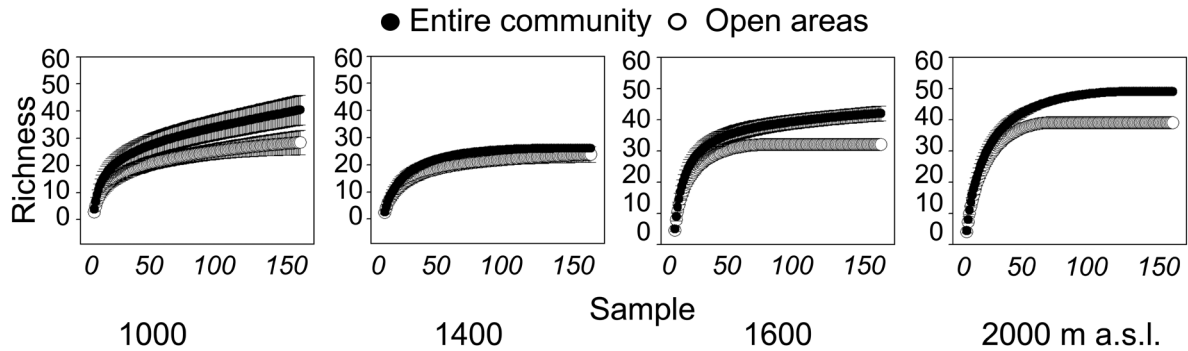


Figure 1. Species accumulation curve (species richness) from 1000 to 2000 m a.s.l., for the community (black symbols) and the sub-set of species located in open areas (white symbols) obtained using the sample-based rarefaction and extrapolation method. Richness estimates are provided with their corresponding 95% confidence intervals. Nurse contribution to total richness can be estimated as the difference between the two curves at the asymptote. Curves are statistically significant when the confidence intervals do not overlap.

Interactions intensity and phylogenetic distances

According to RII, we found 14 shrub species that acted as nurses, with at least one positive interaction between the nurse and its associated species (Table 2). Overall, 56% of the plant–plant interactions detected across the elevation gradient were positive (i.e. facilitative) while 44% were negative (i.e. competitive), but a huge variability in the nurse effect along the elevation gradient occurred (Fig. 2). There were species that acted as nurse for some species and as competitor for others (Fig. 2).

The frequency of positive interactions differed along the elevation gradient, being less frequent than negative interactions at 1000 m (38%; $\chi^2 = 4.1$, $p = 0.04$), no different from negative interactions at 1400 m (68%; $\chi^2 = 3.57$, $p = 0.058$), and more frequent at 1600 m (64%; $\chi^2 = 5.55$, $p = 0.01$) and 2000 m (62%; $\chi^2 = 4.5$, $p = 0.03$). Overall, the intensity of these interactions (RII) were significantly positive (RII = 0.16 ± 0.04 (mean \pm SE), $t = 3.72$, $p = 0.0002$), indicating the prevalence of facilitation. Nevertheless, mean RII differed across elevations: while RII did not differ from zero at 1000 m (RII = -0.07 ± 0.15 , $t = -0.91$, $p = 0.36$), it was significantly positive for higher elevations (1400 m a.s.l.: RII = 0.39 ± 0.12 , $t = 3.38$, $p = 0.002$; 1600 m a.s.l.: RII = 0.23 ± 0.09 , $t = 2.81$, $p = 0.006$; and 2000 m a.s.l.: RII = 0.26 ± 0.08 , $t = 3.19$, $p = 0.002$). However, the differences in RII between the lowest and the other elevations were marginally detected by the linear mixed model (Supplementary information for the whole model), which shows that RII tended to follow both linear and quadratic marginal trends with elevation (linear effect $t = 1.7$, $p = 0.09$; quadratic effect $t = -1.85$, $p = 0.08$). The positive linear effect indicates that RII increased with

elevation, but the quadratic negative term which was slightly stronger than the linear one, indicates a trend where RII increased from 1000 to 1400 and then decreased slightly at 1600 and 2000 m a.s.l. (Fig. 3).

The inclusion of phylogenetic distance in the model testing RII versus elevation showed that only the interaction between the linear effect of elevation and phylogenetic distance was statistically significant (0.19 ± 0.09 ; $t = 2.1$; $p = 0.03$; Table 3). The interaction plot showed that the slope of RII versus elevation increases with the phylogenetic distance between the nurse and the facilitated species (Fig. 4).

Discussion

To properly understand how facilitative interactions shape plant communities across environmental gradients, it is crucial 1) to account for the diversity that nurses add to the communities and 2) to account for the specificity of the interactions. This study revisits facilitation effects by nurse plants at the community level across two elevation gradients, evaluating the effect of nurses on species richness and considering evolutionary relatedness as a proxy for the specificity of interactions. As far as we know, this is the first time that the phylogenetic specificity of all nurses and their facilitated plants has been studied along a stress gradient.

Our results evidenced that facilitation is a prevalent ecological interaction shaping the structure of plant communities at mid elevations (1000–2000 m a.s.l.) of the Andes of central Chile. Indeed, 56% of the plant–plant interactions detected across the elevation gradients were positive (i.e. facilitative) while 44% were negative (i.e. competitive). As expected, the frequency of facilitation changed along the gradient, being less prevalent than negative interactions at low elevation (1000 m a.s.l.), not different at mid elevation (1400 m a.s.l.) and more frequent at high elevations (1600 and 2000 m a.s.l.). Similarly, the intensity of interaction (RII) differed across elevations, ranging from a value not departing from zero at 1000 m a.s.l. to significantly positive values at higher elevations (1400, 1600 and 2000 m a.s.l.).

Table 1. Richness at habitat level and increase in species richness by elevation (1000, 1400, 1600 and 2000 m a.s.l.).

| Elevation | Habitat | | | Increase |
|-----------|---------|------|-------|----------|
| | Nurse | Open | Total | |
| 1000 | 35 | 23 | 38 | 0.395 |
| 1400 | 21 | 21 | 26 | 0.192 |
| 1600 | 37 | 32 | 41 | 0.219 |
| 2000 | 44 | 39 | 49 | 0.204 |

Table 2. Number of facilitated species per nurse. Numbers in parenthesis show how many of these facilitated species are new for the community. Data are shown by elevation (1000, 1400, 1600 and 2000 m a.s.l.) and site (F=Faellones; L=Lagunillas). Dash indicates that the nurse is not present.

| Nurse | 1000 | | 1400 | | 1600 | | 2000 | |
|-------------------------|------|------|------|------|-------|------|-------|-------|
| | F | L | F | L | F | L | F | L |
| Richness | 16 | 24 | 21 | 8 | 29 | 22 | 35 | 22 |
| <i>A. caven</i> | 1(0) | 1(1) | – | – | – | – | – | – |
| <i>B. linearis</i> | 8(1) | 4(4) | – | – | – | – | – | – |
| <i>B. neaei</i> | – | – | – | – | – | – | – | 10(6) |
| <i>B. rhomboidalis</i> | – | – | – | – | – | 3(3) | – | – |
| <i>C. odorifera</i> | 2(0) | – | – | – | – | – | – | – |
| <i>G. foliolosa</i> | – | 1(0) | – | – | – | – | – | – |
| <i>G. trinervis</i> | – | – | 6(0) | – | 8(1) | 7(0) | – | 4(0) |
| <i>K. angustifolia</i> | – | – | 7(2) | – | 19(6) | 9(0) | 21(3) | – |
| <i>L. caustica</i> | 1(0) | 0(0) | – | – | – | – | – | – |
| <i>N. lanatum</i> | – | – | – | – | – | – | 3(0) | – |
| <i>Q. saponaria</i> | – | 3(3) | – | – | – | – | – | – |
| <i>R. rubiginosa</i> | – | – | – | – | – | – | – | 2(0) |
| <i>T. alatum</i> | – | – | – | – | – | – | 4(1) | 1(0) |
| <i>T. quinquenervia</i> | – | 9(5) | – | 6(3) | – | – | – | – |

Our study is based on species spatial associations, and therefore we could be confounding facilitation with shared microhabitat preferences. However, spatial associations due to facilitative interactions have been amply demonstrated in the Mediterranean matorral of Chile (Fuentes et al. 1984, Del Pozo et al. 1989, Peñaloza et al. 2001). For instance, it has been shown that shrubs ameliorate abiotic stress conditions related to intensity of photosynthetic photon flux, evaporation, air and soil temperatures and snow accumulation (Del Pozo et al. 1989, Peñaloza et al. 2001, Ginocchio et al. 2004). These abiotic amelioration factors under shrubs increase the survival of their associated seedlings (Fuentes et al. 1984, Del Pozo et al. 1989, Peñaloza et al. 2001), and the community diversity richness of the community (Ginocchio et al. 2004). Furthermore, the importance of facilitation at the community level found here is consistent with other studies focused on the nurse effect of particular species in scrublands of central Chile (Fuentes et al. 1984, Peñaloza et al. 2001, Cavieres and Peñaloza 2012). These studies have shown that many species are more abundant under or close to the canopy of shrub clumps formed by *Q. saponaria*, *L. caustica*, *C. odorifera*, *Azara dentata* and *A. caven* than away from them. We found that *Q. saponaria*, *L. caustica* and *C. odorifera* facilitate species at 1000 m a.s.l. In addition, *Kageneckia angustifolia* has been documented as a nurse species favoring the establishment of conspecifics, possibly due to a decrease in snow accumulation under its canopy (Peñaloza et al. 2001, Cavieres and Peñaloza 2012). The microclimate mitigation induced by this nurse species also seems to benefit other species because we have found *K. angustifolia* facilitating a long list of species at high altitude (2000 m a.s.l.). The shrub *Baccharis linearis* has been documented as a nurse in areas with human disturbance (Cuevas et al. 2013), which is consistent with our findings of *B. linearis* facilitating species at 1000 m a.s.l. We also report for the first time nursing effects for the species *Trevoa quinquenervia*. Interestingly, the literature had reported nursing effects for its congeneric species *Trevoa*

trinervis (Holmgren et al. 2000), reinforcing the hypothesis that closely-related species tend to behave similarly in terms of their facilitation role, as demonstrated by (Valiente-Banuet and Verdú 2007) in a large worldwide database of species.

Altogether, these nurses facilitate the establishment of up to 14 species that would not otherwise survive, increasing species richness at the community level by up to 35%. The contribution of nurses to species richness differed between communities across elevations, with the highest contribution at 1000 m a.s.l. The highest contribution of nurses to the richness of the community at low elevation was not expected under the SGH when we consider that stress increases with temperature. Other environmental gradients, correlated with elevation, may be also acting. For example, precipitation increases with elevation, and plants at low elevations may be more water-limited. This effect could have been recently magnified in Chile because of the ‘megadrought’ (a persistent rainfall deficit prevailing in central Chile since 2010, Boisier et al. 2016). Droughts certainly play an important role in facilitation interactions, generating an increase in the nurse effect, for example in seedling recruitment (Lloret et al. 2005).

On the other hand, we detected marginal elevation trends in the intensity of pairwise interactions (RII), with neutral mean RII at lowest elevation, the highest intensity at middle elevation and a slight decrease toward higher elevations. The marginal trends in the intensity of pairwise interactions have a nonlinear shape. This is consistent with other studies indicating that facilitative interactions reach their maximum importance under intermediate severity conditions because extreme severity weakens the positive effects of nurses (Michalet et al. 2006, Holmgren and Scheffer 2010, le Roux and McGeoch 2010).

The evolutionarily-inherited traits of a species greatly determine the species with which it will interact (Butterfield and Callaway 2013) and therefore species-specificity in the interaction may interfere with simple SGH predictions

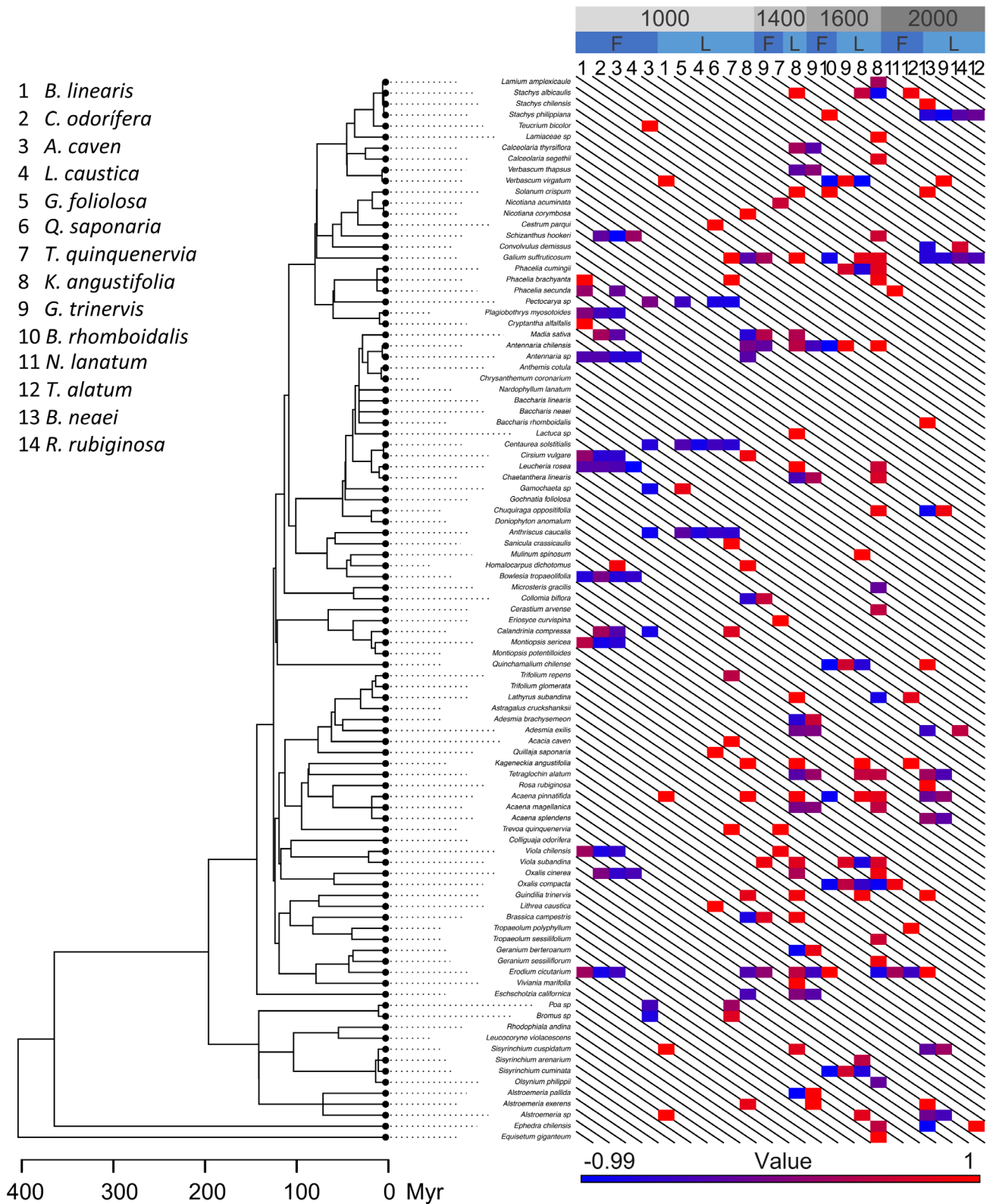


Figure 2. Heatmap showing the relative interaction index (RII) between nurses (in columns) and associated species (in rows) across different elevations and sites (F= Farellones; L=Lagunillas). Bluish marks are indicative of competition while red marks indicate facilitation. The phylogeny of the associated species is also shown.

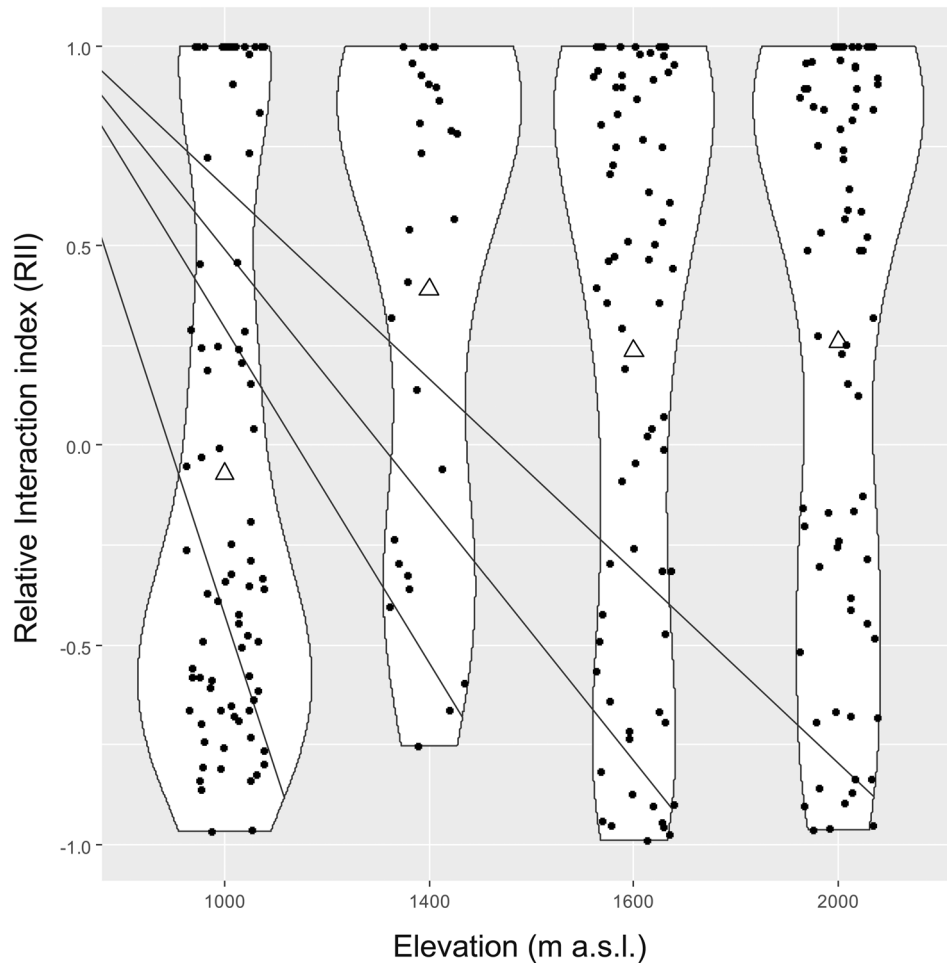


Figure 3. Violin plot showing the relative interaction index (RII) at different elevations. Black dots represent the RII values for each pairwise interaction and white triangles show the average RII per elevation.

based exclusively on variation in abiotic stress conditions (Soliveres et al. 2015). Consequently, we must also consider that the specificity of the interactions may be the result of the evolutionary relationships between the species. Supporting this phylogenetic specificity, we found here that facilitation intensity increased with elevation for interactions involving distantly-related lineages, following the severity gradient. The benefits of facilitation in stressful habitats are magnified as phylogenetic relatedness is reduced because the plants not only compete less but also can cooperate more (Montesinos-Navarro et al. 2017, 2019a). Competition is lower between phylogenetically distant species because they tend to have different physiological and life history traits and therefore to segregate their niches (Webb et al. 2002, Cavender-Bares et al. 2004, Verdú and Pausas 2007). Also, recent evidence indicates that the cooperation between distantly related species may explain plant facilitation due to nutrient transfer through common mycorrhizal networks (Montesinos-Navarro et al. 2019b). Reduced competition and increased cooperation can be especially important for survival in stressful growing conditions, as we have found in the elevation gradients in the Chilean Andes. Our results highlight the inescapable

Table 3. Summary of the linear mixed effect model testing for the effect of elevation and phylogenetic distance between nurse and associated species on relative interaction index (RII). Elevation is coded as an ordered factor with four levels (1000 < 1400 < 1600 < 2000 m a.s.l.), and the three corresponding polynomial contrasts (linear, quadratic and cubic) are shown. The variance estimates along with the significance of the random factor (nurse within site) are also shown.

| Groups | Var ± SD | p-value | | |
|----------------------------|---------------|---------|---------|--|
| Random effects | | | | |
| Nurse within Site | 0.09 ± 0.30 | 0.001 | | |
| Residual | 0.41 ± 0.64 | | | |
| | Estimate ± SE | t-value | p-value | |
| Fixed effects | | | | |
| Intercept | 0.40 ± 0.25 | 1.590 | 0.1113 | |
| Elevation | | | | |
| Linear effect | -0.81 ± 0.50 | -1.619 | 0.1068 | |
| Quadratic effect | -0.86 ± 0.47 | -1.817 | 0.0705 | |
| Cubic effect | -0.35 ± 0.45 | -0.781 | 0.4375 | |
| Phylogenetic distance | -0.04 ± 0.04 | -1.011 | 0.3129 | |
| Elevation × phyl. distance | | | | |
| Linear effect | 0.19 ± 0.09 | 2.114 | 0.0356 | |
| Quadratic effect | 0.12 ± 0.08 | 1.394 | 0.1645 | |
| Cubic effect | 0.07 ± 0.08 | 0.867 | 0.3868 | |

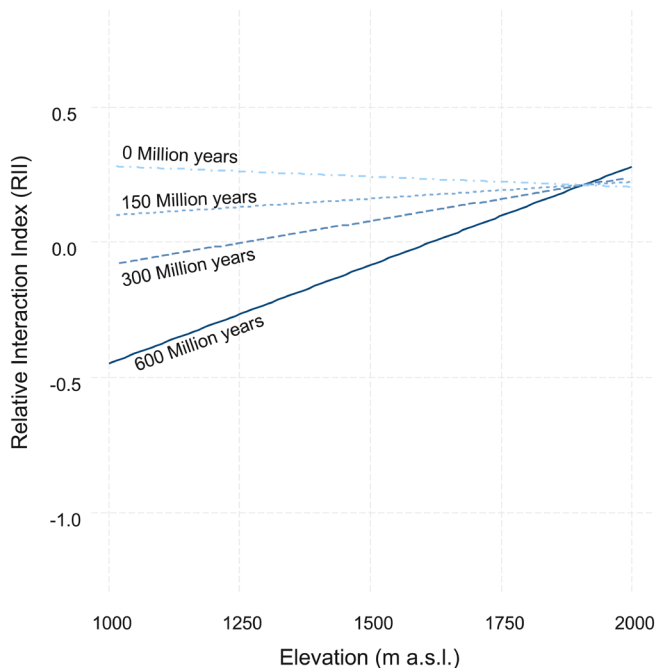


Figure 4. Interaction plot showing the relative interaction index (RII) along the elevation gradient for pairs of species with different phylogenetic distances. For illustrative purposes, we represent elevation as a continuous variable.

relationship between the ecological and evolutionary factors determining the frequency of facilitating interactions (Verdú and Valiente-Banuet 2011). There is consensus about the importance of facilitation in shaping different facets of biodiversity, including taxonomic, functional and phylogenetic diversity (Hacker and Gaines 1997, Cavieres and Badano 2009, Soliveres et al. 2012b, Navarro-Cano et al. 2016, Vega-Álvarez et al. 2019). Understanding how these components are altered along elevation gradients may be determinant to conserve vulnerable and threatened communities facing new climatic scenarios, such as those located in Mediterranean ecosystems (Duarte et al. 2019). Although we have focused on the role of facilitation along a particular, albeit complex, gradient like that found in the Andean ranges, we claim that future studies in other regions worldwide including gradients of different nature might benefit from the inclusion of an evolutionary perspective and help to test for the generality of SGH.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.ns1rn8pr7>> (Duarte et al. 2020).

Acknowledgements – We thank Laureana Muñoz, Estefany Goncalvez, Ronny Zúñiga and Sebastián Contreras for field assistance.

Funding – This work has been partially financed by ICM (P05-002) and by CONICYT (21140099). MV is supported by CYTED (Red 418RT0555). ROB and LAC are supported by Project CONICYT

PIA support for CCTE AFB170008 funding the Institute of Ecology and Biodiversity.

Conflicts of interest – We declare no conflicts of interest.

Author contributions

Milen Duarte: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Miguel Verdu:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lohengrin Cavieres:** Conceptualization (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ramiro Bustamante:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Resources (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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