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Phylogenetic distance among beneficiary species in a cushion plant species explains interaction outcome

Nuria Pistón, Cristina Armas, Christian Schöb, Petr Macek and Francisco I. Pugnaire

N. Pistón (npiston@eeza.csic.es) and F. I. Pugnaire, Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Carretera de Sacramento s/n, ES-04120 La Cañada de San Urbano, Almería, Spain. – C. Armas, Depto de Biología, Univ. de La Serena, Casilla 554, La Serena and Instituto de Ecología y Biodiversidad, Casilla 653, Santiago, Chile. – C. Schöb (<orcid.org/0000-0003-4472-2286>), Inst. of Evolutionary Biology and Environmental Studies, Univ. of Zürich, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland. – P. Macek, Faculty of Science, Univ. of South Bohemia, Branisovska 31, CZ-370 05, Ceske Budejovice, Czech Republic.

Determining which drivers lead to a specific species assemblage is a central issue in community ecology. Although many processes are involved, plant–plant interactions are among the most important. The phylogenetic limiting similarity hypothesis states that closely related species tend to compete stronger than distantly related species, although evidence is inconclusive. We used ecological and phylogenetic data on alpine plant communities along an environmental severity gradient to assess the importance of phylogenetic relatedness in affecting the interaction between cushion plants and the whole community, and how these interactions may affect community assemblage and diversity. We first measured species richness and individual biomass of species growing within and outside the nurse cushion species, *Arenaria tetraquetra*. We then assembled the phylogenetic tree of species present in both communities and calculated the phylogenetic distance between the cushion species and its beneficiary species, as well as the phylogenetic community structure. We also estimated changes in species richness at the local level due to the presence of cushions. The effects of cushions on closely related species changed from negative to positive as environmental conditions became more severe, while the interaction with distantly related species did not change along the environmental gradient. Overall, we found an environmental context-dependence in patterns of phylogenetic similarity, as the interaction outcome between nurses and their close and distantly-related species showed an opposite pattern with environmental severity.

Finding out which mechanisms interact at different spatial scales leading to a given species assemblage is a central issue in community ecology. These mechanisms can be separated relative to the spatial scale into external and internal filters, and involve processes acting at regional scale (i.e. beyond single communities) as well as processes within local communities (Ricklefs 2010, Violle et al. 2012). External filters include factors such as climate, which sort species out from the regional pool and are important determinants of plant community composition (Gaston 2000). Similarly, internal filters such as microscale environmental heterogeneity (Fibich et al. 2013) or plant–plant interactions (Armas et al. 2011) can affect community composition and structure. These filters are not independent; for instance, the outcome of plant–plant interaction varies depending on external filters such as climatic conditions (He et al. 2013). Internal filters may interact with each other as well, e.g. when small-scale environmental heterogeneity affects plant–plant interactions (Choler et al. 2001). Therefore, an approach unifying different drivers, including external and internal filters, is needed to disentangle their relative importance and impact on community assembly.

The integration of phylogenetic information in community analyses has proved to be a powerful tool in understanding changes in species composition. Closely related species tend to share similar trait values, hence may have similar requirements and affect their microenvironment in similar ways; as a consequence, competition is stronger between them than with distantly related species (Violle et al. 2011). This idea was formalized as the phylogenetic limiting similarity hypothesis (PLSH; MacArthur and Levins 1967) and assumes that ecological traits influencing species competition are conserved along phylogenetic lineages (Blomberg et al. 2003, Wiens and Graham 2005). However, evidence supporting this hypothesis is inconclusive (Cahill et al. 2008, Mayfield and Levine 2010).

The species pool under mild environmental conditions is larger and shows wider range of ecological niche space than under severe conditions (Grime and Pierce 2012). Opposite, under harsh environmental conditions external filters (e.g. climate) will severely restrict the species pool, favouring only the presence of species adapted to such demanding conditions (Choler 2005). Assuming that species strategies are phylogenetically conserved (Blomberg et al. 2003, but see Mayfield and Levine 2010), the outcome of plant–plant interactions under mild environmental conditions could render communities phylogenetically diverse, including closely related species. Hence, at the local scale closely related species can show strong competition, following PLSH predictions. By contrast, under harsh environmental conditions the species pool is reduced and it could be expected that species will be more phylogenetically related (Webb et al. 2002) as the environment selects for a given suite of traits.

Under harsh environmental conditions nurse plant species allow for the presence of many other species in the community (Callaway 2007). In alpine environments, a particular case of nurses are cushion plants, which usually ameliorate environmental conditions and facilitate growth and survival of other species (beneficiaries) within them (Badano and Cavieres 2006, Cavieres and Badano 2009). These nurse species can create communities more phylogenetically diverse than communities in open habitats (Butterfield et al. 2013). However, environmental severity restricts the species pool, selecting for species sharing similar traits and more phylogenetically related (Soliveres et al. 2012a). This leads to a paradox between competition intensity among phylogenetically related species and environmental severity that needs more exploration.

To test how plant–plant interactions and phylogenetic relatedness affect each other and how they change along a severity gradient, we analysed the phylogenetic relationships between cushions on other species in three sites along an elevation gradient in the alpine belt of the Sierra Nevada Mountains, Spain. This gradient reflects an increase in environmental severity with elevation characterized by changes in temperature, water availability, and soil nutrients (Sánchez-Marañón et al. 2002, Schöb et al. 2013). We used biomass data to assess interaction outcome for resources and to test the PLSH; and richness as a consequence of plant interactions on presence and survival. Specifically, we expected that 1) the effects of cushion species on its closely-related beneficiary species would vary from very negative to neutral as environmental severity increased; however, the outcome of the interaction of the nurse with its distantly-related beneficiary species would change from neutral to very positive with increasing environmental severity; 2) phylogenetic diversity would change along the gradient, from a community mostly characterized by distantly related species in the less severe environment to one made up by closely related species in the most severe environment; and 3) the contribution of cushions to phylogenetic diversity and species richness would make communities within cushions more diverse than in open areas.

Methods

Field sites, species and data collection

The study was conducted on the north-western slope of the Sierra Nevada Mountains, Spain. We selected three field sites at 2720 m (37°05′N, 03°23′W), 3000 m (37°04′N, 03°22′W) and 3240 m elevation (37°03′N, 03°22′W) encompassing an important gradient in temperature and precipitation (Delgado et al. 1988, Schöb et al. 2013). In this mountain system, and in the range of altitudes where the field sites are located, environmental severity increases with elevation due to decreasing temperature and soil quality, while soil water availability may not be limiting (Schöb et al. 2013).

Overall, climate is continental Mediterranean with a hot and rather dry summer. Mean annual rainfall at the closest met station (Pradollano; 2500 m elevation) is 690 mm, and mean annual temperature is 3.9°C (Worldwide Bioclimatic Classification System 1996–2009). Above 3200 m prevail plant communities with perennial herbaceous species such as *Erigeron frigidus*, *Festuca clementei*, *Linaria glacialis* and *Viola crassiuscula*, including a high number of endemic species. Shrublands prevail below 3000 m, with *Genista versicolor, Hormathophylla spinosa*, *Juniperus communis* ssp. *hemisphaerica, Sideritis glacialis* and *Thymus serpylloides* being the dominant species (Valle 2003). Livestock pressure within our study areas was not high due to its regulation as a National Park (Decreto 238/2011 de 12 de Julio).

The dominant cushion species occurring at all three field sites was *Arenaria tetraquetra* ssp. *amabilis* (Caryophyllaceae), a perennial shrub ranging 10–300 cm^2 in area that often acts as nurse for other species (Schöb et al. 2012, 2013). To assess the contribution of *Arenaria* cushions to community structure, we sampled one hundred 50×50 cm quadrats randomly distributed in each site, identified all species and recorded the number of individuals per species growing in cushions and in the open for each plot. In general, there was at least one cushion plant (mean area of 180 $cm^2 \pm 6.17$ cm^2) within each quadrat except a few quadrats without any cushion, i.e. only open areas.

To evaluate the intensity of plant–plant interactions depending on their phylogenetic relatedness we collected aboveground mass of 20 mature individuals of each of the most common species (14, 12 and 9 species at the low, medium and high sites, respectively; Supplementary material Appendix 1), 10 growing inside *Arenaria* cushions and 10 from open areas. Sampling was paired, collecting one individual from within the cushion and another from an adjacent open area. We selected individuals from open areas more than 35 cm away from *Arenaria* cushions in order to avoid any potential interactions with cushions. Samples were oven-dried at 70°C for 48 h and weighed.

Effect of cushions on species biomass

We measured the interaction outcome between *Arenaria* and each of the other target species as the relative change in biomass of individuals growing within *Arenaria* compared to those growing in open areas. We used the relative interaction index (Armas et al. 2004) as $RII = (B_{cushion} - B_{open})/(B_{cushion} + B_{open})$, where B is the biomass of individuals of the target species growing within *Arenaria* ($B_{cushion}$) or in open areas (B_{open}). This index has positive values when *Arenaria* facilitates other species (i.e. the biomass of the individual growing within *Arenaria* is greater than the one growing in open areas) and is negative when the net effect of *Arenaria* is competitive. Zero RII values suggest that negative and positive effects of *Arenaria* on target species are equal. We calculated the mean value of RII per site (Fig. 1a) and tested

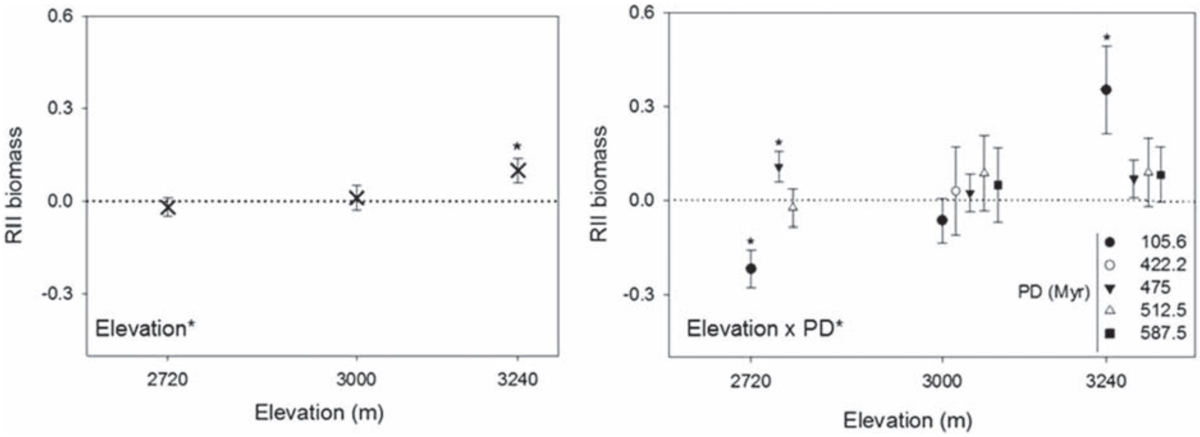

Figure 1. Relative interaction index (RII) between *Arenaria* and selected beneficiary species along the elevation gradient (left panel) (n = 318). RII values as a function of phylogenetic distance (right panel). Data are means ± 1 SE. Symbols with an asterisk represent RII values significantly different from 0. Significant differences ($p < 0.05$) along the elevation gradient and the interaction between the gradient and phylogenetic distances shownd by *.

whether RII depended on phylogenetic relatedness (Fig. 1b). For this, we assembled a phylogenetic tree for all the species recorded at our three sites (54 species) using Phylomatic3 (< http://phylodiversity.net/phylomatic/ >). All families in our dataset matched the family names of Angiosperms megatree used in Phylomatic (R20120829), that reflects the consensus of the Angiosperm Phylogeny Group (2009). Branch lengths were adjusted with the Phylocom Bladj algorithm (< http://phylodiversity.net/phylocom/ >) by computing age estimates for major nodes in our tree (Wikstrom et al. 2001) and distributing undated nodes evenly between those of known ages (Supplementary material Appendix 2). We then obtained phylogenetic distances (PD) among *Arenaria* and the other species using the function cophenetic.phylo (picante library; Kembel et al. 2010) which calculates distances between pairs of tips in our phylogenetic tree using branch length. To test for changes in RII with elevation we used one-way ANOVA; we then used a second model with elevation and phylogenetic distance between *Arenaria* and each target species. As the second model was unbalanced and incomplete, we re-parametrized it in a single factor with 12 'Elevation × PD' levels. We performed one-sample t-tests to check whether RII values within each site and phylogenetic distance were different from zero (i.e. neutral interaction). Post hoc differences were examined with LSD Fisher's tests corrected by Bonferroni for multiple-comparisons.

Contribution of cushions to phylogenetic diversity

We assessed the effect of cushions on phylogenetic community structure at each site by considering all samples in the site (open + cushion) as compared to open areas within plots (open), the latter being a reflection of the intensity of environmental filtering. We calculated two metrics of phylogenetic community diversity per plot, the mean phylogenetic distance (MPD) and mean nearest phylogenetic taxon distance (MNTD) (picante library; Kembel et al. 2010). Both range 0 to infinity; small values represent communities composed of species closely related and large values represent communities with species distantly related. MNTD is typically used to test PLSH as it is sensitive to co-occurrence patterns among closely related species. However, MNTD contains much less information than MPD, which reflects the phylogenetic diversity of taxa over the whole pool of species (Webb 2000). Plots with less than two species were excluded from the analyses as they were uninformative. MPD and MNTD were calculated by weighting species abundance; abundance data were log-transformed to minimize the effect of particularly abundant species (Butterfield et al. 2013). We preferred observed over the expected phylogenetic distances (i.e. NRI and NTI) as we use phylogenetic distances as a factor to explain the intensity of plant–plant interactions. As such, absolute distances between species seem more appropriate than their deviations from a random pattern. To check for changes in MPD and MNTD along the severity gradient and among microhabitats, we used linear mixed models. Elevation and microhabitat (cushion + open versus open) and their interactions were included as fixed factors. We included plot (each of the one hundred 50 × 50 cm quadrats randomly distributed in each site) as a random effect.

Contribution of cushions to species richness

We calculated a third diversity metric, total species richness, to relate patterns of change with MPD, MNTD at each site and along the environmental gradient. Total species richness was calculated at plot level due to differences in area between *Arenaria* cushions and open areas. To test the relationship between total species richness per plot and elevation we used generalized linear models with a Poisson error structure and the log link-function. In addition, to quantify the effect of cushions on species richness at the community level we used rarefaction curves, from which we estimated community-level species richness (S_{total}) and species richness without cushions (S_{open}) per site following Cavieres et al. (2014) (Supplementary material Appendix 3). To assess the magnitude of change in species richness at community level due to the presence of cushion species, we calculated the proportion of increase in non-cushion species richness (ISR) as:

$$ISR = (S_{total} - S_{open}) / S_{total}$$

Rarefaction analyses were performed with the software EstimateS ver. 9.1 (<http://viceroy.eeb.uconn.edu/estimates/>). Statistical analyses were conducted in R ver. 3.0.2 (<www.r-project.org/>) using for linear models the interface implemented in InfoStat-Statistical Software (Di Rienzo et al. 2013).

Results

Overall, the net effect of *Arenaria* on the biomass of other species changed in intensity and sign (RII) along the gradient, showing facilitation at the most severe site (i.e. highest elevation) and neutral effects in other points of the gradient (Fig. 1a). Taking into account phylogenetic relatedness, the RII of species closely related to *Arenaria* (≤ 105.6 Myr) increased with environmental severity but in general, it did not change for medium (≥ 422.2 Myr) and distantly related species (≥ 512.5 Myr). However, there was an exception at the least severe site (i.e. lowest elevation), where species intermediately related to *Arenaria* (475 Myr) were facilitated by the cushion.

Data showed that MPD decreased and MNTD increased with environmental severity (Fig. 2a–b). Specifically, both indices increased from mid to high elevation, while total species richness remained steady (Fig. 2a–c). At each elevation, MPD was always higher in cushion + open than in open areas (Fig. 2a), while MNTD did not vary between cushion + open nor in the open (Fig. 2b).

Total species richness decreased as environmental severity increased, but there were no significant differences between mid and high elevations (Fig. 2c). Total species richness positively correlated with MPD and negatively with MNTD ($r = 0.71$ and $r = –0.32$ respectively, $p < 0.0001$). There was a significant effect of cushions on species richness at mid and high elevations but not at low elevation (Supplementary material Appendix A3).

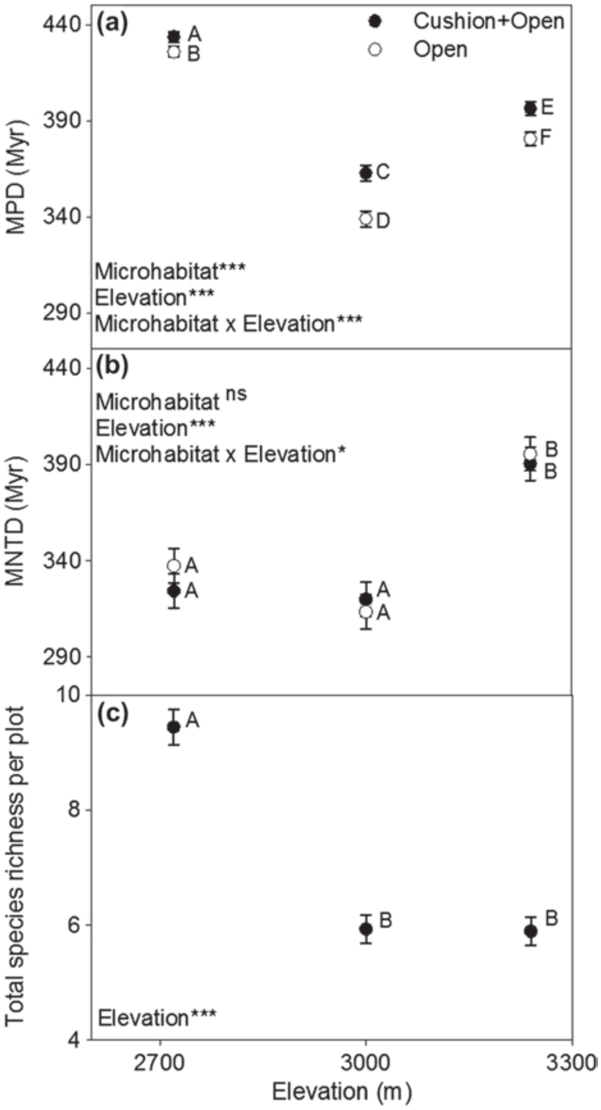

Figure 2. (a) Mean phylogenetic distance (MPD; n = 589), (b) mean nearest taxon distance (MNTD; n = 587) in communities along an environmental gradient; (c) total species richness per plot at the three sites (n = 589). Data are means ± 1 SE. Letters represent differences among factors. In each panel are included the fixed factors and their significance (linear mixed models for MPD and MNTD, and GLMM for total species richness), where * and *** indicate $p < 0.05$ and $p < 0.0001$, respectively. ns indicates non-significant differences.

Discussion

Our data suggest a relationship between phylogenetic relatedness and the outcome of plant–plant interactions along a severity gradient. Specifically, the effect of nurses on their closely related species varied from positive to negative as the environment became less severe while with more distantly-related species it remained mostly neutral. At the site level, MPD and MNTD varied with environmental conditions, with nurses increasing mean phylogenetic distance compared to open areas. Thus, we found a remarkable context-dependent effect of phylogeny on plant–plant interactions.

Relationship between phylogenetic relatedness and plant–plant interactions

Plant–plant interaction intensity and sign are expected to change depending on abiotic conditions; following predictions of the stress gradient hypothesis (Bertness and Callaway 1994) we expected a prevalence of positive interactions in the severe part of the gradient and negative interactions in the milder part. Indeed, we found that facilitation prevailed at the most severe site among closely related species, suggesting that cushions produced an expansion of the realized niche of stress-sensitive species, allowing them to survive in environments too harsh without nurse protection (Butterfield et al. 2013, Valiente-Banuet and Verdú 2013). Thus, the interaction effects of nurses on their closely related species varied from positive to negative as the environment became less severe while with more distantly-related species it remained, in general, neutral, with the exception of intermediately-related species that were facilitated at the less severe site. This data agree with Butterfield et al. (2013), who found that cushions facilitated certain lineages (in our case, those closely related to *Arenaria*) as environmental severity increased, but excluded other lineages (in our case, medium-related species) when environmental severity was highest.

Our results partially support the phylogenetic limiting similarity hypothesis (MacArthur and Levins 1967, Violle et al. 2011), as at the less severe site (i.e. low elevation) closely-related species competed with *Arenaria*. However, when environmental conditions became more severe (i.e. intermediate and high elevation sites) competition became less important in shaping plant interactions. Hence, the observed competition between *Arenaria* and closely-related species disappeared at medium environmental severity and turned to facilitation at high environmental severity.

There is a controversy regarding phylogenetic relatedness and the outcome of plant interactions. Bennett and Cahill (2013) suggested that, should niche conservatism be common, the response of related species to environmental conditions should be similar. Although some studies support existence of the relationship between phylogenetic relatedness and interactions (Castillo et al. 2010, Soliveres et al. 2012b, Verdú et al. 2012), other studies found no relationship (Cahill et al. 2008, Fritschie et al. 2013). In our alpine environment phylogenetic relatedness plays a clear role in the outcome of plant interactions but its effect is context-dependent.

The influence of interactions on community assemblage

Phylogenetic diversity was characterized by a predominance of distantly related species (high MPD) in communities at high and low severity sites and by closely related species at intermediate environmental severity. MNTD changed within species closely related from more distantly related to each other (higher MNTD) in communities at the most severe site to more closely related species in communities at the less severe site. Changes along the severity gradient could be consequence of the positive correlation between MPD with total species richness while this relationship was negative for MNTD. Thus, higher species richness increased the probability of having higher phylogenetic diversity in the community, which in turn increased the probability of higher MPD and lower MNTD.

Nevertheless, significant increases in MPD and MNTD at the high elevation site suggest that closely-related species to each other are replaced by distantly-related species. Despite the similar number of species at the most severe sites, from mid- to high-elevation sites phylogenetic distance changed significantly (33.7 Myr for MPD and 70.5 Myr for MNTD), reflecting that cushions increasingly facilitate closely-related linages and exclude medium-related lineages at high elevations. Changes in phylogenetic diversity, most likely due to environmental filtering caused by climatic severity, did not occur across entire lineages (Arroyo-Rodríguez et al. 2012) (e.g. in our case *Arenaria serpyllifolia* and *Paronychia* sp. disappeared from 3000 m to 3200 m but not the entire clade of Caryophyllaceae); thus, at least at these two sites, environmental conditions appear very important for shaping phylogenetic community structure and may also result in different trait distribution patterns (Cavender-Bares and Reich 2012, Purschke et al. 2013).

Mean phylogenetic distance was always smaller in communities from open areas than in whole communities, while there were no differences for MNTD in any of the three sites. MPD may be more sensitive to the outcome of plant interactions as traits might be conserved within relatively older nodes (i.e. among families); MNTD, by contrast, considers a narrower phylogenetic scale and might not capture relevant trait information when analysing the effects of plant competition on phylogenetic diversity. Therefore, a smaller MPD in open-area communities suggest that harsher environmental conditions promote stronger habitat filtering, leading to a large decrease in species abundance and creating communities with species more related than in less severe sites (Webb et al. 2002). In such conditions, cushion plants may provide suitable habitats for these species that are less abundant or extinct in open areas, allowing them to survive in such an extreme environment while they almost disappear in harsh open areas (Butterfield et al. 2013).

Conclusion

Overall, when environmental conditions were relatively mild (i.e. at low elevation) we found partial support for the phylogenetic limiting similarity hypothesis; the interaction effects of nurses on their closely related species varied from positive to negative as the environment became less severe, while with more distantly-related species it remained, in general, neutral. Thus, under severe conditions (i.e. high elevation), facilitation became more frequent and intense, favouring the growth of closely related species, which suggest that under such conditions closely-related species – i.e. sharing similar traits – cope better with environmental severity, and facilitation prevails over disadvantages of competition. Thus, there is an environmental context-dependence effect of phylogenetic relatedness which influences plant–plant interactions and shapes plant community structure.

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Supplementary material (available online as Appendix oik.01979 at <www.oikosjournal.org/readers/appendix>). Appendix 1–3.

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