

Research article

Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient



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ABSTRACT

In alpine environments facilitator species buffer environmental extremes while building up soil resources above that of open areas. These modulating effects are critical for the persistence of species out of their optimal range and contribute to increase community-level plant species richness and phylogenetic diversity. We analyzed the effects of seven potential facilitator species with contrasting morphologies on subordinate plant species along a crossed environmental gradient, linking such effects to canopy effects. We also used these patches consisting of multiple shrub species to evaluate the effects of the whole shrub community on species richness and phylogenetic diversity, and whether such shrub community effects differed along the gradient. We used ecological and phylogenetic data of alpine plant communities along two altitudinal gradients on opposing aspects of the Sierra Nevada Mountains (Spain). As expected, shrubs buffered harsh abiotic conditions by decreasing mean temperatures and increasing relative humidity with regard to open areas. Composition of subordinate plant communities differed among shrubs and among sites, and correlated with relative humidity along the gradient pointing to the dependence of subordinate species on micro-environments created by shrubs. There were a variety of shrub effects on overall plant abundance and richness depending on shrub identity. In the most extreme sites we recorded generally positive effects of the shrub community, which promoted whole-community species richness and phylogenetic diversity despite species-specific effects ranging from clearly negative to positive. Our data therefore show that the effect of different shrub species on plant community richness and phylogenetic diversity is not redundant, as every shrub species may host unique communities, thereby affecting the structure and composition of the whole community.

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1. Introduction

The impact of species interactions on diversity patterns has been addressed in detail in stressful environments such as the alpine belt (Cavieres et al., 2014; Liczner and Lortie, 2014; Reid et al., 2010). In alpine environments, facilitator species – often cushions and small shrubs – alter microhabitats by buffering temperature extremes and wind, maintaining soil humidity and nutrient availability higher than open areas (Anthelme et al., 2014; Cavieres et al., 2005;

Körner, 2003). The modulating effects of facilitator species under stressful environments are critical for the persistence of subordinate species outside of their optimal range and contribute to higher community richness (Badano and Cavieres, 2006; Schöb et al., 2012). This positive effect of facilitator species changes with abiotic conditions, usually turning from positive to negative between harsh and mild environments (Callaway et al., 2002). In addition, ontogeny of facilitator species (Armas and Pugnaire, 2005; Soliveres et al., 2010), soil organisms (Rodríguez-Echeverría et al., 2013; Rodríguez-Echeverría and Traveset, 2015; Van der Putten, 2009) and different morphologies within and among species may also affect the outcome of facilitator-beneficiary interactions (Bråthen and Ravolainen, 2015; Michalet et al., 2011; Schöb et al., 2012). For example, canopy morphologies among facilitator species vary widely from very compact to loose (Aubert et al., 2014), a fact which may influence microhabitat in different ways leading to facilitation.

Abbreviation: RII, Relative Interaction Index (effect of the interaction on richness and abundance) (Armas et al., 2004).

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Thus, the co-occurrence of disparate facilitator species may fill a larger niche space and create higher environmental heterogeneity than a single facilitator species, increasing species richness at the whole community level.

Plant morphology is not an easy metric to use due to the complex variety of traits involved; alternatively, a useful approach to account for species similarity is to use phylogenetic relationships (Ackerly, 1997; Cavender-Bares et al., 2009). Under the phylogenetic limiting similarity concept (Darwin, 1859; MacArthur and Levins, 1967), functional traits shaping a phenotype are considered conserved along phylogenetic lineages (Blomberg et al., 2003; but see Mayfield and Levine, 2010) including those influencing species interactions (Violle et al., 2011). Given that species sharing traits within close phylogenetic lineages may have similar responses to the environment, severe environmental conditions are likely to sort species out, leading to communities with low species richness and low phylogenetic diversity (Cavender-Bares and Reich, 2012; Soliveres et al., 2012). However, and due to the effect of facilitator species in buffering extreme conditions, facilitators increase species richness and phylogenetic diversity (Butterfield et al., 2013). Thus, diversity patterns would depend on both, environmental severity, and on the effects of facilitator species (Pistón et al., 2015; Valiente-Banuet and Verdú, 2013).

Since different shrub and cushion species create different microhabitats which could be colonized by different species (Díaz and Cabido, 2001), the co-occurrence of several facilitator species would likely increase community-level diversity. However this issue has hardly been addressed (Amat et al., 2015; Zhang et al., 2011). Most reports on positive interactions concerned only one facilitator species per community, even though communities in stressful environments often include different potential facilitator species (Pugnaire et al., 2004) creating microhabitats that fulfill niche requirements of a greater variety of subordinate species. We assume that different shrubs exert net positive (i.e., facilitation) or negative (i.e., competition) effects on subordinate communities, and that the effects of different shrub species are not redundant; i.e., there is a whole range of species-specific effects of shrubs on subordinate plant communities. However, the combined effects of different, non-redundant shrub species would be different, in terms of subordinate species diversity, from that of individual shrub species.

Our goal in this study was to analyze the effects of several potential facilitator species with contrasting morphologies on subordinate plant communities along an environmental gradient spanning the North and South aspects in a dry mountain ecosystem, linking such effects to microhabitat conditions under the canopy of each shrub species. We were also interested in analyzing the contribution of co-occurring shrub species to community-level species richness and phylogenetic diversity, and whether the effects of facilitator species differed along the gradient. For this purpose we selected in the Sierra Nevada Mountains, Spain, an environmental gradient characterized by changes in temperature, water availability, and soil organic matter (Sánchez-Marañón et al., 2002; Schöb et al., 2013), and recorded plant community composition beneath seven shrub species and in adjacent open areas in 6 sites at different elevations; three sites were in the northern aspect and three in the southern aspect of the Sierra Nevada range. We expected that community composition would change depending on shrub identity, being related to microclimatic conditions beneath them. We expected species-specific effects of different shrubs on subordinate plant communities (i.e., not only affecting intensity and sign of the interaction, but also presence/absence of subordinate species and abundance). We also expected a general trend in the magnitude of effects along the gradient, so that individual shrubs would mostly have overall positive effects on plant community richness and plant abundance under relatively

harsher environmental conditions while the net effect of shrubs would be neutral or competitive under milder environmental conditions, as predicted by the stress gradient hypothesis (Bertness and Callaway, 1994). At the community level we expected a net positive effect of the whole shrub community on subordinate community-level richness and phylogenetic diversity in stressful sites and no effects in relatively milder sites, where negative and positive effects on subordinate species would be leveled.

2. Methods

2.1. Field sites, species and data collection

The field sites are located in the Sierra Nevada Mountains, South-eastern Spain. We selected three sites, each ca. 1 ha, on the northern aspect of the Veleta peak at 2315 m, 2720 m and 3240 m elevation, and three on the southern aspect of the Mulhacén peak at 2040 m, 2570 m, and 2900 m elevation. Both peaks are separated by a distance of 30 km approx. The bedrock is mica-schist, and determines the rounded and gentle hillside landscape (Delgado et al., 2001).

Climate is dry continental Mediterranean with a hot and dry summer with means of 17 °C and 5 mm rainfall in July and –2.5 °C and 90 mm rainfall in January (Pradollano (37°05' N 03°23' W); 2500 m elevation; <http://pendientedemigracion.ucm.es/info/cif/station/es-prad2.htm>). Mean annual temperature decreases about 0.61 °C/100 m at the North aspect and 0.59 °C/100 m at the South aspect; mean annual precipitation increases around 30 mm/100 m at the North aspect and 28 mm/100 m at the South aspect (Delgado et al., 1988). Abiotic factors change with elevation, resulting in a crossed gradient where temperature and soil organic matter decrease with elevation while precipitation – and soil water – increase with elevation (Pugnaire et al., 2015a; Schöb et al., 2013) as in other dry mountains (Pugnaire et al., 2015b).

Plant communities in Sierra Nevada are characterized by a great diversity of species with a high level of endemism (Delgado et al., 2001). Subalpine-alpine shrubland communities (“piornales-enebrales”) are dominated by prostrate shrubs like *Cytisus galianoi* Talavera and P. E. Gibbs. (Fabaceae), *Genista versicolor* Boiss. (Fabaceae) or *Hormathophylla spinosa* (L.) P. Küpfer (Brassicaceae), and cushion-forming species like *Arenaria tetraquetra* ssp. *amabilis* (Bory) H. Lindb. fil. (Caryophyllaceae). Our analyses focused on seven species that dominated plant communities at our field sites, *A. tetraquetra* ssp. *amabilis*, *Bupleurum spinosum* Gouan (Apiaceae), *C. galianoi*, *G. versicolor*, *H. spinosa*, *Juniperus communis* ssp. *nana* Syme (Cupressaceae), and *Plantago holosteum* Scop. (Plantaginaceae). For simplicity we will refer to them as shrubs, although two of them, *A. tetraquetra* and *P. holosteum* are cushions. Regarding their morphology, and following the description of different canopy shapes by Aubert et al. (2014), *A. tetraquetra* shows a semi compact creeping canopy, *B. spinosum* and *H. spinosa* are thorny compact shrubs, *C. galianoi* and *G. versicolor* are radial hollow hemispherical shrubs, *J. communis* is a thorny-prostrated shrubs and, *P. holosteum* is a tufted compact cushion. Shrubs and surrounding open areas were colonized by predominantly small perennial herbs and grasses (see Table S1 in Supporting Information for a list with the number of species that were shrub-dependent and Table S2 for the full list of species present at the sites).

In July 2010, at the peak of the growing season, we selected 30 individuals of each of the dominant shrub species present at each site and did a paired sampling beneath them and randomly in nearby open areas (but at least 1 m away the shrub canopy); we recorded the number of all plant species and the their number of individuals (number of shoots in the case of clonal species). For small cushions such as *A. tetraquetra* ssp. *amabilis* (mean ± 1SE; 209 ± 12 cm²) and *P. holosteum* (190 ± 19 cm²) the sampling was

done for the whole cushion canopy and paired with open plots of equal size (Schamp et al., 2013). For *B. spinosum* ($4,992 \pm 506 \text{ cm}^2$), *C. galianoi* ($8,689 \pm 684 \text{ cm}^2$) and *G. versicolor* ($10,641 \pm 834 \text{ cm}^2$) we randomly placed one 625 cm^2 quadrat per canopy paired with a similar area in the open. As *G. versicolor* was larger at the low North site, we used $1,250 \text{ cm}^2$ quadrats. For *J. communis* ssp. *nana* ($115,582 \pm 9340 \text{ cm}^2$) we sampled five randomly placed 625 cm^2 quadrats per shrub and an equal number of open area plots. For *H. spinosa* ($1,573 \pm 101 \text{ cm}^2$) we sampled the whole canopy area and a 625 cm^2 quadrat in open areas.

2.2. Micro-environmental conditions along the gradient

We recorded air temperature and relative humidity (RH) at hourly intervals with iButtons (Maxim Integrated Products, Sunnyvale CA, USA). At each site three temperature sensors were randomly placed in the open and three into the canopy, in the mid-point between the stem and the edge of the canopy, of *B. spinosum*, *C. galianoi*, *G. versicolor*, *H. spinosa* and *J. communis* when the species were present. Sensors were placed 5 cm above ground and protected from direct solar radiation with a wooden cube placed above the sensor allowing free airflow near the sensor. Using hourly values, we calculated the mean air temperature and RH for August 2010 (peak of the growing season at Sierra Nevada) and checked for differences between aspects (North and South), elevation (low, middle and high) and microhabitat (cushion vs. open areas) with a three-way factorial ANOVA. Temperature data were transformed with a power of two to meet the homogeneity of variances and normality assumptions. Post hoc differences along the gradient were examined with Fisher's LSD tests and significant differences among shrub species at each site were tested by separate contrasts within each site.

2.3. Sign and intensity of plant interactions

To test whether and which shrub species had positive effects on species richness and overall plant abundance (i.e., total number of individuals irrespective of the species) along the environmental gradient we measured the interaction outcome between each shrub species and the subordinate community at each site. Since there were no observable spatial distribution patterns and the substrate was homogenous, we assumed no microsite effects other than caused by shrubs. In addition, it is unlikely that hidden microsites would select rare rather than common species under nurses (Soliveres et al., 2015). Interaction outcome was measured as the relative change in species number and abundance beneath shrubs compared to open areas. We used the Relative Interaction Index (Armas et al., 2004) as $\text{RII} = (S_{\text{shrub}} - S_{\text{open}}) / (S_{\text{shrub}} + S_{\text{open}})$, where S_{shrub} and S_{open} are the values of species richness and plant abundance of the subordinate community measured in the presence and absence of a dominant shrub. This index is positive when species richness or plant abundance is higher beneath shrubs than in open areas and negative when species richness or plant abundance is higher in open areas than below shrubs. Values of RII not differing from zero suggest that species richness and plant abundance are equal underneath shrubs and in open areas. We calculated the mean value of RII per site and shrub species and tested for differences among sites and among shrub species with general linear models. As our model was unbalanced and incomplete (not all shrub species were present at all sites), we re-parametrized the model using a single fixed factor with 18 "Site.Species" levels. We performed one-sample *t*-tests to check whether RII values within each site and cushion species were different from zero (i.e., neutral interaction). We excluded *H. spinosa* from all these analyses due to

the differences in sampling areas between the shrub and its paired open areas.

2.4. Assessing species diversity along the environmental gradient

We tested for differences in community composition analyzing plant density (number of individuals of each subordinate species per cm^2) of all subordinate species associated to each shrub species and at each elevation by performing a Principal Coordinates Analysis (PCoA). For this analysis, we excluded subordinate species with a frequency below 5% in order to avoid rare species effects. We used Bray–Curtis distances and extracted 3 axes, which explained a total of 43% of the variance. To test if differences in community composition among shrub species were significant we used a multivariate mean comparisons test (gDGC test) based on cluster analysis, using a diagonal covariance matrix with a single linkage and a Monte Carlo simulation with 500 permutations (Valdano and Di Rienzo, 2007). We used plant density instead of abundance or composition because, given differences in plot size of different shrubs, the latter could be prone to plot-size effects while density would be less affected. Finally, to test the relationship between microhabitats (temperature and RH along the environmental gradient) and community composition (the site scores for axis 1, 2 and 3 extracted from PCoA analysis) we calculated Spearman's rank correlation (r_s).

2.5. Community level species richness and phylogenetic diversity

We assembled a phylogenetic tree with the 86 sampled species using Phylomatic3 (<http://phylodiversity.net/phyloomatic/>). All families in our database matched family names of the angiosperm megatree (R20120829), based on the Angiosperm Phylogeny Group (Stevens, 2001). Branch lengths were adjusted with the Bladj algorithm taking age estimates for the main nodes from Wikstrom et al. (2001) and distributing undated nodes evenly among nodes of known age as implemented in Phylocom 4.2 (<http://phylodiversity.net/phylocom/>).

To quantify the effect of all shrubs on community-level species richness and phylogenetic diversity we used rarefaction curves that allowed accounting for differences in sampling effort (i.e., different plot sizes) among microhabitats (i.e., shrubs and open areas). With community-level we refer to the whole community at each of the sites (i.e., all the species including all shrubs and species in open areas). In the case of species richness, we used the function *specaccum* with the rarefaction method (Oksanen et al., 2013) which finds the expected number of subordinate species by re-sampling at random the pool of shrub and open samples, plotting the average number of species for a pre-determined number of shrub and open samples (Gotelli and Colwell, 2001). For phylogenetic diversity, the total branch length of a phylogenetic tree, we used the function *phylocurve* (<http://davidnipperess.blogspot.com.es/>), which generates an individual-based rarefaction curve. It calculates expected phylogenetic diversity for a number of individuals per branch and per sample, and using sampling without replacement (Nipperess and Matsen, 2013). These two measurements provide different information, as species richness considers species as equally distinct from one another while phylogenetic diversity considers how much evolutionary history is behind the species in a community (Faith, 1992). Phylogenetic diversity represents individuals by their relative branch lengths without the need to establish absolute species identity (Nipperess and Matsen, 2013). Thus, different shrubs can increase species richness to a similar extent but may differ in the composition of species they host and thus in their effects on the phylogenetic diversity of subordinate communities (i.e., if two shrub species equally increased the number of species compared to open areas but species within one of the shrub species were closer in the phylogenetic tree than species

within the other shrub, then the rarefaction curves for richness will be equal for the two shrub species but those for phylogenetic diversity will be quite different). To evaluate the effect of shrubs on species diversity or phylogenetic diversity we calculated two rarefaction curves per site for each variable; one including open areas only and one taking into account all shrubs along with open areas, and plotted them for each site. All statistical analyses were conducted in InfoStat v. 2014 (Di Rienzo et al., 2014) and R 3.0.2 (<http://www.r-project.org/>).

3. Results

Mean temperature in summer was higher in the southern than in the northern aspect, decreasing by $6.2 \pm 1.8^\circ\text{C}$ (mean $\pm$ 1SE) and $5.3 \pm 1.5^\circ\text{C}$ from low to high elevation sites in the North and South aspects, respectively. Mean temperature beneath shrubs was $1 \pm 0.3^\circ\text{C}$ and $1.6 \pm 0.4^\circ\text{C}$ lower than in open areas in the North and South aspects, respectively. All along the gradients, temperatures were higher in open areas than beneath shrubs, except in the highest sites where temperatures did not differ ($13.7 \pm 0.4^\circ\text{C}$ vs. $13.5 \pm 0.4^\circ\text{C}$ for shrubs and open areas, respectively, in the North, and $16.3 \pm 0.2^\circ\text{C}$ vs. $16.8 \pm 0.5^\circ\text{C}$ in the South). The most important effect of shrubs on temperature were at the low South site where the differences between shrubs and open areas ranged 1.3–2.5°C (Fig. 1a, and Tables S3 and S4 for statistical results).

Mean relative humidity in summer increased with elevation by $4.2 \pm 1.6\%$ in the North, and decreased with elevation by $2.0 \pm 1.0\%$ in the South aspect. Mean relative humidity beneath the shrubs was $7.5 \pm 2.9\%$ and $8.3 \pm 2.4\%$ higher than in open areas in the North

and South aspects, respectively. Moreover, relative humidity was always higher beneath shrub species than in open areas all along the gradient except for *H. spinosa* at middle sites in both aspects. The most important effect on relative humidity by shrubs were found at the low South site, where values ranged 6.9–14.9% (Fig. 1b and Table S3 and S4 for statistical results).

The net effect of shrubs (RII) on plant abundance (i.e., total number of individuals) and species richness changed in intensity and sign depending on shrub identity and environmental conditions. In general, we found positive and neutral effects at the most severe sites (i.e., highest and lowest elevations in both aspects), yet one shrub species (*J. communis*) always had negative effects irrespective of environmental harshness. We found neutral to negative effects at milder environments (Middle sites; Fig. 2). In general, *A. tetraquetra* and *C. galianoi* had positive effects under harsher conditions and showed neutral or weak positive effects in milder environments. By contrast, *G. versicolor* and *P. holostium* showed consistent neutral interactions at all sites where the species occurred.

Community composition of subordinate species (i.e., number of individuals per species and cm^2) differed among shrub species as shown by PCoA analysis (Fig. 3a) and post-hoc gDGC tests (Fig. 3b). It was significantly different under the different shrub species within a site, with some exceptions (e.g., *C. galianoi* and *H. spinosa* at the low South site; *C. galianoi* and *G. versicolor* at the middle South site, and *H. spinosa* and *J. communis* at the high South site). However, this data could be prone to plot size effects and thus should be taken with caution. The number of dependent subordinate species (i.e., species found only under shrubs) ranged from 1 under *P. holostium* at the middle North site up to 13 under *C. galianoi* at the low South

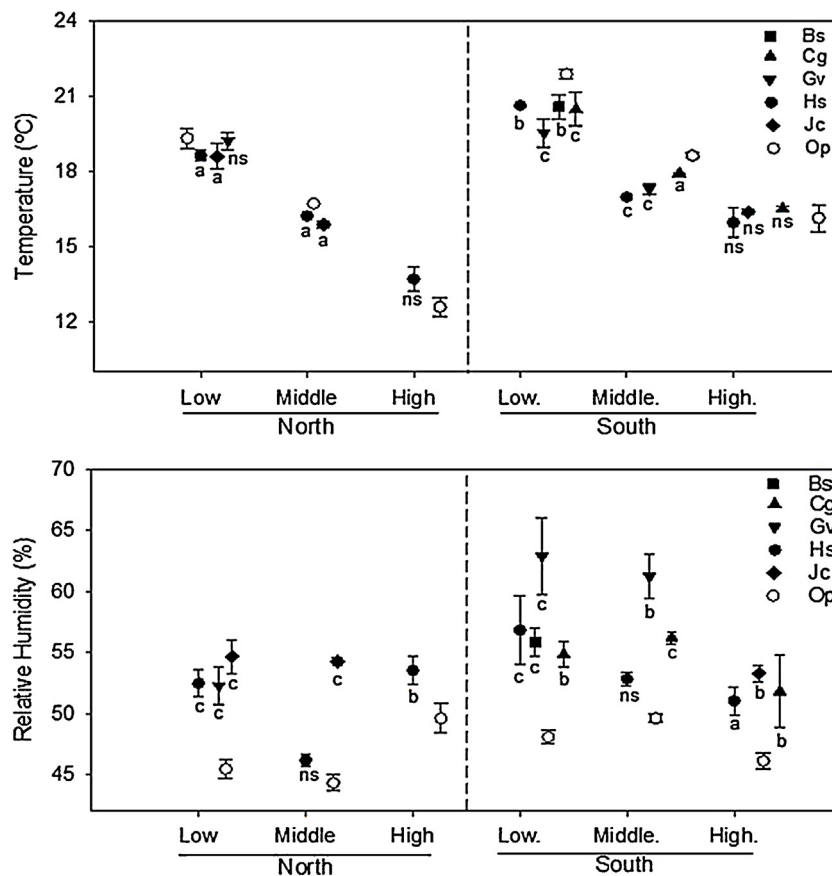


Fig. 1. Mean temperature and relative humidity (RH) of air beneath shrub species and open areas along two elevational gradients in Sierra Nevada, Spain. Values are means $\pm$ 1SE ($n=3$). L: Low elevation; M: Middle elevation; H: High elevation; Bs: *Bupleurum spinosum*; Cg: *Cytisus galianoi*; Gv: *Genista versicolor*; Hs: *Hormathophylla spinosa*; Jc: *Juniperus communis* ssp. *nana*; Op: open microhabitats. Asterisks indicate the results of contrasts between each shrub species compared to open areas at each site: * $p < 0.05$, ^b $p < 0.01$, ^c $p < 0.001$ and ^{ns}not significant results.

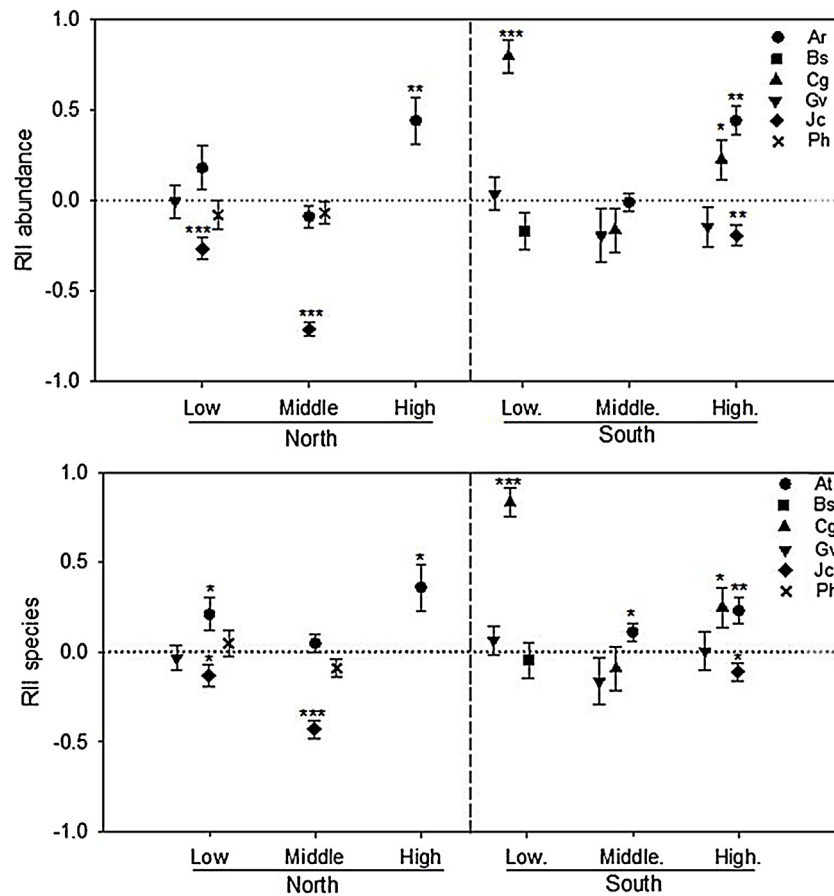


Fig. 2. Relative Interaction Index (RII) showing every shrub effect on abundance (i.e., total number of individuals over all species) (a) and on species richness (b) of subordinate communities along the elevation gradient ($n = 30$). Data are means $\pm$ 1SE. L: Low elevation; M: Middle elevation; H: High elevation; At: *Arenaria tetraquetra* ssp. *amabilis*; Bs: *Bupleurum spinosum*; Cg: *Cytisus galianoi*; Gv: *Genista versicolor*; Hs: *Hormathophylla spinosa*; Jc: *Juniperus communis* ssp. *nana*; Ph: *Plantago holosteum*. Symbols with an asterisk represent RII values significantly different from 0; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The “site.shrub species” factor was significant ($p < 0.001$) for both RII measures.

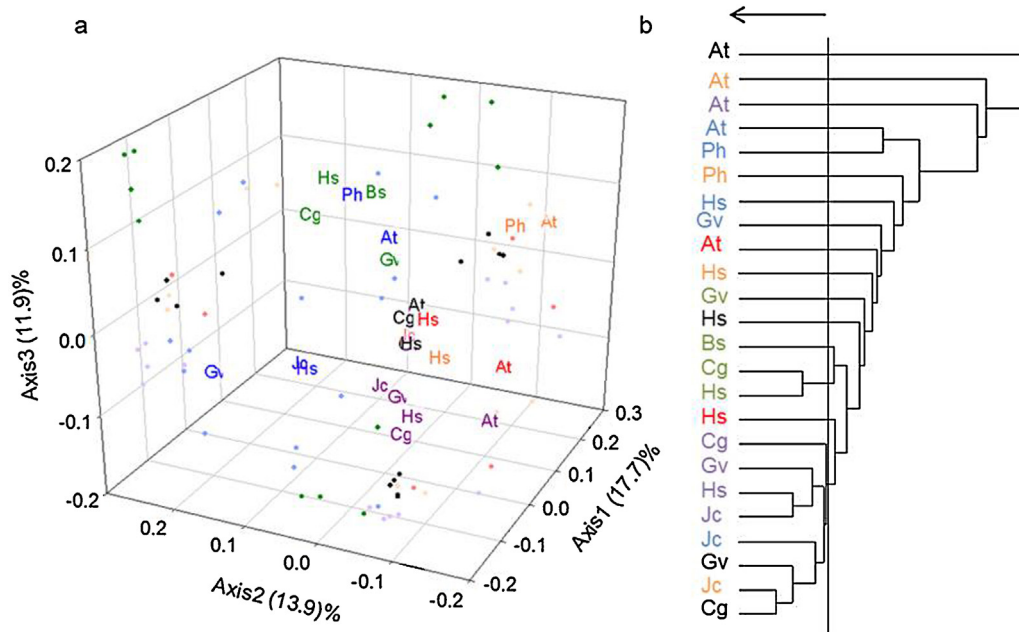


Fig. 3. Differences in subordinate species composition (individuals per species and cm²) among sites and shrubs. Species with a frequency less than 5% were excluded (a) ($n = 59$). Multivariate mean comparisons (gDGCtest) testing differences in plant densities among shrubs along elevational gradients at the Northern and Southern aspects of the Sierra Nevada mountains based on cluster analysis. We used a diagonal covariance matrix with a single linkage and Monte Carlo simulation with 500 permutations. The direction of the arrow indicates significant differences in the subordinate plant species density ($p < 0.05$) among each shrub (b). North aspect low in blue; North middle in orange; North high in red; South aspect low in green; South middle in black; South high in magenta. At: *Arenaria tetraquetra* ssp. *amabilis*; Bs: *Bupleurum spinosum*; Cg: *Cytisus galianoi*; Gv: *Genista versicolor*; Hs: *Hormathophylla spinosa*; Jc: *Juniperus communis* ssp. *nana*; Ph: *Plantago holosteum*.

Table 1

Spearman correlation (r_s) of mean temperature and mean relative humidity (RH) beneath shrubs and community composition (site scores extracted from axis 1, axis 2 and 3 of the PCoA analysis of subordinate plant density for each shrub species at each site; Fig. 3a). n is the total number of microhabitats along a severity gradient with environmental data, and p -value is the significance test of the correlation analysis. Significant results are shown in bold.

	Temperature		p -Value	RH	p -Value
	n	r_s		r_s	
Axis 1	16	0.18	0.49	−0.08	0.76
Axis 2	16	−0.06	0.83	0.38	0.15
Axis 3	16	0.33	0.21	0.49	0.05

site (Table S1). Subordinate communities changed with microhabitat conditions along the gradient. Axis 3 extracted from the PCoA analysis positively correlated with RH; however, axes 1 and 2 from the PCoA did not correlate with any of the abiotic factors measured (i.e., temperature or RH, Table 1).

Shrubs increased community-level species richness (Fig. 4) at the most environmentally extreme sites of the gradient (i.e., low

and high sites in both aspects). The highest contribution was recorded at the warmest site (the low South site) (Figs. 4f and 5f) with the highest differences in abiotic conditions (temperature and RH) beneath shrubs vs. open areas (Fig. 1). At this site, *C. galianoi* showed strong positive effects on the subordinate plant community whereas other shrub species had neutral effects (Fig. 3). Furthermore, shrubs increased community-level phylogenetic diversity at all sites (Fig. 5). The effect was stronger at the middle and low North and at the highest South where community-level phylogenetic diversity increased due to the presence of the shrubs species by 146,562 Myr, 154,003 Myr and 153,801 Myr, respectively.

4. Discussion

As a whole, shrub buffered harsh abiotic conditions by decreasing summer temperatures and increasing RH in their understories with respect to open areas along the gradient. Subordinate communities differed not only across shrub species but also across sites, although occasionally different shrub species hosted similar communities within a site. Such differences in subordinate

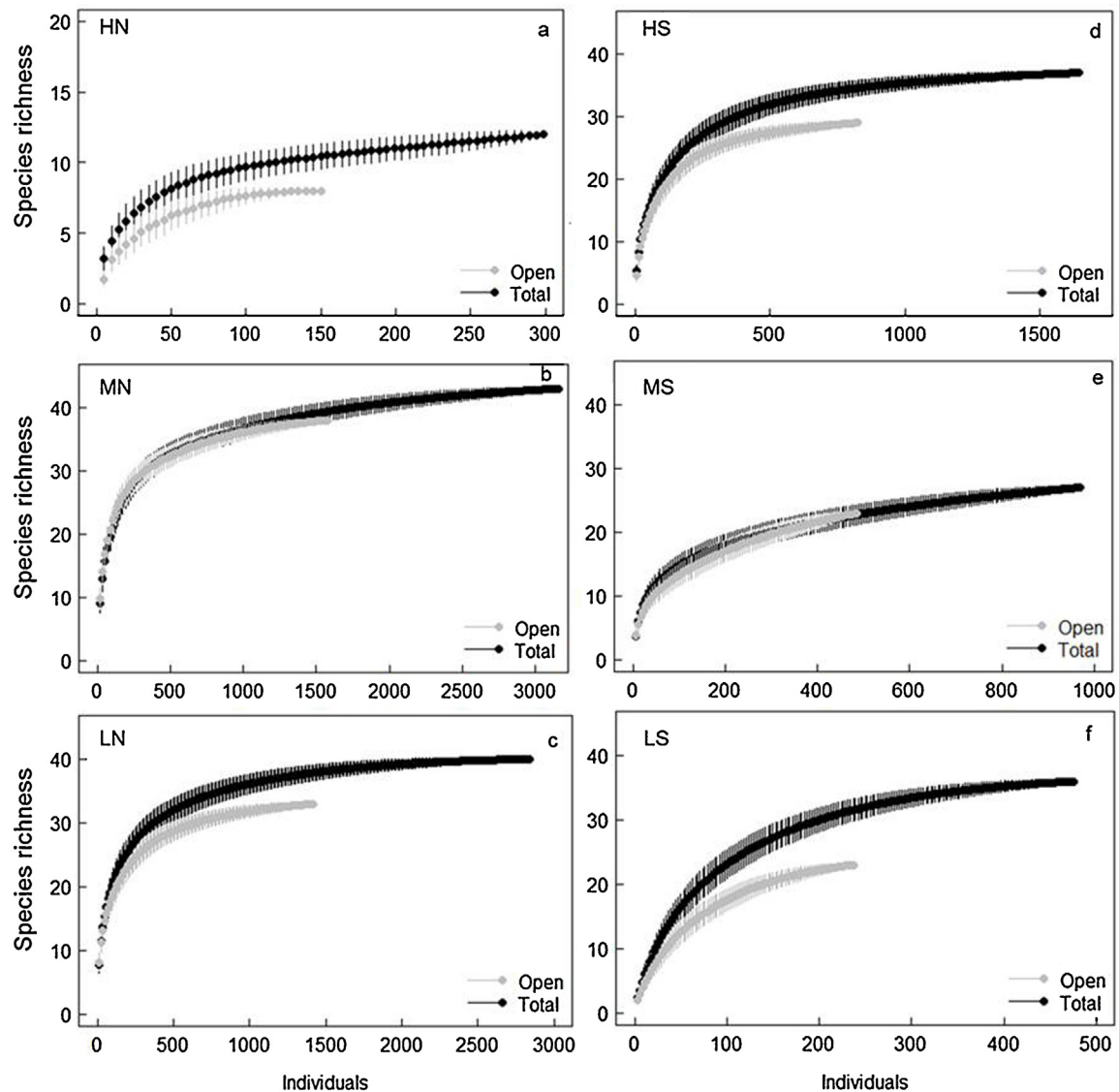


Fig. 4. Shrub contribution to community species richness at each site. (a) HN: Northern aspect high with two shrub species; (b) MN: Northern middle with four shrub species; (c) LN: Northern low with five shrub species; (d) HS: Southern aspect high with five shrub species; (e) MS: Southern middle with four shrub species; (f) LS: Southern low with four shrub species. Values are mean $\pm$ SD. Significant differences are indicated by non-overlapping error terms of the curves at the asymptote.

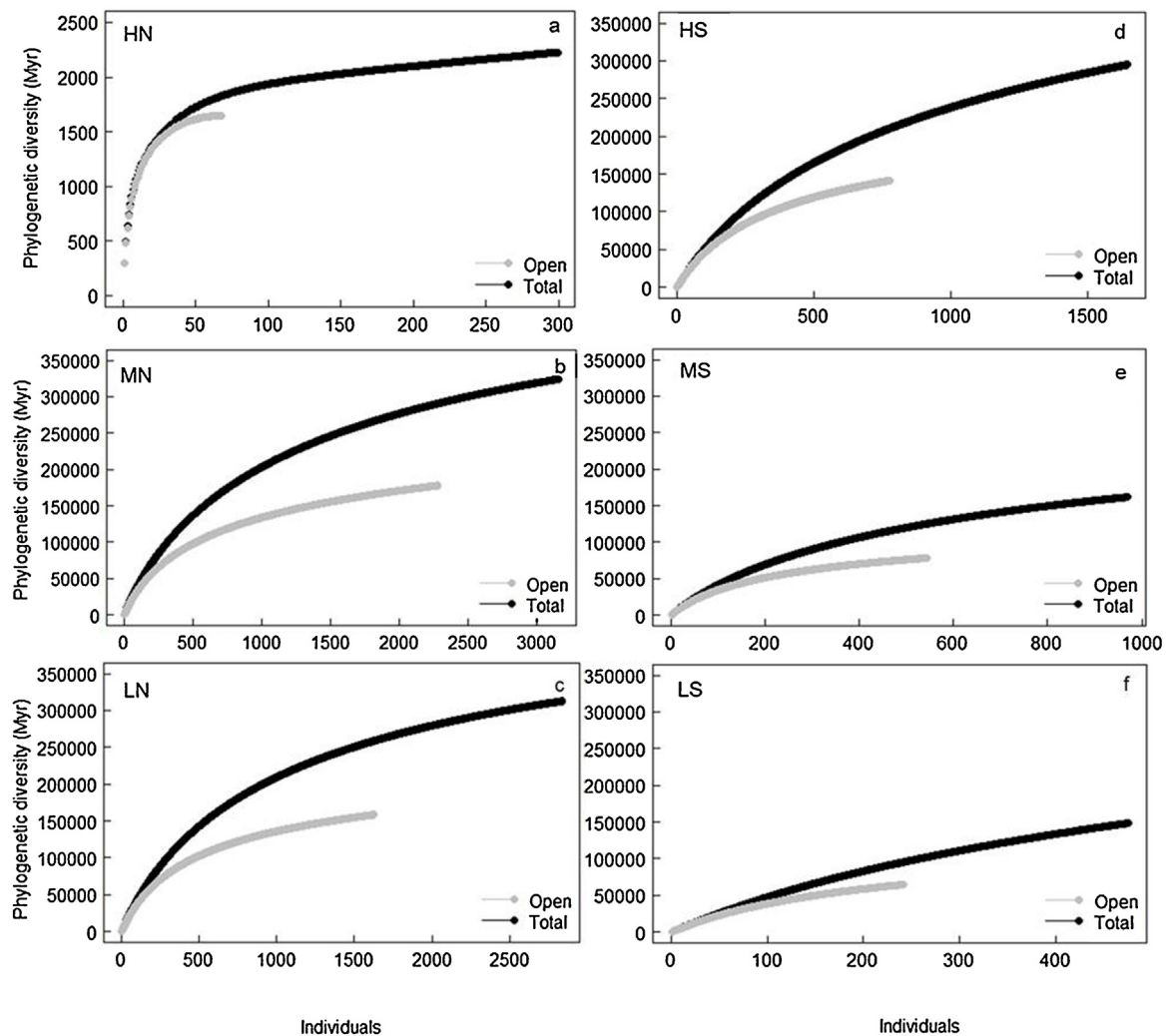


Fig. 5. Shrub contribution to community phylogenetic diversity (total branch length of the tree in Myr) for each site. (a) HN: Northern aspect high with two shrub species; (b) MN: Northern middle with four shrub species; (c) LN: Northern low with five shrub species; (d) HS: Southern aspect high with five shrub species; (e) MS: Southern middle with four shrub species; (f) LS: Southern low with four shrub species. Displayed are means.

community composition were mostly related to microhabitat conditions created by shrubs (i.e., water balance), suggesting a dependence of beneficiary species on their facilitators. The effects of shrubs on overall plant abundance and species richness differed with shrub identity and elevation. In sites where abiotic conditions were most extreme (i.e., high North due to low temperatures or low South due to high temperatures and low relative humidity), the combined effect of shrubs on subordinate species richness increased whole-community richness compared to open areas. This effect was evident when at least one shrub species showed positive effects on species richness and abundance compared to open areas. Interestingly, shrubs increased community phylogenetic diversity at all sites.

4.1. Differences in microhabitat conditions

Shrubs can modify the microhabitat beneath their canopies influencing growth and survival of beneficiary species (Anthelme et al., 2014; Brooker and Callaway, 2009; Cavieres and Badano, 2009; Pugnaire et al., 2015a; Pugnaire et al., 2015b). For example, they can buffer temperature extremes under their canopies reducing summer heat shock, transpiration, and soil water evaporation and reducing winter frost damage (Körner, 2003). In our case not

all shrub species within a site changed their microhabitat in the same way during the growing season, suggesting that species with different canopy morphology created different microhabitats with contrasting effects on communities of subordinate species. Molina-Montenegro et al. (2006) showed significant differences between microhabitat conditions of two cushion species (*Azorella monantha* and *Laretia acaulis*) in an alpine zone of Central Chile but they did not evaluate their effects on subordinate plant communities, and most studies performed in alpine systems that measured more than one cushion species did not distinguish the different effects of cushions on microhabitat conditions (Cavieres et al., 2007; Chu et al., 2009; Wang et al., 2008).

4.2. Shrub effects on subordinate species richness and abundance

Usually there is a range of net positive to net negative effects among species in plant communities (Callaway et al., 1991; Holzapfel and Mahall, 1999; Maestre et al., 2003; Pugnaire et al., 2004; Wang et al., 2008). Moreover, plant interaction intensity and sign are expected to change along environmental gradients depending on abiotic conditions so that net positive interactions would prevail at the most severe part of the gradient while net negative interactions would prevail at the milder part, as predicted by

the stress gradient hypothesis (SGH; Bertness and Callaway, 1994). Indeed, we found that at sites where abiotic conditions were most extreme, and at least one shrub species had positive effects, there was an increase of community-level species richness and phylogenetic diversity. This was also the case along the North aspect of the Sierra Nevada mountains, where Pistón et al. (2015) found that the effect of nurses on closely related species varied from positive to negative as the environment became less severe while on more distantly-related species it remained neutral. These, and our own results, support the role of facilitation in expanding the distribution range of beneficiary species (Armas et al., 2011; Butterfield et al., 2013; Pugnaire et al., 2015b; Valiente-Banuet and Verdú, 2013).

Shrubs showing positive effects on plant species richness and abundance under harsh conditions changed their effect to neutral under milder conditions (i.e. *A. tetraquetra* at both middle sites and *C. galianoi* at the middle South site), while shrubs that always showed neutral or negative effects on plant diversity along the gradient, never had positive effects (i.e., they were always non-facilitator species irrespective of environmental conditions; *B. spinosum*, *G. versicolor*, *J. communis* and *P. holosteam*). In severe environments plant interactions rely on morphological and physiological traits, which have many species-specific consequences (Armas and Pugnaire, 2011; Aubert et al., 2014; Schöb et al., 2013). Thus, two shrub species may have similar canopy morphology but one may have negative effects on subordinate species, i.e., allelopathic effects, such as *J. communis* in our field sites (Castro et al., 2005), whereas other shrubs may host symbionts (e.g., N-fixing bacteria, such as *C. galianoi*), plant growth-promoting bacteria or mycorrhizae that would positively affect the subordinate community (Martínez and Pugnaire, 2009; Martínez-García and Pugnaire, 2011; Rodríguez-Echeverría et al., 2013). Therefore, niches created by coexisting shrub species may be similar but rarely identical, and these species-specific differences could influence subordinate plant communities.

4.3. Differences in subordinate community composition among shrub species

Communities of subordinate species differed among shrub species along the gradient, with few exceptions. Although shrub species may appear functionally redundant under certain environmental conditions, the microhabitats they create could actually differ. For example, *C. galianoi* and *G. versicolor* share similar morphology but the microclimate beneath their canopies was vastly different, hosting different communities of subordinate species. Overall, shrubs had net positive effects in our sites, which means that assemblages of shrub species could fill larger niche spaces and create more environmental heterogeneity (Harper, 1977; Jones et al., 1994) than a single species. Kikvidze et al. (2015) found, however, that niche space constructed by cushion species was more homogeneous than that in open areas. In any case, the combined effects of shrub species in a community deeply influence whole-community species richness, phylogenetic diversity and ecosystem function (Cadotte, 2013; Loreau et al., 2001).

4.4. Context-dependence of co-occurring shrub species effects on community diversity

The increase in community-level species richness due to the presence of different shrub species was parallel to an increase in phylogenetic diversity except at the middle sites. The highest contribution of shrubs to whole-community species richness was found at the low South site, where the facilitative effect of *C. galianoi* on subordinate species was strongest. In this site, the net effect of the different shrub species on richness was positive although among individual shrub species there were simultaneous

neutral and positive effects. Furthermore, the combined effects of all shrub species increased phylogenetic diversity at all sites along the environmental gradient. Previous studies showed that cushions create phylogenetically unique communities relative to open areas in severe environments (Butterfield et al., 2013; Pistón et al., 2015). Our results suggest that species richness and phylogenetic diversity responded differently to the dominant shrub species.

As environmental severity decreased toward middle sites, whole-community species richness was similar to that of open areas. This result suggests that coexistence was stable at these sites following the spatial storage effect; this mechanism is the most feasible in a heterogeneous environment, enabling coexistence by buffering population growth rates (also called “source-sink dynamics”; Dias, 1996). This mechanism prevents the exclusion of species inhabiting the whole community (Amarasekare, 2003; Sears and Chesson, 2007). Therefore, shrubs could act as source habitat for some species (i.e., those more abundant within shrubs than in open areas) and as sinks for species that dominate open habitats (i.e., those less abundant under shrubs than in the open areas). In some places e.g., the highest site in the South aspect, open areas could be acting as sinks and the understories of *A. tetraquetra* and *C. galianoi* as sources. However, to verify the presence of such source-sink dynamics in our system we would need to quantify the *per capita* growth rates of each subordinate species (Dias, 1996), which we did not. Nevertheless, just comparing the number of dependent subordinate species on specific shrubs could be indicative of such processes. For example, 13 shrub-dependent species were found under *C. galianoi* at the low South site, and 8 species were found under *G. versicolor* in the low North site (Table S1). These are clear indication that shrubs may act as a source habitat for these species at a specific site and that spatial storage effects could indeed be quite relevant in our study system.

5. Conclusions

Our study showed the importance of the combined effect of co-occurring shrubs on species richness and phylogenetic diversity at the community level, despite individual shrub effects ranging from positive to negative. These differences in species-specific effects are most likely due to the creation of different niche spaces which allow stress-sensitive species to survive in environments otherwise too harsh for them. Thus, the effect of different shrub species on plant community richness and phylogenetic diversity is not redundant as they host unique communities, particularly under harsh environmental conditions. This highlights the importance of conserving the variety of co-occurring shrub species, as their net effects on community diversity may be critical to maintain biodiversity and ecosystem functions in this fragile ecosystem.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.02.002>.

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