

Shrub–ephemeral plants interactions in semiarid north-central Chile: Is the nurse plant syndrome manifested at the community level?



Jaime Madrigal-González ^{a, b, *}, Douglas A. Kelt ^c, Peter L. Meserve ^d, Francisco A. Squeo ^{b, e}, Julio R. Gutiérrez ^{b, e}

^a Forest Ecology and Restoration Group, Department of Life Sciences, Science Building, University of Alcalá, ctra. A-2 km 33.6, 28805, Alcalá de Henares, Spain

^b Instituto de Ecología y Biodiversidad, Casilla 653, Santiago, Chile

^c Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA

^d Department of Biological Sciences, University of Idaho, Moscow, ID 83843, USA

^e Departamento de Biología and Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad de La Serena, Chile

ARTICLE INFO

Article history:

Received 29 September 2014

Received in revised form

28 July 2015

Accepted 3 August 2015

Available online 21 August 2015

Keywords:

Ephemeral plant communities

Facilitation

Nurse plant syndrome

Precipitation

Semiarid scrub

Biomass production

Diversity

ABSTRACT

Models of plant–plant interactions suggest that nurse plants are critical for the maintenance of biodiversity and ecosystem functions in arid and semiarid lands. At the community scale, however, empirical support of this idea is limited and context-dependent. Following on a preliminary work which suggested that a dominant shrub in north-central Chile (*Porlieria chilensis*) had nurse plant effects, we tested the effects of this and two other shrubs (*Adesmia bedwellii* and *Proustia cuneifolia*) on community biomass production, species density, and species composition of ephemeral plants in the semiarid scrub of the Bosque Fray Jorge National Park (Chile) over four consecutive years. We tested for main and interactive effects of shrubs and precipitation on total biomass production and species density of ephemeral plant communities using Generalized Linear Mixed Models (GLMM). To analyze the effects of shrubs and precipitation on species composition we used Canonical Correspondence Analysis (CCA) and t-value biplot analysis. Total biomass production increased significantly with precipitation and was consistently lower beneath shrub canopies, particularly under *A. bedwellii* and *P. chilensis*. Although ephemeral plant species density generally was higher in open areas, differences between open and shrub canopy samples diminished with increasing precipitation. Finally, despite significant differences in ephemeral plant species composition between open areas and shrub canopies, we found no evidence of shrub species-specific effects. In conclusion, our results do not support a classical nurse plant syndrome in the semiarid scrub of the Bosque Fray Jorge National Park although shrubs can increase local diversity by favoring some ephemeral plant species that are absent in open areas.

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1. Introduction

In geographical areas where low rainfall and nutrient availability strongly limit plant survival and growth, woody species may facilitate herbaceous plants through amelioration of abiotic stresses via shading and redistribution of soil water and nutrients (Callaway, 2007). Study of plant–plant interactions strongly supports the nurse plant syndrome in semiarid lands worldwide (He et al., 2013)

and suggests that positive interactions could be critical mechanisms for the maintenance of ecosystem functions and biodiversity in severe environments (Flores and Jurado, 2003; Brooker et al., 2008). Three major hypotheses have been formulated to link mechanisms underlying the nurse plant syndrome with structure and functioning of beneficiary plant communities (see Filazzola and Lortie, 2014). First, nurse plants enhance fitness or productivity of beneficiary plants in their vicinity through direct and indirect mechanisms of interaction (Segoli et al., 2012). Among other benefits, increased water availability through hydraulic lift (Caldwell et al., 1998; Prieto et al., 2010), increased soil nutrient availability (Rodríguez-Echeverría and Pérez-Fernández, 2003; Pugnaire et al., 2004), reduced evapotranspiration and photoinhibition due to

* Corresponding author. Forest Ecology and Restoration Group, Department of Life Sciences, Science Building, University of Alcalá, ctra. A-2 km 33.6, 28805, Alcalá de Henares, Spain.

E-mail address: ecojpg@hotmail.com (J. Madrigal-González).

interception of direct solar radiation (Callaway and Pugnaire, 1999), and protection against herbivore pressure (Smit and Ruifrok, 2011) are the most conspicuous mechanisms in arid and semiarid environments. Second, it is commonly hypothesized that net positive interactions are more likely under severe conditions (Stress Gradient Hypothesis; Bertness and Callaway, 1994). Plant–plant interactions can shift from being net negative to net positive as resource availability declines along spatial gradients (Pugnaire and Luque, 2001; Pugnaire et al., 2004; Holzpfel et al., 2006; Armas et al., 2011). Although it is generally accepted that abiotic stress due to low resource availability promotes facilitative interactions, current theory suggests that positive interactions tend to collapse under extremely severe environments (Michalet et al., 2006) leading to a hump-backed relationship between facilitation and stress (Maestre et al., 2009). Third, and particularly under warmer and drier conditions, nurse plants increase local diversity of beneficiary plant communities by altering spatial dynamics of species with particular life strategies that are more likely to be facilitated (Davies et al., 2007; Soliveres et al., 2012).

Empirical support for these hypotheses at the community or ecosystem levels is limited, however, and at times contradictory (Cavieres and Badano, 2009; Soliveres and Maestre, 2014; Michalet et al., 2015). At the community level, indirect interactions along with nurse species-specific effects (Blank and Carmel, 2012) and/or disparate functional strategies of beneficiary plants could result in idiosyncratic plant responses to open and shrub conditions leading to complex scenarios of interactions (Schöb et al., 2013; Michalet et al., 2015). For example, many plant species in arid and semiarid environments have evolved tolerance mechanisms such as increased root–shoot ratios, or shortened vegetative–reproductive periods to restrict resource use to episodic favorable periods (Noy-Meir, 1973). Such life strategies are frequently incompatible with survival under shading conditions as suggested by the existence of functional trade-offs between tolerance to drought and shading in drylands (Smith and Huston, 1989; Holmgren et al., 1997). Accordingly, differences in species composition between open areas and under the canopy of shrubs in some semiarid ecosystems have been previously observed (López-Pintor et al., 2006). These findings at the community level question whether the outcome of net plant–plant interactions would scale up to multispecies interactions following the stress gradient hypothesis. Data obtained during a one-year study focusing on the nurse plant *Porlieria chilensis* in north-central Chile suggested species-specific responses of ephemeral plants and neutral interactions at the community level (Gutiérrez et al., 1997). However, it is still poorly known whether interannual variability of precipitation or different shrub species can shift the shrub–ephemeral interaction outcomes at the community level (Tielbörger and Kadmon, 2000, but see Pugnaire et al., 2004).

These uncertainties led us to pursue a field study to test the three hypotheses outlined above in the semiarid scrub of north-central Chile, and to expand this to consider the three most abundant shrubs in this system throughout four consecutive years. First, we hypothesized that these three shrub species would enhance annual plant community productivity, as observed in other semiarid habitats. Second, we predicted that the intensity and direction of shrub–ephemeral interactions would shift across a temporal (multi-year) precipitation gradient (i.e., lower precipitation should lead to higher facilitation but this benefit should be diffused when rainfall is sufficiently high that no microhabitat is water-stressed; Tielbörger and Kadmon, 2000). Most experimental and observational approaches to plant responses across stress gradients in arid and semiarid lands have considered spatial gradients of water availability, but our long-term study provides us with an unusual opportunity to complement these studies with an

approach emphasizing temporal variation in stress associated with variation in rainfall. Third, we hypothesized that patterns of species density and composition would differ between open areas and shrubs, and microhabitats beneath shrub canopies, leading to qualitatively distinct annual plant community structure (i.e. species composition and density).

2. Materials and methods

2.1. Study area

Our study area is near the coast of north-central Chile, in Bosque Fray Jorge National Park (71°40'W, 30°38'S) 100 km S La Serena and 350 km N Santiago. This 10 000 ha park contains semiarid thorn scrub vegetation and remnant fog forest, all of which has been protected from livestock grazing and disturbance since 1941. The flora of the lower elevated scrub zone includes spiny drought-deciduous shrubs and understory herbs on a primarily sandy substrate (Gutiérrez et al., 1993). Total cover of shrubs is ca 55%, dominated by *P. chilensis* L. M. Johnst. (Zygophyllaceae, 30% cover), *Adesmia bedwellii* Skottsb. (Fabaceae, 5% cover), and *Proustia cuneifolia* D. Don (Asteraceae, 6% cover). The climate is semiarid Mediterranean with 90% of the mean annual 122.6 mm (± 91.8 mm; data from 1989 to 2014, both years included) precipitation falling in winter (May–September) and precipitation from May to July is critical for seed germination and growth; summer months are warm and dry and during this period no ephemeral communities are present/growing. After a rainy 2002 (282.6 mm May–July rainfall) associated with an El Niño event, 2003 and 2005 were relatively dry (77.2 and 42.8 mm, May–July rainfall respectively), whereas 2004 and 2006 were relatively wet years (98.8 mm and 127.4 mm, May–July rainfall respectively).

2.2. Interacting species

Ephemeral plant communities in semiarid Chile are comprised of plants growing in a few weeks after the end of discrete water pulses, mostly in the winter season (Vidiella and Armesto, 1989). As water becomes limiting, these plants die, leaving a seed bank for the next favorable period. This strategy makes such species “stress-avoiders” with respect to summer drought in the broad sense (Slatyer, 1967) although variability of functional strategies is particularly high in this biogeographical area (Armesto et al., 1993).

Dominant shrub species in semiarid Chile are evergreen (i.e. *P. chilensis*) or drought-deciduous (e.g., *A. bedwellii* and *P. cuneifolia*) and have dimorphic root systems that passively mobilize water from shallow horizons during winter (Muñoz et al., 2008). Less is known about whether specific morphological-functional features of shrubs are related to shifts in the balance of their interactions with annuals. Perhaps most notably, the three shrub species selected provide very different levels of shading. According to the foliage density and Plant Area Index (PAI) the three shrub species can be arranged as follow from highest to lowest PAI: *P. chilensis*, *A. bedwellii* and finally *P. cuneifolia* (Tracol et al., 2011). Additionally, *A. bedwellii* is a N-fixer which could contribute to soil nutrients and enhance the performance of herbaceous plants (Aguilera et al., 1999).

2.3. Sampling design

We selected 3 individuals of each shrub species (*A. bedwellii*, *P. chilensis*, *P. cuneifolia*) and 3 representative open areas nearby in 4 random plots in the study area (Quebrada de las Vacas). It is important to note that shrub individuals, as well as nearby open areas, were different in each sampling year to avoid potential legacy

effects of biomass yields of previous years; thus there were 192 plant assemblages distributed in 36 shrub individuals and 12 open areas during the four years of study (2003–2006). Precipitation was continuously recorded with a meteorological station located at the study site, and winter precipitation was assessed as the sum of rainfall from May to July; this is the major period for biomass production of ephemeral plants in this area. All plots were fenced in 1989 but exclusion of all herbivores was established in 2001; this allowed us to avoid potential bias due to top-down impacts of herbivores on plant interactions. At the peak of the growing season for ephemeral plants (late August), we tallied all plants within 30×30 cm sampling quadrats located randomly under each individual shrub, identified ephemeral plant species, and finally, harvested them (including above- and belowground biomass). We applied the same procedure to the randomly located quadrats (30×30 cm) in open areas. Plants were oven-dried and weighed in the laboratory for biomass determination. We treated these four treatments (i.e. open areas vs. understory of the three shrubs) as a single variable named microhabitat. Since we sampled different quadrats under each plant in each year (e.g., no repeat sampling), we treat samples as independent (not repeated) measurements. We assessed biomass production at the community level as the summed above- and below-ground biomass of all the plant individuals in each quadrat. Finally, we computed species density as the number of species in each sampling quadrat.

2.4. Statistical analysis

We studied the effects of shrubs on biomass production of ephemeral plant communities using Generalized Linear Mixed-effects Models (GLMM) with a gamma distribution of error and a log-link function. Selection of fixed effects was conducted by comparing all possible candidate models, from the full model including Microhabitat \times Precipitation, to a null model that included only an intercept parameter (i.e. no environmental variables). Since community measurements were systematically recorded in the same plots throughout the study period, we treated plots as the random term affecting the intercept parameter in the model (i.e., biomass production can differ among plots). We used Akaike's Information Criterion corrected for small samples (AICc) assuming that two models are different when Δ AICc exceeds 2 units. Parameters were estimated with the Laplace approximation using the glmer function in the R environment (R Core Team, 2013). To study the effects of shrubs and precipitation on species density we applied GLMM with a Poisson error distribution and a log-link function. Model selection and the random term were identical to previous models applied to biomass production. In all the above analyses we included precipitation as a continuous numeric variable whereas microhabitat was coded as a discrete categorical variable with four categories: i.e., open, *A. bedwellii*, *P. chilensis*, *P. cuneifolia*.

To test the influence of microhabitat and precipitation on the ephemeral plant community composition we applied canonical correspondence analysis (CCA) to the species \times quadrats abundance matrix. Independent variables (i.e., microhabitat and precipitation) were tested using Markov-Chain Monte Carlo with 9999 permutations restricted to plots assuming a potential spatial dependence among quadrats within plots. Because microhabitat is a categorical variable, it was included as four different dummy variables coded with 0–1. This implies that each microhabitat category is tested separately as a single binomial variable in the MCMC process.

To seek for indicator species of the different microhabitats we used a t-value biplot analysis. T-value biplot is a graphical representation of significant linear relationships between species and

environmental variables based on t-values associated with regression coefficients. It is assumed that t-values equal or higher than 2 units represent a significant relationship between species and the focal environmental variable. Significant relationships are represented by the Van-Dobben circles such that species vectors fully falling within a Van Dobben circle are indicator species of positive or negative effects of the focal environmental variable, i.e. a particular microhabitat (Ter Braak and Šmilauer, 2002). Ordination analysis and t-value biplot were conducted using CANOCO 4.5 (Ter Braak and Šmilauer, 2002).

3. Results

Although community biomass production was highly variable across both years and microhabitats it was significantly higher in open patches and wet years (Fig. 1a). On the one hand, the best supported model suggested significant negative effects of the three shrub species (i.e. mostly *A. bedwellii* and *P. chilensis*) on ephemeral biomass production and this pattern remained constant throughout the four years of study. On the other hand, precipitation was included in the best supported model with consistent positive

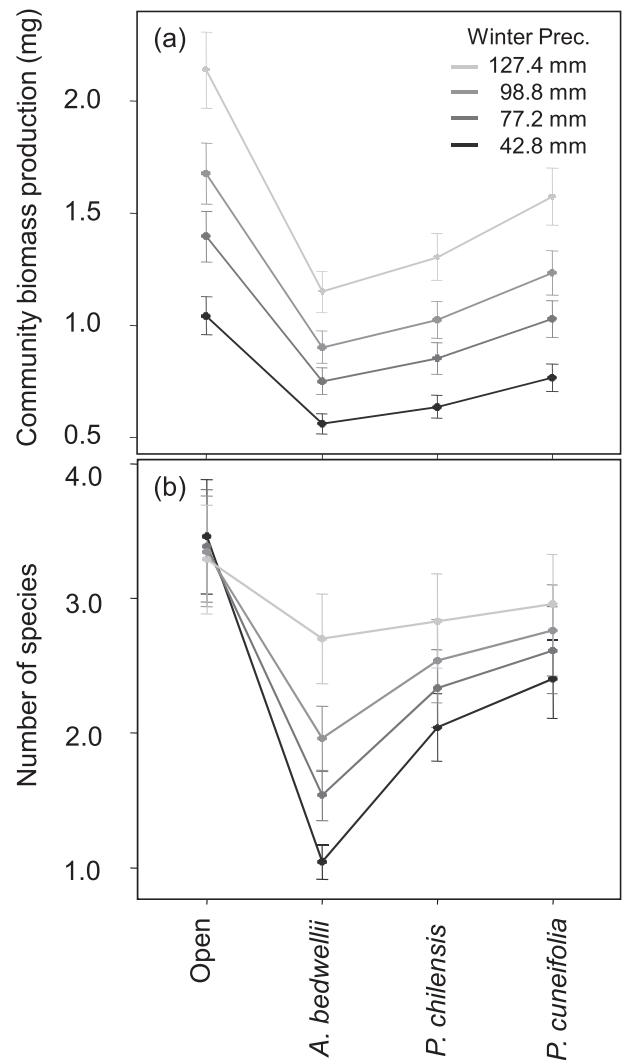


Fig. 1. Predicted values \pm standard error of ephemeral community biomass (a) and species density (b) as function of microhabitat (i.e. open patches, *A. bedwellii*, *P. chilensis*, *P. cuneifolia*) and winter precipitation (color gradient represent winter precipitation) during the four years of study.

effects on ephemeral biomass production (Table 1; see parameter estimates in Table 2).

Model selection suggested the inclusion of interactive effects of precipitation and microhabitat on species density of ephemeral plant communities (Table 1). This interaction suggested that differences in species density between open and shrub patches decreased during wetter years (Table 3): i.e. while the lowest number of species was found beneath shrub canopies in the driest year, particularly beneath *A. bedwellii* and *P. chilensis*, maximum values of species density were always reached in open areas (Fig. 1b).

Canonical correspondence analysis showed a principal gradient associated with microhabitat and a second gradient associated with precipitation (Fig. 2). Both variables were significantly included in the supported canonical model (Table 4) and all the canonical axes were significant ($R^2 = 0.28$; F-ratio = 4.899, $p < 0.001$). However, only open areas had significant effects on ephemeral plant species composition as shown by the MCMC test with 9999 permutations (Table 4, see also Table S1 for regression coefficients). The t-value biplot analysis suggested that species such as *Moschardia pinnatifida*, *Apium laciniatum* or *Oxalis micrantha* were almost exclusively ephemeral plant species of shrub understory because of their significant negative relationship with open areas, whereas *Adesmia tenella*, *Alstroemeria diluta*, *Camissonia dentata*, *Chaetanthera linearis*, *Calandrinia* sp., *Crassula closiana*, *Erodium botrys*, *Eryngium coquimbantum*, *Lastarriaea chilensis*, *Pectocarya dimorpha*, *Pectocarya linearis*, *Plantago hispidula*, *Schismus arabicus* or *Schizanthus litoralis* were most typical ephemeral plant species of open areas (Fig. 3).

4. Discussion

We found no clear evidence of nurse plant effects at the community level over four years of study. On the one hand, our results showed negative effects of shrubs on biomass production of ephemeral plant communities in this semiarid Mediterranean ecosystem. On the other, although species composition significantly varies among microhabitats, higher or similar number of species in open areas was observed. Contrary to our findings, Holzapfel et al. (2006) in the most arid site of its geographical resource gradient in Israel, Holzapfel and Mahall (1999) in the Mojave Desert (US) or Armas et al. (2011) and Pugnaire et al. (2004) in semiarid Iberian Peninsula inferred net positive or neutral effects of shrubs on the ephemeral plant community from significant higher values of above-ground annual plant biomass beneath the shrub canopies. Only a case of significant interference was detected by Pugnaire et al. (2004) in southern Iberian Peninsula associated with the small shrub *Thymus hyemalis*, a woody species which is known to have negative effects on the soil biota and thus decomposition rates and soil nutrient availability. The apparent

Table 1

Model selection separately for community biomass production and species density using the Akaike Information Criterion corrected for small sample sizes (AICc). We assumed the inclusion of a parameter in the best supported model when its elimination from the full model (i.e. Microhabitat × Precipitation) determines an increment of at least 2 units of AICc. When two models have similar AICc (i.e. $\Delta AICc < 2$) we selected the one with lower number of parameters.

Models	No. parameters	Community biomass		Species density	
		AICc	$\Delta AICc$	AICc	$\Delta AICc$
Microhabitat × Precipitation	10	760	0	784	0
No interaction	7	760	0	786	2
No Microhabitat	4	775	15	802	18
No Precipitation	6	784	24	788	4
Null (intercept only)	3	801	41	805	21

Table 2

Parameter estimates of the best supported model for ephemeral plant biomass production (i.e. Microhabitat + Precipitation).

Best supported model	Estimates	s.e.	t-value	Pr(> z)
Intercept (Open patches)	0.667977	0.204976	3.259	0.00112
<i>A. bedwellii</i>	−0.620487	0.155984	−3.978	6.95E−05
<i>P. chilensis</i>	−0.493981	0.155984	−3.167	0.00154
<i>P. cuneifolia</i>	−0.306775	0.155984	−1.967	0.04922
Precipitation	0.008502	0.001785	4.765	1.89E−06

contradiction between these and our results may, however, be resolved. First, there may be bias associated with using only aboveground biomass measurements as a surrogate of total biomass production. Plants in open habitats tend to increase the root-shoot ratio to maximize soil water uptakes while minimizing transpiration rates. Conversely, plants tend to allocate more resources to aboveground photosynthetic structures to maximize light interception in shaded habitats (Smith and Huston, 1989). Second, without information on herbivore pressure these authors may inadvertently reach misleading conclusions about the nurse plant syndrome (Eldridge et al., 2013). For example, herbivore exclusion in arid parts of South Australia had significantly greater effects in open areas compared to the understory beneath *Maireana sedifolia* (Facelli and Temby, 2002). To avoid these potential sources of bias, we used total biomass (i.e. above- and below-ground biomass) as a measurement of biomass production in fenced plots where mammal herbivores have been excluded since 2001.

In southern Australia the shrub *M. sedifolia* has negative effects on the annual plant community (Weedon and Facelli, 2008). In this system, above- and below-ground competition outweighs the amelioration of soil properties due to shading, resulting in net negative effects on annuals. Shading in particular has been proposed as a chief candidate to explain most negative plant–plant interactions in arid and semiarid environments (Forseth et al., 2001). As hypothesized by Holmgren et al. (1997), shading and drought impose functional trade-offs that can significantly alter nurse plant effects. Thus, positive effects of shading by nurse plants (i.e., protection against photoinhibition, reduced temperature, increased soil moisture) exceed negative effects only when sufficient water availability compensates for increased evaporative demands associated with larger above-ground photosynthetic biomass. In agreement with this idea and contrary to the second hypothesis (that facilitation by shrubs should be more evident under increasing stress during the driest years) our results suggest that shrub shading even exacerbates declines in biomass production associated with low precipitation in the driest years (Valladares et al., 2008). This result, along with the absence of significant species-specific effects of shrubs on annual plant species composition reinforces the idea that functional/morphological differences among the three shrub species considered here (i.e., Plant Area Index and N-fixing) do not outweigh the effects that they hold in common, chiefly solar radiation interception. Although plant–plant interactions strongly support the stress gradient hypothesis in semiarid lands (He et al., 2013), the opposite pattern has been also reported as a consequence of predominant negative effects of deep shading (Forseth et al., 2001; Weedon and Facelli, 2008). Accordingly, the strongest negative effects were observed in the shrub species with higher plant area index in our study site (i.e., *P. chilensis* and *A. bedwellii*; see Tracol et al., 2011).

In agreement with the third hypothesis (i.e., that nurse plants increase local diversity by altering spatial dynamics of species with distinct life histories), different functional strategies have emerged in annual plants to address increased drought in open areas and greater shading beneath shrub canopy. This variety of species leads

Table 3
Parameter estimates of the best supported model for ephemeral plant species density (i.e. Microhabitat × Precipitation).

Best supported model	Estimates	s.e.	Z-value	Pr(> z)
Intercept (Open × Precipitation)	1.24806	0.2523822	4.94	7.61E-07
<i>A. bedwellii</i>	-1.7053522	0.4380517	-3.89	9.90E-05
<i>P. chilensis</i>	-0.7194675	0.3702007	-1.94	0.051
<i>P. cuneifolia</i>	-0.4966302	0.3559133	-1.39	0.16
Precipitation	-0.0005965	0.0025404	-0.23	0.814
<i>A. bedwellii</i> × Precipitation	0.0118428	0.0044664	2.65	0.008
<i>P. chilensis</i> × Precipitation	0.0044727	0.0039524	1.13	0.257
<i>P. cuneifolia</i> × Precipitation	0.0030746	0.0038317	0.80	0.422

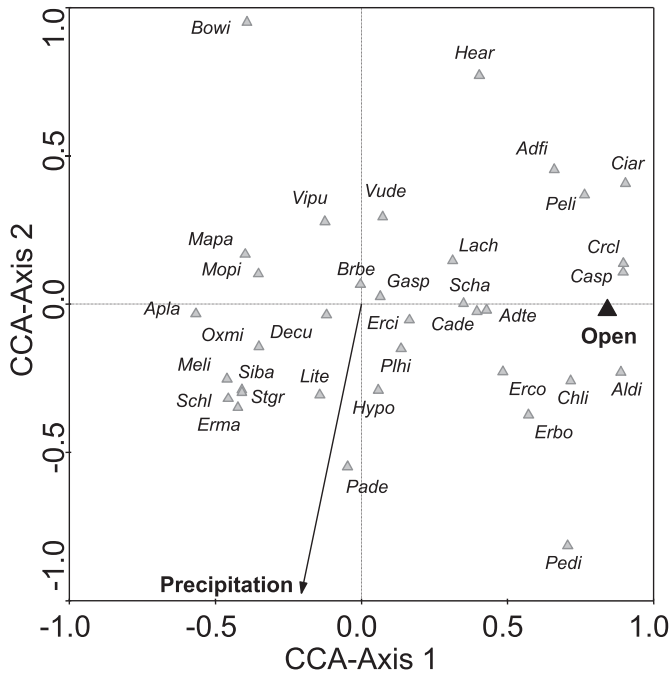


Fig. 2. Ordination plot (axes 1 and 2) showing species and significant environmental variables in the CCA. The black arrow represents precipitation and the black triangle the open microhabitat. Small gray triangles represent species scores on principal CCA axes. Species legend: Adfi – *Adesmia filifolia*; Adte – *Adesmia tenella*; Aldi – *Alstroemeria aromatica*; Apla – *Apium laciniatum*; Bowi – *Bowlesia incana*; Brbe – *Bromus berterianus*; Cade – *Camissonia dentata*; Casp – *Calandrinia* sp.; Chli – *Chaetanthera linearis*; Crcl – *Crassula closiana*; Decu – *Descurainia cumingiana*; Erci – *Erodium cicutarium*; Erbo – *Erodium botrys*; Erco; *Eryngium coquimbantum*; Hear – *Helenium aromaticum*; Hypo – *Hypochaeris* sp.; Lach – *Lastarriaea chilensis*; Mapa – *Malva parviflora*; Meli – *Menonvillea litoralis*; Mopi – *Moscharia pinnatifida*; Oxmi – *Oxalis micrantha*; Pade – *Parietaria debilis*; Pedi – *Pectocarya dimorpha*; Peli – *Pectocarya linearis*; Plhi – *Plantago hispidula*; Scha – *Schismus arabicus*; Schl – *Schizanthus litoralis*.

Table 4
Lambda parameter and associated F-statistic for environmental variables in the canonical model (CCA) obtained using 9999 random permutations of environmental data in the Markov-Chain Monte-Carlo test. The best supported model includes significant effects of Precipitation and open areas only.

Parameters	Lambda	F	p
Open patches	0.16	10.44	>0.01
<i>A. bedwellii</i>	0.00	2.05	0.29
<i>P. chilensis</i>	0.03	2.77	0.09
<i>P. cuneifolia</i>	0.04	2.78	0.10
Precipitation	0.05	2.99	>0.01

to an increment of local diversity and complexity although species density tends to be relatively lower in shrub patches. On the one hand, shading is particularly negative for drought-tolerant species that maximize the root-shoot ratio to cope with low soil moisture

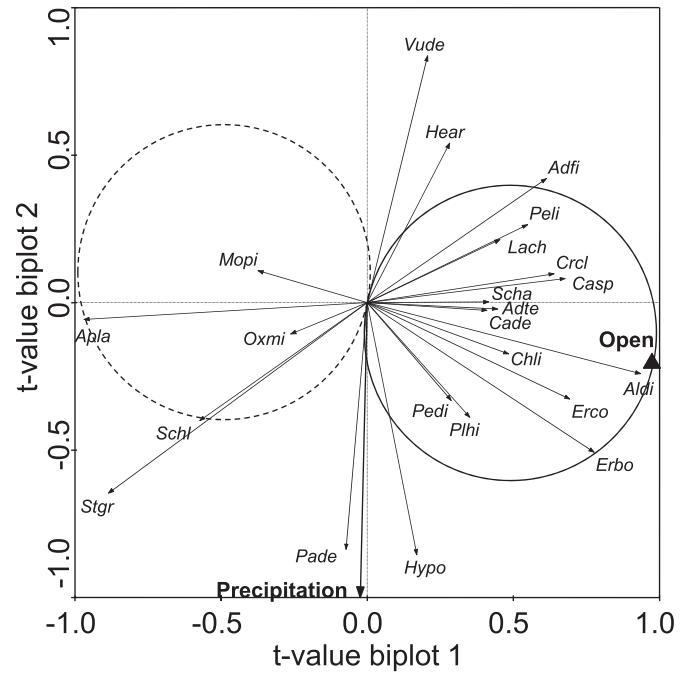


Fig. 3. T-value biplot for the relationship between open habitats and ephemeral plant species. Species arrows fully falling within a Van-Dobben circle indicate a significant relationship between the focal species and the environmental variable. Relationships can be positive (solid line circle) or negative (dashed line circle). See Fig. 2 legend for species names and acronyms.

(Maestre et al., 2009). On the other, shading negatively affect stress-avoiding species that require rapid investment of energy and resources to develop reproductive structures during brief and episodic winter rains (Werk et al., 1983; De Lillis and Federici, 1993, respectively). Ephemeral plants of open habitats often perform like stress-tolerant or stress-avoider species in semiarid ecosystems, making use of brief winter mesic periods to emerge and successfully complete their life cycles (Jara et al., 2006). Simultaneously, some ephemeral plants are almost exclusive of shrub microhabitat. The most typical species under the canopy of shrubs is *M. pinnatifida*, a dominant shade-tolerant species that also inhabits the understory of remnant forests on the top of coastal hills in the Bosque Fray Jorge National Park. Curiously, the genus *M. pinnatifida* has effective adaptations to hyper-aridity that allow for its distribution along the coastal desert of Chile where it is associated with nurse plants and dry forests (Katinas and Crisci, 2000). The spatial segregation of annual plant species in other arid ecosystems has been explained through differential responses to shading (Facelli and Temby, 2002; Osem et al., 2007; Weedon and Facelli, 2008; Pugnaire et al., 2011). Light availability has been previously put forward to explain local plant heterogeneity gradients from open areas to shrub patches in dry shrublands

(López-Pintor et al., 2006). From a mechanistic point of view, complex direct and indirect interactions may operate simultaneously to shape species composition and diversity outside and under the canopy of shrubs (Schöb et al., 2013). Thus, increased competition among potential beneficiary species can indirectly reduce the species density beneath nurse shrub canopies when soil water is limited. Our results support this idea since species density beneath shrub canopies decreased in the driest year, when competition for extremely scarce resources is stronger. In wetter years, abundant resources (chiefly soil water) allow for coexistence of a larger number of species beneath shrub canopies because shrub shading indirectly facilitates poor competitors by limiting growth of dominant species (Michalet et al., 2015).

5. Conclusions

The nurse plant syndrome at the community level seems to be rather unlikely in the semiarid scrub of the Bosque Fray Jorge National Park. In fact, and contrary to expectations that stress promote facilitation interactions in plant communities, increased stress in dry years led to stronger negative effects of shrubs on the ephemeral plant community. Our results, however, support the idea that shrub species increase local diversity and complexity of surrounding ephemeral plant communities through modification of environmental conditions. Shrub microhabitats in this ecosystem harbor annual plant species such as *M. pinnatifida* and *O. micrantha* that are almost absent in open areas. Shrub species are thus important elements in this semiarid area that enhance biodiversity and other ecosystem functions associated with nutrient and water relocation even though a classical nurse plant syndrome on ephemeral plant biomass is lacking at the community level.

Acknowledgments

We thank Gina Arancio (Herbarium Curator, Universidad de La Serena) for plant identification. Several field research assistants. Financial support has been provided by the U.S. National Science Foundation and FONDECYT Chile including most recently NSF-LTREB DEB-1456729 to DAK and PLM, and FONDECYT No. 1070808 to J. R. Gutiérrez. This work also is funded by Institute of Ecology and Biodiversity, Millennium Scientific Initiative (IEB-ICM P05-002) and INTERCAMBIO (BIOCON06_039) Fundación BBVA.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2015.08.001>.

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