# Species-specific influences of shrubs on the non-dormant soil seed bank of native and exotic plant species in central-northern Monte Desert

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**Abstract**    Deserts shrubs are well known to facilitate vegetation aggregation, mostly through seed trapping, and stress amelioration during and after plant establishment. Because vegetation aggregation effects are a by-product of shrub presence, beneficiary species may not only be native, but also exotic. However, despite the high risk that exotic invasive species pose to ecosystem services, little is known of the role of desert shrubs on plant invasions. We assessed the influence of two shrub species on the non-dormant soil seed bank (i.e. the number of seeds that readily germinate with sufficient water availability) of an invasive annual grass (*Schismus barbatus*) and of coexisting native species in a central-northern Monte Desert (Argentina). Soil samples were collected beneath the canopies of two dominant shrub species (*Bulnesia retama* and *Larrea divaricata*) and in open spaces (i.e. intercanopies) in May 2001. Overall, the density of germinated seedlings of *Schismus* and that of the native species were negatively associated across microsite types. *Schismus* density was similar to that of all native species pooled together (mostly annuals), and was highest in *Larrea* samples (with no significant differences between *Bulnesia* and intercanopies). On the contrary, the density of all native species pooled together was highest in *Bulnesia* samples. Our results suggest that shrubs may contribute to plant invasions in our study system but, most importantly, they further illustrate that this influence can be species specific. Further research is needed to assess the relative importance of *in situ* seed production (and survival) and seed redistribution on soil seed bank spatial patterns.

**Key words:** invasion facilitation, *Schismus barbatus*, seed redistribution, vegetation nucleation, vegetation patch.

## INTRODUCTION

Desert shrubs are well known as foci for vegetation aggregation (Aguiar & Sala 1997; Flores & Jurado 2003). This pattern is the result of net positive influences exerted by shrubs, which may either be direct or indirect, and may act on more than one life-stage of the beneficiary species (Bruno *et al*. 2003; Flores & Jurado 2003; Brooker *et al*. 2008). Many studies have reported positive influences on post-dispersal stages that ultimately determine *in situ* seed production of beneficiary species (mostly growth, survival and fecundity), and frequently invoked mechanisms include stress amelioration, resource enrichment and sheltering from natural enemies (see reviews in e.g. Bruno *et al*. 2003; Flores & Jurado 2003; Brooker *et al*. 2008). Such interactions among established plants are often referred to as facilitation (e.g. Callaway 2007). Nonetheless, seed trapping by shrubs, which acts on seed dispersal, may be even more important than interactions among established plants in explaining vegetation aggregation in deserts (Aguiar & Sala 1997; Flores & Jurado 2003).

Given that aggregation effects of shrubs are a by-product of their presence (and of the associated changes in the environment around them; Callaway 2007), beneficiary species may not only be native, but also exotic. Surprisingly, despite the high risk that exotic invasive species pose to ecosystem services in deserts (Milton & Dean 2010), little is known of the role of woody species on plant invasions in these ecosystems (but see Lenz & Facelli 2003; Cavieres *et al*. 2005).

Many plant species that aggregate around desert shrubs are annuals or ephemerals (Gutterman 2002; Whitford 2002; Ward 2009). Desert annual species usually form persistent soil seed banks from which only a fraction of seeds germinate when water is available (Gutterman 2002; Venable 2007). This strategy buffers the risk of reproductive failure associated with (frequent) dry years (Cohen 1966; Venable 2007). As

a consequence, persistence of annual plant populations in deserts is driven by seed production during infrequent favourable years (Cohen 1966; Venable 2007). Hence, the non-dormant soil seed bank, that is, the number of seeds that can readily germinate under favourable soil moisture conditions, may be used as an indicator of annual-plant community dynamics because it reflects the potential species composition during key favourable years.

Here we examined the spatial heterogeneity of the non-dormant soil seed bank of resident native herbaceous species, and of an invasive annual winter grass (*Schismus barbatus*) in relation to the distribution of shrub species in central-northern Monte Desert, in western Argentina. The Monte is a warm desert that extends latitudinally from the foothills of the Andes (24°35′S) down to the Atlantic coast (40°20′S) (Fig. 1; Abraham *et al.* 2009). Annual rainfall varies from <100 mm in the north to over 350 mm in the south, with winter precipitation increasing along the same gradient (Labraga & Villalba 2009). *Schismus barbatus* is native to the winter-rainfall deserts of the Mediterranean Basin and has spread into most deserts around the globe (Brooks 2000a). This species has become particularly problematic in North America's deserts as a competitive, fire-promoting weed (Brooks 1999, 2000b; Rodríguez-Buriticá & Miriti 2009). *Schismus barbatus* has been only recently found in the central-northern Monte Desert, where it can form large non-dormant soil seed banks (Pucheta *et al.* 2011). Results of a preceding seed bank study in central-northern Monte Desert suggest positive effects of multi-specific shrub clusters on the native annual plant community (Quevedo-Robledo *et al.* 2010), although species-specific influences of shrubs were not studied.

We particularly asked: (i) are the non-dormant seed banks of *S. barbatus* and of coexisting native annual species positively associated with shrubs? And (ii) are these patterns species-specific, that is, are species in the non-dormant seed bank associated with different dominant shrub species? To answer these questions we examined the non-dormant soil seed bank beneath the canopies of two dominant shrubs (*Bulnesia retama* and *Larrea divaricata*; Zygophyllaceae) and in open spaces in a site of central-northern Monte. It should be noted here that the non-dormant soil seed bank in a given location is a function of seed number and germination fraction. The former results from the balance of *in situ* seed production and survival and of immigration *versus* emigration rates, whereas the latter depends on mechanisms of seed dormancy. Such processes will be inevitably entangled in the interpretation of our results. That is, we interpret positive (or negative) spatial associations between species in the non-dormant seed bank and shrubs as indicative of positive (or negative) influences of shrubs summarized over all the demographic processes that ultimately determine the spatial distribution of non-dormant seeds in the soil. Hence, influences detected at this stage (i.e. non-dormant seed) will not be regarded as indicative of ultimate, fitness-based influences, because interactions may shift from positive to negative from one life-stage to the next (e.g. Soliveres *et al.* 2010).

## MATERIALS AND METHODS

### Study site

Our study was conducted in Médanos de Guayamas, San Juan, Argentina (31°43′18″S, 68°08′17″W; 576 m of elevation), which is one of the driest areas of the Monte Desert. The site is located on private land mostly used for extensive goat ranching. Mean temperature in the region is 27.0°C in January (min/max: 19.5/34.7°C) and 7.9°C in July (min/max: 0.9/16.6°C) (San Juan Airport, 32 km NW of site; 1979–2010). Mean annual precipitation is 94.4 mm (CV 44.4%), with a relatively predictable summer peak: summer precipitation (December–February) averages 49.9 mm (CV 59.0%), whereas winter average precipitation (June–August) is only 9.5 mm (CV 122.3%); autumn (March–May) and spring (September–November) average precipitations are 19.6 mm (CV 83.7%) and 15.5 mm (CV 76.4%) respectively. Soils are sandy and deep (>6 m depth) and topography is nearly flat. The vegetation is an open shrubland
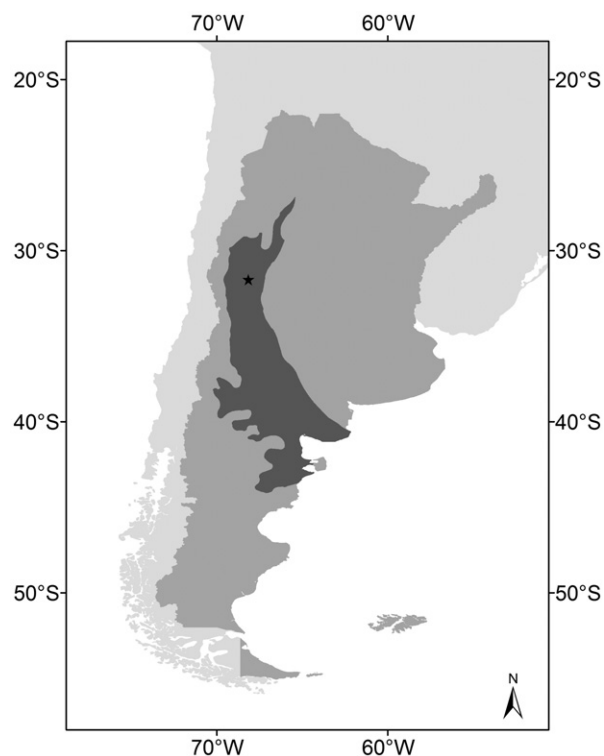


**Fig. 1.** Geographic location of the Monte Desert (dark grey), Argentina, and of our study site (star).

dominated by *B. retama* and *L. divaricata* (hereafter named by genus), with presence of other sub-shrub species such as *Capparis atamisquea* and various *Lycium* and *Atriplex* species. The dominant shrub species have different physiognomies: individuals of *Bulnesia* are aphyllous, but larger and with denser canopies than the microphyllous *Larrea* shrubs. The herbaceous vegetation is mostly composed of annual species, although perennial grasses (e.g. *Setaria mendocina*) and herbs (e.g. *Glandularia tenera* and *Heliotropium* spp.) are also present. Annual species can be roughly classified as 'winter species' (e.g. *S. barbatus* and *Chenopodium papulosum*), or as 'summer species' (e.g. *Bouteloua barbata* and *Portulaca grandiflora*) according to their main vegetative period. Species nomenclature follows Zuloaga and Morrone (1996, 1999).

## Soil seed bank sampling

Within a 10-ha area, we selected 13 replicates of each of three microsite types: beneath the canopy of adult *Larrea* shrubs, beneath the canopy of adult *Bulnesia* shrubs, and open spaces among shrubs (i.e. intercanopy). Sampled microsites were at least 8 m away from each other. In each selected microsite, three sub-samples of superficial soil were collected (separated by 30–50 cm) using a 10 cm diameter and 5 cm deep iron corer. This depth has been found sufficient for collecting almost all buried seeds in a similar desert (Marone *et al.* 1998). Sampling was carried out early in the cool season (May) in 2001, after seed set of most summer species but before seedling emergence of winter species. The 39 composite soil samples (13 replicates × 3 microsites) were stored at 4°C for 45 days to simulate winter conditions and subsequently incubated in 25 × 18 × 3 cm plastic trays arranged in a growth chamber. Growth chamber conditions were set at 25/18°C day/night, with a 12-h long photoperiod, which are typical of the early autumn and late spring months (March and November, respectively) and were considered to be simultaneously favourable for both winter and summer species. Trays were rearranged daily and regularly watered to field capacity. Germination in each tray was registered weekly and all emerged seedlings were carefully removed after counting. After 1 month of incubation, the soil in each tray was crumbled and mixed, and another round of germination registration was performed.

Our experimental methods may lead to an underestimation of seed germination of winter species in relation to germination under natural conditions. If low temperatures trigger dormancy of winter species seeds (e.g. Baskin *et al.* 1993), incubation after cold stratification (i.e. at 4°C for 45 days in mid-winter) of soil samples collected in autumn may hinder seed germination of winter species. Conversely, it is unlikely that cold stratification would affect the estimation of germination of summer species because, under natural conditions, summer species germinate after being exposed to the low winter temperatures. Hence, our results regarding germination of winter species will be conservative with respect to those of summer species.

## Data analysis

General patterns of seedling distribution among microsites were described using Discriminant Analysis (DA). Discriminant Analysis is an ordination procedure useful to identify species associated with groups of plots defined *a priori*, and to display simultaneously both species and plots (Dillon & Goldstein 1984). Our data set did not satisfy DA's requirements for statistical inference (normality and homogeneity of variance), although this does not interfere with our aim of pattern description. Preliminary analyses showed that results of this procedure were considerably less sensitive to rare species and to extremely high density values than other ordination procedures, such as Detrended Correspondence Analysis and Principal Component Analysis (data not shown). Species composition was compared across microsite types following a Multi Response Permutation Procedure based on the Euclidean distance (McCune & Mefford 1999). This procedure compares the average within-group distance in species space (usually called observed delta) with that of random collections of sampling units drawn from the entire population. A *P*-value is calculated as the fraction of permuted deltas smaller than the observed delta. Both Discriminant and Multi Response Permutation Procedure analyses were performed using PC-ORD (McCune & Mefford 1999). Data were 'shifted log' transformed (i.e. ln[1 + n]) prior to these analyses to downweight extremely high density values.

Density of emerged seedlings was compared for each species across microsite types following a method based on the Poisson distribution and its link with the chi-square distribution (Ulm 1990). This method allowed us to calculate confidence limits of density averages for all combinations of species and microsite types, including those with null values (i.e. where no germination occurred). Upper and lower confidence limits were calculated as $UCL = X^2_{2(n+1),1-\alpha/2}/2q$ and $LCL = X^2_{2n,\alpha/2}/2q$, where n is the total number of germinated seedlings for each combination of species and microsite type, $X^2_{v,\alpha}$ is the chi-square quantile for upper tail probability on v degrees of freedom, and q is the number of replicates (Ulm 1990).

## RESULTS

Overall, seedlings of 13 species germinated from the soil samples. Annuals were clearly more abundant than perennials (Table 1). Floristic variation (of soil samples *a priori* classified into microsite types) was mostly accounted for by differences between intercanopy and *Bulnesia* microsites, which were separated along the first axis of the DA (Fig. 2). Samples taken from *Larrea* microsites occupied the mid-portion of DA's first axis and stretched along the second axis, for which *S. barbatus* (hereafter named by genus) was the most contributive species (Fig. 2). Species composition differed significantly among the three microsite types (observed delta = 1.905, *P* < 0.001), and all pair-wise comparisons between microsite types yielded significant differences (data not shown).

The density of five native species varied significantly across microsite types (Table 1). *Chenopodium papulosum*, the most frequent species, was more abundant beneath shrub canopies than in intercanopies, with no significant differences between *Bulnesia* and *Larrea*

**Table 1.** Number of seedlings germinated from soil samples (average and 95% confidence interval) of native and exotic species across three microsite types (*n* = 13 per microsite type)

| Species | Habit | Propagule size (mm) | Freq | *Bulnesia* | *Larrea* | Bare soil |
|---|---|---|---|---|---|---|
| *Sclerophylax arnotii* (scar) | FAS | 5.5 × 2.5 | 19 | 2.38 (1.62–3.38)[a] | 0.69 (0.32–1.31)[b] | 0.69 (0.3–1.31)[b] |
| *Eragrostis pilosa* (erpi) | GAS | 0.6 × 0.3 | 10 | 0.85 (0.42–1.51)[a] | 0.31 (0.08–0.79)[b] | 0 (0–0.28)[b] |
| *Senna aphylla* (seap) | Sh | 3 | 2 | 0.15 (0.02–0.56) | 0 (0–0.28) | 0 (0–0.28) |
| *Bulnesia retama* (bure) | Sh | 30 | 1 | 0.08 (0–0.43) | 0 (0–0.28) | 0 (0–0.28) |
| *Chenopodium papulosum* (chpa) | FAW | 1 | 27 | 1.38 (0.82–2.19)[a] | 1.46 (0.88–2.28)[a] | 0.54 (0.2–1.11)[b] |
| *Aristida mendocina* (arme) | GP | 7 × 0.5 | 1 | 0.15 (0.02–0.56) | 0 (0–0.28) | 0 (0–0.28) |
| *Setaria mendocina* (seme) | GP | 2 | 1 | 0 (0–0.28) | 0.15 (0.02–0.56) | 0 (0–0.28) |
| *Chloris castilloniana* (chca) | GP | 2 × 0.4 | 1 | 0 (0–0.28) | 0.08 (0–0.43) | 0 (0–0.28) |
| *Glandularia tenera* (glte) | HP | 5 × 0.7 | 1 | 0.08 (0–0.43) | 0 (0–0.28) | 0 (0–0.28) |
| *Gomphrena mendocina* (gome) | FAS | 2 | 3 | 0 (0–0.28) | 0.08 (0–0.43) | 0.15 (0–0.56) |
| *Schismus barbatus*[†] (scba) | GAW | 0.4 | 24 | 1.15 (0.65–1.9)[b] | 19.38 (17.06–21.93)[a] | 1.08 (0.6–1.81)[b] |
| *Portulaca grandiflora* (pogr) | FAS | 0.8 | 20 | 0.62 (0.27–1.21)[b] | 0.62 (0.27–1.21)[b] | 1.54 (0.9–2.38)[a] |
| *Bouteloua barbata* (boba) | GAS | 1 × 0.5 | 1 | 0 (0–0.28)[b] | 0 (0–0.28)[b] | 0.62 (0.3–1.21)[a] |
| All perennials | | | 6 | 0.46 (0.17–1.00)[a] | 0.23 (0.05–0.67)[ab] | 0 (0–0.28)[b] |
| All annuals | | | 39 | 6.38 (5.09–7.91)[b] | 22.54 (20.03–25.27)[a] | 4.62 (3.50–5.94)[c] |
| All species | | | 39 | 6.85 (5.50–8.42)[b] | 22.77 (20.25–25.52)[a] | 4.62 (3.52–5.94)[c] |

Soil samples were approx. 78.5 cm² and 5 cm deep. Freq: absolute frequency of species in total sample (*n* = 39). Summed density and group frequency are also shown for all perennials, all annuals and all species pooled together. Within each row, different lowercase letters indicate significant differences (*P* < 0.05). Species' habit according to Zuloaga and Morrone (1996, 1999); F: forb, G: grass, A: annual, P: perennial, Sh: shrub. Annual species can vegetate during winter (W), or summer (S). [†]Exotic species. Sizes of species' propagules (seeds or indehiscent fruits) were drawn from the literature (Di Fulvio 1961; Burkart 1979; Kiesling 1994, 2003, 2009; Gutterman 2002); average length and width are shown for clearly oblong propagules. Species are ordered according to first axis scores of Discriminant Analysis. Abbreviations of species' names used in Figure 2 are shown in parenthesis.
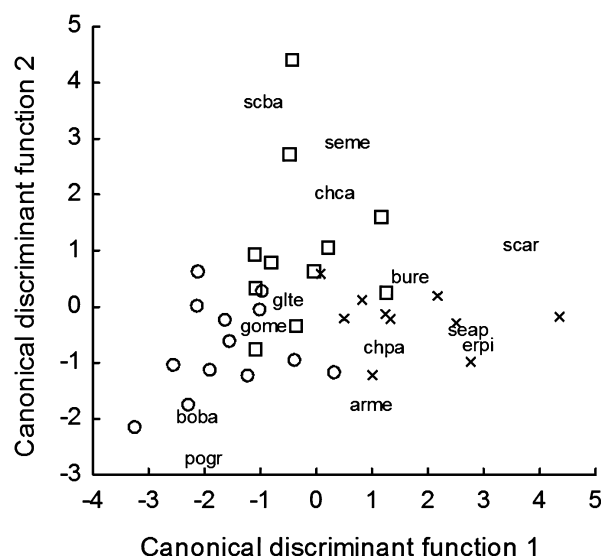


**Fig. 2.** Ordination based on Discriminant Analysis of species density (log transformed) across three microsite types: *Larrea* (squares), *Bulnesia* (crosses) and intercanopy (circles). Species scores are standardized values multiplied by 4 to scale plot scores. Abbreviations of species' names as in Table 1.

microsites (Table 1). *Sclerophylax arnotii* and *Eragrostis pilosa* showed their highest density beneath *Bulnesia*, whereas *P. grandiflora* and *Bo. barbata* were significantly associated with intercanopies (Table 1; Fig. 2). Perennial native species pooled together were most abundant beneath *Bulnesia*, and there was no emergence of these species in intercanopies (Table 1).

We found significant differences in the association of exotic and native species with the different microsite types. The exotic *Schismus* showed the highest density overall and was significantly associated with *Larrea* microsites, whereas no differences were found between *Bulnesia* and intercanopy microsites (Table 1). On the contrary, overall germination of native annual species was significantly more profuse beneath *Bulnesia* than either of the other two microsites (Fig. 3). Despite its association with *Larrea*, density of *Schismus* in intercanopies was relatively high and comparable to that of the most abundant native species in this microsite type (Table 1).

## DISCUSSION

### Influences on coexisting native species

We found 12 annual and perennial native species in the non-dormant seed bank. In particular, perennial
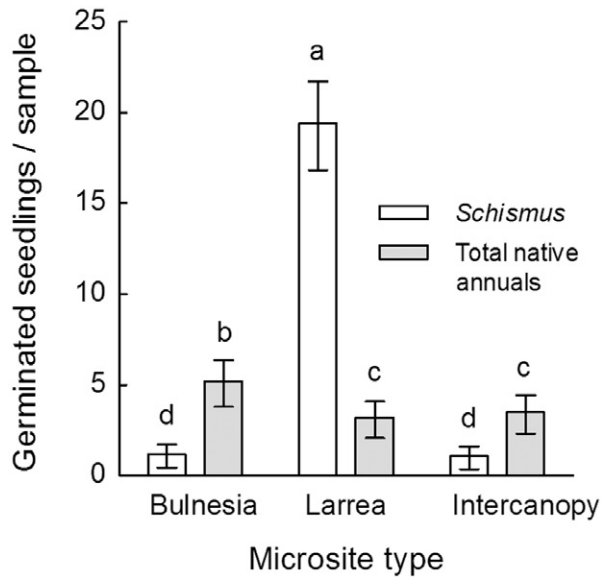
**Fig. 3.** Average number of seedlings of *Schismus* and of native annual species (pooled together) that germinated from soil samples collected in three microsite types (*n* = 13 per microsite type). Soil samples were approx. 78.5 cm² and 5 cm deep. Bars indicate 95% confidence intervals. Different letters above bars indicate significant differences (*P* < 0.05).

species showed very low seedling densities. Absence or rarity of perennial plants in the non-dormant seed bank may be due to low seed input, low persistence in the soil, and/or high dormancy (see, e.g. Thompson & Grime 1979; Thompson 2000). For rare species in the community (e.g. *Senna aphylla* and *Aristida mendocina*), low densities in the non-dormant seed bank can be equally attributed to any of these reasons. For dominant shrub species (*B. retama* and *L. divaricata*) though, which produce seeds roughly every year (E. Pucheta, pers. obs. 2011), seed input is less likely to be limiting. Rather, density of non-dormant seeds of *B. retama* (and possibly of *L. divaricata* as well) is more likely to be limited by a combination of low persistence in the soil and high dormancy (see Ribas-Fernández *et al.* 2009).

Despite their low density, perennial species were, as a whole, associated with shrub microsites. Three abundant annual species – *C. papulosum*, *Scl. arnotii* (succulent) and *E. pilosa* (grass) – were also associated with shrub microsites. Overall, these results suggest that shrubs may exert a positive influence on the distribution of non-dormant seeds of perennial species and some annual species.

Mechanisms underlying seed aggregation beneath shrub canopies include seed trapping, and those promoting *in situ* seed production of beneficiary species – mainly enhancement of nutrient and water availability, and protection from herbivores (Flores & Jurado

2003). For our study case, we disregard herbivore-mediated facilitation as domestic goats and native rodents can easily reach the areas under shrub canopies. In fact, aggregated populations may even benefit from animal activity (e.g. nutrient deposition, nesting, and microdisturbances), which tends to concentrate under woody plants in arid environments (Dean *et al.* 1999). Strong winds (especially during winter) and sheet runoff (especially during summer) are relatively frequent in our study area, so that seed trapping appears to be a plausible explanation for the observed pattern. Nutrient concentration was found to be higher beneath canopies of both *Bulnesia* and *Larrea* than in intercanopies (Pucheta *et al.* 2006), which suggests that nutrient enrichment is also a possible underlying mechanism. Undoubtedly, further research is needed to disentangle habitat – from dispersal-based mechanisms on soil seed bank distribution.

Our results also showed evidence of species-specific effects of shrubs. The density of *Scl. arnotii* and *E. pilosa* was higher beneath *Bulnesia* canopies than beneath those of *Larrea*. This suggests that shrub identity may contribute to the spatial heterogeneity of at least part of the native non-dormant seed bank. Consistently, overall floristic composition in soil samples differed significantly among microsite types and variation was mainly arranged along an intercanopy-*Larrea*-*Bulnesia* gradient. This pattern correlates well with microhabitat differences associated with shrub species, as soil nutrient concentration (Pucheta *et al.* 2006) and shade increase towards *Bulnesia* microsites. Possibly, habitat provisioning through stress amelioration, and/or resource enrichment may partially explain the observed pattern. Alternatively (or complementarily), the larger and more compact *Bulnesia* shrubs may function as larger and perhaps more effective seed traps (and larger foci for beneficial animal activity) than *Larrea* shrubs.

As opposed to shrub-associated species, the density of two annual species (the succulent *P. grandiflora* and the grass *Bo. barbata*) was highest in samples from intercanopies. The seeds of these species are relatively small (<1 mm) and similar in shape and size to those of the species positively influenced by shrubs (e.g. *C. papulosum* and *E. pilosa*; Table 1). On this base, we would expect them to disperse similarly when moved by wind and sheet runoff (and to respond similarly to potential seed traps, such as shrubs), but our data suggest the contrary. Hence, the distribution of non-dormant seeds of these species may not be ascribed to seed redistribution. We suggest that the association of *P. grandiflora* and *Bo. barbata* with intercanopies may result from differences in plant performance and *in situ* seed production and/or seed survival. It is possible that

individuals of these species find a relative advantage in intercanopies, which are likely to be more stressful in terms of abiotic conditions but less competitive. Seed predation, usually concentrated around shrubs (López de Casenave *et al.* 1998; Taraborelli *et al.* 2003), may also contribute to this pattern.

Interestingly, different grass and succulent annual species were associated with different microsite types. The summer annual grass *E. pilosa* and the (mostly) summer annual succulent *Scl. arnotii* were associated with *Bulnesia* whereas the summer annual grass *Bo. barbata* and the summer annual succulent *P. grandiflora* were associated with intercanopies. This suggests that simple, qualitative functional group classifications may not be enough to predict the distribution of herbaceous species in this desert. Functional strategies may need to be considered in the context of other processes, such as localized competition, resource fluctuations and dispersal limitation (see Shmida & Ellner 1984; Angert *et al.* 2009) in order to achieve a comprehensive understanding of the dynamics of herbaceous species in the Monte Desert.

### Influences on the exotic *S. barbatus*

Seedling density of *Schismus* was significantly higher in soil samples collected from *Larrea* microsites than in those from intercanopies. This suggests that *Larrea* may exert some sort of positive, species-specific effect on the non-dormant seed bank of *Schismus*. In the Sonoran Desert, data on the distribution of seedlings suggested that dispersal distances of seeds of *Schismus* are short, with most seeds travelling less than a metre (Venable *et al.* 2008). The Sonoran Desert is environmentally and physiognomically similar to the Monte (Solbrig 1972), thus we suspect seeds of *Schismus* may move little in the Monte Desert as well. If this holds true, the observed pattern of non-dormant seeds of *Schismus* in the soil should result mostly from *in situ* seed production. We thus suggest that the positive effect of *Larrea* on the non-dormant seed bank of *Schismus* may be mediated by positive effects on established plants. On this base, our results support the view that habitat-forming species, such as shrubs, may contribute to plant invasions in stressed ecosystems (Bruno *et al.* 2003; Bulleri *et al.* 2008).

However, field surveys carried out in the Sonoran Desert suggest that shrubs (i.e. *Ambrosia* and *Larrea* species) may have a neutral effect on the distribution of established plants of *Schismus* (Halvorson & Patten 1975; Patten 1978; Rodríguez-Buriticá & Miriti 2009). Moreover, detailed observational and experimental studies within this desert showed that *Schismus* had higher germination fraction, mean survival and

fitness in the open than under *Larrea* shrubs (Pake & Venable 1995, 1996). Our results appear to be inconsistent with these observations, and suggest that the influence of *Larrea* spp. on *Schismus* may differ between these deserts.

Notably, seedling density of *Schismus* in *Bulnesia* microsites was relatively low and similar to that in intercanopies, suggesting that there was no effect of *Bulnesia* adults on *Schismus* non-dormant seed bank. We cannot attribute this to differential seed redistribution, as there is no good reason to suggest that *Larrea* shrubs act as more effective seed traps than *Bulnesia* shrubs. As discussed above, we may expect the opposite, given that *Bulnesia* shrubs are larger and have denser canopies than those of *Larrea*. Contrary to the pattern observed for *Schismus*, overall germination of annual native species (and particularly of the succulent forb *Scl. arnotii*) was significantly more profuse in samples from *Bulnesia* microsites. Such negative spatial association between *Schismus* and some of the native annual species may result from either species-specific responses to the abiotic environment or a negative interaction between them (or both). We suggest that our results may be consistent with a framework of hierarchical organization of natural communities in which competitive interactions are nested within positive influences of habitat-forming species (Bruno & Bertness 2001; Bruno *et al.* 2003). However, further investigation is required to test whether the overall influence of *Bulnesia* on *Schismus* consists of an indirect interaction (see, e.g. White *et al.* 2006) mediated by aggregated native competitors, seed predators, or both.

### Implications for plant diversity conservation

Density of germinated seedlings of *Schismus* was similar to that of all native species pooled together. This supports previous findings in our study area, which showed very high densities of *Schismus* (Pucheta *et al.* 2011) and relatively low densities of native species (Quevedo-Robledo *et al.* 2010). *Larrea* microsites appeared to be more susceptible to be invaded by *Schismus* than *Bulnesia* microsites, which in turn appeared to harbour a higher abundance of native species. As *Larrea* species are the most characteristic and widespread shrubs in the Monte Desert (Kiesling 2003), we believe that attention should be drawn to the ecological controls of *Larrea–Schismus* interactions across the region. Furthermore, our results stress the importance of *Bulnesia* shrub conservation as a management tool to protect native herbaceous populations and constrain the success of *Schismus* in these deserts.

## ACKNOWLEDGEMENTS

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