Shrub facilitation increases plant diversity along an arid scrubland–temperate rain forest boundary in South America

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Abstract

Aim: Theoretical models predict nurse plant facilitation enhances species richness by ameliorating stressful environmental conditions and expanding distributional ranges of stress-intolerant species into harsh environments. We studied the role of nurse facilitation on the recruitment of perennial plants along an arid scrubland–temperate rain forest boundary to test the following predictions: (1) nurse shrub canopy increases seedling abundance and species richness along the rain forest–scrubland boundary; (2) scrubland species are less dependent on facilitative interactions than temperate rain forest species, especially at the moister, upper end of the gradient.

Location: Bosque Fray Jorge National Park, north-central Chile, South America (30° 39′ S – 71° 40′ W).

Methods: We examined seedling abundance and species richness of perennial plants in the open and under different types of patches that may facilitate species recruitment (living shrubs, dead shrubs, perennial grasses and trees) along an arid scrubland–temperate rain forest boundary. To assess whether the potential role of the shrub canopy on seedling survival in the scrubland and forest differs, we designed a 2 × 2 factorial field experiment with shrub canopy (under shrub or open patch) and small mammal herbivory (access or closed) as factors. At both sides of the scrubland–forest gradient, we planted young seedlings of scrubland (*Senna cumingii*) and forest (*Myrceugenia correifolia* and *Griselinia scandens*) species under the four treatment combinations.

Results: Nurse living shrubs increased seedling abundance and diversity. Under living shrubs, the number of recruiting species was 100% and 30% larger than in open patches of the arid scrubland and temperate rain forest patches, respectively. Seedling abundance was 60% and 300% larger under living shrubs compared to open patches of the scrubland and the temperate rain forest, respectively. Despite their low cover, dead shrubs were particularly important for recruitment of young seedlings in the scrubland. Seedlings of forest species were extremely rare. The field experiment demonstrated the importance of nurse plant facilitation for the survival of the forest species at both sides of the boundary. In contrast, scrubland species were less dependent on nurse plants than forest and intermediate forest–scrubland species.

Conclusions: Our results show that facilitative interactions increase seedling abundance and species richness along an arid scrubland–temperate rain forest boundary, notably by enhancing seedling establishment of forest species. Despite increasing nurse shrub–seedling competition in the arid scrubland, shrubs have a net positive effect on plant community diversity.

Introduction

Positive and negative interactions shape the structure and composition of ecological communities by differently affecting the growth, survival and fecundity of individuals. Several theoretical models suggest that facilitative interactions can contribute to maintaining species richness by expanding the range of environmental conditions where a species can survive (Bruno et al. 2003). As environmental conditions become more stressful, the relative importance of facilitation is predicted to increase linearly (Bertness & Callaway 1994) or to peak at intermediate stress conditions (Michalet et al. 2006; Maestre et al. 2009; Holmgren & Scheffer 2010). Under very stressful conditions, the ameliorating effect of facilitators on facilitated species can become insufficient and the net effect of positive and negative interactions shifts from facilitation towards competition (Holmgren et al. 1997; Holmgren & Scheffer 2010). Shifts from facilitative to competitive interactions have been documented in several arid ecosystems (Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Callaway 2007). Facilitation is expected to promote species richness at medium to high environmental severity by expanding the range of stress-intolerant species into harsh abiotic conditions (Bruno et al. 2003; Michalet et al. 2006; Maestre et al. 2009). However, facilitative interactions may be more common than often expected also in less stressful environments, especially for stress-intolerant species (Holmgren & Scheffer 2010). The impact of nurse plants on species richness will not only depend on the severity of the abiotic environment but also on the characteristics of both facilitators and facilitated species (Maestre et al. 2009; Cavieres & Badano 2010).

In north-central semi-arid Chile (30° S), temperate rain forest patches grow on the coastal mountain-tops in a region receiving only 150 mm of annual rainfall (López-Cortés & López 2004) and surrounded by arid scrub communities (Squeo et al. 2004). The occurrence of these rain forest patches under extremely dry conditions has fascinated scientists for a long time (Philippi 1884; del-Val et al. 2006) because they are floristically close to the southern Chilean forests found 1500 km further south (up to 43°S), where rainfall can reach more than 2600 mm (Villagrán & Armesto 1980; Smith-Ramírez et al. 2005). These temperate rain forest patches seem to be remnants of vegetation once dominant during the colder and more humid glacial periods before the Tertiary (Villagrán et al. 2004), and persist because frequent coastal fog subsidizes moisture, thus providing additional water (del-Val et al. 2006; Garreaud et al. 2008). This scrubland–temperate rain forest boundary provides an interesting opportunity to study the role of nurse facilitation on plant species richness along a moisture stress gradient and its consequences for the recruitment of species and for plant community diversity. Clearly, the net direction of the nurse effect on seedling recruitment is likely to depend on species tolerance to thermal stress, drought and shade. It can be anticipated that arid scrub species may be less dependent than temperate rain forest species on nurse cover on the moister foggy mountain-tops and be able to colonize open spaces in the fragmented temperate forest, whereas forest species may be more dependent on nurse plant cover.

We examined the abundance and species richness of perennial plant seedlings (grass, shrub and tree species) in different types of patches along the arid scrubland–temperate rain forest boundary and conducted a field experiment to evaluate the role of nurse plant facilitation on the survival of scrub and forest species in order to test the following predictions: (1) nurse shrub canopy increases seedling abundance and species richness along the rain forest–scrubland boundary; (2) scrubland species are less dependent on facilitative interactions than temperate rain forest species, especially at the moister upper end of the gradient.

Methods

Study area

The study area was located within Bosque Fray Jorge National Park, north-central Chile (30° 39′ S, 71° 40′ W) where elevation varies from 250 to 650 m a.s.l. Temperate rain forest patches are located on the coastal mountain slopes facing the Pacific Ocean. The forest is dominated by olivillo trees (*Aextoxicon punctatum*) but contains a diversity of life forms, including trees (e.g. *Myrceugenia correifolia, Drimys winteri, Rhaphithamnus spinosus*), woody climbers and shrubs (e.g. *Griselinia scandens, Adenopeltis serrata*), epiphytic ferns, herbs, lichens and mosses (Villagrán & Armesto 1980; Squeo et al. 2004). The forest becomes fragmented into smaller patches on the mountain plateau and is replaced by a matrix of semi-arid scrub vegetation on the inland-facing slopes and lowlands (Squeo et al. 2004). The scrubland is located at lower altitudes and dominated by xerophytic vegetation, with shrub patches surrounded by bare soil that is only covered by annual forbs and perennial grasses in rainy years (Gutiérrez et al. 1993a). Dominant shrub species include *Porlieria chilensis, Adesmia bedwellii, Proustia cuneifolia, Senna cumingii, Bahia ambrosioides, Flourensia thurifera, Haplopappus foliosus* and *Baccharis* sp. (Gutiérrez et al. 2004).

The regional climate is semi-arid mediterranean, with warm dry summers and cooler wet winters and a mean annual temperature of 13.6 °C. The mean maximum temperature in the warmest month (Jan) is 24 °C, and the mean minimum temperature in the coolest month (Jul) is 4 °C (López-Cortés & López 2004). Rainfall is concentrated

in the winter months from May to Aug, with high inter-annual variability associated with the El Niño Southern Oscillation (ENSO) phenomenon (Montecinos & Aceituno 2003). During 2004, the year in which this study was carried out, total annual precipitation reached 135 mm, which is close to the mean annual precipitation of 147 mm in recent decades (1983–2003). Longer meteorological records from La Serena (85 km north) report a mean precipitation of 114.4 mm (1878–1998; Soto & Ulloa 1997).

Natural seedling abundance and species richness

We sampled the vegetation along two parallel transects of 2 m × 75 m from north to south, separated by 50 m from each other in both the upper and lower end of the rain forest–scrubland boundary (i.e. vegetation transition zone). The upper boundary end was located in a sector of fragmented forests called 'El Mineral' (30° 39'34" S, 71° 41'06" W) and the lower end was downhill in the dry scrubland (30° 39'23" S, 71° 39'56" W) (Supporting Information Appendix S1). This sampling effort was sufficient to assess the species richness in both habitats (Appendix S2).

Along these four transects, we identified and counted all perennial grass, shrub and tree seedlings and the type of patch in which they were growing. We distinguished between (1) open; (2) under living shrubs; (3) under dead shrubs; (4) under trees; and (5) under perennial grasses. The last two patch categories were only present in forest and scrubland, respectively. We distinguished between two types of seedling: 'young seedlings' as those younger than 1 yr old (with one or two new sprouts indicating they had emerged that same year), and 'old seedlings' as those with a lignified stem and up to 25-cm tall, often multi-branched, indicating they had established at least in the previous year. Based on the flora description of Arancio et al. (2004), we further classified the species into three habitat categories: (1) scrubland species (those that grow only in the arid scrubland); (2) forest species (those that grow only in forest or forest edges); and (3) scrubland–forest intermediate species (those that occur in scrubland, forest edges and forest). We estimated the cover and mean height of the distinct patch types and identified the species forming them, using the line intercept method along the central transect line (Bauer 1943).

We calculated seedling abundance and species richness for each patch type and species separately. In the upper and lower sides of the boundary (i.e. forest fragments and scrubland), we used χ^2 homogeneity tests to test whether seedling species richness (species richness) and abundance (number of seedlings) followed a different distribution than could be expected according to the relative propor-tion of the patch types. We compared the proportions of species (or number of seedlings) observed in each patch with the relative availability of each patch type. We also examined whether the scrubland, intermediate and forest species were more often found under particular patch types at the upper and lower sides of the scrubland–forest boundary. We used χ^2 homogeneity tests to assess shifts in the distribution of seedlings in different microsites as they grow older. We compared the proportions of young and old seedlings found in open patches, and living and dead shrubs (insufficient numbers of seedlings were established under tree canopy and perennial grasses to allow statistical analyses).

Field experiment: testing nurse facilitation in forest and scrubland

To assess the differential role of nurse facilitation in the forest and scrubland sides of the boundary, we conducted a field experiment at both sites with seedlings of two forest (M. correifolia and G. scandens) and one scrubland (S. cumingii) species (Appendix S1). Myrceugenia correifolia is an evergreen tree species up to 5-m tall (Arancio et al. 2001), and is the most drought-tolerant tree species in the forest patches (del-Val et al. 2006) and thus potentially able to colonize open patches at the upper end of the scrubland–forest boundary and expand forest patches. The genus Myrceugenia (Myrtaceae) contains about 40 species that grow in temperate, wet and subtropical climates and are distributed in Chile, Argentina and south Brazil (Landrum 1981). In Chile, M. correifolia is restricted to isolated patches along the central coast that are sufficiently humid (Pais 2000). In the forest patches of Bosque Fray Jorge National Park it is one of the dominant tree species, especially in the smaller patches in the northern part of the park (del-Val et al. 2006). The genus Griselinia (Cornaceae) contains seven species, of which four are endemic to Chile and three to New Zealand (Enciclopedia de Flora Chilena 2011). Griselinia scandens is an evergreen climber that occurs along the Chilean coast, and in Bosque Fray Jorge National Park is restricted to the moist forest patches. Senna (Caesalpinioideae) is a genus of about 350 shrub and herb species occurring worldwide in tropical and temperate regions (Marazzi et al. 2006). Senna cumingii is a semi-deciduous shrub that is common to the semi-arid scrubland of north-central Chile (Gutiérrez et al. 2004).

At both sides of the boundary, we designed a factorial experiment with two factors, each of them with two levels: shrub canopy (under shrub or open patch) and small mammal herbivory (access or closed). Herbivory was included as an experimental factor because it has been identified as a critical limiting factor in the regeneration of arid and semi-arid plant communities in Chile and is

affected by the proximity to shrub availability (Jaksic & Fuentes 1980; Fuentes et al. 1984; Holmgren et al. 2000; Gutiérrez et al. 2007). Each of the four treatment combinations had six complete replicates, giving a total of 24 experimental units in each site (forest and scrubland). Accordingly, the total number of experimental units was 48. In each 120 cm × 80 cm experimental unit, we planted eight seedlings of each of the three species on *in situ* soils. Seedlings were randomly distributed over four rows of six seedlings each, planted at 10 cm from the edges of the experimental unit and separated by 20 cm from each other. Seedlings of *S. cumingii* and *G. scandens* were produced from seeds collected at the study area and nursed for 5 wk in a greenhouse at the Universidad de La Serena, Chile. Because *M. correifolia* seedlings are difficult to germinate and grow very slowly, we used 1.5-yr-old seedlings provided by the local CONAF, the Chilean Forestry Corporation. At planting time, seedlings had a mean height of 6 cm (*S. cumingii*), 1.5 cm (*G. scandens*) and 5.6 cm (*M. correifolia*). We transplanted all seedlings to the field within 10 d and protected them with a temporary plastic enclosure until all seedlings were planted. Each seedling was irrigated with 0.5 dm^3 of water at planting time. Before starting the experiment, we removed the plastic protection, replaced dead seedlings and provided complementary irrigation so that each seedling received in total an initial irrigation of 1 dm^3. We monitored seedling survival for 5 mo until the end of the first summer drought, which has been identified as a main environmental filter for seedling establishment in arid Chile (Fuentes et al. 1984; Holmgren et al. 2000; Gutiérrez et al. 2007; León et al. 2011).

To test for the nurse canopy effect, we selected *Baccharis vernalis* at the forest and *P. chilensis* at the scrubland as nurse shrubs. Both species are abundant and have previously been considered as nurse species (Gutiérrez et al. 1993b). Unfortunately, forest and scrubland had no common nurse shrub species. Nevertheless, both *Baccharis* and *Porlieria* share an umbrella-shaped crown and were present in sufficient numbers to allow replication. All selected nurse shrubs were between 120- and 150-cm tall. Experimental plots under the shrub treatment were placed with a southwest orientation towards the fog input direction (del-Val et al. 2006). For the open treatment, experimental plots were placed in open places about 1 m away from the shrub canopy.

The herbivore treatments (access or closed) were designed to test for the effect of small native mammals such as rodents (*Phyllotis darwini, Akodon olivaceus, Octodon degus*), rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), which are the main herbivores in both forest and scrubland. At present, there are very few guanacos (*Lama guanicoe*) and no domestic livestock in Bosque Fray Jorge National Park. To exclude small mammals, we used galva-

nized wire cages of 120 cm × 80 cm × 45 cm, with a 0.5-cm wire mesh on the sides and bottom and 1-cm wire mesh on top, that were placed over the seedlings. The bottom mesh was perforated with holes of 4 cm^2 at each seedling planting point to facilitate seedling growth. In all treatments the proportion of surviving seedlings was monitored every 3 wk.

We used a repeated measures (rm) two-way ANOVA to assess the effects of shade and herbivory treatments on seedling survival. Separate analyses were made for each species at each site. Since the proportion of surviving seedlings did not follow a normal distribution even after several variable transformations (log, square root and arcsin), we ordered for each date the rates of seedling survival into ranks before applying *F* analyses. This is a function of the Friedman statistics, which can be treated as a normal distribution for *F*-tests (Conover & Iman 1981).

To verify if soil water content was higher under the shrub canopy, we compared the soil water content of the top soil layer (20 cm) between the open patch and shrub shade treatments. We took two samples for each experimental unit every month and estimated the percentage water content per gram of soil by subtracting dry soil weight from fresh soil weight. Differences between open patches and shrub shade and between the two vegetation types were examined with a (rm) ANOVA.

Results

Natural patterns of seedling abundance and species richness

Species recruitment was highest under living shrubs in both the arid scrubland and the temperate rain forest sites (Fig. 1, Appendix S3). Species richness was twice as high under living shrubs compared to open places in the scrubland and increased by one-third in the forest (Fig. 1, Appendix S3). The total number of seedlings increased from 41 (0.32 seedlings·m^{-2}) to 66 (0.48 seedlings·m^{-2}) and from 137 (1.40 seedlings·m^{-2}) to 491 (3.08 seedlings·m^{-2}) under living shrubs in scrubland and forest, respectively (Appendix S3). Despite their low cover, patches of dead shrubs appeared to be important for recruitment, in addition to living shrubs, particularly in the scrubland (Fig. 1, Appendix S3). Perennial grasses in the scrubland, and trees in the forest, were particularly poor in seedlings (Appendix S3). Species richness and seedling abundance at both sides of the scrubland–rain forest boundary did not follow a frequency distribution, as expected by the relative availability of each patch type (Fig. 1, Appendix S3; species richness in both sites, $\chi^2_3 > 33.15$, $P < 0.0001$; seedling abundance in scrubland, $\chi^2_3 > 33.15$, $P < 0.0001$; seedling abundance in forest, $\chi^2_3 = 15.23$, $P = 0.0015$).
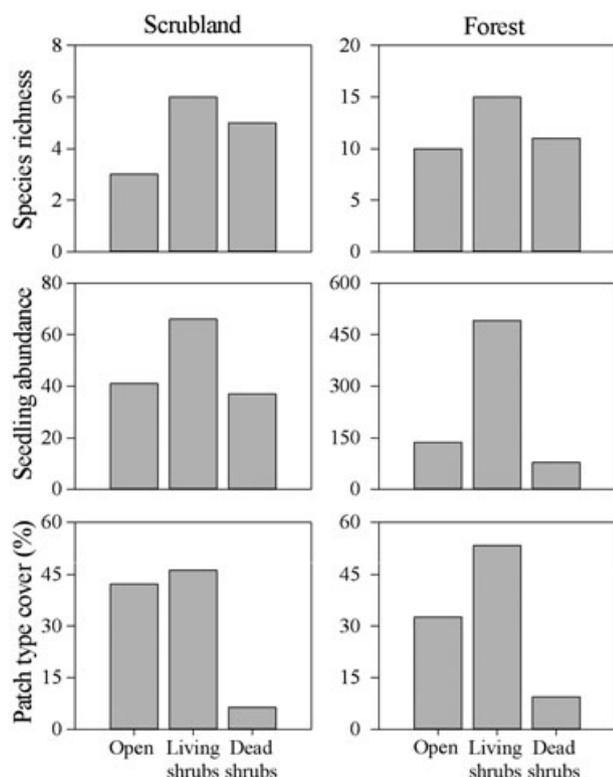
Fig. 1. Seedling species richness (number of species) and abundance (number of seedlings) in patch types found at both sides of the arid scrubland–temperate rain forest boundary in Bosque Fray Jorge National Park, Chile. For all microsites see Appendix S3.
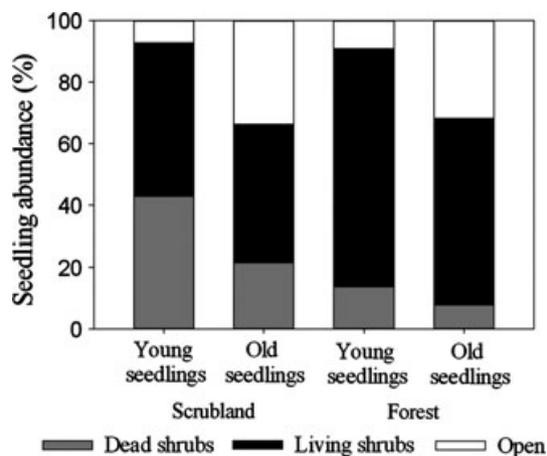

Fig. 2. Relative abundance of young and old seedlings established under different patch types at both sides of the arid scrubland–temperate rain forest boundary in Bosque Fray Jorge National Park, Chile.

Table 1. Species richness (number of species) and abundance (number of seedlings) in the seedling bank under nurse living shrubs at both sides of the arid scrubland–temperate rain forest boundary in Bosque Fray Jorge National Park, Chile.

	Nurse cover (%)	Species richness	Seedling abundance
Scrubland			
Porlieria chilensis	29.9	3	14
Proustia cuneifolia	14.6	3	11
Adesmia bedwellii	10.2	3	9
Chenopodium petiolare	31.6	2	25
Senna cumingii	5.8	2	3
Baccharis vernalis	0	2	2
Anisomeria littoralis	1.2	1	2
Fuchsia lycioides	4.0	0	0
Baccharis paniculata	2.6	0	0
Forest			
Baccharis vernalis	43.9	14	342
Haplopappus foliosus	6.6	7	28
Fuchsia lycioides	5.8	5	28
Bahia ambrosioides	4.1	5	20
Senecio planiflorus	4.3	5	9
Berberis actinacantha	1.0	5	8
Aristeguietia salvia	5.6	4	21
Puya chilensis	16.9	3	7
Ribes punctatum	2.6	2	4
Baccharis paniculata	1.3	1	2
Senecio coquimbensis	2.3	0	0
Valeriana peltata	1.8	0	0
Chenopodium petiolare	0.3	0	0
Erigeron luxurians	0.3	0	0
Unknown	3.2	6	22

Seedlings of forest species were extremely rare. We found only one forest species, *Myrceugenia correifolia*, growing exclusively under living shrubs in the forest (Appendix S3). Scrubland species recruited along the whole scrubland–forest boundary gradient, mostly under living and dead shrubs, but were also able to recruit in the open patches, especially in the upper forest end of the gradient (Appendix S3). Seedlings of species classified as intermediate scrubland–forest species only recruited in the forest borders, where they established mostly under the living and dead shrub canopy (Appendix S3). In the semi-arid scrubland, we only found seedlings belonging to species classified as typical of scrubland systems according to Arancio et al. (2004) (Appendix S3).

Dead shrubs were particularly important for young seedlings in the scrubland, i.e. 41% of all young seedlings established under dead shrubs in comparison to 14% in the fragmented forests (Fig. 2). In the open patches of the scrubland, there were proportionally more old than young seedlings (Fig. 2; $\chi^2_2 > 33.15$, $P < 0.0001$). A rather similar pattern was found in the forest (Fig. 2; $\chi^2_2 = 28.36$, $P < 0.0001$).

Nurse characteristics

In the forest, *Baccharis vernalis*, the most common shrub, was also the most successful nurse shrub, with the most abundant and diverse seedling community recruiting

under its canopy (Table 1). Species recruitment was also high under the canopy cover of the shrub *Haplopappus foliosus* (Table 1). In the scrubland, most seedlings were found under the canopy of the dominant subshrub *Chenopodium petiolare* (Table 1). Seedling richness in the scrubland was high under the canopies of *Porlieria chilensis*, *Proustia cuneifolia* and *Adesmia bedwellii* (Table 1). Living shrubs were on average taller than dead shrubs. Mean height of living shrubs in the forest boundary was 104.9 cm compared to 70.9 cm for dead shrubs (*t*-test; $n = 186$ for living shrubs, $n = 22$ for dead shrubs, $P = 0.0003$). Also in the scrubland, living shrubs were taller than dead ones, but the difference was not statistically significant (80.7 vs 60 cm respectively; *t*-test; $n = 132$ for living shrubs, $n = 17$ for dead shrubs, $P = 0.054$).

Field experiment: shrub canopy and herbivore effects in forest and scrubland

Seedlings of all three experimental species survived better in the forest borders than in the scrubland (Fig. 3; Appendix S4): *Senna cumingii* ($F_{1,46} = 13.74$, $P = 0.001$), *Griselinia scandens* ($F_{1,46} = 82.13$, $P < 0.001$) and *M. correifolia* ($F_{1,46} = 139.71$, $P < 0.001$). All seedlings of the forest species *G. scandens* and *M. correifolia* died earlier in the semi-arid scrubland. Shrub canopy had no effect on seedling survival of the scrubland species *S. cumingii* (forest borders $F_{1,20} = 0.42$, $P = 0.53$; scrubland $F_{1,20} = 1.90$, $P = 0.18$) but extended the seedling survival of the two forest species, *G. scandens* (forest borders $F_{1,20} = 12.84$, $P = 0.02$; scrubland $F_{1,20} = 39.52$, $P < 0.001$) and *M. correifolia*
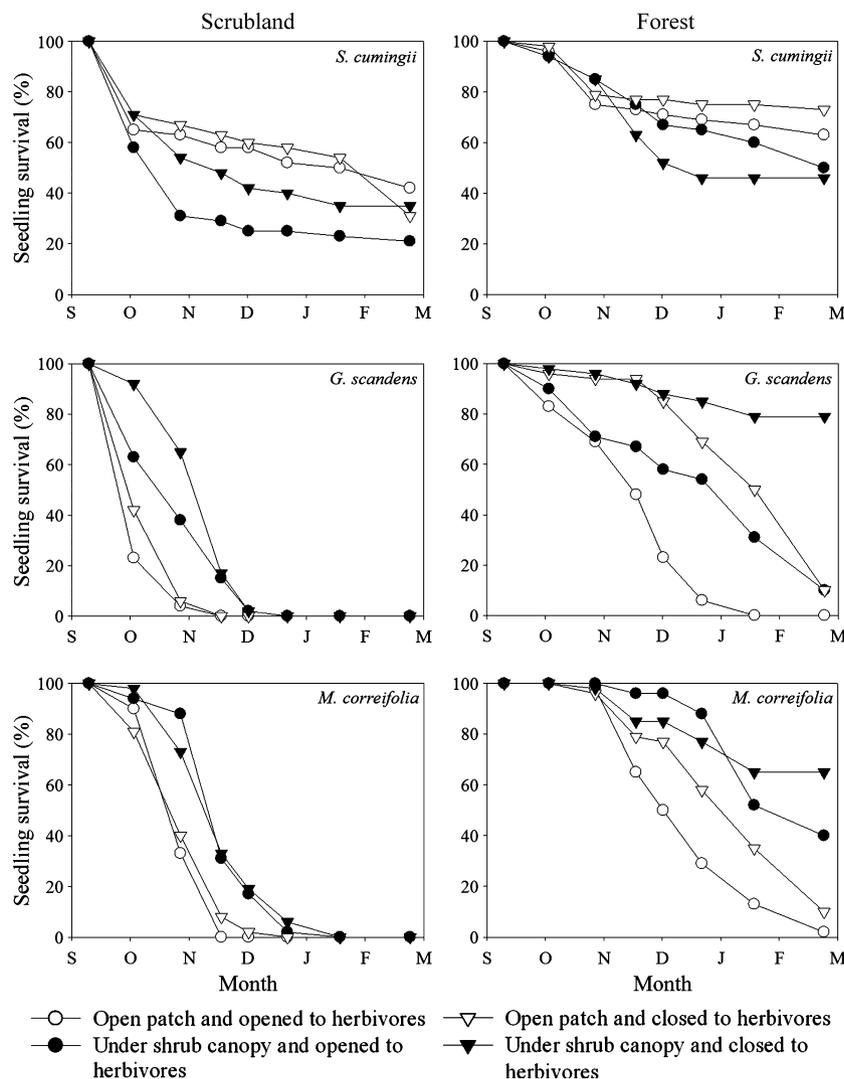

Fig. 3. Survival of experimental seedlings of *Senna cumingii*, *Griselinia scandens* and *Myrceugenia correifolia* in scrubland and forest fragments in Bosque Fray Jorge National Park, Chile.

(forest borders $F_{1,20}$ = 15.83, P = 0.001; scrubland $F_{1,20}$ = 19.76, $P < 0.001$). Herbivores reduced the survival of *G. scandens* seedlings in the forest border ($F_{1,20}$ = 41.27, $P < 0.001$) but not in the scrubland. Herbivores had no effect on the survival of *S. cumingii* and *M. correifolia* seedlings in any habitat (Appendix S4). In both sites there were no significant interactions among factors (Appendix S4).

Soil water content was higher in the forest border than in the scrubland ($F_{1,46}$ = 195.47, $P < 0.001$). In both sites, soil water content decreased during the time period of the field experiment but remained higher under the shrub canopy (forest borders, $F_{1,20}$ = 147.49, $P < 0.001$; scrubland, $F_{1,20}$ = 37.21, $P < 0.001$).

Discussion

Nurse shrub facilitation and species richness

We expected higher species richness under nurse plants than in open places as result of a larger occurrence of stress-sensitive plant species. We found three species in the scrubland (50% of total seedling species richness) and five species in the forest fragments (33% of total seedling species richness) exclusively establishing under nurse plants, i.e. under living shrubs, dead shrubs and/or perennial grasses (Appendix S3). In contrast, there were no species that recruited exclusively in open patches; species that were established in open patches recruited in all cases also under nurse plants. This indicates that some species have a broader stress tolerance range, whereas some rely on nurse facilitation for successful establishment.

In the forest fragments, we could compare overall patterns of seedling establishment between dry scrubland species and intermediate scrubland–forest species. We found that the establishment of intermediate species was more restricted to nurse plants than that of scrubland species. About one-third of the intermediate species exclusively recruited under the nurse canopy while all scrub species established in both open patches and under shrub shade. These results suggest that shrubs may be more important for the amelioration of abiotic stress and the seedling recruitment of intermediate and forest species. Our field experiment demonstrates that seedlings of the scrubland species *Senna cumingii* can perform equally well under both shrub canopy and open patches in both the scrubland and forest sides of the boundary, whereas seedlings of the forest species *Myrceugenia correifolia* and *Griselinia scandens* perform better under a nurse canopy. However, climate in the dry scrubland is too harsh for these species to survive even under a nurse canopy. All our experimental seedlings of *M. correifolia* and *G. scandens* died in the scrubland, despite their longer survival under shrub shade.

Shrub facilitation along the arid scrubland–temperate rain forest boundary

The distribution patterns of naturally established seedlings demonstrate that shrub canopy is crucial for perennial plant species recruitment in both the upper and lower sides of the scrubland–temperate rain forest boundary. The number of species and the number of seedlings that recruit under shade is higher than in open patches. This supports the hypothesis that nurse plant facilitation may also be important in milder environments like these temperate rain forest fragments (Holmgren & Scheffer 2010). Our experimental results indicate that the positive nurse effects are more likely related to improvement in microclimatic conditions than to reduced herbivore pressure. In both vegetation types, soil moisture was higher in the experimental units under shrub canopy than those in open sites. Many studies have demonstrated that nurse plant shade can improve microclimatic conditions, thus reducing water stress (Holmgren et al. 1997, 2011; Gómez-Aparicio et al. 2004), as also found in the scrublands of Bosque Fray Jorge National Park (Tracol et al. 2011). In the temperate forest fragments, shrubs probably facilitate seedling establishment also by increasing water availability through fog combing (del-Val et al. 2006). The inverted cone shape and the numerous small-sized leaves of *Baccharis vernalis* allow efficient interception of the fog coming from the Pacific Ocean. Similar mechanisms seem to occur in the temperate rain forest of New Caledonia, where isolated trees facilitate succession from maquis to rain forests by improving water conditions of recruiting plants through cloud combing and a shady cooler microclimate (Rigg et al. 2002).

Shrubs could potentially affect herbivore pressure (Callaway 2007) but we found very weak herbivore effects in our field experiment, in contrast to previous studies in north-central Chile where small herbivores have been identified as a major bottleneck for seedling recruitment. In the scrubland habitat surrounding Fray Jorge, long-term field experiments have detected transient top-down control during and after high rainfall years (Meserve et al. 2003). Here, herbivore damage can completely preclude shrub and tree seedling recruitment (Holmgren et al. 2006a; Gutiérrez et al. 2007). In the rain forest forest fragment, field experiments have found about a 25% decline in tree seedling survival due to small mammal herbivores (del-Val & Armesto 2010).

Despite the net positive effect of shrubs, increasing abiotic stress severity and competition in the scrubland probably explains switches in the role of dead shrubs compared to living shrubs as nurses. Although dead shrubs played an important role in both vegetation types, proportionally more young seedlings recruited under dead shrubs in the

scrubland than in the forest borders. This pattern suggests stronger competition between living shrubs and establishing seedlings in the dry scrubland than in the forest fragments. Dead nurse plants can ameliorate thermal stress without the potential negative cost of reduced soil water content (Anthelme et al. 2007). The ameliorating effect of dead woody branches can also facilitate plant recruitment after disturbances. For instance, lower soil temperature and higher soil moisture under remaining burned branches increases seedling recruitment in burned Mediterranean pine forests (Castro et al. 2011). The role of dead shrubs is comparable to the role of abiotic–nurse associations described for other systems. For instance, nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti in Mexican deserts (Peters et al. 2008). The relative importance of living plants vs dead or abiotic structures as nurses will depend on their effects on environmental stresses that affect plant performance. For facilitation to occur, the positive ameliorating effect on air and soil temperature, soil moisture, soil nutrients or herbivore damage should be larger than the unavoidable negative effects of lower photosynthetic radiation under shade. Since plant facilitation is the net result of positive and negative effects between neighbouring plants (Holmgren et al. 1997), one can expect dead or abiotic structures to become increasingly important as abiotic conditions become more stressful and competition for limiting resources overrides the positive effects of a living nurse canopy.

Our study shows the importance of dead shrubs as nurse plants. However, some plant functional traits may have a strong effect on resources and shift the balance towards living plants as nurses. For example, hydraulic lift could potentially have a stronger positive effect on soil moisture under a living canopy than reduced soil evaporation under the shade of dead or abiotic structures. Also, nitrogen fixation by nurse plants could improve soil fertility more effectively than the controlled soil run-off from abiotic structures. The importance of different plant functional traits to explain the facilitative role of living nurses certainly deserves attention and is starting to be explored (Butterfield & Briggs 2011). In our study, the most successful living nurses, with the most abundant and diverse seedling bank, were the most abundant shrubs *B. vernalis* in the forest and *Chenopodium petiolare* in the scrubland. This suggests that probably no particular functional trait is strongly linked to their role as nurses. Other species acting as important nurses were *Haplopappus foliosus* (in the forest), *Porlieria chilensis*, *Proustia cuneifolia* and *Adesmia bedwellii* (in the scrubland). The last three shrub species have root systems capable of hydraulic lift (Muñoz et al. 2008) and *A. bedwellii* also fixes nitrogen through *Rhizobium*–root associations (Aguilera et al. 1999). However, it is currently unknown if these traits really explain the nursing role of these species.

Very few naturally established seedlings of forest tree species were found in the forest site (only three seedlings of *M. correifolia*), all of them under living shrubs. This suggests that the establishment of forest tree species is extraordinarily difficult and that these temperate rain forest patches cannot easily grow and expand. It is possible that establishment of very drought-sensitive species occurs during particular climatic conditions. Rainy years, like those associated with ENSO events, are windows of opportunity for plant recruitment in several arid and semi-arid ecosystems around the world (Holmgren et al. 2001, 2006a,b), including Chilean drylands (Gutiérrez et al. 2007; Squeo et al. 2007; León et al. 2011). However, for the dominant canopy species in these forests, the endemic *Aextoxicon punctatum*, establishment seems to be only weakly correlated with rainfall and ENSO (Gutiérrez et al. 2008). Changes in fog frequency due to changes in sea-surface temperature or the height of the inversion (Cereceda et al. 2002) could also have consequences for tree growth and recruitment patterns. Long-term monitoring of forest species recruitment is required to understand the interplay between seedling establishment and the effects of inter-annual climatic variability on rainfall and fog frequency patterns.

In summary, we conclude that facilitative interactions increase the species richness and abundance of seedlings recruiting along the arid scrubland–temperate rain forest boundary by ameliorating abiotic stress and enhancing the establishment of stress-sensitive species in the forest and scrubland. Our study demonstrated that forest species recruitment is restricted to the nurse microhabitat and, hence, without the presence of nurses, these species would be condemned to disappear from the community. Therefore, the presence of nurse shrubs is crucial for forest species recruitment but less important for some scrubland species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Locations where the transects and the factorial experiment were established.

Appendix S2. Species – area curve per transect.

Appendix S3. Total number of established seedlings of each recruiting species under the patch types at both ends of the arid scrubland–temperate rainforest boundary in Bosque Fray Jorge National Park, Chile.

Appendix S4. ANOVA tests of between-subjects effects for the factorial experiment.

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