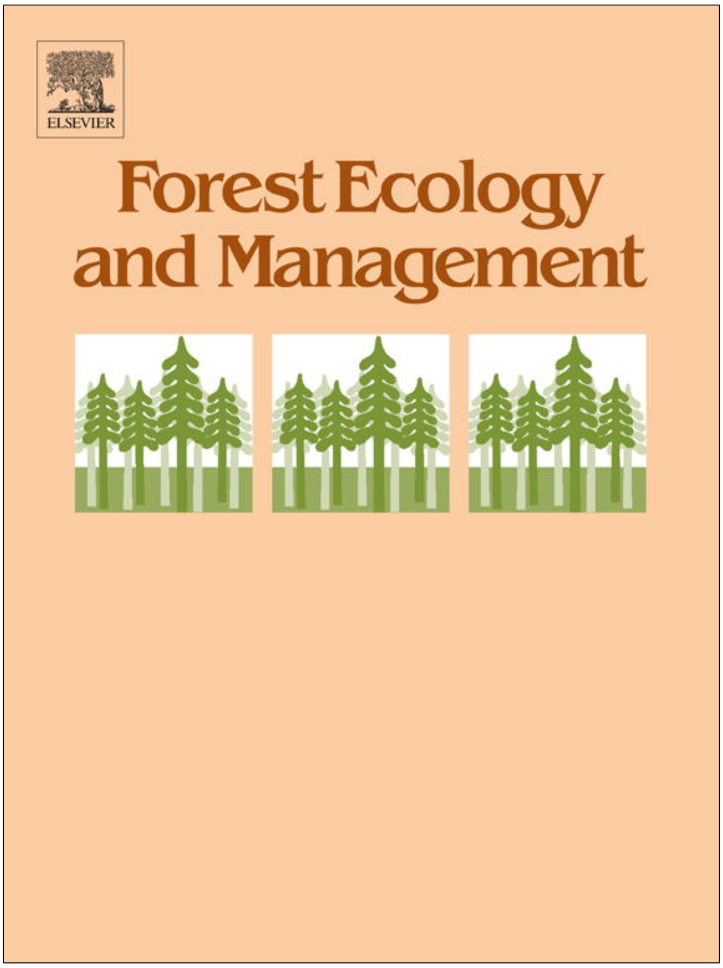

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The exotic shrub *Rosa rubiginosa* as a nurse plant. Implications for the restoration of disturbed temperate forests in Patagonia, Argentina

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ABSTRACT

Facilitation of forest native species under exotic nurse plants may differ between climatic regions and microsites. Recruitment of other exotic species should be taken into account when areas invaded by exotic shrubs are considered for forest restoration. Natural regeneration of native and exotic species and survival of planted native saplings under the deciduous exotic *Rosa rubiginosa* (shrub microsite = SM) and in open microsites (OM) were studied in preexisting shrublands of mesic and wet regions in North Patagonia. Light levels, soil chemical composition and seasonal variation of soil moisture were analyzed in SM and OM and the content of N and C was compared between mature and senescent *R. rubiginosa* leaves. In the SM, native species received less light and soils had higher C:N rate and moisture in spring than in the OM. *R. rubiginosa* reabsorbs this nutrient before leaves fall. Natural native forest species recruitment occurred only in the SM. In shrublands of the mesic region native species richness and abundance increased under bigger nurse plants. In the wet region, where herbivory was higher, moderate climatic conditions allowed greater species richness and abundance than in the mesic region, independently of the nurse plant volume. The height of the exotic shrub and the protected species showed a positive and negative relationship in the mesic and wet region, respectively. Exotic species grew under 5–15% of the nurse plants ($n = 60$). Survival of planted saplings, shoot resprouting and herbivore-related mortality were highest in the SM and in wet regions. Sapling mortality due to drying out was highest in the OM of the mesic region. It is possible for forest restoration in areas previously invaded by *R. rubiginosa* to achieve highly positive results in mesic regions where plants are protected from desiccation. In areas with moderate climatic conditions, facilitation against herbivores has beneficial initial effects, but as the nurse plant competes with taller native individuals, forest restoration would depend on effective control of the nurse plant biomass. In both areas other exotic species would be well represented in the long term.

1. Introduction

Plant facilitation consists in a positive interaction between species and is essential at community level (Callaway, 1995; Callaway and Walker, 1997). It plays a major role particularly in ecosystems suffering from high abiotic stress or intense herbivory (Niering et al., 1963; Bertness and Callaway, 1994; Withgott, 2000; Aerts et al., 2007). Nurse plants improve species survival and plant growth by reducing excessive solar radiation, conserving soil moisture, increasing soil nutrients, protecting plants against livestock grazing (Callaway et al., 1991; Callaway, 1995; Pugnaire et al., 1996; Withgott, 2000; Aerts et al., 2007) and acting as seed traps (Verdú and García-Fayos, 1998). For naturally established seedlings, facilitative effects may operate during the seed dispersal, germination and/or seedling stages (Aerts et al., 2007). Plant facilitation is important in restoration projects where the unsuccessful recovery of plant cover may be ultimately limited by insufficient safe sites (Urbanska, 1997).

Natural regeneration of native vegetation (passive restoration, Lamb and Gilmour, 2003) in disturbed areas may be facilitated by invading exotic species (De Pietri, 1992; Quinos et al., 1998; Otsamo, 2000; Lugo, 2004; Tecco et al., 2006; Williams et al., 2006; Yang et al., 2009). Since frequently they are the only abundant species in disturbed environments, exotic trees and shrubs could be used as nurse plants during the first stages of restoration projects (Ewel and Putz, 2004). This does not involve the planting of exotic shrubs, but only their use when they are dominant in the restoration areas and native nurse plants are not available (Becerra and Montenegro, 2012). Positive interaction could be considered for restoration purposes, assuming that in the long term

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native woody species would replace the nurse shrub, due to shading (McAuliffe, 1984; Valiente-Banuet et al., 1991) as is mentioned for *Rosa rubiginosa* by Damascos (2008).

Becerra and Montenegro (2012) found that the plants growing under exotic and native nurse species studied in arid areas were mainly shade tolerant species. However, saplings of heliophilous exotic woody plants may be the most abundant species protected by the nurse plant in disturbed temperate areas (Tecco et al., 2006).

Disturbed areas of the Andean Patagonian forest in Argentina are invaded by the exotic species *R. rubiginosa* L. (Rosaceae), a deciduous fleshy-fruited shrub which forms extensive shrublands (Damascos and Gallopín, 1992; Zimmermann et al., 2011). Eradication of this species would be costly and labor-intensive, as demonstrated for two other species of the genus *Rosa* with similar traits (Loux et al., 2005; Isermann, 2008). De Pietri (1992) determined that natural regeneration of native species under this thorny shrub occurs by vegetative resprouting of remaining roots or by seeds from nearby *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri (Cupressaceae) forest species. However, the pronounced rainfall gradient occurring in the Andean Patagonian region along 80 km determines the presence of different forest types (Mermoz et al., 2000) and consequently plant regeneration under the exotic shrub would differ between wet and mesic regions and forest types. In addition to natural regeneration of native vegetation in these different regions, the exotic shrub would promote the recruitment of other exotic species. Finally, survival of planted saplings of native species would differ between wet and mesic regions.

The aim of this work was to study the nurse effect of *R. rubiginosa* on different spatial scales. We compared abiotic conditions and natural plant recruitment under and outside the exotic shrub. As *R. rubiginosa* is a deciduous shrub with a short leaf turnover we compared the nitrogen content in mature and senescent leaves and the soil nutrients under and outside the shrub canopy. Since *R. rubiginosa* grows in mesic and wet areas we analyzed the regional differences in natural species regeneration and the survival of planted saplings of the more frequent native forest species under and outside the exotic nurse plant.

The specific hypotheses tested were: (1) *R. rubiginosa* would reabsorb foliar N before fall, and therefore would not alter soil nitrogen content; (2) with regard to positive effects of the nurse shrub, the recruitment of native species in *R. rubiginosa* shrublands would occur in particular under the shrub canopy where plants evade higher radiation and have greater water availability; (3) passive restoration would be greater in terms of species richness and abundance in mesic shrublands than in those of the wet region; (4) plants protected by the nurse shrub would grow more in height in shrublands with higher rainfall; (5) the nurse plant environment would not favor exotic species recruitment because these are mainly shade intolerant species; and (6) the survival and vigor of planted native species saplings would be higher under the nurse plant than in the open areas next to shrubs and the differences between open and shrub microsites would be more pronounced in the shrublands of the mesic than in those of the wet region.

2. Methods

2.1. Study area

The study was carried out in *R. rubiginosa* shrublands present in disturbed forest areas of the Nahuel Huapi and Lanín National Parks and in the surroundings of Bariloche city, Patagonia. The climate is temperate cold and the mean annual temperature is 8.4 °C (Ezcurra and Brion, 2005). Mean annual precipitation decreases along a west–east gradient (Barros et al., 1983; Ayesa et al., 2002) mostly occurring during winter (May–September). The plant growth period coincides with the dry season (spring and summer), when plants use mainly soil water. Soils are formed from volcanic ash and pyroclastic materials (Mermoz et al., 2000). The altitude varies between 610 and 869 m.a.s.l. (Appendix I). *Nothofagus dombeyi* (Mirb.) Oerst (Fagaceae) forests are dominant in the wet region while *A. chilensis* forests or mixed forests of *N. dombeyi* and *A. chilensis* are present in the mesic region (Mermoz et al., 2000). Forests in the latter region are generally distributed on north-facing slopes receiving high radiation (Kitzberger et al., 2000).

Forest disturbed by clearing, fires, and livestock grazing are invaded by the exotic shrub *R. rubiginosa*. This species was introduced into Argentina at the beginning of the 20th century and forms extensive thickets by vegetative multiplication in forest and steppe (Damascos and Gallopín, 1992). Herbaceous species, especially Poaceae, grow around *R. rubiginosa* plants.

We studied 12 *R. rubiginosa* shrublands; six located in degraded areas of the mesic region and six in the wet region. The mean seasonal rainfall values of the shrublands studied were estimated using regional maps (Barros et al., 1983), revealing that summer values were indeed significantly lower (Student *t* test, $p < 0.001$) in the mesic (121.43 ± 10.10 mm) than in the wet (166.67 ± 10.54 mm) region. Autumn (M: 600.00 ± 53.45 mm, W: 666.67 ± 42.16 mm), winter (M: 485.72 ± 40.40, W: 533.00 ± 21.08 mm), and spring values (M: 185.71 ± 21.03, W: 200 mm) were similar in both regions.

Only *R. rubiginosa* canopy area (calculated using the average of two perpendicular diameters) and plant volume (determined from plant height and two perpendicular diameters) measured in ten plants per shrubland for the 12 studied shrublands differed (Mann–Whitney test, $p = 0.039$) between mesic and wet regions. *R. rubiginosa* plants in the wet region had greater canopy area (6.64 ± 1.26 m^2) and volume (40.74 ± 10.11 m^3) than plants in the mesic region (3.18 ± 0.45 m^2, 17.75 ± 3.35 m^3, respectively). Plant height (W: 2.65 ± 0.14 m^2, M: 2.31 ± 0.09 m^2) was similar ($p = 0.168$) in plants of both regions.

The presence of horses and cows was observed in 83% and 67% of shrublands of wet and mesic regions, respectively.

2.2. Experimental design

In all 12 shrublands we studied two microsites associated with the nurse plant. The area under the canopy of the *R. rubiginosa* thicket (hereafter plant) was defined as shrub microsite (SM) and was extended 50 cm inside the plant from the outer edge of its canopy. The open interspace (open microsite, OM) was located at least 1 m from the external edge of the plant canopy. Samples were paired. Each *R. rubiginosa* plant represents one SM and has one associated OM.

Micro environmental characteristics in SM and OM were exemplarily analyzed in one mesic shrubland. Photosynthetic active radiation (PAR) was measured in the SM and OM of ten randomly selected *R. rubiginosa* plants during one summer day with a Li-250A Light Meter (Li-cor, USA).

Soil samples for moisture determination were collected in October (spring), January (summer), May (autumn) and August (winter) in the SM and OM of ten *R. rubiginosa* plants. Four soil subsamples per microsite were collected in the SM and OM of each nurse plant and pooled by microsite per plant. Soil samples were weighed and stove dried at 105 °C until constant weight was reached, and then stored in a desiccator. The same method of sampling was used to obtain soil samples of the SM and OM of four plants for chemical determination. Soil samples were air dried and sieved through a 2 mm mesh. Following Blakemore et al. (1981) and Sparks et al. (1996) the following analyses were conducted in each sample: (a) pH in water (soil: water 1:2.5) and (b) extractable P in 0.5 M $NaHCO_3$ at pH 8.4 (soil solution 1:20). Total soil C and N content was determined with a CN analyzer (Flash EA 1112 Thermo Electron Cop.). In the same shrubland, 50 mature and 50 senescent leaves of three *R. rubiginosa* randomly selected plants were collected in summer and autumn, respectively. Leaf samples were dried at 60 °C until constant weight was reached and then stored in desiccators. Total N and C content were determined as described above in mature and senescent leaves.

To study natural plant regeneration at different microsites, one 100 × 100 m plot was delimited in each one of the 12 *R. rubiginosa* shrublands (six per region) and a 50 m transect was marked in the plot. Ten random points were determined on the transect and the *R. rubiginosa* plant closest to each point was selected. We recorded woody (native and exotic) species present in the SM and OM of ten *R. rubiginosa* selected plants per shrubland and measured the height of each sapling up to 2.5 m.

Sapling planting was conducted in four of the 12 shrublands (two in each climatic region). Inside each shrubland, saplings were planted under the canopy of five *R. rubiginosa* plants (SM) and in the five paired OM.

The woody species planted and sapling numbers were selected according to their abundance in the undisturbed forests (data from Damascos, 2005). We chose the three most frequent species in each forest and the proportion 3:1:1 for the total native species saplings (5 individuals) planted at each microsite, three saplings of the most frequent species and one of each of the two species following in abundance. The distance between sapling in each microsite was 50 cm. In the two shrublands of the mesic region the species planted were: *A. chilensis*, *Maytenus boaria* Molina (Celastraceae) and *Schinus patagonica* (Phil.) I.M. Johnst. (Anacardiaceae) while in the wet region saplings of *N. dombeyi*, *M. boaria* and *A. chilensis* (Molina) Stuntz (Elaeocarpaceae) were planted. Saplings (less than 30 cm in height) of these native species were dug out in forests situated near *R. rubiginosa* shrublands and planted during autumn (April 2007). One month after sampling we monitored the sampling sites and determined the absence of sapling mortality due to transplant. Nine months after planting we registered: (i) planted sapling survival, (ii) main shoot meristem persistence or main shoot mortality and basal resprouting, reviewing each planted sapling in each microsite, and (iii) plant mortality due to drying out (presence of fully dried stems and leaves) or herbivory (absence of the planted individual).

2.3. Data analysis

All data were analyzed with the statistical software R Development Core Team (2009). Soil moisture, soil chemical and PAR variables were compared between microsites using the Paired *t* test. Nitrogen, C and C:N relationship of mature and senescent *R. rubiginosa* leaves were analyzed with the Student *t* test.

Because saplings were found only in the SM, floristic analyses are referred to only in relation to this microsite. The mean number of saplings and height of native species present in the SM of *R. rubiginosa* were compared between shrublands of mesic and wet regions using the Mann–Whitney test.

The chi square (X^2) or the Fisher Exact tests were used to compare the two climatic regions with respect to the height class distribution of different plant species growing by natural regeneration in the SM.

We used the Sorensen coefficient to compare floristic composition of species present at microsites between: (a) shrublands of mesic and wet regions and (b) shrub microsite (present study data) and undisturbed *A. chilensis* and *N. dombeyi* forests (data from Damascos, 2005).

The numbers of species and individuals growing in 0.25 m^2 of the SM (calculated using the values of the nurse plant canopy area) were compared between climatic regions using the Mann–Whitney test.

The Pearson Product Moment Correlation was used to analyze: the dependence between (1) the number of species or individuals and the nurse plant volume and (2) the height of native species and those of the nurse plant.

With a two-way ANOVA we compared the number of surviving saplings (pooled species data) between microsites and regions. The survival of planted saplings of each species was compared between microsites in each climatic region using the Wilcoxon test.

The percentage of planted saplings: (a) surviving with apical meristem persistence, (b) surviving with basal resprouting, (c) dead due to drying out, and (d) dead due to herbivory were compared between shrublands and microsites and between microsites and regions using two-way ANOVAs.

3. Results

3.1. Abiotic microsite characteristics and nutrient content of R. rubiginosa leaves

PAR was 30% lower ($n = 10$ plants, $p < 0.001$) in the SM (82.20 ± 16.51 μmol m^{-2} s^{-1}) than in the OM (305.00 ± 34.50 μmol m^{-2} s^{-1}),

Differences in soil chemical characteristics (pH, P, N and C) were found to be non-significant between microsites (Table 1). The C:N relationship was higher in SM than OM (Table 1). Soil moisture was higher in the SM than the OM during spring ($p = 0.001$), while during other seasons it was similar at both microsites.

The percentages of N and C in *R. rubiginosa* mature leaves were higher than in senescent leaves while the latter had a higher C:N ratio than mature leaves (Table 2).

3.2. Microsites and regional differences in natural species recruitment

Native species dominated the SM (Appendix II) but were absent in the OM (data not shown). Exotic shrubs and trees also found only in the SM represented 15% (wet region) and 17% (mesic region) of all species surviving under *R. rubiginosa* (Appendix II). Under the nurse plant grew 1–6 native and 1–2 exotic species (Fig. 1). The frequencies of nurse plants with native species varied from 45% to 70% while exotics were present in 5–15% of nurse plants (Fig. 1). Similarity of native species composition in the SM between shrublands of the two climatic regions was 61%. These species represent 25% (mesic region) and 40% (wet region) of the native species belonging to these undisturbed temperate forests.

The mean individual number of each native species growing in SM was similar in both climatic regions (Table 3). Native species number and density of individuals (in 0.25 m^2 of nurse plant) were lower in the mesic than in the wet region (Table 4). A positive cor-

Table 1
Soil mean (±SE) values for pH, carbon (C), nitrogen (N), phosphorous (P), C:N ratio and the seasonal variation of soil water content under the canopy of *R. rubiginosa* (SM = shrub microsite) and the open microsite (OM) measured in one shrubland of the mesic region. *p* = associated probability, Paired *t* test. Bolded values indicate *p* < 0.05.

Abiotic soil conditions	SM	OM	(*p*)
Soil chemistry[a]			
pH	6.30 ± 0.07	6.25 ± 0.06	0.731
C (%)	6.28 ± 0.59	6.96 ± 0.62	0.304
N (%)	0.42 ± 0.04	0.50 ± 0.04	0.155
P (mg kg^{-1})	3.62 ± 0.41	5.02 ± 0.42	0.175
C/N	14.73 ± 0.11	13.84 ± 0.24	**0.034**
Water content (%)[b]			
Spring	28.20 ± 3.26	23.5 ± 3.91	**0.001**
Summer	12.30 ± 1.42	9.92 ± 0.85	0.054
Autumn	25.92 ± 0.63	24.98 ± 0.75	0.216
Winter	32.86 ± 1.63	33.06 ± 1.55	0.929

[a] Soil samples ($n = 4$ plants).
[b] Soil moisture ($n = 10$ plants).

Table 2
Mean (±SE) values of carbon (C), nitrogen (N) and C/N ratio for mature and senescent leaves of *R. rubiginosa* measured in one shrubland of the mesic area. p = associated probability, Student t test. Bolded values indicate $p < 0.05$.

	Mature leaves	Senescent leaves	(p)
C%	46.98 ± 0.22	44.75 ± 0.55	**0.019**
N%	2.38 ± 0.09	1.45 ± 0.01	**0.002**
C/N	19.75 ± 0.67	31.16 ± 0.67	**0.011**

relation was determined for the relationships between the number of native species ($r = 0.499$, $p < 0.001$) or individuals ($r = 0.417$, $p < 0.001$) and the nurse plant volume in the mesic region. In the wet region correlation of these variables was not significant (species number, $r = 0.005$, $p = 0.690$; individual number, $r = 0.182$, $p = 0.165$).

Only saplings of *L. hirsuta* and *A. chilensis* differed in height between regions (Table 3). Native and exotic species plants smaller than 25 cm in height were the most frequent in the SM (Fig. 2). In the mesic region the height of native species correlated positively with nurse plant height ($r = 0.499$, $p = 0.001$), while in the wet region this relationship was negative ($r = -0.368$, $p < 0.001$).

3.3. Sapling survival and vigor after planting

Survival of planted saplings was higher in the SM than the OM ($p < 0.001$) and similar between studied regions ($p = 0.267$, Fig. 3). Saplings of the trees *A. chilensis* and *M. boaria* planted in the mesic region survived only in the SM (Fig. 4). Furthermore, the shrubs *S. patagonica* (mesic region) and *A. chilensis* (wet region) showed higher survival values in the SM than in the OM ($p = 0.016$ and $p = 0.022$, respectively, Fig. 4). In contrast, *N. dombeyi* ($p = 0.500$) and *M. boaria* ($p = 0.500$) planted in wet region shrublands exhibited similar survival in both microsites (Fig. 4).

The percentage of surviving saplings showing main shoot apical meristem persistence was higher ($p < 0.001$) in the SM than in the OM but did not differ ($p = 0.666$) between regions (Fig. 5). The saplings with main shoot mortality and basal resprouting exhibited similar frequencies independently of microsites ($p = 0.184$) and regions ($p = 0.099$). The dead dry saplings were more frequent in OM than in SM ($p = 0.004$) and under mesic than wet conditions ($p = 0.016$), while mortality due to herbivores was higher only in the latter region ($p = 0.004$, Fig. 5). In all comparisons interaction was not statistical significant (data not shown).

4. Discussion

4.1. Natural species regeneration under the exotic nurse plant

Invasive exotic species may play a positive role in the restoration of degraded forest areas, protecting native plants (Ewel and Putz, 2004; Lugo, 2004; Fischer et al., 2009). Despite harsh environmental conditions in *R. rubiginosa* shrublands in comparison with

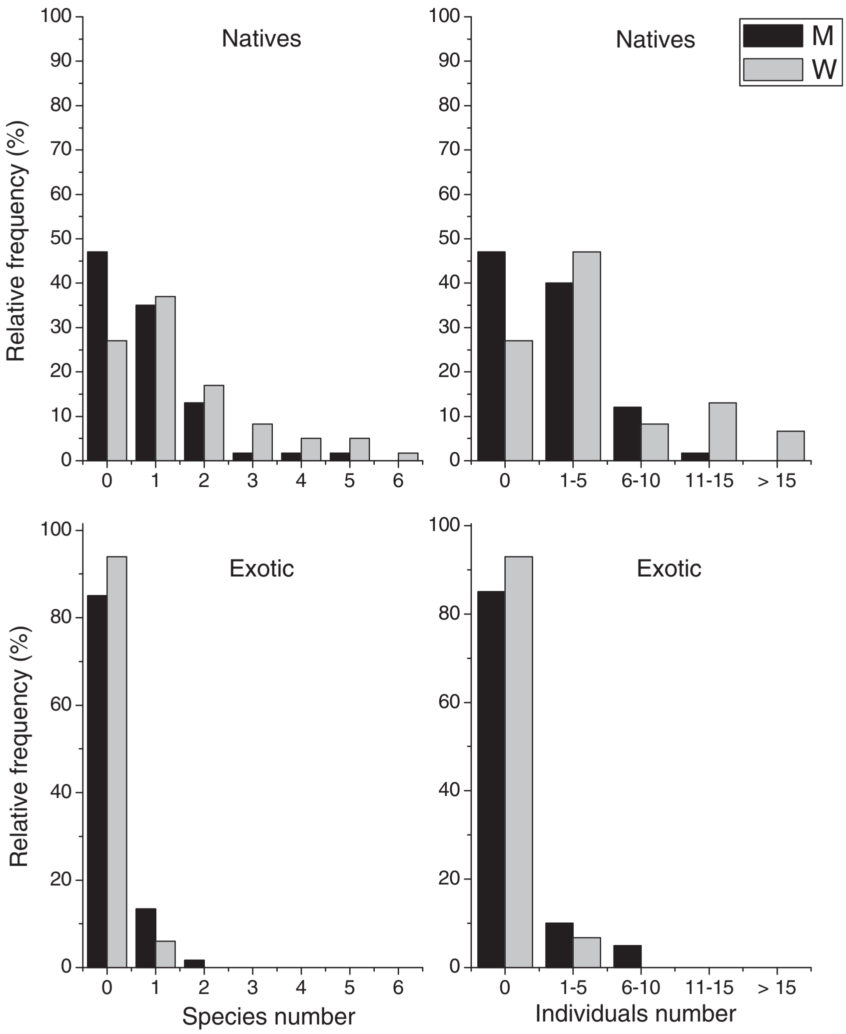

Fig. 1. Relative frequency (%) of native and exotic species and individuals of these species growing under *R. rubiginosa* in shrublands of the mesic (M) and wet (W) regions.

Table 3
Mean (±SE) values for sapling number and height (m) of the native and exotic species growing under the nurse plant in *R. rubiginosa* shrublands of the two climatic regions studied. M: mesic region; W: wet region. *p* = associated probability, Mann–Whitney test. Numbers in brackets are the number of individuals used to calculate the mean height of saplings of each species. Bolded values indicate $p < 0.05$.

Species	Sapling number			Sapling height (cm)		
	M	W	*p*	M	W	*p*
Native						
Schinus patagonica	0.11 ± 0.06	0.25 ± 0.10	0.310	0.61 ± 0.32 (7)	0.57 ± 0.14 (15)	0.481
Maytenus boaria	0.43 ± 0.10	1.80 ± 0.96	0.937	0.38 ± 0.10 (26)	0.74 ± 0.48 (107)	0.742
Lomatia hirsuta	0.25 ± 0.21	0.60 ± 0.26	0.310	0.17 ± 0.02 (13)	0.72 ± 0.14 (36)	**0.001**
Berberis microphylla	0.40 ± 0.27	0.61 ± 1.24	0.093	0.80 ± 0.14 (24)	0.52 ± 0.08 (37)	0.199
Aristotelia chilensis	0.42 ± 0.25	0.17 ± 0.13	0.394	0.23 ± 0.05 (25)	0.15 ± 0.10 (10)	0.635
Berberis darwinii	0.06 ± 0.06	0.38 ± 0.17	0.240	0.66 ± 0.32 (4)	0.45 ± 0.10 (23)	0.453
Austrocedrus chilensis	0.15 ± 0.13	0.23 ± 0.12	0.310	0.49 ± 0.11 (19)	0.35 ± 0.17 (14)	**0.011**
Maytenus chubutensis	0.03 ± 0.03	0.17 ± 0.11	0.589	0.06 (2)	0.26 ± 0.08 (10)	–
Myoschilos oblongum	0.03 ± 0.02	–	–	1.45 ± 0.25 (2)	–	–
Baccharis linearis	0.03 ± 0.03	–	–	0.75 ± 0.25 (2)	–	–
Nothofagus dombeyi	–	0.62 ± 0.30	–	–	0.26 ± 0.03 (37)	–
Escallonia virgata	–	0.01 ± 0.02	–		0.21 (1)	–
Nothofagus antarctica	–	0.01 ± 0.02	–	–	0.50 (1)	–
Exotic						–
Crataegus monogyna	0.50 ± 0.20	–	–	0.18 ± 0.05 (30)	-	–
Cotoneaster franchetii	0.01 ± 0.02	–	–	0.50 (1)	-	–
Pinus ponderosa	–	0.06 ± 0.05	–	–	0.65 ± 0.11 (4)	–
Acer pseudo-platanus	–		–	–	0.26 ± 0.04 (13)	–

Table 4
Number (mean ± SE) of native species and saplings growing under *R. rubiginosa* plants in shrublands of mesic (M) and wet (W) regions. Data calculated for 0.25 m^2 of *R. rubiginosa* plant canopy. *p* = associated probability, Mann–Whitney test. Bolded values indicate $p < 0.05$.

Number	Shrublands		(*p*)
	M	W	
Species	0.10 ± 0.02	0.32 ± 0.09	**0.031**
Individuals	0.25 ± 0.07	0.64 ± 0.13	**0.004**

the forest environment, natural regeneration of woody native trees and shrubs does occur under the studied exotic nurse plant in different climatic regions. The absence of native and exotic species saplings in the open microsite next to the nurse plant may be explained by differences in abiotic conditions and high herbivory. Low radiation and high soil moisture during the plant growing period (spring) are the main variables facilitating plant recruitment under *R. rubiginosa*. These results were also found for other native (Tielbörger and Kadmon, 2000; Puerta-Piñero et al., 2007; Gómez-Aparicio et al., 2008) and exotic (Quinos et al., 1998; Otsamo, 2000; Lugo, 2004; Tecco et al., 2006; Williams et al., 2006; Yang et al., 2009) nurse plants.

The soil nutrient content could increase under the exotic nurse plant (Ehrenfeld, 2003; Lugo, 2004) or not show significant differences in comparison with the surrounding environment (Vanderhoever et al., 2006). In the *R. rubiginosa* shrubland, the absence of differences between microsites in most of the soil chemical variables studied may imply similar organic matter input by leaves of the deciduous nurse plant as by herbaceous vegetation into the OM, balancing the nutrient supply between microsites. Another factor explaining the similarity in the soil nitrogen content between microsites is the resorption of this element by the *R. rubiginosa* leaves before autumn. Nitrogen resorption was also determined for other exotic species, such as *Lonicera makii* in its invasion area (Demars and Boerner, 1997) and *R. canina* in its native area (Ammar et al., 2010), and is also frequent among native deciduous species of Patagonian forests where nitrogen content is a limiting factor (Diehl et al., 2003). On the other hand, soils with low C:N ratio have high organic matter decomposition and mineralization (Melillo et al., 1982). In the SM the soil C:N ratio was significantly higher than in the OM, indicating a greater structural C contribution from the nurse plant leaves under its canopy than those incorporated into the OM by herbaceous vegetation. Both microsites are colonized by different biological forms in terms of structural C content which affects the instantaneous C:N rate. Since nutrient soil values for both microsites are similar to those determined by Satti et al. (2003) for well-conserved *A. chilensis* forests, the shrubland soils are favorable for natural plant regeneration.

Native woody species (mostly trees) growing in the SM have the highest frequency in the undisturbed temperate forests (Damascos, 2005). They are pioneer native plants, frequent in different communities along the regional climatic gradient and tolerant to varying light conditions (Damascos, 2005), which initiate the passive restoration of forests in disturbed areas previously invaded by *R. rubiginosa*. The native flora growing in shrublands of mesic and wet regions is similar, but in the latter region the floristic similarity with the vegetation of the undisturbed forest, the native species richness and abundance under the nurse plant are higher than in the mesic area. Contrary to our expectations, these results imply that in relation to passive plant restoration, *R. rubiginosa* would not have a greater facilitation effect on plant growth in the mesic, more stressed region, than in the shrublands of the wet region, even though the mean number of species was similar in undisturbed forests of both regions (Damascos, 2005). Tielbörger and Kadmon (2000) also reported higher native species facilitation with increasing precipitation conditions. Considering floristic similarity between shrublands of both regions, seed dispersion from near forests may also be similar, but in the *R. rubiginosa* shrublands of the wet region, the absence of water stress could allow higher germination and survival of native species and individuals under the nurse plant, independently of its volume. In the mesic region plant mortality may be higher, and species richness and abundance depend on nurse plant canopy size, evaluated here by volume. Considering that livestock grazing is more frequent in shrublands of the wet region, and environmental conditions are more moderate, we think that nurse plant facilitation there is mainly against herbivores, while in the mesic region nurse plant facilitation is against plant desiccation.

In shrublands of both studied regions, saplings less than 25 cm in height are the most frequent in the SM, showing high initial plant recruitment. However, the long-term survival of these individuals is not assured. Analysis of plant height class distributions may allow the determination of mean values for species growing

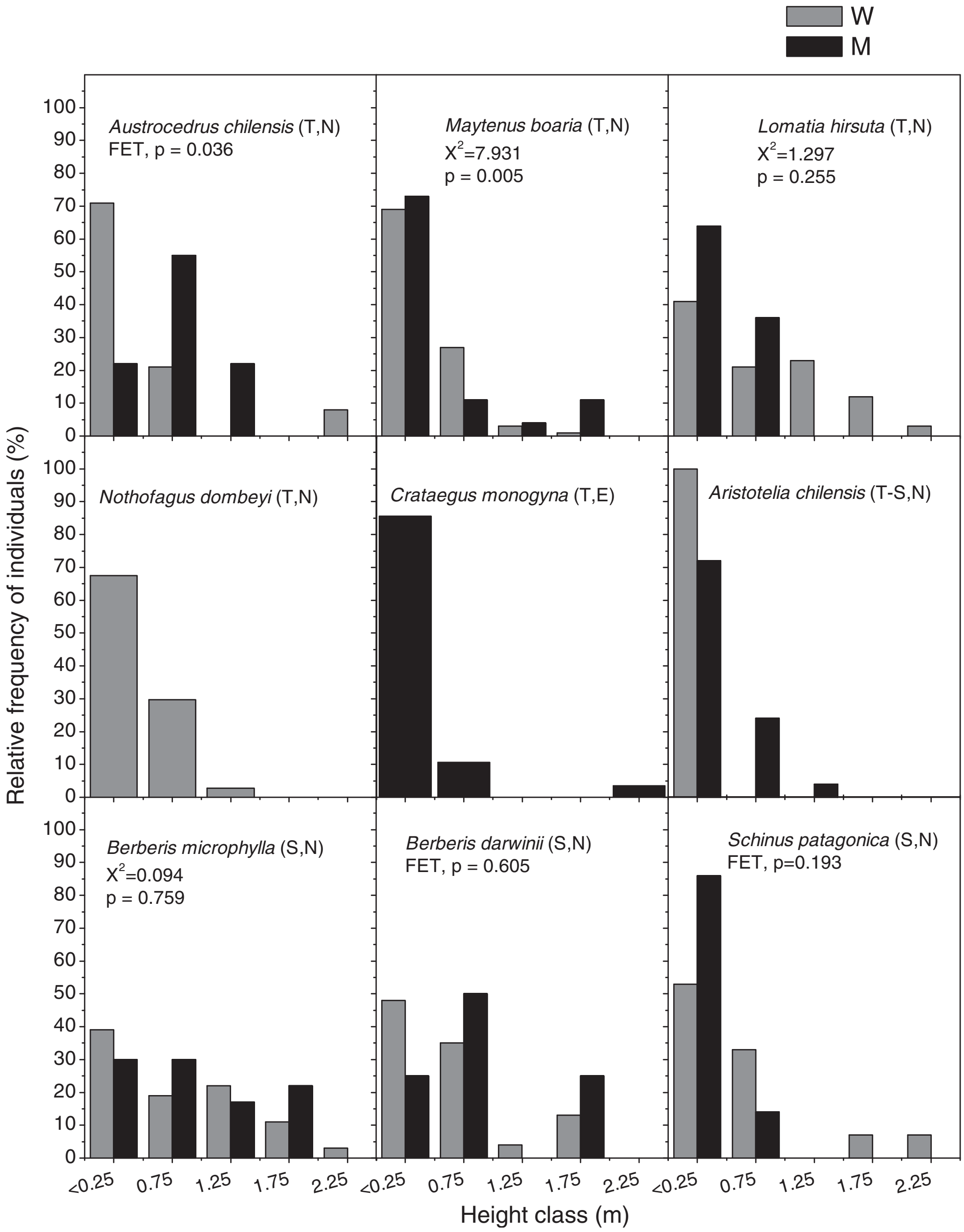

Fig. 2. Different height classes of tree (T) and shrub (S) individuals of eight native and one exotic (E) species growing under the *R. rubiginosa* canopy in shrublands of the mesic (M) and wet (W) regions. *p* = associated probability, X^2 = Chi square test, EFT = Exact Fisher test.

under *R. rubiginosa* canopy or growing among its branches, and is a suitable tool for the selection of target species for restoration. Young trees present in the SM do not all exhibit the same pattern in terms of height growth. Although *L. hirsuta* shows similar distribution of height classes in both climatic regions, only in shrublands of the wet region do individuals reach heights of between 1.25 and 2.5 m, and it is possible that this species continues growing in the long term. *N. dombeyi*, the dominant tree in wet forest, grew up to 1.25 m under the nurse shrub. This tree regenerates in gaps and disturbed areas (Veblen, 1989) not requiring a nurse plant. However, in *R. rubiginosa* shrubland *N. dombeyi* grows mainly in the SM because it is protected against livestock grazing. Caccia et al. (2009) documented this escape from herbivores in *N. dombeyi* seedlings growing under the native species *Chusquea culeou* Dev. (Poaceae). However, the few *N. dombeyi* individuals present under *R. rubiginosa* may not survive due to the low light level, or they may survive with a change in architecture, restricting shoot development and increasing specific leaf area, as was documented by Calabria and Puntieri (2008) for saplings growing in shaded areas. *A. chilensis* and *M. boaria*, another two frequent tree species, grow more in height in the SM of the mesic region. They grow in different light environments but require a nurse plant in the early stages because they are stressed either by drought (*A. chilensis*, Rovere, 2000) or by herbivory (*M. boaria*, Raffaele and Veblen, 1998; Veblen et al., 1992). In addition, in the mesic region the relationship between the height of the native species and those of the nurse plant is positive, while in the wet region it is negative. This means that in the medium to long term they could compete by shading. As was indicated by Maestre et al. (2009), when climatic conditions are moderate the relationship between the nurse plant and the protected species is mainly one of competition. Fischer et al. (2009) indicated that with the structural change itself, one exotic

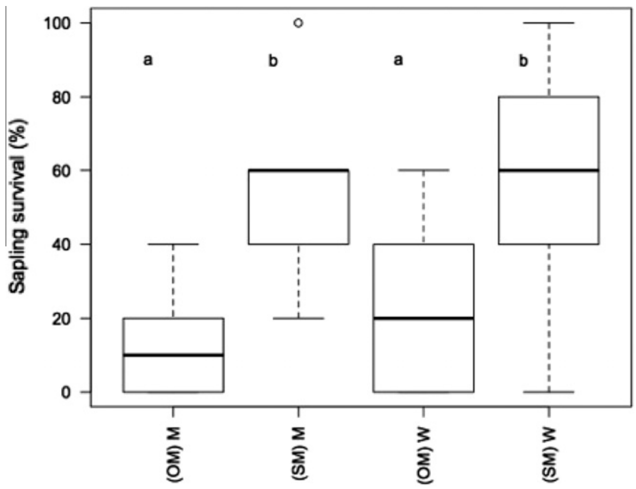

Fig. 3. Box plot of sapling survival in shrub (SM) and open (OM) microsites in shrublands of wet (W) and mesic (M) regions. Different letters indicate significant differences between microsites and regions (two-way ANOVA, $p < 0.001$).

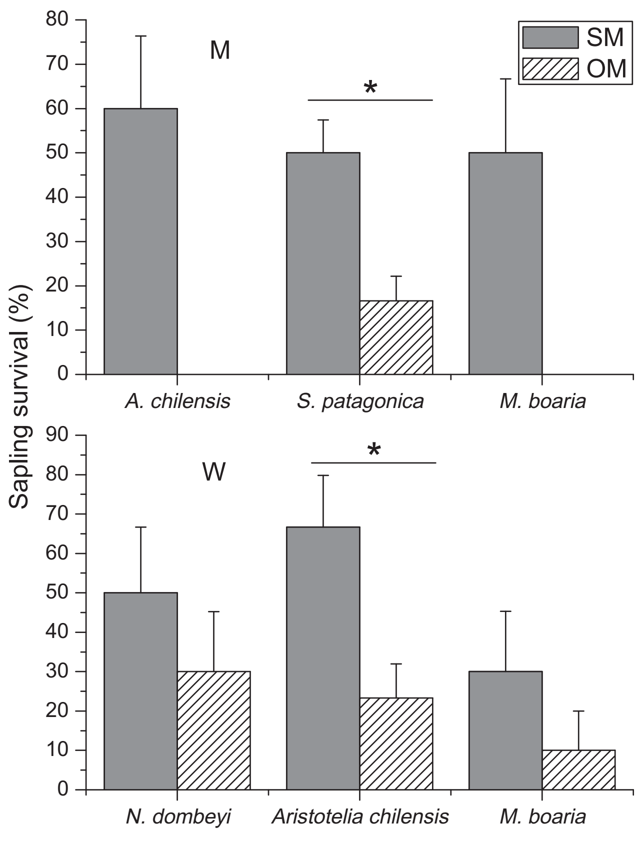

Fig. 4. Survival (%) of each of five native species saplings planted in the *R. rubiginosa* shrub (SM) and open (OM) microsites in shrublands of mesic (M) and wet (W) regions, compared using the Wilcoxon test. The symbol * indicates significant differences between microsites for species.

species would cause divergent effects. This will affect forest restoration carried out using exotic nurse plants and determine the need for different management practices according to environmental conditions. Ours results suggest that, particularly in the mesic region, the growth of the native species canopy could eliminate the nurse plant. In the wet region shrublands, control of the exotic shrub could be more difficult and should be carried out early in the restoration process.

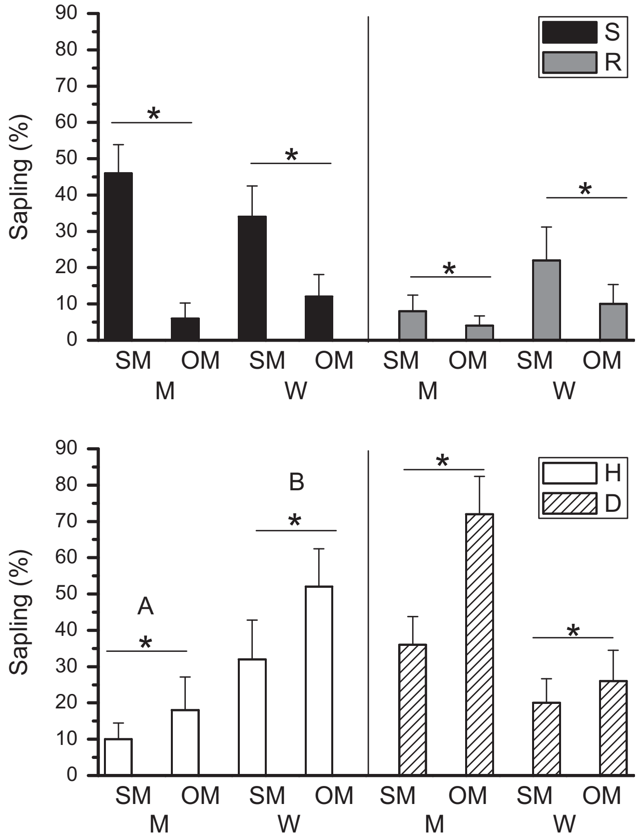

Fig. 5. Percentage of planted native species saplings surviving with persistence of the apical meristem on the main shoot (S), with only resprouted basal shoots (R), or dead due to herbivory (H) or drying out (D) in the shrub (SM) and open (OM) microsites in *R. rubiginosa* shrublands of mesic (M) and wet (W) regions. The symbol * indicates significant differences between microsites in the same region, while different letters indicate differences between regions.

One positive effect of restoration emerging from the present study is that other exotic woody species found in the SM have a low representation in relation to the total species richness and their presence under the nurse plant is also very low. Tecco et al. (2006) found a higher proportion of exotic fleshy-fruited than native species under one exotic shrub and the same richness of native and exotic species. Under *R. rubiginosa* the only frequent exotic species was *Crataegus monogyna*. Exotic trees and shrubs recorded under *R. rubiginosa* are shade-intolerant species; they do not need a nurse plant for initial recruitment but they do not grow in the OM because they suffer heavy grazing pressure and do not survive as well as native species. However, their presence and growth should be monitored because there are several examples where exotic plants cause long-term problems in restoration areas (Zavaleta et al., 2001; D'Antonio and Meyerson, 2002; Ranjan, 2008). Becerra and Montenegro (2012), studying natural regeneration under the exotic *Pinus radiata* recommend analysis of the potential for nurse plant elimination before using this strategy for forest restoration. This aspect has not yet been studied for *R. rubiginosa*.

4.2. Planting native species in R. rubiginosa shrublands

In disturbed areas the time required for restoration can be minimized, by making use of fast growing exotic shrubs that facilitate the regeneration of native species (Otsamo, 2000). The results of the present study show that one exotic species that has already invaded a disturbed area is a suitable nurse plant for planting native forest species. The main effect is evident on a microsite scale for most species studied. Planted saplings need a nurse plant and although the first-year individuals of some of the planted species also remain in the OM, irrespective of the climatic region, the survival difference between microsites is more marked in the mesic than in the wet region. When we consider sapling survival and vigor and discriminate between mortality causes, both survival and sapling resilience are higher in SM than in the open shrub interspaces of the mesic climatic region. In the latter region, the saplings of the dominant tree species (*A. chilensis*) survive only under the nurse plant while another very common tree (*M. boaria*), present in shrublands of both regions, did not survive without nurse plant protection when it was planted under mesic conditions but survived in both microsites under wet conditions. It is known that young *A. chilensis* up to 50 cm high show less water stress under a native nurse plant in comparison with open areas in xeric forests (Nuñez et al., 2009). Protection with respect to abiotic stress by a nurse plant would be more relevant than protection against herbivores (Gómez-Aparicio et al., 2008; Chaneton et al., 2010). This is observed among saplings planted in the mesic region. *N. dombeyi* shows similar mortality in both microsites because it suffers heavy grazing, perhaps by cattle and small vertebrates. In addition, *N. dombeyi* did not exhibit basal resprouting and depended exclusively on seed reproduction for plant recruitment (Veblen et al., 2003). *S. patagonica* also survives without the protection of the exotic shrub canopy because is a light generalist species (Damascos, 1998) common in disturbed areas, where it acts as a nurse plant (Raffaele and Veblen, 1998). Although *A. chilensis* suffers a high level of herbivory (Relva et al., 2010), its resprouting capacity enables it to survive in different microsites.

5. Conclusion

Preexisting *R. rubiginosa* shrublands invading disturbed areas could be sites of forest restoration since pioneer woody species regenerate naturally under the nurse plant. Because of its high light requirement, young plants of this and other exotic shrubs will not represent an initial source of competition for the naturally regenerating or planted woody species under the nurse plant. Differences in planted sapling mortality were more pronounced between microsites in the mesic than in the wet region. Although species responses depend both on environmental factors and endogenous species attributes, in the short term, most of the planted native species exhibit lower survival in the absence of the nurse shrub.

Forest restoration in areas previously invaded by *R. rubiginosa* can reduce the time required to obtain the first results and the mortality risk of planted species, especially in mesic regions where plants are protected from desiccation. In areas with moderate climatic conditions, facilitation against herbivores has positive initial effects but the nurse plant competes with taller native individuals and forest restoration would be dependent on effective control of the nurse plant biomass. Cattle exclusion and early cutting of the nurse shrub are required to allow growth of small saplings (lower than 25 cm). In both regions other exotic species would be well represented after the closure of restoration areas and the mechanical control of the exotic nurse plant.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.09.037.

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