

Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina

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Question: What are the effects of fire in native shrubland communities and in pine plantations established in these shrublands?

Location: Northern Patagonia, Argentina.

Methods: We surveyed four sites in Chall-Huaco valley, located in northwest Patagonia. Each site was a vegetation mosaic composed of an unburned *Pinus ponderosa* plantation, a plantation burned in 1996, and an unburned matorral and a matorral burned by the same fire. We recorded the cover of all vascular plant species. We also analysed species richness, total cover, proportion of exotic species, abundance of woody species and herb species, cover of exotic species, abundance of woody and herb species and differences in composition of species. For both shrubs and tree species we recorded the main strategy of regeneration (by resprouting or by seed).

Results: We found that fire had different effects on native matorral and pine plantations. Five years after fire, plantations came to be dominated by herbs and exotic species, showing differences in floristic composition. In contrast, matorral communities remained very similar to unburned matorral in terms of species richness, proportion of woody species, and herb species and proportion of exotics. Also, pine plantations were primarily colonized by seedlings, while matorrals were primarily colonized by resprouting.

Conclusions: Matorrals are highly fire resilient communities, and the practice of establishing plantations on matorrals produces a strong reduction in the capacity of matorral to return to its original state. The elimination of shrubs owing to the effect of plantations can hinder regeneration of native ecosystems. Burned plantations may slowly develop into ecosystems similar to the native ones, or they may produce a new ecosystem dominated by exotic herbs. This study shows that plantations of exotic conifers affect native vegetation even after they have been removed, as in this case by fire.

Keywords: Exotic species; Matorral; Pine plantation; *Pinus ponderosa*; Resilience; Resprouting.

Nomenclature: Correa (1969–1984).

Introduction

Exotic conifer plantations are an important part of the economy in several countries, but they are associated with negative impacts on natural communities (Richardson 1998). In recent years, the replacement of native communities by extended exotic monocultures has been criticized (e.g. Donoso Zegers 1993; Lara & Veblen 1993; Richardson 1998). Effects of these plantations are particularly detrimental in non-forest communities, since they can reduce natural biodiversity, change life-form composition, increase vegetational biomass, increase water consumption, and change fire dynamics (Armstrong & Van Hensbergen 1996; Jackson et al. 2005; le Maitre 1998; Richardson et al. 1994). Also, these monocultures can reduce soil sustainability (Michelsen et al. 1996; Frank & Finch 1997; Hofstede 1998), increase the risk of disease and fires (Richardson & Higgins 1998), invade native neighbouring ecosystems (Richardson et al. 1994; Simberloff et al. 2002, 2003), and generate local biodiversity loss when native biota cannot occupy these areas (e.g. Clout & Gaze 1984; Lebreton & Pont 1987; Hofstede 1998; Lindenmayer et al. 1999).

The effects of exotic conifer plantations on native communities in the southern hemisphere have been studied in Chile (e.g. Lara & Veblen 1992; Frank & Finch 1997) and in more detail in Australia, South Africa and New Zealand (e.g. Friend 1982; Fiembel & Fiembel 1996; Higgins & Richardson 1998; Richardson et al. 1994; Lindenmayer et al. 1999). However, in Argentina there are few studies on the impact of exotic conifer plantations on native communities (e.g. Raffaele & Schlichter 2001; Sarasola et al. 2006; Simberloff et al. 2002, 2003).

From 1970 onwards, plantations of several introduced tree species increased rapidly in northwestern Patagonia, Argentina (Schlichter & Laclau 1998). By 2001, 90% of the total area planted consisted of *Pinus ponderosa* (Anon. 2001). In this region there are presently ca. 50 000 hectares of plantations, but that figure is growing

rapidly, (Anon. 2001). Between 700 000 and 2000000 ha are considered suitable for such plantations in north-western Patagonia (Schlichter & Laclau 1998).

In northern Patagonian forests and shrublands (matorral), the most important ecological disturbance is fire (both natural and anthropogenic) (Veblen & Lorenz 1988). In this region, fire is the major determinant of vegetation structure and landscape pattern (Veblen et al 2003). Following burning of shrublands and xeric open forests, re-sprouting shrubs often dominate the post-fire regeneration, while regeneration of non-resprouting tree species is rare. The establishment of tree species is often facilitated by already established shrubs that operate as nurse plants (Raffaele & Veblen 1998).

The ecotone between forest and steppe consists of xeric open forests and shrublands (matorral communities) where many of the plantations are being established. In such areas in Patagonia, the Argentinean government and the World Bank aggressively promote planting exotic conifers (Olivera 2003). Ecotone areas are not protected as are most native forest zones, where legislation bans afforestation with exotic conifers. In addition, these highly flammable pines have been planted in areas that were formerly open woodland or steppe, where lack of fuel continuity was an important limitation to fire spread. Today, however, large areas of these exotic conifers have burned and/or created the potential for extensive crown fires in habitats formerly characterized only by surface fires (Veblen et al. 2003). However, the effects of fire on the regeneration of communities where exotic conifers have been introduced have not been studied.

The objective of this work is to study early post-fire successional changes in ecotone matorral areas in which native communities were partially replaced by exotic conifer plantations. We compare a series of sites with burned plantations and matorrals, and we also study unburned matorral communities and plantations to analyse possible trajectories of change. We expect changes in composition, structure and regeneration strategies after fire in plantations and matorrals, because afforestation largely consists of replacing native shrubland with a monoculture of an exotic tree species.

Study area

The study area is located ca. 1000 m above sea level in the Chall-Huaco valley (41°12' S and 71°20' W), 10 km from the city of San Carlos de Bariloche, Argentina. This valley is located in the ecotone between the humid Andean forest, with precipitation from 1000 to 3000 mm per year, and the Patagonian steppe, with less than 700 mm precipitation per year (Dimitri 1972).

In this valley, the dominant vegetation is northern Patagonian shrubland. This is a matorral community

(Raffaele & Veblen 2001) of *Schinus patagonicus*, *Diostea juncea*, *Nothofagus antarctica* and *Berberis buxifolia*. These species can reproduce vegetatively from root crown, trunk bases, or rhizomes. In this ecotone, dominant species of the Patagonian steppe, such as *Acaena splendens* and *Mullinum spinosum*, coexist with species that are abundant in the understory of the south American temperate forest, such as *Berberis darwinii* and *Alstroemeria aurea*, and vines such as *Mutisia spinosa* and *Loasa bergii*. This system is highly diverse compared to the surrounding areas.

These systems are open, tall (ca. 2.5 m) shrublands and in general form shrub clumps of varied size. They are usually found near human settlements and often highly disturbed by human activity. The primary disturbance is fire, followed by cutting of firewood, cattle ranching (Kitzberger & Veblen 1999; Raffaele & Veblen 2001), and, during the last three decades, planting of exotic conifers (Veblen et al. 2003; Schlichter & Laclau 1998). Young pines are planted inside the shrublands without removal of the native vegetation. However, pine plantations replace these systems as they grow (M.A. Nuñez & E. Raffaele pers. observ.).

Chall-Huaco valley has a rich fire history, but most of the fires occurred in the late 19th and early 20th centuries (Anon. 1996). In the austral summer 1996 Chall-Huaco valley had a large fire. This fire affected different types of communities: grasslands, pure forest of *Nothofagus pumilo*, *Pinus ponderosa* plantations, and matorrals (Anon. 1996). The fire was stopped and lasted 45 days. As a result a large part of the valley was burned. The total area affected included 395 ha of *Nothofagus pumilo* forest, 207 ha of grassland, and 676 ha of matorral communities and pine plantations. This fire affected 30 % of the valley area and produced distinct patches of burned and unburned vegetation (Anon. 1996). A list of the most abundant species and their relative abundance in the different studied systems is presented in App. 1.

Methods

Research design

We surveyed four sites in the Chall-Huaco valley. Each site was a vegetation mosaic composed of burned and unburned matorrals and ponderosa pine plantations (22 years old when the fire started). Surveys were conducted at the four sites, where each site was a block replicate and every block had four treatments (vegetation patches); i.e., each site had a burned ponderosa pine plantation and a burned matorral, and an unburned plantation and matorral. Each treatment (e.g. burned matorral) in each site was located in the same

aspect of the valley, and had similar slope. The soil type in the area is medium-textured udand (Anon. 1990).

In the four treatments in each site, during the austral summer of 2001 we surveyed five 9-m² plots in which we recorded the cover (%) of all vascular plant species. We also measured species richness, total plant cover, abundance of woody species and herb species, cover and richness of exotic species, and species composition. For both shrubs and tree species we recorded the main type of regeneration by digging into their root systems to see if they regenerated by resprouting or by seed.

Our experimental design consisted of a 2 × 2 factorial block arrangement in which vegetation type (plantation or matorral) and fire (burned or unburned) were the two main factors. Dependent variables included total understory plant cover, total species richness, herb species richness and cover, woody species richness and cover, percentage of plants regenerating by resprouting, and native and exotic species richness and cover.

Data analysis

Main effects of plantations and fire, as well as their interactive effects on the dependent variables, were assessed by factorial ANOVAs. We pooled data on the different variables by obtaining an average of the five 9-m² plots per site per treatment. Normality of the residuals between observed and predicted values of dependent variables was evaluated by using normal plots (Sokal & Rohlf 1995). We used SAS 9.1 for these analyses (Anon. 2003).

Multivariate community analyses were undertaken using the computer package PAST (Hammer et al. 2001) to assess an overall change in plant species composition. Analyses of similarity (ANOSIM) were used to establish if there were significant differences in plant composition among the four treatments and between the two burned treatments (burned matorral and plantation). ANOSIM produced an R-statistic that is an absolute measure of distance between the treatments (Parr et al. 2004). An R-value close to 1 indicates that communities are strongly distinctive, while a value close to 0 indicates communities cannot be differentiated. A P-value associated with this statistic quantifies the level of significance of the

results. The relationship between the different treatments is shown with a Non-metric Multidimensional Scaling (NMDS) ordination. Analyses were based on similarity matrices produced using the Bray–Curtis similarity measure to define a similarity coefficient between every pair of species (species ordinations) in terms of their varying abundances across all samples (Murray et al. 2006). All ordinations were run using 5000 iterations. For this analysis we used data from all the species (50 species total) and their cover in each site.

Results

Effects on community structure

Vegetation type and fire interacted by affecting several vegetation parameters. Plant cover, richness, herb and woody cover as well as numbers of woody and herb species were affected by the interaction of plantation and fire (Table 1). The dependent variables showing main effect differences are total plant cover and richness, richness and cover by life form (resprouting or seed), and richness and cover of native and exotic species (Table 1).

Richness and cover was similar in all treatments except for the unburned plantations where they were significantly lower (Fig. 1). In plantation plots, total plant cover and total richness increased from 0.4 to 100% and from 1 to 8 species/9 m², respectively, in burned plots compared with unburned plots ($P < 0.001$, Table 1 and Fig. 1 a, c). However, total cover and richness in matorral patches were similar between burned and unburned plots (Fig. 1).

There were large differences in herbaceous cover between burned plantation and burned matorral plots ($P < 0.0001$), with more herb cover in burned plantations compared to burned matorral plots (Fig. 1, Table 1). Notable differences in herb cover were found between the burned plantations with 96 % cover and the unburned plantations with just 0.33 % cover. A different pattern was observed in matorral plots, where the herb cover was similar (ca. 30 %) in both burned and unburned plots (Fig. 1b). Total herb richness did not differ significantly between burned and unburned matorral plots (Fig. 1e).

Table 1. F-values and significance level of 2 × 2 factorial ANOVAs for the effect of fire and vegetation types (plantations and matorrals) on species richness, total plant cover, herb cover, woody plant cover, number of herbs and number of woody species. NS = $P > 0.1$; * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.01$; df = 1.

	Species richness	Total plant cover	Herb cover	Woody plant cover	Number of herb species	Number of woody species
Vegetation type	30.9 **	80.75***	4.12*	263.7***	2.0 NS	83.9***
Fire	34.54**	28.56***	64.13***	21.7***	22.1 ***	5.77**
Veg. type * Fire	26.65**	113.51***	36.8***	40.21***	16.72***	4.19*

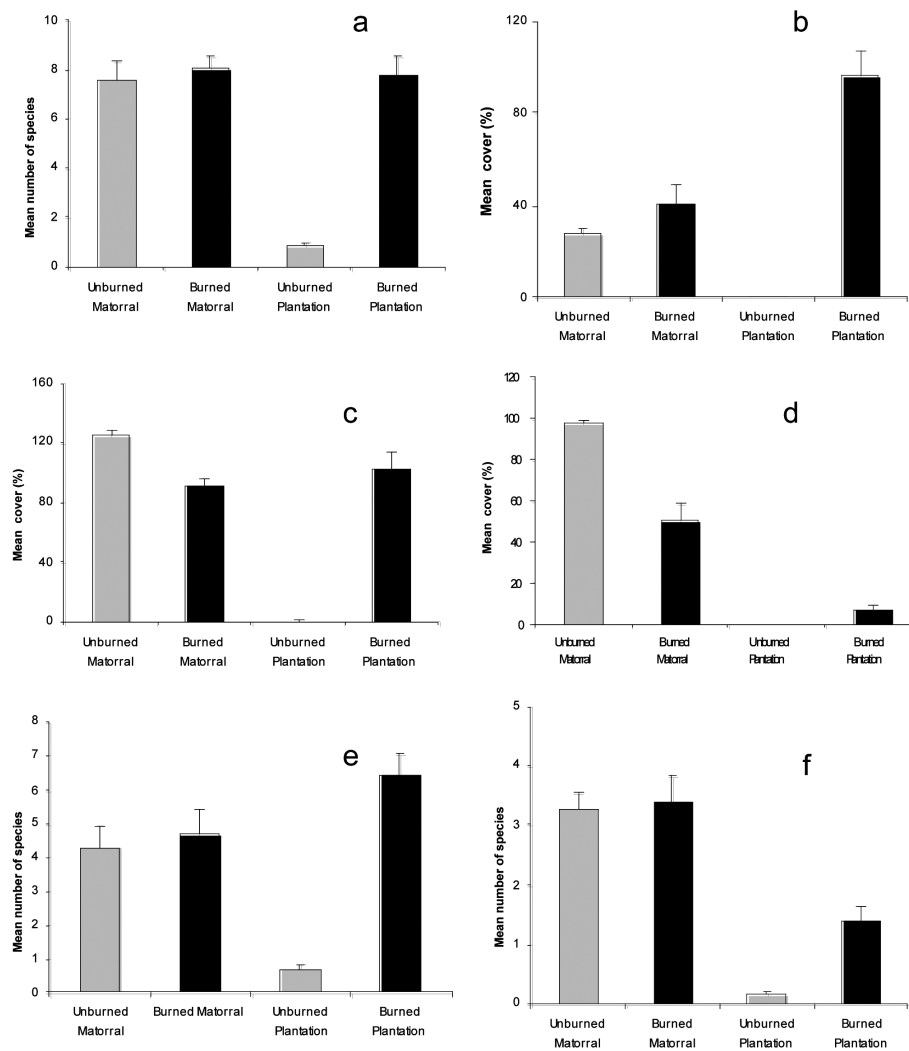


Fig. 1. Vegetation parameters in burned and unburned matorrals and burned and unburned pine plantations sites (\pm SE); (a) species richness, (b) cover by herbaceous species; (c) total species cover, (d) cover by woody species, (e) number of herbaceous species, and (f) number of woody species.

However, plantations showed significant differences (Table 1) in the mean number of species, with $0.7 (\pm 0.2$ SE) species in average in unburned plantation plots and $6.4 (\pm 0.9$ SE) species in burned plantation plots. Herb richness increased after fire in plantation plots, and mean richness was greater than in matorral plots ($P < 0.0001$, Fig. 1e).

The mean total cover by woody species was 97% and 50% in unburned and burned matorral plots, respectively, while in the unburned and burned plantations plots it was much lower: 0.04% (± 0.02) and 4% (± 2.1), respectively (Fig. 1d). We did not find individuals of ponderosa pine in our plots in the burned matorral and the cover of ponderosa pine in burned plantations averaged 0.5% over the four sites (App. 1). The number of woody species in the matorral plots was similar between burned and unburned plots, while in the plantation plots

the number of woody species was significantly greater in burned than in unburned plots (Fig. 1f, Table 1).

Richness of species of exotic and native plants differed significantly between matorral and plantation plots. Overall, the numbers of native species in unburned and burned matorral plots were very similar, while in plantations numbers of native species increased after fire (Fig. 2a, Table 2). Also, the mean cover of natives was higher in matorrals than in plantations (Fig. 2b). On the other hand, the number of exotic species showed different patterns depending on plantation and fire effects. The number of exotic plants was larger in burned plantation than in burned and unburned matorral plots, which reflects a strong influence of both effects, fire and plantation (Fig. 2, Table 2). Despite the fact that the number of native species was larger than the number of exotic species in burned plantations, cover of exotics was significantly

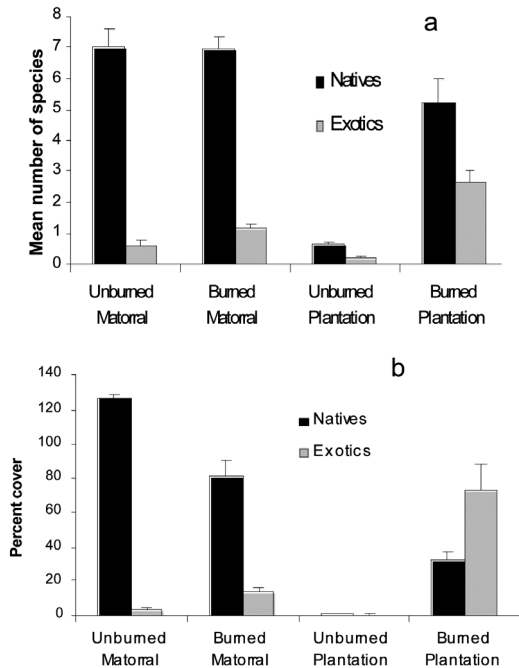


Fig. 2. Native and exotic species richness in burned and unburned matorrals and pine plantations sites (\pm SE). **a.** Mean number of native and exotic species in the different treatments. **b.** Cover (%) of native and exotic species.

larger than cover of natives, and burned plantations had the highest values of exotic cover among all treatments. Therefore, cover of exotics depends on both plantation and fire effects (Table 2).

The mean total value of resprouting cover versus non-resprouting cover was significantly different between matorral and plantation plots after fire ($P < 0.008$, $F = 33.33$, $df = 7$). The cover after resprouting was 64.9% (± 4.2) in burned matorrals and 3.6% (± 1.06) in burned plantations. Resprouting was the dominant type of regeneration in matorrals and seed the main type of regeneration in plantations.

Floristic analyses

ANOSIM revealed that there were significant differences between the treatments in terms of floristic composition. The R -value was 0.81 for the comparison among all the treatments (values close to 1 show differ-

ences between communities) with a P -value < 0.00001 . ANOSIM showed differences among burned communities with an R -value of 0.99 ($P < 0.023$). Fig. 3 shows the ordinations of the different systems, where matorrals (burned or unburned) occupy the same area and the other treatments occupied distinctive non-overlapping areas of the plot.

Discussion

The presence of fire and pine plantations affects matorral community structure in many different ways. We found that the effect of fire on early regeneration differs greatly between matorral communities and exotic conifer plantations established on matorral. The most important changes were observed in the structure of the community (i.e. changes in the proportion of life forms and species composition, increase in exotic species) and in the regeneration strategies. After five years, burned plantations changed from ponderosa pine monocultures to grasslands with a high proportion of exotics. On the other hand, burned matorrals changed in relatively few aspects compared with the unburned matorrals. Also, resprouting was the main type of regeneration in matorrals, and regeneration by seed was dominant in burned plantations.

These results could be due to several, not necessarily exclusive, causes. Some of these are (1) the unburned pine plantations eliminate the fire-resilient shrubs, and with them the possibility of fast regeneration by resprouting after fire. Loss of these shrubs could also reduce biotic resistance (*sensu* Elton 1958) of the ecosystems to the establishment of exotic species. (2) Loss of native resprouting shrubs below pines eliminates the possibility of colonization by resprouting after fire, with colonization inside the burned plantation restricted to seed-dispersed plants. And (3) soil characteristics could be different among the treatments because of previous differences or because of the greater amount of fuel in plantations than in the matorral, which could increase fire intensity, causing greater changes of soil properties in the burned plantations.

Fire in plant communities, as does most disturbances, often promotes invasion. However, fire effects are very

Table 2. F -values and significance level of 2×2 factorial ANOVAs for the effect of fire and vegetation type (plantations and matorrals) on the origin of the species (native and exotic) during early regeneration. NS = $P > 0.1$; * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.01$; $df = 1$.

	No. native species	No. exotic species	Cover native species	Cover exotic species
Vegetation type	46.35***	5.67**	183.9***	11.77***
Fire	14.81***	42.19***	1.44 NS	25.51***
Vegetation type * Fire	15.47***	16.92***	36.6 ***	14.25***

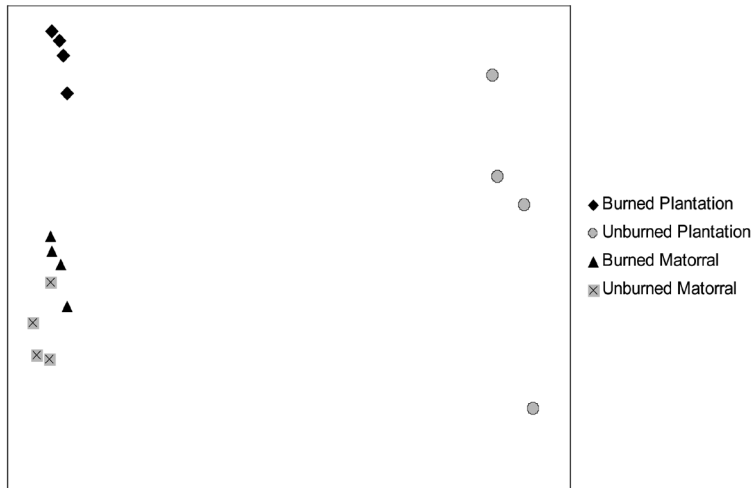


Fig. 3. Non-metric Multidimensional Scaling ordination of plant species in the four treatments. Burned and unburned matorrals tend to occupy the same sector in the graph while the other two treatments are found in different areas.

community-specific (D'Antonio 2000). Ponderosa pine is well adapted to fire and regenerates quickly after it, like the herbaceous vegetation that composes the understory of most ponderosa pine ecosystems, also after fire, these systems tend to be invaded by exotic plants (Agee 1998). In shrublands with a long evolutionary history with fire, like the Californian chaparral, fire tends to reduce the abundance of exotics (D'Antonio 2000). In our systems, we observed a small increment in the number of exotics in burned matorrals compared with unburned matorral communities, and a large increase of exotics in the burned plantations over unburned ones.

Matorral communities in northwestern Patagonia are well-adapted to regenerate by resprouting after fire (Veblen et al. 1997). This strategy permits this system to reach its pre-fire biomass and composition in a few years, giving this system an extraordinary resilience to this kind of disturbance (Bellingham 2000). Pine plantations eliminate this capacity and with it the natural resilience of this system after fire. The nurse plant syndrome has been reported in matorral communities, and particularly during early regeneration after fire (Raffaele & Veblen 1998). Thus, the results of the present study imply that where these shrub species disappear or decline in abundance because of pine plantations, the capacity of other species to regenerate is seriously impeded. Elimination of resprouting does produce changes in regeneration in the middle term, producing local extinction of some species. An extreme case of this effect is seen with the dominant species *Nothofagus antarctica*, which has very low seed viability (Premoli 1991) and which was not found inside plantations burned five years previously (App. 1). This situation could lead to a less diverse system in terms of woody species, owing to the limited capacity for seed dispersal of some matorral species.

The structural changes that plantations produce on na-

tive communities are important not only because of biodiversity losses but also because they affect recolonization processes after fire. These changes affect native species establishment, as well as possible successional trajectories during the recolonization process. These results demonstrate that five years after fire, matorral and ponderosa pine plantations have different communities. We can only speculate as to what future succession in these two different systems will look like. Probably the burned matorral will approximate mature matorral in the next few years. However, it seems unlikely that burned pine plantations will converge to mature matorral, since the plantations do not share many intrinsic characteristics of the matorral, such as low proportion of exotics, and a relatively high diversity and abundance of nurse woody species.

In summary, this study shows that plantations of exotic conifers induce significant changes in native communities where they have been established. This implies that establishment of plantations of exotics conifers can profoundly affect native communities while they are established and after they are removed, as in this case by fire.

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App. 1. Average percent cover of the most abundant species in the four treatments (\pm SE). Exotic species are denoted by an asterisk (*). Species not found in the study are denoted by a minus sign (-).

Species	Life form	Percent cover in the different treatments (\pm SE)			
		Burned matorral	Unburned matorral	Burned plantation	Unburned plantation
<i>Acaena splendens</i>	Herb	0.7 \pm 0.4	4.9 \pm 1.3	2.05 \pm 0.7	-
<i>Alstroemeria aurea</i>	Shrub	13.7 \pm 8.5	9.7 \pm 2.2	1.0 \pm 1	-
<i>Berberis buxifolia</i>	Shrub	3.7 \pm 1.3	12.3 \pm 5.1	-	-
<i>Carduus nutans</i> *	Herb	0.1 \pm 0.1	-	1.6 \pm 0.6	-
<i>Diostea juncea</i>	Shrub	18.1 \pm 4.4	23.5 \pm 7.1	1.97 \pm 1.2	-
<i>Discaria chacaye</i>	Shrub	0.15 \pm 0.15	5.8 \pm 4.1	-	-
<i>Elymus andinus</i>	Grass	-	0.95 \pm 0.55	1.5 \pm 1.42	-
<i>Epilobium glaucum</i> *	Herb	9.5 \pm 4.6	0.08 \pm 0.05	41 \pm 7.2	-
<i>Fabiana imbricata</i>	Shrub	-	-	1.87 \pm 1.3	-
<i>Geranium magellanicum</i>	Herb	1.25 \pm 0.3	1.2 \pm 0.9	8.6 \pm 2.5	0.17 \pm 0.05
<i>Maytenus chubutensis</i>	Shrub	0.75 \pm 0.57	0.17 \pm 0.05	0.1 \pm 0.1	0.04 \pm 0.03
<i>Mutisia decurrens</i>	Herb	1.5 \pm 0.7	9.7 \pm 2.2	2.15 \pm 1.5	0.07 \pm 0.04
<i>Nothofagus antarctica</i>	Shrub	10.6 \pm 4.1	35.9 \pm 9.0	-	-
<i>Oxalis valdiviensis</i>	Herb	0.56 \pm 0.38	-	1.8 \pm 1.5	-
<i>Pinus ponderosa</i> *	Tree	-	-	0.5 \pm 0.69	-
<i>Rumex acetosella</i> *	Herb	3.25 \pm 2.5	1.3 \pm 0.6	28.7 \pm 8.7	0.11 \pm 0.1
<i>Schinus patagonicus</i>	Shrub	8.5 \pm 1.1	8.5 \pm 1.0	0.26 \pm 0.2	0.05 \pm 0.05