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FACILITATION BY PIONEER TREES AND HERBIVORE EXCLUSION ALLOW
REGENERATION AND SUCCESSION OF WOODY SPECIES IN A SEMIARID
ECOSYSTEM

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Abstract

In semiarid ecosystems, pioneer nurse plants facilitate regeneration of woody species, however, colonization in open areas and under nurse tree canopy could be limited by the presence of herbivores. The goal of this study was evaluated the effect of cattle and rabbit exclusion and the *Acacia caven* on natural regeneration of woody species, in a seven-year experiment in two localities (Pirque and Peñuelas) of central Chile. Six exclosures and control areas were established in degraded savannas of *A. caven* close to sclerophyllous forest fragments, where sexual and asexual (resprouts) regeneration was sampled in plots located under the canopy of *A. caven* and in open sites. After seven years, species richness and abundance of plants of sexual regeneration (size 0.5-2m) was significantly greater within exclosures than in control areas. Species richness and abundance of both type of regeneration was greater Under *A. caven* than in open sites in both localities. In Peñuelas, abundance of asexually regenerated seedlings was significantly greater within exclosures than in control areas, in both localities. In no variable or locality some significant effect of the interaction between *A. caven* and exclosure was detected. Our results suggest that when cattle and rabbits are present, the use of exclosures may allow colonization of open sites and successional advance under canopy of *Acacia caven*. Instead, asexual regeneration does not seem to be importantly affected by herbivores, and hence it may contribute to recover this forest when exclusion of large surfaces is not possible.

Key words: facilitation, herbivory, recruitment, regeneration, resprouting.

1. Introduction

Native forest loss and degradation produced by human activity have become a major concern for many countries during the last decades (Monastersky, 2014), whereby many of them have been taking conservation and restoration actions (Chazdon & Guariguata, 2016; FAO & UNEP, 2020). Restoration processes in degraded forests are especially needed when recolonization by pioneer, mid or late-successional species is limited by human-related factors or this recovering is extremely slow (Vásquez-Grandón et al., 2018).

One of the main anthropic drivers limiting recovering of native forest has been the herbivory of introduced mammals, like cattle horses and the European rabbit (Nomiya et al., 2003; Fensham et al., 2011). In the long term herbivores may change the community of herbaceous and woody plants, and impede recovering of the ecosystem structure and functionality (Perrin et al, 2006; Hejmanová et al., 2010; He et al. 2011; Listopad et al. 2018). These long-term effects frequently are produced because of the impacts on regeneration. Plant regeneration is affected by herbivores mainly when recently germinated seedlings are trampled and/or browsed, which directly kills seedlings or reduces foliar area for photosynthesis and growth (Cooper & McCann, 2011; Etchebarne & Brazeiro, 2016; Hackworth et al., 2018). This process may randomly occur among species, or selectively, browsing on more palatable species (Harmer, 2001; Cooper & McCann, 2011; He et al., 2011; Etchebarne & Brazeiro, 2016). Other studies have shown that herbaceous species, many of them exotics, increase their cover and biomass when herbivores are excluded, competing and indirectly causing a decrease of woody native species regeneration (Laurent et al., 2017; Listopad et al., 2018). On the other hand, herbivores may alter the seed dispersal and germination processes (Williams & Ward, 2006), and some studies have observed that this may enhance the exotic weed establishment (Juan-Baeza et al., 2015; McGarvey et al., 2013). Trampling and browsing can also change the abiotic conditions of the habitat through soil compaction, increasing runoff and changing light and soil moisture availability (Etchebarne & Brazeiro, 2016), which indirectly may also affect regeneration of plant communities. Thus, herbivores such as cattle and rabbits, may impede the regeneration of some species, reducing species richness and abundance of regeneration, and may also allow the presence of some plant species excluded by other species when herbivores are absent.

On the other hand, natural recovering of woody vegetation in degraded areas is frequently limited by high radiation and/or low water soil content, especially in more arid and semiarid ecosystems (Badano et al., 2019; Gómez-Aparicio, 2009; Zhang et al., 2017). Open areas of degraded ecosystems may be colonized by some woody pioneer species, although frequently the number of these species is reduced compared to the whole plant community of the original ecosystem (Armesto & Pickett, 1985; Corlett, 1991). Presence of these woody pioneer plants may reduce water stress and increase soil nutrient availability, which may become crucial for regeneration of mid and late-successional species (Calle & Holl, 2019; Cuevas et al., 2013; Devaney et al., 2014). In addition, pioneer woody plants can play the role of perch for birds or other animals, facilitating seed dispersal and seed rain in degraded areas (Calle & Holl, 2019; Holt et al., 2014; Miranda et al., 2019). Thus, species richness and abundance of species regenerating under canopy of pioneer species is frequently greater than that of open areas, where only pioneer species may recruit (Cuevas et al., 2013). Additionally, pioneer species are usually inhibited to regenerate under its own canopy, producing also an important change in species composition regenerating between open areas and under the canopy of pioneer species.

The Mediterranean-type climate ecosystems have suffered a long history of human disturbances which have drastically reduced their remaining area and impacted its functionality, structure and species composition (Palahi et al., 2008; Van de Wouw et al., 2011). Forest restoration in these ecosystems is important to recover the habitat of a great number of endemic species (Myers et al., 2000; Van de Wouw et al., 2011). This is the case of central Chile whose Sclerophyllous native forests during the last centuries have strongly been replaced by agriculture and human settlements (Schulz et al., 2010), and degraded by tree cutting, wildfires and livestock (Ovalle et al., 2006; Van de Wouw et al., 2011). Most degraded natural areas became open grasslands, which in many cases, have been colonized by the native tree *Acacia caven* (Mol.) Mol., forming savannas at early successional stages. In the last decades only 34.5% of the native sclerophyllous forest has persisted, and the rest has been mainly transformed in *A. caven* savannas (46.1%), agricultural crops (9.6%) and naked soil (Schulz et al., 2010; Van de Wouw et al., 2011). However, most of these savannas show no evidence of successional advancement or recovery of the original forest (Ovalle et al., 2006; Van de Wouw et al., 2011). Only 6.3% of the *A. caven* savannas has been able to transform into

Sclerophyllous forest, although this trend seems to decrease over the time (Van de Wouw et al., 2011). Therefore, it is needed to find solutions to recover this endangered ecosystem.

Despite *A. caven* savannas are characteristics of degraded ecosystems (Ovalle et al., 1996), they can provide ecological conditions to trigger restoration processes since *A. caven* trees may act as nurse plants facilitating the recruitment of herbaceous and woody species under their canopy (Castro et al., 2010; Ovalle et al., 1996; Root-Bernstein et al., 2017), due to their capability to fix nitrogen, provide organic material on the soils and ameliorate environmental conditions, increasing soil humidity and decreasing temperature (Aronson et al., 1993; Ovalle et al., 1996; Soto et al., 2015). Besides, it has been shown that *A. caven* can play the role of perch tree where birds or other animals can disperse seeds of native tree species (Miranda et al., 2019). However, the high frequency of cattle and rabbits may be impeding regeneration of mid and late successional woody species of the original forest under the canopy of *A. caven*, as well as limiting colonization of open areas by *A. caven* or other pioneer woody species (Root-Bernstein et al., 2017), which may explain the slow rate of recovering of this forest (Schulz et al., 2010; Van de Wouw et al., 2011).

The goal of this study was to assess the effect of cattle and rabbit exclusion and the role of *A. caven* in the natural regeneration of woody native species of the Sclerophyllous forest of central Chile, through exclusions in a seven-year experiment between 2010 and 2017. The study was conducted in two localities of central Chile in order to explore geographical variability of the effects of herbivores and *A. caven* on regeneration in this region. The following hypotheses were tested: richness and abundance of naturally regenerating woody species should be higher under the canopy of *A. caven* than in open sites, and both canopy conditions should present exclusive species. Also, species richness and abundance of the regeneration should be greater with than without excluding herbivores, and both exclusion conditions should present exclusive species. In this way, this study explore the effect of more than one restauration strategy in native forest regeneration, as previous works suggest (Nomiya et al., 2003; Perrin et al., 2006), in the best possible conditions: close to native forest patches and without the presence of introduced herbivores.

2. Materials and methods

2.1 Study sites

The study was conducted in two sites representing the two main bioclimatic ranges of the area of the Sclerophyllous forest of central Chile: a coastal and a pre-Andean range. In a pre-Andean area, we worked in the farm “El Principal”, Pirque, located adjacent to the city of Santiago (33° 44.036'S, 70° 31.148'W) (hereafter Pirque), and in a coastal area we worked in the Lago Peñuelas National Reserve (33° 10.827'S, 71° 25.741'W) (hereafter Peñuelas), located near the city of Valparaíso.

Both localities are characterized by a Mediterranean-type climate of marked seasonality, with rainy winters and hot and dry summers (Luebert & Plischoff, 2017; Salas et al., 2016). Pirque has an annual mean temperature of 10.1°C and an annual mean precipitation of 463 mm. The dry season can last six or eight months (Table 1) and generate 1253 mm of evapotranspiration annually (Soto et al., 2015). The soil has a silty texture with 12 to 24% of clay, 35 to 48% of loam and 31 to 43% of sand (Soto et al., 2015). The Lago Peñuelas National Reserve has an annual mean temperature of 14.8°C, an annual mean precipitation of 589 mm (Table 1) and 983 mm of evapotranspiration during the year (Soto et al., 2015). The soil texture is mainly silty loam with 7 to 18% clay, 53 to 75% of loam and 15 to 23% of sand (Soto et al., 2015; Table 1).

The herbivores potentially browsers on woody seedlings in both localities are the exotic species rabbit (*Oryctolagus cuniculus*), cow (*Bos taurus*), horse (*Equus caballus*), the rodent *Rattus norvegicus*, and the native rodent *Abrothrix olivaceus*. In addition, in Peñuelas the native rodent *Spalacopus cyanus* and some few reintroduced individuals of the native camelid Guanaco (*Lama guanicoe*) were also present (Correa-Solis 2020). Among these herbivores, the larger ones may also produce trampling. Regarding to tree species *Maytenus boaria*, *Schinus polygamus*, *Kageneckia oblonga* and the exotic specie *Crataegus monogyna* were only found in the forest patches of Pirque (Table S1). While *Peumus boldo*, *Escallonia revoluta*, *Schinus latifolius*, *Azara celastrina* were only present in Peñuelas (Table S1).

2.2 Experimental design

During autumn of 2010, in each locality six 30 x 40 m exclosures were established in zones of savannas dominated by *Acacia caven*, in sites next to sclerophyllous forest fragments. Exclosures were located 300-800 m apart and fenced with 1.5 m height mesh and barbed wire above the mesh. This protection allowed us to exclude any medium and large mammal such as rabbits, cows, horses, and guanacos. These fences did not exclude small herbivores like rodents, birds or marsupials, although these species do not eat on seedlings (except rodents). Near each exclosure (20-50 m apart) an unfenced plot of the same surface (30 x 40 m) was established as a control treatment. Within each exclosure and control plot a number between 6 and 22 *A. caven* trees (> 2 m height) were present. Total cover of *A. caven* trees reached between 14.49 and 56.96% in Peñuelas, and 9.55 and 33.98% in Pirque. Thus, four treatments were analyzed in this study: (i) Exclosure and under *A. caven*, (ii) Exclosure and open site, (iii) Control and under *A. caven*, and (iv) Control and open site.

Regeneration coming from germination (sexual) and sprouts (asexual) was evaluated. The measurements were realized in autumn (April-May) of the years 2012, 2013, 2014, 2015 and 2017. However, asexual regeneration was not assessed the year 2014. The method to record data between 2012 and 2015 was carried out with one methodology and in the year 2017 with another. This change was applied in order to increase and improve the sampling effort, enhancing the number of *A. caven* trees sampled within and outside the exclosures. For the years 2012-2015 the following protocol was followed: after building the exclosures in the year 2010, six *A. caven* trees (> 2m height) within each exclosure and other six trees in each control area were randomly selected. When two *A. caven* taller than 2 m were growing together without mixing canopies, they were considered as different individuals. In the cases where the trees were overlapping canopies with less than one meter of distance between their main trunks, they were considered as one individual. Under each tree four 1 x 0.5 m sampling plots located to the south, north, east and west of the trunk and perpendicular to it were installed (2 m² overall under each *A. caven*). Also, six 1 x 2 m plots were installed in open sites in randomly selected positions, within each exclosure and control area. In this way, the same area was sampled within and outside exclosures, under canopy and in open sites. In each plot all woody plants <0.5 m height were registered differentiating by their

origin (coming from sprouts or seed germination) and species. All *A. caven* plants <0.5 m height were considered as regeneration.

In 2017, under the canopy of each *A. caven* >2 m height present within each exclosure and control area, a circular plot with a diameter equal to the shorter diameter of the canopy was installed. These plots were considered as “under *A. caven*” treatment. In an open site next to each *A. caven*, another circular plot with the same diameter than the one established under the nearer *A. caven*, was also installed. The locations (distance and direction) of the open site plots were randomly chosen. These sites were considered as “open site” treatments. In each plot all woody individuals <2m height were registered differentiating by their origin (coming sprouts or seed germination), species and height range (<0.5 m or 0.5-2 m height). All *A. caven* plants <2 m height were considered as regeneration, otherwise, they would have been considered as nurse tree used to evaluate the treatment “under *A. caven*”.

2.3 Data Analysis

We first quantified the total abundance of regenerating plants (< 0.5 m or 0.5-2m height) (combining all species) as well as the species richness present in each plot used in both sampling protocols. Then, we quantified an average for total abundance and species richness among all plots sampled within each exclosure and control area, separately for those sampled under *A. caven* trees and open sites, obtaining a total number of six replicates per treatment and locality. Because of differences of area of plots used in both sampling protocols we standardised the data of every year, although the analyses were made separately for each year, controlling for the surface of subplots. To do this, species richness was divided by the natural log of the area of the plot, while abundance values were extrapolated to 1 hectare. These quantifications were performed separately for each size class sampled the year 2017.

In order to compare the different treatments, and given that the transformed data were continuous with a large amount of zeros, generalized linear mixed model (GLMM) with tweedie distribution and log link function were applied using the package *glmmTMB* of the R software (version 4.0.0) (Brooks et al., 2017; Candy, 2004). In all analyses we used exclosure and *A. caven* presence as fixed factors. Due to exclosures and control

plots were paired, we used each of these pairs (named as station) as a random factor. The significance of random effects was assessed following the same protocol than Carvajal et al. (2017) based on the difference in Akaike's Information Criteria (AICs) between the full model (i.e. model with random factor included) and a model in which the random factor was removed (i.e. generalised linear model – GLM). For the years 2012 to 2015 the analyses were performed only for regeneration <0.5 m height (because we did not measure other size class of regeneration during these years). Instead, for the year 2017 we evaluated the effect of the treatments for the height size classes (<0.5 m and 0.5-2m), separately. The effect of the different treatments on herb cover and height was evaluated in the same way than woody species.

3. Results

3.1 Sexual regeneration

Species richness of the regeneration <0.5 m was significantly greater within exclosures than in control areas the years 2014 and 2017 in Pirque, while only the year 2014 in Peñuelas (Table 2, Fig. 1). Species richness of the regeneration size class 0.5-2 m the year 2017 was significantly greater within exclosures than in control areas in both localities (Table 2, Fig. 2). Species richness of the regeneration <0.5 m was significantly greater under *A. caven* than in open sites the year 2014 in Pirque, while the years 2013, 2014, 2015 and 2017 in Peñuelas (Table 2, Fig. 1). Species richness of the size class 0.5-2m was also significantly greater under *A. caven* than in open sites the year 2017 in both localities (Table 2, Fig. 2). No interactive effects between *A. caven* and exclosure were detected for species richness in any size class and year (Table 2).

Total abundance of the regeneration <0.5 m was significantly greater within exclosures than in control areas the years 2014 and 2017 in Pirque, while only the year 2014 in Peñuelas (Table 2, Fig. 1). Total abundance of the regeneration size class 0.5-2 m the year 2017 was significantly greater within exclosures than in control areas in both localities (Table 2, Fig. 2). Total abundance of the regeneration <0.5 m was significantly greater under *A. caven* than in open sites the year 2014 in Pirque, while all years in Peñuelas (Table 2, Fig. 1). Total abundance of the regeneration size class 0.5-2m was

significantly greater under *A. caven* than in open sites the year 2017 in both localities (Table 2, Fig. 2). No interactive effects between *A. caven* and exclosure were detected for total abundance in any size class and year (Table 2).

The random factor “station” had a variable effect on species richness and abundance through the years (Table 2) in both localities.

On the other hand, a high number of exclusive species in both localities and size classes of regeneration was observed under *A. caven* pooling both exclusion conditions, and within exclosures pooling both *A. caven* conditions (Table 4, Table S2). Only the combination under *A. caven* within exclosures presented high number of exclusive species (Table 4). Nevertheless, open sites and controls outside exclosures also presented one exclusive species in Peñuelas (Table 4, Table S2).

3.2 Asexual regeneration

Species richness of both size classes of regeneration did not differ between herbivore exclusion treatments any year in both localities (Table 3, Figs. 3 and 4). Species richness of the regeneration <0.5 m was significantly greater under *A. caven* than in open sites all years in Peñuelas, while in Pirque no significant difference was found (Table 3, Fig. 3). The year 2017, species richness of the size class 0.5-2m was significantly greater under *A. caven* than in open sites in both localities (Table 3, Fig. 4). No significant interactive effects between *A. caven* and exclosure were detected for species richness in any size class and year (Table 3).

Total abundance of the regeneration <0.5 m was significantly greater within exclosures than in control areas the year 2012 in Peñuelas and 2013 in Pirque (Table 3, Fig. 3). The year 2017, total abundance of the size class of regeneration 0.5-2 m was significantly greater within exclosures than in control areas only in Peñuelas (Table 3, Fig. 4). Total abundance of the regeneration <0.5 m was significantly greater under *A. caven* than in open sites all years in Peñuelas, while no significant difference was found in Pirque (Table 3, Fig. 3). The year 2017, total abundance of the size class 0.5-2m of regeneration was significantly greater under *A. caven* than in open sites in both localities (Table 3, Fig. 4). No interactive effects between *A. caven* and exclosure were detected for total abundance in any size class and year (Table 3).

The random factor “station” had significant effects on species richness and abundance every year in both localities ($\Delta AIC > 2$, Table 2).

A high number of exclusive species in both size class of asexual regeneration was observed in Peñuelas in the treatment under *A. caven* when both exclusion conditions are pooled, and also secondarily within exclosures pooling both *A. caven* conditions, and in control areas when both *A. caven* conditions were pooled (Table 4, Table S3). Furthermore, only the combination under *A. caven* within exclosures presented high number of exclusive species in Peñuelas (Table 4, Table S3). Instead, in Pirque very few exclusive species resprouting were observed in the treatments studied (Table 4, Table S3).

3.3 Herb cover and height

In the case of herb species, in both localities herb cover and height were higher inside the exclosures (Table 5), but just herb height was higher under *A. caven* (Table 5). On the other hand, just in Peñuelas we found an interactive effect of exclosures and *A. caven* in herb cover (Table 5).

4. Discussion

Our results indicate that the effects of *A. caven* and herbivores are similar but not equal for sexual and asexual regeneration and vary between localities and years. In Pirque, regarding the last assessment of sexual regeneration (2017) seven years after installing exclosures, species richness and abundance of the older and probably more established regeneration (0.5-2m) were enhanced by *A. caven* and reduced by herbivores. However, this year, recently recruited regeneration (<0.5 m) was only reduced by herbivores, and not facilitated by *A. caven*. It is possible that facilitation observed on older plants the year 2017 resulted from a previous facilitation by *A. caven* on recently recruited plants, probably the fourth year (2014) of the experiment. Similarly, the negative impact of herbivores observed on the older regeneration in Pirque is probably consequence of previous negative impacts produced on younger seedlings, probably that observed the year 2014. Nevertheless, the year 2017 herbivores also reduced recently recruited

seedlings, which suggests that in this locality detrimental effects of herbivory on seedlings may be more frequent than facilitation by *A. caven*. Interestingly, we found no significant statistical interaction between *A. caven* and herbivory, suggesting that the effects of them on species richness and abundance of the regeneration are orthogonal and independent.

On the other hand, in Peñuelas, facilitation by *A. caven* seems to be a permanent process as this interaction was observed almost every year of the experiment, including older plants the year 2017, in terms of both species richness and abundance of plants. Instead, the negative effects of herbivory were observed only the year 2014 on recently recruited seedlings, and the year 2017 on older plants. The negative effect of herbivory on the older regeneration was probably the result of the negative impact of herbivory observed the year 2014 on recently recruited regeneration. In Peñuelas, the statistical interactions between *A. caven* and exclosure were not significant, suggesting that these factors produce independent effects on species richness and abundance of the regeneration in this locality. All these results suggest that in Peñuelas, both factors are producing an important impact on sexual regeneration of woody species, but the effect produced by *A. caven* is more frequent than that produced by herbivores.

Asexual regeneration (resprouts) was affected by *A. caven* and herbivores in a relatively different way than sexual regeneration. In Pirque, only older plants were facilitated by *A. caven*, while herbivores did not affect this type of regeneration. Nevertheless, the year 2013 the abundance of recently resprouted plants was significantly reduced by herbivores, which did not apparently have influences on older plants the year 2017. The fact that older resprouted plants were facilitated the last year of the experiment without no previous facilitation on younger resprouted plants could be produced by a facilitation during the year 2016 or even 2017, and a fast growth of resprouts. Resprouts have usually rapid growing rates, and frequently reach size higher than 0.5 m in few months (Moggridge & Gurnell, 2009; Shenoy et al., 2011). Statistical interactions between both factors were not significant, indicating that *A. caven* and herbivores have independent effects on asexual regeneration. These results suggest that in Pirque the effect of *A. caven* was more frequent than that of herbivores, although both factors seem to be little relevant for asexual regeneration in this locality.

On the other hand, in Peñuelas, species richness and abundance of resprouts were facilitated by *A. caven* every year of the experiment, while herbivores had a negative

impact only on abundance of older plants, suggesting that the effect of herbivores on asexual regeneration is less frequent and important than that of *A. caven* in this locality. However, both factors showed no significant statistical interaction between them, suggesting that they produce independent impacts on species richness and abundance of the asexual regeneration.

The high numbers of species sexually regenerating exclusively under *A. caven*, compared to open sites, and within exclosures, compared to control areas, suggest that many species of this region only grow under these conditions. Also, the low or null number of species growing exclusively in open sites or outside exclosures suggests that very few species of this region are exclusive pioneers or benefited by herbivores. This pattern was also observed in the asexual regeneration, although in this case only in Peñuelas. This suggests that asexual regeneration is less specialized than sexual regeneration, at least in terms of canopy cover and herbivory. However, the fact that there are species regenerating only under *A. caven* outside the exclosures, suggests that there may be species that require herbivores and cover of pioneer woody species to regenerate. Similarly, the presence of species exclusively regenerating in open sites inside exclosures, suggests that, in some localities, there may be species with a colonizer strategy but that require excluding herbivores to regenerate.

Interestingly, we observed no species sexually regenerating in open sites without excluding herbivores, suggesting that recovering of the native forest is very difficult in open areas when herbivores are present. This may explain observations from other studies documenting very low or null recovering of this forest type in strongly degraded areas (Schulz et al., 2010; Van de Wouw et al. 2011). Nevertheless, our results suggest that sexual regeneration under canopy of *A. caven* is also reduced by herbivores. Thus, the exclusion of herbivores such as cattle and rabbits could enhance sexual regeneration and thus triggering the successional advance with more species than when herbivores are present. These results support other findings of studies performed in central Chile (Fuentes et al., 1983; Fuentes et al., 1984; Holmgren, 2002; Holmgren et al., 2006; Cuevas et al., 2013; Morales et al., 2015), and other semiarid regions of the world (Moreno & Villafuerte, 1995; Bird et al., 2012; Abraham et al., 2018; Perea et al., 2020), all of which suggest that woody regeneration is strongly affected by herbivores. Nevertheless, we are not able to differentiate if herbivory effects observed were produced

by cattle, rabbits or both. In our studies sites both types of herbivores were present, and in particular, the cattle was very abundant in both localities (Salinas 2013; Correa-Solís, 2020). On the other hand, some studies have observed positive rather than negative effects of cattle, in this case, through indirect effects by reducing the negative impact of the herbaceous layer (Laurent et al., 2017; Mata-González et al., 2007). In our study area, the herbaceous layer is effectively reduced by cattle and rabbits (Salinas 2013), which could be related with the forest regeneration. Specifically, taller and higher cover herbs inside the exclosures seems to negatively affect woody species richness and abundance below 0.5 m just in Peñuelas, while taller herbs under *A. caven* could be affecting species richness and abundance in Pirque. On the other hand, tree seedlings between 0.5 and 2 m could not be affected by herbs, so these would only affect tree species recruitment but not their growth in sexual regeneration. Regarding asexual regeneration, in Pirque only abundance under of seedlings between 0.5 and 2 m *A. caven* seems not be affected by a higher cover of herbs. While in Peñuelas they would decrease forest regeneration inside exclosures except the abundance of older seedlings.

The facilitative effect of the pioneer woody species, such as *A. caven*, on mid or late-successional species, is consistent with those of other studies performed in central Chile (Fuentes et al., 1984; Armesto & Pickett, 1985; Fuentes et al., 1986; Bustamante & Simonetti, 2000; Holmgren et al., 2000; Becerra & Montenegro, 2013; Cuevas et al., 2013; Root-Bernstein et al. 2017; Velasco & Becerra, 2020) as well as with several works from other regions with semiarid climates (Callaway, 1992; Bonet, 2004; Gómez-Aparicio et al., 2005; Maestre et al., 2009; Caldeira et al., 2014; Lloret & Granzow-de la Cerda, 2013; Pugnaire & Haase, 2019). It is probable that facilitation by *A. caven* was produced by amelioration of the drought under canopy (Velasco & Becerra, 2020), as well as by acting as perches increasing seed rain under its canopy (Miranda et al., 2019), since both mechanisms have been documented in this pioneer species. Interestingly, this effect could be detected even in sites without exclusion of herbivores in both localities. For example, regarding the older and more established sexual and asexual regeneration combined, in Pirque, the mid-successional species *Quillaja saponaria* and *Maytenus boaria* were facilitated by *A. caven* when herbivores were excluded, while only *M. boaria* was facilitated in presence of herbivores. In Peñuelas, the mid and late-successional species *Cryptocarya alba*, *Maytenus boaria*, *L. caustica* and *Schinus latifolius* were

facilitated when herbivores were excluded, and very similar species composition when herbivores were present (*C. alba*, *M. boaria*, *L. caustica* and *Q. saponaria*).

Although the time lapse of our experiment was relatively shorter than other studies documenting increases of regeneration along time (Hejcmanová et al., 2010; Listopad et al., 2018), we expected an increase of the species richness and abundance of seedlings along time, at least within exclosures and under *A. caven*. However, we observed no increase, and by contrast, both sexual and asexual regeneration showed a slight decreasing between 2012 and 2017. This could be related to an intensification of drought since 2010 (Garreaud et al., 2020). It is known that dry seasons and water availability in Mediterranean regions are important limiting factors for regeneration (Lloret et al., 2005; Holmgren et al., 2006), hence, it is probable that a continuous reduction of soil moisture along time has impeded an accumulation of regeneration, producing an oscillation or even a reduction of the regeneration along the experiment. However, the influence of rainfalls during the experiment on the natural regeneration is unclear, since the maximum values of species richness and abundance (2013 and 2014) in Pirque were not preceded by years with high precipitation. Similarly, the year with greater rainfalls (2016) was followed by a year with very low species richness and abundance in the regeneration. Thus, higher values of rainfall observed during some years had no relevant effect on regeneration, and instead the generalized low values of precipitation were slowly increasing the drought of these sites, producing no increment or accumulation of regeneration. It is important to note that in Pirque there was some species recruiting (<0.5m) but not present among older plants (0.5-2m), not even under *A. caven* canopies, for example, *Cryptocarya alba* and *Lithrea caustica*. These species were able to recruit probably due to winter rainfall, however, the dry conditions during spring and summer (and even autumn) in this locality are halting survival, growth and establishment of a future population, which may become permanent regarding predictions of climate change for this region (Bozkurt et al., 2017).

5. Conclusions and implications

The findings of this study suggest that when cattle and rabbits are abundant, and although the impact of them vary and oscillate along time, the use of exclosures may

allow sexual regeneration of woody species to colonize open sites, and advance successional under canopy of *Acacia caven*, which may help recovering this semiarid forest. Instead, asexual regeneration does not seem to be importantly affected by herbivores, and hence it may strongly contribute to recover this forest when excluding large surfaces is not possible. Nevertheless, given the importance of sexual regeneration for the long-term persistence of this and any forest, restoration of sexual regeneration is critical. Our results also suggest that active reforestation with the pioneer tree *A. caven* may accelerate succession and recovering of this forest through facilitative interactions, especially when herbivores are excluded.

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Resumen

En ecosistemas semiáridos, las plantas nodrizas pioneras facilitan la regeneración de especies leñosas, sin embargo, la colonización en áreas abiertas como bajo árboles nodriza podría verse limitada por los herbívoros. El objetivo de este estudio fue evaluar el efecto de la exclusión de ganado y conejos y de *Acacia caven* sobre la regeneración natural de especies leñosas, en un experimento de siete años en dos localidades (Pirque y Peñuelas) de Chile central. Se establecieron seis exclusiones y zonas control en sabanas degradadas de *A. caven* cercanas a fragmentos de bosque esclerófilo donde muestreó la regeneración sexual y asexual bajo dosel de *A. caven* y en sitios abiertos. Después de siete años, la riqueza de especies y abundancia de plantas regeneradas sexualmente de tamaño 0,5-2 m fue significativamente mayor dentro de exclusiones que en áreas control en ambas localidades. Bajo *A. caven* la riqueza de especies y abundancia de ambos tipos de regeneración fue mayor que en sitios abiertos. En Peñuelas la abundancia de plántulas regeneradas asexualmente fue significativamente mayor dentro de exclusiones que en áreas control. En ninguna variable o localidad se detectó efecto significativo de la interacción entre *A. caven* y exclusión. Nuestros resultados sugieren que cuando ganado y conejos están presentes, el uso de exclusiones permitiría la colonización de sitios abiertos y el avance sucesional bajo dosel de *Acacia caven*. En cambio, la regeneración asexual es menos afectada por los herbívoros por lo que puede contribuir a recuperar este bosque cuando no es posible excluir grandes áreas.

Palabras clave: facilitación, herbivoría, reclutamiento, regeneración, rebrote vegetativo.

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Tables

Table 1. Rainfalls in both localities during the study period (CR2, 2018).

Year	Pirque			Peñuelas		
	Total	Winter/Autumm	Summer/Spring	Total	Winter/Autumm	Summer/Spring
2010	304.6	241.3	63.3	362.5	344.5	18.0
2011	214.6	202.9	11.7	386.5	373.7	0.8
2012	354.5	263.4	91.1	626.0	505.7	119.8
2013	233.8	233.5	0.3	347.6	346.4	1.2
2014	231.1	221.9	9.2	537.5	531.0	6.5
2015	345.3	235.8	109.5	676.8	558.3	118.5
2016	421.0	354.9	66.1	436.9	263.9	54.0

Table 2. Statistical results (GLMM) for the effect of Exclosures and *A. caven* on species richness and total abundance of plants of the sexual regeneration every year (both size classes in 2017) (NA= Not enough regeneration to run statistical analyses). Δ AIC values of the random factor (station) are also shown, indicating the variance between replicates. When Δ AIC > 2, results including the factor “station” are shown. When Δ AIC < 2, results excluding the factor “station” are shown.

Variable		Pirque			Peñuelas		
Size class and year		Acacia	Exclosure	Exclosure x Acacia	Acacia	Exclosure	Exclosure x Acacia
Species richness							
<0.5 m 2012	Chi2	NA	NA	NA	3.33	0.23	0
	P	NA	NA	NA	0.07	0.63	1
	Δ AIC		NA			0	
<0.5 m 2013	Chi2	0	0.15	0	17.33	0.24	0
	P	1	0.71	1	<0.001	0.62	1
	Δ AIC		1.8			3.8	
<0.5 m 2014	Chi2	10.47	8.25	0	13.46	11.13	0
	P	0.01	0.04	1	<0.001	<0.001	1
	Δ AIC		4.1			2	
<0.5 m 2015	Chi2	NA	NA	NA	9.06	0.17	0
	P	NA	NA	NA	0.003	0.68	1
	Δ AIC		NA			2.4	
<0.5 m 2017	Chi2	0.02	9.52	0.02	5.49	1.13	0
	P	0.89	0.002	0.89	0.02	0.29	1
	Δ AIC		0.3			0.3	
0.5-2m 2017	Chi2	9.82	8.51	0	13.47	13.09	0
	P	0.002	0.004	1	<0.001	<0.001	1
	Δ AIC		5.1			5.6	
Total Abundance							
<0.5 m 2012	Chi2	NA	NA	NA	14.52	1.61	0.48
	P	NA	NA	NA	<0.001	0.21	0.49
	Δ AIC		NA			3.5	
<0.5 m 2013	Chi2	0	0.40	0	13.50	1.72	0
	P	1	0.53	1	<0.001	0.19	1
	Δ AIC		5.8			0.1	
<0.5 m 2014	Chi2	5.95	7.26	1.15	17.79	19.55	0
	P	0.01	0.01	0.29	<0.001	<0.001	1
	Δ AIC		8.9			0.4	
<0.5 m 2015	Chi2	NA	NA	NA	9.93	0.01	0
	P	NA	NA	NA	0.002	0.91	1
	Δ AIC		NA			2	
<0.5 m 2017	Chi2	0.02	9.46	0.02	6.49	2.35	0
	P	0.89	0.002	0.89	0.01	0.13	1
	Δ AIC		1.1			0.5	
0.5-2m 2017	Chi2	8.37	8.13	0	18.38	17.92	0
	P	0.04	0.04	1	<0.001	<0.001	1
	Δ AIC		6.2			2.7	

Table 3. Statistical results (GLMM) for the effect of Exclosures and A. caven on species richness and total abundance of plants of the asexual regeneration every year (both size classes in 2017) (NA= Not enough regeneration to run statistical analyses). Δ AIC values of the random factor (station) are also shown, indicating the variance between replicates. When Δ AIC > 2, results including the factor “station” are shown. When Δ AIC < 2, results excluding the factor “station” are shown.

Variables		Pirque			Peñuelas		
Size class and year		Acacia	Exclosure	Exclosure x Acacia	Acacia	Exclosure	Exclosure x Acacia
Species richness							
<0.5 m	Chi2	NA	NA	NA	5.81	1.39	0
2012	P	NA	NA	NA	0.02	0.24	0.99
	Δ AIC		NA			5.7	
<0.5 m	Chi2	1.67	0	1.67	14.19	0.12	1.67
2013	P	0.19	0.99	0.19	<0.001	0.73	0.19
	Δ AIC		3.8			9	
<0.5 m	Chi2	0.07	0.81	1.05	11.68	0	0
2015	P	0.79	0.37	0.31	<0.001	1	1
	Δ AIC		3.4			23.1	
<0.5 m	Chi2	1.28	0.01	0	4.54	1.32	0
2017	P	0.26	0.93	1	0.03	0.25	1
	Δ AIC		2.6			2.7	
0.5-2m	Chi2	25.94	1.04	1.85	6.79	0.58	0.85
2017	P	<0.001	0.31	0.17	0.01	0.45	0.36
	Δ AIC		5.5			5.6	
Total Abundance							
<0.5 m	Chi2	NA	NA	NA	11.99	6.19	0.01
2012	P	NA	NA	NA	<0.001	0.01	0.94
	Δ AIC		NA			4.8	
<0.5 m	Chi2	1.46	4.58	1.45	11.,73	0.49	0.92
2013	P	0.23	0.03	0.23	<0.001	0.49	0.34
	Δ AIC		8.8			4.8	
<0.5 m	Chi2	0.01	1.11	1.31	13.31	0.03	0
2015	P	0.98	0.29	0.25	<0.001	0.87	1
	Δ AIC		3.8			6.6	
<0.5 m	Chi2	1.23	0.21	0	11.15	3.35	0
2017	P	0.27	0.65	1	<0.001	0.07	1
	Δ AIC		3.4			4.6	
0.5-2m	Chi2	27.89	3.33	0.21	4.59	5.26	0.43
2017	P	<0.001	0.07	0.65	0.03	0.02	0.51
	Δ AIC		7.9			2.9	

Table 4. Exclusive species in each treatment or combination of treatment of the factors *A. caven* and exclosure per size class and source of regeneration.

Treatment			Pirque			Peñuelas		
			<0.5	0.5-2	Total	<0.5	0.5-2	Total
Sexual regeneration								
Under <i>A. caven</i>			4	3	5	7	5	5
Open sites			1	0	0	1	0	1
Exclosure			5	3	6	5	5	3
Control			0	0	0	1	1	1
Under <i>A. caven</i>	-	Exclosure	4	2	5	4	4	3
Under <i>A. caven</i>	-	Control	1	0	0	1	0	1
Open sites	-	Exclosure	0	0	0	1	1	1
Open sites	-	Control	0	0	0	0	0	0
Asexual regeneration								
Under <i>A. caven</i>			0	1	1	3	5	6
Open sites			0	0	0	1	0	0
Exclosure			0	2	1	3	1	3
Control			0	0	0	1	2	2
Under <i>A. caven</i>	-	Exclosure	0	1	1	2	1	3
Under <i>A. caven</i>	-	Control	0	0	0	1	0	2
Open sites	-	Exclosure	0	0	0	1	2	0
Open sites	-	Control	0	0	0	0	0	0

Table 5. Effect of the different treatments on herb regeneration

		Pirque			Peñuelas		
		Acacia	Exclosure	Exclosures x Acacia	Acacia	Exclosure	Exclosures x Acacia
Herb cover							
<0.5m	Chi2	0.06	18.05	0.001	0.52	40.85	4.46
	p	0.81	<0.001	0.99	0.47	<0.001	0.04
	ΔAIC			9.7			8.8
Herb height							
<0.5m	Chi2	8.97	93.03	1.16	4.72	24.02	2.37
	p	0.003	<0.001	0.28	0.03	<0.001	0.12
	ΔAIC			9.1			8

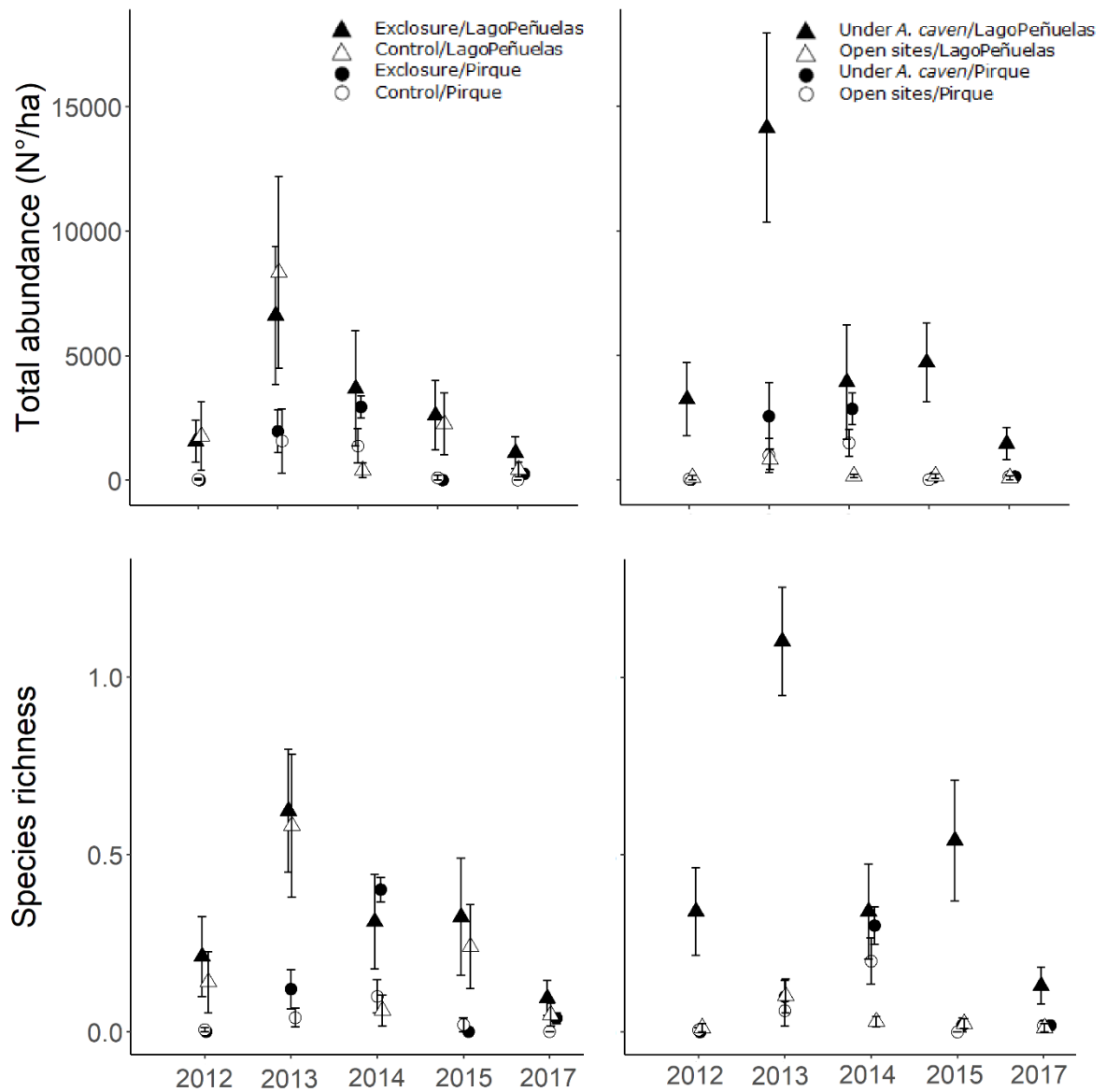


Figure 1. Sexual regeneration of the size class <0.5 m height (mean $\pm$ 1 SE) through the years in Pirque and Peñuelas. Left panels indicate the effect of exclosures and right panels indicate the effect of *A. caven*. Combination of treatments of both factors are not shown because the statistical interactions between both factors were not significant in any year. Species richness indicate the number of species per subplot/Ln (area of subplot).

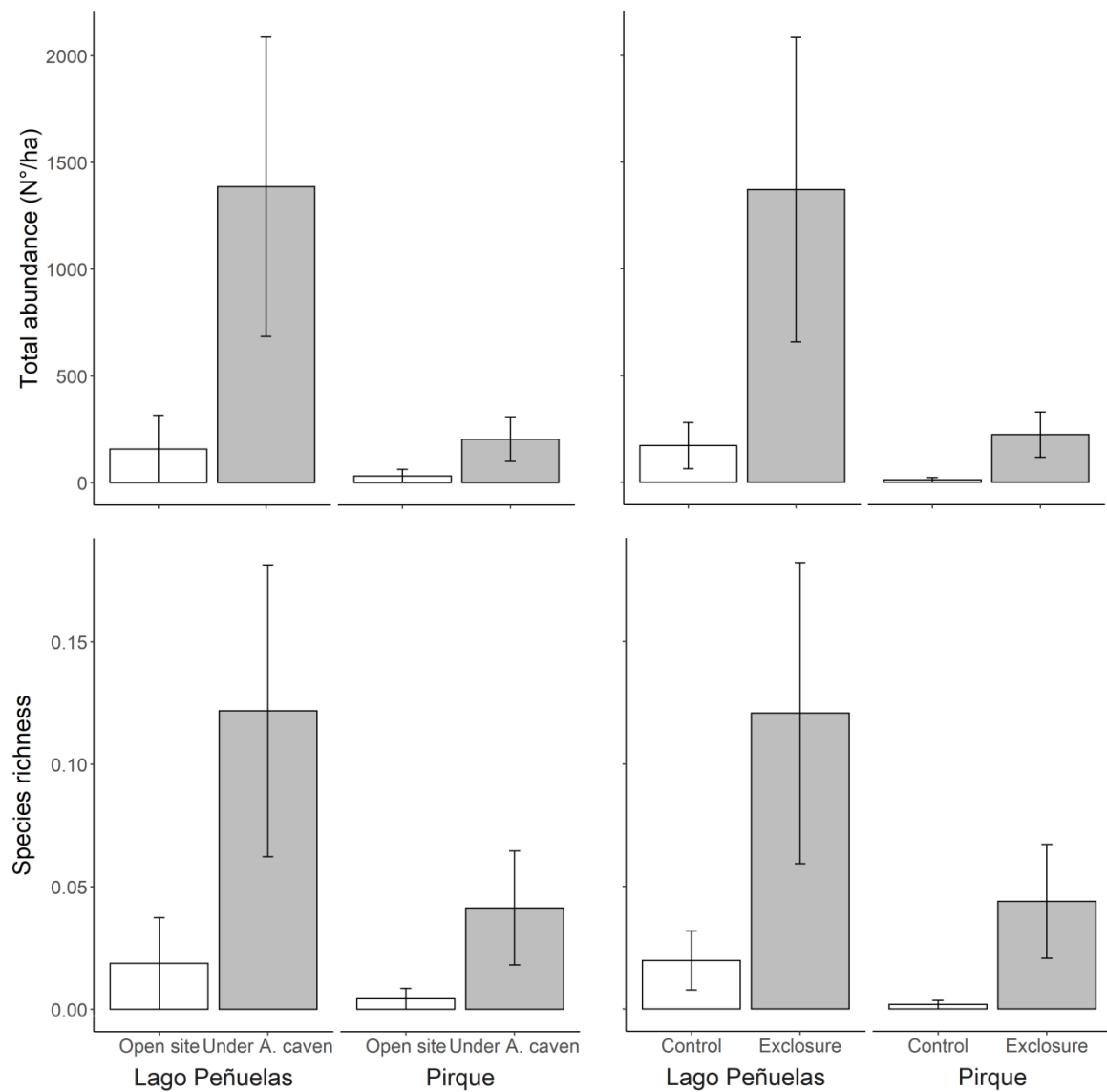


Figure 2. Sexual regeneration (mean $\pm$ 1 SE) of the size class 0.5-2 m (data of the year 2017) in Pirque and Peñuelas. Left panels indicate the effect of *A. caven* and right panels indicate the effect of exclosures. Combination of treatments of both factors are not shown because the statistical interactions between both factors were not significant in any year. Species richness indicate the number of species per subplot/Ln (area of subplot).

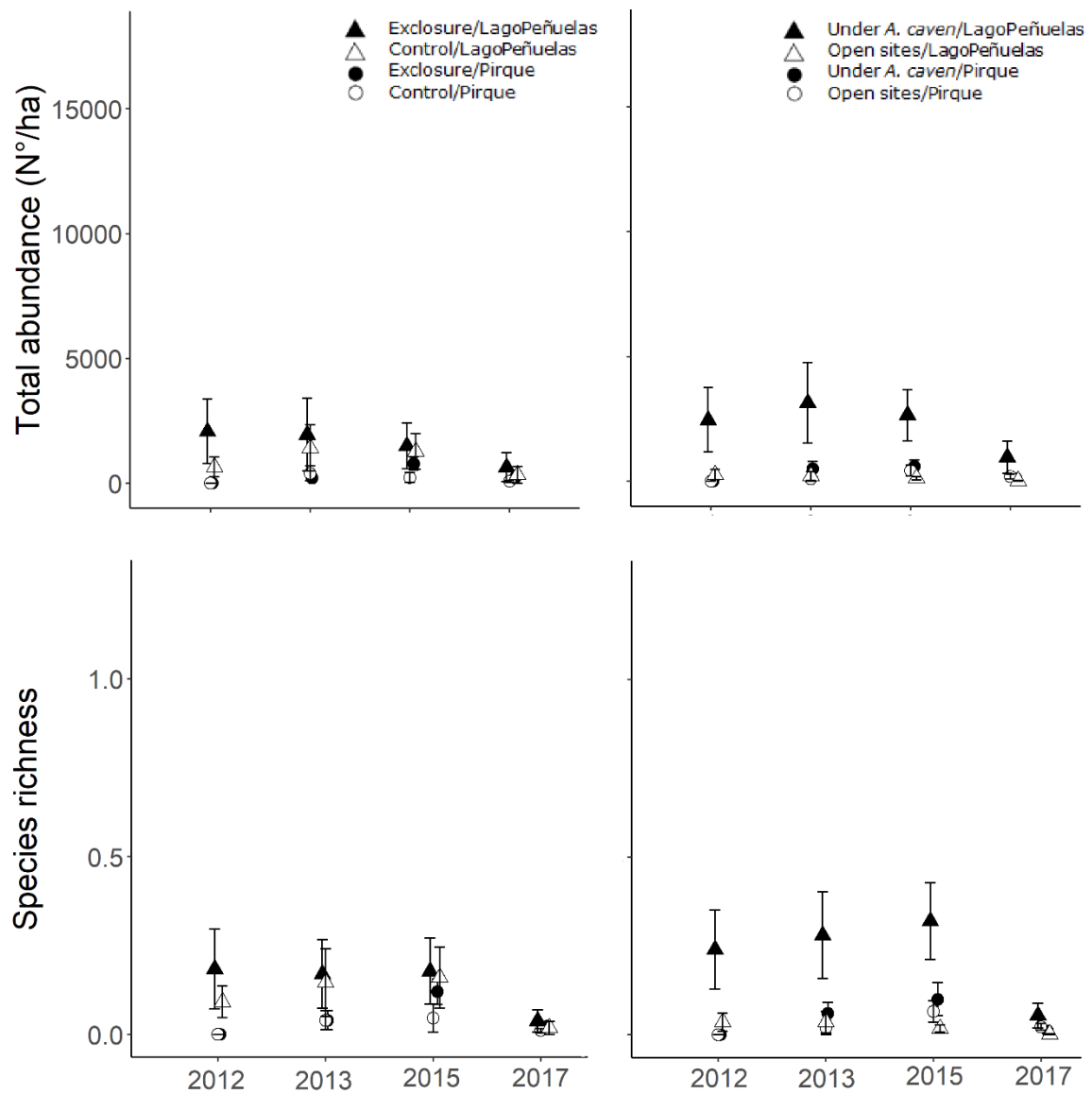


Figure 3. Asexual regeneration of the size class <0.5 m height (mean $\pm$ 1 SE) through the years in Pirque and Peñuelas. Left panels indicate the effect of exclosures and right panels indicate the effect of *A. caven*. Combination of treatments of both factors are not shown because the statistical interactions between both factors were not significant in any year. Species richness indicate the number of species per subplot/Ln (area of subplot).

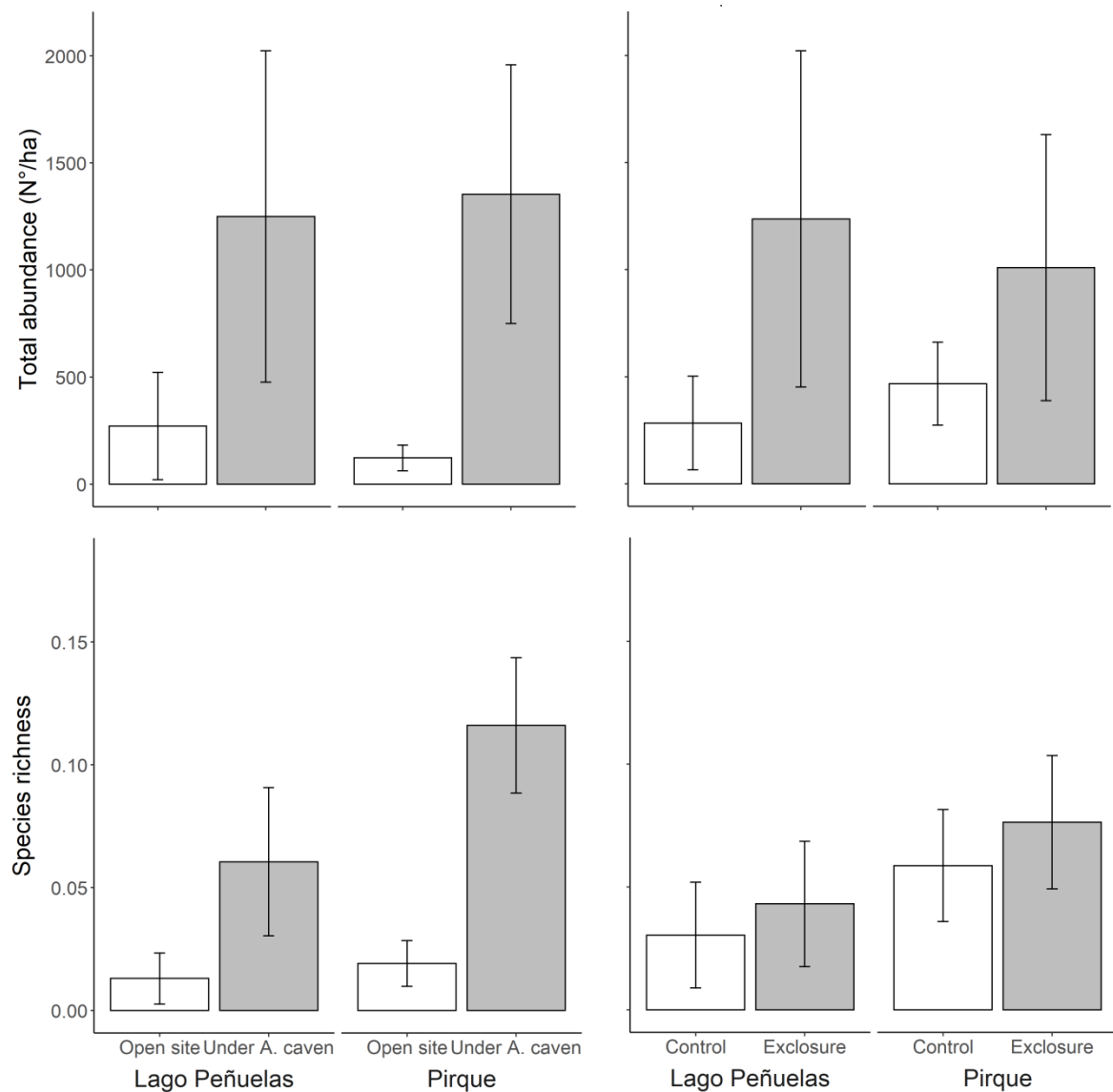


Figure 4. Asexual regeneration (mean $\pm$ 1 SE) of the size class 0.5-2 m (data of the year 2017) in Pirque and Peñuelas. Left panels indicate the effect of *A. caven* and right panels indicate the effect of exclosures. Combination of treatments of both factors are not shown because the statistical interactions between both factors were not significant in any year. Species richness indicate the number of species per subplot/Ln(area of subplot).

Supplementary material

Table S1. Species cover and abundance per hectare

Specie	Pirque		Peñuelas	
	Abundance/ha	cover (%)	Abundance/ha	cover (%)
<i>Lithraea caustica</i>	93,33	25,63	20	17,08
<i>Maytenus boaria</i>	1,67	0,08	0	0
<i>Schinus polygamus</i>	6,67	1,88	0	0
<i>Kageneckia oblonga</i>	5	0,5	0	0
<i>Quillaja saponaria</i>	11,67	8,75	55	20,83
<i>Cryptocarya alba</i>	65	14,75	128,33	25,42
<i>Peumus boldo</i>	0	0	68,33	22,92
<i>Acacia caven</i>	6,67	1,46	45	4,58
<i>Escallonia revoluta</i>	0	0	1,67	0,21
<i>Schinus latifolius</i>	0	0	11,67	5,08
<i>Azara celastrina</i>	0	0	6,67	0,71
<i>Crataegus monogyna</i>	1,67	0,42	0	0

Table S1. Mean abundance (N° ind/ha) of the sexual regeneration per treatment the last year of the experiment (2017).

Species per size class	Pirque				Peñuelas			
	Exclosures		Control		Exclosures		Control	
	Under Acacia	Open sites	Under Acacia	Open sites	Under Acacia	Open sites	Under Acacia	Open sites
Plants <0.5 m								
<i>Lithraea caustica</i>	28.5	0	0	0	95.9	0	60.6	0
<i>Maytenus boaria</i>	21.8	0	0	0	1159.1	61.7	314.1	0
<i>Trevoa trinervis</i>	0	0	0	0	37.1	0	0	0
<i>Cestrum parqui</i>	104.5	0	0	0	0	0	0	0
<i>Quillaja saponaria</i>	0	0	0	0	97.7	16.7	32.9	0
<i>Cryptocarya alba</i>	125.1	0	0	0	90.3	0	0	0
<i>Peumus boldus</i>	0	0	0	0	0	0	23.9	0
<i>Acacia caven</i>	0	29.6	0	0	0	0	0	0
<i>Schinus latifolius</i>	0	0	0	0	57.1	0	110.1	0
<i>Muehlenbeckia hastulata</i>	0	0	0	0	31.1	0	0	0
<i>Baccharis linearis</i>	0	0	0	0	23.5	46.9	32.9	0
<i>Colliguaja odorifera</i>	0	0	0	0	251.6	0	0	0
<i>Azara celastrina</i>	0	0	0	0	0	16.7	0	0
Plants 0.5-2 m								
<i>Lithraea caustica</i>	0	0	0	0	0	16.7	47.9	0
<i>Maytenus boaria</i>	50.8	0	28.5	0	997.4	81.6	96.3	0
<i>Trevoa trinervis</i>	0	0	0	0	74.3	0	0	0
<i>Cestrum parqui</i>	147.3	0	0	0	23.1	0	0	0
<i>Quillaja saponaria</i>	55.9	0	0	0	0	0	23.5	0
<i>Cryptocarya alba</i>	0	0	0	0	28.1	0	15.9	0
<i>Acacia caven</i>	134.1	41.2	0	0	0	0	0	0
<i>Schinus latifolius</i>	0	0	0	0	56.4	0	0	0
<i>Muehlenbeckia hastulata</i>	0	0	0	0	30.3	0	0	0
<i>Baccharis linearis</i>	0	0	0	0	346.8	152.6	63.4	0
<i>Colliguaja odorifera</i>	0	0	0	0	380.7	38.4	0	0

Table S2. Mean abundance (N° ind/ha) of the asexual regeneration per treatment the last year of the experiment (2017).

Species per size class	Pirque				Peñuelas			
	Exclosures		Control		Exclosures		Control	
	Under Acacia	Open sites	Under Acacia	Open sites	Under Acacia	Open sites	Under Acacia	Open sites
Resprouts <0.5 m								
<i>Lithraea</i>	0	0	0	0	0	0	30.3	0
<i>caustica</i>								
<i>Maytenus</i>	87.1	0	0	21.6	573.4	0	295.7	0
<i>boaria</i>								
<i>Cestrum</i>	29.0	0	0	29.6	0	0	0	0
<i>parqui</i>								
<i>Acacia caven</i>	37.3	55.9	0	46.1	0	0	0	0
<i>Baccharis</i>	0	0	0	0	0	26.8	0	0
<i>linearis</i>								
<i>Colliguaja</i>	0	0	0	0	38.4	0	0	0
<i>odorifera</i>								
<i>Azara</i>	0	0	0	0	33.4	0	0	0
<i>celastrina</i>								
Resprouts 0.5-2 m								
<i>Lithraea</i>	0	0	0	0	30.3	0	30.0	0
<i>caustica</i>								
<i>Maytenus</i>	435.3	0	0	0	720.7	0	160.5	0
<i>boaria</i>								
<i>Cestrum</i>	911.4	78.4	640.0	0	0	0	0	0
<i>parqui</i>								
<i>Quillaja</i>	31.3	37.5	0	0	0	0	23.5	0
<i>saponaria</i>								
<i>Acacia caven</i>	35.6	30.1	158.9	47.74	29.5	0	0	0
<i>Baccharis</i>	0	0	0	0	371.9	461.5	60.3	35.9
<i>linearis</i>								
<i>Rubus</i>	0	0	0	0	0	0	23.0	0
<i>ulmifolius</i>								

