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Ungulates can control tree invasions: experimental evidence from nonnative conifers and sheep herbivory

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Abstract Invasive conifer species are increasingly recognized as a serious problem in many parts of the world, where they are having large ecological and economic impacts. Understanding factors that trigger and can control invasion is key to management. Grazing and browsing by large herbivores have been suggested as a mechanism that may halt conifer invasions, although conflicting results have been reported (i.e. positive, negative or no effect of grazing on invasion). We believe that some of these opposing responses arise due to the absence of well-planned and replicated experiments, since current evidence is mostly observational, and for example, differences in animal densities can produce different results. Thus, in this study, we tested whether large herbivores can control invasion by nonnative conifers and whether the severity of the invasion process would be lessened by increased herbivory intensity. We evaluate experimentally herbivore damage on *Pinus contorta*, a highly invasive species in many countries of the Southern Hemisphere, under different sheep stocking rates in Patagonia, Argentina. We used four stocking rates, corresponding to 1, 2, 4 and 8 times the recommended sheep herbivory intensity for the study area. The response was not linear but rather presented a threshold. The greater stocking rate, the greater the browsing, higher reduction in seedling height, and decrease of survival of *P. contorta*. Also, the highest stocking rate damaged and killed 99% of them. This study provides evidence that large domestic herbivores can play a key role in the invasion process and, if managed properly, would provide a tool to help limit conifer invasion.

Keywords Biological invasion · Browsing · Large mammalian herbivore · *Pinus contorta* · Sheep · Steppe

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Introduction

Biological invasions are a global concern owing to their impact on biodiversity and ecosystem services, and to the high economic costs they entail (Mack et al. 2000; Simberloff 2011; Lockwood et al. 2013). Among plant species, it was not until a few decades ago that invasive woody species were recognized as global drivers able to alter natural ecosystems (Richardson and Rejmánek 2011). Pinaceae, almost exclusively native to the Northern Hemisphere, have been introduced and planted in the Southern Hemisphere, mainly for forestry and erosion control. Fast-growing conifers have been planted since the 1800s in Australia, New Zealand and South Africa, and later, since the 1950s, in South America (e.g., Argentina, Brazil, Chile and Uruguay) (Simberloff et al. 2010). As a result, many of these pine species became invasive in many places with several impacts such as replacement of native treeless vegetation (Rundel et al. 2014), disturbance of soils and nutrient cycles, and changes in fire and water regimes (Simberloff et al. 2010).

Many hypotheses have been proposed to explain non-native plant success as invasive and major advances have been achieved in revealing mechanisms underlying invasions (Daehler 2003; Hierro et al. 2005; Richardson and Pyšek 2006; Lamarque et al. 2011). These studies take into account both intrinsic properties of the species (invasiveness) and emergent properties of the ecosystems (invasibility). Particularly, Pinaceae is one of the best-studied taxa and can be considered a model group that has allowed identification of mechanisms operating in plant invasions (Richardson 2006; Gundale et al. 2014). The success of conifers as invaders (i.e. invasiveness) has mainly been attributed to a set of life-history traits: small seeds, short intervals between high seed production and short juvenile period (Rejmánek and Richardson 1996). However, these intrinsic traits have not always sufficed to predict completely the success of conifer invasion; rather, multiple factors interacting in a complex manner are important (Simberloff et al. 2002; Nuñez et al. 2011). Thus, external mechanisms that could influence pine invasions (i.e. invasibility) are, among others, changes in disturbance regimes (Hobbs and Huenneke 1992; Lonsdale 1999), forestry use (McGregor et al. 2012), climate suitability (Nuñez and Medley 2011), ground-cover, structure and composition of the receiving community (Richardson et al. 2011), and herbivory (Relva et al. 2010).

It is widely recognized that ungulates (domestic and wild), through herbivory and associated disturbances (e.g., trampling), can influence plant community composition, nutrient dynamics, hydrology and fire regimes (Hester et al. 2006; Hobbs 2006). The role of introduced ungulates in facilitating plant invasions has been demonstrated by many studies (Hobbs 2001; Parker and Hay 2005; Vavra et al. 2007; Knight et al. 2009; Loydi and Zalba 2009; Spear and Chown 2009; Oduor et al. 2010; Nuñez et al. 2013), and changes in grazing pressure are cited as a disturbance that may decrease or promote the invasion of conifers depending on its magnitude (Richardson and Bond 1991). However, the evidence concerning how ungulates affect conifer invasions is conflicting. For example, some studies link the timing of conifer invasion with grazing cessation (Sarasola et al. 2006; Ledgard and Norton 2008; Boulant et al. 2008), while others found positive responses or no effect of conifer invasion to grazing and browsing by ungulates (Relva et al. 2010; Osem et al. 2011; de Villalobos et al. 2011; Six et al. 2013). The information on herbivore type and intensity with and without invasion is often anecdotal, and for example, differences in animal densities can produce different results. Intensity of herbivory has been recognized as a key factor in plant responses (Eschtruth and Battles 2008); however, the empirical evidence on its role in plant invasion is scarce, and specifically is nil for invasion by conifers. Manipulative studies controlling intensity level and type of herbivory (e.g., animal species, density, grazing history) are required for a better understanding of the ungulate–plant invasion relationship.

On the one hand, in Patagonia Argentina, livestock activity constitutes the main agricultural production (Easdale et al. 2009) and, in the other hand, since the early 1970s, plantation forestry of several nonnative species has increased rapidly. There are about 97,400 ha forested (Bava et al. 2015), mainly with *Pinus ponderosa*, *Pinus contorta*, and *Pseudotsuga menziesii* of the 700,000–2,000,000 hectares estimated as suitable for plantation (Schlichter and Laclau 1998). Taking into account the scale of planting in a short time period and with species recognized as very invasive in the Southern Hemisphere, and the currently observed levels of invasion, it is possible to predict a rapid rate of invasion in the near future (Richardson et al. 2007; Simberloff et al. 2010). Given the productive context of Patagonia and other areas of the world where most of the ranches combine pine plantations with livestock, the idea of controlling pine spread near the plantations by domestic livestock may be feasible. Thus, we hypothesize that ungulates can control the invasion of conifers through herbivory on seedlings and that their effectiveness depends on the intensity of herbivory. Thus, the objective of this study was to evaluate the effect of grazing intensity by sheep on seedlings of *Pinus contorta,* one of the most invasive conifer species in Patagonia and the Southern Hemisphere (Langdon et al. 2010). We expected to register further damage in seedlings undergoing major sheep stocking rate, reaching a point where the invasion can be efficiently controlled. Understanding how variation in grazing intensity affects seedlings of nonnative conifers may provide a practical guidance of prescribed grazing regimes (timing, density, frequency) that might work as effective control and for prevent future scenarios of invasions.

Methods

Study area

This research was conducted in NW Patagonia in the Fortín Chacabuco ranch, located in Neuquén province in Argentina (41°0′16.67″S and 71°10′46.62″W). The landscape is composed of mountains, mountain ranges and hills, and it is crossed by many rivers and streams. The climate is Mediterranean, with 60% of precipitation occurring in autumn and winter. The annual rainfall ranges between 300 and 700 mm per year and the average annual temperature does not exceed 10 °C (Bran et al. 2002). The vegetation corresponds to a semiarid Patagonian steppe in the Andean piedmont. The vegetation forms a mosaic depending on exposure and soil. The dominant vegetation is the steppe of tussock grasses, *Pappostipa speciosa* in the lower sectors and *Festuca pallescens* in higher areas, with scattered shrubs of *Acaena splendens*, *Senecio bracteolatus*, and *Mulinum spinosum*. There are many flood meadows with *Juncus balticus*, *Poa pratensis* and *F. pallescens* associated with shrub of *Ochetophila trinervis, Discaria chacaye*, *Escallonia virgata*, *Berberis microphylla* and *Maytenus boaria* (Bran et al. 2002).

Fortin Chacabuco ranch has a long livestock farming history in northern Patagonia and its management has changed over the years. Sheep grazing has been the land use that has prevailed in the ranch, with a peak of 6000 animals in the 1980s when the ranch was twice the current surface. This land use has gradually declined to this day (TNC 2016). Currently, despite having a low number of animals (225 sheep, 46 cows and 8 horses in 4460 ha), the quality of the paddocks is variable due to a lack of grazing management in the last years. There are sites over-grazed and sites with abundant litter accumulation from un-grazed senescent plants because of the heterogeneity of grazing patterns (Paramidani et al. 2014). Since 2014 the ranch is in process of obtaining GRASS certification (Grassland Regeneration and Sustainability Standard) (Borrelli et al. 2013), a grazing management that include Holistic Management (Butterfield et al. 2006). Particularly the paddock where we established the enclosures have a vegetation type corresponding to a steppe of tussock grasses of moderate quality (Paramidani et al. 2014). Taking this into account we calculate the stocking rates applied in the experiment (see "Experimental design" section). In the ranch, there are also plantations of *P. contorta* and *P. ponderosa* and there are some areas with pine invasions. Many of the individuals escaped from plantations have signs of herbivory damage. Beside domestic herbivores, there are invasive nonnative herbivores like red deer (*Cervus elaphus*) and European hare (*Lepus europaeus*) and native herbivores such as guanaco (*Lama guanicoe*).

Experimental design

To determine whether ungulates drive invasion by nonnative conifers we exposed *Pinus contorta* seedlings to different stocking rates of sheep (*Ovis aries*). We selected the sheep, all Merino wethers (male castrated sheep) of the same age; all had a similar initial diet with similar nutritional components and had been exposed to conifers before the experiment. The exposure is important because individuals may develop a preference for one species or another over time (Squibb et al. 1990; Walker et al. 1992).

Within the study area, we installed five blocks of experimental enclosures (Fig. 1 Online Resource 1). Each block was a 50 × 50 m area divided in four plots of 25 × 25 m with a 1.50 m tall fence. Each plot has a hardware cloth 0.6 m tall buried into the soil to prevent the access of other herbivores, such as European hare (*L. europaeus*). Each plot received one of four different sheep densities, ranging from densities recommended typically for the study area (0.2 sheep/ha/year) to very high densities (1.6 sheep/ha/year). These densities were based upon assessment of the forage condition of the sites. For this assessment, we used guidelines for pastures developed by specialists from INTA (Instituto Nacional de Tecnología Agropecuaria) for the study area (Bonvissuto et al. 2008; Siffredi et al. 2013), which are the standard for the area and are widely used by ranchers. Since these guidelines provided stocking rate recommendations per hectare per year and dry forage production per year, we calculated the area and grazing time corresponding to 1, 2, 4 and 8 times the recommended sheep stocking rate on that site. Because wethers (male castrated sheep) have a 920 g day^{-1} forage intake, the corresponding stock rate was 2, 4, 8 and 16 wethers in each enclosure for 3 days. In each plot we planted 42 seedlings of *P. contorta* (17.85 cm average height, SD 5.5) in a systematic way and similar microsites from a greenhouse where they had been grown under identical conditions. The seedlings were less than 2 years old, because it has been suggested that before that age they are susceptible to herbivore attack (Crozier and Ledgard 1990). The number of total and browsed branches, the maximum height before and after treatment and the survival immediately after the treatment were recorded for all seedlings. Each block was conducted in a different but adjacent place and at consecutively times but nevertheless, the environmental conditions and the forage available at each block was similar. The experiment and measurements were conducted in September and October 2014. All seedlings were removed at the end of the experiment.

Data Analysis

The percentage of damage (number of browsed branches/total number of branches) and the survival of seedlings were analyzed using hierarchical Bayesian models. These response variables were modeled with a binomial distribution where the probability that any branch was browsed or the probability of survival of each seedling was related via a logit link to the sheep stocking rate (explanatory variable, four treatments corresponding to 1, 2, 4 and 8 times the recommended sheep stocking rate on that site). Because each block was conducted in a different place and at a different time, from the hierarchical analysis we can explicitly consider that each one has characteristics that differentiate them (e.g., forage quality of each site, abiotic factors affecting sheep behavior) but they also have common sources of variation (Gelman and Hill 2007). We used a Markov Chains Monte Carlo (MCMC) method to obtain samples from parameter posterior probabilities, and we obtained their 95% credibility intervals (by calculating the HPD, highest posterior density interval). We set non-informative prior distributions. Statistical analyses were carried out with the Jags program (Plummer 2003). The JagsUI and Coda package of R version 3.2.0 was used (R Development Core Team 2015). Details of the analysis are available as electronic supplementary material (Online Resource 2).

Relative reduction in height of *P. contorta* seedlings under the treatments 1×, 2×, 4× and 8× sheep stocking rate was calculated as Relative differences = (initial height – final height/initial height) * 100. This relative difference was analyzed with the Kruskal–Wallis test.

Results

After 3 days of exposure of the *P. contorta* seedlings to sheep grazing ca. 95% were browsed and the severity of seedling damage (number of browsed branches/total branches per seedling) increased with sheep stocking rate. For treatments 1×, 2×, 4× and 8×, the percent of seedling damage was 79.2, 85.8, 93.8 and 99% respectively (Fig. 1). Whenever the seedling was browsed, the terminal bud was browsed (Table 3.1 for estimated means and 95% HPD interval values, Online Resource 3).

After 3 days of sheep browsing, the height of *P. contorta* seedlings was reduced by ca. 78% on average, ranging from seedlings with a mean height of 17.85 (5.5 SD) cm at the beginning of the experiment to a mean height of 3.77 cm (3.4 SD) at the end. All stocking rates produced a strong height reduction of *P. contorta* seedlings, increasing with level of treatment. Stocking rates at 4× and 8× produced a significantly higher reduction in seedling height than stocking rates of 1× and 2×. At the same time, there is no significant difference on height reduction when stocking rate is doubled from 1× to 2× (Fig. 2).

On the other hand, increasing sheep stocking rate negatively affected the probability of survival of *P. contorta*. Estimated probability of survival for treatments 1×, 2×, 4× and 8× was 56.1, 38.3, 12.7 and 0.8% respectively (Fig. 3, Table 3.2 for estimated means and 95% HPD intervals values, Online Resource 3).

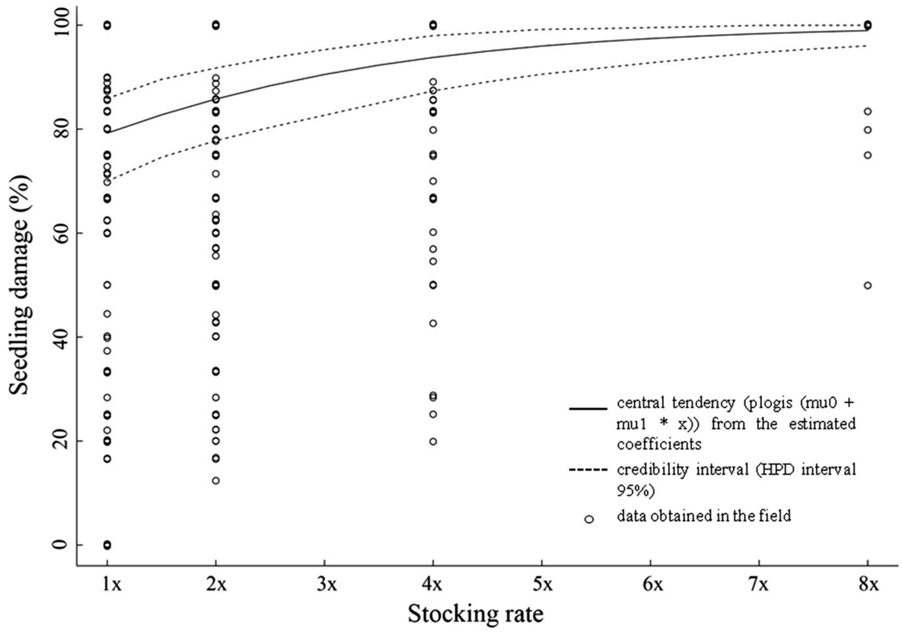

Fig. 1 Percentage of seedling damage (number of browsed branches/total branches per seedling) of *Pinus contorta* as a function of sheep stocking rate treatment

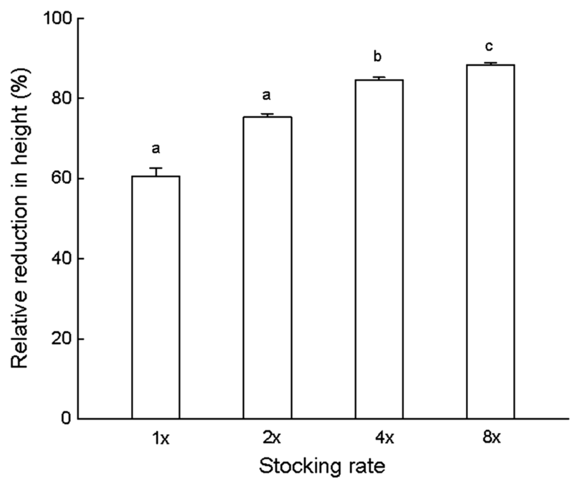

Fig. 2 Relative reduction in height (mean ± SE) of *Pinus contorta* seedlings under the treatment 1×, 2×, 4× and 8× sheep stocking rate. Relative reduction = ((initial height – final height)/initial height) * 100. Kruskal–Wallis test H(3) = 248.04 $p < 0.005$. *Different letters* above *bars* indicate significant differences

Discussion

Our results show that large mammalian herbivores can control conifer invasion by strongly damaging seedlings, reducing drastically their height and survival. In addition, and consistent with our hypothesis, the results indicate that severity of damage is determined by the stocking rate. In a systematic review, Richardson and Bond (1991) observed that grazing and browsing were the main types of disturbance implicated in conifer invasions (57% of studies). Previous studies have reported a negative effect of large herbivores (e.g., mainly cattle and sheep) on conifer invasions, but, in most of them, information on the animal species and herbivory intensity is lacking (Sarasola et al. 2006; Becerra and Bustamante 2009; de Villalobos et al. 2011). In this study we quantified the level of damage for every stocking rate tested. Yet, at the stocking rate recommended for the study area, sheep severely damage 2-years old seedlings of *P. contorta*, but only at the highest stocking rates (4× and 8×) do sheep consume practically all branches and thus effectively control *P. contorta*.

Beside the herbivory intensity, the severity of damage and thus the potential of large herbivores to control conifer invasion will also depend on the palatability of the species. In this case, *P. contorta* is considered one of the most preferred species by sheep, among Pinaceae such as *P. radiata, P. sylvestris*, *P*

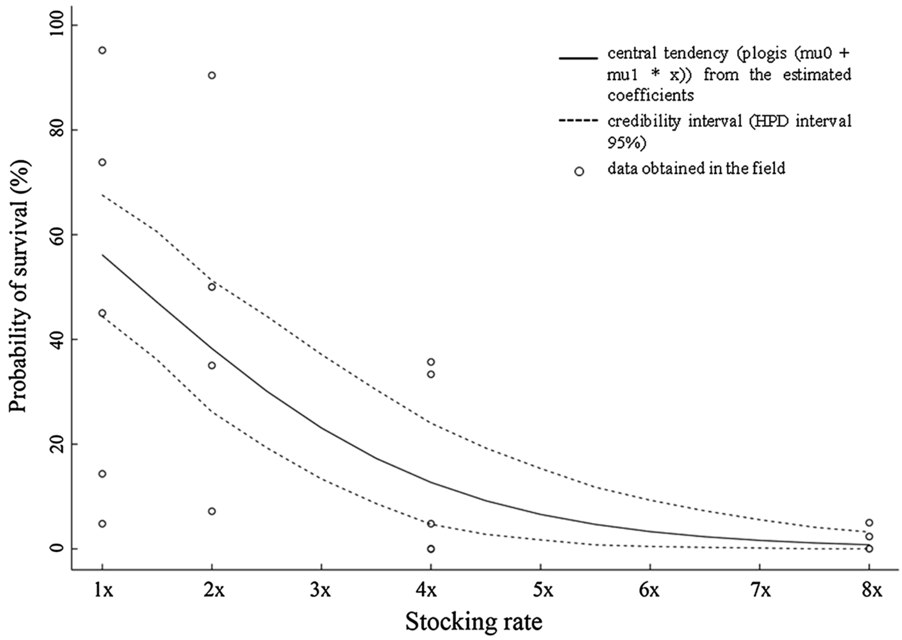

Fig. 3 Probability of survival of *Pinus contorta* as a function of sheep stocking rate

ponderosa and *P. nigra,* (Crozier and Ledgard 1990). So, future activities of management of conifer invasion with herbivory should consider this possible differences in palatability.

The experimental approach in this study allowed us to control by type and number of animals since we restrict the entry of others herbivores. This allowed us to conduct a detailed analysis of the implications of herbivory intensity for management of conifer invasion. Estimation of densities and interpretations of their effects from observational studies can be complicated, so this experimental approach sheds light on the importance of sheep densities for invasive tree management. Our results have the limitation that the sheep were kept in small plots, which could change their feeding behavior. However, these highly controlled plots of 625 m^2 are appropriate for the densities that we aimed for and in no plots were sheep alone (minimum number was two sheep per plot).

In most places where *P. contorta* is introduced, it is highly invasive (e.g., New Zealand, Chile and Argentina), so grazing might become a valuable and useful tool to control conifer invasion in the introduced range. Since it is known that conifers can regenerate at moderate levels of browsing, to be effective as control of invasions, browsing must occur before the lignifications of branches and the damage must be below the base of the live needles in order to ensure mortality (Crozier and Ledgard 1990; Edenius et al. 1993). In this study, stocking rate at 4× produced enough damage to avoid branch resprouting. Also, when a seed source remains close, annual periods of grazing in key seasons (i.e. spring) should be applied.

Several grazing managements have been proposed seeking to reduce the selective livestock behavior and to obtain a more homogeneous patterns of grazing (Savory 1983; Porath et al. 2002; Bailey 2004; di Virgilio and Morales 2016). Among these practices, many of them propose that high stocking rates increase the consumption of low palatable species and reduce litter accumulation from un-grazed senescent plants promoting better resource uses and productivity (Butterfield et al. 2006; Kurtz et al. 2016). These practices must be properly timed with continuous rotations and appropriated rest periods, taking into account the climatic variations and having a constant forage assessment. The results of using high stocking rates were variables and some of these proposed methods generated broadly debates (Briske et al. 2013; Cibils et al. 2014; Teague 2014) with favorable and unfavorable results both at global scale and locally in Patagonia (Oliva et al. 2012; Lalampaa et al. 2016;

Odadi et al. 2017). Nevertheless, conducting these practices in forestry sites could be an efficient tool to invasion control. Logically, farmers will prioritize their production rather than guarantee total mortality of pine seedlings with highest stockings rates, but the management practices proposed in our study are feasible and would significantly decrease the number of pines seedlings, and could delay the growth rate and retard the reproductive age of pines (Zamora et al. 2001).

Herbivory pressure will depend on the palatability of the target species. Chemical compounds differ greatly among conifer species, rendering them more or less palatable (Moreira et al. 2014). Since *P. contorta* is one of the most preferred conifers (Crozier and Ledgard 1990), our results may underestimate the herbivory intensity needed for other conifer species. Other control techniques could complement the use of sheep (Nuñez et al. in press). For instance, mechanical tools to eliminate the bigger trees in areas where they are superabundant can be important and can complement the effect of sheep well.

Our results indicate that large herbivores could be used for effective management of conifers at an early age in invaded areas such as Patagonia and suggest that prescribed grazing by sheep could be paired with other forestry practices to reduce risks of nonnative conifer expansion. This approach is not the ideal way to reduce densities in areas with conifers already widely established. Rather it could be effective in areas with a recent invasion, with young seedlings and with the possibility of moderate to high sheep stocking rate.

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