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Livestock reduces juvenile tree growth of alien invasive species with a minimal effect on natives: a field experiment using exclosures

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Abstract Many alien invasive tree species were originally introduced to their non-native ranges for use in forestry and as urban trees. These alien species were selected for their fast growth and not necessarily for possessing mechanisms which deter browsing. Instead, many tree species native to semiarid areas of the world evolved mechanisms which deter browsing, presumably at the cost of slower growth. In a semiarid rangeland we observed that livestock exclusion greatly promoted the growth of juveniles of several alien species but not of native species, and we hypothesized that this increase in growth of aliens was due to livestock preference for alien and not native trees. With the objective of quantifying our observations and understanding the mechanism underlying the increased growth rates of alien juvenile trees under livestock exclusion, we assessed growth and browsing levels in juveniles of two alien invasive and four abundant native tree species within three parcels where livestock was excluded and three parcels with livestock at 0.20 cattle equivalents.ha^{-1}. Alien species grew around four-fold faster under livestock exclusion than with livestock and, as predicted, received five times more browsing than natives. Instead, native species did not significantly increase their growth rate with livestock exclusion. The results support our hypothesis and the implications for management would be that stocking paddocks with livestock to browse existing alien juveniles and re-growth of felled adults should be effective in delaying invasions of trees used for forestry without significantly affecting the growth of the most abundant native trees.

Keywords Browsing · Herbivory · Cattle · Non-native · Exotic

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Introduction

Reducing alien tree invasions is a difficult but important task that will give native species more time to adapt to their new neighbors thus reducing adverse impacts of invasion such as alteration of nutrient cycling, hydrology and fire regimes (van Wilgen and Richardson 2014). As domestic livestock is known to retard juvenile tree growth through browsing (Giorgis et al. 2010; Speed et al. 2011), there exists the possibility of using livestock to control growth of juvenile alien trees. Livestock and large wild herbivores are powerful modulators of plant growing

conditions and a selective agent that can affect the function, structure and development of ecosystems (Milchunas et al. 1988; Cingolani et al. 2005, 2013). Furthermore, livestock has the potential to influence plant invasions in around 25 % of the terrestrial surface where it is present (Asner et al. 2004).

Many alien invasive tree species were originally introduced to their non-native ranges for use in industrial forestry and as urban trees (i.e. for USA Gavier-Pizarro et al. 2010; for Central Argentina Giorgis et al. 2011a). These alien species were selected for introduction due to their fast growth and not necessarily for possessing mechanisms which deter browsing. Most have acquisitive set of traits, which include broad, tender and thinner leaves, low wood density, high specific leaf area and high growth rate (Grotkopp and Rejmanek 2007; Tecco et al. 2010; van Wilgen and Richardson 2014). Because of existing resource use tradeoffs, trees with high growth rates are likely to produce less anti-herbivore defenses than slow growing trees (Herms and Mattson 1992).

Using livestock to control alien juvenile tree growth could be especially effective in ecosystems where alien invasive trees are highly browsed and native trees are less browsed or not browsed at all. Juvenile trees species that are unlikely to be highly browsed include species with physical defenses such as thorns, and species that are unpalatable to grazing animals, which typically have conservative traits including slow growth rates with tough and small leaves, high wood density, low specific area and low nutrient content (Vendramini et al. 2002; Skarpe and Hester 2008; Zeballos et al. 2014). These plants are often associated to arid and semiarid areas of the world which have had a long history of grazing by large herbivores, where many adaptations to aridity are convergent with adaptations to dissuade large herbivores (Milchunas et al. 1988).

We test these ideas in the seasonally dry mountains of central Argentina, a region where it is assumed that vegetation is adapted to a long evolutionary history of large herbivore grazing including past populations of *Lama guanicoe* and more recently replaced by domestic herbivores (Cingolani et al. 2008). Here, our personal observations suggest livestock exclusion greatly increases alien tree invasion as already reported for the alien shrub *Rosa rubiginosa* (Mestre et al. 2014). Additionally, in the past recent decades livestock farming has been partially suppressed at the urban—semi natural interface due to conflicts between ranchers and urban duelers (authors personal observations), which coincides with a significant expansion of alien tree invasions in these areas (Giorgis et al. 2011b; Gavier-Pizarro et al. 2012; Aguirre-Acosta et al. 2014). We hypothesize that in semiarid ecosystems livestock reduces juvenile tree growth of alien invasive species with a minimal effect on natives because livestock browses preferentially on fast growing aliens while native trees are less browsed by livestock. We quantify seasonal growth rates with and without livestock presence and predict that the proportion of browsed shoots will be higher in alien than in native juvenile trees. Our objective was to understand the mechanism underlying the increased growth rates of alien juvenile trees with livestock exclusion and thus propose livestock management scenarios which could be used to reduce alien tree invasions.

To the best of our knowledge, only two empirical studies have assessed the impact of large wild herbivores on the growth dynamics of native and alien tree species (Knapp et al. 2008; Relva et al. 2010), with no studies using domestic herbivores and no studies in ecosystems where most native tree species have conservative traits.

Methods

Study area

The study was conducted in a private property in the locality of "San Antonio de Arredondo" (S31°28′; W64°32′), Córdoba province, Argentina. The site contains forest remnants of different sizes and isolated trees and is used for tourism and for cattle grazing. The vegetation of the area corresponds to the Chaco Serrano phytogeographical region, with *Acacia* spp., *Geoffroea decorticans, Condalia montana, Schinus fasciculata, Celtis ehrenbergiana, Prosopis* spp. and *Jodina rhombifolia,* as the most abundant native tree species and with *Ulmus pumila, Gleditsia triacanthos, Ligustrum lucidum* and *Pyracantha angustifolia* as the most important alien tree species in the area (Giorgis et al. 2011a). The site is at 700 m a.s.l. and mean annual precipitation is 830 mm, which is concentrated in the warm season. Winters are relatively dry and cold, with mean annual temperature of 16.5 °C (Colladon and Pazos 2014).

Experimental design

Measures were taken in 2010 and 2011 on six permanent parcels of 2.1 to 2.3 ha that were established in October 2007. Three of the parcels were fenced to prevent livestock access whereas the other three parcels were open and located nearby in a pair wise fashion. All parcels are located within a large paddock of 213 ha with a livestock load of 0.20 cattle equivalents.ha^{-1}. All parcels with and without livestock share a similar topography and vegetation type (more details in Torres and Renison 2015).

The selection of alien and native tree species was based on their relative abundance within the study site. The selected alien tree species were *Ulmus pumila* L. (Ulmaceae), from Central Asia (Fu et al. 2003) and *Gleditsia triacanthos* L. (Fabaceae), from USA (Blair 1990). The native species *Geoffroea decorticans* Gillies ex Hook. and Arn. (Fabaceae), *Schinus fasciculatus* (Griseb.) I. M. Johnst. (Anacardiaceae), *Condalia montana* A. Cast. (Rhamnaceae) and *Acacia caven* (Molina) Molina (Fabaceae) are known as successful pioneer species present in the early successional stages of Chaco Serrano forest (Giorgis et al. 2011a).

Growth and browsing

In each parcel we selected and marked 7 juveniles per species (basal diameter 2–4 cm) (N total = 42 individuals per species). We only selected juveniles that were accessible to livestock browsing, thus our study does not contemplate indirect facilitation by protection from surrounding spiny trees (Torres and Renison 2016). We monitored for growth in height and browsing every two months throughout a year (6 measurements). Juvenile height was measured with a meter tape from a fixed point at the base to the highest shoot. Cumulated growth in height after a year was calculated as the difference in height (cm) between last and first measurements. We also calculated a relative growth rate in height (RGR$_H$; Hunt 1990) per juvenile as: (LnH2 − LnH1/T2 − T1), where LnH1 and LnH2 are the natural logarithm of juvenile height measured every 60 days across 12 months (i.e., T2 − T1 = 60). Browsing was estimated as the proportion of recently browsed shoots in 20 randomly selected shoots per individual (as in Giorgis et al. 2010). We distinguished recent from old browsing because browsed tips dried with time.

Data analysis

Analyses were performed in R environment (R development Core Team 2009). Our response variables were annual growth in height (cm), relative growth rate in height (cm day^{-1}), and mean proportion of browsed shoots per individual. We used linear mixed effects model (*lme* function, Pinheiro et al. 2009) for the quantitative response variable (growth in height and RGR$_H$) and generalized linear mixed effect models (*lmer* function, Bates and Maechler 2009), for the binomial-distributed response variable (browsing proportion). Each variable was analyzed separately for each tree species. We used livestock as the fixed main effect with two levels (presence and absence), and parcel as a random effect (N = 6) nested within livestock condition. When analyzing relative growth rate in height (RGR$_H$) we included growth season as another fixed factor with two levels (wet and dry seasons). We subsequently run post hoc tests (Tukey honest significant difference) to determine differences among the two main factor levels. Because no herbivory was observed within livestock-excluded parcels, we further tested for browsing differences among native and alien tree species within parcels with livestock. For this analysis we used origin as the fixed main effect with two levels (alien and native) and parcels with livestock as a random effect (N = 3) nested within origin condition. Significance of fixed effect was assessed with *F*-tests in linear mixed models and with Wald-*Z* in generalized linear mixed models. Model parameters were estimated with restricted maximum likelihood methods and Laplace approximation for *lme* and *lmer* functions, respectively.

Results

Growth

Annual growth in height of the alien *U. pumila* and *G. triacanthos* was on average 4 and 4.5 times higher, respectively, in the livestock-excluded parcels as compared to the parcels with livestock (Fig. 1). Instead, in the four native tree species annual growth in height was similar in the livestock-excluded parcels as compared to the parcels with livestock; furthermore, annual growth
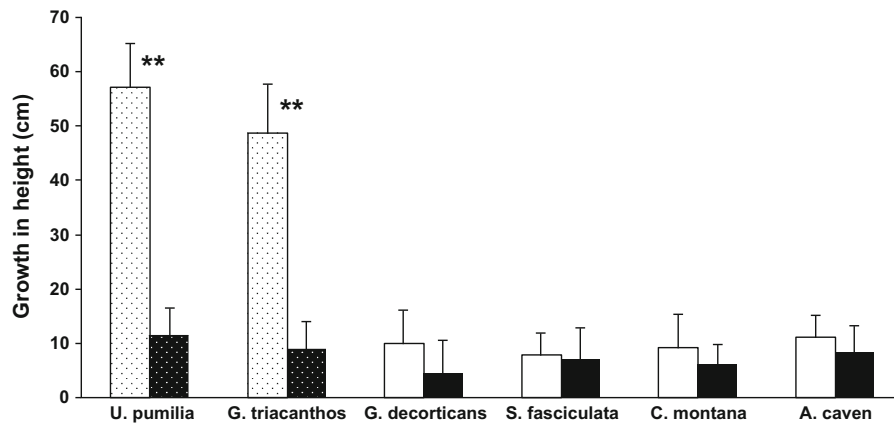
Fig. 1 Annual growth in height of juveniles belonging to six tree species in the absence (*white bars*) and presence (*black bars*) of livestock. The two alien species are denoted with white and black dotted patterns. *Asterisks* indicate statistical significant differences ($P < 0.05$) in growth with or without livestock (see text for model description and genus names)

in height of native species was comparable to the growth of aliens with livestock presence (Fig. 1).

Interestingly, livestock presence significantly decreased the relative growth rates (RGR_H) of alien species but had almost no effects on the RGR_H of native tree species (Table 1). The only exception was the native tree *G. decorticans* that showed a small decrease in RGR_H during the wet season in parcels with livestock as compared to parcels without livestock (Table 1). As expected, seasonality in precipitation regime had significant effects on RGR_H in all alien and native tree species. All species showed the highest RGRs during the wet season from October to April (Table 1; Fig. 2a, b). The only exception was the alien tree *G. triacanthos* that showed no significant changes in RGR_H in parcels with livestock across wet and dry seasons (Table 1). During the dry season (from April to October), RGR_H substantially decreased for all tree species but in livestock-excluded parcels alien species still showed overall higher RGR_H than native trees (Table 1; Fig. 2a). Parcels subjected to livestock showed similar RGR_H among alien and native tree species during the wet season (Table 1; Fig. 2b). However, while RGR_H of native trees approached nil values in parcels with livestock during the dry season, alien species showed negative RGR_H values as a result of increased livestock browsing during this period (Fig. 2b). Parcel identity as a random factor nested within livestock condition had no significant effects on RGR_H for any of the studied species (not shown).

Browsing

As would be expected, in parcels without livestock there was no browsing at all in any of the measured individuals. Instead, in parcels with livestock, browsing varied among species and months within the year (Fig. 3). Alien tree species were subjected to the highest browsing percentages, especially during the beginning of the wet season with around 96 % of the growth buds with recent signs of browsing (Fig. 3). During the rest of rainy season (December–April) browsing decreased to 20 and 10 % in *U. pumilia* and *G. triacanthos*, respectively. Native tree species, however, were subjected to less browsing during the same time period, with the highest browsing percentages ranging from 43 to 12 % and decreasing to nearly 0 % by April (Fig. 3). During the dry season browsing strongly decreases for most of the species (Fig. 3). On average, across months and species, alien tree species suffered 5 times more browsing than native tree species ($Z = -7.812$; $P < 0.001$; Fig. 4) in parcels with livestock.

Discussion

The results obtained here support our hypothesis that in semiarid areas with a long evolutionary history of grazing livestock reduces juvenile tree growth of alien invasive species with a minimal effect on natives because livestock consistently consumed the shoots of

Table 1 Mean relative growth rate (cm day^{-1}) in dry and wet seasons for each alien and native tree species growing in parcels with and without livestock

| | Parcels without livestock | | Parcels with livestock | | F-values from main factors and their interaction | | |
	Wet season	Dry season	Wet season	Dry season	Livestock condition	Season	Livestock condition X Season
Alien tree species							
Ulmus pumila	0.374 ± 0.121**a**	0.016 ± 0.059**b**	0.042 ± 0.111**c**	0.005 ± 0.063**b**	$F_{[1,\,72]} = -22.44$***	$F_{[1,\,72]} = 44.05$***	$F_{[1,\,72]} = 13.49$**
Gleditsia triacanthos	0.316 ± 0.118**a**	0.078 ± 0.114**b**	0.020 ± 0.085**c**	0.029 ± 0.061**c**	$F_{[1,\,72]} = 12.75$**	$F_{[1,\,72]} = 3.04$^{NS}	$F_{[1,\,72]} = 8.81$*
Native tree species							
Geoffroea decorticans	0.049 ± 0.037**a**	0.008 ± 0.011**b**	0.014 ± 0.009 **b**	0.012 ± 0.017**b**	$F_{[1,\,72]} = 4.59$*	$F_{[1,\,72]} = 8.51$**	$F_{[1,\,72]} = 6.42$*
Schinus fasciculata	0.037 ± 0.017**a**	0.008 ± 0.006**b**	0.047 ± 0.025**a**	0.001 ± 0.001**b**	$F_{[1,\,72]} = 0.112$^{NS}	$F_{[1,\,72]} = 34.85$***	$F_{[1,\,72]} = 2.10$^{NS}
Condalia montana	0.048 ± 0.031**a**	0.004 ± 0.002**b**	0.032 ± 0.021**a**	0.002 ± 0.001**b**	$F_{[1,\,72]} = 1.80$^{NS}	$F_{[1,\,72]} = 6.98$***	$F_{[1,\,72]} = 0.25$^{NS}
Acacia caven	0.065 ± 0.026**a**	0.009 ± 0.006**b**	0.043 ± 0.025**a**	0.004 ± 0.001**b**	$F_{[1,\,72]} = 0.423$^{NS}	$F_{[1,\,72]} = 26.96$***	$F_{[1,\,72]} = 0.22$^{NS}

NS stands for not significant, different letters in the cells indicate significantly different values ($P < 0.05$)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$
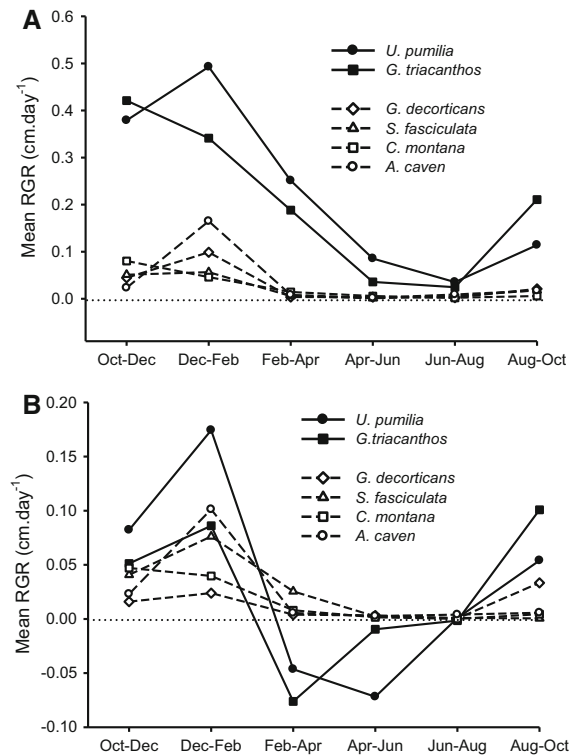
Fig. 2 Mean relative growth rate per day every 2 months for each alien and native tree species in parcels where livestock was excluded (**a**) and in parcels with livestock presence (**b**)

alien trees and to a much lesser extent of native trees. This is in line with evidence reviewed by Daehler (2003), which suggests that invasive aliens outperform natives under most, but not all growing conditions, with our study providing for the first time the suggestion that livestock can favor native tree species over alien invasive trees in semiarid areas with a long evolutionary history of grazing.

The reduced browsing observed in the studied native species as compared to the studied alien species is probably explained by the native species conservative growth traits, which imply slower growth rates and the development of physical and chemical defenses against browsing by large mammals such as thorns and secondary compounds, respectively (Cooper and Owen-Smith 1986; Hanley et al. 2007). Interestingly, although the alien G. triacanthos also presents thorns in trunk and branches, livestock still heavily browsed it. One important difference of such defenses in G. triacanthos at our study area in comparison with that of native species is that at initial
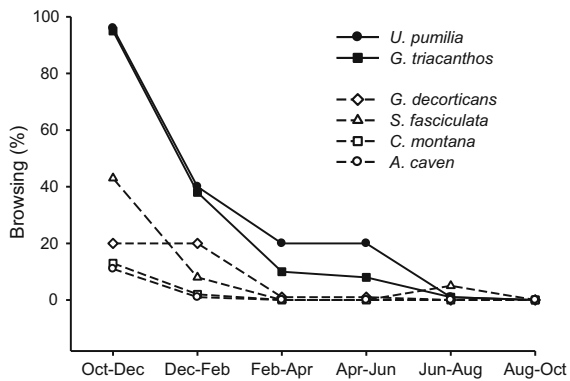
Fig. 3 Proportion of newly browsed shoots per species as measured every 2 months throughout a year, between October 2010 and October 2011 at parcels with livestock. The two alien species are shown filled in *black*, while native species are filled in *white*

development and growth, thorns in *G. triacanthos* juveniles are green, soft, and flexible as any other bud and leaf. Such characteristic would make *G. triacanthos* as vulnerable to browsing in early stages of development as the other alien tree of our study area, *U. pumila*.

Two previous studies have assessed the relative effects of browsing by large mammals on alien and native plant species and have found contrasting response patterns (Knapp et al. 2008; Relva et al.
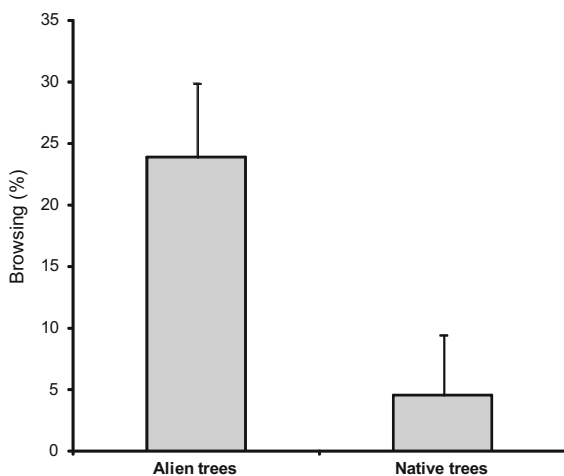
Fig. 4 Overall mean browsing throughout a year for alien (N = 2) and native (N = 4) tree species growing in parcels with livestock presence ($Z = -7.812$; $P < 0.001$; see text for model description)

2010). These studies were conducted in temperate forests and showed that large mammal browsing can have negative and positive effects on growth in both alien and native plant species. Contrary to such preceding evidence, here, the studied native tree species representative of early successional Chaco Serrano subtropical dry forest tree species are resilient to browsing by livestock due to their conservative growth traits. Thus, although alien species grow much faster under livestock exclusion than native trees, the growth rate of alien and native species tends to be similar with the presence of livestock. Hence, livestock can act as a biological control agent that can limit growth of alien tree species such as *U. pumila* and *G. triacanthos* in their sapling and juvenile stages. In our study system, livestock use as a biological control could be restricted to the early rain season from October to February as browsing was mainly concentrated within this period. In the long term, however, we expect that once alien trees reach heights at which livestock browsing is greatly reduced (e.g., larger than 354 cm; Pollice et al. 2013), their growth rate will become higher than that of their native counterparts. Thus, after a certain height threshold, alien trees will have a larger contribution to seed production and population growth rate.

We can anticipate several drawbacks to the use of livestock as biological control of alien juvenile trees. Firstly, it will only function at micro-sites accessible to livestock browsing. Steep escarpments, ravines and dense patches of spine shrubs and trees are usually less used by livestock and would escape control (Renison et al. 2015; Torres and Renison 2015, 2016). Second, livestock can also affect the recruitment of native species by trampling and soil compaction (e.g., Torres et al. 2008), and due to browsing of late successional native species not contemplated in our study (Torres and Renison 2015, 2016). Lastly, livestock often serves as dispersal agent of several alien plant species with nutritive fruits such *G. triacanthos* (Ferreras et al. 2014) and often promotes plant invasion through reducing plant competition and augmenting open spaces where new individuals may establish (Chaneton et al. 2002). Thus, alien species can benefit from livestock to increase their ranges and occupy vacant sites in human-disturbed systems (Ashworth et al. 2015).

Given the anticipated drawbacks to the use of livestock as a biological control for alien species, we

propose livestock should be considered when pad-docks have a large portion of the invaded area accessible to browsing and when recruitment of native species by trampling and soil compaction is not seriously delayed. The use of livestock should be restricted to early successional stages and must be discontinued to promote establishment of susceptible late successional species out of protected sites, and should be restricted to the target species that are not dispersed by livestock as for example the wind dispersed *U. pumila* or when invasion is not limited by seed dispersal as would be the case of highly invaded sites where *G. triacanthos* adults and seeds are already present at high densities in all the paddock. Not withstanding the drawbacks, livestock could be used in extensive areas of central Argentina and the world where early successional forests are now prevailing (Zak and Cabido 2009) and being invaded by alien trees which are selected for browsing.

More research needs to be conducted to validate and generalize these results to other alien plant species, assessing different life stages of plants and also different livestock loads and species for a better understanding of its potential as control agent of alien species growth. Studies should also compare the relative efficiency of livestock versus other control techniques on alien species that imply direct human interventions. In particular, we expect that felling of large and fecund alien trees (i.e. higher than 2 m) in combination with the maintenance of livestock that browse smaller trees and felled re-sprouting trees may be a especially successful method for controlling alien trees in systems where native trees are resilient to browsing, while producing an economic income to land managers through livestock rearing.

References

Aguirre-Acosta N, Kowaljow E, Aguilar R (2014) Reproductive performance of the invasive tree *Ligustrum lucidum* in a subtropical dry forest: does habitat fragmentation boost or limit invasion? Biol Invas 16:1397–1410

Ashworth L, Martí L, Calviño A, Aguilar R (2015) Offspring performance and recruitment of the pioneer tree *Acacia caven* (Fabaceae) in a fragmented subtropical dry forest. Austral Ecol 40:634–641

Asner GP, Elmore AJ, Olander LP et al (2004) Grazing systems, ecosystem responses, and global change. Annu Rev Environ Resour 29:261–299. doi:10.1146/annurev.energy.29.062403.102142

Bates D, Maechler M (2009) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-32. http://CRAN.R-project.org/package=lme4

Blair RM (1990) *Gleditsia triacanthos* L. (honeylocust). In: Burns RM, Honkala BH (eds) Silvics of North America, 2, hardwoods. Agricultural Handbook. Department of Agriculture, Forest Service, Washington, DC, pp 358–364

Chaneton EJ, Perelman SB, Omacini M, León RJC (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. Biol Invasions 4:7–24

Cingolani AM, Noy-Meir I, Díaz S (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecol Appl 15:757–773. doi:10.1890/03-5272

Cingolani AM, Renison D, Tecco PA, Gurvich DE, Cabido M (2008) Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. J Biogeogr 35:538–551

Cingolani AM, Vaieretti MV, Giorgis MA et al (2013) Can livestock and fires convert the sub-tropical mountain rangelands of central Argentina into a rocky desert? Rangel J 35:285–297

Colladon L, Pazos I (2014) Anuario pluviometrico 1992/93—2011/12, Cuenca del Río San Antonio, vol 1. Instituto Nacional del Agua, Ezeiza, pp 1–86

Cooper SM, Owen-Smith N (1986) Effects of plant spinescence on large mammalian herbivores. Oecologia 68:446–455

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu Rev Ecol Evol Syst 34:183–211

Ferreras AE, Funes G, Galetto L (2014) The role of seed germination in the invasion process of Honey locust (*Gleditsia triacanthos* L., Fabaceae): comparison with a native confamilial. Plant Species Biol 30:126–136

Fu L, Xin Y, Whittemore A (2003) Ulmaceae. In: Wu Z, Raven P (eds) Flora of China, Vol. 5 (Ulmaceae through Basellaceae). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, USA, pp 1–10

Gavier-Pizarro GI, Radeloff VC, Stewart SI et al (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecol Appl 20:1913–1925

Gavier-Pizarro GI, Kuemmerle T, Hoyos LE et al (2012) Monitoring the invasion of an exotic tree (*Ligustrum lucidum*) from 1983 to 2006 with Landsat TM/ETM + satellite data and Support Vector Machines in Córdoba, Argentina. Remote Sens Environ 122:134–145

Giorgis MA, Cingolani AM, Teich I, Renison D, Hensen I (2010) Do *Polylepis australis* trees tolerate herbivory? Seasonal patterns of shoot growth and its consumption by livestock. Plant Ecol 207:307–319

Giorgis MA, Cingolani AM, Chiarini F, Chiapella J, Barboza G, Espinar LA, Morero R, Gurvich DE, Tecco PA, Subils R, Cabido MR (2011a) Composición florística del Bosque

Chaqueño Serrano de la provincia de Córdoba, Argentina. Kurtziana 36:9–43

Giorgis MA, Tecco PA, Cingolani AM, Renison D, Marcora P, Paiaro V (2011b) Factors associated with woody alien species distribution in a newly invaded mountain system of central Argentina. Biol Invas 13:1423–1434

Grotkopp E, Rejmanek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. Amer J Bot 94:526–532

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. Perspect Plant Ecol Evol Syst 8:157–178

Herms DA, Mattson WJ (1992) The Dilemma of plants: to grow or defend. Quart Rev Biol 67:283–335

Hunt R (1990) Basic growth analysis. Unwin Hyman, London

Knapp LB, Fownes JH, Harrington RA (2008) Variable effects of large mammal herbivory on three non-native versus three native woody plants. Forest Ecol Manag 255:92–98

Mestre L, Chartier M, Renison D (2014) Effect of livestock on the growth of *Rosa rubiginosa* in a mountain range: a dendrochronological approach. Appl Ecol Environ Res 12:855–866. doi:10.15666/aeer/1204

Milchunas DG, Sala OE, Laurenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106

Pinheiro J, Bates D, Debroy S, Sarkar D (2009) The R Core team. nlme: Linear and nonlinear mixed effects models. R package version 3.1-96

Pollice J, Marcora P, Renison D (2013) Seed production in *Polylepis australis* (Rosaceae) as influenced by tree size, livestock and interannual climate variations in the mountains of central Argentina. New For 44:233–247. doi:10.1007/s11056-012-9313-0

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3 900051-07-0

Relva MA, Nuñez MA, Simberloff D (2010) Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol Invasions 12:303–311

Renison D, Chartier MP, Menghi M, Marcora P, Torres RC, Giorgis M, Hensen I, Cingolani AM (2015) Spatial variation in tree demography associated to domestic herbivores and topography: insights from a seeding and planting experiment. For Ecol Manage 335:139–146

Skarpe C, Hester AJ (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: Gordon IJ, Prins HHT (eds) The Ecology of Browsing and Grazing. Springer, Berlin, pp 217–261

Speed JDM, Austrheim G, Hester AJ, Mysterud A (2011) Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. For Ecol Manag 261:1344–1352

Tecco PA, Dí-az S, Cabido MR, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? J Ecol 98:17–27

Torres RC, Renison D (2015) Effects of vegetation and herbivores on regeneration of two tree species in a seasonally dry forest. J Arid Environ 121:59–66. doi:10.1016/j.jaridenv.2015.05.002

Torres RC, Renison D (2016) Indirect facilitation becomes stronger with seedling age in a degraded seasonally dry forest. Acta Oecol 70:138–143. doi:10.1016/j.actao.2015.12.006

Torres RC, Renison D, Hensen I et al (2008) *Polylepis australis*' regeneration niche in relation to seed dispersal, site characteristics and livestock density. For Ecol Manag 254:255–260

van Wilgen BW, Richardson DM (2014) Challenges and trade-offs in the management of invasive alien trees. Biol Invasions 16:721–734

Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytol 154:147–157

Zak MR, Cabido MR (2009) Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. Appl Vege Sci 5:213–226

Zeballos SR, Giorgis M, Cingolani AM et al (2014) Do alien and native tree species from Central Argentina differ in their water transport strategy? Austral Ecol 39:984–991. doi:10.1111/aec.12171