



Spatial variation in tree demography associated to domestic herbivores and topography: Insights from a seeding and planting experiment



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ABSTRACT

Tropical and subtropical high mountains forests are mainly situated within ravines. Two alternative and often confronted explanations have been proposed for this pattern: that abiotic environmental conditions are favourable for tree establishment only within ravines, or that ravines are less affected by grazing and fires which negatively affect establishment in other sites. Here we propose a mixed explanation and hypothesize that abiotic environmental conditions associated to spatial variation are important during early seedling establishment and that grazing is the main determinant during later stages through its negative effect on survival and growth of larger saplings. We sowed 302,400 seeds and planted 360 saplings of the dominant tree species from the upper Córdoba Mountain range (Central Argentina) with and without grazing in three contrasting sites: a ravine, a valley and a ridge. We monitored seeding plots 5 years until the seedlings reached the height of the planted saplings and we monitored the planted saplings for 12 years. We integrated life stages using matrix multiplications, which resulted in data simulating 17 years of the trees' early development. Our results showed that seedling establishment was lower in the ravine and ridge sites and higher in the valley site with negative differences due to grazing only in the valley. Planted sapling survival increased but growth decreased from ravine to valley and ridge sites in the absence of large herbivores, while both survival and growth were substantially lower in the presence of large herbivores. Matrix multiplications indicated that differences between sites were 5.0 times more important than grazing when integrating up to year 5, but grazing by large herbivores was 5.4 times more important than differences between sites when assessed across the whole 17 year period. We conclude that there could be a strong influence of grazing in restricting high montane forests to sites like ravines where large herbivores are less frequent and show how the relative importance of site characteristics and grazing changes as a result of the length and the differing life stages which are monitored.

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1. Introduction

Subtropical and tropical mountains forests situated above the continuous timberline are often found in ravines, with little or no tree cover in open sites such as valley floors, gentle slopes, ridges and convex summits (Körner, 2012). In South America much debate exists on the causes of this prevalence of forests to ravines and the issue has been termed “the *Polylepis* problem” (Kessler, 2002) because in this continent it is mainly species of the genus *Polylepis* which dominate the canopy of the high mountain forests

above the timberline in a 5400 km forest belt which ranges from Venezuela to Central Argentina.

Proponents of the natural distribution explanation suggest that *Polylepis* forests are mainly situated within ravines due to a combination of more favourable micro climate conditions including protection from freezing, wind and radiation, and due to deeper soils with better moisture conditions (review in Kessler, 2002). Studies supporting this view have been performed in absence of grazing and fires. For example, better microclimatic growing conditions were determined within forest as compared to forest gaps and surrounding paramo vegetation for *Polylepis sericea* in Venezuela (Rada et al., 2009). Also, better soil nutrient and water conditions are reported within ravine woodlands as compared to shrublands

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situated in higher topographies for *Polylepis australis* in Argentina (Enrico et al., 2004).

Proponents of the anthropogenic explanations note that in most tropical and subtropical mountains herbivory is largely exerted by free roaming domestic livestock (Messerli and Ives, 1997) and that it is well established that in alpine environments browsing by herbivores affects woodland regeneration by retarding or even hampering juvenile growth (Cairns and Moen, 2004; Speed et al., 2011). Forest restriction to ravines could be explained at least in part because here trees may find protection from browsing because at these sites domestic herbivores are more exposed and vulnerable to predation than in open sites (i.e. for wild herbivores; Ripple and Beschta, 2003). Also, in ravines fire incidence is reduced due to higher moisture content and the tendency of fire to spread uphill, and hence in ravines we find fewer domestic herbivores which are attracted to post-fire plant re-growth (Renison et al., 2006; Coblenz and Keating, 2008). Studies performed in sites with differing herbivore densities show mixed support for the anthropogenic explanation. In Ecuador more *Polylepis incana* seedlings are found in sites with higher livestock impact (Cierjacks et al., 2007). In central Argentina more *P. australis* seedlings are found at intermediate livestock densities than without livestock or at high livestock densities (Torres et al., 2008; Zimmermann et al., 2009), but juvenile growth is severely hampered by livestock (Giorgis et al., 2010). Thus, seedling studies do not seem to support the anthropogenic explanation and juvenile studies support it.

Population filters due to microclimate, soil conditions and browsing may exert their effects at different plant life stages. Small seedlings may be more vulnerable to stressing microclimatic conditions such as wind, strong radiation and lack of moisture, which could easily desiccate a seedling in its early stages. When seedlings grow larger (i.e. >3 cm) they become accessible to large herbivores and thus became vulnerable to browsing (Fenner and Thompson, 2005). Fires may affect all life stages in complex patterns where some life stage may be more affected than others. The use of fire to sustain grazing areas and improve forage quality is certainly very relevant to understand the spatial pattern of *Polylepis* forests (i.e. Renison et al., 2002; Cierjacks et al., 2008; Coblenz and Keating, 2008). The forest belt occupied by small *Polylepis* forest patches and isolated trees found above the continuous timberline in subtropical and tropical mountains forms part of what has been termed the “ecosystem uncertain” climate envelope where vegetation types dominated by grasses and by different types of woody vegetation coexist (Whittaker, 1975). Under these climatic conditions the balance between vegetation types may be driven to a certain extent by large herbivores but also by fires which can be thought of as a non-selective consumer (Bond, 2005).

Here, we experimentally manipulate livestock presence and control for seed and plant density at different sites. We report elsewhere the important influences of fire (Alinari et al., in press). Our objective is to gain insight into demographic filters that show the relative importance of site characteristics as compared to grazing, and discuss its implications in the debate over the causes of the restriction of *Polylepis* forests to ravines. We hypothesised that differences between sites would be the main driver during early establishment, when seedlings are most vulnerable to harsh micro climatic and abiotic conditions prevalent out of ravines (Enrico et al., 2004). We additionally hypothesized that grazing would be the main driver of survival and growth after the seedling stage, as grazers are known to eat parts of tree saplings when accessible (Giorgis et al., 2010; Marcora et al., 2013). We therefore predict a greater influence of contrasting site characteristics at the early life stages with an increasing influence of livestock at the later stages.

Polylepis forests contain an important richness of endemic species which in many cases is endangered, forest extension and density has been reduced in many regions and soil loss has been

prominent in extended areas within the *Polylepis* forest belt (Jameson and Ramsay, 2007; Gareca et al., 2010; Robledo and Renison, 2010; Renison et al., 2013). Obtaining insights into the drivers of high altitude *Polylepis* forest distribution is important to provide information to assist the many ongoing *Polylepis* forests restoration projects by pointing at the spatial variation in tree demography associated to domestic herbivores and topography.

2. Materials and methods

2.1. Study area and species

The Córdoba mountains in Central Argentina (31°34' S; 64°50' W; 500–2800 m) have a mean temperature of 5.0 and 11.4 °C at 2100 m for the coldest and warmest months, respectively, with occurrence of below zero temperatures all year round. Mean annual precipitation from 1992 to 2010 averaged 900 mm. The long, dry and cold season lasts from May to September and 83% of the rainfall is concentrated in the warmer months between October and April (Colladon et al., 2010). Soils are mainly derived from weathering of the granite substrate and fine-textured Aeolian deposits (Cabido et al., 1987). The main economic activity is livestock rearing (cattle, sheep, horses and goats), which began in the 17th century, and all large native herbivores went extinct by the 1920s. At present, local livestock densities range from 0.1 to 4.8 cattle equivalents/ha (von Müller et al., 2012). The main livestock predator in the area is the puma (*Puma concolor*) which is still fairly abundant in the higher mountains (Pia et al., 2013) and according to local ranchers is often found within forested ravines (personal communications).

The vegetation belts in the study area have been traditionally described as a lower seasonally dry forest dominated by trees such as *Lithraea molleoides* and *Celtis ehrenbergiana* with a timberline at around 1300 m asl (Luti et al., 1979). The areas above the timberline, up to the highest altitudes of 2884 m asl, consist of a mosaic of tussock grasslands, short grazed grasslands, exposed granite surfaces and rock outcrops. In addition, around 12% of the area comprises scattered forest stands and shrublands largely restricted to ravines and gorges (locally called “quebradas”), but also found in rock outcrops and in the slopes of open valleys in areas with less human disturbance (Cingolani et al., 2008). The canopy of the forest patches above the continuous timberline is dominated by *P. australis*, which at lower altitudes mixes with other tree species, mainly *Maytenus boaria* (Renison et al., 2011).

P. australis is endemic to the mountains of Central and North-Western Argentina (Renison et al., 2013) and is strongly consumed by livestock which on average browses from 85% of the accessible shoots when at moderate stocking rates and 98% of the accessible shoots under the heavy grazing pressures typical of the area (Giorgis et al., 2010). *P. australis* can reach up to 14 m in height, the fruits are single seeded nutlets (hereafter referred to as seeds) that ripen and fall from the trees between January and April; they usually germinate immediately after dispersal at the end of the wet season in March and April. Seed viability is variable, ranging from 0% to 60% with an average viability of around 20% (Renison et al., 2004).

2.2. Seeding and planting experiments

We performed two seeding and one planting experiments in the northern part of the higher Córdoba Mountain range (Los Gigantes, 31°25' S; 64°48' W; 2270 m asl) in three sites of contrasting topography: the bottom of a ravine, the lower slopes of an open valley, and a flat ridge site (hereafter ravine, valley and ridge, respectively). We selected these particular sites because they were

available within short distances thus controlling for other possible confounding factors such as altitude, latitude, rainfall or biotic factors such as possible local insect outbreaks. Vegetation at all sites was composed of short grasses and forbs dominated by *Alchemilla pinnata*, *Carex fuscula*, sometimes together with small tussocks of *Deyeuxia hieronymi*. The taller tussock *Poa stuckertii* increased in abundance from the ridge, to the ravine site with intermediate covers in the valley, in accordance to its better performance in sites with more moisture (Cingolani et al., 2003, 2014). In December 2000 we removed livestock from half of each of the sites differing in topography by constructing an 8 ha enclosure (Fig. 1). The other half of each site was thereafter grazed by cattle and horses (0.13 ± 0.01 cattle equivalents/ha⁻¹, as estimated from five dung counts performed throughout the years using the model developed for the study area, von Müller et al., 2012). Livestock densities were constant throughout the experiment and the three sites provided similar levels of accessibility to livestock, though it was evident after 12 years that the ravine site was less used by livestock, as judged by the height of tussock grasses (see Table 1; Cingolani et al., 2003).

The seeding experiments were performed in March 2001 when vegetation was very similar in and out of the enclosure, and in March 2004 when vegetation was taller within the enclosure than out. We used pooled seeds collected from over 30 trees. Timing for seeding was chosen to simulate a late natural seed fall, allowing 30 days for seed processing from collection of the ripe fruits to seeding. In each date we seeded 252 plots (42 for each combination of grazing and site) of 400 cm² with 6 g of seeds each (approximately 600 ± 5 seeds, as estimated by counting). Seeded plots were distributed irregularly with the restriction that they were separated from each other by at least 5 m. We annually monitored the plots at the end of the winter in August. We carefully searched for seedlings in the plot and surroundings and upon detection we marked seedlings with metal pins, recorded their heights (cm) and checked for signs of browsing (cut stems). To control for spontaneously appearing seedlings, the presence of seedlings was also checked in a control plot and surroundings where no seeding had taking place. However in the 252 control plots we only detected a total of only one seedling, so we disregarded any possible influence of incoming seeds. Seeding plots were monitored until the

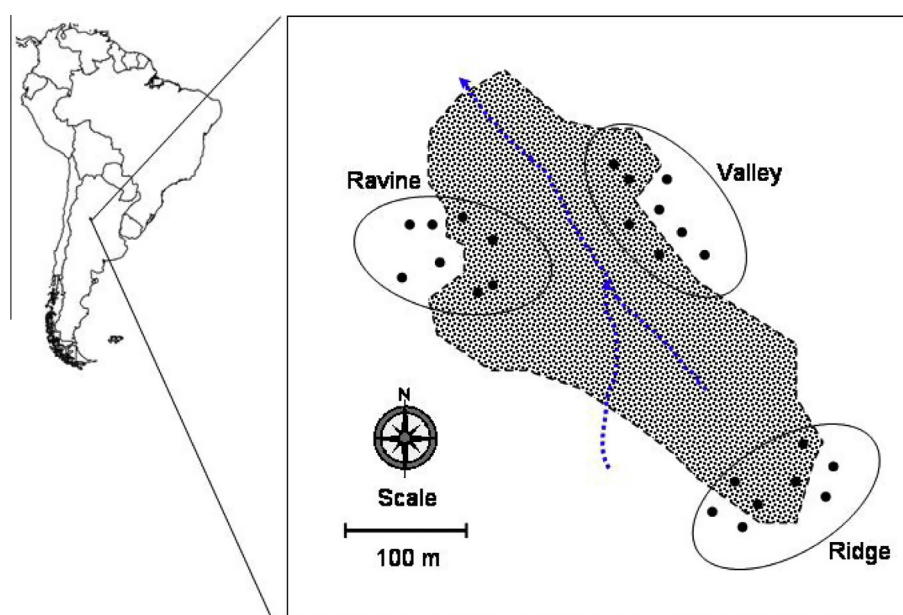


Fig. 1. Location of the study sites within South America and a schematic representation of the disposition of the ravine, valley and ridge study sites (oval circles), study plots (black circles within – only a sample), and of the area without livestock (dotted texture) and with livestock (in white).

Table 1

Summary information on abiotic and biotic characteristics of the three sites used for seeding and planting experiments. Where relevant, minimum/maximum values are reported.

Site characteristics	Topographic position		
	Ravine	Valley	Ridge
Sun incidence (degrees)	20–60	80–110	120–170
Inclination (degrees)	20–40	15–25	0–10
Aspect	East	West	North
Altitude (m asl)	2280–2305	2260–2275	2295–2305
Mean annual temperature (°C)	8.86	9.12	9.39
Absolute minimum (°C)	–11.70	–12.17	–12.88
Soil depth at 120 planting sites (cm)	48.8 ± 2.0	47.8 ± 1.5	36.3 ± 1.9
Vegetation cover around 60 planting sites (%) 12 years after livestock exclusion	With livestock	With livestock	With livestock
	87.8 ± 2.6	99.6 ± 0.2	72.9 ± 4.2
	No livestock	No livestock	No livestock
Vegetation height around 60 planting sites (cm) 12 years after livestock exclusion	96.2 ± 1.5	99.9 ± 0.04	75.7 ± 4.2
	With livestock	With livestock	With livestock
	19.0 ± 1.5	4.3 ± 0.9	2.8 ± 0.1
No livestock	No livestock	No livestock	
	72.1 ± 3.7	37.6 ± 3.5	15.8 ± 2.0

average seedling height reached the average height of the planted saplings.

The planting experiment included 360 planting plots with one *P. australis* sapling each (60 per treatment). Planting plots were intermingled between seeding plots and followed the experimental design described for the seeding experiments (three sites \times two livestock conditions). We produced the saplings in a greenhouse using seeds and individual tubes of 5 cm in diameter and 15 cm in height. Saplings were outplanted during the first week of January 2001, when 8 month old and 2.01 ± 0.06 cm of mean height. In the field we monitored for survival, growth and browsing at years 5 and 12. Time of the year for planting the saplings was chosen to coincide with the month of most rain and optimize out-planting survival (Renison et al., 2002).

To characterize each site, we estimated in every planting plot ($N = 60$ per treatment) (1) soil depth by hammering a 70 cm pin into the soil until we judged that the underling rock had been reached, (2) the cover of grasses and forbs, and (3) the height of grasses and forbs at three random points, two to three meters away from the plot to discard the influence of the planted saplings on other vegetation. At the plots with the minimum and maximum values of the following variables we estimated (4) sun incidence as the trajectory of the sun not covered by mountains, rocky outcrops or other obstacles as calculated with a clinometer (in a flat area with no obstacles 180 degrees), (5) the general slope inclination and (6) aspect. At the midpoint of each site we measured (7) altitude above sea level using GPS. We also assessed (8) mean temperatures, as recorded every hour by Hobo data loggers. The data loggers were situated 1 m above ground level in complete shade (Marcora et al., 2008). Temperatures were recorded for 1 year from 1/7/2009 to 30/6/2010, and all other data in June to September 2013.

2.3. Statistical analysis

We describe the seedling and sapling dynamics using means and standard errors. We used univariate Generalized Linear Models (GLM) to determine differences between sites and livestock conditions. For both seeding experiments (2001 and 2004), the response variables were the number of registered seedlings at year 5 after sowing (Poisson distribution and log linear link). For the planted sapling experiment the response variables were survival (Binary Logistic distribution) and height (normal distribution after log transformation) at year 5 and 12 after planting. In all cases, the factors were: (1) site with three levels (the ravine, valley and ridge sites), and (2) livestock with two levels (with and without). We checked residuals for normality and homoscedasticity and used the program Infostat (2001).

To integrate seedling counts, survival and height of planted saplings we estimated a single performance indicator using a method analogous to matrix modelling (Caswell, 2001). For each treatment,

we calculated the sum of the seedling heights produced by 1000 sown seeds using the following equation:

$$CSH_{5+i} = 1000 \times Se_5 \times SaS_i \times SaH_i,$$

where CSH = Cumulative Sapling Heights achieved by 1000 seeds ($\text{cm } 1000 \text{ seeds}^{-1}$), Se_5 = seedlings recorded at the fifth winter as a proportion of total sown seeds, SaS_i = mean planted sapling survival to the i th year (proportion), and SaH_i = mean planted sapling height (cm) for the i th year ($i = 0, 5$ and 12 years) to calculate values for years 5, 10 and 17, respectively. Here we assumed on the basis of their similar height (data shown in the next section) that 5 year old seedlings derived from the field seeding were equivalent to the 8 month old seedlings produced in the greenhouse. We standardized the number of seeds to 1000 for easier interpretation.

To determine whether differences in estimated cumulative sapling heights differed between sites and livestock conditions, we used bootstrap procedures (after Hesterberg et al., 2005). Cumulative sapling height was calculated 1000 times for each treatment, with each calculation involving a recalculation of the Se_5 , SaS_i and SaH_i values from a bootstrap sample of the original dataset, and using sampling with replacement to generate datasets of identical size consisting of random sets of values derived from the original dataset. Thus, for each of the six treatments, we calculated a 1000 means from the original dataset of sown plots per treatment ($N = 84$; 42 plots per treatment combining data from the 2001 and 2004 seeding experiments), a 1000 means from the survival data of planted saplings ($N = 60$ per treatment), and a 1000 means of variable 'N' of heights per treatment (N according to survivals). We therefore simulated 1000 cumulative sapling height values per treatment which resulted in 95% confidence intervals, with CSH_{5+i} being considered significantly different when no overlap existed between treatments in the confidence intervals.

3. Results

3.1. Seedling and sapling dynamics

In the 2001 seeding experiment we recorded newborn seedlings through years 1–5 of 0, 1191, 64, 27 and 22, respectively, out of approximately 151,200 sowed seeds, representing 0%, 0.79%, 0.04%, 0.02% and 0.01% of the sowed seeds (Fig. 2a). We recorded total seedling numbers (newborns and seedlings surviving from previous years) through years 1–5 of 0, 1191, 725, 452 and 306 seedlings, percentage wise representing 0%, 0.79%, 0.48%, 0.30% and 0.20% of the sown seeds, respectively. In the 2004 seeding experiment, newborn peak counts were recorded in year 1 and not in year 2 as in the 2001 seeding experiment, and their number doubled the peak counts of the 2001 seeding experiment. Thereafter, newborn seedlings were registered at low proportions every year and by year 5 total seedling counts declined to levels lower than those recorded in the 2001 seeding experiment (Fig. 2b).

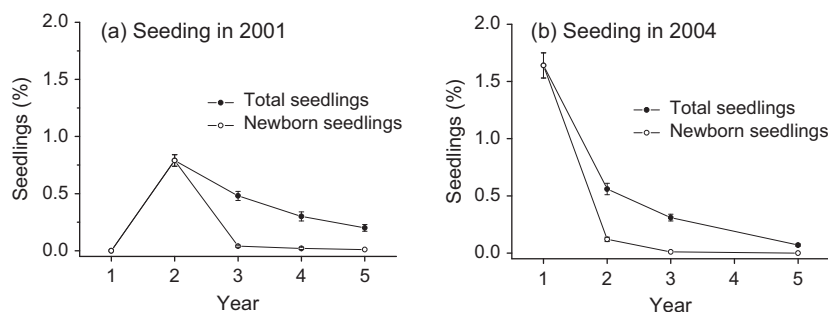


Fig. 2. Seedling counts as registered during years 1–5 after seeding. Solid and empty circles represent total seedlings and newborn seedlings respectively, and are expressed as a proportion of the sown seeds (%) for experiment seeded in 2001 (a) and in 2004 (b). For both experiments, $N = 252$ seeding plots with approximately 600 seeds each.

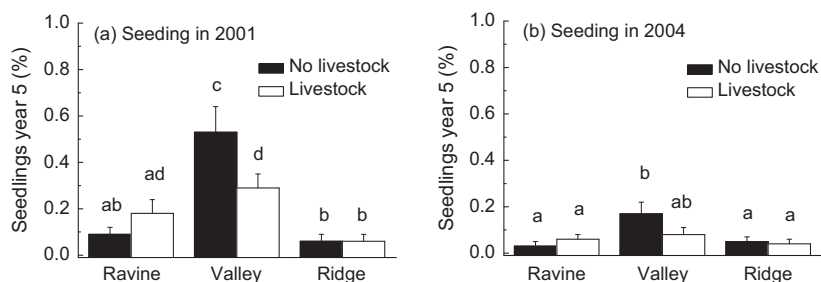


Fig. 3. *Polylepis australis* seedling counts expressed as a percent of the sown seeds across three topographies with and without livestock. (a) Corresponds to the seeding trial performed in 2001 and (b) to the seeding trial performed in 2004. In all cases we report average number of seedlings \pm standard error. Different letters above the bars indicate significant differences ($P \leq 0.05$).

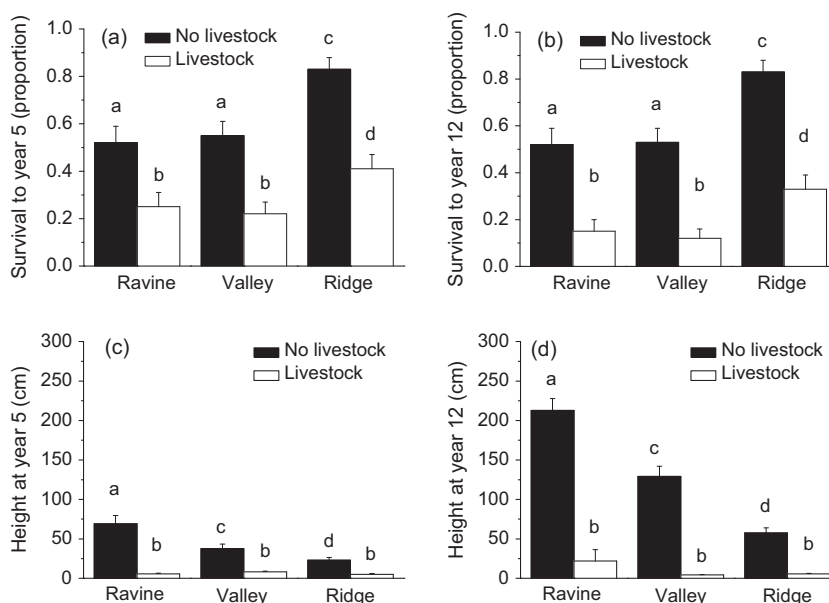


Fig. 4. Survival (a and b) and height (c and d) of *Polylepis australis* saplings 5 and 12 years after planting as a function of topographic position and livestock presence. In all cases we report average number of seedlings \pm standard error. Different letters above the bars indicate significant differences ($P \leq 0.05$).

Seedling heights reached the height of the planted saplings at year 5, with average heights per plot in the experiments of years 2001 and 2004, respectively, of 2.68 ± 0.45 cm ($N = 81$ plots with seedlings and 306 seedlings) and 2.37 ± 0.50 cm ($N = 49$ plots with seedlings, 90 seedlings).

The planting experiment showed survivals of saplings to years 5 and 12 of 46% and 41% respectively ($N = 360$ planted saplings), with average heights at years 5 and 12 of 29.24 ± 2.52 and 93.60 ± 7.66 cm, respectively.

3.2. Site and grazing differences

In the 2001 seeding experiment, seedling counts in year 5 were around four times higher in the valley site than in the ravine and ridge sites, with a negative effect of livestock only for the valley (Fig. 3a; GLM site Wald $\chi^2 = 105.3$; $P < 0.001$; livestock $\chi^2 = 0.01$; $P = 0.908$; site \times livestock $\chi^2 = 15.8$; $P < 0.001$). In the 2004 seeding experiment, seedling counts in year 5 were also around four times higher in the valley than in the ravine and ridge sites, with a tendency for a negative effect of livestock in the valley (Fig. 3b; GLM site Wald $\chi^2 = 18.8$; $P < 0.001$; livestock $\chi^2 = 0.2$; $P = 0.690$; site \times livestock $\chi^2 = 5.3$; $P = 0.070$).

The survival of planted *P. australis* saplings to year 5 was 1.6 times higher in the ridge site (mean 0.62 ± 0.04) than in the ravine

or valley sites (both means 0.38 ± 0.05). In addition, survival was two times higher without livestock (0.63 ± 0.03) than with livestock (0.29 ± 0.03) (Fig. 4a; GLM site Wald $\chi^2 = 20.2$; $P < 0.001$; livestock $\chi^2 = 41.5$; $P < 0.001$; site \times livestock $\chi^2 = 0.4$; $P = 0.412$). Survival to year 12 followed a very similar pattern as in the year 5 records, with a slight decline in survival for sites with livestock and almost no decline in the livestock exclusion sites (Fig. 4b; site Wald $\chi^2 = 23.7$; $P < 0.001$; livestock $\chi^2 = 63.7$; $P < 0.001$; site \times livestock $\chi^2 = 0.7$; $P = 0.694$).

Without livestock, average sapling heights in year 5 at the ravine, valley and ridge were 69.1 ± 10.5 , 37.5 ± 5.7 and 23.0 ± 3.5 cm, respectively. With livestock sapling height only reached 6.31 ± 0.53 cm with no differences being attributed to sites differing in topography (Fig. 4c; GLM site Wald $\chi^2 = 19.3$; $P < 0.001$; livestock $\chi^2 = 184.4$; $P < 0.001$; site \times livestock $\chi^2 = 14.6$; $P = 0.001$). Sapling heights in year 12 followed a very similar pattern to those of year 5, with heights becoming a lot larger in the sites without livestock and almost no growth in sites with livestock (Fig. 4d; GLM site Wald $\chi^2 = 42.1$; $P < 0.001$; livestock $\chi^2 = 106.2$; $P < 0.001$; site \times livestock $\chi^2 = 28.6$; $P < 0.001$). Without livestock the highest sapling at the ravine, valley and ridge was 355, 273 and 187 cm, respectively, and the number that reach seed producing heights (without livestock 87 cm or more; Pollice et al., 2013) at the ravine, valley and ridge was 29, 18 and 12, respectively. With

Table 2

Cumulative height (cm 1000 seeds⁻¹) of *Polylepis australis* seedlings and saplings as a function of topography and livestock presence and absence. Cumulative height was calculated using matrix multiplications (see methods) as a single performance value which integrated seedling counts and their heights with 12 year survival and growth rates of planted saplings. Cumulative height may be conceptualized as the height that would be reached if all the seedlings and saplings produced from 1000 seeds were summed, and it should be directly related to the biomass produced in each situation. Different letters indicate significant differences within lines (bootstrap procedures $P < 0.05$).

Topography	Ravine		Valley		Ridge		
	Livestock	Absent	Present	Absent	Present	Absent	Present
Year 5		1.61 (a)	3.22 (a)	9.38 (b)	5.09 (c)	1.34 (a)	1.61 (a)
Year 17		66.42 (a)	3.92 (b)	239.54 (c)	0.98 (d)	23.86 (e)	1.13 (d)

livestock the highest sapling at the ravine, valley and ridge was 137, 7 and 11 cm, respectively, and only one sapling reached seed producing height (with livestock 107 cm or more; Pollice et al., 2013).

Browsing inside the exclosures was almost null, with exceptions of one browsed sapling in year 5, presumably due to a hare (*Lepus europaeus*), and seven saplings registered in year 12, which were planted too close to the fences. Browsing out of the exclosures in the sites with livestock was also almost null for seedlings in years 1 through 4 and very low in year 5 (4 seedlings in the 2004 experiment). For saplings we registered browsing in years 5 and 12 in 96% and 97% of the individuals, respectively. The abiotic and biotic characteristics of the three study sites are shown in Table 1.

3.3. Matrix integration

The estimated cumulative sapling heights (CSHs) are shown in Table 2. Without livestock, CSH increased throughout time, as mortality was amply compensated by growth. With livestock, CSH remained relatively similar throughout time due to mortality being more or less compensated by growth. Thus, CSH without livestock was 1.2 times greater than with livestock at year 5, while this ratio increased to 54.7 for year 17 (ratio calculated as the sums of CSH values for all sites without livestock/the sums with livestock, see values in Table 2). The greatest differences in CSHs between sites differing in topography was detected without livestock, with CSH values seven times greater in the valley than in the ridge at year 10, and 10 times greater at year 17 (9.38/1.34 and 239.54/23.86, see values in Table 2). Thus, at year 5 differences between the two livestock conditions were 5.8 times smaller than the largest difference attributed to sites, but at year 17 the importance of livestock condition and sites reversed, with differences between livestock conditions being 5.4 times greater than the largest differences between sites.

4. Discussion

Our main results strongly suggest that the seedling stage of *P. australis* life cycle is influenced by the microenvironment imposed by site differences and relatively less by herbivory, while the survival and growth of saplings is strongly affected by herbivory and relatively less by the abiotic environment, at least within the range of abiotic environments studied here. This highlights the importance of considering these two key stages of tree establishment in conjunction and not separately, and highly suggests that herbivory as opposed to abiotic environment is the main filter to the distribution of *Polylepis* in our study area, and possibly of other similar subtropical and tropical mountain ranges where forests are found mainly within ravines. We encourage the replication of this study in other tropical and subtropical mountains, as has been performed in temperate and boreal mountains where it has been shown that sheep can keep *Betula pubescens* trees from

expanding upward into the alpine zone in the Scandes mountains (Speed et al., 2011), that cattle greatly retard post-fire re-growth of *Nothofagus dombeyi* and *Austrocedrus chilensis* trees in the Southern Andes (Blackhall et al., 2008) and that browsing by deer on *Pinus sylvestris* suppresses natural regeneration under some situations in the Highlands of Scotland (Palmer and Truscott, 2003). Our work also highlights the importance of long-term studies as fewer years would have incorrectly assigned a larger influence of the abiotic environment as compared to a longer monitoring.

The low seedling establishment that we encountered is in accordance to those reported for the same species by Landi and Renison (2010), and within the range of values for treeline taxa (Körner, 2012). The low seed establishment could be due to harsh abiotic conditions imposed by altitude, seed predation or to the long dry winter of our study area which desiccates exposed seedlings (Fenner and Thompson, 2005; Vieira and Scariot, 2006; Torres et al., 2014). Competition with grasses and forbs is also known to reduce seedling establishment, but we found no differences between the 2001 and 2004 seeding experiment even though in the later experiment vegetation was much taller within the exclosure. In accordance, previous studies in our area found very few differences between establishment rates on bare sites, grassy pasture vegetation and tussocks (Landi and Renison, 2010). Sapling survival and growth in our study was also within the range reported for plantations in seasonally dry forest areas (Verzino et al., 2004), including that of previous studies on *P. australis* (Renison et al., 2005, 2013; Marcora et al., 2013).

As hypothesised, the effects of sites differing markedly in topography where relatively important at the early establishment stage. In our study area, ridges and other upper topographies have shallower and drier soils than ravines and valleys which are characterized by their deeper soils which persist for longer periods with moisture due to the downhill movement of water. Additionally, ravines have lower sun incidence and temperatures than open valleys which share the deep soils with ravines (Table 1; Cingolani et al., 2003; Enrico et al., 2004). Such differences are probably the main determinants of germination and early establishment, the growth stages most susceptible to prolonged drought and frost (Fenner and Thompson, 2005) and could explain why the valley site was the topographic position with the highest seedling establishment, as it had moist conditions and was warmer than the ravine site (Fig. 3). The ridge site was also more exposed to wind, which may exacerbate transpiration in pioneer seedlings, but once trees become well established and provide greater shelter, it is likely this could facilitate further establishment by reducing wind influence and other harsh climatic conditions such as dry surface soils (Callaway et al., 2002; Wesche et al., 2008). Interestingly, it was not the ravine site which had the best early establishment, but the valley site. This result is consistent with the observation that in the less disturbed sites of our mountain's *Polylepis* forests are also found in valley sides similar to the experimental site (Cingolani et al., 2008).

Also as hypothesised, the effect of livestock was relatively small for *P. australis* early establishment and evident only for the valley site (Fig. 3a), while livestock presence became consistently negative in the later stages (i.e. planted saplings at year 12) (Fig. 4). Importantly, without livestock almost 1/3 of the planted samplings (59 out of 180) reached seed producing heights, while with livestock only one sapling out of 180 reached this height. At the sapling stage all studies report negative effects of livestock on *P. australis* survival, growth rates or forest cover (Cingolani et al., 2008; Giorgis et al., 2010; Marcora et al., 2013), a scenario also reported for other timberline species (i.e. Speed et al., 2011). Given the generality of the negative effect of livestock on sapling performance we consider our results are robust and probably applicable to other similar systems.

The performance indicator we used to integrate the seedling and sapling stages with matrix multiplications demonstrated that in the long-term, the effects of livestock were far more important than differences between the three sites with different topographies, but if our study would have ceased after the first 5 years or earlier we would have arrived at the opposite conclusion (Table 2). Furthermore, with no matrix multiplications, the interpretation of the results regarding the three topographies would have been complicated by the fact that survival and growth had opposing trends in the planting experiment (i.e. more survival associated to less growth) (Fig. 4). We therefore encourage future studies to adopt such an approach where practicable, as it can facilitate clearer insights into the consequences of management changes, an approach also encouraged by Daehler (2003) in the context of understanding plant invasions.

5. Management implications

Our results challenge the explanation put forth in the past to explain the restriction of woodlands to ravines mainly as a result of abiotic environmental conditions such as climate, soil moisture, soil depth and other local factors (Luti et al., 1979; Enrico et al., 2004). In concordance with Cingolani et al. (2008), we suggest that at present the current system is strongly ‘consumer controlled’ (Bond, 2005), indicating that it should be regarded as an integrated landscape, as opposed to forests being exclusively in ravines and grasslands out of ravines. We advocate a management of the system as a long-term shifting patchwork of exclusions to allow forests to creep out of ravines and coexist in a mosaic of grasslands and forests which we hope will reduce the present day undesirable levels of soil erosion caused by the continued inclusion of livestock and associated fires (Cingolani et al., 2013, 2014). Under this system, grasslands would be preserved in sites with livestock and also to a lesser extent in sites without livestock due to fire ignitions from lighting which would spread more successfully in higher and dryer topographies burning saplings before they reach heights large enough to escape fires (as in Wakeling et al., 2012).

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