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## Do we need livestock grazing to promote *Polylepis australis* tree recruitment in the Central Argentinean Mountains?

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**Abstract** South American *Polylepis* mountain forests are endangered due to centuries of logging, fire clearance, and intensive livestock grazing. *Polylepis australis* (Rosaceae) dominates the tree canopy in the Central Argentinean Mountains, where livestock have been excluded or reduced to very low densities over wide areas. Lowered plant and bird diversity in these abandoned grazing areas suggest that some livestock grazing may be beneficial for conservation purposes. Our study aimed to determine whether this may also be true for forest regeneration. In 300 plots of 1 m<sup>2</sup> distributed in sub-regions of high to moderate grazing pressure as well as grazing exclusion, we recorded the presence of *P. australis* seedlings and grazing indicators. Topographical parameters as well as vegetation and soil characteristics were also assessed. Seedling frequencies were highest in the region with moderate grazing, intermediate with grazing exclusion, and the lowest with high grazing pressures. Logistic regression models revealed that seedling occurrence was highest close to seeder trees, with intermediate litter coverage and at intermediate altitudes above sea level. Since grazing ultimately affects seeder tree occurrence through browsing and reduces litter cover and predominates in higher areas, we con-

clude that grazing is an important driving factor for *P. australis* regeneration. We confirm previous studies determining high grazing pressure to be detrimental for *P. australis* regeneration, but also provide data suggesting that its complete exclusion may not be recommendable either. Management should aim to alternate between a moderate grazing intensity to promote seedling recruitment, with subsequent exclusion to accelerate the growth of the established seedlings.

**Keywords** High-altitude forests · Livestock · Logistic regression · Tree regeneration · South America

### Introduction

South American mountain ecosystems have been subjected to intensive anthropological pressure for thousands of years (Ellenberg 1979). Logging and fire clearance notwithstanding, grazing has represented the most prominent land use to date (Fjeldså and Kessler 1996). Domestic herbivores negatively affect tree regeneration both directly by browsing on seedlings (Dezzotti et al. 2003; Mountford and Peterken 2003; Teich et al. 2005; Torres et al. 2008), and indirectly by reducing fitness in the parental tree due to excessive biomass extraction (Cierjacks and Hensen 2004). In addition, the burning of forests to produce more pasture land leads to forest fragmentation and thus reduces population sizes (Hensen 2002; Renison et al. 2006); which may result in genetic erosion and inbreeding depression (Hedrick and Kalinowski 2000; Oostermeijer et al. 2003; Seltmann et al. 2009). Furthermore, Renison et al. (unpublished data) found that several indicators of land degradation correlated to human impact, such as tree-canopy cover, soil impedance, and organic matter content. All these factors have been shown to affect seed quality (Fischer and Matthies 1998; Cierjacks and Hensen 2004; Renison et al. 2004) and seedling growth (Renison et al. 2005).

Recently, lower beef prices, together with the cultural and economic attraction of urban centers, have led to

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the abandonment of many marginal South American montane rangelands, thus reducing land degradation and creating potentially interesting opportunities for conservation (Aide and Grau 2004). However, it is contested as to whether livestock grazing should be totally excluded from these areas. South American mountain ecosystems have always been a habitat for large herbivores like Camelids and Rheas. In several areas, native herbivores are now locally extinct and their function may have been replaced by domestic livestock. However, domestic livestock show dietary differences to native guanacos (Puig et al. 2001), their hoofs exert more pressure and their stoking rates could be up to ten times higher than native herbivores (Cingolani et al. 2008), thus it is unclear whether both types of herbivory are functionally similar.

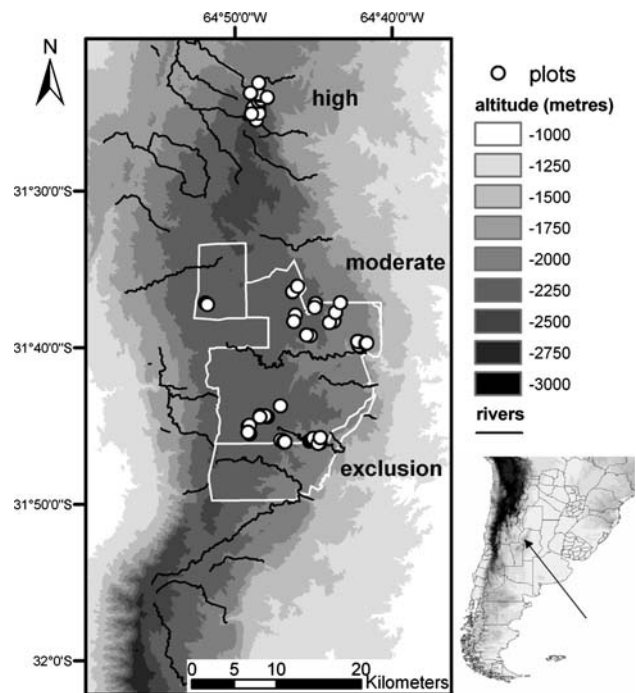
Some case studies have indicated that complete exclusion of livestock in South American mountains may lead to a decline in plant and bird diversity (Cingolani et al. 2003; García et al. 2008), and studies in Africa have shown that forest regeneration may even decline with the complete exclusion of livestock (Reed and Clokie 2000). In South America, Cierjacks et al. (2008) found no evidence suggesting that the regeneration of *Polylepis incana* and *P. pauta* at the upper tree line in Ecuador is negatively affected by moderate cattle grazing. In effect, moderate stocking rates may even promote the establishment of tree saplings (Ramirez-Marcial 2003). Germination and establishment of woody species may be encouraged by consumption of competing herbs and grasses (Posada et al. 2000), yet this advantage diminishes where the young trees themselves are palatable to the associated grazer (Timmins 2002; Vandenberghe et al. 2006).

The genus *Polylepis* is endemic to South America where it forms almost all tropical tree lines. Thus, its protection is implicit to the survival of these mountain ecosystems, which not only contain a high number of endemic species, but are known to be highly important for the regional water balance (Hensen 1995; Fjeldså and Kessler 1996; Renison et al. 2006). Since successful germination and establishment are basic requirements of forest regeneration, we investigated seedling occurrence of *Polylepis australis*, the southernmost species of the genus, by comparing three regions with differing grazing impact and land-use histories in the mountains of central Argentina. We assessed: (1) whether grazing affects *P. australis* seedling occurrence; and (2) which environmental parameters facilitate or hamper rejuvenation. Data on the influence of grazing pressure and grazing exclusion on *Polylepis* species are urgently needed in order to develop management schemes that promote the natural regeneration of these highly threatened forests. A previous study by Torres et al. (2008) that compared areas with high and moderate livestock densities close to our study areas found that most regeneration occurred in areas with moderate stocking rates, but to date, it is not known whether low or complete grazing exclusion is advantageous or not for *P. australis* regeneration.

## Methods

### Study area and study species

The study area is situated in the Córdoba Mountains (31°20'–31°50' S, 64°40'–64°90' W, maximum elevation 2,880 m a.s.l.) located in central Argentina (Fig. 1). The climate is temperate humid (Cabido et al. 1987; Acosta et al. 1989), with an average precipitation of 650 mm/a and an average temperature of 10.3°C at 2,000 m a.s.l. Frost occurs throughout the whole year, while snow events are rare since winter coincides with the dry period (Cabido et al. 1987). The mountainous study area is formed by a granite dome that culminates into an alti-plano (high plain) region (Zeil 1986). The main rivers have eroded deep gorges into this mountain range while the higher regions are weathered into more gentle forms. Grasslands dominate the landscape, with *P. australis* trees occupying 4.2% of the area (Cingolani et al. 2004). The first humans settled in the area some 8,000 years ago and started altering the environment by using fire for hunting (Berberian 1999; Pastor 2000). European settlers reached Córdoba 400 years ago and diminished forest area through logging and an intensified fire regime in order to create grazing grounds for horses, sheep, goats and cattle (Diaz et al. 1994). Large native herbivores such as *Lama guanicoe* and *Rhea americana* became extinct in the area at the beginning of the 20th century. Nowadays, livestock composition has shifted



**Fig. 1** Study region (arrow) and sub-regions characterized by different grazing intensities. The white lines encircle the national park (data derived from the Global Land Cover Facility, <http://www.glc.f.umiacs.umd.edu>)

towards cattle-grazing (Diaz et al. 2001). The average stocking rate ranges from 0.16 to 2.24 cattle equivalent/ha (Teich et al. 2005).

*Polylepis australis* BITT., an evergreen phanerophytic Rosaceae, grows up to 15 m high. The species is wind-pollinated (Simpson 1979; Seltsmann et al. 2007); fruits are 5 to 10-mm-long nutlets (hereafter referred to as seeds) lacking any special attachments to promote dispersal.

## Experimental design

Field sampling was carried out in autumn 2003. The study area was divided into three sub-regions in accordance with their land-use histories. Sub-regions 1 and 2 form part of a national park created for conservation purposes in 1997 ("Parque Nacional del Condorito", Fig. 1). Sub-region 1 had endured the least historical human impact and is characterized by dense and extensive *P. australis* forests covering 15% of the area (Cingolani et al. 2004). From 1998 to 2002, livestock was excluded but re-introduced in some of the paddocks for 3–4 months in the summer of 2003 (labeled 'exclusion' hereafter). In sub-region 2, where dense *P. australis* forests cover approximately 6% of the area, the current livestock-management regime is different: livestock was excluded in 1998 and then progressively reintroduced into several paddocks from the year 2000 (labeled as 'moderate' grazing intensity). Sub-region 3 is located outside the national park, has experienced a long history of heavy grazing, and is fairly representative of livestock management for most of the Córdoba Mountains. No more than a few isolated *P. australis* individuals and small woodland patches can be found in relatively inaccessible areas covering 3% of the total area (labeled 'high' grazing intensity).

Using a GIS of the area, which included elevation and vegetation layers (Cingolani et al. 2004), 20 randomized squares per sub-region were derived within vegetation units that were assumed to contain woodlands or sparse shrublands (*P. australis* cover generally >5%). Due to the mapping resolution (Landsat ETM+), each square represented 30 × 30 m. We stratified the sampling to obtain an even distribution of samples along the altitudinal gradient (1,700–2,400 m a.s.l.) in each sub-region, resulting in five squares for every 200 m. In the field we located 30 × 30 m squares using a GPS receiver and selected them for the study when: (1) there was at least one adult *P. australis* individual taller than 2 m, and (2) all occurring individuals were accessible for measurement. When the selected plot location was inaccessible or without trees higher than 2 m we moved to the nearest 30 × 30 m area that met the requirements (Renison et al. 2006). In each square, five 1 × 1 m plots located at the four corners and centre of the square were established, which yielded a grand total of 300 plots. For each plot we recorded the presence of *P. australis* seedlings and saplings lower than

30 cm. Larger saplings were regarded as established (Renison et al. 2002). We also recorded grazing indicators (presence/absence of browsed vegetation and cowpats). Additional variables measured included: grass cover (%), herb cover (%), moss cover (%), shrub cover (%), litter layer (%), bare soil (%), gravel (2 mm–2 cm, %), stones (2–20 cm, %) and rocks (> 20 cm, %); as well as topographical parameters including altitude above sea level (m), aspect (northness [ $\cos^\circ$ ], eastness [ $\sin^\circ$ ]) and inclination, and, as an indicator of seed rain, the distance from the nearest seed carrying *P. australis* tree (m), hereafter called "seeder tree".

## Statistical analyses

First, we tested whether the observed grazing frequencies were consistent with the predefined sub-regions, and if *P. australis* seedling frequencies differed between the three sub-regions using a Chi-square-test ( $P < 0.05$ ,  $n = 300$ ).

In order to test for spatial autocorrelation of our plots, we compared the residuals of mixed models containing the UTM-coordinates of plot positions as a spatial correlation matrix, with the residuals of logistic regression models (R 2.6.0, packages = MASS, glmPQL). The resulting correlograms based on Morans indices did not indicate significant autocorrelation of any of the 300 study plots for any of the measured parameters (packages = ncf, correlog). Occurrence of *P. australis* seedlings as a function of environmental parameters was modelled using logistic regression and forward selection (ter Braak and Looman 1986; Jongman et al. 1995; Quinn and Keough 2002; Leyer 2005). Therefore, a generalized linear model was constructed with a binomial error structure, which calculates the probability of occurrence of *P. australis* seedlings ( $p = \exp(a + b_1x_1 + \dots + b_kx_k) / [1 + \exp(a + b_1x_1 + \dots + b_kx_k)]$ , where  $a$  = intercept,  $b$  = regression coefficient and  $x$  = explanatory variable). In addition, we tested if the same environmental variables that explained seedling occurrence explained grazing occurrence. We thereby performed a similar procedure using the occurrence of grazing indicators as a response variable and the variables that predicted seedling occurrence as explanatory variables. We refrained from using other continuous grazing indicators for the model procedure since the presence of *P. australis* trees could influence livestock presence, thus grazing indicators and seedling presence may not be entirely independent from each other.

The total data set was randomly split into two halves for model validation. As a permutation-method, we repeated this random sampling procedure 100 times. The first half was used as a training subset to develop the prediction models. The significance of each model in comparison with the null model or a different model was tested by comparing the explained deviance of the models using a Chi-square test (Crawley 2002). The

second half was used as a testing subset necessary for model validation. The Receiver Operating Characteristic (ROC) technique was performed as a threshold-independent method to estimate the predictive power of the models (Zweig and Campbell 1993). We therefore used AUC (area under ROC function) values as validation indices. An AUC-value of 0.5 indicates a random model without any power of prediction; values between 0.6 and 0.7 indicate weak power of prediction; values between 0.7 and 0.8 represent acceptable models, while values  $\geq 0.8$  indicate excellent to outstanding models (Hosmer and Lemeshow 2000).

We used the open source statistical software “R” (2.6.0) (R Development Core Team 2007) for all analyses.

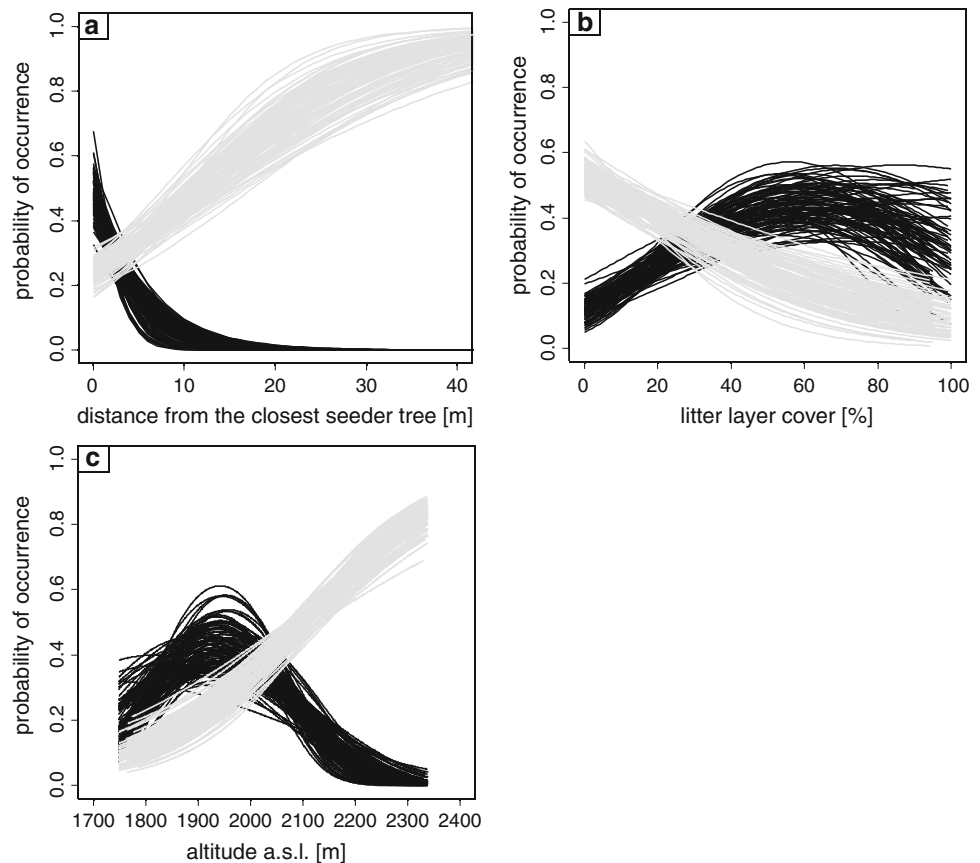
## Results

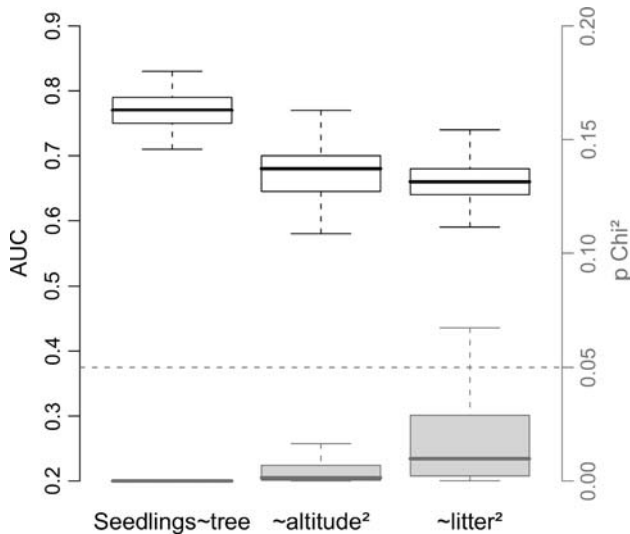
Signs of grazing were found in 5, 36, and 78% of the plots located in the sub-regions characterized by grazing exclusion, moderate and high grazing pressure, respectively ( $\chi^2 = 112$ ;  $df = 2$ ;  $P < 0.0001$ ). Seedling occurrence was lowest (16%) in the sub-region with high grazing intensity, intermediate (24%) in the sub-region with grazing exclusion, and highest (33%) in the sub-region with moderate grazing intensity ( $\chi^2 = 7.86$ ;  $df = 2$ ;  $P = 0.02$ ).

*P. australis* seedling occurrence was best predicted by three logistic regression models with distance from the closest seeder tree, proportion of litter cover and altitude above sea level serving as single predictors. The probability of seedling occurrence was almost 0.5 directly beneath the seeder tree, and decreased to almost zero at a distance of only 10 m (Fig. 2a). The model explained 13–30% of the total deviance and the AUC-values for 100 repeated logistic models varied from acceptable to excellent in predictive power (Fig 3). In addition, the probability of *P. australis* seedling occurrence was highest at intermediate litter cover and altitudes above sea level (Fig. 2b, c), although AUC values were clearly lower than for proximity to seeder tree. AUC-values for 100 repeated logistic models indicated weak to acceptable predictive power for both litter layer cover and altitude above sea level (Fig. 3). The highest numbers of seedlings occurred at about 55% litter layer cover and around 1,950 m a.s.l. (Fig. 2c). The explained deviance for litter cover ranged from 1 to 12% for the altitudinal model and from 3 to 16% for the litter cover model. In contrast, the probability of grazing occurrence increased with distance from the tree, and was negatively related to litter cover and steadily increased with elevation (Fig. 2a–c).

Aspect, vegetation cover, inclination of the study site, and the proportion of open soil, gravel, stones and rocks were not significant predictors of seedling occurrence

**Fig. 2** Logistic regression curves generated in 100 iterations showing the probability of occurrence of seedlings (black lines) and of grazing (grey lines) in relation to **a** distance from the closest seeder tree, **b** litter layer cover, and **c** altitude





**Fig. 3** AUC- and significance-values ( $P \chi^2$ ) of the three logistic regression models for 100 iterations (from the left to the right) distance from the closest seeder tree (seedlings~tree), altitude (~altitude<sup>2</sup>) and litter layer cover (~litter<sup>2</sup>). The top and bottom of the box show the 25th and 75th percentiles of the data, and the whiskers show 1.5 times the interquartile range of the data. Outliers, which represent more than 1.5 times the interquartile range, are not plotted (for altitude the maximum  $P$  value is 0.05, for litter layer cover the maximum  $P$  value is 0.58 and the maximum AUC-value is 0.75). The significance threshold is indicated by the dotted line at 0.05  $P \chi^2$

( $P > 0.05$ ). Neither additive models nor interactions between variables were significant.

## Discussion

### Effects of grazing

Our study suggests that *P. australis* seedling occurrence in the Córdoba Mountains is highest in the sub-region with moderate grazing intensities, as compared to the sub-region with grazing exclusion or high stocking rates. Consequently, seedling number was lowest in the sub-region where intensive land use is still practiced, which is the case for most parts of the Córdoba Mountains. Here, poor rejuvenation can easily be explained by the direct effects of grazing or browsing (Teich et al. 2005). Indirect explanations are presented by Renison et al. (2004), who confirmed a significant negative relationship between *P. australis* seed viability and soil degradation due to overgrazing; Torres et al. (2008) also found less seedlings in areas with livestock induced soil erosion.

Although fewer *P. australis* seedlings were found under conditions of intensive grazing, seedling occurrence was higher in the sub-region with moderate grazing compared to that with grazing exclusion. Our results of the logistic regressions indicate that this might be an effect of litter quantity. The increase of litter layer seems to have a positive effect on *P. australis* seedling occur-

rence until cover exceeds 55%, at which point a general decline and increased variability in seedling occurrence is observed (Fig. 2b). Litter derives mainly from herbs and tussock-grasses, as a consequence of the absence of grazing animals (Noy-Meir 1995). Hence, overgrazing—which diminishes litter layer cover—as well as grazing exclusion—which favors high litter layer cover—negatively affect seedling survival. This corresponds with Cierjacks et al. (2008), who found significantly greater seedling emergence in two Ecuadorian *Polylepis* species after litter removal in sowing experiments, and higher seedling numbers at trampled *Polylepis* sites than at untrampled sites. A deep litter layer is known to limit successful germination due to the higher distance between seed and soil, and to the reduced solar radiation where seeds are covered by litter (Steven 1991; Facelli 1994; Christie and Armesto 2003). Furthermore, lower radiation intensity in the denser forests of the national park might hamper rejuvenation. Cierjacks et al. (2007) demonstrated that canopy cover significantly affected seedling and sapling numbers in the two *Polylepis* species mentioned above. Since large herbivores were present before the introduction of domestic livestock in the Córdoba Mountains, it is likely that the regeneration strategy of *P. australis* is adapted to a herbivore controlled ecosystem.

The best logistic regression models that predict seedling occurrence displayed only 30% of the total deviance; this indicates that we failed to sample all important predictor variables. Rodent abundance and low seed viability on a microhabitat scale may also inhibit plant regeneration (Wada et al. 1995; Cabin et al. 2000; Renison et al. 2004), but these factors were not investigated in this study. In addition, our results show that the pre-stratification of the study area into the three sub-regions does outline differing grazing regimes; yet heterogeneity within the sub-region may also explain the low AUC-values.

### Influence of environmental parameters

The only significant parameter defining a suitable regeneration niche was litter cover. Other standard parameters, such as vegetation cover and soil composition as well as inclination and aspect, did not influence seedling occurrence. However, *P. australis* seedling establishment was highly determined by the proximity of seeder trees: at a distance of about 10 m from the potential parental tree the probability of occurrence of seedlings equaled almost zero. This result coincides with Torres et al. (2008), who used seed traps to determine dispersal distances of *P. australis* seeds but failed to capture any seeds further than 6 m from seeder trees. This confirms the species to be gravichorous; and no secondary dispersal agents such as rodents are known neither for any of the other *Polylepis* species studied so far. Apart from limited seed dispersal distance as an explanation of seedling distribution, the probability of

grazing was lowest directly beneath the seeder tree, suggesting fewer seedlings are browsed by livestock in the immediate vicinity of the trees—possibly due to lower forage availability or low branches physically impeding access. Furthermore, the high and moderately grazed sub-regions also have lower tree densities, leading to the assumption that this pattern results from the combined effect of seed dispersal, grazing preference, and land-use history. Seedling occurrence was also negatively related to altitude. However, we do not expect any climatic constraints on rejuvenation (Bader et al. 2007), as in northern Argentina the highest occurrences of *P. australis* are located at 3,500 m a.s.l. In addition, in a transect study covering the elevation range of 900–2,700 m a.s.l., Marcora et al. (2008) found *P. australis* seed viability and germination rates under laboratory conditions to correlate positively with altitude. The low seedling occurrence at the lowermost locations could be explained by the low *P. australis* seed viability at these altitudes (Marcora et al. 2008). As the probability of grazing occurrence was found to increase with altitude, we expect higher grazing intensity to be responsible for this pattern (Fig. 2c). The mountains of Córdoba culminate into a high plain, which is more accessible for cattle than the lower situated steep hillsides.

#### Implications for nature conservation

Since trees have to survive a long critical juvenile phase, forests require centuries to recover (Vellend et al. 2005). As seedling recruitment in *P. australis* was shown to be mainly seed limited (see also Torres et al. 2008), the initial focus of conservation should be to preserve the existing *P. australis* trees as seed sources for the recovering forests. Our data reveal that a complete exclusion of all grazing animals would not match the natural grazing regime of this ecosystem, which is likely to have adapted to a low but fluctuating grazing pressure by native Guanacos, Rheas, and several small mammals. Therefore our results suggest that the adjustment of a moderate grazing intensity is essential for *P. australis* rejuvenation. However, as seedling and sapling growth was shown to be severely hampered by browsing, even at low stocking rates (Teich et al. 2005), livestock may have to be temporarily excluded, once a seedling bank has been formed, in order to facilitate their growth to a height at which they escape browsing. Comparable studies on tree regeneration from other temperate humid montane rangelands with a similar grazing history would be desirable to confirm our results.

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