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Impacts of cattle on the South American temperate forests: Challenges for the conservation of the endangered monkey puzzle tree (*Araucaria araucana*) in Chile

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ABSTRACT

Notwithstanding the increasing cattle activity on the South American temperate forests, its impacts on the forests regeneration are yet poorly understood. We investigated the influence of cattle on the regeneration of monkey puzzle tree (*Araucaria*), an endangered conifer of the temperate forests of Chile and Argentina, on properties of small landowners and of timber companies. In thirty-six 100 × 20 m plots, we recorded the number of seedlings and saplings from seeds and resprouts, the number of cattle dung pats and the density of parent trees. We used the cattle dung pats as a surrogate of cattle activity (the cattle intensity index, CAI). The regeneration was analyzed as a function of the CAI, land tenure regime, the study site, and the number of parent *Araucaria* trees. We used likelihood methods and model selection for data analysis. Overall, there was a negative exponential influence of the CAI on all response variables. In small landowner forests, even low cattle intensities caused regeneration to drop rapidly to zero, whereas in plots owned by timber companies regeneration decreased smoothly as the CAI increased. The CAI affected regeneration of *Araucaria* qualitatively by decreasing the ratio of sexual/asexual regeneration, which may lead to problems of genetic drift in the long-term. Our results suggest that conservation of a single species does not necessarily ensure its long-term persistence. It is necessary to protect the ecosystems in which the species grows and involve local stakeholders in the development of management strategies that reduce the impacts of cattle ranching.

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1. Introduction

Araucaria araucana (Molina) K. Koch (Araucariaceae) is an impressively large and long-lived conifer, reaching 50 m in height, 2.5 m in diameter and up to 1300 years in age (Montaldo, 1974). This conifer is commonly known as the monkey puzzle tree, *Pehuén* or *Araucaria*, and its current distribution spans only three degrees of latitude and is divided between a main area straddling the Chilean and Argentinian slopes of the Andean *Cordillera*, and two unconnected populations in the Coastal Range of Chile (Fig. 1). The current distribution derives from a previously more extensive range, which has been severely reduced and fragmented by logging, man-made fires and land clearance since European colonization (Veblen, 1982). The ecology of *Araucaria* is disturbance-driven, principally by volcanism, natural and human ignited fires, landslides and wind, and it has effective adaptations to thrive under these disturbance regimes such as thick bark and epicormic buds (Burns, 1993; González et al., 2006). *Araucaria* is generally dioecious, but may occasionally be monoecious with predominantly gravity-dispersed seeds and wind-dispersed pollen. Most of the *Araucaria* seeds fall directly under the canopy or a few meters away from the parent tree, due to their large size (2–4 cm long, 1–2 cm wide) and heavy weight (3.5–5.0 g, González et al., 2006). *Araucaria* seeds can also be dispersed over greater distances by birds, rodents and other animals (Veblen, 1982; González et al., 2006). Asexual reproduction by root suckering has been reported on the Andes and the Coastal Range (Schilling and Donoso, 1976;

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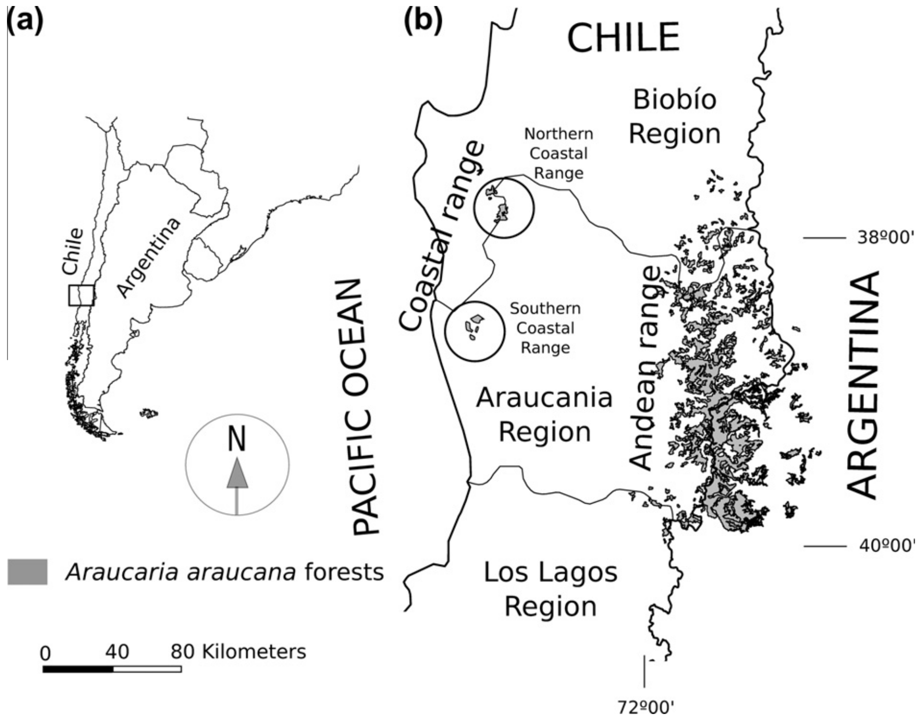

Fig. 1. (a) Location of the study area, and (b) distribution of *Araucaria* forests within the Coastal and Andean ranges, and location of the two main populations of monkey puzzle that were sampled in this study in the Coastal Range.

Cortés, 2003), particularly under severe disturbance regimes (Cortés, 2003; González et al., 2006). Yet it is unknown how important this process is for population maintenance and expansion (Veblen et al., 1995).

Araucaria is a socially significant species, producing high-quality timber and providing a unique resource for tourism and recreation. The tree has a relevant role in the culture of the indigenous Pehuenche people and is also valued for its large, edible seeds, which are extensively collected for local markets (Aagesen, 1998a). *Araucaria* has been classified under the IUCN guidelines as vulnerable (Farjon and Page, 1999), and is currently officially protected in both Chile and Argentina as well as internationally through its listing in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Despite its protected status and outstanding ecological, economic and cultural significance, *Araucaria* forests continue to experience intense human-induced pressures, such as grazing and harvesting, both for timber and seeds (Aagesen, 1998b). Its thick bark and resprouting ability may confer the *Araucaria* a competitive advantage under fire regimes relative to other coexisting species with thin bark such as *Nothofagus pumilio* and *Nothofagus dombeyi* (Schilling and Donoso, 1976; González and Veblen, 2007). Nevertheless, grazing and high-frequency human set fires may have profound effects on the species long-term persistence, mostly by altering its regeneration capacity. Nowadays, the most obvious sign of *Araucaria* forest degradation is the lack of natural regeneration, which might be exacerbated by livestock and feral exotic animals as wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*), which consume seeds in autumn and seedlings in spring, and trample seeds, seedlings and saplings during grazing (Gallo et al., 2004; Shepherd and Ditgen, 2005; Sanguinetti and Kitzberger, 2009a). In addition, cattle ranching can cause soil compaction, which may change soil structure and contribute to the increased incidence of water stress, tree mortality during dry periods and erosion (Fleischner, 1994; Hobbs, 2001).

Studies about the regeneration of the species include the effects of biophysical factors (Veblen, 1992; Christie and Armesto, 2003) and stand variables (Donoso and Nyland, 2005) on seedling densities in late-successional and old-growth evergreen (Valdivian) forests in Chile. More recently, the effects of masting, seed predation and understory vegetation on seedling establishment (Sanguinetti and Kitzberger, 2008, 2009a,b), and the long-term implications of fire in the regeneration of the species (Burns, 1993; González et al., 2005; González and Veblen, 2007) have been addressed. However, notwithstanding the widespread coincidence of cattle and the distribution of *Araucaria* forests, the impacts of animal husbandry on the regeneration of this tree species are yet poorly understood. The effects of grazing on *Araucaria* may vary under different land tenure regimes, namely rural properties of small landowners and large properties of timber companies. Currently, most of Chile's forests on the Coastal Range are owned by a small number of large timber companies. During the last decades, these companies have been responsible for the replacement of large tracts of native forests by exotic *Pinus radiata* and *Eucalyptus* spp. plantations (Taylor, 1998; Lara and Veblen, 1993; Echeverría et al., 2006; Lara et al., 2010). Paradoxically, some of the properties owned by timber companies, where exotic plantations are expanding, are nowadays refuge to some of the last remnants of *Araucaria* forests in the Coastal Range. Improving our understanding of how *Araucaria* regeneration responds to cattle intensity under these two major land tenure regimes might therefore contribute to manage the conservation and sustainable use of this endangered species more efficiently.

This study is aimed to elucidate whether there is a negative effect of cattle on the regeneration of *A. araucana* in the Coastal Range, which are more exposed to human disturbance compared to the Andes. We analyzed how the impact of cattle on regeneration varies according to land tenure regime, site (northern and southern) and density of *Araucaria* parent trees. Specifically we investigated the impacts of cattle ranching on: (1) the number of seedlings and saplings; (2) the number of seedlings and saplings originated from seed (sexual reproduction); (3) the number of resprouting seedlings and saplings (asexual reproduction); and (4) the ratio between seedlings and saplings originated from seed and those from resprout.

2. Materials and methods

2.1. Study area

The study was carried out in the Nahuelbuta mountain range, within the coastal distribution range of *Araucaria* in Chile (Fig. 1). We selected this study area for three main reasons: (1) *Araucaria* populations in the southern limit of its distribution in the Coastal Range are genetically distinct to the other populations: populations in the northern Coastal Range do not differ genetically from those in the Andean range (Bekessy et al., 2002). Thus, our study includes two genetically distinct extant populations; (2) human disturbance represents a serious threat for forest conservation in the Coastal Range, mainly due to its physiographical features; elevations rarely exceed 1500 m, and therefore provide greater accessibility and represent higher vulnerability (Armesto et al., 1995); and (3) the scarcity of protected areas in this region (Armesto et al., 1998) poses an additional threat for *Araucaria* populations. Most *Araucaria* forests are included within large properties of timber companies, and to a lesser extent, are within the properties of small landowners that extract firewood and timber for charcoal from associated species, and use the forest for cattle grazing.

Nahuelbuta is characterized by abundant endemic flora and fauna, which probably reflects the location of vegetation refuges during the last glacial period (Armesto et al., 1995). The main forest association in the study area is *Araucaria–N. dombeyi* forest. Sampling was conducted in two different sites: the northern Coastal Range (NCR), and the southern Coastal Range (SCR, Fig. 1). The NCR site bordered the Nahuelbuta National Park (37°44′S, 72°55′W; 37°51′S, 73°03′W, elevation between 700 and 1400 m). The SCR site matches the southern limit of *Araucaria* distribution in the Coastal Range (38°29′ W, 73°12′ W, elevation between 450 and 700 m). The predominant climate is temperate with Mediterranean influence, with average temperatures between −1 °C in winter and 9 °C in summer, and an average annual precipitation of 1500–2500 mm (Di Castri and Hajek, 1976; González et al., 2006). Soils derived from metamorphic material and granitic rocks are thin to moderately deep (15–180 cm), loamy-clay to clay at depth, extremely acidic to very strongly acidic (pH = 3.0–5.5), and have moderate to high erodibility, and low nutrient levels (IREN-CORFO, 1964; Montaldo, 1974).

2.2. Sampling methods

We established thirty-six 100 × 20 m sampling plots: 20 plots were located in rural properties of small landowners (sampling size: NCR = 17 plots, SCR = 3 plots) and 16 plots in large properties of timber companies (sampling size: NCR = 9 plots, SCR = 7 plots). Within each plot, we counted monkey puzzle seedlings (<1.3 m in height) and saplings (>1.3 m tall and <5 cm in diameter at breast height, DBH) in thirty 2 × 2 m sub-plots set at 10 m intervals from each other along three 100 m line transects running parallel to the longest axis of the plot. Using a non-destructive technique we dug around each sapling and seedling by hand and hand shovel to differentiate between sexual (seeds) and asexual (resprouts, *sensu* González et al., 2006) regeneration. For the sake of brevity we will refer henceforth to seedlings and saplings from seeds and resprouts, although seedlings in a strict sense refer only to young plants grown from seeds. Once we made the observations, we put back and compacted the soil around the seedlings and saplings. In each 100 × 20 m plot we counted the number of cattle dung pats and estimated the number of dung pats/ha as a surrogate of the current cattle density and trampling pressure. The dung pats have a very slow decomposition rate in this region due to the cold temperatures that prevail during most of the year. Therefore our estimation of cattle intensity is likely to include the accumulated activity of cattle for a broad period of time, spanning at least the last 1–2 years (C. Zamorano, pers. obs.). Henceforth we will refer to this variable as the cattle intensity index (CAI). Measurements of damage by grazing were not YY considered since *Araucaria* is not a palatable species. In each of these plots we also counted the number of parent trees, defined as those individuals >5 cm in DBH. Even though 5 cm in DBH might seem a low size for trees to become reproductive, we must note that reproductive capacity in this species is more related to age than to size. *Araucaria* reaches sexual maturity between 15 and 25 years old (Montaldo, 1974), and since it is a slow growing species, individuals >5 cm in DBH often attain this age (Cortés, 2003). We did not determine the sex of adult *Araucaria* trees because of the difficulties to do such distinction in tall trees and/or in dense stands.

2.3. Statistical analyses

We fitted models for the following response variables: total number of seedlings and saplings; number of seedlings and saplings originated from seed (sexual reproduction); number of resprouting seedlings and saplings (asexual reproduction); and the ratio between seedlings and saplings originated from seed and resprouts (sexual/asexual ratio). The latter was calculated as follows for seedlings (we applied the same formula to saplings):

$$\text{Sexual/asexual ratio} = \frac{\text{Number of seedlings from seed} + 1}{\text{Number of resprouting seedlings} + 1}$$

These response variables were analyzed as a function of the cattle intensity index (CAI), land tenure regime (small landowner, timber company), the study site (NCR, SCR), and the number of parent trees. We used likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland, 2004; Canham and Uriarte, 2006) for data analysis. Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the regeneration measured in the field, given a suite of alternative models. We examined eight different nested models. For each model, we conducted separate analyses for each individual response variable, namely overall seedling and sapling regeneration, as well as analyses considering sexual and asexual seedling and sapling regeneration. For each response variable (Y), our simplest model takes the form:

$$Y = a \cdot e^{b \cdot \mathrm{CAI}} \tag{1}$$

The first term in the model, a, is an estimated parameter that represents the average *Araucaria* regeneration in the absence of cattle effects. The second term, $e^{b \cdot \mathrm{CAI}}$, controls for the effect of cattle intensity. This model implies that regeneration changes exponentially as a function of the number of dung pats, where b is an estimated parameter that controls for the slope of the curve.

We tested three variants of Eq. (1). A first variant allowed the effect of the cattle intensity on *Araucaria* regeneration to vary depending on land tenure:

$$Y = a \cdot e^{b_i \cdot \mathrm{CAI}} \tag{2}$$

where b_i defines the slope of the exponential curve between regeneration and cattle intensity for the two classes of land tenure analyzed. To test for the possibility of a site effect independent of cattle intensity, we ran a modified version of the simplest model in which the average *Araucaria* regeneration (i.e. term b in Eq. (1)) was estimated separately for the NCR and the SCR study sites:

$$Y = a_j \cdot e^{b \cdot \mathrm{CAI}} \tag{3}$$

The last variant included both the effects of land tenure on the slope of the exponential curve, and the inclusion of separate terms for average *Araucaria* regeneration in the two study sites:

$$Y = a_j \cdot e^{b_i \cdot \mathrm{CAI}} \tag{4}$$

We also ran variations of Eqs. (1)–(4) including a density effect of parent trees on regeneration. The most complex model, a variant of Eq. (4), takes the form:

$$Y = a_j \cdot e^{b_i \cdot \mathrm{CAI} + c \cdot \mathrm{Number\ of\ trees}} \tag{5}$$

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e. the parameters that maximize the log-likelihood) given our observed data (Goffe et al., 1994). We used a Poisson error structure for variables involving a count number of seedlings and saplings, and a normal error structure with the variance as a power function of the mean for the sexual/asexual ratio of seedlings and saplings. The latter required estimating an additional parameter, *delta*, to determine the scaling of the variance to the mean. Alternative models were compared using the Akaike Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson, 2002). Models with a difference in $AIC_c < 2$ units are considered to have equivalent empirical support, whereas a difference value within only 4–7 units of the best model has considerably less support. Differences in $AIC_c > 10$ indicate that the worse model has virtually no support and can be omitted from further consideration. We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards, 1992). These are simply the range of parameter estimates for which 'support' (log-likelihood) is within two units of the maximum log-likelihood, and were determined by incrementally varying parameter estimates above and below the maximum likelihood estimated until log-likelihood had dropped by two units. The R^2 of the model fit (1 – SSE/SST, sum of squares error (SSE); sum of squares total (SST)) of observed versus predicted was used as a measure of goodness-of-fit. All analyses were performed using the 'likelihood' package (Murphy, 2008) written for the R environment (R Development Core Team, 2010).

3. Results

Seedlings were almost threefold more abundant than saplings (Table 1). Sexual regeneration in seedlings was more frequent than asexual regeneration, whereas saplings showed the opposite trend. Mean density of seedlings and saplings was considerably higher in plots of timber companies than in those of small landowners (Table 1).

Table 1
Mean density and standard deviation (in parentheses) of *Araucaria* seedlings and saplings in sampled plots of small landowners and timber companies, including sexual (i.e. from seed) and asexual (i.e. from resprouting) regeneration.

	Mean density (plants/ha)		
	All plots	Small landowners	Timber companies
Total seedlings	861 (761)	613 (874)	1172 (1870)
Sexual regeneration	571 (938)	467 (729)	703 (1160)
Asexual regeneration	289 (504)	146 (145)	469 (710)
Total saplings	333 (241)	229 (392)	463 (517)
Sexual regeneration	134 (261)	96 (154)	182 (353)
Asexual regeneration	199 (218)	133 (238)	281 (164)

Comparison of alternate models revealed the best-fits for the different response variables (Table 2). For total and sexual seedlings, the best-fit models showed site-specificity and an effect of land tenure on the response of *Araucaria* regeneration to cattle intensity, without an effect of the parent tree density (R^2 = 0.40 and 0.33, respectively). For total saplings and asexual regeneration of seedlings, the best-fit model included the effects of land tenure and tree density (R^2 = 0.25 and 0.27, respectively). Site specificity and density-dependence were the main effects included in the best-fit model for regeneration of sapling resprouting (R^2 = 0.28). For seedlings, the results suggest a slight response of the sexual/asexual ratio to cattle intensity of land tenure regimes and sites (R^2 = 0.16), whereas for saplings this response was even lower, with the best-fit model including only site-specificity (R^2 = 0.13, Table 2). There was a density effect in total saplings, and seedling and sapling resprouts (Table 2), indicating that the higher the number of parent trees, the more regeneration from resprouting. Overall, there was a negative influence of cattle intensity on all response variables, except for sapling resprouts (Fig. 2).

The northern Coastal Range (NCR) had, on average, greater regeneration than the southern Coastal Range (SCR, see model coefficients in Table 3). In addition, the estimated sexual/asexual ratio of seedlings was about threefold larger in the NCR than in the SCR, and almost eightfold larger for saplings (Fig. 3). It must be noted that the estimated mean value of the sexual/asexual ratio of saplings in the SCR (parameter a_{SCR} in Table 3) was below one, thus indicating a predominance of asexual as compared to sexual regeneration even in the absence of cattle (Fig. 3). Parameter b in the exponential term of the models was approximately one order of magnitude higher in small properties than in forest companies (Table 3). As a result, in small landowner forests, low cattle intensities (100–200 dung pats/ha) caused regeneration to drop rapidly to zero, whereas in plots of timber companies, regeneration decreased smoothly as cattle intensity increased, and models predicted some degree of regeneration even at high levels of cattle intensity (>1000 dung pats/ha), particularly for seedlings (Fig. 2). The same applied to the sexual/asexual ratio of seedlings (Fig. 3). No density effect was detected in the sexual/asexual ratio of seedlings and saplings.

4. Discussion

4.1. Cattle impacts on the regeneration of Araucaria

During the last decades, the native forests of the Nahuelbuta mountain range have been exposed to substantial loss as a result of the expansion of commercial plantations, agricultural activities and urban and industrial sprawl (Aguayo et al., 2009). Despite legal protection, *Araucaria* forests in Chile are still exposed to constant direct and indirect human disturbances, similarly to what has been reported in mixed ombrophyllus forests with *Araucaria angustifolia* in southern Brazil (Vibrans et al., 2011). Cattle, fire, and selective logging of forest species associated with this conifer, especially *N. pumilio* and *N. dombeyi* for timber and *N. antarctica* for firewood and charcoal, are common disturbances in these forests. Cattle ranching may have profound impacts on forest ecosystems (Hobbs, 2001; Floyd et al., 2003). Free-ranging cattle grazing on seedlings and saplings can diminish, damage or prevent the recruitment of many tree and other species by trampling, thus promoting changes in species composition (Hobbs, 2001; Floyd et al., 2003; Wassie et al., 2009). In Nahuelbuta, soil compaction caused by intensive cattle ranching since the late 1940s in the NCR and early 1950s in the SCR has probably aggravated the restrictive natural soil

Table 2
Comparison of alternate models (using AIC_c) for seedling and sapling *Araucaria* regeneration, including sexual (i.e. from seed) and asexual (i.e. from resprouting) regeneration. The best model (lowest AICc) is indicated in boldface type. The number of parameters *k* and R^2 refer to the best model (see Table 3).

Response variable	AIC_c[a]									
	Basic model[b]		Land tenure model[c]		Site-specific model[d]		Site-specific land tenure model[e]			
	No-density effect	Density effect	No-density effect	Density effect	No-density effect	Density effect	No-density effect	Density effect	k[f]	R^2
Seedlings density	516.25	478.29	414.97	378.43	476.44	406.31	**360.70**	432.20	4	0.40
Sexual regeneration	485.20	480.43	395.32	391.59	426.93	405.38	**318.13**	355.23	4	0.33
Asexual regeneration	285.75	240.23	268.09	**223.39**	286.74	232.02	268.65	288.48	4	0.27
$Ratio_{S/A}$	185.95	188.27	171.81	174.60	180.31	183.16	**165.40**	168.83	5	0.16
Saplings density	227.16	211.44	209.11	**192.97**	227.56	214.08	210.37	230.25	4	0.25
Sexual regeneration	166.81	164.98	145.33	144.25	159.28	152.67	**133.06**	146.64	4	0.24
Asexual regeneration	161.11	148.25	159.47	146.02	576.55	**141.19**	144.71	149.96	4	0.28
$Ratio_{S/A}$	110.71	113.29	111.22	114.16	**90.85**	93.46	93.00	99.66	4	0.13

[a] Akaike Information Criterion corrected for small sample sizes.
[b] This model predicts *Araucaria* regeneration only as a function of the CAI.
[c] This model allows variations in the response of *Araucaria* regeneration to the number of cattle dung pats between the two land tenure classes.
[d] This model estimates different average responses of *Araucaria* regeneration in the two study sites.
[e] This model is a combination of the previous two models.
[f] Number of model parameters.

conditions that characterize the region, especially in properties of small landowners (Torrejón and Cisternas, 2003; Zamorano et al., 2008).

Our study reveals that *Araucaria* regeneration is severely affected by cattle ranching, both in properties of timber companies and of small landowners. In the large properties of private timber companies, forests are used by neighboring farmers and even by those from nearby towns as a source of fodder and refuge for cattle. In some cases, companies allow this use through the "leasing of grazing rights", but this does not include any control over livestock density or the amount of forest area that is grazed. The negative exponential models show that small increases in cattle intensity may lead to a substantial decrease in the regeneration of the species, particularly for seedlings. The effect of cattle ranching on the regeneration of *Araucaria* appears much less dramatic in plots owned by timber companies than in small rural properties (Fig. 2). Two complementary explanations may account for such differences in the response to cattle ranching. On the one hand, forests owned by private companies are often used by cattle as a winter refuge, whereas cattle ranching in small rural properties take place throughout the entire year. Thus, although not directly accounted for in our study, the frequency of a disturbance might be as important as its intensity on the regeneration of a species. On the other hand, firewood and timber extraction are one of the main sources of income in small rural properties (Zamorano et al., 2008). Although current legislation prohibits logging of *Araucaria*, extraction of forest species associated with this conifer, especially *Nothofagus* spp. is allowed. Such disturbances, which occur less intensively in lands of timber companies (C. Zamorano, unpublished results), may act synergistically with cattle ranching (Hobbs, 2001; Laurance and Useche, 2009), amplifying its impact on monkey puzzle regeneration.

The response of regeneration to cattle intensity was also site-specific in most cases. The SCR displayed, in average, lower values of seedlings and saplings than the NCR (Fig. 2). Overall differences found in regeneration between the NCR and the SCR can be explained by two main reasons: (1) soils in the NCR have better physical and chemical properties than those in the SCR (Cortés et al., 2001). Unfortunately, soil measures were not directly accounted for in this study; and (2) *Araucaria* forests in the NCR are, in general terms, better conserved, display more complex structure and hold a larger number of plant species than forests in the SCR (Cortés et al., 2001; Cortés, 2003; Zamorano et al., 2008).

Among seedlings, the proportion of resprouts was relatively high (ca. one third of the total number of seedlings) compared to other studies in *Araucaria* stands at the Andes that describe ca. 10% of seedlings from asexual regeneration (e.g. Sanguinetti and Kitzberger, 2009b). This figure was even higher for saplings, with more than half the total number of saplings having an asexual origin (Table 1). Best fit models of the sexual/asexual ratio of seedlings and saplings (Fig. 3) might indicate that, in the face of disturbance, resprouts are expected to have higher chances of survival than plants germinating from seeds. Resprouts have advantages, including an already established root system with a large surface area for water and resource acquisition and high stored energy reserves (Simões and Marques, 2007; Miller and Kauffman, 1998), which enables them to withstand disturbances and compete more efficiently for resources. It is also important to remark that density of parent trees does not play an important role in explaining the observed regeneration of seedlings and saplings from seed, but might be important in determining regeneration from resprouts (Fig. 2). This implies that *Araucaria* densities of about 50 trees/ha, the minimum number recorded in our plots, would suffice to produce the current observed figures of seedling and sapling regeneration from seed.

4.2. Conservation prospects

For some species, a limited level of grazing can increase regeneration by removing competitive vegetation, reducing fire hazards and through fertilization from manure (Kuiters et al., 1996; Blackhall et al., 2008). Although *Araucaria* is highly tolerant to disturbances (Burns, 1993; González et al., 2006), increasing levels of cattle ranching have a rapid response in its regeneration, both quantitatively, by reducing the number of seedlings and saplings, and qualitatively, by decreasing the ratio of sexual/asexual regeneration. These impacts may lead to problems of genetic drift which would ultimately have profound implications for the conservation of this species, especially for populations in the southern limit of

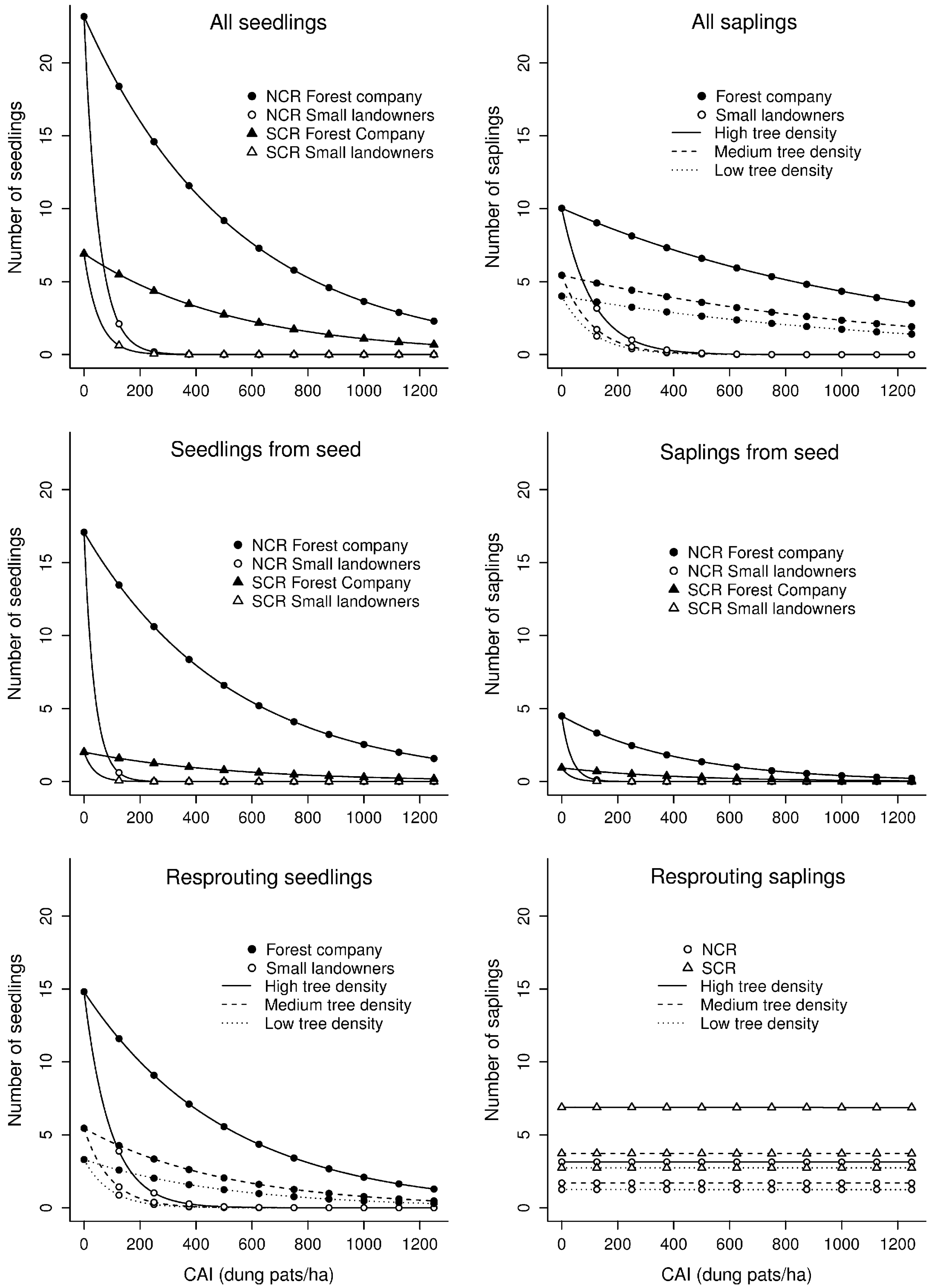

Fig. 2. Predicted decrease of seedling and sapling density (number per ha) as a function of the cattle intensity index (CAI) for the best selected models (see Table 1). For simplicity, only three tree density classes were represented in those models for which this term was important: high density = 200 *Araucaria* trees/ha; medium density = 100 trees/ha; low density = 50 trees/ha.

Araucaria distribution, which are genetically distinct from the other populations (Bekessy et al., 2002).

Overall, the results of this study reveal that partial conservation actions focused on a single species and limited to cutting prohibitions do not necessarily ensure its long-term persistence. It is necessary to develop scientific-based conservation plans focused on the species autoecology, considering its particular germination and growth characteristics, as well as the optimal environmental conditions that determine its distribution. This involves developing synergies between single-species (Simberloff, 1998) and ecosystem approaches (Walker and Salt, 2006; Lindenmayer et al., 2007).

Even though our results suggest the incompatibility of the conservation of *Araucaria* with cattle ranching, cattle eradication is not a feasible solution. It is unpractical to control livestock access to

Table 3
Parameter estimates and two-unit support intervals (in brackets) for the most parsimonious models of seedling and sapling *Araucaria* regeneration, including sexual (i.e. from seed) and asexual (i.e. from resprouting) regeneration, as well as the sexual/asexual ratio ($Ratio_{S/A}$).

Response variable	*a*	a_{NCR}	a_{SCR}	*B*	$b_{small\ property}$	$b_{forest\ company}$	*c*	*delta*[a]
Seedlings		23.18	6.92		−0.0096	−0.0009		
		[20.67, 25.59]	[4.84, 9.64]		[−0.0116, −0.0077]	[−0.0011, −0.0006]		
Sexual regeneration		17.09	2.02		−0.0133	−0.0009		
		[14.85, 19.42]	[0.92, 3.54]		[−0.0166, −0.0105]	[−0.0013, −0.0006]		
Asexual regeneration	2.00				−0.0053	−0.0009	0.005	
	[1.70, 2.38]				[−0.0075, −0.0033]	[−0.0016, −0.0004]	[0.004, 0.006]	
$Ratio_{S/A}$		3.94	1.46		−0.0038	−0.0002		1.147
		[3.22, 5.13]	[0.92, 2.40]		[−0.0046, −0.0025]	[−0.0008, 0.0006]		[0.902, 1.466]
Saplings	2.95				−0.0046	−0.0004	0.003	
	[2.52, 3.53]				[−0.0046, −0.0027]	[−0.0008, −0.0001]	[0.002, 0.004]	
Sexual regeneration		4.49	0.93		−0.0146	−0.0012		
		[3.35, 5.77]	[0.26, 2.08]		[−0.0217, −0.0090]	[−0.0024, −0.0005]		
Asexual regeneration		0.92	2.01	−9.19e−07			0.003	
		[0.66, 1.21]	[2.75, 0.71]	[−0.0005, 0.0004]			[0.002, 0.004]	
$Ratio_{S/A}$		1.75	0.31	−0.0006				0.853
		[1.39, 2.15]	[0.23, 0.51]	[−0.0009, −0.0002]				[0.662, 1.081]

[a] Parameter delta determines the scaling of the variance to the mean.

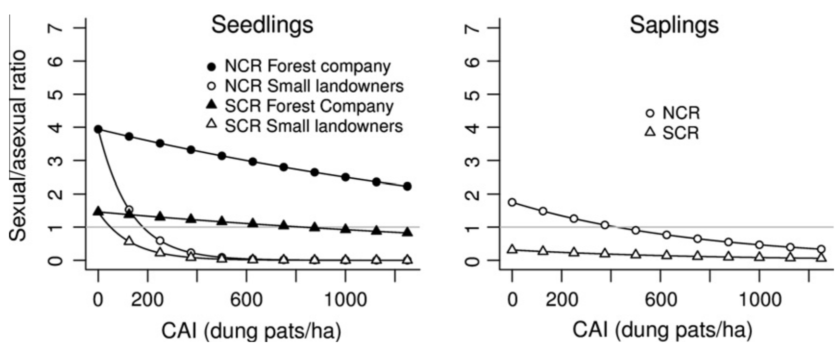

Fig. 3. Predicted decrease of seedling and sapling sexual/asexual ratio as a function of the cattle intensity index (CAI) for the best selected models (see Table 1). Horizontal gray lines indicate the point below which asexual regeneration surpasses sexual regeneration.

the properties of timber companies or even the National Park, given their wide ranges and lack of fences. A tighter control in small and medium-sized properties would inevitably increase pressure of illegal cattle ranching in larger uncontrolled properties, as well as unsustainable productive pressure on small farms and rural poverty of families that depend on livestock as their main source of income (Zamorano et al., 2008). Current policies oriented towards poverty reduction in rural areas of Chile mainly target agriculture, livestock or planting of exotic forest species, whereas conservation and sustainable management of native forests has been systematically neglected (Tecklin and Catalán, 2005). As a result, inevitably contradictory interests arise between current production-oriented agricultural and silvicultural policies and partial and limited species-focused conservation policies for *Araucaria*. So what is the path forward? An important step is to promote the regulation of livestock densities and *Araucaria* protection among local actors, instead of relying on policies imposed that have small chances to assure sustainable long-term solutions for the conservation of this species. Multiscale approaches offer nowadays a unique opportunity to conciliate policies for rural development and *Araucaria* conservation through the concerted interaction of all relevant stakeholders (Reed, 2008) in order to attain long-term sustainable land use planning at local and landscape scales, considering both the local interests and the environmental features of the region. To guarantee the success of multiscale approaches, stakeholder participation must be institutionalized, promoting organisational cultures that can facilitate processes where goals are negotiated and outcomes are necessarily uncertain (Reed, 2008).

Notwithstanding that timber companies have been responsible for the conversion of large extensions of native forests to exotic plantations during the last decades (Taylor, 1998; Echeverría et al., 2006; Lara et al., 2010), the lower cattle impact recorded on *Araucaria* regeneration as compared to properties of small landowners offer an excellent opportunity for the conservation of these forests, as these remnants are less exposed to the negative effects of cattle and other disturbances. Some practices to foster conservation of this species include active restoration by planting *Araucaria* seedlings on patches where regeneration is very scarce or absent, promoting reconversion of exotic plantations established in formerly *Araucaria* forest patches, and implementing monitoring programmes to control the invasion of exotic forest species within *Araucaria* remnants. In addition, timber companies might contribute to conservation of the species by identifying pasturelands or areas more suitable for cattle ranching in order to reduce cattle pressure on the extant *Araucaria* remnants (Polasky et al., 2008), particularly when leasing grazing rights.

In Chile, it has recently been promulgated a legal instrument for the conservation and sustainable management of native forests (Law No. 20283 of Development and Recuperation of the Native Forests). This law defines subsidies for afforestation with threatened forest species, which may represent a first step towards developing further forest restoration initiatives. In addition, there are currently several ongoing governmental subsidies that support productive systems of small landowners, such as pastureland improvement through fertilization and erosion control. In the long-term this could help regulate and even exclude cattle ranching activities from *Araucaria* forests.

Further investigation is needed to fully understand the multiple factors that affect the long-term maintenance of *Araucaria* populations, as well as the interactions between natural and human-driven disturbances, in order to develop and promote effective measures for the restoration and conservation of these endangered unique forests. Although there are still many unsolved questions, our results can help identify urgent policies and promote initiatives to reverse or mitigate the degradation processes that affect *Araucaria* regeneration.

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