Tree survival and growth in the highlands of central Argentina: impact of wildfires and land management

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Abstract

High-mountain forests of subtropical and tropical South America are dominated by *Polylepis* trees. Forest fragmentation is believed to result from human-caused wildfires, livestock grazing and deforestation. Since the 1990s, management of *Polylepis* forests has included the establishment of conservation areas. We assessed survival and growth of *P. australis* trees in central Argentina, examining wildfires and land management effects. We monitored 880 trees over 15 years (2003-2018) in 139 plots distributed across conservation and ranching areas. Tree survival rate was 99.2% yr^{-1}, net height growth 1.4 cm yr^{-1}, and crown dieback 17%. Fire affected 16% of plots in ranching areas and 25% in conservation areas. Compared to unburned plots, fire damage resulted in a 3% yr^{-1} reduction in survival rate, a 4 cm yr^{-1} reduction in height growth, and a 15% increase in crown dieback. Land management did not affect survival, growth, or crown dieback when controlling for wildfire incidence. However, survival rate and net growth were 0.3% and 0.6 cm lower in the conservation areas than in ranching areas when wildfire incidence was considered. Plot tree cover was not linked to survival but was positively associated with net growth, elevation was positively associated with survival and negatively with net growth, and tree height was negatively associated with both survival and growth. No logging evidences were observed. We conclude that wildfires are the primary human-induced impact on *P. australis* trees; therefore, strengthening fire reduction policies is crucial.

Keywords: elevation, Cordoba, dieback, livestock, *Polylepis*, ranching, tree mortality

1. Introduction

High-elevation tropical and subtropical forests and woodlands dominated by trees of the genus *Polylepis* (hereafter "*Polylepis* forests") spread over 5,000 km in latitude across South America, from Venezuela to central Argentina. Due to increasing anthropogenic impacts, many areas suitable for *Polylepis* forests now only have scattered trees that could become important seed sources for passive restoration of the surrounding areas (Segovia-Salcedo et al., 2021; Cuyckens & Renison, 2024). Expanding *Polylepis* forest cover is crucial, since the species provides key ecosystem services, such as biodiversity and endemism conservation, water retention, and soil protection. Additionally, forest restoration could aid in conserving the 36 of the 45 *Polylepis* species classified as threatened (Boza Espinoza & Kessler, 2022).

For millennia, fire has been used in South America highlands to clear land for agricultural uses, including grazing by domestic animals (e.g., Chepstow-Lusty et al., 2009). Even though many tree species resprout after fires, fires usually increase tree mortality and cause top-kill or crown dieback, thereby reducing aboveground biomass and seed production. Furthermore, post-fire basal resprouts are browsed by livestock, which further delays forest recovery (Renison et al., 2002). Consequently, many *Polylepis* forests are thought to be restricted to fire-refugia like rocky areas or stream banks (Fjeldså & Kessler, 1996; Renison et al., 2002; 2006). Grazed grasslands do not adequately protect mountain soils from erosion, resulting in widespread down-slope soil movement and degradation (e.g., Chepstow-Lusty et al., 2009, Renison et al., 2013).

In the 1900s, a new approach to managing *Polylepis* forests was implemented, focusing on the establishment of conservation areas. In Argentina, conservation management involved exclusion of livestock exclusion or reduction of their density, along with enhanced fire control policies (Renison et al., 2013). Conservation management has been effective in reducing soil erosion and increasing the survival and growth rate of *Polylepis* saplings and juveniles in central Argentina, where most of assessments have been made (Cingolani et al., 2013; Giorgis et al., 2020). However, the effects of conservation management on trees can be both negative and positive. Negative effects include the accumulation of fuel, which is thought to promote larger and more intense fires than in grassed areas, where fuel accumulation is low (Bernardi et al., 2019). In turn, these fires may negatively affect tree survival and growth (Alinari et al., 2015; Argibay & Renison, 2018). Negative effects of livestock exclusion not caused by fires are also to be expected from the increased competition between trees and grasses for nutrients and water (Scholes & Archer, 1997). Positive effects of conservation management involve the reduction of soil erosion, which contributes to the maintenance of soil fertility, favoring seed production (Renison et al., 2004, 2010; Pollice et al., 2013) and, possibly, tree survival and growth rates.

Our main objective was to provide baseline data on the survival, growth, and dieback of *Polylepis* trees. We also evaluated the impact of land management on fire incidence and tree performance, while controlling for plot tree cover, elevation, and tree height, since these factors are known to influence tree performance (Marcora et al., 2008; Smith et al., 2015; Ceballos et al., 2021). Our study focuses on *P. australis*, the southernmost species of the genus. We hypothesize that increased fuel accumulation leads to more frequent wildfires, thereby reducing tree performance. Consequently, tree performance will be lower in conservation-managed forests than in ranching areas. In the absence of fire, we expect tree performance to be similar in both management types. To

assess tree performance, we measured 15-year tree survival, changes in height (both positively associated with performance), and crown dieback (negatively associated with performance). Based on this information, we test the following predictions: (1) The number of study plots affected by wildfires will be higher in conservation areas than in ranching areas. (2) Tree performance will be lower in study plots affected by wildfires than in non-affected plots. (3) When fire incidence is considered, tree performance will be lower in conservation areas than in ranching areas. (4) When fire incidence is controlled for, tree performance will be similar in both conservation and ranching areas.

2. Methods

2.1. Study area

The "Sierras Grandes" mountain range in Córdoba province (central Argentina) is oriented in a north-south direction and varies in elevation from 900 to 2800 m a.s.l. (lat -31.6723; lon -64.8270). Mean annual temperature decreases from 15.7 °C to 7.4 °C between 900 m to 2700 m a.s.l., while annual precipitation increases from 600 to 1000 mm between 600 to 2200 m a.s.l. Precipitation was 907 mm yr^{-1} during the study period (from 2003 to 2018), 23 mm below the 1992-2020 average. The dry-cold season spans from May to September, while most of precipitation is concentrated in the warmer months, between October and April (Cingolani et al., 2023).

The landscape consists of a mosaic of tussock grasslands, grazed lawns, granite outcrops, eroded areas with exposed rock surfaces and *Polylepis australis* (Rosaceae) forests or woodlands. Forests cover 3%, woodlands 9%, and scattered *P. australis* trees occur in 55%, and are nearly absent in the remaining 33% (Cingolani et al., 2004). The main economic activity, which was already established in the 17th century, is livestock ranching with cattle, sheep, horses and goat. Local livestock densities range from 0.1 to 4.8 cattle equivalents ha^{-1} (von Müller et al., 2017). Mean annual fire incidence between 1999 and 2017 ranged from 1.7 to 3.2%, depending on elevation, with at least 91% of wildfires being human-caused (Argañaraz et al., 2020).

2.2. Monitoring

We monitored 880 trees across 139 30 × 30 m plots spread on 1500 km^2 and along an elevational range from 1400 to 2500 m a.s.l. (Fig. 1). Preliminary plot locations were selected using a geographic information system within vegetation units that were supposed to contain *P. australis* trees (Cingolani et al., 2004; 2008). We used Global Positioning System (GPS) to locate eligible plots and selected those that: (1) contained at least one *P. australis* tree 2 m or taller, and (2) had accessible trees for measurement. If a plot did not meet the criteria, it was relocated to the nearest 30 × 30 m area that did. A 2-m height threshold was chosen because *P. australis* already produces a substantial seed crop at this height and is considerably less susceptible to browsing by livestock (Pollice et al., 2013). Plots were marked with metal pins at the center and four corners; coordinates and elevation were recorded using a GPS.

The plots were established in 2003 and were re-measured 15 years later, in 2018. In 2003, we tagged all living *P. australis* trees and measured tree height to the nearest cm from the base to the top of the highest living stem. The percentage of the plot covered by tree crowns was estimated visually. In 2018, we surveyed each plot for a maximum of 45

tagged trees and classified them as alive or dead. Given that *P. australis* trees are semi-deciduous, we considered a tree to be dead if all the aboveground tissues were leafless and the trunks were dry. We re-measured tree height and visually estimated crown dieback as the proportion of dry to total stem biomass. We also searched for signs of logging, such as cut trunks and tree stumps.

We found tags in 75% of all the examined trees that were supposed to contain tags (662 trees with tags out of 880 tagged trees). We identified 179 of the 218 trees with lost tags by locating their position relative to nearby tagged trees with sequential tag numbers and verifying that their height matched the measurements recorded in 2003. In these cases, we assessed their survival, but, as a precaution, we did not record their height in 2018 because of the sensitivity of calculating growth based on a potentially incorrect initial height. For the remaining 39 trees with a lost tag (4% of the total), we were not able to determine individual survival or height due to other uncertainties in their identification. Instead, we recorded the collective survival of the trees with a lost tag at the plot level. We distinguished deaths during the 2003-2018 period from previous deaths by checking our list of trees already dead in 2003 (Renison et al. 2011).

2.3. Wildfires, land management and tree cover

Plots affected by wildfires between 2003 and 2018 were identified by overlaying the plot locations with a fire map created from Landsat TM and ETM+ imagery (30-m spatial resolution, Path/Rows: 229/81 and 229/82) using automatic burned area mapping software (Argañaraz et al., 2020). The plot was considered to be affected by fire (for simplicity, hereafter “burned” plots) if the fire polygon completely or partially included the plot area. Due to protection from rocky outcrops, streams, or surrounding vegetation, not all trees on a burned plot were necessarily scorched.

Our study area falls entirely under some level of protection, which we classified into two conservation categories. (1) *Privately-owned lands with minimal restrictions*, where traditional livestock grazing is permitted (hereafter “ranching areas”; 68 study plots). These areas typically support 0.15–0.3 free-ranging cattle ha^{-1} in paddocks of up to 3000 ha (von Müller et al., 2017). Compared to more strictly protected areas, ranching areas exhibit more grazed lawns, visible soil erosion at active erosion edges, and limited regeneration of tree saplings, even at low livestock densities (Cingolani et al., 2008; Giorgis et al., 2020). (2) Strictly protected areas (hereafter “conservation areas”; 71 study plots) include the state-managed “Quebrada del Condorito” National Park (26,000 ha, established in 1996) and the NGO-managed “Fundación Biosférica” reserve (700 ha, established in 2007). Livestock management was variable in conservation areas: Livestock were gradually removed from 1997 to 2002 and not present thereafter in 56 plots, while livestock grazing occurred at low density (0.05 cattle ha^{-1}) throughout the study in 15 plots.

2.4. Statistical analyses

To test whether land management influenced the likelihood of fire, we fitted a Generalized Linear Model with Bernoulli distribution to plot-level data (N = 139; 0 = unburned, 1 = burned). The explanatory variable was land management, considered as a fixed-effects factor (ranching vs. conservation areas). We describe this and all other models in more detail in the supplementary information (SI).

To assess how trees were affected by land management and fire, we used individual-tree performance indicators. Survival was modeled using all 880 trees, including the 39 unidentified trees for which we knew their collective survival at the plot level. We included unidentified trees to avoid biased results, because their survival was lower than average. Since models considered initial tree height as a covariate, we needed to estimate the identity of each unidentified tree to obtain this value. We solved this by treating the unidentified trees as an additional parameter to be estimated, using as a basis the known initial tree height of the unidentified trees in the plot (see SI). For the analysis of tree net growth and crown dieback, we used 661 tagged trees that had survived.

We fitted a Generalized Linear Mixed Model for each response variable: (a) survival, assuming a Bernoulli distribution (0 = dead, 1 = alive) with logit link; (b) average annual net growth (cm) as the difference in height between 2018 and 2003 divided by the number of years, assuming a Student-t distribution; and (c) crown dieback (%), assuming a logit-skew-normal distribution (i.e., modeling logit-dieback as skew-Normal). Land management (ranching vs. conservation areas) and fire (unburned vs burned plots) were treated as fixed-effects factors. Plot tree cover, elevation and initial tree height were treated as covariates. We also included study plot as a random effect on the intercept.

First, we specified linear effects for continuous predictors and no interactions. When the model residuals showed patterns as a function of predictors, we included additional terms: a quadratic effect for tree cover in the net growth model and for elevation in the crown dieback model, and a linear effect of tree height on the standard deviation in the net growth model. Additionally, we included an interaction term between management and fire in the models for net growth and crown dieback and modeled the dispersion parameter considering these factors and their interaction (more details in SI).

By including management and fire in the models, the fitted effects of management represent the direct effects on the response variables, i.e., the effects not mediated by fire. To assess the whole management effect (direct + mediated by fire), we compared the predicted means for ranching and conservation areas not controlling for fire, which is analogous to the effect of land management that would be estimated in a model that ignores fire. For each response variable, the predicted mean was calculated for each combination of management and fire, with the continuous predictors fixed at their means. We then calculated the mean for each management level, not controlling for fire incidence, as the weighted average of predictions for burned and unburned conditions. Weights were based on the fire probability specific to each management level, as estimated by the fire probability model.

We fitted all models using a Bayesian approach, where knowledge about model parameters after observing the data is represented by their posterior distribution (Hobbs and Hooten, 2015). This approach allows for probabilistic statements about model parameters and their functions. We summarized the posterior distribution with its mean and 95% equal-tailed credible intervals, the Bayesian analog of point estimates and confidence intervals. In addition, we computed the probability of each parameter being positive ($Pr(x > 0)$ in Table 2), with values varying from 0, indicating a negative effect of a covariate, to 1, indicating a positive effect. Probability 0.5 indicates complete uncertainty about the sign of the effect. For the mean tree performance variables, we also computed the posterior probability of being higher in ranching than in conservation areas. We used Stan (Stan Development Team 2020) to sample the posterior distribution and defined weakly informative priors (details on models in SI). For each model, we ran six Monte Carlo Markov chains with 2000 iterations, leaving 1000 iterations for warm-up,

resulting in 6000 samples for inference. All models converged and showed large effective sample sizes, with an adequate fit to the data based on DHARMa residuals (Fig. S1 to S6). All analyses and figures were made in R 4.2.0 (R core team, 2022). The code and data can be downloaded from https://github.com/barberaivan/polylepis_survival.git); data can also be downloaded from http://hdl.handle.net/11336/245364.

3. Results

Over the 15-year period, the average tree survival rate was 88.7% (781 out of 880 trees) and tree height increased by 21 cm, corresponding to an annual survival rate of 99.2% and an annual net growth of 1.4 cm. Crown dieback, assessed in 2018, was on average 17%. We found no evidence of logging activities.

3.1. Wildfires and land management

Over the 15 years, fire reached 21% of the plots (29 out of 139 plots, with 17 plots burning once and 2 plots burning twice). The analysis of each land management showed that fires reached 16% of the plots in ranching areas (11 out of 68) and 25% in the conservation areas (18 out of 71). The posterior probability that ranching areas would burn less than conservation areas was 0.92.

The burned plots had lower values of annual tree survival rate and net annual growth (3% and 4 cm, respectively), and 15% higher crown dieback than the unburned plots (Fig. 2, Table 1). When we controlled for fire incidence, tree survival rate, net growth and crown dieback were similar in the ranching and conservation areas (Fig. 2, Table 1). However, when we did not control for fire incidence, tree survival rate and net growth were 0.3% and 0.6 cm lower, respectively, in the conservation areas than in the ranching areas (Fig. 3).

Tree cover was not related to survival rate but showed a large positive effect on net growth, which remained constant below 60% cover and increased above this threshold. However, plot tree cover slightly increased crown dieback (Fig. 2, Table 1). Annual survival rate increased by 2% from the lowest to the highest elevation, while annual net growth decreased by 3 cm. In turn, crown dieback was lowest at intermediate elevation, although the differences from low or high elevation were small (Fig. S7 in SI). Tree height was one of the strongest predictors of survival and the strongest predictor of net growth: tall trees showed lower survival rate and lower net growth than short trees. In line with these results, tree height led to increased crown dieback, but only with a small effect (Fig. S8 in SI, Table 1).

In general, the explanatory power of the models was low at the observation (tree) level based on the R^2, but moderate-high at the plot level (Table 2).

4. Discussion

The present study reports the first values for tree survival rates, net growth and crown dieback for a *Polylepis* tree species. The results support the working hypothesis that wildfires have a greater effect on treesin conservation areas, where livestock is excluded or reduced, than in rangelands, and that fires reduce tree survival and growth rates due to the dieback of above ground tissues. Moreover, the effects of land management were null

when we controlled for wildfire incidence, but negative for trees under conservation management compared to rangelands when we did not control for fire incidence.

The 99.2% annual survival rate of *P. australis* trees is similar to that reported for planted saplings of the same species from the fourth year after out-planting onward (e.g., Simoes Macayo & Renison, 2015). Our survival values are also similar to those of trees in high elevation forests in Colorado, USA (99.0 to 99.6% yr^{-1}, Smith et al., 2015; Andrus et al., 2021) and in the semiarid Chaco of Central Argentina (99.4% yr^{-1}, Iturre et al., 2020). In contrast, tree survival in our study was higher than in the subtropical mountain forests of northwestern Argentina (97.3% yr^{-1}, Ceballos et al., 2021), southwestern USA (98 to 98.7% yr^{-1}, Bradford & Bell, 2017), Switzerland (98.5% yr^{-1}, Etzold et al., 2019) or African Savannas (91.2 to 97% yr^{-1}, Das et al., 2022). Regarding the growth of *P. australis*, under livestock exclusion saplings and juveniles grow 8 to 13 cm per year (Simoes Macayo & Renison, 2015; Giorgis et al., 2020), which is significantly higher than the 1.4 cm annual growth observed in trees. This is consistent with our result of a negative association of tree height with height growth (and survival), as reported in other tree species (e.g. Smith et al., 2015; Andrus et al., 2021). Fire incidence in our study area also contributed to the low growth rates of the studied trees. In general, larger trees are older, and tend to be more vulnerable to damage from fungi, wind, or drought (Robledo & Renison, 2010; Stovall et al., 2019). The high survival and low growth rate of *P. australis* are surprising, given the relatively low wood density of the species, a trait usually associated with low survival and high growth rate, and may be explained by the climate in the high elevation where *P. australis* is distributed (Greenwood et al., 2017; Ferrero et al., 2022).

Over the 15-year study period, 21% of the plots were affected by wildfires, including two plots that were affected twice. These values correspond to 1.5% of plots per year and a fire cycle of 67 years, which is a short fire cycle for a woody ecosystem. Fire incidence in our study is slightly lower than the average reported for all vegetation types at similar elevations (1.5% compared to 1.7 - 3.2% yr^{-1}, Argañaraz et al., 2020). The lower fire incidence in our study could be related to the selection of plots in areas with occurrence of *P. australis* trees, which on average are better protected from fire due to higher rockiness and lower tussock cover (Cingolani et al., 2004; 2008). Although ranching activities, such as illegal burning of tussocks to promote palatable regrowth, increase the number of fires, the incidence of wildfires was higher in conservation areas. As we suggested, this result can be explained by increased fire spread in conservation areas, driven by reduced grazing and fuel accumulation (Cingolani et al., 2008; Vaieretti et al., 2018), without sufficient implementation of fire mitigation strategies.

Three previous studies on the effects of wildfires on *P. australis* trees report survival rates of burned trees of 90%, 82% and a range varying with elevation of only 20 to 50%, while all report important reductions in tree height due to above-ground scorching of tissues (Renison et al., 2002; Alinari et al., 2015, Argibay & Renison, 2018). The present findings are consistent with previous studies reporting negative effects of fire, but the magnitude of the effects is difficult to compare due to differences in methodologies, including different monitoring periods. Post-fire recruitment of *P. australis* is low, as indicated by the only assessment made (Alinari et al. 2015), suggesting that a reduction in fire incidence would lead to an expansion of forests from the current fire-refugia. Ecological studies on wildfires in the high mountain *Polylepis* forests are urgently needed, since fires are widely used as a management tool in the Andes. In addition, so far only one *Polylepis* species has been studied, in which survival was found to be 6.2% two years after

the fire (*P. incana* from the highlands of Ecuador, Cierjacks et al., 2008), showing that there is a wide range of responses to fire in the genus *Polylepis*. No effects of land management on tree survival and net growth were detected when fire incidence was controlled for, which is likely due to tree resilience to change, and a balance between negative and positive effects of livestock (Scholes & Archer, 1997). It is surprising that, given the high palatability of *P. australis* to livestock, management did not influence survival or growth in burnt areas. After a fire, most trees resprout from the base, and the tissues are accessible to livestock and heavily browsed (Alinari et al., 2015, Argibay & Renison 2018). However, it is possible that the lower accumulation of fuel in ranching areas resulted in wildfires that were less damaging to trees than in conservation areas, thereby compensating for the browsing of resprouts.

Regarding covariates, while we found no relationship between plot tree cover and tree survival, crown dieback increased with crown cover, suggesting competition rather than facilitation among trees (e.g., Bradford & Bell, 2017; Ceballos et al., 2021). Furthermore, elevation was associated with increased tree survival and decreased growth, which is consistent with reports on *P. australis* saplings and juveniles (Marcora et al., 2013; Renison et al., 2022), whereas trees grew and survived less as they became taller and older. Our finding of null evidence of logging is encouraging for the conservation of *P. australis* and suggests effective implementation of logging restrictions.

Without experimental data and a 15-year monitoring period without intermediate evaluations, our study did not allow for an examination of the proximate causes of variation in tree survival, growth and crown dieback, except for the evident effects of fires, tree height, tree cover and elevation. Based on our case study, future research on *P. australis* should include: (1) Defoliation by leaf-cutter ants, since it was recorded in planted saplings below 2170 m a.s.l. in the same region (Renison et al., 2022; Peirone-Cappri et al., 2024); (2) lightning strikes, as described for lowland forests in Panama (Yanoviak et al., 2020), and considering that our study area has annual averages of 50 thunderstorm days yr^{-1} (Bertone et al., 2022); (3) wind-throw, exacerbated by ice and snow accumulation in the tree structure (DR personal observations); (4) pest outbreaks; and (5) anomalous droughts or heat waves, as studied in many forest types but not for *Polylepis* forests (e.g., Das et al., 2016; Choat et al., 2018).

5. Management implications

On the one hand, we found that scattered trees had high survival rates, so that good-quality seed input to the surrounding areas can be expected for many decades (Renison et al., 2004). If regeneration around scattered trees is not already present in conservation areas, it will be necessary to create vegetation gaps where seedlings can establish, and then promote sapling growth by reducing or excluding grazing (Zimmerman et al., 2009; Renison et al., 2015; 2022). On the other hand, while the exclusion of livestock is essential to reduce soil erosion and allow the growth of *P. australis* juveniles (Cingolani et al., 2013, Renison et al., 2015), it has been associated with an increase in fire frequency, which can undermine its benefits. Therefore, more investment is needed to reduce wildfire incidence.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table 1. Parameter estimates for tree survival, growth and crown dieback models. Pr(x > 0) is the posterior probability of each parameter being positive; hence, it is zero (or one) if there is complete certainty that the parameter is negative (or positive), and 0.5 if either sign is equally probable. Rhat < 1.01 indicates convergence of the Markov Chain Monte Carlo algorithm. The continuous predictors were standardized before fitting the models. The following mean and sd values were used for standardization: elevation = {1898, 233.4} m a.s.l; tree height = {385.5, 119.9} cm; forest cover = {22.8, 23.3}%. The levels management = ranching areas and fire = unburned were absorbed in the intercepts. Sigma (plot) is the standard deviation among plots. The parameters controlling dispersion in the growth and crown dieback models are indicated with "(Sigma)" and "(Omega)", respectively. Nu is the degrees of freedom of the Student-t distribution, and Alpha is the slant parameter of the skew-normal distribution. Abbreviations: Manag = management; C = conservation areas; R = ranching areas; B = burned, U = unburned. See models details in SI.

	Posterior mean	95% CI	Pr(x > 0)	Effective sample size	R hat
Survival					
Intercept	5.912	[5.325, 6.602]	1.000	3917	1.001
Manag=C	-0.256	[-0.992, 0.471]	0.243	4750	1.000
Fire=B	-1.715	[-2.463, -0.985]	0.000	4460	1.000
Tree cover	-0.086	[-0.401, 0.229]	0.291	4677	1.000
Elevation	0.391	[0.009, 0.789]	0.978	5279	1.000
Height	-0.270	[-0.439, -0.075]	0.003	6002	1.000
Sigma (plot)	0.901	[0.409, 1.447]	1.000	1315	1.004
Growth					
Intercept	1.282	[-0.398, 2.956]	0.932	1250	1.004
Manag=C	-1.007	[-3.164, 1.195]	0.178	1474	1.008
Fire=B	-3.544	[-6.987, -0.022]	0.024	1848	1.002
Manag=C;Fire=Burned (interaction)	0.349	[-4.318, 4.906]	0.564	1789	1.004
Tree cover	-0.468	[-1.934, 1.027]	0.262	1255	1.003
Tree cover ^ 2	0.903	[0.108, 1.684]	0.988	1329	1.000
Elevation	-0.570	[-1.5, 0.366]	0.111	2117	1.002
Height	-2.600	[-3.084, -2.121]	0.000	6627	1.000
Manag=R;Fire=U (Sigma)	1.262	[1.078, 1.435]	1.000	3918	1.000
Manag=R;Fire=B (Sigma)	1.295	[0.898, 1.696]	1.000	4246	1.001
Manag=C;Fire=U (Sigma)	1.322	[1.197, 1.443]	1.000	4108	1.000
Manag=C;Fire=B (Sigma)	1.382	[1.066, 1.697]	1.000	4795	1.000
Height (Sigma)	0.262	[0.205, 0.323]	1.000	7710	1.000
Nu	4.074	[2.881, 5.804]	1.000	3845	1.000
Sigma (plot)	3.839	[3.115, 4.684]	1.000	1666	1.002
Crown dieback					
Intercept	-4.228	[-4.585, -3.85]	0.000	2838	1.000
Manag=C	-0.308	[-0.779, 0.155]	0.095	2515	1.001
Fire=B	-0.459	[-1.546, 0.519]	0.192	3054	1.002
Manag=C;Fire=Burned (interaction)	0.804	[-0.491, 2.163]	0.888	2895	1.001
Tree cover	0.196	[-0.003, 0.392]	0.973	2681	1.001
Elevation	-0.090	[-0.301, 0.113]	0.197	4036	1.001
Elevation ^ 2	0.208	[0.049, 0.36]	0.994	3925	1.000
Height	0.086	[-0.01, 0.183]	0.959	6296	1.000

Manag=R;Fire=U (Omega)	2.160	[1.87, 2.484]	1.000	5048	1.001
Manag=R;Fire=B (Omega)	3.609	[2.747, 4.767]	1.000	6033	1.000
Manag=C;Fire=U (Omega)	2.441	[2.213, 2.679]	1.000	4471	1.001
Manag=C;Fire=B (Omega)	3.493	[2.779, 4.381]	1.000	5445	1.000
Alpha	4.327	[2.913, 6.608]	1.000	2287	1.002
Sigma (plot)	0.657	[0.474, 0.862]	1.000	1747	1002

Table 2. Bayesian R^2 (Gelman et al. 2019) for the three models, expressed as percentage. Each R^2 is summarized by the mean and 95% equal-tailed credible interval of the posterior distribution (in brackets). The observation-level R^2 was computed by marginalizing over the plot random effect, and plot-level R^2 was calculated by fixing tree height at the mean (see SI for details).

Model	Observation level	Plot level
Survival	0.52 [0.15, 1.00]	43.87 [15.27, 78.19]
Growth	15.30 [10.65, 20.47]	26.06 [12.45, 40.72]
Crown dieback	6.85 [3.22, 11.81]	44.81 [22.95, 65.72]

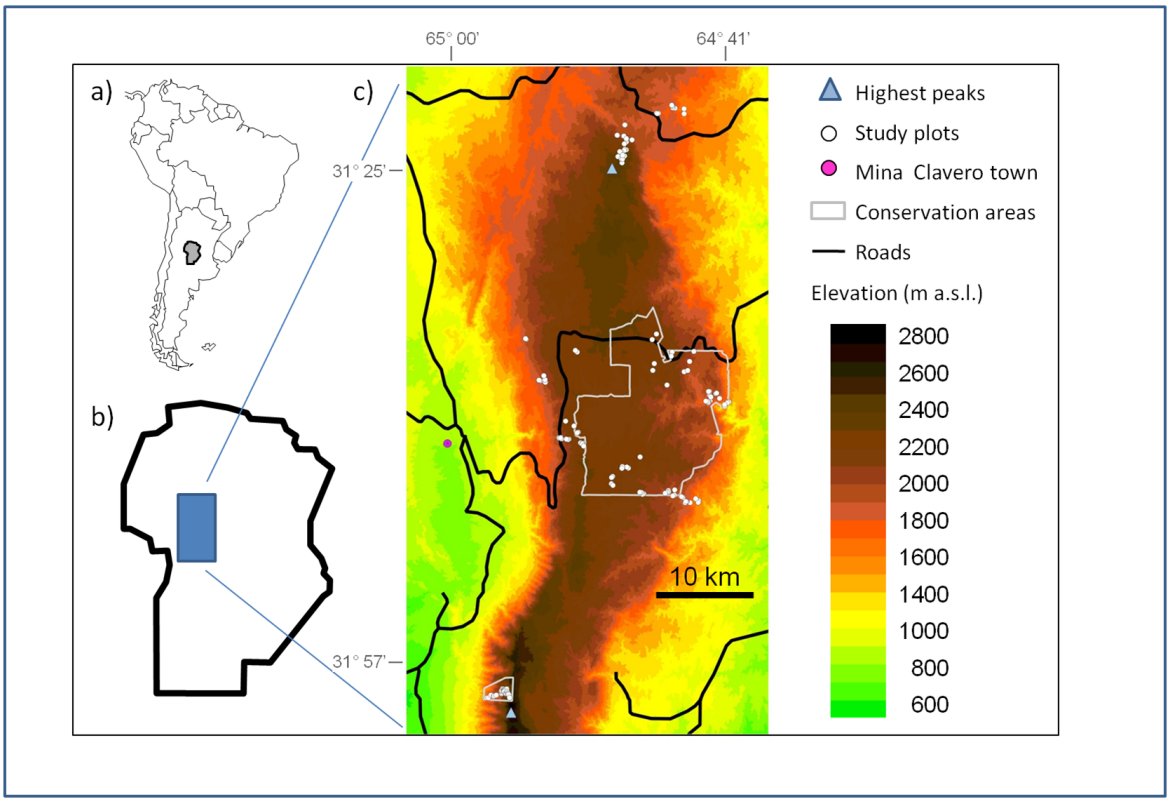

Figure 1. Study area and plot locations. (a) Córdoba province in Argentina and South America. (b) Study area in the province of Córdoba. (c) Plot locations (white squares) in the study area.

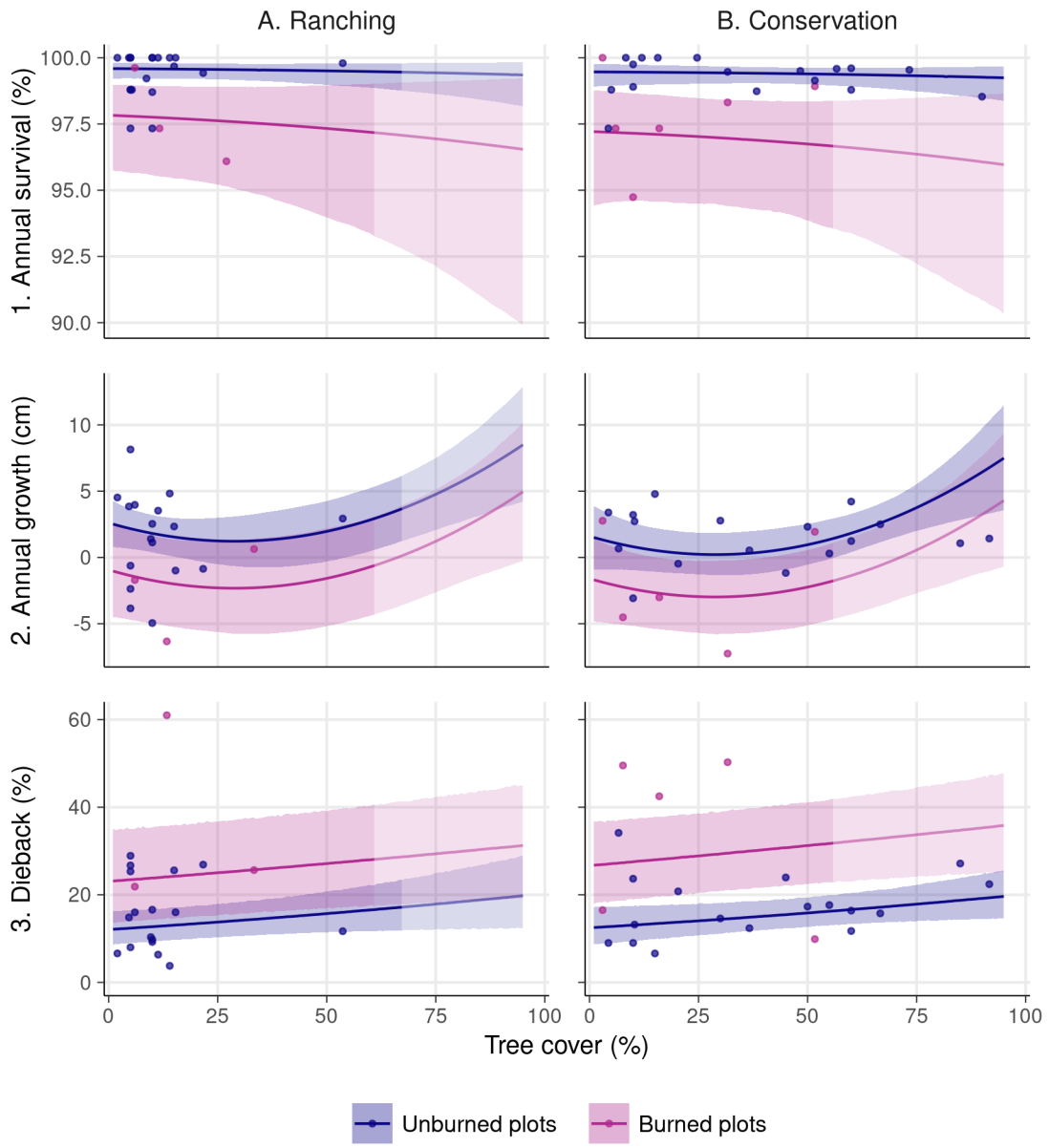

Figure 2. Annual tree survival, net annual growth in height, and crown dieback due to land management and fire as a function of tree cover. Lines show predicted mean for an average plot using the posterior mean, and bands show 95% equal-tailed credible intervals. Predictions were calculated by fixing elevation and tree height to their means across plots (elevation = 1898 m a.s.l.; tree height = 385.5 cm). Points show the mean values at the plot-level, averaged in groups of three plots (for survival proportions, these values were raised to the 1/15th power to approximate the annual values). Lighter shade: tree cover values exceeding the maximum observed in each subset of the data. Points do not usually reach these limits because they are averages of three plots.

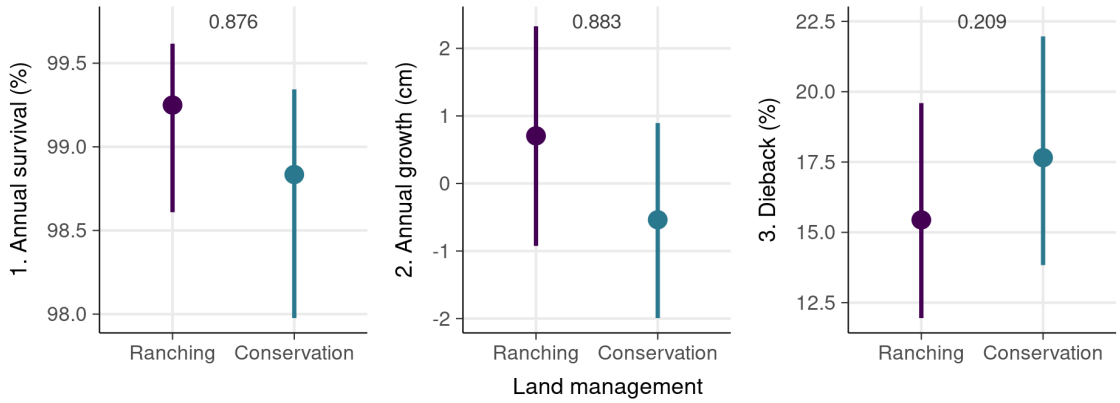

Figure 3. Annual tree survival, net annual growth in height, and crown dieback as a function of land management, without controlling for fire occurrence. The dots show the predicted mean for an average plot using the posterior mean, and the lines, the 95% equal-tailed interval. The continuous predictors were fixed at their means across plots (elevation = 1898 m a.s.l.; tree height = 385.5 cm; tree cover = 22.8%). The numbers in the upper part of the panels show the posterior probability of ranching areas showing higher mean than conservation areas, where 1 indicates complete certainty of this being true, 0 indicates complete certainty about the opposite pattern (the mean is *lower* in ranching areas), and 0.5 indicates complete uncertainty about the sign of the difference.