



## The contribution of fire damage to restricting high mountain *Polylepis australis* forests to ravines: Insights from an un-replicated comparison.

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**ABSTRACT.** High mountain forests are often restricted to ravines and much debate has existed on the explanations of this distribution, with arguments ranging from abiotic site conditions being more favorable in ravines to there being reduced herbivory or reduced fire frequency and damage in ravines. We aim at understanding the contribution of fire damage and provide data to help test the hypothesis that fires are less damaging and that trees recover faster in ravines as compared to ridge sites. We evaluated crown damage, post-fire survival, regeneration by resprouts and seeds, and browsed stems in burned and unburned control *Polylepis australis* trees situated in a ravine and in a ridge forest in the west slope of the mountains of Central Argentina. The proportion of the tree crown scorched by fire was 28 % higher on the ridge than in the ravine ( $94.3 \pm 1.9$  % and  $66.1 \pm 4.5$  %, respectively) and was negatively related to tree height which was lower on the ridge. Survival was not differentially affected, but post-fire re-growth and establishment through seeds was lower in the ridge as compared to the ravine. Browsed stems were about twice as frequent in the ridge as in the ravine, more so in the resprouting burned trees. Our study provides evidence that forests are restricted to ravines in part because the effects of fires are less severe at these sites than in ridges, which adds to other possible causes like reduced livestock use of ravines, enhanced regeneration by seed and faster tree growth within ravines all of which are probably mediated by abiotic factors.

[Keywords: Montane woodlands, regeneration, topography, tree line, sprouting; ridge]

**RESUMEN.** La contribución del daño por fuego en restringir los bosques montanos de *Polylepis australis* a las quebradas: aportes de una comparación sin réplicas: Con frecuencia los bosques de altura están restringidos a quebradas y existe controversia sobre los motivos de esta distribución, con un rango de argumentos que van desde los que afirman que en las quebradas existen mejores condiciones abióticas, hay menos herbivoría, la frecuencia de fuegos es menor o que allí los fuegos hacen menos daño. Nos propusimos entender la contribución del daño por fuego y proveemos datos para poner a prueba la hipótesis de que los fuegos hacen menos daño en las quebradas en comparación con los filos. Evaluamos el daño por fuego, la supervivencia post-fuego, la regeneración por rebrote y por semilla y el ramoneo entre árboles quemado y controles no quemados situados en una quebrada y en un filo de la ladera occidental de las Sierras Grandes de Córdoba, Argentina. El daño a las copas fue 28 % mayor en filo que en quebrada ( $94,3 \pm 1,9$  % y  $66,1 \pm 4,5$  %, respectivamente) y estaba negativamente relacionada con la altura de los árboles, que además era menor en filo. La supervivencia post-fuego no fue afectada diferencialmente por la topografía, pero el crecimiento de rebrotes y el establecimiento por semilla fue menor en filo que en quebrada. El ramoneo por animales domésticos fue dos veces más frecuente en el filo que en quebrada y mayor en los árboles quemados que en los árboles no quemados. Nuestro estudio aporta evidencias de que los bosques de *Polylepis* están en parte restringidos a quebradas debido a que allí los efectos de los fuegos son menos severos, lo cual se agrega a otras posibles causas como un uso más reducido por ganado, mayor crecimiento de los rebrotes y regeneración por semillas, las cuales seguramente están mediadas por condiciones abióticas.

[Palabras clave: Bosquecillos montanos, regeneración, topografía, línea arbórea, rebrote, filo]

### INTRODUCTION

The higher tropical and subtropical mountains of South America often have isolated forest patches above the timberline which are mainly situated in ravines, rocky outcrops and other protected situations, with a few shrub-like individuals found in other topographic positions such as ridges (Körner

2012). Some authors propose that these forest patches are remnants of a potentially larger forest belt which was destroyed and fragmented by long-term human land-use, mainly due to livestock rearing and associated fires used to promote grass re-growth (Kessler 2002; Cingolani et al. 2008). Browsing by livestock is also known to affect woodland regeneration by retarding or even hampering

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juvenile growth (Giorgis et al. 2010). However, other authors note the importance of abiotic influences (e.g., Rada et al. 2011) and the fact that *Polylepis* forests were fragmented even before human colonization of the Americas (Gosling et al. 2009).

Fires may in part explain the distribution of forest patches if they are less frequent or damaging in deep ravines, canyons and rocky areas (Kessler 2002; Coblenz & Keating 2008). Supporting this hypothesis more fire scars were detected in forests situated at higher topographical positions than in forests situated in valley bottoms and ravines of Central Argentina (Renison et al. 2006). However, other authors argue that forests are restricted to ravines mainly because in these sites trees find more favorable conditions for regeneration and growth, such as protection from chilling winds and moist soils (Miehe & Miehe 1994 cited in Kessler 2002; Enrico et al. 2004). Moreover, in some situations fires may even be necessary for forest regeneration and expansion, for example, when post-fire establishment is favored by the removal of herbaceous understory and adult trees are tolerant to fire (Grau & Veblen 2000).

In South America *Polylepis* species dominate the canopy of the high Andean forests from Venezuela to Argentina, forming an impressive 5,400 km long patchwork of forest islands which concentrate a large number of endemic species, provide numerous ecological services such as maintenance of biodiversity, control of soil loss, provision of clean water and carbon capture (Gareca et al. 2010; Renison et al. 2010). Almost every study within *Polylepis* forests mentions fires as one of the main causes of forest decline, and a quick evaluation performed in Argentina showed that over 60 % of the forests had evidence of fire in three of the five studied *Polylepis* species (Renison et al. 2013). Thus, studying the effects of fires seems the logical starting point to understanding the present day distribution of *Polylepis* forests, but to the best of our knowledge only two studies have examined the effects of fires on *Polylepis* survival, growth and reproduction (Renison et al. 2002; Cierjacks et al. 2008), while none have compared fire effects in different topographic positions. An important consideration when studying fire effects is that in many ecosystems woody species persist in situ through re-sprouting to multiple disturbances, including fires. This strategy has been termed the persistence niche and may substantially contribute to

species resilience (Bond & Midgley 2001; Torres et al. 2013). However, this strategy has been less studied than post-fire regeneration by seed. Moreover, this may be the key-point to understand *Polylepis* forest present day distribution patterns.

Our goal was to understand fire effects on *Polylepis australis* survival, growth, sprouting and regeneration by seed, in two contrasting topographic positions, a deep ravine and a ridge-top. Because in our study area soils in ravines are wetter than in ridges we hypothesized that fire damage would be reduced at the ravine site and post-fire recovery would be faster. Alternatively, fires could be affecting both topographic positions in a similar manner suggesting that forests are restricted to ravines for other reasons, e.g., lower fire frequency or better growing conditions. Because livestock are often attracted to re-growth in burned areas we also quantified browsed stems.

## METHODS

### *Study area and species*

The study was carried out in the western slopes of the Sierras de Córdoba mountain range in central Argentina (31° 58' S; 64° 57' W). Mean temperatures of the coldest and warmest months at 2100 m asl are 5.0 and 11.4°C respectively, with no frost-free period (Cabido 1985). Mean annual precipitation is 840 mm, with 83 % of all rainfall concentrated in the warmest months, between October and April.

The present-day vegetation consists of a mosaic of tussock grasslands, grazing lawns, granite outcrops, eroded areas with exposed rock surfaces, *Polylepis* forests (12 % of the surface) generally restricted to ravines but also found in steep slopes and low topographic positions like open valleys (Cingolani et al. 2004; Renison et al. 2011). The upper forest strata is dominated by *Polylepis australis* with other less abundant woody species such as the tree *Maytenus boaria* (Celastraceae), the shrubs *Escallonia cordobensis* (Glossulariaceae), *Berberis hieronimii* (Berberidaceae), *Satureja* spp. (Lamiaceae) and the dwarf shrub *Gaultheria poepigii* (Ericaceae) (Cingolani et al. 2004, Renison et al. 2011).

The main economic activity in the Córdoba mountains is livestock rearing (cattle, sheep, horses and goats), which began early in the 17th century. Large native herbivores (*Lama guanicoe* and *Rhea pennata*) were completely replaced by domestic livestock by the beginning of the 20th century (Medina et al. 2011) and *L. guanicoe* is being re-introduced in the Córdoba mountains (Flores et al. 2012) but not present in our study area. Due to its intrinsic fragility and four centuries of domestic grazing, vegetation cover and soils have been lost in

around 20 % of the mountain range, leaving behind bare rock (Cingolani et al. 2008, 2013).

Our study species, *Polylepis australis* (hereafter *Polylepis*), is an evergreen tree or shrub endemic to the mountains of Argentina (Renison et al. 2013). Seed production per tree can reach up to 224,000 seeds per year but is reduced considerably by fires with most completely burned individuals producing no seeds for at least 4 years after the fire event (Renison et al. 2002; Pollice et al. 2013). Seed viability is variable, ranging from 0 to 60 % with an average of around 20%. Unviable seeds do not contain embryos and over 98 % of the seeds containing a full embryo germinate when in adequate moisture conditions. The species maintains no significant seed bank (Enrico et al. 2004; Renison et al., 2004; Seltmann et al. 2007).

### Methods

The study was performed after a fire which burned over 1,000 hectares on August 17, 2003 in the "Los Molles" river basin under hot and windy weather. We did not measure fire intensity but according to the local fire brigade personnel the fire caused intense vegetation and soil burning (personal communication). The area was previously grazed by free ranging livestock at relatively low densities. Our study was carried out in two sites differing in topographic position: (1) a *Polylepis* forest on the flat top of a ridge (0.36 ha, 2140 m asl) and (2) a comparison forest which was closest to the ridge and which we judged as a typical *Polylepis* forest in a ravine (2 ha, 1534 m asl). In our study system this is the only location we know of where a *Polylepis* forest is found on a ridge (Cingolani et al. 2004; Renison et al. 2006), thus no other ridge-top forests were available. Although our results are difficult to extrapolate beyond the study sites, we believe that accumulating local studies of this type is the only approach for obtaining general patterns.

In each site we selected 17 unburned control *Polylepis* trees situated in an area not reached by the fire and 59 trees within the burned area. We selected more burned than unburned trees because we expected a greater variability in their responses. We attempted to ensure that control trees were situated under similar conditions than burned trees regarding solar incidence, rock under the crown and slope but this was not possible for all variables (see first result). Study trees were selected haphazardly with the restriction that we attempted to distribute them evenly throughout the forests. We tagged and geo-positioned individuals after the fire (September 2003), and re-visited them during the dormant season (winter) two years after the fire (September 2005). We considered that monitoring two years after the fire was optimal on the basis of a previous study where trees were monitored every year for four years but all post-fire effects were already evident in the first year and the pattern of results did not change after this (Renison et al. 2002). We monitored during the second year to be conservative. For each tagged individual, on

the first visit we estimated: (1) fire damage as the proportion of the crown that was scorched (%); (2) pre-fire height (cm) as determined by the tree skeleton which survived the fire largely intact. For the area under the tree crown we estimated: (3) solar incidence at the crown level measured with a clinometer as the trajectory of the sun not covered by mountains, rock outcrops or other obstacles (in a flat area with no obstacles: 180 degrees), (4) proportion of rock (%); (5) slope inclination with a clinometer. On the second visit two years later we estimated: (6) Survival (trees were classed as alive when trees had at least one green leaf); (7) Height from the tallest live growth bud to the ground (cm); (8) and proportion of browsed stems (%) by counting up to 100 browsed and non-browsed stems per individual, which in our study area are mainly browsed by livestock (Giorgis et al. 2010).

To determine whether fire favored *Polylepis* establishment by seed differentially in both topographic positions, we sowed 40 groups of 600 seeds each, distributed in the burned and control sites. Seed addition was performed in December 2003 and we re-visited the area eight months later in August 2004 to register seedling presence.

### Statistical analysis

We described microsite and tree characteristics of control and burned trees in the two topographic positions calculating mean  $\pm$  SE values and using a one-way ANOVA (one factor with 4 groups) to determine significant differences. For the variable solar incidence we used non-parametric Kruskal-Wallis ANOVA because many trees had identical values, thus tests using rankings were more adequate. For rock under crown, slope and tree height (ln transformed) we used parametric ANOVAs. To determine differences in fire damage in the two sites differing in topographic position we used logistic regression for the trees in the burned treatment only. We performed a logistic regression and classified tree crowns as scorched more and less than 50 % (1 and 0, respectively) because the distribution of the variable was bimodal with a smaller peak in crowns scorched less than 25 %, very few values between 25 and 75 % and many values of more than 75 %, thus we could not use statistics with an assumption of normal distribution. As explanatory variables we considered topographic position as a categorical variable (ravine and ridge) and tree height. Since solar incidence, rock under tree crown and slope were strongly correlated with topographic position those variables were not included in the analysis. Post-fire survival (0-1) was also analyzed using logistic regression while change in tree height (height 2 yrs after the fire - pre-fire height) and proportion of browsed stems (ln transformed) of surviving trees was analyzed with ANOVA. In all post-fire analysis (survival, change in height and proportion of browsed stems) we first built a model where the factors were burned status (unburned and burned) and topography (ridge and ravine), and then added proportion of the crown

**Table 1.** Microsite and tree characteristics for unburned and burned trees at the two studied topographic positions. In the first row we show the number of sampled trees under each situation, below are the mean  $\pm$  SE values for the corresponding variable. Different letters indicate significant differences according to post-hoc tests.

**Tabla 1.** Características de los micrositios para árboles quemados y no quemados en las dos posiciones topográficas estudiadas. En la primera línea mostramos el número de árboles muestreados en cada situación, abajo están los promedios  $\pm$  EE para las correspondientes variables. Las letras distintas indican diferencias significativas según las pruebas a posteriori.

Variable	Ridge		Ravine		P value
	Unburned N = 17	Burned N = 59	Unburned N = 17	Burned N = 59	
Solar incidence (degrees)	150.0 $\pm$ 1.2 A	149.1 $\pm$ 0.9 A	120.6 $\pm$ 1.0 B	113.4 $\pm$ 1.1 B	H = 110.12 P < 0.001
Rock under crown (%)	53.2 $\pm$ 6.2 A	27.6 $\pm$ 2.8 B	37.1 $\pm$ 6.7 B	13.2 $\pm$ 2.0 C	F = 18.854 P < 0.001
Slope %	6.8 $\pm$ 1.5 A	15.9 $\pm$ 0.9 B	24.7 $\pm$ 1.2 C	33.0 $\pm$ 1.2 D	F = 77.854 P < 0.001
Pre-fire height (m)	1.8 $\pm$ 0.4 A	1.8 $\pm$ 0.2 A	1.7 $\pm$ 0.4 A	2.33 $\pm$ 0.2 B	F = 4.401 P = 0.005

which was scorched as a covariate to determine if more variance was explained.

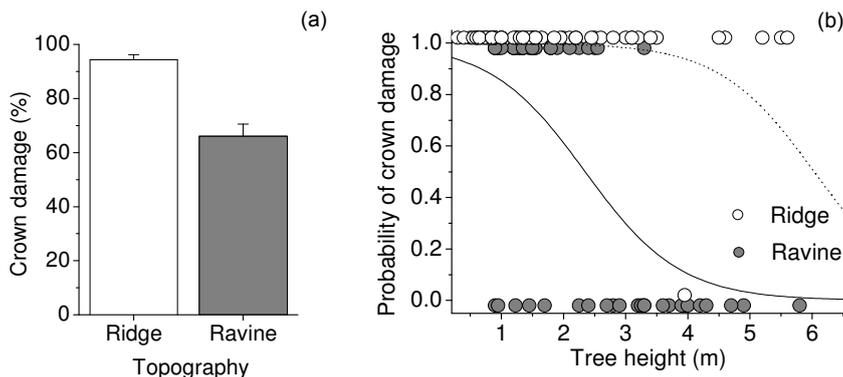
We analyzed establishment through seeding with a two way GLM, with assumption of Poisson distribution and Log-link function. As before, the factors were burned status and topography. Analyses were performed using Infostat 2001.

## RESULTS

Solar incidence was 34 degrees greater at the ridge than in the ravine with no significant differences between control unburned trees and burned trees, while rock under tree crowns was about double on the ridge as compared to the ravine with the unburned control trees having more rock than the burned trees of both

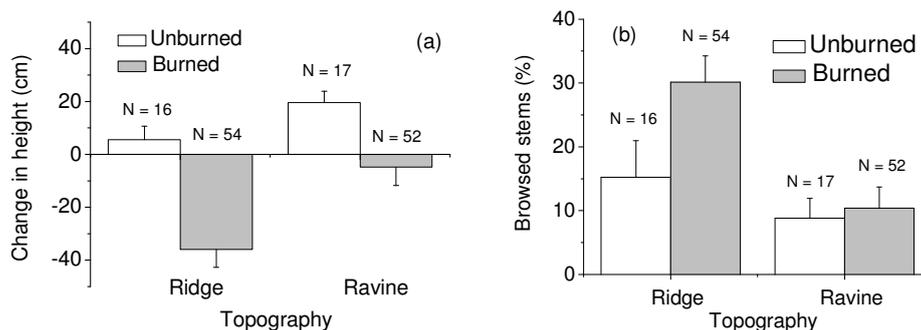
topographic positions. Slopes were flatter in the ridge than in the ravine and more so in the unburned control trees of both locations. Finally, pre-fire tree size averaged around 1.8 m in all situations, except burned trees in the ravine were 30 percent taller (Table 1).

The proportion of the tree crown scorched by fire was 28 percent lower in the ravine than in the ridge (66.1  $\pm$  4.5% and 94.3  $\pm$  1.9%, respectively). Correspondingly, the logistic regression model showed that fire damage (categorized as more and less than 50% scorched) was significantly lower at the ravine than at the ridge (P < 0.001). Additionally, larger trees were scorched less than smaller trees (P < 0.001; Figure 1).



**Figure 1.** *Polylepis australis* crown damage as a function of (a) topography, and (b) height, for 118 individuals affected by a wildfire. In (a) we show average  $\pm$  SE crown damage expressed as a percentage, and in (b) we show the probability of crown damage for each topographic location as a function of pre-fire tree height, where 0 = burned less than 50%; 1 = burned more than 50%. The dotted line indicates probability values as estimated by the logistic regression model for ridge trees:  $Y = 1/(1+2.71828^{-(7.89092-1.30882*X)})$ ; and the continuous line corresponds to ravine trees:  $Y = 1/(1+2.71828^{-(3.071-1.309*X)})$ . Note: all circles have either 0 or 1 values, but for better visualization we drew them slightly above or below their corresponding values.

**Figure 1.** Daños a la copa individuos de *Polylepis australis* en función de la (a) topografía y (b) altura, para 118 individuos afectados por un incendio. En (a) se muestra la media  $\pm$  EE de la proporción de la copa dañada (%), y en (b) se muestra la probabilidad de daños de la copa en una función de la altura pre-fuego del árbol, donde 0 = son los árboles que se quemaron menos de 50%; y 1 = los que se quemaron más de 50%. La línea punteada indica los valores de probabilidad estimada por el modelo de regresión logística para los árboles ubicados en filo:  $Y = 1/(1+2.71828^{-(7.89092-1.30882*X)})$ ; y la línea continua corresponde a los árboles ubicados en quebrada  $Y = 1/(1+2.71828^{-(3.071-1.309*X)})$ . Nótese que los círculos tienen valores de 0 o 1 pero para una mejor visualización los ubicamos levemente por debajo o arriba de los valores correspondientes.



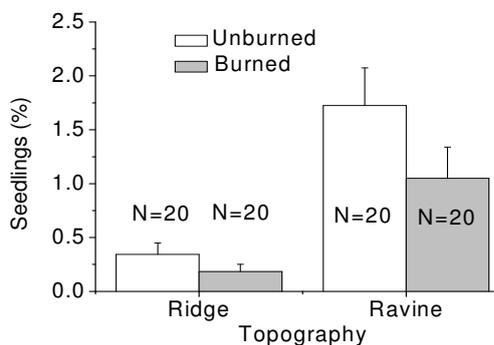
**Figure 2.** (a) Change in height (height two years after the fire - height before the fire) and (b) proportion of browsed stems (%) in relation to topography for unburned (white columns) and burned surviving *Polylepis australis* trees (light grey columns). Above the columns we indicate the number of trees on which the averages are based.

**Figure 2.** (a) Cambio en la altura (dos años después del fuego - altura antes del fuego) y (b) proporción de tallos ramoneados (%) en relación a la topografía para árboles de *Polylepis australis* no quemados (columnas blancas) y quemados (columnas de color gris claro). Por encima de las columnas se indica el número de árboles en los que se basan los promedios.

Probability of survival to the second year of unburned trees was 1 and 0.94 in the ravine and ridge, respectively ( $N = 17$  each), and for burned trees survival was 0.88 and 0.92 in the ravine and ridge, respectively ( $N = 59$  each). The effects of burned status, topography and the interaction between burned status  $\times$  topography on probability of survival were not significant (Logistic regression: Nagelkerke  $R^2 = 0.058$ ;  $P = 0.266$ ). When we added to the model proportion of crown which was scorched, the percentage of explained variance went up considerably but still no explanatory variables were significant (Nagelkerke  $R^2 = 0.261$ ;  $P = 0.103$ ).

Net change in height for unburned trees averaged 20 and 6 cm in the ravine and ridge,

respectively, while burned trees had negative net changes in height of -5 and -36 cm in the ravine and ridge, respectively, due to partial crown die-off and sprouting from the base or upper stems which did not compensate die-off (Figure 2a). Growth in height was significantly higher for unburned than burned trees ( $F = 13.6$ ;  $P < 0.001$ ) and lower in the ridge than in the ravine ( $F = 6.4$ ;  $P = 0.013$ ) with no significant interaction between burned status  $\times$  topography ( $F = 0.9$ ;  $P = 0.34$ ). The overall model only explained 15 % of the variation in tree growth (ANOVA: adjusted  $R^2 = 0.15$ ;  $P < 0.001$ ). When we added as a covariate the proportion of crown which was scorched the model explained an extra 21 % of the variance (adjusted  $R^2 = 0.36$ ;  $P < 0.001$ ), and topography was no longer significant.



**Figure 3.** Proportion of *Polylepis australis* seeds registered as seedlings (%) for a ridge and ravine situation with seedlings in unburned and burned soils. Sample sizes are shown in the bars and represent plots with 600 sown seeds.

**Figure 3.** Proporción de semillas de *Polylepis australis* registrados como plántulas (%) para un filo y una quebrada en siembras en suelos no quemados y quemados. Los tamaños muestrales se muestran en las barras y representan parcelas con 600 semillas sembradas.

Livestock influence was greater in the burned areas as judged by the proportion of browsed stems which was two times greater in burned trees as compared to unburned trees in the ridge. However, livestock influence was not significant in the ravine where browsing was lower overall (ANOVA: Burned status,  $F = 2.13$ ,  $P = 0.14$ ; Topography,  $F = 8.44$ ;  $P = 0.004$ ; Burned status  $\times$  topography,  $F = 4.11$ ,  $P = 0.045$ , Adjusted  $R^2 = 0.17$ ; Figure 2b).

We recorded as seedlings 0.82 percent of the sown seeds when checked eight months after sowing. Number of recorded seedling was around 5 times greater in the ravine as compared to the ridge ( $P < 0.0001$ ), and 1.6 times greater in unburned as compared to burned sites ( $P < 0.0001$ ) with no detected topography  $\times$  burned status interaction ( $P = 0.66$ ; overall GLM model:  $\chi^2 = 473.7$ ;  $P < 0.0001$ ;  $df = 76$ ; Figure 3).

## DISCUSSION

The ridge and ravine sites represent two unreplicated contrasting topographical situations and the generalization of our results to a broader region will mainly depend of further studies performed in other mountain ranges. At the local scale our results maybe used to explain present day forest distribution only if the studied fire event and topographical situations are fairly typical of the region, which we believe they are. In the ridge, the forest is exposed to winds and higher solar radiation, and presumably has lower moisture in soil due to downhill water runoff, as generally occurs in our study area (Cingolani et al. 2003). The ravine is protected from the winds and solar radiation by surrounding hillsides, and presumably has a higher supply of moisture from the stream and surrounding hillsides, as also been proven to be the case in our study area (Cingolani et al. 2003). Furthermore, although we have no other ridge forests as references, it is logical to assume that lower tree height in the ridge forest is not an exceptional condition as in our study area trees often become shorter and more shrub-like outside of ravines even when not reaching the uppermost ridges (Enrico et al. 2004). Not so similar are the altitudes above sea level of the ridge and ravine with a difference of 600 m, however both altitudes are well within the optimal growth conditions for *Polylepis* in our region (Marcora et al. 2008; 2013), and of course on average ridges are always higher than ravines as in our case. Thus, we can consider our ridge and ravine situations as fairly typical in many aspects to other ridge and ravine sites in our region. We did not measure fire intensity and conditions during the fire, and we are not aware of any other study in the region which measured fire characteristics so it is very difficult to know whether the study fire had a typical behavior. Fire date and weather conditions during the fire were typical for the region during the fire season (end of the dry season on hot windy days), and our study fire is probably representative of the many small to medium sized fires in the area.

Supporting the hypothesis that fire causes less damage in ravines, we found that the proportion of the tree crowns that were scorched was lower in the ravine, even though ravine trees had less protective rock under their crowns. Renison et al. (2006) reported less fire scars in ravines as compared to other topographic locations, suggesting fires are also less recurrent in ravines. Thus, we can

presume reduced fire damage and frequency in ravines.

The fire damage did not affect post-fire *Polylepis* survival which was high in accordance with a previous study performed in the same species (survival of 88%, Renison et al. 2002), but contrasting to post-fire survivals of 6% as determined in a fire event affecting *Polylepis incana* of Ecuador (Cierjacks et al. 2008). The high *Polylepis* survival in our study may be explained by the multiple layers characteristic from the bark of *P. australis*. Its particular bark serves to protect it from low temperatures in the high mountains (Rada et al. 2001) and may also protect it from high temperatures of fires as has been shown for many species around the globe where bark thickness increases fire survival (Whelan 1995).

However, even if *Polylepis* survival is high after our study fire, their growth in height was retarded due to crown die-off, more so in the ridge situation where trees were more scorched and growth was slower. As short trees were also more scorched, recurrent fires can have a positive feedback, especially in sites like ridges where fire frequency is higher (Renison et al. 2006) and damage greater (the present study). Livestock then tends to browse sprouts after fires, especially in the more accessible and flat ridge-top forest. Therefore, the *Polylepis* forest stand at the ridge was subjected to a second positive feedback which could ultimately lead to local extinction of *Polylepis* due to the combined effects of enhanced herbivory, higher fire frequency and higher fire damage, a scenario which has also been described for other forest types under livestock influence (Blackhall et al. 2008).

Sown seeds established better in the ravine than in the ridge probably due to the higher moisture in soil. This topographical divergence in post-fire tree regeneration by seed was reported in other woody species (Kennard et al. 2002; Diaci et al. 2005). Seedling recruitment is usually abundant in environments such as deep ravines, not only due to increased establishment per seed, but also because deep ravines tend to retain seeds. Conversely, in convex summits tree stands were predominantly covered by adults with a low number of saplings because seed regeneration possibilities were limited to certain years with favorable environmental conditions as occurs in other ecosystems (Silla et al. 2002; Turner et al. 2003). In arid environments, competition for water is high among seedlings and grasses and

sprouting is less affected by this competition than seeds (Lloret et al. 2005), which may explain the preponderance of sprouting in our ridge site. The lower seed recruitment in the ridge could also be due to livestock trampling and soil compaction (Torres et al. 2008). It is unlikely that livestock would be responsible for the lower seed recruitment through seedling browsing because at eight months the seedlings are less than 2 cm tall and thus too short to be affected by browsing.

As our study only encompassed a single fire and topographic position was un-replicated, it is difficult to infer up to what extent the results will apply to other fires and situations. Our study area included the largest ridge-top *Polylepis* forest stand that we know of, with only a few smaller ridge forests, all with less than 20 trees still remaining, so it is very unlikely there will be more opportunities to compare effects of fires between ravine and ridge forests in our study area. Often, more grazed areas burn less often or less intensely (e.g., Carilla & Grau 2010), so shifting grazing regimes could change the patterns we found. However, it is interesting that the ridge area we studied – besides having more rock than the ravine – also had a lot more livestock use, and even so, burnt with more damaging consequences, suggesting this pattern holds true under situations with less livestock in the ridge. To be able to make generalizations we encourage further studies of fire frequency, intensity and consequences under different situations. Because fires are illegal in all the Andean countries with *Polylepis* forests, it is often not acknowledged that they occur and permits to study fires are difficult to obtain, so every opportunity must be taken.

Our results suggest that ravines can have the function of “shelter areas” because of their protection from anthropogenic and natural fires which may lead to the local extinction of *Polylepis* forests in the most susceptible sites like ridges, especially with presence of livestock. Conversely, forest conservation and restoration may be feasible out of ravines if fires frequency was reduced and livestock excluded after fires to avoid browsing of sprouts.

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