

RESEARCH ARTICLE

# Landscape Structural Complexity of High-Mountain *Polylepis australis* Forests: A New Aspect of Restoration Goals

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## Abstract

Forest restoration efforts should aim at creating landscapes with a balanced array of forest stands at varying successional stages, thus providing habitat for a wealth of species and multiple ecosystem services. In most high-mountain ecosystems of South America, long-term livestock rearing activities that include fires, browsing, and trampling have delayed or stopped forest succession resulting in simplified landscapes. To determine appropriate restoration goals for *Polylepis australis* mountain forests of Central Argentina, we established 146 plots of 900 m<sup>2</sup> plots throughout five river basins with different historic livestock stocking rates. In each plot, we measured tree heights, canopy cover, estimated age of oldest tree, volume of standing and fallen dead wood, fern cover, and abundance of shade tolerant *Maytenus boaria* trees. K-means cluster analysis using tree heights and canopy cover as classificatory variables yielded

four biologically meaningful clusters. Clusters 1, 2, 3, and 4 comprising 68, 10, 13, and 9% of the plots, respectively, showed increasing amounts of standing and fallen dead wood, fern cover, and abundance of shade tolerant *M. boaria* trees. Plots in clusters 1 and 2 were proportionally more abundant in basins with high human impact and at the altitudinal extremes of *P. australis* distribution, whereas plots in clusters 3 and 4 were relatively more abundant in well-preserved basins and at the optimum of their altitudinal distribution. We interpret clusters 1, 2, 3, and 4 as degraded, regenerating, young, and mature forests, respectively. Restoration goals should focus on attaining an even distribution of forest types similar to that found in our best-preserved basins.

**Key words:** Argentina, forest mosaics, forest structure, forest succession, land use, livestock.

## Introduction

The structure of natural forests is a product of their history of recruitment events and disturbances, such as wildfires, windstorms, diseases, logging, and browsing by herbivores. All of these factors interact with topographical features that influence both disturbance rates and post-disturbance forest succession (Hunter 1990; McComb 2008). Succession occurring in post-disturbance forest stands typically involves a change from open areas colonized by disturbance-prone species to mature forests characterized by a larger proportion of shade-tolerant species, large trees, standing stags, and fallen logs. Most often, succession is reset by new disturbances, and thus forest's

landscape structural complexity may be conceptualized as a changing mosaic of stands at varying successional stages; each stand having a tree age and size structure that benefits certain species' assemblages and differs in the ecosystem services they provide (Hunter 1990; Heilmann-Clausen & Christensen 2005; Lindenmayer et al. 2006). In the management and restoration of landscapes aimed at balancing land use, wildlife conservation, and ecosystem services, it is therefore important to attain a balanced array of forest stands at differing developmental or successional stages where all requirements are considered (Lindenmayer et al. 2006).

Human impact has greatly reduced the surface area occupied by high-mountain forests of Central Argentina and other tropical and subtropical mountain forests of South America, which would otherwise be dominated by trees of the *Polylepis* genus. Many *Polylepis* forest remnants are now restricted to rocky outcrops where the impact of livestock and burning is low. The restoration of forest extension to pre-human intervention levels has been highly recommended because *Polylepis* forests harbor a high richness of endemic species and provide important ecological services to humans, such as the provision of clean water, soil generation, and carbon sequestration (Ellenberg 1979; Hensen 1995, 2002; Fjelds  & Kessler 1996; Purcell & Brelford 2004; Renison et al.

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2006; Cingolani et al. 2008). *Polylepis* forests' presence, patch size, and connectivity have been highlighted as important components of biodiversity and restoration goals (for birds: Fjeldså 2002; Herzog et al. 2002; García et al. 2008; Lloyd & Marsden 2008; for plants: Fernández et al. 2001; Fernández-Terrazas & Ståhl 2002; for rodents: Tarifa & Yensen 2001; Yensen & Tarifa 2002), and more recently *Polylepis* forests' structural complexity has been emphasized (Robledo et al. 2006; Cahill & Matthysen 2007; Lloyd 2008). However, we are not aware of any study determining what the restoration goals should aim for regarding *Polylepis* forest structural complexity.

In Central Argentina, many opportunities to contribute to *Polylepis* forest restoration are arising as an extensive water shed protection area and a National Park were created in 1997 (Cingolani et al. 2004). In addition, many mountain inhabitants are migrating to the lowlands, thus decreasing human pressure on mountain resources as is occurring in other Central and South American regions (Grau & Aide 2008). We studied forest structure in the mountains of Central Argentina where *Polylepis australis* dominates the tree canopy. *P. australis* is the southernmost species of the genus and endemic to Argentina (Kessler & Schmidt-Lebuhn 2006). Its distribution has been greatly reduced due to fires and livestock browsing, with most forests growing in valley bottoms of steep ravines and at around 1,850 m asl where the species finds optimum growth conditions (Cingolani et al. 2008; Marcora et al. 2008). As we lack knowledge of past forest types and structure (as in Lindbladh et al. 2007), we adopted a retrospective approach by comparing areas with differing historical human impact (as in Cingolani et al. 2008).

Our objective was to determine the proportion of *P. australis* forest stands in each successional stage that we should aim for when restoring landscape structural complexity. We did this by: (1) categorizing a wide range of forests by stand successional stage, according to tree size structure and cover, and correlating these stages to ecosystem attributes such as tree age, dead wood, and understorey vegetation; and (2) determining the association of long-term human impacts and natural topographical features with the proportion of stands in each successional stage. Our hypothesis was that human impact has both augmented stand-replacing disturbances and delayed stand recovery, in particular where growing conditions are more adverse. We predicted that: (1) basins with a long-term history of recurring human impacts, as indicated by rock exposed by soil erosion and density of rancher houses, will have less complex landscapes mostly dominated by early successional stands, whereas the proportion of forest successional stages will be more balanced in areas with a lower degree of human impact; (2) areas situated at the altitudinal extremes of *P. australis*' distribution and in high topographical positions will have less complex landscapes mostly dominated by early successional stages compared with sites at the altitudinal optimum and in lower topographical positions.

## Methods

### Study Area

The higher Córdoba Mountain range (Central Argentina, North–South direction, rising up to 2,884 m asl, 31° 34'S, 64° 50'W) has mean temperatures of 5.0 and 11.4°C for the coldest and warmest months, respectively, with no frost-free period (Cabido 1985). Mean annual precipitation was 920 mm, with 83% of the rainfall being concentrated in the warmer months, between October and April (Colladon 2002; Renison et al. 2002a). Vegetation consists of a mosaic of tussock grasslands, grazing lawns, degraded grazing lawns, eroded areas with exposed rock surfaces, granite outcrops, closed and open *Polylepis australis* forests or shrublands (2.5 and 9.4% of the area, respectively). The main economic activity in the Córdoba Mountains is livestock rearing (cattle, sheep, horses, and goats), which began in the seventeenth century, and represents the main driver affecting vegetation and faunal composition at the local scale (Cingolani et al. 2003; 2004; 2008; Teich et al. 2005; Renison et al. 2006; García et al. 2008).

### Sampling Plots and Data Collection

From March to December 2003, we established 146 plots of 30 × 30 m distributed throughout five river basins. Using a geographic information system (GIS) that included a vegetation map (Cingolani et al. 2004), we chose a plot location by manually selecting 30 points per basin imitating a random distribution of points within vegetation units that were supposed to contain forests or open shrublands (*P. australis* covers generally > 5%). After the initial selection, we verified that within each basin there was a similar distribution of samples within altitudinal belts (range from 1,400 to 2,500 m asl), and where necessary plots were moved. In the field, we located plots using global positioning system (GPS) and selected them for the study when: (1) there was at least one *P. australis* of 2 m or taller; and (2) all individuals present were accessible for measuring. When the selected plot location was inaccessible without climbing gear or there were no trees > 2 m ( $n = 29$ ), we moved the plot location to the nearest 30 × 30 m area that met the requirements (final plot locations may be requested of the first author). Following these procedures, we established 30 plots per river basin except one basin with 26 plots where we were unable to find 30 adequate areas due to extensive forest destruction.

For each plot we recorded: (1) percentage of *P. australis* canopy cover (visual estimation, projection of canopy cover); (2) height of all living *P. australis* individuals taller than 30 cm; (3) basal circumference of the largest tree and proportion of rock under its canopy—both to estimate the tree age following Suarez et al. (2008); (4) standing; and (5) fallen dead volume of wood by measuring length and average circumference; (6) visual estimation of the proportional fern cover (%); (7) density of *Maytenus boaria* individuals (the only tree species accompanying *P. australis*) taller than 30 cm; (8) altitude above the sea level; (9) topographic

position in three categories: (i) valley bottoms and lower slopes (hereafter called valley bottoms), (ii) mid-slopes, and (iii) upper-slopes and convex summits (hereafter called upper-slopes); (10) slope inclination with a clinometer (RECTA SA, CH-2501); (11) slope aspect with a compass (RECTA SA, CH-2501); (12) sun incidence at the canopy level measured as the trajectory of the sun not covered by mountains, rock outcrops, or other obstacles as calculated with the clinometer (in a flat area with no obstacles: 180°).

### Measuring Anthropogenic Disturbances

As in most South American Mountains, few livestock owners were willing to report their past stocking rates and most of them refused to report fire events (which are illegal but widespread, Renison et al. 2006). As no precise records on human impact were available for this study, we used a coarse human impact categorization by river basin. According to Renison et al. (2006), the five river basins selected for this study may be ordered from the least to the most preserved as (1) Mina Clavero, (2) Yuspe, (3) Condorito, (4) Molles, and (5) Santa Clara, with respectively 34, 31, 14, 7, and 7% rock exposed by soil erosion and 0.65, 0.51, 0.09, 0.21, and 0.02 rancher houses per square kilometer, both of which in our study area are good indicators of the past human use (Cingolani et al. 2004; 2008). The Los Molles and Santa Clara river basins represent a “benchmark” as they are relatively inaccessible and extensive *P. australis* forests still exist under conditions of relatively low human impact (Renison et al. 2006).

### Data Analysis

We categorized tree heights in 11 classes at intervals of 85 cm: (1) 31–115; (2) 116–200; (3) 201–285; (4) 286–370; (5) 371–455; (6) 456–540; (7) 541–625; (8) 626–710; (9) 711–795; (10) 796–880; and (11) >881. We chose 85 cm limits to produce an interval coinciding with 200 cm—being the criteria for including a prospective plot in the study if it had at least one tree of height 200 cm or taller. Smaller size intervals (e.g., 50 cm) produced histograms with missing intermediate columns, whereas larger intervals would produce a loss of information for the cluster analyses (see below). To determine differences between size classes we performed analyses of variance (ANOVAs) and “Student–Newman–Keuls” post hoc tests with ln transformed densities per hectare. We used K-means non-hierarchical cluster analysis for classifying plots into four clusters according to the abundance of trees in each size class and total tree canopy cover. Although cluster analysis is not often used for classification of forest stands, in our case the analysis was adequate because we did not have stands where regeneration occurred in tree fall patches, which could induce their clustering with young stands due to the preponderance of small individuals in both (Frelich 2002). We compared estimated age of oldest living tree, volume of fallen and standing dead wood, fern cover, and abundance of *M. boaria* trees between clusters using

ANOVA and “Student–Newman–Keuls” post hoc test. The volume of fallen dead wood and standing dead wood was square-root transformed. The index of dead wood volume (IDWV) was calculated as  $IDWV = hC^2/4\pi$ , where  $h$  is the length and  $C$  the average circumference. Age of the largest tree was estimated as:  $\text{Log}(\text{age in years}) = -0.16 + (0.85 \times \log(\text{circumference in cm})) + (0.0013 \times \% \text{ rock under the tree canopy})$ , which in our study area explains 48% of variation in age over a wide range of habitat types (Suarez et al. 2008).

We used chi-square tests to determine differences in forests types among river basins, topographical positions, and altitude above the sea level (three altitudinal belts: 1,200–1,750 m, 1,750–2,100 m and 2,100–2,450 m asl) We chose these altitudinal limits to get an even distribution of plots. To avoid expected frequencies of less than five in more than 5% of the cells, we regrouped the four cluster types into two biologically meaningful groups (clusters 1–2 and 3–4) and the five river basins into three (Mina Clavero/Yuspe, Condorito, Molles/Santa Clara; Siegel & Castellan 1988). To determine differences in slope, aspect, and sun trajectory we compared the means of each cluster through ANOVA. In all ANOVAs, we used Type III sums of squares, which can handle unbalanced designs better than Types I and II, and all residuals were tested for normality and homocedasticity (Milliken & Johnson 2002).

## Results

### Overall Size Structure

We assessed 3,952 *Polylepis australis* individuals 30 cm or taller, at an average density of 302 individuals per hectare ( $n = 146$  plots). Overall distribution of *P. australis* sizes approximated an inverse J-shaped curve (Fig. 1a), with many small individuals and progressively fewer taller individuals. The tallest recorded tree was 14 m high and 350 cm in basal circumference, which suggests an age of up to 117 years.

### Forest Types

K-means cluster analysis yielded four clusters, which we numbered in increasing order of tree canopy cover. Canopy cover and the number of trees at each of the 11-size categories differed significantly between clusters (ANOVA: all  $F$  values > 10; all  $p$  values < 0.0001). Cluster 1 ( $n = 99$  plots; 68% of total plots) and cluster 2 ( $n = 15$ ; 10%) encompassed the plots with the lowest tree canopy cover (8 and 23% cover, respectively). In both cases, the distribution of height classes approximated to the shape of an inverse J. However, in comparison to cluster 1, cluster 2 included plots with a clearly higher abundance of individuals, especially in the two lowest height classes, indicating higher regeneration rates. In cluster 3 ( $n = 19$ ; 13% of total plots, canopy cover 54%), trees from 116 to 200 cm (class 2) were the most abundant, whereas trees larger than 540 cm (class 6 onwards) were completely absent. Plots of cluster 4 ( $n = 13$ ; 9% of total plots, canopy cover

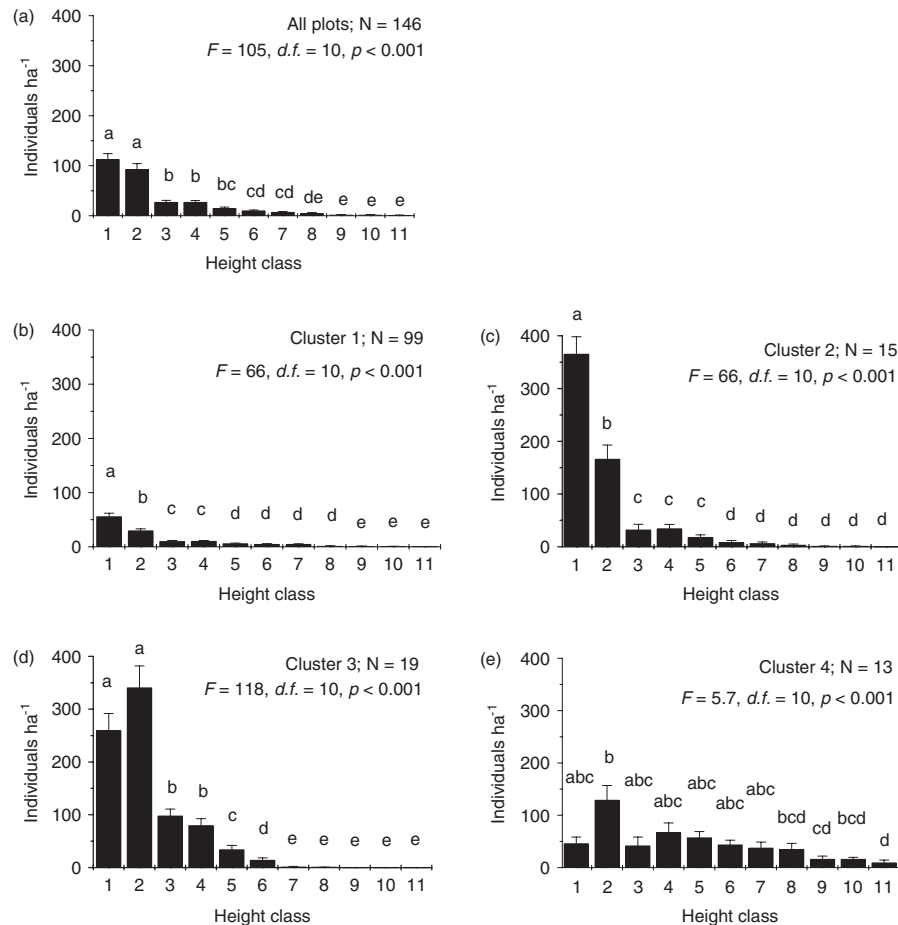


Figure 1. Density of *Polylepis australis* individuals in each height class per hectare as calculated from 146 forests plots of 900 m<sup>2</sup> for: (a) all plots and (b–e) four types of plots as classified by K-means cluster analysis using the abundance of individuals in each height class and proportion of tree canopy cover. Height classes of 85 cm starting from: 31, 116, 201, 286, 371, 456, 541, 626, 711, and 796 cm for classes 1–10, respectively, whereas class 11 corresponds to heights > 881 cm. ANOVA results are indicated, different letters above the bars indicate significant differences within each figure ( $p < 0.05$ ) according to “Student–Newman–Keuls” post hoc tests.

72%) contained the highest abundance of large trees and a fairly even distribution of height classes (Figs. 1 and 2).

Estimated age of the largest tree, volume of fallen and standing dead wood, and fern cover were low in plots belonging to clusters 1, 2, and 3 and significantly higher in cluster 4. *Maytenus boaria* abundance was lowest in plots belonging to clusters 1 and 2 and significantly higher in clusters 3 and 4 (Table 1).

#### Long-Term Livestock Rearing and Topography

The proportion of plots in clusters 1 and 2 decreased with river basin preservation status from 96% in the two river basins that were most degraded by long-term livestock rearing, to 73% for plots in the basin with intermediate human intervention and to 63% in the two best-preserved river basins. Conversely, the proportion of plots in clusters 3 and 4 increased with river basin conservation status from 4% in the two least-preserved river basins, to 27% in the intermediate situation and 37% in the two best-preserved basins (Fig. 3,  $p < 0.001$ ).

Lower and higher altitudes above the sea level contained more plots in clusters 1 and 2 than expected by chance, whereas at intermediate altitudes plots in clusters 3 and 4 were relatively more abundant (Fig. 4,  $p < 0.001$ ). No significant differences were found in the proportion of plots (clusters 1–2 vs. 3–4) occupying different topographical positions ( $\chi^2$  test:  $\chi^2 = 3.2, df = 2, p = 0.20$ ). Slope, relative North–South and relative East–West aspect, and sun trajectory did not differ between forest types (respective ANOVAs  $F = 0.29, p = 0.83$ ;  $F = 1.11, p = 0.35$ ;  $F = 0.57, p = 0.63$ ;  $F = 1.34, p = 0.26$ , all  $df = 3$ ).

## Discussion

### Overall Size Structure

Many factors influence the size structure of plant populations including patterns of dispersal, early establishment, later plant survival and growth rates, and seed productivity—all of which may be induced by climatic shifts—altitude above the sea

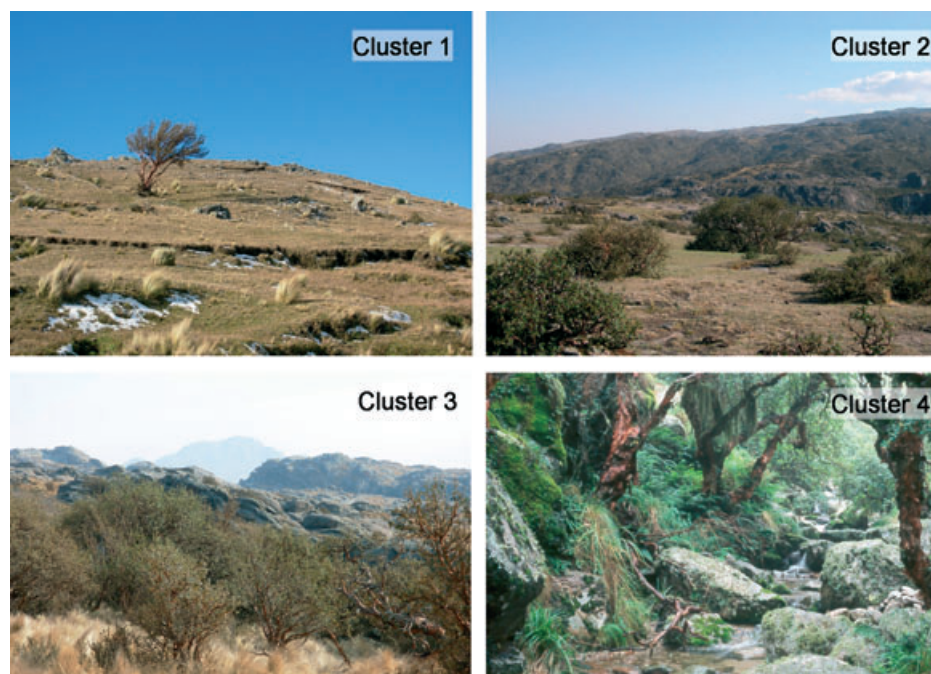


Figure 2. *Polylepis australis* study plot photographs representative for clusters 1–4, as classified by K-means cluster analysis using the abundance of individuals in each height class (85 cm, Fig. 1) and proportion of tree canopy cover.

**Table 1.** Biotic attributes of *Polylepis australis* forest plots as grouped in four clusters according to the abundance of trees in different height classes and total tree canopy cover.

Cluster/Variable	Cluster 1 (n = 99)	Cluster 2 (n = 15)	Cluster 3 (n = 19)	Cluster 4 (n = 13)	ANOVA df = 3
Age of largest living tree (years)	43.1 ± 2.3	47.3 ± 4.5	36.8 ± 3.6	66.7 ± 5.3	F = 5.77
	a	a	a	b	p < 0.001
Fallen dead wood (m <sup>3</sup> /ha)	0.8 ± 0.5	0.9 ± 0.6	1.1 ± 0.5	11.4 ± 8.6	F = 9.3
	a	a	a	b	p < 0.001
Standing dead wood (m <sup>3</sup> /ha)	0.1 ± 0.1	2.7 ± 1.7	1.1 ± 0.5	19.5 ± 7.5	F = 21.7
	a	a	a	b	p < 0.001
Fern cover (%)	3.3 ± 0.5	5.1 ± 2.6	6.8 ± 1.6	30.0 ± 5.0	F = 45.1
	a	a	a	b	p < 0.001
Abundance of <i>Maytenus boaria</i> trees	2.0 ± 0.5	5.7 ± 1.8	19.2 ± 6.5	15.6 ± 5.7	F = 12.72
	a	a	b	b	p < 0.001

The values are indicated as means ± standard error, different letters indicate significant differences ( $p < 0.05$ ) according to “Student–Newman–Keuls” post hoc ANOVA tests.

level, slope exposure, variation in animal browsing, pathogens, and anthropogenic disturbances among others (Wang et al. 2004; Hertel & Wesche 2008). The overall inverse J-shape structure presented for *Polylepis australis* in the mountains of Central Argentina suggests that regeneration, survival, and growth rates have been relatively stable for the last few centuries (stable stage structure: Caswell 1989), implying no masting years, rare large-scale regeneration events, or disturbances at landscape scales. Rather, relatively small, continuous and recurring fires would explain the young age of most trees, which did not exceed an estimated age of 117 years according to the predictive model of Suarez et al. (2008). Nowadays, in most of the Córdoba Mountains, low-intensity fires spread only a few hectares due to the overall high proportion of rock exposed by erosion, natural rock outcrops,

and small amounts of accumulated biomass; however, ignition rates are as high as 70% of our plots and 36% of the examined trees presented fire scars (Renison et al. 2006). This differentiates our *P. australis* study populations from those of, e.g., *Austrocedrus chilensis* in northern Patagonia where establishment only occurs during rare cool-wet conditions, and of those regions where the predominance of large areas of evenly aged trees is due to large-scale fire events (Villalba & Veblen 1997; Spies & Turner 1999).

#### Forest Types

Our comparisons of stand characteristics between the four *P. australis* cluster types found in our study region provide a first quantitative characterization of four successional stages.

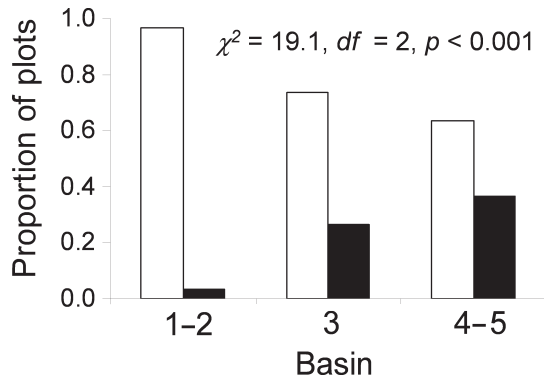


Figure 3. Proportion of *Polylepis australis* forest plots categorized by cluster type in each study basin. Empty bars represent clusters 1 and 2, filled bars represent clusters 3 and 4. Clusters were numbered by increasing order of canopy cover. River basins are ordered from least (1) to best preserved (5) on the basis of density of houses and proportion of rock exposed by erosion used as a long-term index of human impact (Renison et al. 2006). The chi-squared test value is indicated.

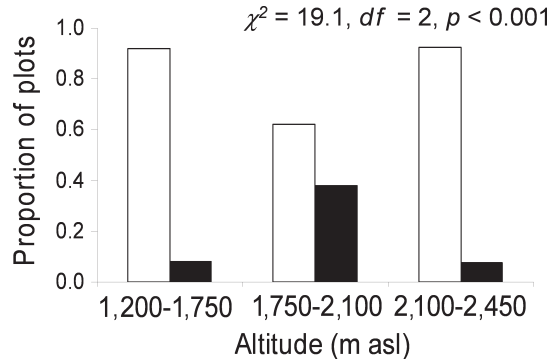


Figure 4. Proportion of *Polylepis australis* forest plots categorized by cluster type along each altitudinal belt. Empty bars represent clusters 1 and 2, filled bars represent clusters 3 and 4. Clusters were numbered by increasing order of canopy cover. The chi-squared test value is indicated.

Clusters 1 and 2 both approximate an inverse J-shape structure, which in our study area is typical of accessible areas with presumably high human impact. The few remaining *P. australis* trees < 2 m are usually unaffected by fires or livestock because they grow between rocks or short grazing lawns, and their canopy is out of reach of livestock. Their continuous seed production, seed germination, and early establishment is affected by livestock only when it implies soil erosion, but otherwise may even be favored due to less competition from other grasses and forbs (Renison et al. 2004; 2005; Torres et al. 2008). In contrast to, e.g., Bolivia (Hensen 1995, 2002)—where saplings are indeed almost completely consumed by goats and sheep—in the mountains of Central Argentina, saplings (30–115 cm) and juveniles (116–200 cm) are grazed by cattle that tend not to eradicate them completely. However, continuous browsing severely hampers their growth and development, and leads to banks of dwarf trees that only reach maturity if partially protected from browsing by rock outcrops (Teich et al. 2005). A similar scenario was reported

by Hofgaard (1997) for the Central Scandes mountains of Norway, where sheep maintained a viable but browsed population of birch (*Betula pubescens*) saplings with an average height of 0.2 m. Plots in cluster 1 are differentiated from plots in cluster 2 because they have a lower percentage of canopy cover and seeder trees, resulting in a lower number of saplings and juveniles (Fig. 1). In addition, exposed and degraded soils in cluster 1 plots might reduce seed retention and germination (Torres et al. 2008). Thus, clusters 1 and 2 could be interpreted as degraded and regenerating stands, respectively.

Clusters 3 and 4 did not generally correspond to an inverse J shape, suggesting either the influence of shade, competition, or litter layer on sapling occurrence (Cierjacks et al. 2007), or a larger-scale stand dynamics with fires top-killing individuals over relatively large areas, which simultaneously respresent in the following growing seasons (Renison et al. 2002b, 2006). Stands that are similar to plots in cluster 3 are also typical of degraded and regenerating forest areas (like our cluster 1 and 2 stands) which have been freed from livestock activity 15–30 years before (personal observations)—although this does not apply to our study plots. The difference between plots of clusters 3 and 4 can be explained by time-span, since the last stand scale disturbance and their features correspond to those reported for dense *P. incana* forests in Ecuador (Wesche et al. 2008). Plots in clusters 3 and 4 could be interpreted as young and mature forests, respectively.

Rare mature *P. australis* forests presented several attributes indicating higher environmental quality, such as considerable volumes of standing and dead wood, a typical fern understorey, and the presence of the rare *Maytenus boaria* shade-tolerant trees. Dead wood typically harbors an array of species like wood degrading fungi, which in many ecosystems belong to the most threatened species groups (Lonsdale et al. 2008). The first studies on wood degrading fungi in our study area revealed several new species to science, which are endemic to *P. australis* mature forests (Robledo et al. 2006). Bird studies also suggest an important influence of forest structure (Lloyd 2008), and there is abundant literature from other regions on the association between forest structural complexity and biological diversity (e.g., Hunter 1990; Lindenmayer et al. 2006; McComb 2008). Moreover, mature forests provide a large set of valuable ecosystem services such as regulation of water supply, reduction in soil erosion, and carbon sequestration (Kremen 2005).

#### Long-Term Livestock Rearing and Topography

The use of fire together with livestock browsing is most probably the two main forces maintaining forests in what we have called the degraded and regenerating stages. Our quantitative measurements and field observations both suggest that if grazing intensity was reduced or stopped, these forests would probably develop along a successional pathway to young and mature forests (Teich et al. 2005; Renison et al. 2006). In support of this idea, the most impacted basins were found to have proportionately more degraded and regenerating forests than the better-preserved basins.

Knowledge on land-use history is very important to understand forest structure and the degree of ecological degradation (Fulé & Laughlin 2007). European livestock introduction in the mountains of Central Argentina began around 400 years ago, and fires are very much associated with livestock rearing activities—with few natural ignitions as lightning coincides with the rainy season. Thus, domestic livestock and fires represent relatively recent disturbances for these mountains. In accordance, Cingolani et al. (2008) showed that remote mountain regions have five times more forest areas than those close to roads and rancher houses where livestock and fire ignitions are more frequent. As *P. australis* is to a certain extent resistant to browsing and fires, the species has persisted in numerous areas—but not as mature forests—since the landscape of most of the Córdoba Mountains is similar to that of our degraded river basins (Cingolani et al. 2004). Negative consequences of grazing on regeneration and stand structure have also been reported for *Polylepis* forests in Bolivia (Hensen 2002; Kessler 2002), but not in Ecuador (Cierjacks et al. 2008) where the dominant *P. incana* species is avoided by livestock which, through trampling, even enhance seedling emergence. A high proportion of small tree height classes was also reported by Hoch and Körner (2005) for *P. tarapacana* along the highest Andean treeline on Mt Sajama (Bolivia), and by Gareca et al. (2007) for *P. subtusalbida* in the Parque Nacional Tunari (Bolivia) in stands that are also subjected to both livestock grazing and fire. However, in both cases, it is not known whether tree height corresponds to tree age or rather is a result of browsing.

Within accessible areas, where our study plots are situated, topographical features played a minor role in forest structural complexity—with the exception that *P. australis* performs best at intermediate altitudes of around 1,850 m asl. This pattern was also found by Renison et al. (2006) and Cingolani et al. (2008) for tree canopy cover, and Marcora et al. (2008) for radial tree growth, tree vitality, and seed production. At higher altitudes the species is presumably limited by temperature, and at lower altitudes by water availability and competition with other tree species better adapted to warmer climates (Marcora et al. 2008). The fact that no patterns emerged between forest structural complexity and topographical position—in particular, we expected more advanced successional stands in valley bottoms—is in line with the findings of Cabido and Acosta (1985) and Renison et al. (2006), but is in contrast to those of Enrico et al. (2004) who, in one of our study regions, attributed differences in structural complexity to topographic position. We assume that these differences in structural complexity historically derive from higher stocking rates and fires in the flatter upper-slopes over time than in the valley bottoms and deep ravines—an issue which is not considered or discussed in Enrico et al. (2004).

### Restoration and Management Implications

Long-term livestock rearing activities which involve fires and livestock browsing, besides altering forest cover and producing extensive soil erosion and compaction (Cingolani et al.

2003, 2008; Renison et al. 2006), have profoundly simplified *P. australis* forest structural complexity at the landscape level. This scenario is very likely for most high-altitude mountain forests of tropical and subtropical South America (Hensen 2002; Kessler 2002; Renison et al. 2006; Lloyd 2008). Thus, in order to enhance biodiversity at a landscape level, restoration should aim not only at the promotion of forest expansion, as suggested by Cingolani et al. (2008), but also at the conversion of the degraded *P. australis* forests to an even mix of regenerating, young, and mature stands similar to the situation found in the better-preserved basins. Exceptions would include forests at their altitudinal extremes, which are presumably more climatically driven (Marcora et al. 2008) and where *P. australis* may persist as isolated trees, even with natural disturbance regimes. To attain this conversion, human-induced fires have to be reduced—a policy that is ongoing but will have to be maintained for decades or centuries. It will encourage a balanced array of forest stands at different successional stages including mature forests with adequate regeneration of shade-tolerant *M. boaria* trees, and fallen and standing dead wood. In addition, to promote the conversion of degraded and regenerating stands to young and mature stands, livestock will have to be excluded from these areas to minimize browsing pressure on the abundant *P. australis* dwarf saplings and juveniles. *P. australis* is a clearly selected forage item, and livestock consume a high proportion of their biomass even at low stocking densities (Teich et al. 2005). If necessary, due to economic reasons, livestock could be tolerated in young and mature forest stands, because in these forests most trees are out of reach of livestock browsing. In fact, the biomass consumption may moderate fire impact and, due to the local extinction of all large native grazers, livestock is required for conservation reasons (Cingolani et al. 2003; García et al. 2008). The ongoing reintroduction of native grazers (*Lama ganacoe*) may provide the benefits of grazing without the consequent soil erosion associated with European livestock (Cingolani et al. 2008).

### Implications for Practice

- *Polylepis australis* forest restoration goals should be set to augment landscape structural complexity aiming at an even distribution of regenerating, young, and mature forests.
- To achieve goals, anthropogenical-ignited fires must be reduced in all areas. Livestock must be excluded in degraded and regenerating forest stands, whereas it could be tolerated in young and mature forests where most aboveground tree biomass is out of reach of livestock browsing.

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