



Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence?

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ABSTRACT

Aim To determine whether the cover and growth habit of the main forest forming species (*Polylepis australis* BITT.) in a mountain range with low human population density is mainly affected by anthropogenic activities or by environmental influences.

Location Central Argentina.

Methods Using GIS and field surveys we established 146 plots of 30 × 30 m located in five river basins differing in human impact. We measured *P. australis* cover, growth habit of each individual (number of basal ramifications), index of long term human impact (percentage of rock exposed by soil erosion due to livestock and fires), evidence of logging, fire scars, local relief, percentage of rock outcrops and altitude above sea level. We analysed the influence of independent variables on *P. australis* cover and growth habit (average number of basal ramifications per plot) using correlations and General Linear Models.

Results *Polylepis australis* cover was greater at intermediate altitudes above sea level and in areas with reduced long term human impact. Contrastingly local relief, percentage of rock outcrops and logging in the recent past did not have a major influence on *P. australis* abundance. Growth habit varied in complex patterns. Individuals with fewer ramifications were found in valley bottoms and more disturbed basins, while more ramifications were found at mid- and upper slopes and well preserved basins. In valley bottoms, ramifications decreased with increasing altitude whereas the opposite trend was observed for mid-slopes. Ramifications were positively related to fires in two river basins and in mid- and upper slopes but not in valley bottoms. Fire impact was always less in valley bottoms than at mid- and upper slopes.

Main conclusions Human impact had a major role on *P. australis* cover, while growth habit was determined by complex combinations of potentially cumulative natural and anthropogenic factors. Even in sparsely populated mountains, both human impact and their interaction with natural environmental gradients influence plant communities and need to be understood for effective management.

Keywords

Argentina, fire, forests, grazing, high mountains, *Polylepis australis*, *Polylepis* woodlands, topography.

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INTRODUCTION

The upper timberline is a conspicuous natural vegetation limit in many upper montane settings, but the causes determining its elevation and structure are still poorly understood. Modern

forest distributions and particular characteristics such as species distributions, growth habits and fitness, need to be seen in the context of historical human land use, natural disturbances and site conditions (Foster *et al.*, 1999; Guyette & Spetich, 2003). However, in many inaccessible mountain

regions of the world where human activities are centred around livestock rearing at low densities (Price, 1981), obvious human influences such as clear-cutting and agriculture are rare. In these areas it has been tempting to ignore human disturbances and only consider site conditions and natural disturbances as the main structuring forces of the upper timberline. To date, the issue of whether humans have, or have not, had a considerable influence on the development of high mountain forests or alternative communities such as grasslands, shrublands or woodlands remains controversial (Miehe & Miehe, 1994; Fjelds  & Kessler, 1996; Sarmiento, 2002; K rner, 2003; Wesche & Kessler, 2004).

In the mountains of South America the human influence issue has led to two opposed and often confrontational points of view explaining high altitude *Polylepis* woodland distribution and characteristics (Kessler, 2002). According to some authors *Polylepis* tree species at the upper limit of their distribution form dense woodlands in deep ravines where they are presumably more protected from wind and freezing (Koepcke, 1961; Walter & Medina, 1969; Simpson, 1986; Rauh, 1988; Arce, 1990; Ibsch, 1993). In exposed topographic positions tree growth is presumably hampered, and, when present, *Polylepis* species often produce lateral basal ramifications forming shrublands (Enrico *et al.*, 2004).

However, in the South American mountains the long history of human disturbances has led to the suggestion that human impact is the main factor explaining *Polylepis* woodland distribution and characteristics (Beck & Ellenberg, 1977; Ruthsatz, 1977, 1983; Jordan, 1983; Frimer & M ller Nielsen, 1989; Beck & Garcia, 1991; L gaard, 1992; Kessler & Driesch, 1993; Hensen, 1995, 2002; Kessler, 1995; Fjelds  & Kessler, 1996; Lauer *et al.*, 2001). *Polylepis* species are somewhat fire tolerant as they are able to re-sprout after fire, but usually develop a shrubby growth habit that changes woodland structure and appearance (Kessler, 2000). Browsing is known to affect woodland regeneration by retarding or even hampering juvenile growth (Kessler & Driesch, 1993; Hensen, 1995, 2002; Fjelds  & Kessler, 1996). Thus, both fire and browsing delay stand recovery processes, prolonging the time-span in which grasses and forbs dominate an area (Hunter, 1990), and causing a shrubby growth habit in many tree species (Vera, 2000). The recognition of the strong influence of human impact on the present-day distribution of the South American *Polylepis* woodlands (Ellenberg, 1979; Fjelds  & Kessler, 1996; Kessler, 2000) led to their listing as one of the most endangered woodland ecosystems in the world (UNEP-WCMC, 2004).

Whether *Polylepis* woodland distribution and characteristics are due to natural or anthropogenic factors is unclear because several poorly understood interactions between environmental factors and anthropogenic disturbances might be influential. For example, fires are less prone to affect protected deep ravines, damper valley bottoms and rocky areas (Fryer & Johnson, 1988; Renison *et al.*, 2002). Uneven grazing by free ranging livestock may result from physical barriers such as deep ravines and rocky slopes (Coughenour, 1991; Cingolani

et al., 2003), and in this way livestock may mediate the vegetation–environment relationships.

In the high C rdoba mountains where *Polylepis australis* BITT. (Rosaceae) is the dominant woody species, Enrico *et al.* (2004) reported that topography and other environmental factors underlay observed differences in the occurrence of *P. australis* dense woodlands vs. sparse shrublands. However, they did not discuss the possibility of synergistic effects between these factors and anthropogenic disturbances. In contrast, Cabido & Acosta (1985) and Cingolani *et al.* (2004) suggested that sparse shrublands of *P. australis* could be totally or partially derived from dense woodlands after burning followed by grazing. There is an urgent need for research that examines the influences of multiple factors on patterns of woodland landscape dynamics across a range of spatial scales (Wimberly & Ohmann, 2004). Here, we aim to analyse combined and interactive effects of historical human impact and local relief on two variables related to the development of *P. australis* woodlands and shrublands: tree canopy cover and dominant growth habit.

METHODS

Study area

The study was carried out in the C rdoba Mountain range (central Argentina, north–south orientation, 1200–2800 m a.s.l., 31°34' S, 64°50' W; 124,700 ha). Mean temperatures of the coldest and warmest months at 2100 m a.s.l. 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 warmer months, between October and April (Renison *et al.*, 2002).

The present-day vegetation consists of a mosaic of tussock grasslands, grazing lawns, granite outcrops, eroded areas with exposed rock surfaces, *P. australis* woodlands (2.5% of the surface) and sparse woodlands or shrublands (9.4%) (Cingolani *et al.*, 2004). *Polylepis australis* is generally restricted to steep slopes in mid- to low topographic positions, but sometimes this species is also found on the flat terrain of ravine bottoms, on convex summits or gentle slopes (Cingolani *et al.*, 2004). *Polylepis australis* dominates the upper strata of woodlands and shrublands with other less abundant woody species such as the tree *Maytenus boaria* (Celastraceae), the shrubs *Escallonia cordobensis* (Glossulariaceae), *Berberis hieronimii* (Berberidaceae) and *Satureja* spp. (Lamiaceae), and the dwarf shrub *Gaultheria poepigii* (Ericaceae) (Cabido & Acosta, 1985). Woody species occasionally form dense stands that cover most of the surface and could be called forests, but are usually intermingled with patches of tussock grasslands, ferns or rock outcrops (Cingolani *et al.*, 2004) and have traditionally been called woodlands or shrublands.

The main economic activity in the C rdoba mountains is the rearing of livestock (cattle, sheep, horses and goats), which began early in the seventeenth century. Large native herbivores (*Lama guanicoe*, and probably *Rhea americana*) were

completely replaced by domestic livestock by the beginning of the twentieth century (Díaz *et al.*, 1994). Due to its intrinsic fragility and four centuries of domestic grazing, vegetation cover and soils have been completely destroyed in c. 20% of the area leaving behind bare rock (Cingolani *et al.*, 2003, 2004). In 1997, 26,000 ha of the best preserved areas were set aside to create the 'Quebrada del Condorito' National Park. A further buffer area of 129,000 ha of private land surrounding the Park were declared National and Provincial Water Reserves, but with no expropriation taking place. Soil erosion remains a severe problem in most of the privately owned areas used for livestock rearing (Cingolani *et al.*, 2004).

Basin characterization

Our research was performed in five hydrographical basins chosen due to their different land-use history and in order to represent both East and West river catchments: Condorito, Molles, Mina Clavero, Santa Clara and Yuspe. We characterized the five basins according to human impact indicators, physical characteristics, and *P. australis* cover using a Geographical Information System (GIS) of the area. The GIS includes a vegetation and erosion layer (based on Landsat TM image, pixel width 30 × 30 m, Cingolani *et al.*, 2004), and layers of altitude, slope, trails and human settlements. The physical characteristics we measured were percentage of gentle, moderate and steep slopes (< 10%, 10–30% and > 30%, respectively), and percentage of natural rock outcrops. As human impact indicators we considered the number of human settlements per km² (abandoned as well as permanent households) and the percentage of rock exposed by erosion.

Plot establishment

From March to December 2003, we established 146 plots of 30 × 30 m distributed in the five river basins. Plot location was initially selected using a GIS (Cingolani *et al.*, 2004). We randomly chose areas within vegetation units that were supposed to contain woodlands or sparse shrublands (i.e. *P. australis* cover generally > 5%) and stratified the sampling to obtain an even distribution of samples within each altitudinal belt (1400–2500 m a.s.l.) and river basin. In the field we located plots using a GPS and selected them for the study when: (1) there was at least one adult *P. australis* individual 2 m or taller, and (2) all occurring individuals were accessible for measuring. This procedure excluded plots in steep ravines and cliffs that were inaccessible without specialized climbing gear. When the selected plot location was inaccessible or without trees > 2 m ($n = 29$) we moved the plot location to the nearest 30 × 30 m area that met these requirements. Following this procedure we established 30 plots in four of the river basins. In the fifth, we set up only 26 plots as we were unable to find 30 adequate areas.

In each plot we recorded: (1) percentage of *P. australis* cover (visual estimation, projection of canopy cover per 900 m²); (2) height and number of basal ramifications of all *P. australis*

individuals taller than 30 cm (recorded as an indicator of shrubby growth habit; Renison *et al.*, 2005); (3) topographic position in three categories: (i) valley bottoms and shallow slopes (hereafter called valley bottoms), (ii) mid-slopes, and (iii) upper slopes and convex summits (hereafter called upper slopes); (4) altitude above sea level; (5) slope inclination; (6) slope aspect; (7) percentage of natural rock outcrop; and (8) sun incidence measured as the trajectory of the sun not covered by mountains, rock outcrops or other obstacles (in a flat area with no obstacles: 180°).

Measuring anthropogenic effects

Past anthropogenic disturbances are extraordinarily important for understanding woodland dynamics and measuring ecological degradation (Fulé *et al.*, 2002). Ideally, stocking rates and fire events would need to be known for several centuries to understand present *P. australis* cover, which is the product of environmental and anthropogenic influences on several *P. australis* generations. To understand growth habit, a shorter time history is needed as growth is presumably influenced by the environment that affected the tree during its life span. However, as in most South American mountains, no records were available on historical stocking rates and fires in the Córdoba Mountains. Paddock construction dates to the early twentieth century and is still incomplete, with > 25% of the area having free-ranging livestock. Few livestock owners are willing to report their past stocking rates and virtually no owners will report fire events, as burning woodlands and grasslands is illegal.

As no records on human impact were available, we used a surrogate index obtained from the vegetation and erosion map (Cingolani *et al.*, 2004). The index of human impact was determined as the proportion of bare rock exposed by erosion in the non-woody map units, in a square of 90 × 90 m around our study plots (similar to Renison *et al.*, 2004; woodlands were discounted to avoid circular reasoning, because they protect soils to a higher degree than do open vegetation types). In the Córdoba Mountains bare rock exposed by erosion should be a good indicator of long-term grazing pressure, because grazing (estimated through dung deposition) and cover of bare soil on vertical surfaces where erosion is active are highly correlated (Cingolani *et al.*, 2003). Thus, bare rock exposed by erosion integrates the whole period of domestic grazing, i.e. from the time livestock was introduced into the mountains to the present. Although this indicator is not completely independent of topographic position (Cingolani *et al.*, 2003), by considering a large area around our plot we included several topographic positions, minimizing the bias due to this cause. Fire use is largely associated with livestock breeding and contributes to soil erosion by decreasing vegetation cover.

To quantify fire events at a shorter time scale, we visually evaluated fire scars (based on Renison *et al.*, 2002) for each *P. australis* individual > 30 cm tall as follows: 0, no fire scars; 1, scars, which judging by their position, were most likely caused by fire but too old to find traces of charcoal; 2, scars with most of

the surface covered by bark but with traces of charcoal; 3, open scars with charcoal only on the surface of the main stems, no signs of fire on smaller stems, burnt wood usually present on the soil; 4, signs of burnt bark, scars with charcoal in main and smaller stems, fire probably occurred within the last 2–3 years; and 5, burnt bark in main and smaller stems, fire probably occurred within the last year. In the best scenario, these scores represent fire events in the last few decades, so we can only use index of fire impact to explain shrubbiness (and not cover). To determine the influence of logging, we recorded if there were stumps or evidences of cut stems within the plot.

Statistical analysis

We used simple Pearson correlations across the basins ($n = 5$) to explore the associations between the average *P. australis* cover per basin, density of human settlements, slope, natural rock outcrops and rock exposed by erosion.

We performed exploratory statistics at the plot level ($n = 146$) to determine to what extent the variability in percentage of *P. australis* cover and average number of basal ramifications were explained by the abiotic variables and human impact indicators using General Linear Models (GLM). Two factors and, depending on the analysis, six or seven covariates were considered as independent variables in the models. Factors were river basin (five levels) and topographic position (three levels). Covariates were altitude above sea level, slope inclination, relative north and east aspect (calculated from slope and aspect, through cosine and sine transformations, respectively, of slope aspect, multiplied by the slope inclination, Cushman & Wallin, 2002), percentage of natural rock outcrops, index of human impact and index of fire impact (only for the GLM where the dependent variable was the number of basal ramifications). All two-way interaction terms were considered in the models, as well as the quadratic terms of the covariates altitude (for *P. australis* plot cover) and index of human impact (for number of basal ramifications). Quadratic terms were included to detect unimodal relationships after visual examination of scatter plots of all relevant combinations of variables.

For both analyses, we performed an initial GLM with all factors and covariates. In further steps, we deleted independent variables in a backward stepwise procedure until only significant variables remained in the model. We applied square root transformation to *P. australis* plot cover and the number of basal ramifications to approximate normality and homocedasticity of residuals. When the model detected interactions between a factor and a covariate the interaction was interpreted by visual observation of the corresponding plots of each factor separately (Underwood, 1997). To assist visual interpretation we drew lines that indicated the best linear fit to the predicted values of the dependent variable (*Polylepis* cover or number of basal ramifications) according to the respective GLM with all significant factors included. When the model detected interaction between two factors, we interpreted the interaction by visual examination of bar figures aided by

ANOVA and Tukey *post hoc* test using only the two factors involved in the interaction.

To allow a better interpretation of the mechanisms involved in our results regarding fire frequency, we performed a third GLM considering the index of fire impact as a dependent variable, and the remaining factors and covariates as independent variables. As in the previous analyses, all two way interaction terms were considered, and a backward stepwise procedure was performed to select the best predictor variables.

As fire scars are more likely to accumulate on older trees, differences in tree age between plots could bias the results. Therefore, in order to check for potential biases we repeated the two analyses where the index of fire impact was involved (GLMs where the dependent variables were with number of basal ramifications and index of fire impact) using indices of fire impact calculated separately from trees in one of the following height categories: 30–60 cm, 60–100 cm, 100–200 cm and > 200 cm. However, when calculating separate indices using trees of the four different size categories we always obtained a similar pattern of results as when we used all size classes, although in some cases fewer variables were found to be significant and R^2 was always smaller. In no case did the results using a special category of tree size contradict the results using another tree size category, so for simplicity we only report results of all sizes averaged.

RESULTS

Basin characterization

The physical characteristics and human impact indicators of the five study basins are summarized in Table 1. Basins were ranked by degradation status from 1 to 5 according to the percentage of rock exposed by soil erosion; basins 4 and 5 were also ranked by the number of human settlements. Pairwise correlations across the five basins showed four significant associations: the percentage of rock exposed by erosion was positively correlated with human settlement density ($r = 0.93$, $n = 5$, $P \leq 0.05$) and negatively with *P. australis* cover ($r = -0.93$, $n = 5$, $P \leq 0.05$), whereas the percentage of natural rock outcrop was positively correlated with both the number of human settlements ($r = 0.93$, $n = 5$, $P \leq 0.05$) and the percentage of rock exposed by erosion ($r = 0.91$, $n = 5$, $P \leq 0.05$). The latter relationship reflects the fact that rangelands with a low percentage of rock outcrops belong to large ranches with few human settlements and low erosion. This relationship does not reflect a tendency of more naturally rocky habitats to get more eroded, because at smaller scales the relationship was not significant (results not shown). Percentages of different slope categories were not significantly correlated with rock exposed by erosion, human density or *P. australis* cover per basin.

Cover per plot

The percentage of the plot covered by *P. australis* ranged from < 1% to 95% with an average of $21 \pm 1.96\%$ SE ($n = 146$).

Table 1 Data on basin characterization obtained from a GIS of the Córdoba Mountains (Cingolani *et al.*, 2004)

	(1) M. Clavero	(2) Yuspe	(3) Condorito	(4) Los Molles	(5) Sta. Clara
Exposed rock (%)	34	31	14	7	7
Settlements km ⁻²	0.65	0.51	0.09	0.21	0.02
<i>Polylepis</i> cover (%)	1	3	6	15	15
Natural outcrops (%)	25	27	19	20	16
Area (ha)	8925	3899	20888	468	6057
Slopes < 10%	29	37	62	< 1	52
Slopes 10–30%	65	56	34	11	43
Slopes > 30%	6	7	4	89	4
General aspect	W	E	E	W	E
Paddock fencing	No	Some	Yes	No	Yes
Current stocking rate	Very high	High	No	Moderate	No
Reported fires	No information	In 7 years 16 fires < 3–4 ha	No information	In 18 years 3 fires > 10 ha	Repeatedly burnt from 1960s to 1997
National Park from 1997	No	No	Yes	No	Yes

Table 2 Factors and covariables selected by a GLM (General Linear Model) to explain variation in percentage *Polylepis australis* cover across 146 plots in the Córdoba Mountains

Adjusted <i>r</i> ² = 0.44	d.f.	<i>F</i>	<i>P</i>
Full model	7	7.02	< 0.001
Altitude (m a.s.l.)	1	5.02	0.03
Altitude (m a.s.l.) ²	1	5.16	0.02
Index of human impact	1	24.28	< 0.001
River basin × index of human impact	4	6.30	< 0.001

The number of *P. australis* individuals per plot 2 m or taller ranged from 1 to 114 with an average of 27 ± 2.3 SE individuals. We never found stumps, cut branches or any other evidence of logging within our plots.

The independent variables explained 44% of the variation in *P. australis* cover per plot (Table 2). Abiotic environmental variables selected by the model were altitude above sea level and its quadratic term, indicating that *P. australis* cover per plot was highest at intermediate altitudes (Fig. 1). Also selected by the model were the index of human impact and its interaction with the river basin. The interaction implied that *P. australis* cover per plot was always negatively associated with human impact, but this association was less pronounced in basins with higher human impact (Fig. 2). Topographic position, percentage of natural rock outcrop, relative north and east aspect, and sun incidence were not selected by the GLM.

Growth habit

The number of *P. australis* basal ramifications per individual ranged from 1 to 45, with an overall average of 2.95 ± 0.04 SE (*n* = 3969). There was no correlation between percentage of *P. australis* cover per plot and the average number of basal ramifications (*r*_s = 0.11. *n* = 146, *P* = 0.17).

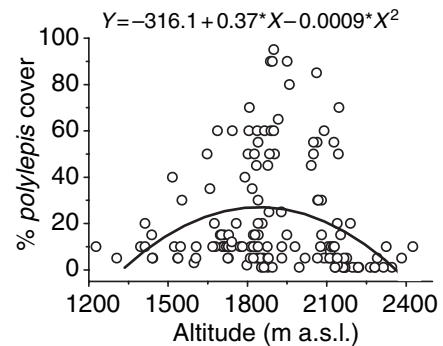


Figure 1 Percentage of *Polylepis australis* cover per plot in relation to altitude (m a.s.l.). The trend line indicates the best fit quadratic model.

The independent variables explained 41% of the variation in average number of basal ramifications per plot (Table 3). The GLM selected topographic position, river basin, index of fire impact, altitude above sea level and several interaction terms (Table 3), while slope inclination, aspect, percentage of natural rock outcrop, index of human impact and sun incidence were not selected.

In valley bottoms, *P. australis* had fewer basal ramifications than at mid- and/or upper slopes (Fig. 3). The interaction between topographic position and river basin (Table 3) indicates that in basins 1, 2 and 4 valley bottoms had fewer basal ramifications than both mid- and upper slopes (Tukey *post hoc* test for each individual basin at *P* ≤ 0.05), while in the basins 3 and 5 the difference was only significant between valley bottoms and mid-slopes (Tukey *post hoc* test for each basin at *P* ≤ 0.05, data not shown).

River basins differed in the number of basal ramifications, showing that less disturbed basins tended to have more basal ramifications (Fig. 4). The number of basal ramifications was positively related to the index of fire impact (Table 3, *P* = 0.05), but this association was only significant in river basins 2 and 4 (Fig. 5). In addition, there were positive significant relationships

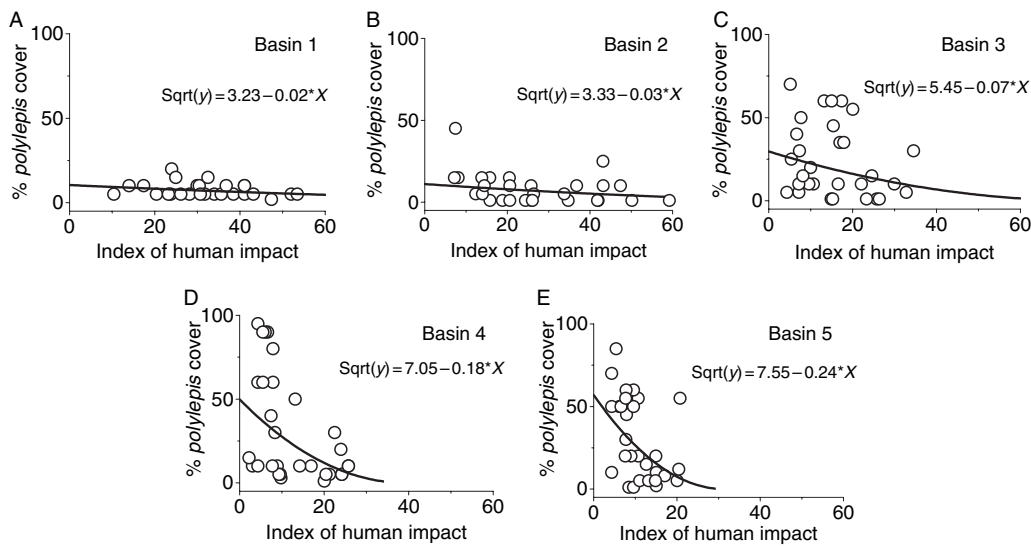


Figure 2 Percentage of *Polylepis australis* cover per plot in relation to an index of human impact (measured by the percentage of rock exposed by soil erosion) for five basins ranked by conservation status from worst (1) to best (5). The trend lines indicate the best linear fit to the squared root of *P. australis* cover (all individual regressions $P \leq 0.05$).

Table 3 Factors and covariables selected by a GLM to explain variation in shrubbiness index across 146 plots in the Córdoba Mountains. Shrubbiness was calculated as the average number of basal ramifications per *Polylepis australis*

Adjusted $R^2 = 0.41$	d.f.	F	P
Full model	22	5.60	< 0.001
Topographic position	2	4.98	0.01
River basin	4	2.39	0.05
Index of fire impact	1	3.97	0.05
Topographic position \times river basin	7	2.69	0.01
River basin \times index of fire impact	4	2.67	0.04
Topographic position \times index of fire impact	2	5.98	0.003
Topographic position \times altitude (m a.s.l.)	2	3.31	0.04

between index of fire impact and number of basal ramifications in mid- and upper slopes but not in valley bottoms (Fig. 6). The number of basal ramifications was also associated with altitude above sea level interacting with topographic position (Table 3, $P = 0.04$). In valley bottoms, the average number of basal ramifications decreased with increasing altitude whereas the opposite trend was observed for mid-slopes. There was no significant association for upper slopes (Fig. 7).

Fire impact per plot

Fire scars were present in at least one *P. australis* individual in 70% of the plots. Altogether, we found evidence of fire in 36% of the examined trees ($n = 3969$ *P. australis* individuals > 30 cm). Even within recently burnt areas many trees showed no fire scars because they were protected by rocks or streams. River basin and topographic position accounted for 28% of the variation in the index of fire impact (total model, adjusted $r^2 = 0.28$, $F_{13} = 5.33$, $P < 0.001$; river basin $F_4 = 8.91$, $P < 0.001$; topographic position $F_2 = 7.23$, $P = 0.001$). Fire

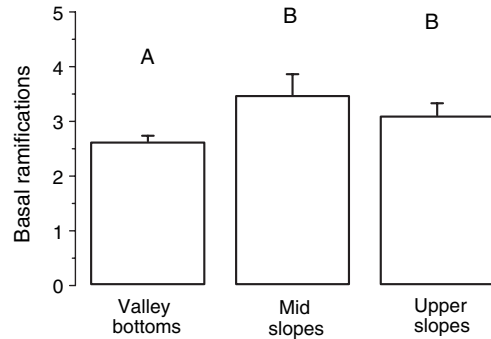


Figure 3 Average \pm SE number of basal ramifications per *Polylepis australis* per plot at three topographic positions. Different letters above the bars indicate significant differences (*post hoc* Tukey test $P \leq 0.05$).

impact differed between basins and appeared unrelated to human impact status of the basins as fire damage was lower in the river basins categorized as 2 and 3, and higher in the river basins 1, 4 and 5 (Tukey *post hoc*, $P \leq 0.05$). Fire impact was always lower in valley bottoms than in mid- and upper slopes (Tukey *post hoc*, $P \leq 0.05$). Altitude above sea level, slope inclination, aspect, percentage of natural rock outcrops and index of human impact were not significant in explaining fire scars, nor did we find any significant interactions.

DISCUSSION

Cover and distribution

South American mountains are usually sparsely populated and sometimes falsely thought of as pristine environments where good opportunities exist to study ‘natural’ systems (Ellenberg,

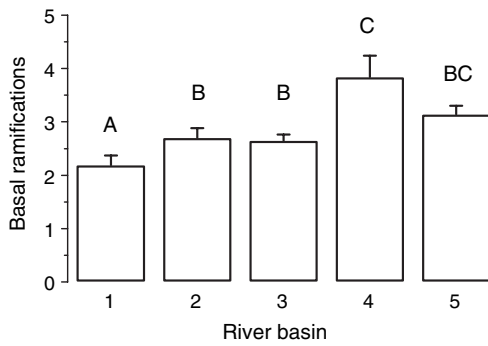


Figure 4 Average \pm SE number of basal ramifications per *Polylophis australis* per plot for each basin ranked by conservation status from worst (1) to best (5). Different letters above the bars indicate significant differences (Tukey *post hoc* test $P \leq 0.05$).

1979; Sarmiento, 2002). In spite of the low number of human settlements in the Córdoba Mountains, we found evidence of fire in 70% of the study plots and signs of livestock in almost all of the plots outside the recently established National Park. The inhabitants of the region burn grasslands and woodlands to promote grass regrowth and to reduce woodland cover, as has been frequently described for other South American mountain regions (Ellenberg, 1979; Verweij & Beukema, 1992; Hensen, 1995, 2002; Fjeldså & Kessler, 1996; Kessler, 2000). Excessive use of fire and the high number of freely moving domestic livestock are thought to be the main reasons for the alarmingly high degree of soil erosion in the Córdoba Mountains (Cingolani *et al.*, 2003, 2004). Thus, it is not surprising that within a certain altitudinal range where *P. australis* finds its optimum (in our study areas this is c. 1750–2100 m a.s.l.) human impact explains *P. australis* cover

and probably a great proportion of its present distribution pattern. Physical landscape attributes such as topographic position or percentage of natural outcrops did not explain a significant portion of variation in *P. australis* cover.

Nevertheless, due to the associations between human disturbance patterns and physical environmental characteristics, it is understandable that some authors (Koeppke, 1961; Walter & Medina, 1969; Simpson, 1986; Rauh, 1988; Arce, 1990; Ibsch, 1993) insisted on the importance of natural topographic features for *Polylophis* woodland cover and characteristics, including *P. australis* in our study area (Enrico *et al.*, 2004). The latter authors report that woodlands with high *P. australis* cover are at low topographic positions, on deep organic soils, and in sites well protected from wind and water stress. In contrast to this, sparse shrublands that contain few or no *Polylophis* occupy higher topographic positions with shallower and sandier soils, and in sites more exposed to wind and water stress (Enrico *et al.*, 2004). However, the study did not include either the effects of fire or the influence of livestock. In our data set, topographic features were also significantly associated with *P. australis* cover when human impact was excluded from the analysis (results not shown). However, as we have shown that fires are more frequent in mid- and upper slopes, and that cattle tend to avoid deep ravines (Fjeldså & Kessler, 1996), we believe that topographic features mainly determine *P. australis* cover indirectly because they have strongly influenced the historical land-use practices. In the past, most of the woodland areas in upper topographic positions were transformed into pastures because of easier access to livestock and fires.

Our data show that the association between *P. australis* cover and index of human impact was less pronounced in the river basins with most human impact. This can be explained by

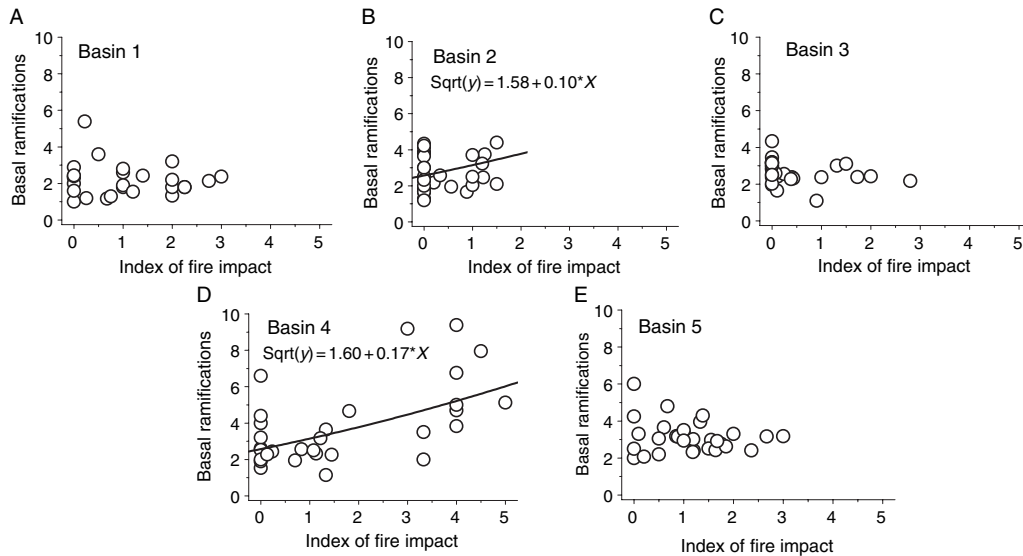


Figure 5 Number of basal ramifications per *Polylophis australis* per plot in relation to the index of fire impact. The trend lines indicate the best linear fit to the square root of the number of basal ramifications. Lines were drawn only when the relationship was significant ($P \leq 0.05$).

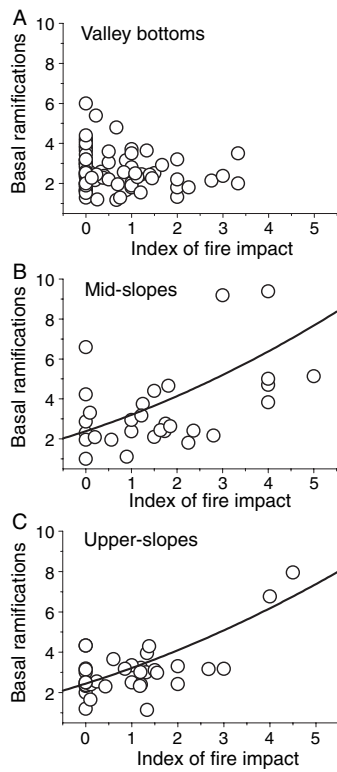


Figure 6 Number of basal ramifications per *Polylepis australis* per plot in relation to the index of fire impact for valley bottoms, mid-slopes, and upper slopes. Trend lines as in Fig. 5.

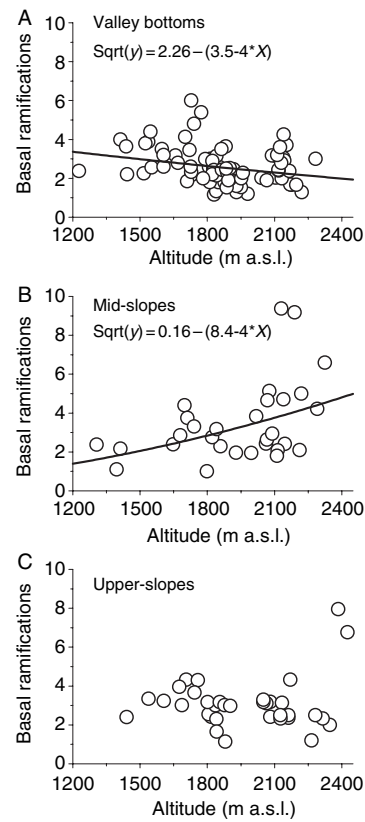


Figure 7 Number of basal ramifications per *Polylepis australis* per plot in relation to altitude (m a.s.l.) for valley bottoms, mid-slopes, and upper slopes. Trend lines as in Fig. 5.

the heterogeneous landscape structure (Cingolani *et al.*, 2004) with high small-scale relief heterogeneity accounting for the differential impact of fire (Renison *et al.*, 2002) and livestock damage (I. Teich *et al.*, unpubl. data). In severely degraded areas, remaining woodlands are simply too inaccessible to be further impacted by fire and livestock.

Our results are in accordance with several other authors who mention the overriding influence of grazing and/or fires on timberline forests of South America (e.g. Hueck, 1961, 1962; Fernández, 1970; Beck & Ellenberg, 1977; Ruthsatz, 1977, 1983; Jordan, 1983; Frimer & Møller Nielsen, 1989; Beck & Garcia, 1991; Lægaard, 1992; Kessler & Driesch, 1993; Mieke & Mieke, 1994; Hensen, 1995, 2002; Kessler, 1995; Fjeldså & Kessler, 1996; Lauer *et al.*, 2001) and the rest of the world (e.g. Hofgaard, 1997; Wesche & Kessler, 2004; Bond *et al.*, 2005). Fire and grazing activity by large herbivores influence numerous processes associated with forest regeneration (e.g. Delarze *et al.*, 1992; Backéus *et al.*, 1994; Lara *et al.*, 1999; Wesche *et al.*, 2000; Hunt, 2001; Fulé *et al.*, 2002; Boer & Smith, 2003; Cierjacks & Hensen, 2004). Disturbance by both fire and grazing generally alter the community structure by reducing biomass, damaging sensitive plant species and promoting growth and establishment of other species (e.g. Gomez Sal *et al.*, 1986; Fernandez Alés *et al.*, 1993; Yates *et al.*, 2000; Fulé *et al.*, 2002; Husheer *et al.*, 2003). In accordance with the results of our study, Cierjacks

& Hensen (2004) found that heavy grazing by sheep and goats has significant effects on the stand structure and regeneration of holm oak forests in south-eastern Spain, producing a decrease in tree density. Thus, natural regeneration might be insufficient at higher grazing intensities as described already by Hensen (1995, 2002) for *Polylepis besseri* woodlands in Bolivia. Several studies have also found historical land-use and landowner behaviour to be more important than physical attributes in the development of forest patch patterns (Hofgaard, 1997; Pan *et al.*, 2001), and in community composition and structure (Bellemare *et al.*, 2002; Gerhardt & Foster, 2002; Wimberly & Ohmann, 2004).

Growth habit

Polylepis australis shrubbiness was found to be the result of complex interactions, including topographic position, river basin, index of fire impact and altitude. Shrubbiness varied independently of *P. australis* cover suggesting that the factors influencing shrub development are not entirely the same as those causing reduction in *P. australis* cover. As predicted by previous studies (Cabido & Acosta, 1985; Enrico *et al.*, 2004), *P. australis* individuals in valley bottoms generally produced fewer basal ramifications than those on mid- and upper slopes. Shrubbiness could be an adaptation to harsher environmental

conditions prevailing in upper topographic positions that are more exposed to wind and have drier soils. In accordance, Pereg & Payette (1998) and Gamache & Payette (2004) described how *Picea mariana* adopts progressively stunted growth habits in response to increasing latitude and wind exposure, which they assumed were the main factors suppressing erect tree growth. Drought stress can severely inhibit tree growth and promote a shrubby character (Barber *et al.*, 2000). Similarly, growth forms of *P. australis* in dry locations may become shrubby as seedlings planted in drier and sandier soils developed a higher number of basal ramifications than seedlings planted in deeper and more humid soils (Renison *et al.*, 2005).

As with many tree species, *P. australis* re-sprouts after fire (Renison *et al.*, 2002) and the shrubby habit becomes more pronounced. Plots with higher fire impact were characterized by higher number of basal ramifications in river basins 2 and 4 (Fig. 5) and in mid- and upper slopes (Fig. 6). That no significant relationship was found between ramifications and fire in valley bottoms may result from the scarcity of fires and the generally favourable growing conditions. Fires are more likely to move upslope than down slope, which explains why fire scars were found more often in upper topographic positions. The reason for the lack of association between shrubbiness and fire scars in the basins 1, 4 and 5 is more difficult to explain. To some extent shrubbiness could be related to fires that occurred too long ago to record with our methods, or there could be genetic differences in growth habit between sites. Supporting the latter hypothesis, Renison *et al.* (2005) noted that seedlings produced from seeds collected in an area with a high number of shrubby *P. australis* individuals showed a higher tendency for the development of a shrubby habit than those collected in an area where the number of basal ramifications per tree was lower.

Finally, altitude above sea level appears to be associated with the number of basal ramifications, but data for valley bottoms indicate an opposite trend to those for mid-slopes (Fig. 7). In valley bottoms, rivers and streams transport thousands of seeds, and many *P. australis* seeds manage to germinate and establish at altitudes where habitat conditions might be suboptimal, favouring the shrubby growth habit. In mid-slopes, on the other hand, most seed sources are neighbouring trees. Individuals on mid-slopes at lower altitudes probably survive in microsites that are very inaccessible to fire and livestock, while at higher altitudes they grow even in areas exposed to shrub-forming fires and browsing.

CONCLUSIONS

We conclude that both anthropogenic and natural environmental features are combined and interact to explain *P. australis* cover and growth habit. We strongly recommend researchers and managers to consider the possible influence of human impact even in sparsely populated and inaccessible mountain areas where topography is correlated with large changes in vegetation. To augment woodland cover we suggest reducing fires and/or livestock stocking rates. Further research on

P. australis should try to determine optimum human impact, because a complete exclusion of fire and livestock may not always be the best measure to conserve the woodlands (Belsky & Blumenthal, 1997; Vera, 2000). In addition, further studies should try to differentiate between the effects of fire and livestock grazing, as we were not able to separate these factors in our human impact index. However, our field impressions are that at present fire might be the factor that plays the larger role in the modification of woodland dynamics, as was also revealed by Fulé *et al.* (2002) for natural forests in the USA.

ACKNOWLEDGEMENTS

We are very grateful to the Volkswagen Foundation Germany for funding this study. We thank M. Caceres, E. Galli, D. Schinner, I. Teich, R. Torre, H. Zimmerman and I. Lett for assisting in the field surveys, and M. B. Bush, I. Teich and two anonymous referees for improving our English. The National Parks authorities provided permits to do part of this study in Quebrada del Condorito National Park. J. Nores, N. Bazan, A. Moreno, J. Cuello, G. Estrada de Ponce, M. López and R. Graph allowed us to carry out part of the study on their lands. Club Andino Córdoba and C. Paz provided lodging and logistics. The first and last authors are assistant researchers of CONICET (Argentina).

REFERENCES

- Arce, R. (1990) Evaluación de la distribución y situación actual de las poblaciones del género *Polylepis* en los Departamentos de Ancash y Lima. PhD Thesis, Universidad Nacional Agronomía, La Molina, Lima, Perú.
- Backéus, I., Rulangaranga, Z.K. & Skoglund, J. (1994) Vegetation changes on formerly overgrazed hill slopes in semi-arid central Tanzania. *Journal of Vegetation Science*, **5**, 327–336.
- Barber, V., Juday, G.P. & Finney, B. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Beck, S. & Ellenberg, H. (1977) *Entwicklungsmöglichkeiten im Andenhochland in ökologischer Sicht*. Federal Ministry for Economical Cooperation, Göttingen, Germany.
- Beck, S. & Garcia, E. (1991) Flora y vegetación en los diferentes pisos altitudinales. *Historia natural de un valle en los Andes: La Paz* (ed. by E. Forno and M. Baudoin), pp. 65–108. Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, Bolivia.
- Bellemare, J., Motzkin, G. & Foster, D.R. (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, **29**, 1401–1420.
- Belsky, J.A. & Blumenthal, D.M. (1997) Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology*, **11**, 315–327.
- Boer, M. & Smith, M.S. (2003) A plant functional approach to the prediction of changes in Australian rangeland vegetation

- under grazing and fire. *Journal of Vegetation Science*, **14**, 333–344.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Cabido, M. (1985) Las comunidades vegetales de la Pampa de Achala, Sierras de Córdoba, Argentina. *Documents Phytosociologiques*, **9**, 431–443.
- Cabido, M. & Acosta, A. (1985) Estudio fitosociológico en bosques de *Polylepis australis* BITT. ('Tabaquillo') en las Sierras de Córdoba. *Argentina. Documents Phytosociologiques*, **9**, 385–400.
- Cierjacks, A. & Hensen, I. (2004) Variation of stand structure and regeneration of Mediterranean holm oak along a grazing intensity gradient. *Plant Ecology*, **173**, 215–223.
- Cingolani, A.M., Cabido, M.R., Renison, D. & Solís Neffa, V. (2003) Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *Journal of Vegetation Science*, **14**, 223–232.
- Cingolani, A.M., Renison, D., Zak, M.R. & Cabido, M.R. (2004) Mapping vegetation in a heterogeneous mountain rangeland using Landsat data: an alternative method to define and classify land-cover units. *Remote Sensing and Environment*, **92**, 84–97.
- Coughenour, M.B. (1991) Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology*, **28**, 71–82.
- Cushman, S.A. & Wallin, D.O. (2002) Separating the effects of environment, spatial and disturbance factors on forest community structure in the Russian Far East. *Forest Ecology and Management*, **168**, 201–215.
- Díaz, S., Acosta, A. & Cabido, M. (1994) Community structure in montane grasslands of central Argentina in relation to land use. *Journal of Vegetation Science*, **5**, 483–488.
- Delarze, R., Caldelari, D. & Hainard, R. (1992) Effects of fire on forest dynamics in southern Switzerland. *Journal of Vegetation Science*, **3**, 55–60.
- Ellenberg, H. (1979) Man's influence on the tropical mountain ecosystems in South America. *Journal of Ecology*, **67**, 401–416.
- Enrico, L., Funes, G. & Cabido, M. (2004) Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. *Forest Ecology and Management*, **190**, 301–309.
- Fernández, J. (1970) *Polylepis tomentella* y orogenia reciente. *Boletín de la Sociedad Argentina de Botánica*, **13**, 14–30.
- Fernandez Alés, R., Laffarga, J.M. & Ortega, F. (1993) Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science*, **4**, 313–322.
- Fjeldsá, J. & Kessler, M. (1996) *Conserving the biological diversity of Polylepis woodlands of the highlands of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes*. NORDECO, Copenhagen, Denmark.
- Foster, D.R., Fluet, M. & Boose, E.R. (1999) Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications*, **9**, 555–572.
- Frimer, O. & Møller Nielsen, S. (1989) *The status of Polylepis forests and their avifauna in Cordillera Blanca, Peru*. Zoological Museum, Copenhagen, Denmark.
- Fryer, G.I. & Johnson, E.A. (1988) Reconstructing fire behaviour and effects in a subalpine forest. *Journal of Applied Ecology*, **25**, 1063–1072.
- Fulé, P.Z., Wallace Covington, W.W., Moore, M.M., Heinlein, T.A. & Waltz, A.E.M. (2002) Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography*, **29**, 31–47.
- Gamache, I. & Payette, S. (2004) Height growth response of tree line black spruce to recent climate warming across the forest-tundra of Eastern Canada. *Journal of Ecology*, **92**, 835–845.
- Gerhardt, F. & Foster, D.R. (2002) Physiographical and historical effects on forest vegetation in central New England, USA. *Journal of Biogeography*, **29**, 1421–1437.
- Gomez Sal, A., De Miguel, J.M., Casado, M.A. & Pineda, F.D. (1986) Successional changes in the morphology and ecological responses of a grazed pasture ecosystem in central Spain. *Vegetatio*, **67**, 33–44.
- Guyette, R.P. & Spetich, M.T. (2003) Fire history of oak-pine forests in the Lower Boston Mountains, Arkansas, United States. *Forest Ecology and Management*, **180**, 463–474.
- Hensen, I. (1995) Die Vegetation von *Polylepis*-Wäldern der Ostkordillere Bolivians. *Phytocoenologia*, **25**, 235–277.
- Hensen, I. (2002) Impacts of anthropogenic activity on the vegetation of *Polylepis* woodlands in the region of Cochabamba/Bolivia. *Ecotropica*, **8**, 183–203.
- Hofgaard, A. (1997) Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography Letters*, **6**, 419–429.
- Hueck, K. (1961) Drei bemerkenswerte Gebirgswaldtypen aus den venezolanischen Anden. *Jahrbuch des Vereins zum Schutze der Alpenpflanzen und -tiere*, **26**, 94–99.
- Hueck, K. (1962) Der *Polylepis*-Wald in den venezolanischen Anden, eine Parallele zum mitteleuropäischen Latschenwald. *Angewandte Pflanzensoziologie. Pflanzensoz.*, **17**, 57–75.
- Hunt, L.P. (2001) Low seed availability may limit recruitment in grazed *Atriplex vesicaria* and contribute to its local extinction. *Plant Ecology*, **157**, 53–67.
- Hunter, M.L. (1990) *Wildlife, forests and forestry*. Prentice Hall, Englewood Cliffs, NJ, USA.
- Husheer, S.W., Coomes, D.A. & Robertson, A.W. (2003) Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *Forest Ecology and Management*, **181**, 99–117.
- Ibisch, P. (1993) *Estudio de la vegetación como una contribución a la caracterización de la provincia de Arque (Bolivia)*. Cuaderno Científico No. 1. PROSANA, Cochabamba, Bolivia.
- Jordan, E. (1983) Die Verbreitung von *Polylepis*-Beständen in der Westkordillere Bolivians. *Tuexenia*, **3**, 101–116.

- Kessler, M. (1995) *Polylepis*-Wälder Boliviens: Taxa, Ökologie, Verbreitung und Geschichte. *Dissertationes Botanicas* 246, Berlin, Stuttgart.
- Kessler, M. (2000) Observations on a human-induced fire event at a humid timberline in the Bolivian Andes. *Ecotropica*, **6**, 89–93.
- Kessler, M. (2002) The *Polylepis* problem: where do we stand? *Ecotropica*, **8**, 97–110.
- Kessler, M. & Driesch, P. (1993) Causas e historia de bosques altoandinos en Bolivia. *Ecología en Bolivia*, **21**, 1–18.
- Koepcke, H.W. (1961) *Synökologische Studien an der Westseite der peruanischen Anden*. Bonner Geographische Abhandlungen 29, Bonn, Germany.
- Körner, C. (2003) *Alpine plant life. Functional plant ecology of high mountain ecosystems*, 2nd edn. Springer-Verlag, Berlin, Germany.
- Lægaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. *Páramo. An Andean ecosystem under human influence* (ed. by H. Balslev and J.L. Luteyn), pp. 151–170. Academic Press, London, UK.
- Lara, A., Fraver, S., Aravena, J.C. & Wolodarsky, F.A. (1999) Fire and the dynamics of *Fitzroya cupressoides* (Alerce) forests of Chile's Cordillera Pelada. *Ecoscience*, **6**, 100–109.
- Lauer, W., Rafiqpoor, M.D. & Theisen, I. (2001) *Physiogeographie, vegetation und syntaxonomie der flora des Páramo de Papallacta (Ostkordillere Ecuador)*. Erdwissenschaftliche Forschung 39, Stuttgart.
- Miehe, G. & Miehe, S. (1994) Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia*, **24**, 53–110.
- Pan, D., Domon, G., Marceau, D. & Bouchard, A. (2001) Spatial pattern of coniferous and deciduous forest patches in an Eastern North America agricultural landscape: the influence of land use and physical attributes. *Landscape Ecology*, **16**, 99–110.
- Pereg, D. & Payette, S. (1998) Development of black spruce growth forms at treeline. *Plant Ecology*, **138**, 137–147.
- Price, L.W. (1981) *Mountains and man: a study of process and environment*. University of California Press, Berkeley and Los Angeles, CA.
- Rauh, W. (1988) *Tropische Hochgebirgspflanzen*. Springer, Berlin, Germany.
- Renison, D., Cingolani, A.M. & Suarez, R. (2002) Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba, Argentina. *Revista Chilena de Historia Natural*, **75**, 719–727.
- Renison, D., Hensen, I. & Cingolani, A.M. (2004) Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. *Forest Ecology and Management*, **196**, 327–333.
- Renison, D., Cingolani, A.M., Suarez, R., Menoyo, E., Coutsiers, C., Sobral, A. & Hensen, I. (2005) The restoration of degraded mountain forests: effects of seed provenance and microsite characteristics on *Polylepis australis* seedling survival and growth in Central Argentina. *Restoration Ecology*, **13**, 1–9.
- Ruthsatz, B. (1977) *Pflanzengesellschaften und ihre Lebensbedingungen in den Andinen Halbwüsten Nordwest-Argentiniens*. *Dissertationes Botanicas* 39, Berlin, Stuttgart.
- Ruthsatz, B. (1983) Der Einfluß des Menschen auf die Vegetation semiarider bis arider tropischer Hochgebirge am Beispiel der Hochanden. *Berichte der Deutschen Botanischen Gesellschaft*, **96**, 535–576.
- Sarmiento, F. (2002) Anthropogenic change in the landscapes of highland Ecuador. *The Geographical Review*, **92**, 213–234.
- Simpson, B. (1986) Speciation and specialization of *Polylepis* in the Andes. *High altitude tropical biogeography* (ed. by F. Vuilleumier and M. Monasterio), pp. 304–315. New York, USA.
- Underwood, A.J. (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, UK.
- UNEP-WCMC (2004) United Nations Environment Programme, World Conservation Monitoring Center; <http://www.unep-wcmc.org>.
- Vera, F.W.M. (2000) *Grazing ecology and forest history*. CABI Publishing, Wallingford, Oxon, UK.
- Verweij, P.A. & Beukema, H. (1992) Aspects of human influence on upper-Andean forest line vegetation. *Páramo. An Andean ecosystem under human influence* (ed. by H. Balslev and J.L. Luteyn), pp. 171–195. Academic Press, London, UK.
- Walter, H. & Medina, E. (1969) Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas. *Berichte der Deutschen Botanischen Gesellschaft*, **82**, 275–281.
- Wesche, K. & Kessler, M. (2004) Die humide tropisch-alpine Stufe – weltweite Gemeinsamkeiten. *Ökologie der Erde*, Bd. 2: Spezielle Ökologie der Tropischen und Subtropischen Zonen, 3rd edn (ed. by H. Walter and S. Breckle), pp. 128–155. Spektrum, München, Germany.
- Wesche, K., Miehe, G. & Kaeppli, M. (2000) The significance of fire for afroalpine ericaceous vegetation. *Mountain Research and Development*, **20**, 340–347.
- Wimberly, M.C. & Ohmann, J.L. (2004) A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) coast range. *Landscape Ecology*, **19**, 631–646.
- Yates, C.J., Norton, D.A. & Hobbs, R.J. (2000) Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. *Austral Ecology*, **25**, 36–47.

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Editor: Mark Bush