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Wood-decaying polypores in the mountains of central Argentina in relation to *Polylepis* forest structure and altitude

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ABSTRACT

To determine how altitude and forest successional stage are related to richness and composition of wood-decaying polypore fungi in *Polylepis* mountain forests of central Argentina we sampled 48 forest plots of 900 m² which included a range of successional stages and altitudes. We recorded a total of 19 species and our main results show that overall richness increased with forest successional stage and altitude, while endemic species richness was positively related only to altitude. Polypore community structure as exemplified by DCA Axes 1 and 2 was also related only to altitude with no pattern with forest successional stage, meaning polypore species are added during succession with no loss of early successional species. We conclude these forests must be managed to promote more mature forests and emphasis must be placed on a range of altitudes, especially highland areas where slow decomposition allows for a more diverse polypore community.

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Introduction

The long land use history of the high mountain forests of central Argentina, and other tropical and subtropical mountain forests of South America, has greatly reduced the surface area occupied by forests dominated by trees of the *Polylepis* genus (Fjeldså & Kessler 1996; Renison *et al.* 2006; Cingolani *et al.* 2008). The restoration of forest extension and connectivity has been highly recommended because *Polylepis* forests harbour a high richness of species many of which are endemics including birds (Fjeldså 2002; Herzog *et al.* 2002; Bellis *et al.* 2009), plants (Fernández *et al.* 2001; Fernández-Terrazas & Ståhl 2002) and rodents (Tarifa & Yensen 2001;

Yensen & Tarifa 2002), and because *Polylepis* forests provide important ecological services to humans such as clean water and carbon sequestration (Fjeldså & Kessler 1996).

Polylepis forests, often called woodlands or shrublands, and mostly have a simple vertical structure. This structure was usually interpreted as a result of high altitude stressful environmental conditions (i.e. Enrico *et al.* 2004). However, a recent study pointed out that the long lasting human impact on *Polylepis* forests has greatly contributed to a reduction of vertical complexity, and that late successional forests with a complex vertical structure may still be found in remote areas (Renison *et al.* 2009). Several recent studies have shown that *Polylepis* forest with a complex vertical structure (mature

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forests) harbours several rare bird endemics (Cahill & Matthysen 2007; Lloyd & Marsden 2008). To the best of our knowledge, the effect of a simplified *Polylepis* forest structure has not been studied in other organisms. Because wood-decaying polypore species are often related to different forest successional stages, including many species which inhabit coarse woody debris only found in mature forests (Renvall 1995; Sippola *et al.* 2001; Junninen *et al.* 2006), they are potential candidate taxa which could highlight the importance of preserving mature *Polylepis* forests.

Studies in eastern US and boreal forests show that forest structure has a profound influence on wood-decay fungi and associated insect fauna (Komonen *et al.* 2000; Siitonen 2001). In boreal ecosystems wood decomposition is slow and hence wood accumulation high. As *Polylepis* forests are also situated in cold environments where wood decomposition may be slow, a similar situation may be suspected, and recent studies have described a diverse wood fungal community inhabiting these forests, with high levels of endemism and new species to science (Urcelay *et al.* 2000; Robledo *et al.* 2003, 2006; Rajchenberg & Robledo 2005).

Here, we study the wood-decaying polypore community of *Polylepis australis* forests from central Argentina. Our objectives were to: (1) describe *P. australis* wood-decaying polypore community in terms of species richness, diversity and composition; (2) determine the association between forest structure, altitude and polypore community; and (3) discuss management implications. Our hypotheses were that: (1) different successional stages harbour unique wood-decaying polypore communities; (2) species inhabiting rare late successional forests could be rare and endangered; and (3) polypore communities could be more diverse at higher altitudes where average temperatures and wood decomposition is slower. To the best of our knowledge, this is the first study in South America that relates changes in wood-decay fungal diversity with forest successional stage or altitude.

Materials and methods

Study area

The Córdoba Mountains (central Argentina, North-South direction, rising up to 2884 m asl, 31° 34' S, 64° 50' W) have an annual precipitation of 840 mm and mean monthly temperatures at 2100 m asl of 5.0 and 11.4 °C in the coldest and warmest months, respectively (Cabido 1985). The landscape is a mosaic of different types of tall tussock grasslands, grazing lawns, natural granitic outcrops, exposed rock surfaces produced by anthropogenic soil erosion, and forest canopies dominated almost exclusively by *P. australis* (Cingolani *et al.* 2004, 2008). For a location map of the study area and *Polylepis* distribution see Robledo *et al.* (2006). *P. australis* is an endemic treeline species of the mountains of central and Northwest Argentina with a maximum height of 16 m and basal circumference of 3.65 m (Simpson 1979; Suarez *et al.* 2008). In central Argentina trees of this species may be found even on the highest peaks at 2900 m asl, but tree performance appears to be best at around 1850 m asl (Marcora *et al.* 2008).

Plot establishment

We established 48 plots of 30 × 30 m, distributed in four river basins, that differed in human impact and successional stage (as in Renison *et al.* 2006, 2009). Plot location was initially selected using a vegetation map (Cingolani *et al.* 2004). We randomly chose areas within vegetation units that were supposed to contain forest or open shrublands (*P. australis* cover generally >5%). In the field we located plots using Global Positioning System and selected them for the study when: (1) there was at least a total of 20 *Polylepis* living stems, snags or logs (hereafter sampling units), and (2) all sampling units were accessible for measuring (i.e. plots on steep cliffs or in gorges were not selected). We attempted to establish a species richness/area curve (and also a species richness/number of sampling units curve) to determine the plot area or number of sampling units at which species richness was well captured. However, due to extensive forest fragmentation and the low relative frequency of all polypore species except one (see Results), the curve did not reach a plateau in degraded areas with small forest patches even when all the patch was sampled. Rather than continue to accumulate species by changing forest patch (thus unintentionally incorporating Beta diversity), or using differing study plot size for small and large forest patches, we opted for a fixed area of 900 m² and more than 20 sample units as a measure of relative density of individuals and species. In the final data set, neither relative species richness nor density per plot were correlated with the number of sampling units per plot (Spearman rank correlation: $r = 0.21$, $P = 0.15$; $r = 0.22$, $P = 0.15$, respectively) showing that sampling effort as measured in wood sampling units was not the main driving force determining relative species richness and abundance per plot, and hence of the patterns found in this study.

Data collection

We sampled plots from May 2003 to Jun. 2005 taking care to evenly distribute sampling periods between river basins (and hence plot successional stage). We recorded all wood broader than 4.5 cm diameter and classified them as (1) living stems, (2) snags (dead standing stems and natural stumps), (3) logs (dead fallen stems) or (4) fallen branches (dead fallen branches and tops) (Table 1), as in Urcelay & Robledo (2004) and Heilmann-Clausen & Boddy (2008). Each stem of multi-stemmed *Polylepis* individuals was considered a separate sampling unit because the colonization strategies and development of the heart rot species in the present study are more associated with stems than individuals (Schwarze *et al.* 2000; GR pers. obs.). We registered the perimeter of all sampling units and the polypore species through the presence of fructifications (a group of one or several fruit bodies in the same sampling unit was considered a single species occurrence).

Specimen identification

Wood-decaying polypore fructifications were identified to species level in the field or collected and studied in the laboratory. Morphological features of basidiocarps were observed

Table 1 – Main structural characteristics of 48 *Polylepis* forest plots of 900 m² as classified according to forest successional stage. Number of plots within each stage is shown in parenthesis, means are shown with standard error of the mean, and different letters indicate significant differences between stages (Post-hoc Tukey test $P = 0.05$). ANOVA F is shown in the last column; degrees of freedom are 4 in all tests

	Early regeneration (N = 10)	Late regeneration (N = 9)	Young (N = 9)	Mixed (N = 9)	Mature (N = 11)	ANOVA ($p < 0.001$)
Basal area (m ²)	0.7 ± 0.1 A	1.2 ± 0.2 B	2.0 ± 0.1 B	1.7 ± 0.1 B	3.3 ± 0.2 B	F = 10.1
Living stems	29.5 ± 3.5 A	88.9 ± 11.4 B	97.3 ± 7.3 B	44.7 ± 4.9 A	84.6 ± 8.7 B	F = 18.3
Snags	2.0 ± 1.2 A	11.9 ± 3.9 B	14.2 ± 2.8 B	7.7 ± 1.9 B	20.8 ± 3.6 B	F = 10.1
Logs	0.9 ± 0.3 A	1.3 ± 0.4 A	1.0 ± 0.3 A	2.8 ± 0.8 AB	5.7 ± 1.0 B	F = 8.4
Fallen branches	7.4 ± 2.0 A	13.0 ± 4.1 AB	21.3 ± 3.4 BC	24.6 ± 4.8 BC	28.6 ± 3.4 C	F = 8.8

with a stereomicroscope. Microscopic examinations and measurements were made from freehand sections mounted in 3–5 % KOH plus 1 % phloxine and in Melzer's reagent. Collections were deposited in the herbarium of the "Museo Botánico, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba" (CORD). For a complete taxonomic description, checklist, habitat and ecological characterization of the polypore taxa found in these forests see [Urcelay et al. \(2000\)](#) and [Robledo et al. \(2003, 2006\)](#).

Data analysis

We categorized plots according to successional stage into five categories adapted from [Renison et al. \(2009\)](#) in order to have a more equal distribution of forest stages: (1) early regeneration had 20–40 sampling units. The remaining had more than 40 sample units. (2) Late regeneration forests had no more than 4 living stems of up to 90 cm in circumference and were not mixed stands. (3) Young forests had 4–8 stems larger than 90 cm in circumference and were not mixed stands. (4) Mixed forests had an even distribution of size classes and were not mature forests. (5) Mature forests had a basal area of more than 2.5 m² and more than 8 stems larger than 90 cm in perimeter.

Statistical analysis

To better interpret the forest group types, we compared mean values of the most relevant structural characteristics using ANOVA. The response variables were the number of living stems, snags, logs and twigs while the independent variable was the forest structure (5 categories). We determined the association between polypore communities, successional stage and altitude using ANCOVA, where the response variables were richness of polypore species per plot (all species and a separate analysis for endemics) and plot species composition summarized as the relevant axes of variation using Detrended Correspondence Analysis (DCA; [Ter Braak 1987](#)). For the DCA analysis we discarded a plot with no recorded polypore fructification, and we used the 14 species with more than two records. The factor in the ANCOVA was plot successional stage and the covariable was altitude. A

visual inspection of the relation between altitude and endemic richness suggested a quadratic relation so we also added altitude squared to the model for endemic richness. We also performed all the same analyses for polypore diversity (Shannon diversity index), but we always obtained the same pattern of results as with species richness with which it is highly correlated (Spearman rank correlation; $r_s = 0.97$, $P < 0.001$). For simplicity we only report species richness. All residuals were checked for normality and homocedasticity, ($P > 0.05$; Shapiro–Wilks and Levenés tests, respectively) and in the case of richness response variables we log transformed to better meet assumptions ([Underwood 1997](#)).

Results

We examined a total of 3304 living stems, 553 snags, 118 logs and 919 fallen branches, and recorded a total of 19 polypore species among 358 fructifications. *Fomitiporia tabaquilio* was the most abundant species with 27 % of the records, followed by a group of 5 species which varied in abundance from 10 to 1 %. At the other extreme 7 rare species were less than 1 % of the records ([Fig 1](#)). Of the 19 species [Robledo et al. \(2006\)](#) classified 12 as mainly saprotrophic and 7 as mainly pathogenic. Endemics were represented by 5 species ([Fig 1](#)).

Plots classified by successional stage as early and late regeneration, young, mixed and mature forests, respectively, had increasing basal area, snags, logs and fallen branches ([Table 1](#)). Overall polypore species richness was associated with both forest successional stage and altitude ([Fig 2](#)). Early and late regeneration stage plots had the lowest richness, young and mixed forest plots had intermediate richness, and mature forest plots had the highest richness ([Fig 2A](#), $P = 0.002$). Moreover, altitude was positively related to richness ([Fig 2B](#), $P = 0.05$), with the overall model explaining 27 % of the variance (ANCOVA; $F = 4.43$; $DF = 5$; $P = 0.003$; R^2 adjusted = 0.27). Endemic species richness was positively related only to altitude ([Fig 3](#); $P < 0.001$) with no pattern with successional stage ($P = 0.34$), with the overall model explaining 37 % of the variance (ANCOVA; $F = 6.37$; $DF = 5$; $P < 0.001$; R^2 adjusted = 0.37). A model for endemics including altitude squared was also only significant for altitude ($P = 0.05$), with $P = 0.09$ for altitude

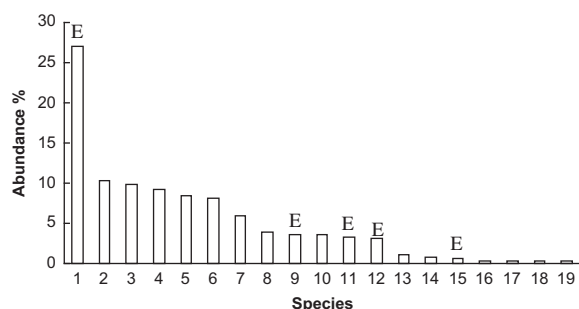


Fig 1 – Polypore abundance (% of collections) in *Polylepis* forests of the Córdoba mountains, Argentina, as a function of the species ordered from the most to the least abundant. Numbers correspond to the following species, with endemics indicated with an (E): (1) *Fomitiporia tabaquilio* (E), (2) *Funalia gallica*, (3) *Trametes versicolor*, (4) *Perenniporia aff. medullapanis*, (5) *Bjerkandera adusta*, (6) *Ganoderma adspersum*, (7) *Gloeoporus dichrous*, (8) *Pycnoporus sanguineus*, (9) *Phellinus uncisetus* (E), (10) *Trametes villosa*, (11) *Phellinus daedaliformis* (E), (12) *Inonotus venezuelicus* (E), (13) *Postia caesia*, (14) *Oxyporus obducens*, (15) *Datronia orcomanta* (E), (16) *Inonotus quercustris*, (17) *Fuscoporia gilva*, (18) *Polyporus arcularius*, (19) *Ceriporia spissa*.

squared and with the overall model explaining a similar percentage of the variance as the model without the quadratic term (ANCOVA; $F = 6.05$; $DF = 6$; $P < 0.001$; R^2 adjusted = 0.38). The seven rarest polypore species (Fig 1) were only found in young, mixed and mature forest plots, and were never found in early and late regeneration woodland plots.

Polypore community composition per plot could be summarized in 2 DCA axes. Eigenvalues were 0.42 and 0.29 for DCA Axis 1 and 2, respectively. The most abundant species were situated in the centre of both DCA axes, while rare species were situated in the extremes of both axes (Fig 4). All endemic species had low values in DCA Axis 1. No significant pattern was found regarding DCA Axis 1 and forest successional stage ($P = 0.16$), while Axis 1 had a significant negative association with altitude ($P < 0.001$; overall ANCOVA: $F = 6.80$; $DF = 5$; $P < 0.001$; R^2 adjusted = 0.39) confirming previous

results of a gradual increment in endemic species with altitude. DCA Axis 2 was not significantly related to forest successional stage ($P = 0.11$) nor to altitude ($P = 0.83$; overall ANCOVA; $F = 1.92$; $GL = 5$; $P = 0.11$; R^2 adjusted = 0.09).

Discussion

The 19 polypore species we found in this study represent the polypore community of *P. australis* forests fairly well, as after 10 yr of study and extensive searches, Robledo et al. (2006) described the community with 23 species. Among the four species not found in our study *Phellinus apiahynus* was only found in mountain ranges further north; *Inocutis jamaicensis* is a characteristic element of the lowland forests and is rarely present in *Polylepis* forests (Robledo et al. 2006), and, *Diplomitoporus lindbladii* and *Polyporus melanopus* are subtropical species rarely found in *Polylepis* forests of central Argentina, found only once and twice respectively (Robledo et al. 2006). We thus consider that our plots are representative of the polypore community of *Polylepis* forests in central Argentina and the observed patterns are well supported.

Polylepis forest successional changes and consequent changes in availability of woody substrata directly affected the richness of polypore species with no accompanying changes in community structure detected by DCA axes. This pattern indicates that polypore species found in early successional forests persist in late successional forests (as defined in our study) with the addition of rare species but no significant community replacement. Higher polypore species richness in mature forests is the norm in most studied forests (Hattori & See 2003; Hattori 2005; Brown et al. 2006; Lonsdale et al. 2008). In particular, the presence of large logs allows the occurrence of threatened and rare polypore species (Bader et al. 1995; Sippola et al. 2001; Penttilä et al. 2004; Stokland & Kauserud 2004; Heilmann-Clausen & Christensen 2005). A similar pattern was found in this study as the rare species *Postia caesia*, *Fuscoporia gilva*, *Polyporus arcularius*, and *Ceriporia spissa* were only recorded on large fallen logs of young, mixed or mature forests. Other rare species, such as *Inonotus quercustris* and *Oxyporus obducens* were found in dead or living trunks of young forests, while the endemic *Datronia orcomanta* was only found in dead attached branches in a young and

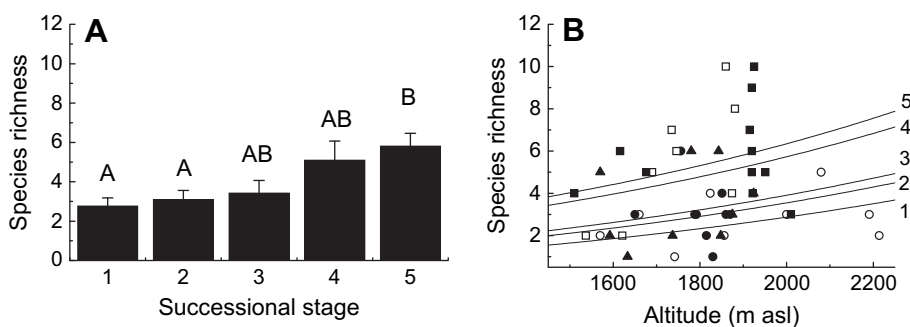


Fig 2 – Relative polypore species richness in relation to (A) forest successional stage, and (B) altitude. Numbers and symbols represent the following forest stages: 1 (○) early regeneration; 2 (●) late regeneration; 3 (▲) young; 4 (□) mixed; and 5 (■) mature. Different letters in (A) indicate significant differences (Post-hoc Tukey test $P = 0.05$). The trend lines in (B) indicate the best linear fit to the logarithm of species richness + 1, for each forest successional stage.

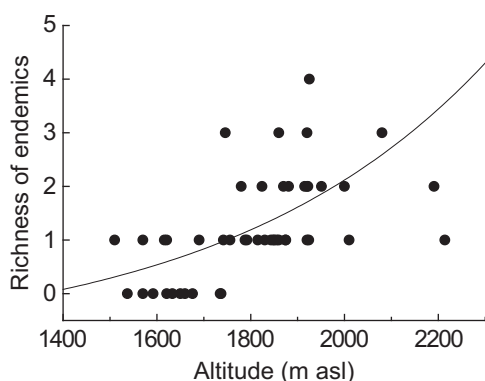


Fig 3 – Relative richness of endemic polypores found in 48 *Polylepis* forest plots in relation to altitude. The trend line indicates the best linear fit to the logarithm of species richness + 1.

mixed forest plots. Although most rare species in this study were not endemic to *Polylepis* forests and are more common in other ecosystems (or even quite abundant like *F. gilva* in the tropics), their conservation status at a local scale should still be of concern, as they are important due to their ecological role, and mature forests are disappearing very rapidly in all the central Argentine region (Zak et al. 2004).

We also found a pattern of increasing species richness (all species and endemics only) and change in polypore community structure with altitude (Figs 2, 3 and 4). The five endemic/specialist species (i.e., host specific, *P. australis* specific or *Polylepis* specific) could be more adapted to environmental conditions at higher altitudes, though an alternative model suggesting a unimodal relationship with an optimum richness at intermediate altitudes could also be feasible as altitude squared reached a nearly significant value of 0.09 when added to the model. Concomitantly, an altitudinal limit of distribution of lowland species was observed, thus the replacement of species with altitude. To our knowledge this is the first report of an altitudinal pattern for wood-decaying fungi. This pattern has to be considered only within *Polylepis* forests altitudinal range of our study (1500–2300 m asl) as polypore richness in

lower “Chaco Serrano” forests of the region increases to 50 species (Robledo & Urcelay 2009).

The relatively low amount of variance explained by our models is probably due to three main factors: (1) the high habitat heterogeneity existing even in 900 m² plots due to the rough terrain of the Córdoba mountains (Cingolani et al. 2004) which may account for differences between plots; (2) the small size of our plots (and forests) combined with the low frequency of occurrences of most polypore species which augment the probability of species not being recorded due to chance effects; and (3) the temporal patterns of fruiting of some polypore species which may have caused many species present as mycelia not to be recorded. However, these factors causing variance in species richness did not completely obscure the patterns found with forest successional stage and altitude.

Conservation and management applications

Long term livestock management, which involves fires and livestock browsing, besides altering forest cover and causing extensive soil erosion and compaction (Cingolani et al. 2004, 2008; Renison et al. 2006, in press), has profoundly simplified *P. australis* forest structural complexity at the landscape level (Renison et al. 2009). 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; Cierjacks et al. 2008). As suggested by Lodge et al. (1995) and Lodge (1997), understanding the main factors driving fungal diversity can give us an important background to suggest areas and policies for conservation. Our polypore study suggests forests in the later successional stages must be protected and other forests must be managed to promote a higher proportion of mature forests. Connectivity between mature forests must also be considered as local distance to mature forests is an important determinant of polypore community structure due to restricted spore deposition (Vasiliauskas et al. 2005). Moreover, special emphasis must be placed on preserving forests at a range of altitudes, but especially highland areas above 1700 m asl where richness of endemic polypores is highest (Fig 3).

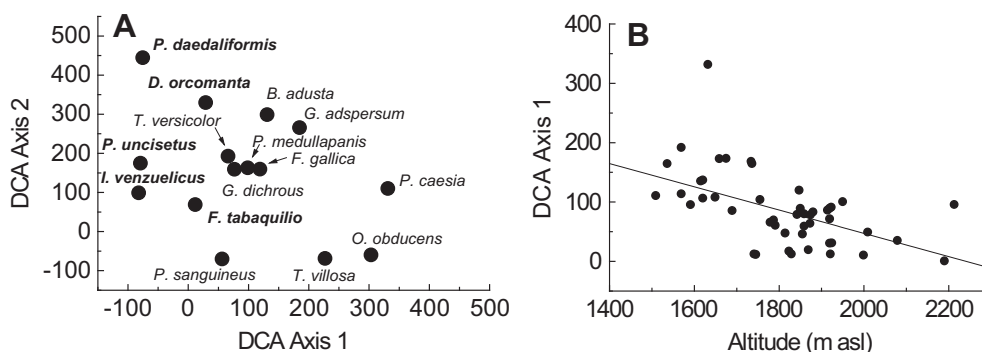


Fig 4 – (A) DCA ordination (Axes 1 and 2) of 47 *Polylepis* forests plots on the basis of 14 polypore species which were recorded with more than two observations. The 5 endemic species are shown in bold. (B) Scores of DCA Axis 1 in relation to altitude. The trend line indicates the best linear fit.

Besides being extremely important in ecosystem processes, wood-decay fungi have key functions in the maintenance of other species, such as providing nesting sites for woodpeckers and substrata for fungivore and saproxylic endemic organisms that depend on fungal fruit bodies and decaying wood (Siitonen 2001; Robledo & Urcelay 2009). Beyond particular taxa, our study supports the hypothesis that every type of habitat with a long evolutionary history of existence is bound to have some kind of organisms that depend on it (Hunter 1990). General management principles that promote a diversity of habitats at all scales would be adequate to manage *Polylepis* forests with the advantage of being less dependent on indicator/key species (Lindenmayer et al. 2006).

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