

**Title Page**

*Short title.—Ecology of gasteroid fungi from Argentinean Polylepis woodlands*

*Title.—Ecology of gasteroid fungi (Agaricomycetidae and Phallomycetidae) affected by different successional stages of Polylepis australis Bitt. woodlands of Córdoba, central Argentina*

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**Abstract:** We conducted the first ecological study of epigeous gasteroid fungi associated with the endangered ecosystem of high altitude *Polylepis australis* woodlands in Córdoba, Argentina. We recollected samples from 48 plots of 900 m<sup>2</sup> each, located in four river basins. Plots were classified according to five successional stage categories: early and late regeneration, young, mixed and mature forests. We performed PERMANOVA and PERMDISP analysis in order to compare species composition among fungal assemblages between the conservation categories. Rank–abundance curves were also generated for the five conservation categories. Twenty species were recollected within the 48 *P. australis* plots. *Bovista pusilliformis* was the most abundant species within the plots classified as the less conserved stages; *Geastrum saccatum* was the most abundant species present in plots classified as mixed forest; plots classified as mature forests presented *G. indicum* and *Lycoperdon pyriforme* as the most abundant species. Plots classified as mixed forest showed the highest species richness values and significant differences in species composition than plots classified as both, early and late regeneration stages. With this work we contribute to the ongoing effort to protect and conserve the endangered ecosystem of our treeline species *P. australis*.

**Key words:** fungal conservation, ecology, endangered ecosystem, fungal diversity, puffball, tabaquillo

## INTRODUCTION

*Polylepis* Ruiz & Pav. (Rosaceae) species form woodlands at elevations between 1300–4400 (–5000) m a.s.l. (Cabrera 1976; Kessler 2006). The current degradation status of these forests due to human activity, environmental conditions and its current degree of fragmentation, place *Polylepis* woodlands within the most endangered ecosystems (Kessler 2006; Renison et al. 2011; UNEP-WCMC 2004; Walter and Gillett 1998). *Polylepis australis* Bitt. woodlands in the Sierras Grandes de Córdoba, Argentina, are considered hotspots of biodiversity as they harbor high richness of species of fungi, plants, and animals (Bellis et al. 2009; Ceballos 2008; Ceballos and Zaragoza, 2008; García et al. 2008; Lescano et al. 2015, Hernández Caffot et al. 2011, 2013, 2016; Robledo et al. 2003; Soteras et al. 2015; Urcelay et al. 2000, Verga et al. 2012). However, livestock rearing and the high incidence of fire caused by human activity have reduced its distribution to isolated patches that are restricted to deep canyons along watersheds and rocky areas (Cabido and Acosta 1985; Cingolani et al. 2004; Enrico et al. 2004; Renison et al. 2006a; Simpson 1979).

Over the past 16 years local fungal diversity from *P. australis* woodlands has been assessed (Gallo et al. 2015; Hernández Caffot et al. 2011, 2013, 2016; Menoyo et al. 2007, 2009; Rajchenberg and Robledo 2005; Robledo and Renison 2010; Robledo et al. 2003, 2006; Soteras et al. 2015; Urcelay et al. 2000) but only a few of these studies focused on the effect of *P. australis* woodlands fragmentation degree on the macrofungal community. Furthermore, the degree of disturbance in *P. australis* forests and how it may affect the epigeous gasteroid mycobiota has never been investigated. Ecological studies involving epigeous gasteroid fungi are still scarce. In Sonora, Mexico, Piña-Páez et al. (2013) and Esqueda-Valle et al. (2000), and Chanona-Gómez et al. (2007) in Chiapas, Mexico, observed changes in the gasteroid community along a vegetation gradient. In Brazil, Trierveiler-Pereira et al. (2013) analyzed the ecological aspects of gasteroid mycobiota in four remnants of the Atlantic Forests. In southern Sweden, Olsson et al. (2010) studied how soil pH and organic matter content determine the presence of certain gasteroid species. Regardless, there are still no ecological studies concerning the epigeous gasteroid mycobiota in Argentina.

Therefore, we conducted the first ecological study of epigeous gasteroid fungi associated with the endangered ecosystem of *P. australis* woodlands in the Sierras Grandes de Córdoba, Argentina. The aim of this study was to evaluate how different forest structures and disturbances stages of *P. australis* woodlands influence the epigeous gasteroid fungal community.

## MATERIALS AND METHODS

**Study area.**— The study took place at Parque Nacional Quebrada del Condorito and the Reserva Hídrica Provincial Pampa de Achala, located at the upper portion of the Sierras Grandes de Córdoba, in Córdoba province, central Argentina, at elevations between 1800 to 2300 m a.s.l. (Cingolani et al. 2003). Mean temperatures of the coldest and warmest month are 5.0 °C and 11.4 °C respectively, with no frost-free period. Mean annual precipitation is 840 mm, with most rainfall concentrated in the warmest months between October and April (Cabido 1985). Surveys were made in four basins of *P. australis* forest (Fig. 1), located in Dpto. Punilla: (a) Macizo Los Gigantes (31°23'58.5"S, 64°48'17.4"W); Dpto. San Alberto: (b) Parque Nacional Quebrada del Condorito (31°39'13.7"S, 64°42'06.6"W); Dpto. San Javier: (c) Quebrada El Hueco (31°58'33"S, 64°57'42"W) and (d) Quebrada del Tigre (i.e. 32°00'39.3"S, 64°57'33.3"W). At each basin we sampled twelve 30 × 30 m (900 m<sup>2</sup>) plots, for a total of 48 plots. These plots were previously established by Robledo and Renison (2010) for the polypore community ecological analysis. The same plots were selected for our

study, not only because of the forest successional stages data they provided us, but also to add information about the gasteroid fungi to the known of the fungal community. Robledo and Renison (2010) recorded all wood broader than 4.5 cm in diameter and classified them. In this classification each stem of multistem *Polylepis* individuals was considered as a separate sampling unit. According to the percentage of each sampling unit and wood diameter, the 48 plots were classified into the five successional stages categories according to Robledo and Renison (2010): “(1) plots classified as early regeneration had 20–40 sampling units. The remaining had more than 40 sampling units. (2) plots classified as late regeneration forests had no more than 4 living stems of up to 90 cm in perimeter and were not mixed stands. (3) plots classified as young forests had 4–8 stems larger than 90 cm in perimeter and were not mixed stands. (4) plots classified as mixed forests had an even distribution of size classes and were not mature forests. (5) plots classified as mature forests had a basal area of more than 2.5 m<sup>2</sup> and more than 8 stems larger than 90 cm in perimeter”. Within the four river basins the distribution of the plots with different successional forest stages was unequal. El Hueco was dominated by mixed forests and there were a low percentage of young forests. Condorito was dominated by late regeneration and followed by young regeneration forests. Gigantes had a high percentage of early regeneration forests, and mixed and mature forests were scarcely represented. El Tigre was dominated by mature forests followed by young forests and a low proportion of early and late regeneration stages (Fig. 2).

**Data collection.**— Each plot in the study area was sampled once during April-May 2007. We recollected all epigeous gasteroid basidiomata that were found inside the plots. In each plot we measured cover percentages (%) of: 1- trees, 2- exposed rock surfaces, 3- grasses, 4- ferns, and 5- cattle dung (number). These variables were selected because they are believed to influence fungal basidiomata and ascomata production (i.e.: Brown et al. 2006; Dickie et al. 2010; Gange et al. 2013; Pöggeler et al. 2006); cattle dung, in particular, constitutes the substrate of two gasteroid species related to cattle (Brodie 1975). For frequency and abundance data, all the basidiomata of the same gasteroid species, within 1 m<sup>2</sup> subplot, were considered as a unique individual and constituted one collection (adapted from Mueller et al. 2004). Information about epigeous gasteroid species involved in this work is detailed in Hernández Caffot et al. (2011, 2013, 2016), where we present a checklist of the gasteroid community inhabiting these woodlands and described two endemic gasteroid species. .

**Processing and examination of specimens.**— Specimens were dried, then kept frozen for a week and deposited at the Herbario del Museo Botánico from Universidad Nacional de Córdoba (CORD). Morphological features were observed in the laboratory using a stereo microscope (Wild M3Z) and a light microscope (Zeiss Axioplan). For microscopic examinations, sections were mounted in 3% KOH, 3% KOH + 1% phloxine, and Melzer’s reagent.

**Data analysis.**— To evaluate if the sampling effort was appropriate on each successional stage category, we compared observed with estimated richness given by Chao 1 estimator using an individual based rarefaction curve, with 1000 iterations in EstimateS (Colwell 2013). We calculated inventory completeness for each site as the difference between the percentages of species observed from the total number of species predicted by Chao 1.

We performed a non-parametric Kruskal Wallis test in order to examine the differences in the five variables believed to influence the presence of gasteroid fungi (cover percentages (%) of: canopy, exposed rock surfaces, ferns, grasses, and number of cattle dung) among plots classified in the five successional stages.

For plots classified within the same successional stage we obtained values of species richness and true diversity of order  $q = 1$ , measured as the effective number of species following Jost (2006). We assessed differences in mean values of species richness and diversity of gasteroid fungi among the five successional stages, with the altitude as a covariable using ANCOVAs.

We assessed differences in species composition among fungal assemblages among plots classified in the five successional stages using a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on a Bray-Curtis similarity matrix. This method compares the variance between groups with the variance within groups for a dissimilarity matrix by means of the sum of squared distances in an ANOVA design. The *p* value was calculated by 1000 permutations. We also performed a Permutational test of Multivariate Dispersions (PERMDISP; Anderson 2006). This complementary analysis tests whether treatments differed in their within-treatment dispersion or beta diversity, and is therefore a measure of compositional heterogeneity (Anderson 2006). When statistically significant differences with PERMANOVA analysis were found, we conducted a paired PERMANOVA tests to explore differences in composition among pairs of successional stages. To compute PERMANOVA, we used the ‘adonis’ function and ‘betadisper’ to compute PERMDISP in the ‘vegan’ package in the R environment (R Development Core Team 2015). We generated rank–abundance curves (Foster and Dunstan 2010; Magurran 2004) for the plots classified in the five forest successional stages. This method represents the combined information on relative frequencies and species ranking, and allows a visual evaluation of species richness as well as species evenness (Montagna et al. 2012). The fitting of species-rank abundance curves was carried out by plotting the relative abundance of species on a scale against their corresponding abundance ranks in each conservation category.

## RESULTS

We obtained 297 field collections comprising 970 basidiomata of epigeous gasteroid fungi from *P. australis* woodlands in the Sierras Grandes de Córdoba-Argentina, and we were able to identify 29 species within these collections. Twenty species were collected within the 48 *P. australis* plots and nine additional species were collected outside the plots (Appendix 1, Fig. 2). The inventory completeness was above 75% for all the five forest successional stages categories (Table 1).

Most of the twenty gasteroid species collected within the 48 plots of *P. australis* woodlands were growing on soil, two of them were on dung: *Cyathus stercoreus* (Schwein.) De Toni and *Sphaerobolus stellatus* Tode. Only one, *L. pyriforme*, was found on *P. australis* living trunks and stumps. *Lycoperdon pyriforme* was the only species growing on a woody substrate, with up to 80 basidiomata within 1 m<sup>2</sup> in the same living tree; also, it was the species with the highest number of basidiomata. *Cyathus stercoreus* and *S. stellatus* also presented up to 40 basidiomata in the same collection.

Agaricaceae Chevall. was represented by twelve species from five genera, whereas Sphaerobolaceae J. Schröt. and Geastraceae Corda were represented by only one genus each. We identified 6 different species of *Geastrum* Pers., being this genus the best represented (Appendix 1). From the 129 individual collected, more than 70% corresponds to species of *Geastrum*, followed by *Lycoperdon* species with 15%, and the remaining species having one finding each representing less than 1% each.

Regarding the five variables believed to influence gasteroid fungi presence (cover percentages (%) of: canopy, exposed rock surfaces, ferns and grasses, and number of cattle dung), as was expected, the successional stages involving the most conserved woodlands (late, young, mixed, and mature stages) exhibited the higher percentages of canopy cover and a lower amount of grasses. The amount of dung was not related to the forest successional stage, as we only found clear differences between the late regeneration and the young forest stages. The highest values of ferns were in the mature forest (Table 2).

Both diversity measures presented significant differences among the forest successional stages (ANCOVA richness,  $df=5$ ,  $F=5.85$ ,  $p<0.01$ ; ANCOVA true div.,  $df=5$ ,  $F=5.67$ ,  $p<0.01$ ). Mixed forest presented the higher mean values of species richness and true diversity of gasteroid fungi among the five forest successional stages (Fig. 4). Altitude was not related to either of these diversity measures (ANCOVA richness and true div.,  $df=1$ ,  $F=1.42$ ,  $p=0.24$  for both). The gasteroid fungal community composition showed clear differences among the five successional stages (PERMANOVA: Pseudo- $F=2.64$ ,  $p\text{-value}<0.01$ ). These differences were not due to differences in the relative dispersion of plots within these successional stages (PERMDISP:  $F=0.52$ ,  $p=0.72$ ). Paired PERMANOVA results showed a statistically significant difference in species composition between mixed forest and both early and late regeneration forests (PERMANOVA, Pseudo- $F=3.3$ ,  $p=0.04$ ; Pseudo- $F=3.74$ ,  $p<0.01$ , respectively). The resulting lower values of true diversity, compared to the ones observed for species richness, denotes some degree of species dominance in each fungal community of each forest stage (Table 1). This result is also shown in the species-rank abundance curves (Fig. 5). The five curves presented a similar slope: with few abundant species and low evenness in species relative abundance. *Bovista pusilliformis* was the most abundant species within the plots classified as less conserved forest stages; in plots classified as early stage forests *B. pusilliformis* represented the 27% (4 individuals); 50% in plots classified as young forests (8 individuals), and 32% in the late stages forests (7 individuals), and was absent in the relatively most conserved forests plots, classified as mixed and mature. These plots did present another species of the genus *Bovista*, *B. cunninghamii*, in lower abundance, representing 2% of total individuals in plots classified as mixed forest and 8% in plots classified as mature forest (one individual each). *Geastrum saccatum* was the most abundant species present in plots classified as mixed forest, representing 20% (13 individuals); in plots classified as mature forests 16.7% (2 individuals); in plots classified as late regeneration stage 9% (2 individuals); and in plots classified as early regeneration stage represented 2% (3 individuals). Mature forests presented *G. indicum* and *Lycoperdon pyriforme* as the most abundant species each species representing 25% of total (three individuals each species) (Figure 5).

## DISCUSSION

In this work we present the first ecological results regarding the gasteroid fungal community from different successional stages of *Polylepis australis* woodlands of Córdoba, central Argentina. We used a plot-based sampling method with the aim of evaluate the influence of *P. australis* forests structure on the gasteroid fungal community. Our results add new information regarding the ecology of the fungal community of this endangered ecosystem.

The predominant wet climate favors the development of fleshy species of fungi in *P. australis* woodlands. Species of *Geastrum* present morphological adaptations to humid environments (Sunhede 1989), as well as species from *Lycoperdon*, *Vascellum*, and *Bovista* (Domínguez de Toledo 1989). All of them present fleshy basidiomata with high water content (Cortez et al. 2013; Jeppson et al. 2012, Sunhede 1989), and some have been registered along mountain environments (Demoulin 1971). We found three *Tulostoma* species in Gigantes and el Hueco. The species of this genus have been described mainly for arid environments or growing on calcareous soil (Baseia and Galvão 2002, Baseia and Milanez 2002, Esqueda et al. 2004, Sesli et al. 2000, Wright 1987), with some exceptions (i.e.: Hernández Caffot et al. 2011, Wright and Wright 2005). Those specimens, from Gigantes and el Hueco, were growing above a rocky surface with low to almost null organic matter content; this ecological feature could explain the presence of all those taxa in *P. australis* woodlands.

Changes in forest structure and type of vegetation generate changes in the availability of substrates thus affecting the richness and community structure of saprophytic fungi, because plants are the habitat and source of energy for most of them (Esqueda-Valle et al. 2000; Gange et al. 2013; Mueller et al. 2004; Trierveiler-Pereira et al. 2013). However, it has been suggested that diversity of decomposers and macrofungi in general is partially related to resource availability, and gasteroid fungi in particular are “somewhat related” to those three variables (Lodge et al. 1995). Nonetheless, in agreement with Hawkes et al. (2011), whom stated that changes in plant community composition, diversity, and productivity may impact negatively in saprophytic fungi, our results suggested that resource availability may be influencing the gasteroid fungal community from *P. australis* forests from Sierras Grandes de Córdoba. Plots classified as early and late regeneration forests, and young forests, presented the lowest values of gasteroid fungal diversity, this turnover may be caused by the lower resources availability (established by Robledo and Renison 2010) for basidiomata production. In addition, we determine that mixed forests harbored the highest diversity levels of gasteroid fungi. Changes in the plant community may affect saprophytic fungi through a change in substrate inputs and chemicals features, thus affecting resource availability (Hawkes et al. 2011). Probably the presence of ferns and grasses, along with the high percentage of canopy cover registered in mixed forests resulted in suitable habitat conditions for fungal development due to a major quantity and quality of different resources availability for basidiomata production. Regarding these differences in fungal diversity among different forests stages, some authors studied the effects of surface water content and soil temperature and they found that basidiomata development depends on these two abiotic factors (Pinna et al. 2010, Cooke 1984, Slakins 1974, Manachere 1998). Fungal phenology is highly susceptible to an extreme variation in temperatures reducing the period in which some species may be present (Pinna et al. 2010). The absence of large *P. australis* trees in early successional stages plots (early and late regeneration, and young forests), would imply absence or scarce canopy cover which would not only increase the solar radiation reaching the surface and involving an increase of soil and environmental heat, but also soil water loss by evaporation (Bonan 2008). It has been showed that gasteroid diversity increases at intermediate and low altitudes (Lodge et al. 1995), our gasteroid fungal diversity did not exhibit any relation with plots altitude, although all the plots were located at high altitude (1510–2000 m a.s.l.), perhaps the altitude range in the selected plots was not so wide to show any diversity changes. We can affirm that successional stages of *P. australis* woodlands from Sierras Grandes de Córdoba affected differentially its inhabiting gasteroid fungal community. Robledo and Renison (2010) observed a positive correlation between the wood-decaying fungal community richness and *P. australis* forests woody structure, with plots classified as mature forest harboring the highest diversity values. These plots presented a wide variety of woody substrates unlike the other plots (see Robledo and Renison 2010). These results may be explained not only because wood-decaying fungi depend on different types of woody substrates, but also because they depend on abiotic factors such as wood drying rate and temperature, and of course woody substrates react differently to these factors according to its nature and size: i.e. stem diameter, dead or living stem, stumps (Gange et al. 2011, Chappela and Boddy 1988, Hendry et al. 2002). Unlike these observations, we found relatively low levels of gasteroid diversity within mature forests (true diversity: 6.17), probably because most of the plots classified as mature forests belong to El Tigre basin located on a steep slope, and this topography facilitates loss of water by runoff with the consequent decrease in fertility and increase the nutrient leaching, thus it could be affecting the survival of some gasteroid species.

Fire and livestock rearing have been reported as human impacts that have greatly reduced the surface area occupied by *Polylepis* forests (Alinari et al. 2015; Cingolani et al. 2008, 2013; Giorgis et al. 2010; Renison et al. 2002b, 2006b).

Results from this study suggest that gasteroid fungal diversity could be negatively related to fire disturbance, since the plots with most fungal diversity correspond to river basins less affected by fire (Renison et al. 2006a). Successional changes among *Polylepis* forest affected not only species richness but also community composition as could be detected by the PERMANOVA analysis and the rank-abundance curves. This pattern indicates that most of the gasteroid fungal species found in early successional forests persist in late successional forests, with the addition of species and a significant community replacement between early and late regeneration forests and mixed forests; this was also observed in Robledo and Renison (2010). Early regeneration stages and mature forests did not present any particular species; all of them were shared with the other categories. Six species (*G. fimbriatum* Fr., *G. fornicatum* (Huds.) Hook., *L. lambinonii* Demoulin, *Tulostoma* sp.1 and *Tulostoma* sp.2, and *T. domingueziae* Hern. Caff. & L.S. Domínguez) were found exclusively in mixed forests. *Geastrum fornicatum* presented only one basidiome and was registered only once, nevertheless it is a common and gregarious species in the xerophytic environments from Córdoba Province (personal observation at Parque Natural y Reserva Forestal Chancaní). *Bovista pusilliformis*, on the other side, was found exclusively in less conserved plots and was the dominant species. This species has been previously registered in disturbed areas among *P. australis* community from the Sierras Grandes de Córdoba (Gallo et al. 2015); based on both results we may consider this species as a good indicator of high habitat disturbance. We encourage further studies as necessary to define if this gasteroid species, *B. pusilliformis*, is actually a global indicator of forests high disturbance. Human activity, environmental conditions, and the current degree of fragmentation of *P. australis* woodlands are negatively affecting the inhabiting gasteroid community. We observed that the epigeous gasteroid species richness and diversity reached a peak in mixed forests and there are no significant differences between the four remaining stages (early and late regeneration, young and mature forests). *Polylepis australis* management strategies to the ongoing effort of their conservation are very important for *P. australis* woodlands survival and for the gasteroid fungal community too. Several forest management strategies have been carried out since the last two decades including: 1- evaluation of the influence of livestock rearing, fire, and human pressure in *P. australis* woodlands distribution (Alinari et al. 2015; Renison et al. 2002b, 2006a, 2006b, 2010, 2015; Teich et al. 2005); 2- restoration involving seedling survival and growth (Pollice et al. 2012; Renison and Cingolani 1998, Renison et al. 2002a, 2004, 2005, 2015; Torres et al. 2008), 3- restoration and tree monitoring (Renison et al. 2011; Simoes-Macayo and Renison 2015, Suarez et al. 2008), 4- effects of elevation and fragmentation in the structure of *P. australis* individuals (Marcora et al. 2008; Peng et al. 2016), and 5- diversity of fungi, plants, and animals associated to its woodlands (mentioned above). Regarding the importance of the fungi and their role in maintaining soil stability, water flow, organic matter decomposing and cycling elements such as nitrogen and phosphorus, and releasing nutrients for plants growth (Brusaard 1997; Fitter et al. 2005; Liu 1984, Rillig and Mummey, 2006; Sato et al. 2012; Smith & Read 2008, Trappe & Luoma 1992); their presence is necessary to the ecosystem functioning. Thus, the management strategies carried out within *P. australis* forests along its distribution range in the Sierras Grandes de Córdoba also contribute with the maintenance and conservation of its gasteroid fungal community.

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