Polylepis woodland remnants as biodiversity islands in the Bolivian high Andes

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Polylepis woodland remnants as biodiversity islands in the Bolivian high Andes

Edgar E. Gareca · Martin Hermy · Jon Fjeldså · Olivier Honnay

Abstract Mountain forests deserve special attention from ecologists and conservation biologists given the ecosystem services they provide to society, and their threat under global change. In the subalpine region of the Andes, *Polylepis* woodlands occur as arboreal islands in a matrix of grassland and scrub. Due to overgrazing and burning, however, these woodland patches are believed to cover only 11% of their potential area in Bolivia, core area for *Polylepis*. We reviewed the knowledge on the species diversity for the Bolivian *Polylepis* woodland remnants, assessed the conservation status of the occurring species, determined their trophic niche, and related species richness with climatic variables and elevation. Based in 31 publications, we found 780 identified species occurring in *Polylepis* woodlands: 425 plants, 266 birds, 46 mammals, 35 butterflies and 8 reptiles. Ten of the 13 Bolivian *Polylepis* species, as well as 7 other plant species, 14 bird species and 4 mammal species were categorized as threatened or near threatened according to IUCN criteria. In general, plant species richness increased with increased precipitation and length of the growth season, while it decreased with increasing elevation. There was a positive relationship between bird species richness, precipitation and length of the growth season. The highest bird endemism in *Polylepis* woodland remnants occurred at intermediate elevations, temperatures and

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precipitation. Mammal species richness decreased with increasing maximum temperature. Finally, we discuss the most important knowledge gaps regarding biodiversity in Bolivian *Polylepis* woodland remnants.

Introduction

Mountain forests offer a variety of ecological services to humans (Douglas 1999; Sidle et al. 2006). They are key sources of wood and non-wood products for human use (Smiet 1992; Moraes et al. 1995; Molles 2002), they mitigate local climate, are an important source of water for domestic, agricultural, and industrial consumption (Beniston 2003; Buytaert et al. 2006), reduce soil erosion, improve soil nutrient status, and they are important biodiversity hotspots (Burgess et al. 2007; Menegon et al. 2008). It has been suggested that mountain ecosystems could be particularly prone to changes in species composition through global change, with consequences for the ecosystem services (Kräuchi et al. 2000; Schroter et al. 2005; Williams et al. 2007), although it has also been suggested that "hotspots of endemism" in tropical mountains may include exceptionally stable local environments (e.g., Fjeldså and Irestedt 2009). For all these reasons mountain forests deserve special attention from ecologists and conservation biologists.

The Andes in South America forms a nearly continuous high-altitude mountain chain in the western part of the continent and contains the largest extension of low-temperature areas within the tropical belt of the world (Sarmiento 1986). Because the environmental conditions change along the altitudinal gradient, several life zones may be found on a single mountain side (Molles 2002; Ghalambor et al. 2006). The ecosystems above the forest limit in the tropical Andes in South America are known by their most distinctive local plant formations, generally defined as *Páramo* in the north, and *Puna* in the central Andes (Vuilleumier and Monasterio 1986), but indeed the vegetation is *Páramo*-like along the humid eastern ridge of Peruvian and Bolivian Andes. These landscapes are patchy and consist of a mosaic of low grass and scrub with occasional oases of more dense vegetation mainly dominated by monospecific stands of one arborescent genus, *Polylepis*. However, these mosaic landscapes are present in a handful of extensive pristine timberline areas where grazing or burning are absent, while in most of the highland these practices have now lead to a monotonous bunchgrass terrain with an abrupt ecotone from closed forest to scrub or grassland (Kessler and Herzog 1998; Jácome et al. 2007). As other mountain forests, these tropical subalpine *Polylepis* woodlands provide valuable ecosystem services (Fjeldså and Kessler 1996; Fernández et al. 2001). Because *Polylepis* woodlands are such an important supply of resources (wood for fuel, tools and house construction, medicinal and nourishing plants) for local people (Kessler 2006), as well as because of the extensive grazing and burning practices, *Polylepis* woodlands have been severely diminished and they are considered as one of the most threatened ecosystems in South America (Kessler 1995; Herzog et al. 2002; Navarro et al. 2005).

Polylepis woodlands are distributed along the Andes from Venezuela (9°N) to Argentina (32°S), and reach elevations as high as 5000–5200 m (Simpson 1979; Navarro et al. 2005). Although the lower altitude *Polylepis* woodlands can be more continuous, most of them are isolated patches in landscapes dominated by grasslands, and they are often found

on rocky slopes or along streams (Fjeldså and Kessler 1996). Early explorers considered these marginal sites as their natural distribution area (e.g. Herzog 1923; Troll 1929 in Kessler 2002). More recent evidence, however, supports Ellenberg's (1958) hypothesis that the patchy distribution of *Polylepis* woodlands is mainly due to thousands of years of human influences (see also Kessler 2002), and that the climax vegetation of parts of the Andean region actually is *Polylepis* woodland (Fernández-Terrazas 1997).

Bolivia is a core area for the genus' diversity, containing 13 out of the c. 26 species of *Polylepis* (Kessler and Schmidt-Lebuhn 2006). In total, *Polylepis* could cover about 51,000 km^2 (20%) of the Bolivian highlands (Kessler 1995); however, it now only covers about 11% of this area: 100% of their potential area in the arid western Andean range, 0.02% in the central high plateau and Titicaca basin, and 1.44% in the eastern highland (Kessler 1995). A new assessment of the latter region revealed a loss between 75–97% of the area and 67–83% of all woodland remnants (Purcell and Brelsford 2004). Twenty out of the c. 26 described *Polylepis* species have been categorized as threatened (IUCN 2008). Given the economical and ecological importance of these high Andean ecosystems, their potential extended distribution, their threatened status, and their uncertain fate under climate change, conservation, monitoring and restoration of *Polylepis* woodland remnants are extremely important.

The primary aim of this study was to present a review of the knowledge regarding the species diversity of the Bolivian *Polylepis* woodland remnants, and to investigate their conservation status. We also aimed at relating species richness with climatic variables and elevation, and at identifying the most important knowledge gaps regarding the biodiversity of *Polylepis* remnants in Bolivia.

Polylepis woodlands

The genus *Polylepis*

The genus *Polylepis* consists of shrubs or trees with usually twisted trunks, which can reach a height of 1–27 m and a diameter of 2 m (Simpson 1979; Fjeldså and Kessler 1996). They are evergreen with small and sparsely to densely packed leaves and usually large amounts of small dead branches in the lower part of the canopy. The bark is thick and rough with even 150 layers which are easy to peel of (Fjeldså and Kessler 1996). The flowers of *Polylepis* are inconspicuous (about 4–10 mm in diameter), apetalous, protogynous, and arranged in racemes. Most species are probably wind pollinated, and self pollination through geitonogamy may occur (Simpson 1979, 1986). The fruits are small (about 4–10 mm in length), indehiscent, one seed achene, composed of the floral cup fused to the ovary. The surface of the fruit of different species has ridges, knobs, spines, or wings, also suggesting animal dispersal (Simpson 1986), although wind dispersal may predominate in some species (e.g. *P. australis*, Simpson 1979).

Regarding the physiognomy of the woodlands, in the arid highlands, and in areas with little regeneration and strong impact of grazing and fires, the *Polylepis* woodlands are open and bushy, and the undergrowth differs little from the surrounding bunchgrass terrain; unlike in mature forests in more humid zones, which have a rich associated flora of herbs and vines.

Phylogenetic analyses suggest that *Polylepis* evolved via polyploidy from *Acaena*, a genus of herbs and subshrubs (Fjeldså and Kessler 1996; Kessler 2006). Radiation and specialization appears to have occurred northward and southward from the vicinity of

northern Peru and to higher elevations (Simpson 1979). The tree form might have evolved since the middle of the Miocene (c. 15 mya) when the Andes first reached 1500 m (Fjeldså and Kessler 1996). As the Andes rose, species of *Polylepis* apparently spread along the eastern slopes of the Andes and across the mountain ranges where there was enough moisture for woody vegetation (Simpson 1986). The most primitive *Polylepis* species occur in the humid forest in the Yungas region (Fig. 1a). The subsequent evolution reduced the number of leaflets and flowers, increased the thickness of leaves and the presence of resins or hairs on leaves, and reduced the tree size; all of these helped surviving the dry and cold conditions of the Pleistocene (Fjeldså and Kessler 1996; Schmidt-Lebuhn et al. 2006). It is very likely that the evolution of the genus was mainly governed by climate fluctuations during this epoch, forcing the migration of the species to places with favorable ecological conditions, and therefore fragmenting the species distribution (Kessler 2006).

Given the potential distribution proposed for *Polylepis* in Bolivia (Kessler 1995), the fact that trees are functional throughout the year, and that most *Polylepis* species are exposed to night frost (frequent in the Andes) and diurnal temperature variations that by far exceed seasonal ones (Goldstein et al. 1994), one of the most important attributes for the survival of most species of the genus is frost tolerance. There might be considerable variation in this
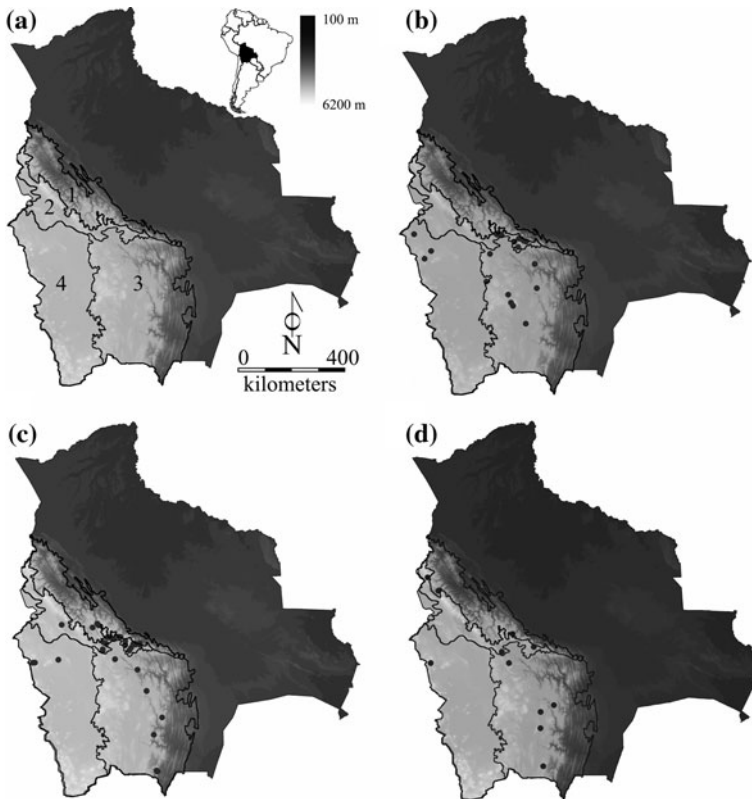
Fig. 1 a Location of the four Andean Biogeographic Provinces of Bolivia. *1* Peruvian-Bolivian Yungas, *2* Peruvian Puna, *3* Tucuman-Bolivian and *4* Altiplanic Biogeographic Province (After Navarro and Maldonado 2002). Distribution of the locations with adequate data for the comparison with climatic variables concerning plant biodiversity (**b**), bird biodiversity (**c**) and mammal biodiversity (**d**)

trait, since species which are basal in the phylogeny generally grow in frost-free cloud-forest habitats. Aditionally, even on high elevations, the interior of dense *Polylepis* forests are generally frost-free (even if areas right outside the forest are covered by snow). Although the species need to cope with frost at night in order to colonize new environments, likely it concerns only few species representing terminal branches in the phylogeny that are adapted to endure strong frost. Comparing this trait between a primitive species (*P. sericea*) and more recent ones (*P. australis* and *P. tarapacana*), Azócar et al. (2007) showed that *P. sericea* presented frost avoidance through supercooling capacity (i.e. injury and freezing temperatures between −8 and −9°C). Whereas *P. australis* and *P. tarapacana* presented frost tolerance (i.e. injury temperatures, −18 to −24°C, and freezing temperature, −3.5 to −9.2°C). Thus, this trait may have evolved from frost avoidance to frost resistance. These results coincide with the proposed evolutionary history of the genus indicating an adaptation to cold conditions (Simpson 1986; Fjeldså and Kessler 1996).

At the species level, the circumscription of taxa in the genus is difficult due to extensive morphological variability within populations, limited variability between many of the recognized species, and apparently extensive hybridization (Kessler and Schmidt-Lebuhn 2006). Therefore, the number of species described within the genus ranges from 15 to 33 (Simpson 1979). A recent study recognizing morphologically, biogeographically and ecologically distinct populations at species rank, suggested a total of c. 26 *Polylepis* species (Kessler and Schmidt-Lebuhn 2006). The number of *Polylepis* species recorded per country is 1 in Venezuela, 3 in Colombia (1 endemic), 7 in Ecuador (2 endemics), 14 in Peru (3 endemics), 13 in Bolivia (4 endemics), 2 in Chile, and 4 in Argentina (1 endemic).

Polylepis species in Bolivia

Thirteen *Polylepis* species are found in Bolivia (Table 1), all of them in the Andean region (Kessler and Schmidt-Lebuhn 2006). This region can be subdivided into four biogeographic provinces (Navarro and Maldonado 2002): the Peruvian Puna province and the Andean Altiplanic province in the inner parts of the highlands, and the Peru-Bolivian Yungas and the Bolivian-Tucuman provinces in the transition to the Bolivian lowlands (Fig. 1a).

The Andean Altiplanic province has a xeric and pluviseasonal bioclimate and an altitude ranging between 3100 m and more than 5200 m. *Polylepis tarapacana* forms dispersed bushy woodlands with associated vegetation of *Mutisia lanigera* at altitudes between 3900 and 4800 m, and some *P. tarapacana* individuals occur above 5000 m (Navarro et al. 2005). The Peruvian Puna has mainly a pluviseasonal climate, it includes altitudes between 2000 m and above 5200 m (Navarro and Maldonado 2002), and seven species of *Polylepis* are found in this province (Table 1). The characteristic communities and distribution of *Polylepis subtusalbida* (with *Berberis commutata*), *P. lanata* (with *B. paucidentata*), *P. tomentella* subsp. *nana* and *P. tomentella* subsp. *incanoides* (both with *B. rariflora*), and *P. besseri* are described in Navarro et al. (2005). *Polylepis incarum* is potentially distributed between 3400 and 4000 m in the Cordillera Real and Titicaca zone, although it is now represented by very dispersed and small groups of trees (Navarro and Maldonado 2002). *P. pacensis* (3250–4130 m) and *P. pauta* (3500–3550 m) are found on the most humid grassland on the transition between the Peruvian-Bolivian Puna and the Yungas slopes (Kessler and Schmidt-Lebuhn 2006).

The Peru-Bolivian Yungas province (500–4200 m) presents xeric to pluvial bioclimates (Navarro and Maldonado 2002). Four *Polylepis* species occur (Table 1), and the characteristic communities of *Polylepis pepei* (with *Gynoxis asteroricha*), *P. lanata* (with *Ilex mandonii*, *Styloceras columnare* and *Berberis edentata*), and *P. triacontandra* (with

Table 1 *Polylepis* species found in Bolivia, endemism, and IUCN category

Polylepis species	Biogeographic Province[a]	Endemism[b]	Conservation status[c]
P. tarapacana	Altiplanic	Bol, P, Ch	NT
P. besseri	Puna	Bol, P[d]	V
P. incarum	Puna	Bol, P	V
P. pacensis	Puna	Bol	
P. pauta	Puna	Bol, P, E	
P. subtusalbida	Puna	Bol	V
P. lanata	Puna, Yungas	Bol	V
P. pepei	Yungas	Bol, P	V
P. sericea	Yungas	Bol, P, V, E, C	
P. triacontandra	Yungas	Bol, P	V
P. crista-galli	Tucuman	Bol, A	V
P. hieronymi	Tucuman	Bol, A	V
P. neglecta	Tucuman	Bol	V
P. tomentella subsp. *incanoides*	Tucuman, Puna	Bol	V
P. tomentella subsp. *nana*	Tucuman, Puna	Bol	CE
P. tomentella subsp. *tomentella*	Tucuman, Puna	Bol, A	NT

[a] *Puna* Peruvian Puna, *Yungas* Peru-Bolivian Yungas, *Altiplanic* Andean Altiplanic, *Tucuman* Bolivian-Tucuman. Following Navarro and Maldonado (2002) and Navarro et al. (2005) and estimated based on the coordinates given by Fjeldså and Kessler (1996) and Kessler and Schmidt-Lebuhn (2006)

[b] *Bol* Bolivia, *P* Peru, *Ch* Chile, *E* Ecuador, *V* Venezuela, *C* Colombia, *A* Argentina

[c] *NT* Near threatened, *V* Vulnerable, *CE* Critically endangered, based on the IUCN Red List (www. iucnredlist.org, March 2009)

[d] A population in the Urubamba Valley of Cuzco, Peru was placed in *P. besseri* by Simpson (1979, cited in Kessler and Schmidt-Lebuhn 2006)

Styloceras columnare) are described in Navarro and Maldonado (2002). *P. sericea* is found sometimes as tall forests in the Yungas at 2950–3700 m. Finally, the characteristic communities of the *Polylepis* species found in the Bolivian-Tucuman region (500-above 5200 m) are described for *P. tomentella* subsp. *tomentella* (with *Azorella compacta* and *Dasyphyllum hystrix*) and *P. neglecta* (with *Schinus microphyllus*) in Navarro et al. (2005), and for *P. hieronymi* (with *Alnus acuminata*) and *P. crista-galli* (with *Escallonia hypoglauca*) in Navarro and Maldonado (2002).

In summary, the high Andes of Bolivia holds species belonging to the most primitive, as well as the most evolved groups of *Polylepis*. The basal group is represented by *P. sericea* and *P. pepei*, which occur in the pluvial bioclimate (Peru-Bolivian Yungas). The phylogenetically terminal species occur in the Peruvian Puna (pluvi-seasonal bioclimate), Bolivian-Tucuman (pluvi-seasonal and xeric bioclimates), and Altiplanic provinces (xeric bioclimate). Thus, Bolivia is a key area to the genus and offers the different adaptations that occurred during the evolution of these high mountain trees.

Endemism and conservation status of *Polylepis* species in Bolivia

Four species and two subspecies of the genus *Polylepis* are endemic to Bolivia (Table 1); they are located in all the Andean biogeographic provinces, suggesting that new

adaptations occurred for all these environments. Four of these endemic species are considered vulnerable (Table 1), denoting the need for research, conservation and restoration to be taken in Bolivia. The other 9 non-endemic species of the genus in Bolivia are shared mainly with Peru or Argentina (Table 1). Concerning the conservation status of the Bolivian *Polylepis* species, nine of the 14 species are considered vulnerable, and one is near threatened (Table 1). Bolivia has one *Polylepis* subspecies near threatened, another vulnerable and one is considered critically endangered by the IUCN red list of threatened species (Table 1).

Methods

In January 2009 we first performed a search in the ISI web of Knowledge with the search terms: "*Polylepis*", "*Polylepis*" AND "Andes", and "*Polylepis*" AND "tree". A second search was made in the Net of Latin-American, Caribbean, Spanish and Portuguese journals, using only the search term "*Polylepis*". Finally, specific searches were made in the journal Ecotropica (holder of the papers of the 1st International Congress on *Polylepis*, 1995–2008), Ecología en Bolivia (August 2001–2008) and the Revista Boliviana de Ecología y Conservación Ambiental (1997–2008) using "*Polylepis*" as the only search term. Admittedly, this kind of search is far from complete, as it overlooks the wealth of information that is scattered in older literature describing Andean habitats (e.g., Troll 1929 and his many other papers on timberline habitats), or which is "buried" in numerous survey reports ("grey literature"), faunistic papers and taxonomic revisions, where habitats were not specified in the list of keywords.

Because of the very large data set we collected from literature, systematic ground truthing was not feasible. We looked for publications with species lists of *Polylepis* woodland remnants in Bolivia or with *Polylepis* species in their list. Then, we compiled species lists of bryophytes and vascular plants that occur in woodland remnants where *Polylepis* is the dominant tree species. Plants were classified by growth form. Birds, mammals, reptiles and Lepidoptera were classified by their trophic niche. The species lists with the names presented by the authors, their guild or growth form and their conservation status (see below) are in Appendices 1 and 2 in Supplementary material. Next, in order to explore the development in knowledge about *Polylepis* woodland remnants in Bolivia, we created species accumulation curves through time using the time of the survey in the *x* axis, starting with the oldest published field work, and ending with the most recent.

Based on the published or derived coordinates of each study location (Appendix 3 in Supplementary Material), local climate variables were retrieved from the Local Climate Estimator New Loc Clim v. 1.10 (Grieser et al. 2006). These included maximum, mean and minimum temperature (°C), annual precipitation (mm), evapotranspiration (mm) and length of the growth season (days). These variables were estimated using Sheppards method and gradient correction (vertical and horizontal, Grieser et al. 2006). Elevation of the study sites was added to the dataset if reported; otherwise it was obtained from Google Earth. For the birds, new survey data was added based in data gathered during earlier expeditions by JF and his field teams. This new data and nine other studies from which it was possible to retrieve the coordinates and the elevation, and that assigned species to a specific locality, were used for studying the relationship between climate and species richness (Appendix 3 in Supplementary Material). Additionally and only for the birds, the habitat quality, defined as good or poor, was added based on the descriptions made by the authors and JF's personal observations (descriptions for poor quality sites: degraded

woodland, relict, scrub, mixed woodland, exotic tree plantations, high human impact; descriptions for good quality sites: substantial woodlands, distinguishable patches, dense vegetation, large areas, low or moderate human impact), and endemism, measured as the inverse of the range-size for each species, was averaged per location for all the species and for the 25% of the species with smallest ranges. Both, mean endemism and species richness per location were related to the local climate variables using Spearman rank correlations in STATISTICA 6.0 (StatSoft 2001). Finally, for the animals, the conservation status of the occurring species in the woodlands was obtained from the IUCN Red List (IUCN 2008), and for the plants, from the latter as well as from Meneses and Beck (2005).

Results

Our search yielded 140 papers mentioning the Andean tree *Polylepis*. The first paper found in the ISI web of knowledge was a review about the pollen morphology of *Polylepis* (Smit 1978). Since then, the number of publications increased with time, and 52 papers were found in our search in the period 2006–2008. During the whole period (Fig. 2a), most of the publications were in the ISI web of Knowledge database (63%), followed by publications in Bolivian journals (20%) and Latin American journals plus Ecotropica (17%). The most important input in the latter category took place the year 2002 with the papers of the 1st International Congress on *Polylepis* held in Bolivia in 2000 (Fig. 2a; Herzog et al. 2002). Twenty four of the retrieved studies dealt with plant and animal species diversity of Bolivian *Polylepis* woodland remnants (Fig. 2b), and next to seven additional documents were used for subsequent analyses.

Cumulative species richness

Data on associated plant species richness were found for six out of the 14 species of *Polylepis* species occurring in Bolivia (*P. lanata*, *P. subtusalbida*, *P. tomentella* subsp. *incanoides*, *P. tomentella* subsp. *nana*, *P. besseri*, *P. tarapacana* and *P. neglecta*). Three of these species include data for the bryophyte species richness (*P. lanata*, *P. subtusalbida* and *P. tomentella* subsp. *nana*).

The six *Polylepis* species with data of associated plant species richness occur in the four biogeographical provinces of the Bolivian Andes (Fig. 1b). Most of the lists were from the
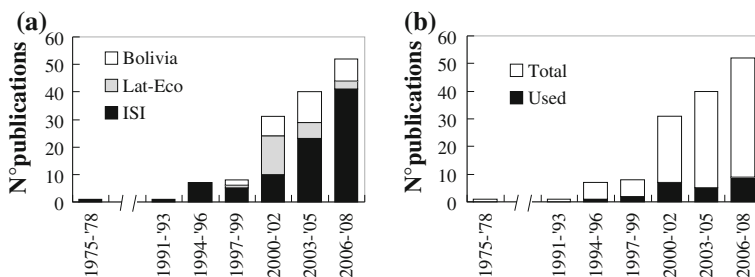
Fig. 2 a Number of publications found in a literature survey in January 2009 with the search terms "*Polylepis*" in the ISI web of knowledge (*black area*), in Latin American journals and Ecotropica (*gray area*) and in Bolivian journals (*white area*). **b** Number of publications used for the analyses presented in this review. For details see text

Fig. 3 Cumulative species richness of the organisms reported for the *Polylepis* woodland remnants. The numbers of publications with suitable data are in *parenthesis*
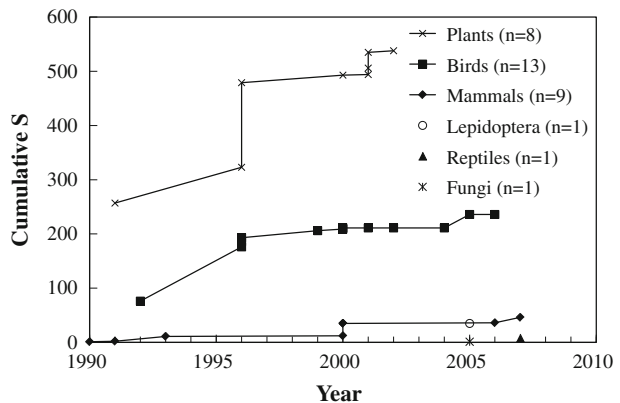

Cochabamba region (Fernández-Terrazas 1997; Mercado-Ustariz 1998; Balderrama and Ramirez 2001; Fernández et al. 2001; Navarro 2001; Hensen 2002). Two studies list plants from other departments (Mueller et al. 2002; Navarro et al. 2005), increasing the cumulative species richness found in the *Polylepis* woodland remnants with 6%. The species accumulation curve for plants (Fig. 3) did not level off. The first study (1990–1991) reports 257 species of plants from *Polylepis* woodland remnants in the Cochabamba region (Hensen 2002). The second major input to the cumulative plant species richness, also performed in the Cochabamba region, described 254 species (Fernández-Terrazas 1997), of which 155 were not described in previous work. The most species rich families were the Asteraceae (101 spp.), followed by the Poaceae (50 spp.) and Scrophulariaceae (17 spp.); ferns were also abundant (57 spp.).

The cumulative bird species richness was almost half of that of the plants (266 species, Fig. 3). The shape of the species accumulation curve is more flattened than for the plants (Fig. 3) and Fjeldså and Kessler (1996, presenting mainly data from the 1980s) includes most of the birds now known for this habitat (169 species). Another major input comes from the Parque Nacional Tunari in Cochabamba (Balderrama 2006) containing 150 species and adding 11% to the cumulative species richness for the *Polylepis* woodland remnants. Most of the additional species are best regarded as rare visitors from forests at lower elevations.

Tarifa and Yensen (2001) performed the major contribution to the mammal species list (Fig. 3); they reported 30 species of which 23 were new for the *Polylepis* woodland remnants. Their collection was made all over the country (Fig. 1d). The second major input was collected for Parque Nacional Tunari in Cochabamba (Aguirre et al. 2007), containing 17 species, and adding 22% to the cumulated mammal species richness for the *Polylepis* woodland remnants.

Finally, there is only one study on Fungi (Macía et al. 2005), one on butterflies (Lepidoptera, section Rhopalocera) (Quinteros et al. 2006) and one on Reptiles (Aguayo et al. 2007). These three studies are quite recent and less than 40 species were recorded per group (Fig. 3). However, several recent taxonomic revisions of other Lepidoptera groups ("microlepidoptera" and moths, see Fjeldså and Kessler 1996) described numerous species which are narrowly associated with *Polylepis* habitats, as indicated by their striking adaptations for crypsis when they rest on the reddish *Polylepis* bark. In total, we built a list of 537 plants (425 identified to the species level), 266 birds, 46 mammals, 35 butterflies and 8 reptiles (Appendix 1 and 2 in Supplementary Material).
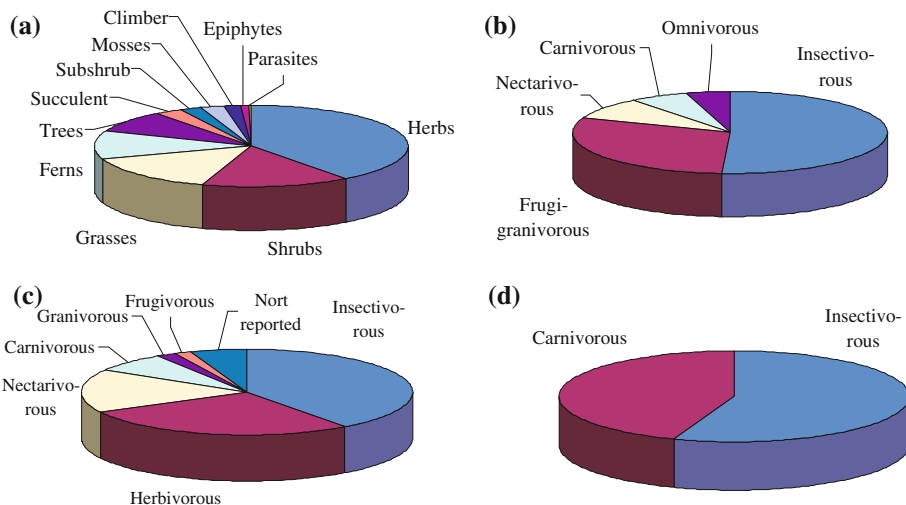
Fig. 4 Percentages of guilds for the **a** plants ($n = 537$, growth form), **b** birds ($n = 266$), **c** mammals ($n = 46$), and **d** reptiles ($n = 8$)

Growth form and trophic niche

The growth form was assigned to 502 plants (93%). Most of the plants found in the *Polylepis* woodland remnants were herbs (40%), followed by shrubs, grasses, ferns, trees, succulents, and others (Fig. 4a, Appendix 1 in Supplementary Material). Fifty one % of the birds were insectivores, followed by the frugi-granivorous, nectarivorous, carnivorous and omnivorous species (Fig. 4b, Appendix 2 in Supplementary Material). Also insectivorous mammals were the most abundant (47%); followed by herbivorous, nectarivorous, carnivorous and frugi-granivores (Fig. 4c, Appendix 2 in Supplementary Material). The reptiles were insectivorous and carnivorous (Fig. 4d, Appendix 2 in Supplementary Material). The adult butterflies are nectarivorous (18 out of 35 species reported for the *Polylepis* woodland remnants, Appendix 2 in Supplementary Material), although their larvae are herbivorous and generally associated with the rich herbaceous vegetation of these forests rather than with the *Polylepis* trees.

Conservation status of the species

Most of the birds (97%) and mammals (85%) recorded for *Polylepis* woodland remnants were considered in the IUCN red list of threatened species, whereas no reptile or butterfly species were evaluated by the IUCN (IUCN 2008). In total, 14 species have been categorized as threatened (vulnerable or endangered, Table 2): 7 plant species, 4 bird species and 3 mammal species; whereas 11 species were categorized as near threatened: 10 birds and 1 mammal (Table 2, Appendixes 1 and 2 in Supplementary Material). Additionally, Appendix 2 in Supplementary Material presents the categories based in the Red Book of wild Bolivian vertebrates which also includes reptiles (Ministerio de Medio Ambiente y Agua 2009).

Table 2 Conservation status of organisms living in the *Polylepis* woodland remnants according to IUCN (2008, birds and mammals) and Meneses and Beck (2005, for plants), and as function of growth form (plants) and trophic niche (birds and mammals)

	Near threatened	Vulnerable	Endangered & critically endangered	Total
Plants				
Herb		1		1
Shrub		1		1
Tree		3		3
Succulent		2		2
Subtotal	0	7	0	7
Birds				
Insectivores	6	1	2	9
Frugi-granivorous	2		2	4
Nectarivorous	1			1
Carnivorous	1			1
Omnivorous	2	1		3
Subtotal	10	1	3	14
Mammals				
Herbivorous		2		2
Omnivorous		1		1
Carnivorous	1			1
Subtotal	1	3	0	4
Total	11	11	3	25

Species diversity vs. climate

A summary of the localities used in our analyses is presented in Appendix 3 in Supplementary Material. Total plant species richness was significantly and positively correlated with precipitation and length of the growth season (Table 3, Fig. 5). The opposite relationship was found for elevation. The species richness of shrubs, grasses and trees decreased with elevation. The species richness of grasses was also positively correlated to precipitation and length of the growth season. Fern diversity increased as length of the growth season increased, as did the number of arboreal species. Tree diversity also increased as precipitation increased.

Regarding the birds, total species richness (245) positively correlated with total precipitation and length of the growth season (Table 3, Fig. 5). This trend was found to hold true for insectivorous, frugi-granivorous, nectarivorous as well as carnivorous birds (Table 2). The endemism (recorded as the mean inverse range-size for all the species present in a locality) was positively correlated to potential evapotranspiration ($r_s = 0.29$, $P = 0.04$, Fig. 6). When the endemism was calculated only for the 25% most range-restricted bird species ($n = 63$), the mean endemism score also increased significantly with precipitation ($r_s = 0.31$, $P = 0.03$). When introducing habitat quality in the graphs, good and poor quality sites were randomly dispersed in the species richness plots (Fig. 5), whereas the endemism plots mostly showed hump-shaped patterns for sites with well matured forest, thus with peak values at intermediate elevations and climates (Fig. 6). Concerning the mammals, a negative relationship was found with the maximum

Table 3 Relationships between the number of species of plants, birds and mammals in relation to elevation and climatic variables (Spearmann rank correlation values)

	Elevation	Tmax	Tmean	Tmin	Precip.	PET[a]	LGS[b]
Species richness							
Plants ($n = 31$)							
Herbs	−0.10	−0.05	0.02	−0.09	0.31	0.08	0.29
Shrubs	−0.57*	−0.04	0.34	0.35	0.22	0.38*	0.33
Grasses	−0.39*	0.06	0.29	0.21	0.40*	0.30	0.40*
Ferns	−0.25	−0.05	0.03	0.04	0.33	0.09	0.37*
Trees	−0.41*	0.20	0.11	0.20	0.53*	0.17	0.67*
Total	−0.47*	0.15	0.29	0.24	0.51*	0.32	0.54*
Birds ($n = 51$)							
Insectivorous	−0.12	0.27	0.09	0.15	0.56*	0.11	0.53*
FG[c]	0.05	0.18	0.07	0.06	0.41*	−0.05	0.33*
Nectarivorous	0.09	−0.02	−0.15	−0.01	0.55*	−0.15	0.56*
Carnivorous	−0.02	0.22	0.04	0.13	0.39*	−0.09	0.41*
Total	−0.07	0.22	0.07	0.13	0.53*	0.03	0.51*
Mammals ($n = 11$)	0.07	−0.65*	−0.34	−0.24	0.47	−0.23	0.51

Number of localities in parenthesis, and * refers to statistically significant values ($P < 0.05$)

[a] Potential evapotranspiration

[b] Length of the growth season

[c] Frugi-granivorous

temperature, but high (although non significant) values of positive correlation were obtained with precipitation and length of the growth season (Table 2). For the other groups, reptiles and butterflies, no test was possible due to the few studies on these organisms.

Discussion

Although it is possible to find structurally similar habitats in mountains of the temperate areas and the tropics, diversity patterns on elevation gradients are different on high and low latitudes, first of all because the amplitude of seasonal change greatly overrides the altitudinal variation at high latitudes (Ghalambor et al. 2006). For this reason, the comparisons below are restricted to tropical mountains.

Cumulative species richness

All surveys of bryophytes were in the vicinity of Cochabamba, in the center of Bolivia, but this is certainly not representative for the diversity of bryophytes of the most humid *Polylepis* habitats of the Yungas province. Surveys of vascular plant species richness covered all the biogeographic provinces in the Bolivian Andes (Fig. 1b). However, they did not include woodland remnants of all the *Polylepis* species. This suggests that our estimates of plant species richness are still too low. This is also supported by the cumulative species richness curve, which does not level off yet, suggesting additional plant species can be found in these high mountain ecosystems.
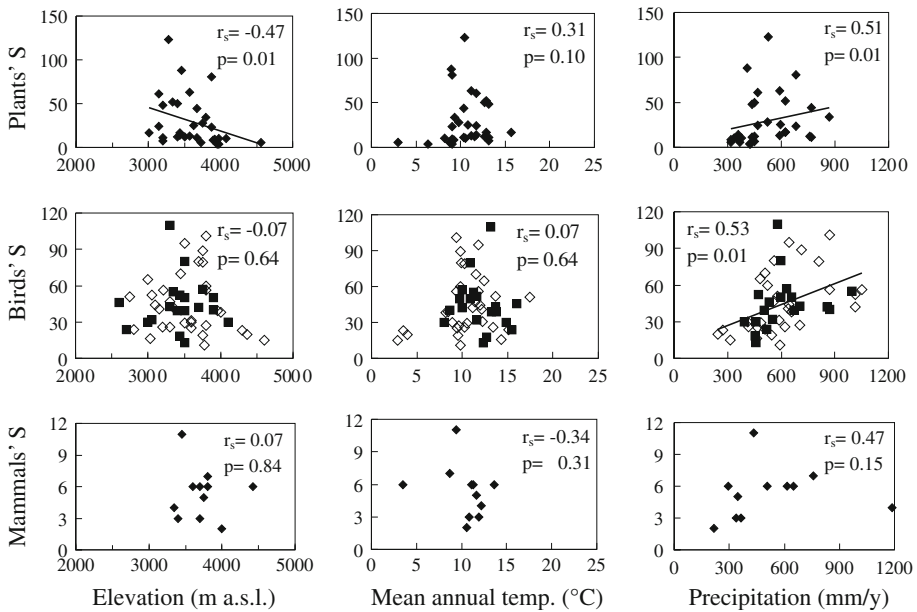
Fig. 5 Relationship between elevation, mean annual temperature and precipitation with the total species richness of plants, birds and mammals reported for the *Polylepis* woodland remnants. Spearman correlation values (r_s) and probabilities (*P*) are indicated. For the birds, *white diamonds* represent good quality sites and *black squares* poor quality sites. The *trend lines* in the significant correlations are for visual purposes only
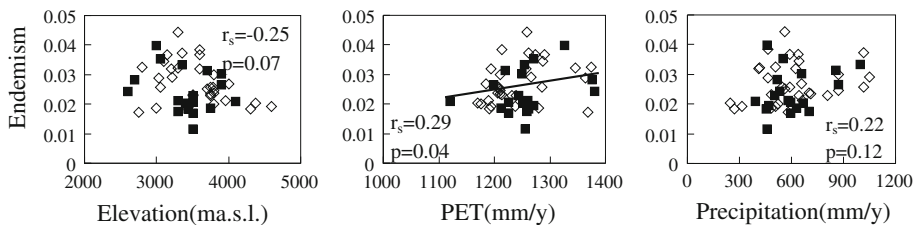
Fig. 6 Relationship between elevation, potential evapotranspiration and precipitation with the bird mean endemism reported for the *Polylepis* woodland remnants. Spearman correlation values (r_s) and probabilities (*P*) are indicated. *White diamonds* represent good quality sites and *black squares* poor quality sites. The *trend lines* in significant correlations are for visual purposes only

Despite these shortcomings, the total plant species richness (537) found in the *Polylepis* woodland remnants is 36% of the species richness estimated for the Bolivian dry Andean valleys at lower elevations than the *Polylepis* woodland remnants (Larrea-Alcázar and López 2005). The maximum species richness per woodland type was 188 vascular plant species in *Polylepis subtusalbida* woodland remnants (Hensen 2002); a value that is higher than the species richness found in the Huaquina sector in Peru (136 spp.; Arteta et al. 2006). Concerning the species richness per family, the *Polylepis* woodland remnants contain 17% of the 601 species of Asteraceae reported in Bolivia (Funk et al. 2005).

The cumulative bird species richness seems to level off during recent years, indicating that most of the bird species may have been found. Many collecting expeditions in Bolivia early in the 20th century collected birds in *Polylepis* forests, but the habitat is not specified

in the publications, so only from the 1970s are bird records for *Polylepis* habitats specifically mentioned (unlike in Peru, where there were several early accounts of the avifauna of this habitat). Most of the publications found for the Bolivian Andes included studies since the 1980s (e.g., Fjeldså 1992, 1993; Fjeldså and Kessler 1996; Fjeldså et al. 1999; Andersen et al. 1999; Herzog et al. 2003; Balderrama 2006). The altitudes included in our study (2600–4600 m, Appendix 3 in Supplementary Material) are relatively species poor compared with the lower parts of an altitudinal transect in the Bolivian Yungas (Herzog et al. 2005). On the other hand, most of the many species of the lower Yungas slope are widespread, and the avifauna of the *Polylepis* zone is outstanding in terms of the numbers of species with restricted distributions.

The cumulative species richness curve of mammals shows a similar tendency as the birds, which reflects a rather complete sampling.

Growth form of plants and trophic niche of animals

More than half of the species richness of plants in the Bolivian *Polylepis* woodland remnants consists of herbs and shrubs (40 and 15%, respectively). Some of them are considered important components of the climax community (Fernández-Terrazas 1997; Navarro et al. 2005), such as the herbs *Azorella compacta* and *Mutisia lanigera*, and the shrubs *Berberis commutata* and *Dasiphyllum hystrix*.

Most of the bird species are insectivorous and frugi-granivorous (together >75%; Fig. 4b), which shows the strong dependency of birds on vegetation and insects. It seems in general that there are few phytofagous insects that live from the *Polylepis* trees, but because of the rich associated vegetation (of well matured forest remnants) and the complex structure of *Polylepis* trees, these trees provide important refuge for insects and large numbers of arachnids (Fjeldså and Kessler 1996). However, the plant and insect species diversity still requires much more study. It is known that the insectivore guild of bird core species (those that regularly breed, winter, or migrate through a given habitat, Remsen 1994) was temporally stable across the year at Sacha Loma, a locality in the Peruvian Puna biogeographic province (Herzog et al. 2003), indicating that an adequate supply of insects may be present during the whole year in these high Andean woodland remnants. Despite this, seasonal variation at the community level reflected that of frugi-granivorous and nectarivorous species, which is lowest in June–July, and highest when food resources were available, from October until November (Herzog et al. 2003).

As in birds, insectivorous, herbivorous and nectarivorous mammals (altogether >75%), were the most abundant guilds; suggesting again the key role of insects in these patches of dense vegetation in the high Andes. Also five of the eight reptiles described for *Polylepis* woodland remnants were insectivorous. Thus, insects may be important part of the *Polylepis* woodland remnants.

Conservation status of the species inhabiting the *Polylepis* woodland remnants

It is noteworthy that most of the birds and mammals living in the *Polylepis* woodland remnants were evaluated by the IUCN as red list species (IUCN 2008), whereas other groups, such as reptiles and butterflies, have no species evaluated. It is clear that for these, additional research is needed. In total, 3% of the species diversity of the *Polylepis* woodland remnants has some degree of threat: 1.6% of the plants, 5.2% of the birds and 8.7% of the mammals. Most of the organisms have been classified as near threatened (11) and vulnerable (11), which show it is time to act in order to avoid their extinction in the

wild (Table 2). There are also three endangered species, which have a very high risk of extinction in the wild: two insectivorous birds (*Anairetes alpinus*, *Cinclodes aricomae*) and one frugi-granivorous bird (*Poospiza garleppi*).

Species diversity vs. climate

The positive correlation between plant species richness (including trees and grasses) and precipitation may represent a more general pattern for tropical forests (Clinebell et al. 1995; Hawkins et al. 2003). The negative relationship between total plant species richness (also for the number of shrubs, grasses and trees) and elevation (Table 3) was also found for trees in neotropical forests (Gentry 1995); although, plant groups which require high air humidity may show peak at mid-elevation or even higher (Kessler et al. 2001; Herzog et al. 2005). Even though the declining species richness at high elevation may be mediated by temperature, which decreases with elevation, no significant relationship was found between temperature and plant species richness. It is worth noting here that well matured *Polylepis* woodlands with a closed canopy are mostly frost-free by night even when the grassland right outside the forest edge is frostbitten (JF, personal observations); furthermore, most *Polylepis* woodlands are found on sloping terrain, in places where cold air does not accumulate by night (Fjeldså and Kessler 1996; Kessler 2002). Thus, plant species richness in the *Polylepis* woodlands may be more related to local temperatures instead of being related to the general ones. The positive correlation between length of the growth season and plant species richness (including grasses, ferns and trees) is related to the fact that a longer growth season and a higher amount of water (precipitation) are related with a higher system productivity, which might lead to increased species richness (Begon et al. 1996).

For birds, we found a positive correlation between total species richness and precipitation, as well as length of the growth season. The same relationships were also significant for all the analyzed guilds and might be linked to a higher plant species richness which is found with higher productivity conditions. The higher plant species richness may offer more resources and niches for birds, increasing the bird species richness. However, this increase is mainly due to widespread species responding mostly to water and energy, and not to the range-restricted ones, whose distributions are better explained by topography and landscape complexity (Rahbek et al. 2007), as well as historical persistence of populations in stable places (Fjeldså et al. 1999; Fjeldså and Irestedt 2009). Concerning the relationship between bird species richness and elevation, a monotonic decline in the species richness with increasing elevation was once considered a general pattern for birds and mammals (Begon et al. 1996), but it seems now that a hump-shaped pattern may indeed be more typical (Rahbek 1995; Lomolino 2001; Herzog et al. 2005). The peak diversity for Andean birds is typically at the lower slopes of the Andean mountain range (c. 500 m a.s.l., Fjeldså and Irestedt 2009), there is a decrease at intermediate elevations (1000–1750 m, Herzog et al. 2005) that may continue until 4000 m (Fjeldså and Irestedt 2009) or may have a plateau (1750–3250 m, Herzog et al. 2005). Finally, there may be local peaks in the montane basins with intermediate humidity, as indicated in Fig. 5 (3300–3800 m). A full understanding of these patterns may require more fine-grained climate data, which detects the local variation such as position of moisture-retaining mist zones and patterns of movements of cold air on the transition between the mountain basins and the high plains.

The distribution of poor quality sites in the plots of species richness (Fig. 5) may reflect the fact that site quality is not much related to species richness under an intermediate disturbance hypothesis (Connell 1978), as the spatiotemporal heterogeneity of habitats can lead to high turnover and species richness. However, the poor quality sites usually

presented lower endemism than the good quality sites (Fig. 6), as the most degraded sites generally have widespread species only. The highest endemism was observed at inter-mediate elevations, temperatures and precipitation. Thus, maximum levels for well-matured habitat patches was at 600 mm, which generally corresponds to elevations above 3000 m in the rain-shadow basins (e.g. in the endemism center of Cochabamba, see Fjeldså 2002). Figure 6 suggests high values also in some of the wettest forests, but often the specialized *Polylepis* species are displaced, may be by competition, by widespread cloud-forest birds from *Polylepis* patches in the humid zone.

Concerning the mammal species richness, we found a significant negative correlation with the maximum average monthly temperature, and high correlation values with the length of the growing season and precipitation. The negative correlation with maximum temperature may be related to an increase in water loss that may occur in small mammals under hot conditions (Cortes et al. 2000). Yensen and Tarifa (2002) found a positive relationship with the precipitation, see Fig. 5 (despite two outliers, one at high precipita-tion values and the other at high species richness values). The expected pattern of declining species richness with increasing elevation (Begon et al. 1996) was not observed in our study. This pattern may be clearer if studies from a broader elevational range were done.

Knowledge gaps and conclusions

The increasing number of publications regarding *Polylepis* in general, and published in Bolivia, in particular, is promising and shows the increasing interest for these threatened woodland remnants. However, more research is still needed. None of the studies analyzed surveyed plant species richness for the woodland remnants with *P. crista-galli*, *P. hier-onymi*, *P. incarum*, *P. pacensis*, *P. pauta*, *P. pepei*, *P. sericea*, or *P. triacontandra*.

Most of the studies for the different groups were conducted in the Cochabamba region, one of the key areas for the conservation of the *Polylepis* woodland remnant avifauna (Fjeldså 2002). Therefore, more research is needed in other regions with *Polylepis* woodland remnants. Comparing the *Polylepis* distribution described by Fjeldså and Kessler (1996) with the distribution of the study sites used in this paper, we suggest the following zones as areas for additional field surveys: (i) for plants (bryophytes and vascular plants), the centre and west of the Peruvian-Bolivian Yungas, the west and centre of the Peruvian Puna provinces, and the south of the Bolivian-Tucuman and Altiplanic provinces. Although the accumulation curves suggest that most of the bird and mammal species have been found in the sampled areas, additional efforts are required: (ii) for birds, in the west of the Peruvian-Bolivian Yungas province, in the west of the Bolivian-Tucuman province, and the south of the Altiplanic province; (iii) for mammals in the south of the Altiplanic biogeographic province, the west of the Bolivian-Tucuman, and the west and centre of the Peruvian Puna and the centre of the Yungas region (Fig. 1d). Regarding the reptiles, insects and Fungi, only one study has been found per group. Obviously more research is needed for these groups. Although clear gaps in knowledge do exist, and more species will be found in these woodland remnants, the total number of species observed in these 31 studies amounts to 780 identified species.

Clearly, *Polylepis* woodlands can be considered high altitude biodiversity islands in Bolivia. So far, most research on *Polylepis* forests in Bolivia was very descriptive, reporting occurring species. Much less research has dealt with the processes threatening the occurring species in Bolivia. Most of the *Polylepis* species themselves in Bolivia are threatened to some extent, and habitat fragmentation, burning, overgrazing, soil erosion and firewood collection have been mentioned as the main processes (IUCN 2008). Studies

regarding the effect of burning, grazing and soil erosion were mainly performed in Argentina and Ecuador (Renison et al. 2002, 2004; Teich et al. 2005; García et al. 2008; Torres et al. 2008; Cierjacks et al. 2008a; Cierjacks et al. 2008b), and only a few studies addressed these issues in Bolivia (e.g., Kessler and Herzog 1998; Hensen 2002). Also the effects of global change on *Polylepis* forest are largely understudied and we found only one study on this issue in Argentina (Marcora et al. 2008). Although field surveys remain required in order to acquire complete accounts of species diversity in *Polylepis* woodlands, much more efforts are necessary to get insight in the processes threatening their exceptional biodiversity.

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