

POLYLEPIS FORESTS – VESTIGES OF A VANISHING ECOSYSTEM IN THE ANDES

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Resumo. Los bosques de *Polylepis* fueron una vez considerados como una clase de vegetación rara y especial de las laderas de barrancos rocosos y los roquedales ("salles") en las partes altas de los Andes. Ahora existe cada vez mas evidencia de que esta ocurrencia muy localizada es causada por la actividad humana como el sobrepastoreo y el manejo de pajonales mediante quemadas, restringiendo la vegetación maderable a habitats especiales, y que estos bosques fueron alguna vez ampliamente distribuidos y contiguos con los bosques nublados a menor elevación. Los cambios vegetacionales antropogenicos fueron modestos en las partes áridas de la zona de la puna y algunos parches de *Polylepis* persisten remacadamente bien, probablemente debido a una actividad de manejo por las comunidades locales. Una comparación de la distribución actual y un modelo de distribución potencial de aves, sugieren una reducción promedio de la riqueza de especies de 26% en las partes húmedas de la zona de puna y 17% en quecas montañosas del centro del Perú. Las áreas mas biológicamente únicas se encuentran en centros culturales antiguos en los Andes, posiblemente reflejando que el clima local es favorable para la agricultura como también para especies raras de animales y plantas. Debido a este vinculo, las iniciativas para evitar la extinción global de animales y plantas deben incluir apoyo para el uso sostenible de la tierra en estos lugares, además de la conservación tradicional por las áreas protegidas sin gente. Nuevas iniciativas de manejo de tierras tienen que proveer alternativas reales para el pastoreo extensivo basado en la quema regular y deben apoyar la reforestación con especies de árboles nativos.

Abstract. *Polylepis* forests were once regarded as a rare and special kind of vegetation of ravines, rocky slopes, and block fields in the high parts of the Andes. There is now increasing evidence that this very localized occurrence is caused by human activity, that chronic overgrazing and pasture management by burning has restricted the woody vegetation to particular habitats, and that these forests were once widespread and contiguous with lower-elevation cloudforests. The human-induced vegetation changes were modest in the arid parts of the puna zone, and some *Polylepis* patches persist remarkably well, probably because of active management by local communities. Comparison of current and modeled potential distribution of birds suggest an average reduction in species richness of 26% in the humid parts of the puna zone and 17% in montane basins of central Peru. The biologically most valuable areas are found close to ancient cultural centers in the Andes, possibly reflecting the fact that the local climate is favorable for agriculture as well as for rare (relict) species of animals and plants. Because of this link, initiatives to minimize global extinction of animals and plants must include support for sustainable land use in these places, in addition to traditional conservation by formal reserving of wilderness areas with few people. New land management initiatives must provide realistic alternatives to extensive pastoralism based on regular burning, and must support reforestation by native trees. Accepted 29 May 2002.

Key words: *Polylepis* forest, South America, threats, birds, species richness, land management.

INTRODUCTION

In most parts of the tropical Andes region the cloud-forest is abruptly replaced, slightly above 3000 m a.s.l., by monotonous shrub- and grasslands, referred to as *páramo* in humid zones, or *puna* in regions with a distinct dry season. Many *páramo* and *puna* plants show striking adaptations to withstand intense radiation, seasonal drought, nightly frost, or periods with snow, and it is therefore surprising to find isolated patches of evergreen woodlands 500–1000 m above the tree-line, often "hidden" in stream ravines, boulder fields,

or steep, rocky terrain. These so-called *Polylepis* woodlands, named after the dominant tree, have long been considered a distinctive vegetation type (Troll 1959, Koepcke 1961).

Hans Ellenberg (1958) was the first to postulate that these woodlands were remnants of a once widespread habitat. Several botanists were skeptical, until in the early 1990s, when various pieces of evidence were put together to form a more complete picture of how the *páramo* and *puna* habitats had been moulded by human activity (Balslev & Luteyn 1992, and papers herein; Fjeldså 1992, 1993; Kessler 1995a). According to this view, the pristine high-Andean vege-

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tation comprised a continuum where cloudforest grades into a patchwork of woodlands, mainly of *Polylepis*, and bushy and grassy páramo vegetation, all the way up to the level of alpine (super-páramo) habitats above 4500 m. The sharp treelines that are seen today are the results of thousands of years of incessant burning, and of extensive grazing by cattle and sheep during the last few centuries (Læggaard 1992, Kessler 1995a, b; Kessler & Herzog 1998).

It is the purpose of this paper to review the current knowledge of the status of *Polylepis* woodlands and, using the example of bird data, to assess the biodiversity loss caused by past habitat fragmentation. Finally I will discuss ways towards better land management in the Andean highlands. Key areas for conservation actions will be identified elsewhere in this volume (Fjeldså 2002a).

POLYLEPIS FORESTS – PAST AND PRESENT

Based on the ecological limits for all *Polylepis* species, Fjeldså & Kessler (1996) estimated the potential total distribution of *Polylepis* forests and woodlands, and suggested that they covered enormous areas in northern and central Peru, on the hills surrounding the northern Titicaca Basin, and in the transition between the dry montane basins ("Valles") and highlands in Bolivia (Fig. 1). The phylogenetically most advanced species of *Polylepis* form open, bushy vegetation on the slopes of the volcanoes of the arid puna of southern Peru and western Bolivia and adjacent Chilean territories. However, most species inhabit distinctive areas in the transition towards warmer or more humid climates, so *Polylepis* forests may have been most developed in zones of frequent mist formation in the upper valleys and in the transition between dry montane basins and the high plateaus, and in high and deeply dissected cordilleras. *Polylepis* may never have been an important element on the level plains, or on the enormous moraine slopes west of Cordillera Oriental (in Puno and La Paz) and in the mountain transitions between Puno and Apurímac/Cuzco.

There are mainly two pieces of evidence linking the present distribution of *Polylepis* to human activity (Kessler 1995a, b, c; Fjeldså & Kessler 1996): (1) The local variation in regeneration patterns correlates very well with present land use, as *Polylepis* zones which are subject to grazing and burning show little evidence of re-growth and therefore gradually vanish. (2) Many

Polylepis patches are found "at random" on puna slopes with ordinary compact soils, indicating that the frequent occurrence in ravines and on rockledges is not due to specific microclimatic requirements. The principal factor affecting the distribution of *Polylepis* forests is therefore the intensity of burning and grazing, which in the end restricts this vegetation to places where fires cannot spread, and where cattle and sheep do not normally roam: in stream ravines and on boulderscree, rock ledges and sandy top ridges. While cutting of firewood represents the most immediately observable threat, there can be little doubt that the use of fire to stimulate regrowth of grasses (*chaqueo*) is more crucial in a long-term perspective. Unfortunately, the long-term decline in productivity and resilience of the ecosystem is not immediately observable, and habitat destruction is therefore allowed to proceed until an unproductive semi-desert is formed.

Unfortunately, the palynological documentation of the past distribution of *Polylepis* is poor and inconclusive, although it seems initially to indicate that *Polylepis* was important only during the Pleistocene glacial periods (Baied 1999a, b). *Polylepis* does not (judging from surface samples taken in contemporary *Polylepis* habitats) produce much pollen, and a predominance of *Polylepis* pollen in glacial periods may simply reflect the paucity of other pollen (A. Chepstow-Lusty in litt.). Furthermore, most drill-cores were taken outside the postulated core areas for *Polylepis*, or in areas, which are suited only for the most specialized, cold- and drought-resistant *Polylepis* species. In these zones the habitats are still fairly pristine, with extensive but very dispersed and bushy *Polylepis*.

Polylepis pollen was important in Lake Junín (a semi-closed glacial refuge in central Peru) throughout the last glacial period but disappeared abruptly 11–12000 years ago (Hansen *et al.* 1984). However, *Polylepis* charcoal is recorded here since the earliest human occupation (10–12000 years ago), although it becomes rare, compared with remains of camelid dung fuel, towards the end of the preceramic periods (3800 years ago) (John Rick, in litt.). *Polylepis racemosa* thrives well today in the area, where planted near houses and on limestone slopes near Lake Junín, and the tree covered extensive zones in the adjacent upper Mantaro valley in historical times (Ansión 1986). In this case, then, the palynological record does not correctly describe the past history of *Polylepis* woodlands.

We cannot exclude that early hunter cultures had a considerable impact on the vegetation (and on the

rapid disappearance of the Andean megafauna, see Wheeler 1984) by using fire to drive animals to places where they could easily be killed or captured. However, the main forest loss probably occurred in the period of agricultural development in the Andes, 3000–5000 years ago. Large parts of the highlands appear to have been treeless since then, with severe signs of soil erosion (see, e.g., Chepstow-Lusty *et al.* 1997). Earls (1991) postulated that the success of the Andean high cultures was based on their ability to enforce environmental policies and to provide food security. Forests were strictly protected during the Inca era. *Polylepis* was important in the Carancas culture, in a currently treeless part of the Altiplano (Capriles & Flores 2002). Chepstow-Lusty *et al.* (1997) documented, for the valley above Ollantaitambo in Cuzco, an abrupt change 1000 years ago from a barren and eroded landscape to one which can best be interpreted as an agroforestry system with *Alnus* trees. Unfortunately, this ecological recovery was only temporary as it was stopped by the Conquista, when earlier regulations and production systems broke down, and when, ecologically very unsound land-use methods were introduced.

Based on comprehensive surveys and analyses of maps and satellite images, Fjeldså & Kessler (1996) estimated that *Polylepis* forests or bushlands now cover little more than 1000 km² in Peru and 5000 km² in Bolivia, the majority of this being very dispersed and bushy growth in the dry southwestern part of the *puna*. This corresponds to 10% of the potential cover in Bolivia and no more than 2–3% in Peru. However, less than 1% is left in the humid parts of the highlands, where *Polylepis* forests can be dense, with 20-m-tall trees. The latter closed and lush *Polylepis* forest is therefore virtually non-existent today, and in many parts of the Andes local people simply do not know that their territories could be forest covered and lush.

Although there can be little doubt about the negative historical impact of humans on Andean ecosystems, it needs to be said that the persistence of *Polylepis* patches today is often a result of active management of firewood resources. In a few places the forests are even used in agroforestry systems, which represent an example of fairly sustainable use (Hjarsen 1999, Mariscal & Rist 1999, Hensen, 2002). In addition to that, many *Polylepis* patches persist because they are already restricted to places that are quite secure. Byers (2000) compared photos taken in the 1930s with ones taken >60 years later, in 1997 and

1998, in P.N. Huascarán (Cordillera Blanca, Peru). Some *Polylepis/Gynoxis* had disappeared in the Honda Valley, but most other valleys exhibited no change or an increase in cover. Improved pasture conditions were documented in some places. Photos of Mt Yanapaccha (5460 m) showed almost exactly identical *Polylepis* patches, which probably have been maintained because the areas are blockfields that are inaccessible to cattle. Active management by national park authorities (since 1975) may also play a role here.

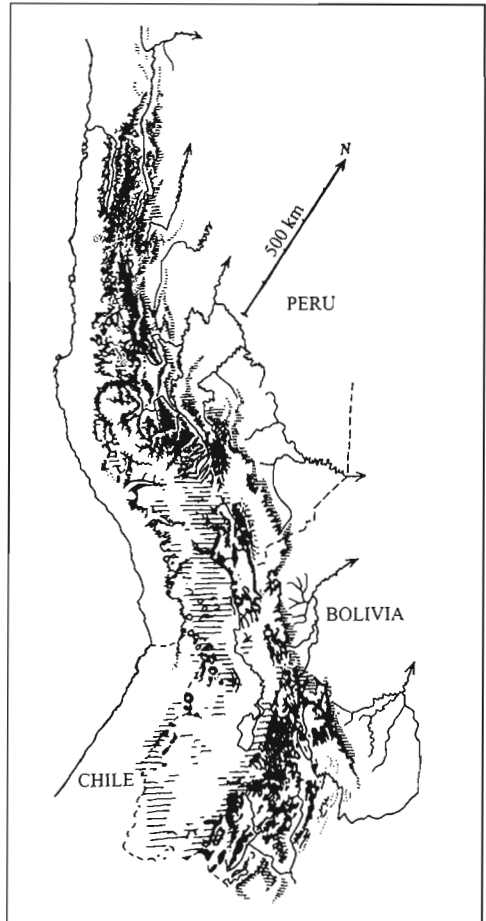


FIG. 1. The potential distribution of *Polylepis* (modified from Fjeldså & Kessler 1996). The horizontal shading marks areas where *Polylepis* can grow (judging from its very scattered occurrence today) but might never have been a significant element.

AN ASSESSMENT OF BIODIVERSITY LOSS IN THE ANDEAN HIGHLANDS

The most open kinds of *Polylepis* woodland are invaded by *puna* plants which, by their adaptations to withstand desiccation and intense radiation, are also well preadapted to resist burning; see Læggaard (1992). Such habitats are biologically rather poor, but patches of denser and undisturbed *Polylepis* represent oases of life in the barren Andean steppe. Places with semi-closed canopies of mature trees have rich soils, an exuberant undergrowth of forbs and herbs (including wild relatives of the Andean tuber crops growing among the rocks) and large amounts of flowering vines.

No comprehensive biodiversity assessment exists for this environment, but Fjeldså & Kessler (1996) provided a general overview, using mainly bird data to describe large-scale patterns of species richness and endemism. Unfortunately the evidence for other groups is still very fragmentary and collection-biased. Mammals may show a similar large-scale variation in species richness to birds, but with fewer specialists and more single-site endemics, according to the available data for Bolivia (Yensen & Tarifa 2002). Plants certainly show more complex and localized patterns since they may depend on special soils, local azonal habitats, and sites with early stages of vegetational succession (e.g., Kessler 1999b).

Since the review by Fjeldså & Kessler (1996) was published, the data available for Andean birds have been improved, and the distributional data computerized for more rigorous analysis. I will present here updated maps of actual and potential avian diversity in the Andean highlands.

Databases. Data compilation and analysis was done using the WORLDMAP software (Williams 1992, 1998), a PC-based graphics tool designed for fast, interactive handling of distributional data for large numbers of taxa. The database, described by Fjeldså *et al.* (1999), Fjeldså (2000), and Fjeldså (2002b), is based on specimens in collections and published records (see Fjeldså & Krabbe 1990 for comprehensive review) and more recent information (especially trip reports) from a large number of people. The primary database was trimmed to include maps for only 670 bird species that are recorded at altitudes where *Polylepis* may grow. This is approximately 2500 m a.s.l. in most parts of the tropical Andes region, lower in the south, and considerably higher in the northern

Andes, where some mountain ranges are too low for *Polylepis*. In this database I tagged, for separate analysis, (1) all 214 species that have been recorded (at least sporadically) in *Polylepis* woodlands or mixed *Polylepis* cloudforest, (2) 51 species which I considered typical of *Polylepis* woodlands, and (3) 14 genuine specialists, which are only very rarely seen away from *Polylepis* (see Fjeldså & Kessler 1996 for species lists).

The records are entered in a geographical projection grid of one-quarter degree (15'x15', or 729 km² at the equator), a compromise between sampling unevenness and the need for a resolution that is fine enough for conservation planning. Reasons for using a grid defined by latitude and longitude, rather than equal-area cells, are given by Rahbek & Graves (2000). Interpolation between the 80000 confirmed records is done to reduce sampling bias (Fjeldså 2002a). The interpolation is based on detailed habitat information but is conservative, since distribution gaps are included where a species is unrecorded in well-researched sites with appropriate habitats.

Estimating potential species richness. In order to assess the degree of biodiversity loss – and the potential for recovery – I also modeled potential species distributions. For this I revised all species distribution maps in accordance with the ecological limits of *Polylepis* (Fjeldså & Kessler 1996). I assumed that *Polylepis* grew back to the limits indicated in Fig. 1, and I also assumed a gradual transition from cloudforest to super-*páramo* vegetation (Kessler & Herzog 1998). Some other positive and negative vegetational changes related to current land use were also taken into account.

When creating new maps, I took into account the specific habitat requirements of different species. Extensive traveling in the Andes (since 1977) provided a good basis for judging the potential distribution of each species. Thus, *Oreomanes fraseri*, which can be found in any kind of *Polylepis* woodland, except the most arid and dispersed types, and *Polylepis* zones that intergrade with humid cloudforest, is modeled to be almost continuously present from 7 to 22°S (Fig. 2b). *Anairetes alpinus*, which is found only in dense *Polylepis* bushes at very high elevations, and in rather humid cordilleras, is modeled to be absent from the high plains and regions with drier conditions (Fig. 2d). I also take biogeographic considerations into account, so in species groups with allo- or parapatric replacements I assume that species distributions were also mutually exclusive in the past. For documentation,

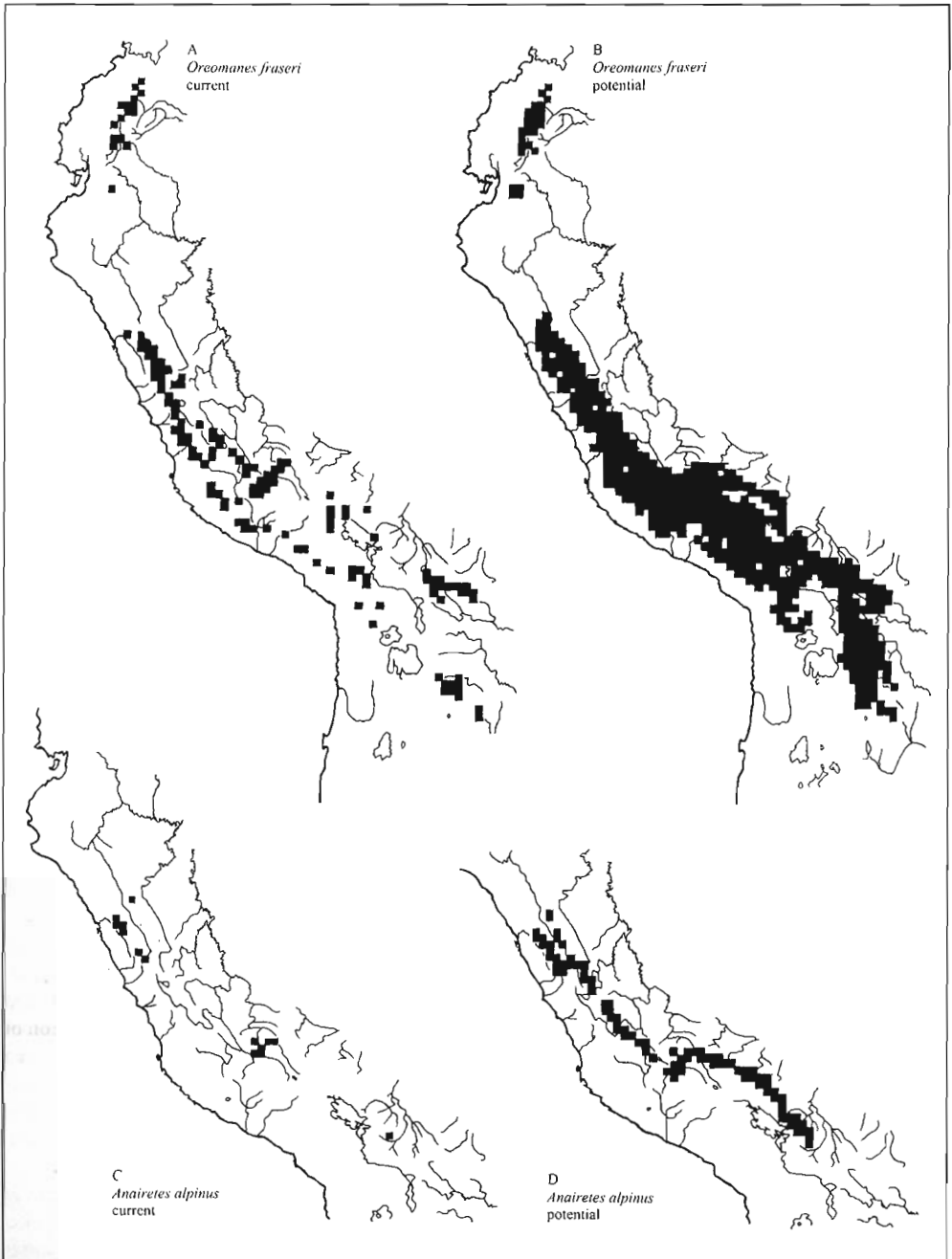


FIG. 2. Modeling of potential distributions. The maps on the left show actual distributions, on the right projected distributions if the highlands were wooded as indicated in Fig. 1. The two examples are: a widespread, *Polylepis*-adapted species *Oreomanes fraseri* (A, B), and a specialist of dense *Polylepis* patches in high cordilleras of relatively high humidity, *Anairetes alpinus* (C, D).

copies are being kept of the two datasets that were developed in this paper ("map andes poly" and "map andes model").

Results. The species richness pattern for highland birds is illustrated in Fig. 3a, and is discussed in some detail in FjeldsÅ *et al.* (1999) and FjeldsÅ (2002b). The highest richness is found in the band of montane forest fringing the upper Amazon Basin (*Ceja de Selva*), with up to 250 species in a 15' cell (on the mountain transition east of Tiraque in Cochabamba, Bolivia). Somewhat lower values characterize the Colombian Cordilleras and the Pacific slope of Colombia and Ecuador, and fairly high values (70–130 species) can also be found in rain shadow valleys with substantial altitudinal amplitudes and mist zones with humid shrubbery. As we pass onto the high plains (grid cells entirely above 3500 m) we find 50–60 species, increasing to >80 species in areas with *Polylepis* or various other shrubby habitats, but with lower levels in the arid parts.

The 214 loosely *Polylepis*-associated species are found mainly in Peru and Bolivia, in areas with moderate rainfall or mist effects and high topographic complexity. They are relatively poorly represented in the *ceja de monte* and in the *páramos* of the northern Andes, where the *Polylepis* zone can best be characterized as having an impoverished cloudforest fauna.

The 51 more typical species of *Polylepis* woodlands (Fig. 4a) show an even more restricted pattern, with very few species present north of the North Peru Low, and even rather few species along the eastern Andean slope of Peru and Bolivia. The highest species numbers are found in Cordillera Blanca, locally on the Pacific slope of Lima, in the montane basins and intervening ridges of Apurímac and Cuzco in Peru, and along the northern edge of the Cochabamba Basin, Bolivia. Fairly high numbers are also found to the northwest of Lake Titicaca, and in southern Peru, where deep canyons intersect the western part of the *puna*.

The 14 *Polylepis* specialists (Fig. 5a) have two absolute peaks, in Cordillera Blanca and Apurímac/Cuzco. This very aggregated pattern suggests that it was only in these two districts that *Polylepis* forests were sufficiently isolated from other forest types in the past to permit a specialization for this forest type. This may have happened during Pleistocene glacial periods, when many cordilleras were ice-covered, and zones of *Polylepis* were isolated from the eastern cloudforest in inter-montane basins (in Apurímac/Cuzco and upper

Marañón valley), or between the glaciated western cordillera and the Peruvian coastal desert (FjeldsÅ 1993).

The pattern of narrow endemism is illustrated in Fig. 3b, as the number of species representing the quartile (25%) with the smallest distributions (see Gaston 1994). The absolute peak value is found on the southern ridge of Cordillera Vilcabamba in Peru, between Abancay (framed) and Machu Picchu. High values are also along the ridge top of Cordillera Central in northern central Peru and in La Paz to Cochabamba in Bolivia, and from Cordillera Blanca to the western Cordillera of Lima, Peru.

The modeled potential distributions show a smoother pattern (Figs. 4 b and 5 b). While the richness peaks are still apparent, the potential richness is quite uniform through the region of montane basins of northern and central Peru and on the transition between the inter-montane valleys and high plains in Bolivia, with a fairly high richness also on the northern part of the Altiplano. In the valley systems of northern Peru the mean richness per cell declined by only 2.4% from 111.0 to 109.2 as an average number of species per cell, reflecting only a rather local species loss in the upper Marañón and Huallaga basins. In the montane basins from Junín (upper Mantaro) to Cuzco it decreased by 17.3% from 98.3 to 81.3, and in rain shadow basins and pre-*puna* habitats in Cochabamba and Chuquisaca, Bolivia, decreased by 14.0% from 114.1 to 98.1. In the humid *puna* (areas entirely above 3500 m) mean richness decreased, overall, by 25.5% from 78.3 to 59.1 species, but in the arid *puna* decreased only by 4.9% from 59.9 to 57.0 species.

According to this comparison, the most serious biodiversity loss took place in the humid *puna* zone, closely followed by rain shadow basins from Junín to Ayacucho. In the latter region, "natural" vegetation is almost non-existent today (replaced by barren *puna* and shrubbery of *Baccharis*, *Colletia*, and *Dodonea* in the upper valleys), and some areas are seriously eroded. This is also the case in many parts of Cochabamba, Chuquisaca, and eastern Potosi in Bolivia.

Estimates of biodiversity loss are of course strongly scale-dependent. Estimates given above are valid as mean values for grid cells of 15'x15', but the losses can of course be much larger locally, for instance where a lush *Polylepis* patch is turned into barren land, or into *Eucalyptus* plantation (see Hjarsen 1999). No total (global) bird extinctions have been documented in this region, but among more or less *Polylepis*-de-

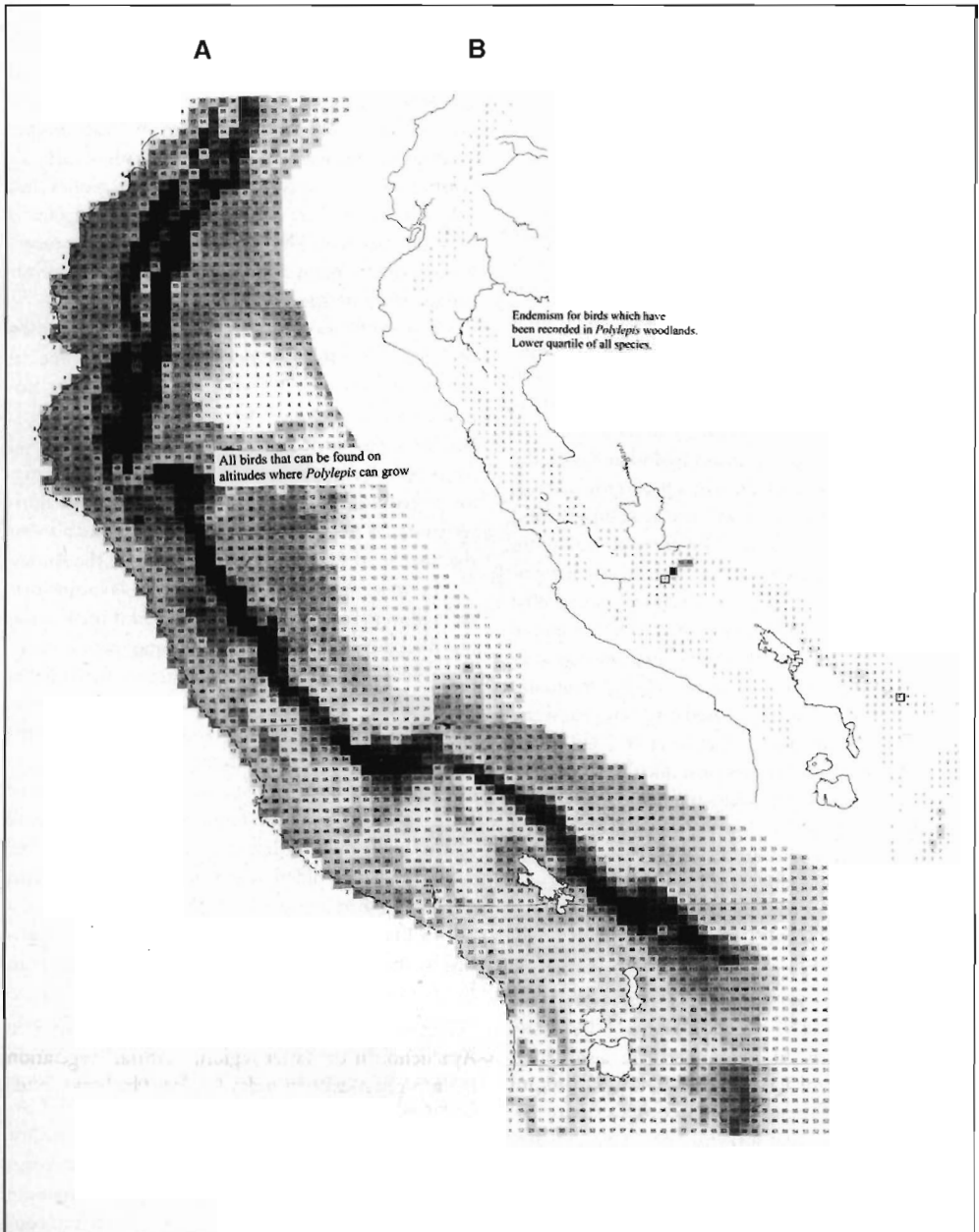


FIG. 3. Patterns of species richness and endemism in the Andes region. A: species richness for birds which, at least locally, inhabit elevational zones where *Polylepis* can grow; B: patterns of endemism, expressed here as presence of species constituting the lower quartile of range-sizes (25% with smallest distributions, with a cut-off limit corresponding to 50000 km²) among those that have been recorded in *Polylepis* woodlands. The three top-priority sites for conserving the 51 more narrowly *Polylepis*-adapted birds (Fjeldså 2002 b) are framed.

pendent species seven are classed as endangered, five as vulnerable and nine as near-threatened (BirdLife 2000). Fjeldså (1993) provides biogeographic evidence suggesting extinctions in central Peru before the start of ornithological exploration.

DISCUSSION

Interpretation of patterns. The difference between actual and potential species richness is, to some extent, constrained by the way in which the modeling was done: modeled distributions are centered around actual distributions and mainly fill in current gaps, but species are not assumed to have extended into other biogeographic zones than those occupied today (Fig. 2). Although the modeling caused a "smoothing" of species-richness peaks (compared with the actual richness pattern) the general pattern persists, and I believe that there is an historic reality behind these peaks (Fjeldså 1992). The areas of maximum endemism (Fig. 3b) are not bound by distinct topographic barriers, but can be described as centered within areas of marked topographic relief and special local climates. An ecological explanation was suggested by the pattern of interannual variability in ground conditions (NDVI and Ts) based on a ten-year series of weather satellite images (Fjeldså *et al.* 1999). Peak values of endemism (in this case calculated as mean reciprocal range-size per species present) corresponded precisely with grid-cells with little variation in ground conditions from year to year. Montane environments are ecologically unstable, overall, but the impact of extreme weather may be moderated locally, where the topography provides shelter against, for instance, cold South Polar winds (*friajes* or *surazos*), which may have been the main determinant of Pleistocene vegetational changes in tropical South America (Servant *et al.* 1993).

This positive correlation between endemism and ecoclimatic stability implies that endemics must (by and large) be relicts that survived only in places where conditions were predictable from year to year (see García-Moreno & Fjeldså 2000 for evolutionary implications). A tantalizing extra dimension is added to this, as it appears that peaks of endemism are often immediately adjacent to areas that have been densely populated by humans for millennia. Peak concentrations of rare *Polylepis*-adapted birds (and of range-restricted kinds of wild potatoes, *Solanum*; see Hijmans & Spooner 2001) are immediately adjacent to the centers of the ancient Chavín culture in Ancash

and of the Wari and Inca cultures in Apurímac/Cuzco, to the Mollo and Inca centers in Cochabamba, and to the Inca/Tomebamba center at Cuenca in southern Ecuador. These areas are also densely populated today, and natural vegetation (with unique avian communities) persists only in places of difficult access in ravines and on adjacent steep slopes and ridges, or where there has been an active management of wood resources. Thus, people seem to prefer exactly those places that were most important in the longer evolutionary perspective.

This correlation between endemism and human settlement is probably not a coincidence. Special ecoclimatic conditions, which permitted relict populations of birds (and other taxa) to survive through periods of past environmental stress, may also be good for people. Crop predictability may have been a major prerequisite for the transition from a life as hunter-gatherers to resident farming systems, and also for the further advancement of agriculture in the Andes.

From a conservation perspective this means that extinction risks can only be eliminated if there is political support for more sustainable land management. Most people may consider that human needs come first, and that conservationists should find other places to interfere with, and it is true that the *ad hoc* approach of conservation planning that has prevailed so far has led to a preference for low-conflict areas. Fjeldså & Rahbek (1998) found that places with peak concentrations of endemic species were, so to say, systematically avoided when national park systems were established in the Andes. P.N. Huascarán in Cordillera Blanca is an exception, which may be explained by the potential income from tourism rather than by rigorous analysis of biological data. Another exception is P.N. Tunari right above Cochabamba town, but this area was partly ruined (from a biodiversity perspective) when *Polylepis* was replaced with *Eucalyptus* as part of a management project. In P.N. Carrasco the initial plan to include the *Polylepis* zone just west of the Tunari watershed had to be given up when angry local people threatened to burn the remaining woodlands so that there would be nothing left to conserve. The park was therefore restricted to the humid *jungas* forests east of the watershed.

This resistance to nature conservation in populated areas means that some of the biologically most unique areas have no protection. It is worth noting that loss of forest habitat in these places not only means a loss of biodiversity but often also a decline

in prosperity for the people who live there, and who used to benefit from various direct and indirect values of the *Polylepis* forests.

Values of Polylepis forests. Shrubbery and *Polylepis* woodlands provide a wide range of plants for local medicinal use (Hensen 1991) and undoubtedly also have considerable potential as genetic resources (e.g., in the case of wild potatoes; Hijmans & Spooner 2001). In the light of modern gene technology, a large potential may exist for (e.g.) enhancing the resilience and frost-resistance of tuber crops. The excellent soils, especially in the more humid types of *Polylepis* forest,

provide a good basis for small-scale agriculture. The crops on small fields inside the forest are protected against wind and nightly frost.

Being rather low and gnarled, *Polylepis* trees are often seen as unimportant, except for charcoal burning, rot-resistant fence-poles, and firewood. *Eucalyptus* plantations are usually favored, because of their higher productivity. However, their very high water consumption, and the detrimental effects on soil chemistry, renders the use of *Eucalyptus* in erosion-prone agricultural areas very questionable (Fjeldså & Hjarsen 1999). Of course *Polylepis* trees also need water, but they also generate water in the sense that they

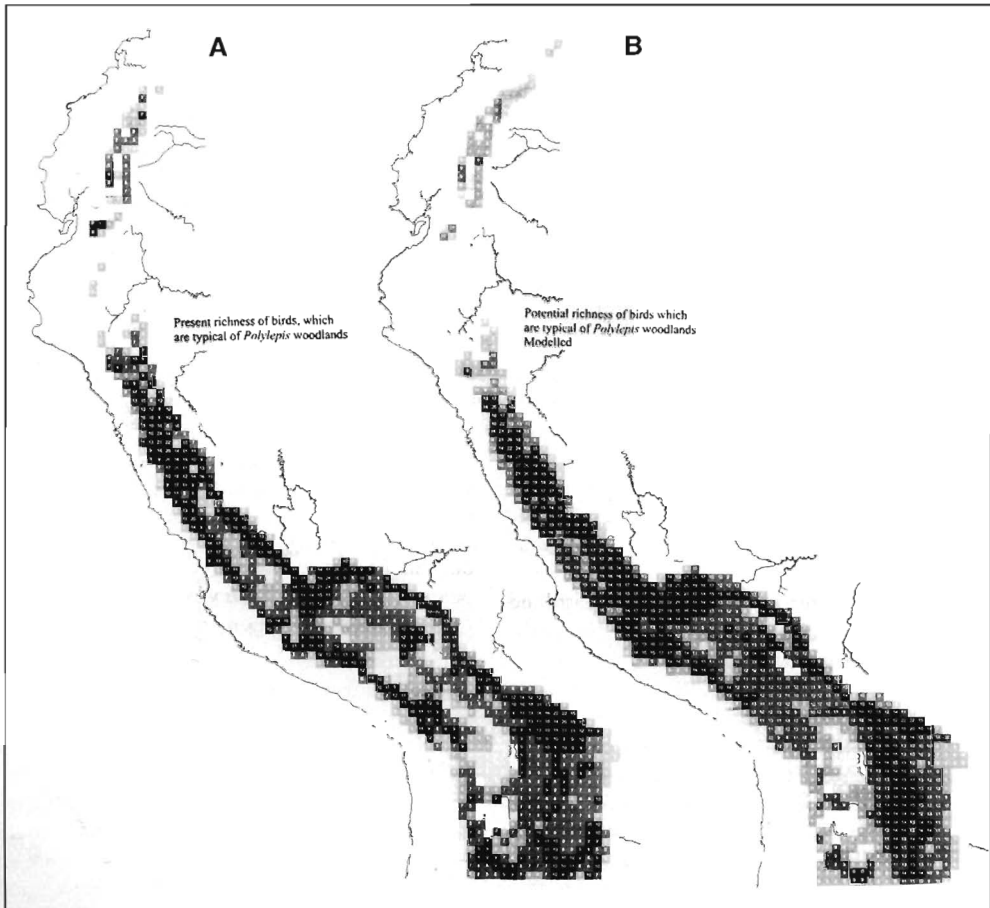


FIG. 4. Actual (A) and potential (B) richness of 51 bird species that are typical for *Polylepis* woodlands.

(unlike *Eucalyptus*) often grow on mist-enshrouded slopes, and have a dense microphyllic foliage structure that can effectively "comb" water out of the atmosphere (Troll 1959). The water is stored in the loose and fertile soil that typically forms in mature and dense *Polylepis* forests (yet another difference from *Eucalyptus*). Boggy habitat (*bofedal*) and wells with clear water are often found right below *Polylepis* forests.

Some consensus seems to exist in local communities in the Cochabamba area (Bolivia) that humidity is maintained in *Polylepis* zones, and that the loss of this vegetation (and planting of *Eucalyptus*) leads to drought (Mariscal & Rist 1999). What developers often overlook is that human livelihood can be improved by allowing natural vegetation to regenerate immediately adjacent to population centers. Dense *Polylepis* vegetation on high ridges and steep slopes is exactly what many communities would need for a secure water supply, and for protecting their infrastructure against incessant landslides. Developers need to consider whether incentives for a land use that allows regeneration of natural vegetation might be cheaper (in the long term) than, for instance, continual road repairs and provision of piped water from remote reservoirs.

It is vigorously debated today how biodiversity and ecological services can be priced, in economic terms, for an effective cost-benefit analysis. Such attempts (e.g., Constanza *et al.* 1997) have been highly stimulating for the political debate, although it seems that putting monetary prices on the environment is only partially possible, and that transparent decision-making processes may be the most realistic substitute where traditional market mechanisms fail. Since many Andean villages have difficult access to external markets, the best way to sustainable landuse seems to be to provide local communities with economic incentives and with better information for making their own decisions about land management (see Beaumont & Walker 1996).

Integrating conservation and development. Because of the general resilience of the vegetation of the high Andes (e.g., Balslev & Luteyn 1992, and papers herein) many components of biodiversity will probably reappear if natural vegetation successions are allowed, and not hindered by chronic overgrazing and burning. Given the lessons of history it is clear, though, that strict reserves should be established to protect unique (and therefore irreplaceable) environments. However,

with the high human population, and traditions of extensive use of the land, it is clear that this approach is acceptable only if communities can anticipate some economic incentives to alter their land-use.

Many areas, such as the Rio Mantaro and Pampas basins of central Peru, and the entire transition (*valles* and pre-*puna*) between the *yungas* forests and high plains of Bolivia, are dominated today by fallow land with extremely eroded slopes (with scattered *Baccharis* and *Dodonea* bushes, and monotonous *ichu* grassland in the higher parts). Low botanical diversity means low drought resilience, inefficient nutrient cycling, and low productivity (Tilman 1999). Needs to use local firewood resources are increasing because of economic changes (Lazcano & Espinosa 2001). Thus, macroeconomic changes and economic support for more sustainable land-use methods could considerably alter the situation for people, as well as for the environment.

A shortage of wood is dealt with (by local communities and project-makers alike) mainly by planting *Eucalyptus* and *Pinus* (ITTO/INEFAN 1994). Unfortunately, plantations of exotic trees are valueless from a biodiversity perspective (Hjarsen 1999; see Pomeroy & Dranzo 1998 for a parallel situation in the Old World tropics), and also aggravate the problems with soil degradation. One needs to consider carefully where to plant these trees to avoid further land degradation. In particular, *Eucalyptus* should be avoided in areas where soil erosion and water scarcity are critical factors. True reforestation with native wood should be encouraged instead. On a larger scale, the most realistic approach may actually be to take advantage of natural vegetation successions, and make agreements with local communities about regulating the burning to allow natural vegetation regeneration on all slopes that are not strictly needed for production.

Today, large parts of the highlands are chronically overstocked by cattle and sheep, as this represents the principal "capital investment" for local people (rather than an efficient food production system). Control of grazing and burning does not mean that livestock numbers need to be reduced. It is well established, in the developed parts of the World, that cattle and sheep are kept most efficiently within fences, or even indoors. In agreement with this, Schad (1995) could demonstrate that in the Andes it is also best to keep animals in *corrales* and feed them with grasses and leguminaceous crops grown on fallow fields. In this way the soil erosion in the fields is reduced, and by

returning the animal dung to the fields, the soil is allowed to recuperate. This approach is less time-consuming than herding free-ranging animals, but the main obstacle is to actually convince farmers to change their behavior.

What is needed, then, is information, together with incentives that make it attractive for people to try new ways of life, and to move planning towards biophysical sustainability (Bolivia 1994). We need support for more intensive use of village areas to

take pressure off the surrounding hills, and get natural vegetation cover back in erosion-prone places and in the mist-zones.

If this happens, and mosaics with natural vegetation can develop, then biodiversity conservation comes 'for free'. A large number of the endangered Andean species seems to benefit from early vegetation successions, where competition is low (e.g., Kessler 1999b for plants). From a conservation perspective, mosaics of fields and forest patches in the Andean

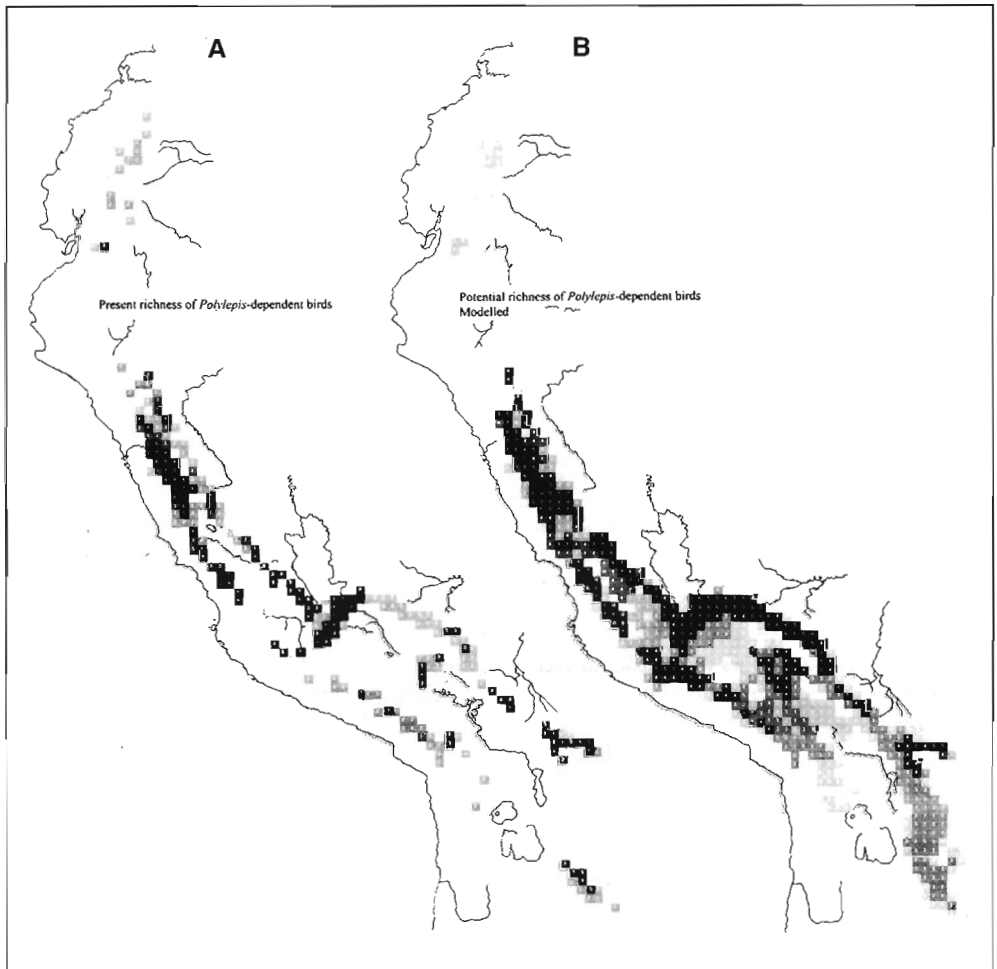


FIG. 5. Actual (A) and potential (B) richness of 14 bird species that are genuine specialists and are only very rarely found away from *Polytepis*.

highlands represent a good alternative to a strict conservation of reserves with no people. Some key areas should be strictly protected, but this will be acceptable only as part of a development plan where local communities find that their food security is improved.

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