

THE “POLYLEPIS PROBLEM”: WHERE DO WE STAND?

Michael Kessler

Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik,
Untere Karspüle 2, 37073 Göttingen, Germany

Abstract. The occurrence of *Polylepsis* stands above the current closed timberline has led to a long-standing discussion as to whether this pattern is natural or due to human activities. I here review the available ecological evidence, reaching the conclusion that the current distribution of *Polylepsis* cannot be explained by natural factors and has been strongly influenced by humans. I identify three main misunderstandings and misconceptions that have so far prevented communication on the subject. Palynological evidence is controversial due to several technical problems. Finally, I discuss the knowledge regarding the ecological factors naturally limiting the distribution of *Polylepsis*. While *Polylepsis* forests represent the natural vegetation on slopes up to elevations of 4000–5000 m (depending on geographical region), large areas within this elevational range are naturally devoid of forests due to salty or water-logged soils and nocturnal cold-air ponding. Well designed palynological studies and plantation schemes can provide important future evidence for a solution of the “*Polylepsis* problem.”
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INTRODUCTION

The genus *Polylepsis* (Rosaceae) consists of about 20 species growing at and above the timberline from Venezuela south to central Argentina (Bitter 1911; Simpson 1979, 1986; Kessler 1995a, c). The various species have adapted to a variety of different habitats, ranging from perhumid cloud forests to desertic puna habitats on the Altiplano. *Polylepsis* has received a lot of attention because throughout its range small stands can be found above the closed timberline. This paradoxical situation, i.e., the occurrence of trees above the timberline, has long baffled biologists and geographers alike and was termed the “*Polylepsis* problem” by Miede & Miede (1994). Originally described by Raimondi (1874), Weberbauer (1907, 1911, 1930), Herzog (1923), and Troll (1929), it was initially believed to represent a natural pattern. This is because most *Polylepsis* stands occur at special microsites such as ravines, boulder slopes, rock faces or in the vicinity of human settlements. Thus, the peculiar distribution of *Polylepsis* was interpreted as being determined by particular microclimatic conditions such as locally higher temperatures or humidity.

In 1958 Ellenberg challenged this view and hypothesized that the patchy distribution of *Polylepsis* trees is mainly due to human influences such as burning,

livestock grazing, and timber extraction. His view was initially severely criticized (e.g., Koepcke 1961; Simpson 1979, 1986; Rauh 1988) and has received support only in the last decade (e.g., Becker 1988; Fjeldså 1992a, b; Lægaard 1992, Kessler 1995a, b). However, a consensus has still not been reached on the relative importance of natural versus human causes in determining the current distribution of *Polylepsis*.

The clarification of the “*Polylepsis* problem” is not merely of academic interest. The potential of large areas of the high Andes to support natural forests presents an immense challenge for ecosystem conservation and restoration (Kessler 1998). The large-scale destruction of forests has had a profound impact on ecosystem functioning and services, affecting biota and human inhabitants alike (Fjeldså & Kessler 1996). Addressing this problem has major knock-on implications for many efforts related to the problems of poverty throughout the Andes today (Chepstov-Lusty & Winfield 2000).

In the present paper, I first review the arguments for and against Ellenberg’s hypothesis, reaching the conclusion that much of the discussion is based on mutual misunderstandings and misconceptions. Ellenberg’s hypothesis is supported by the evidence that the current distribution of *Polylepsis* cannot be explained by present-day ecological conditions and that

many additional sites appear suitable for *Polylepis* growth. Nevertheless, there are natural limitations to the occurrence of *Polylepis* that are still poorly understood. The second part of this paper discusses the current knowledge on the potential distribution and naturally limiting factors.

EVIDENCE SUPPORTING AND REJECTING ELLENBERG'S HYPOTHESIS

Appendix 1 synthesizes the different views and interpretations of the observed current distribution patterns of *Polylepis* and other evidence regarding its occurrence. The available evidence shows that the localized present-day distribution of *Polylepis* cannot be easily explained by ecological factors such as special microclimatic or edaphic conditions, and thus supports Ellenberg's hypothesis. However, there is also clear evidence showing that certain environmental conditions favor or restrict the growth of *Polylepis*.

A closer examination of the "Polylepis problem" shows that much of the discussion is based on three main misunderstandings and misconceptions regarding the idea of a more widespread natural distribution of *Polylepis* forests.

The first problem regards the geographical location of studies on *Polylepis*. Many scientists opposing Ellenberg's view worked in Venezuela, whereas all supporting evidence was obtained in Ecuador, Peru, and Bolivia. The latter three countries each have seven to ten native *Polylepis* species growing under a wide range of environmental conditions (see Kessler 1995a, c for details on Bolivian species). In Venezuela, however, *Polylepis sericea* is the only native species of the genus. This is one of the phylogenetically most basal species (Kessler 1995a) with only limited adaptations to high-elevation conditions. Thus, *P. sericea* is frost-avoiding, rather than frost-tolerant as are some southern taxa (F. Rada, pers. comm.).

In Bolivia, *P. sericea* is the most localized species of the genus and occurs at the most humid and warmest sites of any *Polylepis* species. It is therefore to be expected that in Venezuela *Polylepis* forests would naturally occupy a much more restricted range of environmental niches than in the central Andes. Qualitative observations suggest that some of the colder and more arid sites, which in Bolivia or Peru support such highly adapted *Polylepis* species as *P. tomentella* or *P. tarapacana*, are in Venezuela occupied by stem rosette plants of the composite tribe Espeletiinae (Kessler 1995a). The same situation would apply to Colom-

bia, which only has two *Polylepis* species, with a third species barely reaching in from Ecuador. This should not imply that in Venezuela and Colombia the present distribution of *Polylepis* is completely natural, but it certainly indicates that the potential distribution of the genus as a whole is much more limited than further south in the Andes.

In a recent review of the north Andean páramo vegetation, Luteyn (1999) concluded that there is general consensus that the shrubby subpáramo at (2800) 3000–3500 m would naturally be forested, while the superpáramo above (4000) 4500 m would be devoid of trees. The situation is less clear for the grass páramo (or páramo propiamente dicho) at about 3500–4100 (4500) m. In any case, discussion of the "Polylepis problem" needs to carefully differentiate between the northern and central Andes.

The second misconception is the idea that *Polylepis* forests were mainly destroyed through logging and timber extraction. Opponents of Ellenberg's hypothesis have correctly pointed out that it is very unlikely that early human cultures would have been able to efficiently destroy large forest expanses through logging. However, this has never been claimed. Instead, the main factor in forest destruction is assumed to be the indiscriminate use of fire (Ellenberg 1958; Lægaard 1992; Kessler & Driesch 1993; Kessler 1995a, b; cf. Wesche *et al.* 2000, for the comparable situation in Africa). *Polylepis* populations subjected to regular fires have reduced recruitment and eventually die out (Kessler & Driesch 1993; Kessler 1995a, b). Even hunter-gatherer societies with low population density can effectively destroy large forest areas through the regular use of fire for hunting.

A modern example is given by the situation in Patagonia, where, after the extermination of the indigenous people in the 1880s, who primarily hunted guanacos using fire, the forest has considerably expanded into this former anthropogenic steppe habitat (Veblen & Lorenz 1987, 1988). Similarly, in the high Andes, there is evidence of hunter-gatherer societies from the early Holocene (Wing 1974, 1986; Matos 1977; Wheeler 1984, 1985; Moore 1988). Later on, camelid domestication by pre-Incan cultures led to widespread overgrazing and soil erosion (Bowman 1974, Earls 1976, van der Hammen & Noldus 1985). It is therefore perfectly feasible that through the use of fire early human inhabitants could have destroyed *Polylepis* forests, or even have prevented the colonization of potential sites following the retreat of the glaciers.

Currently, logging and charcoal production play a certain role in *Polylepis* forest destruction, especially in areas with low forest cover and high human population density. There is little evidence that natural fire frequency would have been high enough to restrict the distribution of *Polylepis*. In the northern Andes, natural fire frequency has been estimated at once every 100 years (Verveij 1995). In Peru and Bolivia, I am aware of only one report of a natural fire induced by lightning (R. Bode, pers. comm.).

The third misunderstanding concerns the idea that Ellenberg claimed that "all" of the Andes were naturally forested. This is perhaps the most crucial issue in the whole discussion. Even opponents of Ellenberg's hypothesis do not deny that in many regions *Polylepis* cover has been reduced at least in the last few centuries. The destruction of *Polylepis* forests during the Spanish conquest, e.g., as sources of wood for the mines, is well documented (Ruthsatz 1983, Mansilla 1984, Ansión 1986). In much of the Andes people remember *Polylepis* stands that were present during their childhood, but which have disappeared today (F. Sarmiento, pers. comm.). Conversely, none of Ellenberg's supporters deny that there are habitats which are unsuitable for *Polylepis*.

The question thus is: How much would be naturally forested and how much has been destroyed? For Bolivia, Kessler (1995a, b) estimated that about 20% of the high Andes above 3500 m could potentially support *Polylepis* forests. Of these 20%, however, over 90% have been destroyed and in many regions practically no natural forest is left. In this sense, both groups are correct. Therefore, it follows that if 80% of the Bolivian Andes was naturally devoid of forest, one cannot claim that "all" of the Andes would be forested. However, the destruction of over 90% of the natural *Polylepis* area implies that the current distribution can hardly be explained by natural environmental factors alone.

Probably one of the most critical issues with regard resolving the "*Polylepis* problem" regards the conflicting palynological evidence. The interpretation of palynological diagrams poses several problems:

(a) *Polylepis* pollen is not separable from almost identical pollen of the closely related scrub genus *Acaena* (Salgado-Laboriau 1979, Simpson 1979, Salgado-Laboriau *et al.* 1984), which is common in disturbed, humid areas.

(b) Very few high-Andean pollen records reach back to the Pleistocene and most cores are located at sites which certainly are not suitable for *Polylepis* under pre-

sent-day conditions. Thus it is difficult to determine pre-human *Polylepis* pollen deposition.

(c) Despite flowers morphologically adapted to wind-pollination, *Polylepis* pollen appears not to be wind-transported over distances of more than a few dozen meters (Salgado-Laboriau 1979; J. Fjeldså, pers. comm., J. Vásquez pers. comm.), which could explain low present-day representation of *Polylepis* pollen in core records close to extensive existing forests (e.g., Pelechuco & Quime *in Graf* 1979, Llanganuco *in Graf* 1986).

There are about a dozen existing pollen cores from Peru and Bolivia that contain *Polylepis* pollen (Hansen *et al.* 1984; Ybert & Miranda 1984; Markgraf 1985; Graf 1986, 1992; Hansen 1992; Baied & Wheeler 1993) (see Kessler 1995a for graphs of these cores). The five diagrams reaching into the late Pleistocene all show high depositions of *Polylepis* pollen during that time. Except for the Sajama core, which is located near a volcano currently still extensively covered with *Polylepis* forests, all diagrams show the decline of *Polylepis* pollen at some point during the Holocene. Parallel to this decline, though in some cases involving a time lag of a few thousand years, there is an increase in the frequency of pollen from plants indicating disturbance, such as species of Caryophyllaceae, Malvaceae, Chenopodiaceae, Amaranthaceae, and *Gentiana*. This could be interpreted as showing that *Polylepis* forests declined as human activities increased. However, disturbance indicators might also have increased due to natural causes, particularly increasing aridity. With the exception of unambiguously cultivated plants (e.g., maize), which generally appear rather late in the pollen record, it is currently not easy to distinguish between natural and human-induced disturbances.

The same is true for charcoal remains which are indicative of fires. For example, the El Aguilar core from northern Argentina (Markgraf 1984) has charcoal from about 7500 to 4000 yr BP (years before present) and from 2000 yr BP to present. Particularly the first period corresponds to warmer and drier climatic conditions, but it is not possible to decide whether the increased fire frequency was natural or induced by human activities, e.g., early hunters.

Generally speaking, it is only possible to unambiguously document human activities after the development of agricultural societies, at about 4000 yr BP, while this is more difficult for pastoral societies (after 7500–6000 yr BP). Early hunter-gatherer societies, which appeared in the Andes during the late last glacial period and which may already have had a

strong impact on the *Polylepis* forests through the use of fire for hunting, are very difficult to document in pollen cores.

Turning to the northern Andes, pollen diagrams generally show low levels of *Polylepis* pollen in Venezuela (e.g., Salgado-Laboriau *et al.* 1977, 1992; Rull *et al.* 1987) and a marked decline of *Polylepis* at 20000–30000 yr BP near Bogotá, Colombia (van der Hammen & Cleef 1986), i.e., before the known arrival of humans. However, as previously pointed out, the northern Andes have few *Polylepis* species that may not have been as widespread as those in the central Andes.

In summary, the available palynological evidence is difficult to interpret. It does not provide unambiguous evidence either in favor or against the hypothesis of naturally more widespread *Polylepis* forests. This situation is unlikely to change until several steps are taken. First, methods for separating *Polylepis* pollen from *Acaena* pollen should be explored. Second, more pollen diagrams, and especially longer records, are required from within the potential range of *Polylepis*. Third, palaeoecological studies should focus on additional evidence rather than just pollen, especially charcoal remains (H. Behling, pers. comm.; A.J. Chepstov-Lusty, pers. comm.) and macroremains. Finally, the flight-capability of *Polylepis* pollen has to be studied in order to calibrate observed levels of *Polylepis* pollen.

Summarizing all of the above considerations, Ellenberg's hypothesis is largely supported by the available present-day ecological evidence and cannot be conclusively rejected by the palynological picture. The present-day distribution of *Polylepis* stands cannot be explained by natural factors and is strongly determined by thousands of years of human activity. On the other hand, natural non-forest vegetation certainly occurred extensively in the high Andes. This raises the question:

WHERE WOULD *POLYLEPIS* GROW NATURALLY?

Due to intensive human impact, the potential natural distribution of *Polylepis* forests is difficult to determine. Generally speaking, five different distributional boundaries can be distinguished: upper and lower elevational limits, limits towards arid and wet areas, and unsuitable growth conditions within the distributional range delimited by the previous four factors (Miehe & Miehe 1994; Kessler 1995a, b). The first four boundaries correspond to large-scale macroclimatic patterns, the last boundary to small-scale site conditions.

The causes defining the upper elevational limit of *Polylepis* growth, or of any timberline species for that matter, are still unclear. It has been proposed that tree growth at timberlines is limited by a negative carbon balance, but this hypothesis is not supported by the available evidence (see reviews in Miehe & Miehe 1994, 2000; Körner 1998, 1999). Alternatively, Körner (1998, 1999) recently proposed that timberlines worldwide are primarily determined by low soil temperatures, limiting the investment possibilities of assimilates. However, this hypothesis is not consistent with patterns of tree growth at some natural timberline positions, nor does it specifically address the disadvantages of the tree life-form *vs.* shrubs or herbs (Miehe & Miehe 2000).

Regardless of the underlying mechanisms, the actual position and course of the upper Andean timberline varies considerably. In Bolivia, the uppermost *Polylepis* stands, which are assumed to reflect the natural growth limit of *Polylepis*, are found at 4000–4200 m on the humid eastern Andean versant, rising to above 5000 m on the arid volcanoes of the western cordillera (Jordan 1980, 1983; Kessler 1995a, b). This elevational increase is due to higher solar radiation levels in more arid regions and the overall heating effect of large montane land masses (Hermes 1955, Jordan 1983). Similarly, in the western cordillera *Polylepis* stands reach about 300 m higher on sunny north-facing slopes *vs.* shaded south-facing slopes. This effect is not evident in the cloudy eastern cordillera nor in the equatorial Andes, where insolation differs little with respect to aspect.

The actual course of natural *Polylepis* timberlines is not well understood, as there are almost no natural timberline positions left. Based on comparative observations from other tropical mountains, Young (1993) and Miehe & Miehe (1994) concluded that level valley floors may be avoided because of nocturnal cold air ponding or water stagnation. Ravines and inclined V-shaped valleys are, however, favored by the combined effects of windshelter and more favorable hygric conditions. Generally, tree height, either as closed-canopy forests or scattered tree individuals, would gradually decline at timberlines and grade into shrubby plant formations (Miehe & Miehe 1994, 2000; Kessler 1995b).

The lower elevational limit of *Polylepis* in most cases corresponds to a transition to other forest types. Depending on the biogeographic location and general humidity, these can either be species-rich cloud forests, dominated by *Podocarpus* species, or conver-

sely forests of drought-deciduous Leguminosae. Only in the most arid regions, e.g., on the western Andean slope in northern Chile, do *Polylepis* trees occur as a distinct belt without contact to lower-lying forest types. This situation should not be confused with the presumed pattern of a separate *Polylepis* forest belt in more humid regions (see App. 1).

The aridity limit of *Polylepis* is located at about 100 mm mean annual precipitation at about 4500–4900 m elevation in northern Chile, southwestern Bolivia, and northern Argentina (Kessler 1995a, b; M. Kumar, pers. comm.). At lower elevations, e.g., at 4000–4200 m in southern Bolivia, with higher temperatures and hence higher evapotranspiration, growth of *Polylepis* stops at around 200 mm mean annual precipitation. At its aridity limit, *Polylepis* is restricted to special sites and has a naturally patchy distribution. At high elevations, these stands are restricted to north-facing slopes having higher temperatures, while at lower elevations, south-facing cooler but more humid slopes are preferred (Kessler 1995a, b). Most of the northern and central Andes, with generally more than 500 mm mean annual precipitation, is humid enough for the occurrence of *Polylepis*.

Polylepis also has a humidity limit, being absent from extremely humid mountain ranges on the eastern Andean slope in Ecuador, Peru, and Bolivia, as well as on the western cordillera of Colombia (Kessler 1995a, b). For example, in Podocarpus National Park, southern Ecuador, the natural timberline is located at around 3300 m and is formed by *Weinmannia*, *Clusia*, and other cloud forest trees. *Polylepis* is absent here, but grows to well above 4000 m in less humid areas only about 100 km further north. The physiological or ecological causes for the humidity limit of *Polylepis* are unknown.

These four distributional limits determine the general occurrence of *Polylepis*. In the context of this review, however, the crucial question is how much of the range delimited by these four boundaries would in fact be naturally forested? As is evident from Appendix 1, the current localized distribution of *Polylepis* stands cannot be explained by present-day ecological conditions. Instead, *Polylepis* trees grow on mountain slopes on a variety of geological substrates and soils. There are abundant examples of such forests, some in central Bolivia covering dozens of square kilometers. Thus *Polylepis* forests can be assumed to represent the natural zonal vegetation of large areas of the high Andes.

Apparently, *Polylepis* forests would naturally occur primarily on slopes, avoiding flat valley bottoms. Circumstantial evidence suggests that *Polylepis* is intolerant of even temporarily waterlogged and of salty soils (Kessler 1995a, b). Thus, many flat valley bottoms and large parts of the Altiplano, with its huge salt pans, would naturally be devoid of *Polylepis*. In Chile, mountain slopes adjacent to salt pans lack *Polylepis*, presumably because of wind-blown salt (M. Kumar, pers. comm.). Finally, *Polylepis* would not occur on very steep, shallow-soiled rock faces. In the highest and most arid regions, *Polylepis* would be most susceptible to these factors, while the reverse is true in more benign areas. This would cause *Polylepis* stands to be naturally fragmented near their distributional limits. There is no evidence that biological factors, e.g., parasites or pests, have a limiting effect on the occurrence of *Polylepis* (Kessler 1995a, b).

Thus even within the distributional range of *Polylepis* there is a wide range of site conditions on which *Polylepis* would naturally be absent, providing habitats for many plant and animal species adapted to non-forest vegetation. The actual extent of such sites is difficult to estimate, since the absolute limits of *Polylepis* occurrence have not been quantified. In Bolivia, which has huge areas of salty soils, over 50% of the surface area within the range of *Polylepis* would presumably be devoid of forest (Kessler 1995a, b). In Ecuador and Peru, this percentage would certainly be smaller, since flat waterlogged or salty areas are less widespread. Even further north, the situation would change again, given that only a few *Polylepis* species occur in the páramo zones of Colombia and Venezuela. Here, however, other woody plants, e.g., composites such as *Diplostephium* or *Loricaria*, might potentially form more extensive forests.

While it can hardly be disputed that *Polylepis* forests would naturally have a more widespread distribution than is presently the case, the clarification of the potential distribution of *Polylepis* requires long-term planting schemes. These experimental plantations should be established at suitable sites where no forests are currently present. Such experiments would require the careful selection of site-adapted species and ecotypes and, given the low potential for long-distance dispersal in the genus (Simpson 1986), the translocation of seeds or plantlets. Further research should focus on the population dynamics of *Polylepis*, especially on the requirements for germination and early growth. Finally, ecophysiological studies aimed at determining the causes of the upper distributional limit and the susceptibility of *Polylepis* to wet and salty soils are needed.

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APPENDIX 1. Patterns of *Polylepsis* occurrence and their interpretations in favor and against Ellenberg's hypothesis of a naturally more widespread distribution of *Polylepsis* forests in the high Andes. Evidence lists supporting (+) and rejecting (-) independent evidence for the respective interpretations.

Pattern	Interpretation favoring naturally restricted distribution	Evidence	Interpretation favoring naturally more extensive distribution	Evidence
<i>Polylepsis</i> stands frequently occur on boulder slopes (Raimondi 1874; Weberbauer 1907, 1930; Herzog 1923, Troll 1929; Herrera 1943; Barreda 1951; Hueck 1961, Koepecke 1961, Walter & Medina 1969, Cerrate 1979, Arnal 1983, Salgado-Laboriau <i>et al.</i> 1984, Ferreyra 1986)	Fissures among the rocks allow warm air to penetrate into the soil and hence promote better root development (Walter & Medina 1969)	- Soil temperature measurements have shown soils inside boulder slopes to be colder than adjacent fine-grained soils (Kessler & Hohnwald 1998; see also Richard 1961, Wakonigg 1996, Wunder & Mösel 1996)	Rocks prevent the spread of fire (Ellenberg 1958; Kessler 1995a, b)	+ Observations show that <i>Polylepsis</i> trees on boulder slopes are less affected by fire events (Kessler 1995a, b) + In Bolivia, only 9% of all <i>Polylepsis</i> stands are restricted to boulder slopes, a further 34% of the stands partially cover boulder slopes (Kessler 1995a, b). In Ecuador, there is no restriction of <i>Polylepsis</i> stands to boulder slopes (Lagaard 1992) + There is no elevational increase in the frequency of <i>Polylepsis</i> stands restricted to boulder slopes, as would be expected if low temperatures are the cause of this restriction (Kessler 1995a, b)
<i>Polylepsis</i> stands frequently occur on boulder slopes	Boulder slopes have higher air temperatures than adjacent areas because rocks store solar radiation and slowly release the warmth at night (Weberbauer 1907, 1930; Koepecke 1961)	+ In Mexico, up to 7°C higher temperatures have been measured on boulder slopes than in adjacent areas (Lauer & Klaus 1975)	This effect is unlikely to determine the distribution of <i>Polylepsis</i> because the trees shade the rocks, eliminating the effect; furthermore, this effect would predict <i>Polylepsis</i> plants would grow towards rocks (Miehe & Miehe 1994)	+ In Bolivia, <i>Polylepsis</i> trees frequently shade the rocks among which they are growing and show no sign of better development directly adjacent to rocks; furthermore, in humid areas many rocks are covered by thick moss layers which prevent the heating effect (M. Kessler, pers. obs.)

Pattern	Interpretation favoring naturally restricted distribution	Evidence	Interpretation favoring naturally more extensive distribution	Evidence
<i>Polytepis</i> stands frequently occur on boulder slopes	Boulder slopes are hygrially favored because a) rain water runoff from the rocks is concentrated on the fine-grained soil b) reduced evaporation of soil water due to lower surface area and shading by rocks c) reduced surface runoff (Lauer & Klaus 1975, Geyger 1985, Arce 1990)	+/- In Bolivia, this effect can be observed in areas with less than 300 mm mean annual precipitation, but not in more humid regions (Kessler 1995a, b)	Same interpretation, but the hygrially favored of boulder slopes is assumed to only be effective in arid regions (Kessler 1995a, b)	+/- Same evidence
<i>Polytepis</i> stands rarely occur on flat valley bottoms (Kessler 1995a, b)	Valley bottoms are avoided because a) they tend to have lower nocturnal temperatures than adjacent slope (cold air ponding) (Liberman 1986) b) slopes receive higher solar radiation (Lauer 1982)	+ This is supported by measurements in many temperate and tropical mountain regions (Ruthsatz 1977, Lauer 1982, Liberman 1986, Miehe & Miehe 1994)	Same interpretation, but this effect is only influential near timberline elevations; at lower elevations, only flat valleys with water-saturated soils are avoided (Kessler 1995a, b)	+ In Bolivia, 17% of the <i>Polytepis</i> stands partially occur on flat, deep-soiled sites, although avoiding water-saturated soils (Kessler 1995a, b)
<i>Polytepis</i> stands frequently occur in sheltered ravines and along watercourses (Weberbauer 1911, Troll 1959, Salgado-Labrotiau <i>et al.</i> 1984, Rauh 1988)	Ravines protect the trees from wind, are warmer, are more humid, and have better soils (Troll 1959)	+ This is supported by measurements in many temperate and tropical mountain regions, though measurements in the Andes are few (Miehe & Miehe 1994)	Tree in ravines and along streams are protected from fires which generally burn upslope (Lægaard 1992)	+ Observations show that <i>Polytepis</i> trees along streams are less affected by fire events (Kessler 1995a, b)

<p><i>Polylepsis</i> stands frequently grow where there is regular cloud condensation (Troll 1959; Koepecke 1961; Lauer 1982; Cabido & Acosta 1985; Seibert & Menhofer 1991, 1992; Ibisch 1993, 1994)</p>	<p>Other areas are too dry for <i>Polylepsis</i> (Troll 1959; Koepecke 1961). In addition, fog lowers nocturnal frost intensity and frequency (Cabido & Acosta 1985)</p> <p>+ In the Cochabamba area, central Bolivia, the cloud condensation belt coincides with the belt of highest <i>Polylepsis</i> occurrence (Ibisch 1993, 1994; Hensen 1995; R. Bode pers. comm.)</p> <p>+ In Argentina, higher fog frequency enhances living conditions for trees inside <i>Polylepsis</i> stands (Cabido & Acosta 1985)</p>	<p>While higher humidity certainly favors <i>Polylepsis</i> development (up to a certain degree, see text), this does not imply that <i>Polylepsis</i> cannot grow under more arid situations; stands under optimal humidity conditions are more resilient to human activities and are the last stands to persist</p>	<p>+ In many arid regions, <i>Polylepsis</i> stands occur where there is no cloud condensation belt (Ecuador: Lægaard 1992, Bolivia: Kessler 1995a, b)</p>
<p>In arid regions of eastern Bolivia, <i>Polylepsis</i> stands are restricted to, or are better developed on, south-facing slopes (Hensen 1993; Kessler 1995a, b)</p>	<p>South-facing slopes receive less solar radiation, thus have lower evaporation and higher humidity; in arid regions this favors tree growth (Kessler 1995a, b)</p>	<p>South-facing slopes receive less solar radiation, thus have lower evaporation and higher humidity; in arid regions this favors tree growth (Kessler 1995a, b)</p>	<p>North-facing slopes have higher solar radiation, in cold regions, this favors tree growth (Ruthsatz 1977; Jordan 1980, 1983; Kessler 1995a, b)</p>
<p>In arid western Bolivia, <i>Polylepsis</i> stands are better developed on north-facing slopes (Ruthsatz 1977; Jordan 1980, 1983)</p>	<p>This shows that <i>Polylepsis</i> tolerates a wide range of soil conditions (Kessler 1995a, b)</p>	<p>This shows that <i>Polylepsis</i> tolerates a wide range of soil conditions (Kessler 1995a, b)</p>	<p>This shows that <i>Polylepsis</i> tolerates a wide range of soil conditions (Kessler 1995a, b)</p>
<p>In Bolivia, <i>Polylepsis</i> stands have been found on a wide variety of geological materials and soils, e.g., ranging in pH from 3.9 to 7.2 (Hensen 1993; Kessler 1995a, b)</p>	<p>In Bolivia, <i>Polylepsis</i> stands have been found on a wide variety of geological materials and soils, e.g., ranging in pH from 3.9 to 7.2 (Hensen 1993; Kessler 1995a, b)</p>	<p>In Bolivia, <i>Polylepsis</i> stands have been found on a wide variety of geological materials and soils, e.g., ranging in pH from 3.9 to 7.2 (Hensen 1993; Kessler 1995a, b)</p>	<p>In Bolivia, <i>Polylepsis</i> stands have been found on a wide variety of geological materials and soils, e.g., ranging in pH from 3.9 to 7.2 (Hensen 1993; Kessler 1995a, b)</p>

Pattern	Interpretation favoring naturally restricted distribution	Evidence	Interpretation favoring naturally more extensive distribution	Evidence
Some <i>Polybleps</i> stands do not show any specific adaptations to environmental conditions, but rather grow on regionally typical slopes (Fjeldså 1987, Kessler 1995a, b)	This pattern shows that human use does not destroy <i>Polybleps</i> forests (Koepecke 1961)	- Same evidence	This shows that the patchy occurrence of <i>Polybleps</i> stands cannot be explained by localized environmental conditions	+ In Bolivia, over 50% of all <i>Polybleps</i> stands occur on "typical" slopes, without any elevational preference (Kessler 1995a, b)
<i>Polybleps</i> stands frequently occur immediately adjacent to human habitations, where they are used as a source of firewood (Weberbauer 1911; Koepecke 1961)	Given this ability to resprout, it is unlikely that timber extraction would destroy <i>Polybleps</i> stands (Koepecke 1961)	<i>Polybleps</i> stands are purposefully managed and/or planted near settlements as a source of fire-wood (Kessler 1995a, b)	The destruction of <i>Polybleps</i> stands is not primarily through logging, but through burning and grazing	+ Supported by interviews with local inhabitants (Kessler 1995a, b)
In many areas devoid of <i>Polybleps</i> stands, exotic tree species (especially <i>Encabptus</i> and <i>Pinus</i>) can successfully grow (Ellenberg 1958)	Where grazing and burning are excluded, <i>Polybleps</i> readily colonizes grasslands (Fjelds 1987; Hensen 1993; Kessler 1995a, b)	This shows the potential of natural trees to grow in areas currently devoid of natural forests (Ellenberg 1958,1979, 1996)	The lack of <i>Polybleps</i> in many grasslands cannot be explained by natural factors but is rather the result of burning and grazing	

<p><i>Polytepis</i> stands frequently grow in a separate elevational belt above the upper cloud forest limit without direct contact between them (Herzog 1923; Troll 1959; Hueck 1962; Vareschi 1970)</p>	<p><i>Polytepis</i> stands are not a zonal vegetation type, but rather occur only locally under favorable microclimatic conditions (Troll 1959; Hueck 1962)</p>	<p>Naturally, there would be a broad contact zone between zonal <i>Polytepis</i> forests and cloud forests (Kessler 1995a, b)</p>	<p>+ Direct contact between <i>Polytepis</i> and cloud forests has been documented in Venezuela, Ecuador, Peru, and Bolivia (Kessler 1995a, b) + The <i>Polytepis</i>/cloud forest transition is particularly susceptible to fires, leaving remnant <i>Polytepis</i> stands at high elevations and depressing the closed cloud forest limit (Kessler 2000)</p>
<p>Reports by early Spanish chroniclers (Pedro Cieza de León 1533, 1550; Garcí Diez de San Miguel 1567, Juan de Matienzo 1967, Diego Vaca de Castro 1586, Bernabé Cobo 1653, Guamán Poma de Ayala 1947, Garcilaso de la Vega 1943) show that the Incas actively protected trees and forests, yet by the time of the Spanish conquest the high Andes were largely devoid of trees (Koepecke 1961; Kessler & Driesch 1993; Kessler 1995a, b)</p>	<p>Human cultures always used the high-Andean ecosystems in a sustainable way and did not destroy the forests (Koepecke 1961)</p>	<p>Most forest destruction occurred in pre-Inca times and the forest protection during the Inca empire was a reaction to previous deforestation (Kessler & Driesch 1993)</p>	<p>+/- Interpretation of palynological evidence is controversial (see text); however, 4000-year-old pollen cores from the Cuzco area, Peru, show an increase of trees during Inca times, interpreted as active agroforestry practices following previous deforestation (Cheptov-Lusty <i>et al.</i> 1999)</p>
<p>Human population density is very low in many high-Andean regions (Koepecke 1961)</p>	<p>So few humans could hardly have logged large expanses of forest (Koepecke 1961)</p>	<p>Forest destruction was mainly through burning, which can be conducted by few people over large areas, rather than by logging (Ellenberg 1958)</p>	<p>+ In Bolivia, burning has a stronger negative effect on <i>Polytepis</i> population structure than grazing or logging (Kessler & Driesch 1993; Kessler 1995a, b)</p>

Pattern	Interpretation favoring naturally restricted distribution	Evidence	Interpretation favoring naturally more extensive distribution	Evidence
The high-Andean non-forest vegetation (páramo, puna) is more species-rich in plants than adjacent <i>Polylepis</i> forests (Vareschi 1970)	This shows that non-forest vegetation is naturally dominant and that its flora has had a long evolutionary history (Vareschi 1970; van der Hammen & Cleef 1986)		There are numerous natural non-forest habitats (super-páramo and other alpine habitats, bogs, rock faces, etc.) on which species of open vegetation occur naturally; these species then form the man-made high-Andean vegetation (Budowski 1968, Lægaard 1992); dense forests with low light levels typically have very few ground herbs under generally unfavorable conditions (Kessler in press)	+ In the Venezuelan páramo, there are no grassland species which do not also occur in habitats that are unambiguously naturally devoid of trees (A. Berg, pers. comm.)
Biogeographic analyses of bird and plant distributions reveal affinities between currently disjunct <i>Polylepis</i> regions (Fieldså 1992a, b; Kessler 1995b)			Such biogeographic connections document the occurrence of <i>Polylepis</i> forests in areas where there are none today, pointing to a previously larger forest area (Fieldså 1992a, b; Kessler 1995b)	