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DETERMINANTS OF *POLYLEPIS* (ROSACEAE) FOREST DISTRIBUTION AND TREELINE FORMATION IN THE HIGH ANDES

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For an understanding of the success and defeat of tree life at high elevations,

> *"Trees gets small before they get rare",*
> *and finally,*
> *"The non-adapted are absent".*

Christian Körner

This thesis is based on the following publications and manuscripts, referred to in the text by their Roman numerals.

I   Toivonen, J.M., Horna, V., Kessler, M., Ruokolainen, K, & Hertel, D. 2014. Interspecific variation in functional traits in relation to species climatic niche optima in Andean *Polylepis* (Rosaceae) tree species*:* evidence for climatic adaptations. *Functional Plan Biology* 41: 301-312.

II   Toivonen, J.M., Gonzales-Inca, C.A., Ruokolainen, K., Kessler, M. Terrain features shaping the spatial distribution patterns of *Polylepis* forest stands in the high Andes of southern Peru. *Manuscript.*

III   Kessler, M., Toivonen, J.M., Sylvester, S., Kluge, J. & Hertel, D. 2014. Tree height of *Polylepis* forests (Rosaceae) in the high Andes of Peru: effect of elevation, climatic conditions and human impact. *Frontiers in Plant Science* 5:194. doi: 10.3389/fpls.2014.00194 (uncorrected proof).

IV   Toivonen, J.M., Kessler, M., Ruokolainen, K. & Hertel, D. 2011. Accessibility predicts structural variation of Andean *Polylepis* forests. *Biodiversity and Conservation* 20: 1789–1802.

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Table of contribution.

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JMT = Johanna M. Toivonen, KR = Kalle Ruokolainen, MK = Michael Kessler, DH = Dietrich Hertel, VH= Viviana Horna, CGI = Carlos Gonzales-Inca, SS = Steven Sylvester, JK = Jürgen Kluge

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ABSTRACT

High elevation treelines are formed under common temperature conditions worldwide, but the functional mechanisms that ultimately constrain tree growth are poorly known. In addition to environmental constraints, the distribution of high elevation forests is largely affected by human influence. Andean *Polylepis* (Rosaceae) forests are an example of such a case, forests commonly growing in isolated stands disconnected from the lower elevation montane forests. There has been ample discussion as to the role of environmental versus anthropogenic causes of this fragmented distribution of *Polylepis* forests, but the importance of different factors is still unclear. In this thesis, I studied functional, environmental and anthropogenic aspects determining *Polylepis* forest distribution. Specifically, I assessed the degree of genetic determinism in the functional traits that enable *Polylepis* species to grow in cold and dry conditions. I also studied the role of environment and human influence constraining *Polylepis* forest distribution. I found evidence of genetically determined climatic adaptations in the functional traits of *Polylepis*. High elevation species had reduced leaf size and increased root tip abundance compared to low elevation species. Thus these traits have potentially played an important role in species evolution and adaptation to high elevation habitats, especially to low temperatures. I also found reduced photosynthesis rate among high elevation tree species compared to low elevation species, supporting carbon source limitation at treelines. At low elevations, *Polylepis* forest distribution appeared to be largely defined by human influence. This suggests that the absence of *Polylepis* forests in large areas in the Andes is the result of several environmental and anthropogenic constraints, the role of environment becoming stronger towards high elevations. I also show that *Polylepis* trees grow at remarkably low air and soil temperatures near treelines, and present new evidence of the role of air temperatures in constraining tree growth at high elevations. I further show that easily measurable indices of accessibility are related to the degree of degradation of *Polylepis* forest, and can therefore be used in the rapid identification of potentially degraded *Polylepis* forests. This is of great importance for the conservation and restoration planning of *Polylepis* forests in the Andes. In a global context, the results of this thesis add to our scientific knowledge concerning high elevation adaptations in trees, and increase our understanding of the factors constraining tree growth and forest distribution at high-elevation treelines worldwide.

RESUMEN

El límite altitudinal arbóreo está formado bajo condiciones similares de temperatura a nivel mundial, pero los mecanismos funcionales que finalmente constriñen el crecimiento de los árboles son poco conocidos. Además de los factores ambientales, la distribución de los bosques de alturas está afectada por las acciones humanas. Los bosques andinos de *Polylepis* (Rosaceae) son un ejemplo de este caso: estos bosques crecen en rodales aislados y desconectados de los bosques montanos a menor altitud. Ha habido una amplia discusión sobre el rol de los factores ambientales y antropogénicos que causan esta distribución fragmentada de los bosques de *Polylepis*, pero la importancia de diferentes factores no está todavía clara. En esta tesis estudié los aspectos ecofisiológicos, ambientales y antropogénicos que pueden determinar la distribución de los bosques de *Polylepis*. Específicamente, evalué el grado del determinismo genético sobre las características ecofisiológicas que permiten a las especies de *Polylepis* crecer en condiciones frías y secas. Además, estudié el rol de los factores medio ambientales y antropogénicos que restringen la distribución de los bosques de *Polylepis*. Mis resultados dan evidencias de adaptaciones climáticos genéticamente determinadas en las características ecofisiológicas de las especies de *Polylepis*. Las especies de las zonas altas presentan hojas de tamaño reducido e incremento en la abundancia de ápices radiculares en comparación con las especies de las zonas más bajas. Estas características parecen haber desempeñado un rol importante en la evolución de las especies y en la adaptación a los hábitats de mayor altitud, especialmente a temperaturas bajas. Asimismo, encontré una tasa reducida de fotosíntesis en las especies de las zonas altas en comparación con las especies de las zonas más bajas. Esto apoya la hipótesis de limitación de adquisición de carbono en el límite altitudinal arbóreo. A menor altitud, la distribución de los bosques de *Polylepis* parece estar fuertemente afectada por las acciones antropogénicas. Esto sugiere que la ausencia de los bosques de *Polylepis* en la mayor parte de los Andes es el resultado de una serie de limitaciones ambientales y antropogénicas, donde el rol de los factores ambientales se incrementa hacia las zonas altas. También encontré que los árboles de *Polylepis* cerca del límite altitudinal arbóreo crecen a considerablemente bajas temperaturas del aire y del suelo. Además presento nuevas evidencias del rol de la temperatura del aire en la limitación del crecimiento de los árboles en las zonas altas. Adicionalmente, demuestro que los índices de accesibilidad que son fácilmente medibles están relacionados con el grado de degradación de los bosques de *Polylepis* y pueden ser aplicados para una identificación rápida de los bosques degradados. Esto es de gran importancia para la conservación y planificación de restauración de los bosques de *Polylepis* en los Andes. En el contexto mundial, los resultados de esta tesis contribuyen a incrementar el conocimiento científico relacionado a las adaptaciones de especies arbóreas en hábitats montañosos y el entendimiento de los factores que limitan el crecimiento de los árboles y la distribución de los bosques en el límite altitudinal arbóreo a nivel mundial.

TIIVISTELMÄ

Vuoristopuurajat esiintyvät maailmanlaajuisesti samanlaisissa lämpötila-olosuhteissa, mutta puiden kasvua rajoittavat ekofysiologiset mekanismit tunnetaan kuitenkin huonosti. Ympäristöolosuhteiden lisäksi ihmisvaikutuksella on myös suuri merkitys vuoristometsien levinneisyyteen. Andien *Polylepis*-metsät ovat yksi esimerkki tällaisesta tapauksesta. Metsät kasvavat eristyneinä laikkuina alemman yhtenäisen vuoristometsävyöhykkeen yläpuolella. Ympäristöolosuhteiden ja ihmisvaikutuksen merkitystä *Polylepis*-metsien levinneisyydelle on tutkittu paljon, mutta eri tekijöiden merkitys metsien levinneisyydelle on edelleen epäselvä. Tutkin väitöskirjassani puiden ekofysiologiaan, ympäristöolosuhteisiin ja ihmis-vaikutukseen liittyviä tekijöitä, jotka voivat selittää *Polylepis*-metsien levin-neisyyttä. Tulokseni osoittivat, että osa tutkimistani *Polylepis*-puiden eko-fysiologisista piirteistä ilmensi geneettisesti määräytyneitä ilmastollisia sopeumia: korkean paikan lajeilla oli pienemmät lehdet ja enemmän juurenkärkiä kuin matalampien paikkojen lajeilla. Näillä piirteillä on todennäköisesti ollut tärkeä merkitys lajien evoluutiossa ja sopeutumisessa ylävuoriston elinympäristöihin, erityisesti mataliin lämpötiloihin. Tuloksieni mukaan korkean paikan lajeilla oli myös alentunut fotosynteesikapasiteetti matalampien paikkojen lajeihin verrattuna. Tämä tukee hypoteesia hiilen sitomiseen liittyvistä rajoitteista vuoristopuurajalla. Alemmilla korkeuksilla ihmistoiminnalla näytti olevan erityisen suuri merkitys *Polylepis*-metsien levinneisyyteen. Tuloksieni perusteella voidaan todeta, että *Polylepis*-metsien nykylevinneisyys on seurausta useasta eri ympäristöön ja ihmistoimintaan liittyvästä tekijästä, joista ympäristön merkitys levinneisyyden selittäjänä kasvaa siirryttäessä kohti ylävuoristoa. Tutkimustulokseni myös osoittivat, että *Polylepis*-puut kasvavat huomattavan alhaisissa lämpötila-olosuhteissa lähellä puurajaa, sekä ilman että maaperän lämpötilan suhteen. Lisäksi tulokseni osoittivat, että erityisesti ilman lämpötilalla on merkitystä puiden kasvulle vuoristossa. Havaitsin myös, että helposti mitattavat, metsien saavutettavuuteen perustuvat indeksit selittävät *Polylepis*-metsien rakennetta, ja näin ollen myös metsien kunnon heikkenemistä. Näitä indeksejä voidaan käyttää tunnistamaan nopeasti ja helposti alueita, joilla *Polylepis*-metsät ovat huonokuntoisimpia. Tällä tiedolla on merkitystä *Polylepis*-metsien suojelu- ja kunnostussuunnitelmille Andeilla. Väitöskirjatyöni tulokset lisäävät myös tietoa puiden sopeutumisesta vuoristo-olosuhteisiin ja auttavat ymmärtämään eri tekijöiden merkitystä puiden kasvulle ja metsien levinneisyydelle vuoristo-puurajoilla maailmanlaajuisesti.

1. INTRODUCTION

High elevation treelines are formed at the elevation above which tree growth is prevented by environmental constraints, and tree stature changes to shrubs or other low stature alpine vegetation (Körner 2012). The specific elevation where the treeline is formed varies according to latitude and specific local features, but there appear to be certain globally common temperature conditions for high elevation treelines: a mean growing season soil temperature ranging from 5 to 8°C (Körner 1998, 2003; Körner & Paulsen 2004; Wieser & Tausz 2007) and averaging 6.7 °C±0.8 SD (Körner & Paulsen 2004). Nevertheless, after more than a hundred years of high elevation treeline studies (e.g. Schröter 1908; Troll 1961, 1973; Tranquillini 1979; Lauer 1982; Miehe & Miehe 1994; Körner 1998; Jobbagy & Jackson 2000), both the physiological mechanisms constraining tree growth and the functional adaptations enabling trees to cope with low temperatures remain unclear.

Mountains are environmentally demanding habitats for plants, and are also subject to strong human influence around the world. Activities associated with human land use play a significant role in determining the spatial patterns of natural vegetation in mountain areas. The high Andean tree genus *Polylepis* (Rosaceae) provides an example of this interplay between environmental and anthropogenic factors affecting vegetation. However, the relative importance of environmental *versus* anthropogenic factors in determining the distribution of *Polylepis* forests remains to be clarified. The genus *Polylepis* consists of several evergreen tree species adapted to different temperature and humidity conditions, from relatively warm and wet cloud forests to cold and dry high mountains (Simpson 1986; Schmidt-Lebuhn et al. 2006). The highest forest stands grow near 5000 m of elevation, forming one of the highest alpine treelines worldwide. Forest stands with easy access, usually referring to stands at lower elevations, are extensively affected by human land use (Kessler 1995, 2000; Fjeldså & Kessler 1996; Hagaman 2006). For these reasons, *Polylepis* forests form an interesting study system for investigating the role of functional, environmental and anthropogenic factors determining forest distribution.

1.1. High elevation treelines

The high elevation treeline denotes the upper elevational limit for tree growth, survival and reproduction. It usually forms a natural ecological transition zone, an ecotone, with a gradual shift from high statured trees to lower statured shrubs and other alpine plants (Körner 2003, 2012; Wieser & Tausz 2007). Commonly, "treeline" refers to a boundary at which tree height drops below 3 m (Körner 2003; Smith et al. 2003) and closed forest changes to fragmented forest patches surrounded by alpine pastures (Tranquillini 1979; Holtmeier 2009). However, abrupt high elevation treelines have also been documented (e.g. Miehe et al. 2007). Other high elevation tree boundaries can also be defined: "timberline" commonly refers to the end of closed forests with timber-size trees, while "tree species line"

refs to the upper limit of tree existence; this may conflict with the definition of a tree, i.e. a woody plant at least 3 m in height (Körner 2003; Smith et al. 2003; Körner & Paulsen 2004) (Figure 1).
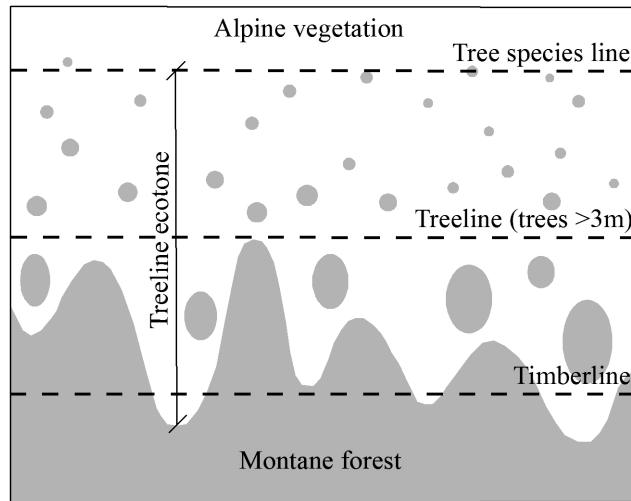

Figure 1. Conceptual representation of timberline, treeline and tree species line (modified from Körner & Paulsen 2004).

Global data on high elevation treeline locations indicate an increasing latitudinal trend in treeline elevations from the poles towards the subtropics, with a decline at the equatorial zone (e.g. Troll 1973; Körner 1998, 2007). Continentality also affects treeline elevation; trees grow at higher elevations in the warmer and sunnier inner parts of mountain areas than in the outer parts, which are exposed to strong winds and rains. This phenomenon is also known as mass elevation effect, discussed in detail for example by Schröter (1908) and Barry (1981).

Temperature is regarded as a main driver of high elevation treeline formation globally (Körner 1998, 2003, 2012; Wieser & Tausz 2007), but the underlying physiological mechanisms of tree function are still unclear, as is the question whether soil or air temperatures are decisive for treeline formation. Körner and Paulsen (2004) found that at high elevation treelines the mean soil temperature during the growing season – defined as the period during which the soil temperature at 10 cm depth consistently exceeds 3.2°C – universally averages 6.7 °C, but substantial regional and taxonomic variation was also observed (Körner & Paulsen 2004). Limited water and nutrient uptake by the fine root system stresses the role of soil temperature in the formation of a high elevation treeline (Wilson et al. 1987; Leuschner et al. 2007; Hertel et al. 2008; Hertel and Schöling 2011; Körner 2012), while the strong atmospheric coupling of high tree stature highlights the role of air temperatures (e.g. Hadley & Smith 1987; Wilson et al. 1987; Grace et al. 1989; Körner 2003). Körner (1998) and Smith et al. (2003)

summarize the following five main hypotheses concerning potential functional explanations for high elevation treeline formation worldwide:

> 1) the stress hypothesis, according to which the growth in particular of young trees is suppressed by physiological tissue damage at cold and dry conditions
>
> 2) the disturbance hypothesis, according to which the decisive factor limiting tree growth involves mechanical damages due to wind, snow accumulation, landslides, avalanches, fungi infection and herbivory
>
> 3) the reproduction limitation hypothesis, emphasizing the role of decreased pollination, seed development, seed dispersal, germination and seedling establishment
>
> 4) the negative carbon balance hypothesis, which suggests that carbon acquisition is insufficient to maintain minimum growth after respiratory carbon loss
>
> 5) the growth limitation hypothesis, according to which impeded tree growth is attributable to reduced carbon investment in the development of new tissues at low temperatures.

In searching for a comprehensive, globally applicable explanation for high elevation treeline formation, the hypotheses which have received the most attention are the last two: the negative carbon balance (carbon source) hypothesis and the growth limitation (carbon sink) hypothesis, related to reduced carbon investment (Körner 1998; 2003; Smith et al. 2003; Hoch & Körner 2005). So far, the carbon sink hypothesis has received more support (Körner 1998, 2003; Hoch & Körner 2005), but there is also some evidence of carbon source limitation at high elevation treelines (Cabrera et al. 1998; Wieser et al. 2010; Wittich et al. 2012). More evidence is needed to clarify the relative importance of these two hypotheses.

1.2. High elevation adaptations in trees

High elevation trees show a number of morphological and physiological responses to cope with low temperatures, in particular, but also with other forms of environmental stress. Examples of such stress factors include water shortage due to higher evaporation and low rainfall (Leuschner 2000), increased solar radiation – especially ultraviolet B radiation – due to reduced absorption from the atmosphere and clouds, and low CO_2 partial pressure (Caldwell 1986; Caldwell et al. 1989; Körner 2003). The responses of trees to these conditions are regulated through different adaptive mechanisms: reversible acclimation, non-reversible modification and evolutionary adaptation (Körner 2003). Evolutionary adaptations are genetically determined and unresponsive to environmental variations, whereas acclimations are plastic changes that respond to environmental conditions (e.g. Clausen et al. 1940; Bradshaw 1965; Schlichting 1986; Sultan 2000).

In general, low temperatures have two types of effect on organisms: gradual effects, which permit important metabolic activities (photosynthesis, respiration and nutrient uptake) but at reduced levels, and threshold effects, which kill the organism if a critical threshold value is exceeded (Körner 2012). High elevation trees have different temperature threshold limits depending on their natural growth conditions and corresponding climatic adaptations. They also have different physiological strategies for coping with low temperatures, including osmotic adjustments, supercooling capacity and/or freezing tolerance (Körner 2003; Azócar et al. 2007).

The most commonly documented response to low temperatures and drought is a reduction in aboveground tree biomass, manifested as a decrease in tree height (e.g. Wilson et al. 1987; Young 1993; Kessler et al. 2007); this correlates with a decrease in leaf size and specific leaf area (e.g. Cordell et al. 1998; Moser et al. 2007; Hertel & Wesche 2008; Macek et al. 2009). These changes are linked to the plant energy economy, but the functional mechanisms behind them are not fully understood. Körner (2003) emphasizes the role of developmental controls over plant organs, in particular cell wall structures, as an underlying cause of the reduced size of aboveground tree parts.

Contrary to aboveground patterns, the size of belowground tree structures has been reported to respond positively to decreasing temperatures (Hertel & Wesche 2008; Moser et al. 2011; Hertel & Schöling 2011) and increasing drought (Gaul et al. 2008; Hertel et al. 2008). Positive responses of root systems to decreased temperatures are explained by a low nutrient supply at low temperatures due to reduced water viscosity and liquid diffusion and to low microbial activity (e.g., Sveinbjörnsson et al. 1992; Tanner et al. 1998; Hertel & Wesche 2008; Hertel & Schöling 2011).

A positive relationship between maximum photosynthesis rate and temperature, as a consequence of increased activity of the RuBisCO enzyme at higher temperatures, has frequently been documented (e.g. Berry & Björkman 1980; Cabrera et al. 1998; Yamori et al. 2005; Zhang et al. 2005; Azócar et al. 2007). However, it is not clear whether reduced carbon acquisition (photosynthesis) limits tree growth at high elevations (Körner 2003; Hoch & Körner 2005; Wieser et al. 2010; Wittich et al. 2012). There is some evidence of decreased carbon acquisition in trees with increasing elevation (e.g. Wieser et al. 2010; Wittich et al. 2012); on the other hand, it has been suggested that the limiting factor for tree growth at high elevations involves metabolic constraints related to carbon investment in tree organs at low temperatures rather than constraints in carbon acquisition (Körner 2003; Hoch & Körner 2005). The higher efficiency of CO_2 utilization (ECU) per unit of leaf area in high elevation trees compared to low elevation ones, measured in experiments carried out at varying CO_2 concentrations, support this view. The higher ECU is apparently caused, at least in part, by increased leaf thickness and the consequently increased N concentration per leaf area (Körner 2013). It thus seems unclear what the high- elevation adaptations of photosynthesis in trees

consist of, or indeed whether such adaptations occur at all. In addition to temperature, net photosynthesis also depends on irradiance and water availability (Körner 2003, 2012; Wieser 2007).

Variations in maintenance respiration are mainly driven by temperature (Larigauderie & Körner 1995; Wright et al. 2006; Wieser 2007). Respiration has been found to be lower among high elevation trees than low elevation ones measured *in situ* (Körner 2003; Wieser & Tausz 2007). This indicates a decreased respiratory carbon loss among high elevation trees due to metabolic adjustments at low temperatures.

1.3. Distribution of high-Andean *Polylepis* forests

Polylepis forests are found in the Andes at high elevations from Argentina to Venezuela, forming one of the world's highest treelines. One of the highest documented sites for *Polylepis* forest is at 4810 m in Volcán Sajama, Bolivia (Hoch & Körner 2005). *Polylepis* trees commonly grow in sparsely distributed stands disconnected from lower-elevation montane forests. There is evidence of both natural and anthropogenic causes for the current fragmented distribution of the forests. Palaeoecological studies, based on fossil pollen records from Salar Uyuni and Lake Titicaca in Bolivia, suggest strong climate-related fluctuations in the extent of *Polylepis* forest cover already 12 000 years ago, providing supporting evidence of the natural fragmentation of *Polylepis* forests (Gosling et al. 2009). The identification and dating of soil charcoal in the northern Ecuadorian Andes also supports fluctuations in forest cover and treeline formation since the beginning of the Holocene due to natural fires (di Pasquale et al. 2008). On the other hand, pollen cores from the Cordillera Urubamba, in southern Peru, suggest a strong decrease in the extent of *Polylepis* forest cover after the arrival of the Spaniards compared to pre-Hispanic times (Chepstow-Lusty et al. 1996; Chepstow-Lusty & Winfield 2000). This supports anthropogenic factors, in particular intensive human land use and unsustainable agro-forestry methods, as one of the main causes for the current fragmented distribution of *Polylepis* forests.

1.3.1. Environmental constraints on Polylepis tree growth and forest distribution

Two main environmental factors controlling *Polylepis* forest distribution are temperature and water availability (e.g. Rada et al. 1996, 2001; Kessler et al. 2007; Macek et al. 2009). These factors are in turn modified by elevation, latitude and topography, and their relative importance seems to vary among species and/or geographical regions. Temperature and solar radiation are the most important factors in humid and cloudy regions, while the importance of water availability increases in dry regions (Braun 1997; Hoch & Körner 2005; Kessler et al. 2007).

Species of *Polylepis* can grow in exceptionally low temperature conditions, apparently lower than several other high-elevation tree species (Kessler & Hohnwald

1998; Lauer & Rafiqpoor 2000, 2002; Hertel & Wesche 2008). Eventually, however, *Polylepis* tree growth is constrained by low temperatures similarly to that of other high-elevation tree species everywhere. Regeneration patterns are likewise affected by low temperatures due to energy-saving needs; thus reproduction from seeds decreases and the proportion of vegetative reproduction increases at low temperatures (Cierjacks 2007; Hertel & Wesche 2008). On the other hand, due to strong solar insolation, high temperatures may cause a heat stress in *Polylepis*. This can be especially critical for seedlings establishment. It has been observed that *Polylepis* seedlings avoid the eastern exposures in Ecuador, probably because of strong solar radiation especially in the mornings when temperatures are still low after cold nights (Sarmiento 1986; Bader et al. 2007; Bader & Ruijten 2008). These conditions can cause water stress in seedlings, as the shoots may lose more water than can be replaced by root water uptake from frozen soil (Körner 2003, 2012; Mayr 2007). Under these conditions photoinhibition may also occur (Ball et al. 1991; Germino & Smith 1999). In Bolivia, in contrast, *Polylepis* forests are taller on the eastern slopes because the increased solar radiation may also increase the average temperature (Kessler et al. 2007).

Figure 2. *Polylepis* forests in nearly natural condition in the Cuzco area, southeastern Peru: a) *P. racemosa* forests at 3900-4000 m in the glacial U-valley of Urubamba. b) *P. subsericans* treeline stand at 4200 m at the base of a slope of glacial erosion, at the border of a wetland in Cancha Cancha valley, Calca. c) Humid *P. pepei* forest with a thick cover of mosses at 4100 m at Abra Malaga. d) *P. sericea* trees after a snow fall at 4200 m on the slope of Mt. Palcay, in the protected area of Machu Picchu. Photographs by J.M. Toivonen.

Drought constrains *Polylepis* tree growth and forest distribution in arid areas. However, *Polylepis* forests, similarly to other treeline forests worldwide, reach their highest elevations in dry regions (Braun 1997; Kessler et al. 2007; Miehe et al. 2007). This is probably related to the positive effect of high solar radiation and temperature conditions favorable to tree growth. The lower limit of annual precipitation for *Polylepis* tree growth, observed for the drought tolerant species *P. tarapacana* in central Bolivia, is 100-200 mm (Fjeldså & Kessler 1996). Fog may allow *Polylepis* to survive in areas of otherwise low water availability. In cloud forest areas, however, the distribution of *Polylepis* is controlled by competition with other tree taxa. The upper soil moisture limit for *Polylepis* is determined by waterlogging. *Polylepis* avoids poorly drained, flat valley bottoms, where cold air masses also tend to accumulate at night (Sarmiento 1986; Young 1993; Kessler 2002; Fjeldså & Kessler 1996).

In addition to constraints caused by temperature and water availability*, Polylepis* avoids soils of high salinity (Fjeldså & Kessler 1996). Geodynamic disturbances (landslides, avalanches, soil erosion) may also control *Polylepis* forest distribution locally by preventing tree colonization. The distribution of *Polylepis* forest stands is often associated with rocky ground. This is presumably related to a favorable microenvironment, in particular temperature (e.g. Fjeldså & Kessler 1996).

1.3.2. Anthropogenic influence on Polylepis forest structure and distribution

It has been estimated that humans first inhabited the Andes approximately 7000–3000 years ago (Baied & Wheeler 1993; Kessler & Driesch 1993). Since then, the Andes have been subject to intensive human land use (Chepstow-Lusty et al. 1996; Chepstow-Lusty & Winfield 2000). The principal land uses have been timber extraction, grazing by domestic animals and the associated burning of pastures (Ellenberg 1958, 1979; Laegaard 1992; Kessler 1995; Purcell and Brelsford 2004). As a consequence, the *Polylepis* forest cover has declined considerably. Human-induced fires in particular have been suggested to contribute significantly to the loss of *Polylepis* forests (Kessler 2000, 2002), and to account for the restriction of forest remnants to habitats protected from fires (Coblentz and Keating 2008). However, it is not clear when this major forest destruction may have happened. It has been suggested that *Polylepis* forest loss occurred at two main times: the first approximately 5000–3000 ago, the second at the time of the Spanish conquest and during the colonial period (Kessler & Driesch 1993). A recent study of the genetic diversity of *P. pauta* and *P. incana* forests in Ecuador supports this view, reflecting both recent and historical genetic isolation (Hensen et al. 2012). Genetic studies of *P. besseri* forests in Bolivia and *P. australis* forests in Argentina, however, do not support the idea of an early anthropogenic forest decline, but indicate relatively recent forest fragmentation, occurring since the Spanish conquest (Julio et al. 2008; Gareca et al. 2013).

Currently, *Polylepis* forests are among the most gravely endangered tropical and subtropical mountain forest ecosystems in the world (UNEP-WCMC 2004). The majority of the ca. 30 species of the genus are classified as vulnerable (IUCN 2013). One of the major threats to remaining *Polylepis* forest stands seems to be habitat degradation, caused especially by livestock grazing but also by wood harvesting for timber and firewood (e.g. Renison et al. 2006, 2010; Jameson & Ramsay 2007). Grazing specifically affects regeneration patterns, favoring vegetative regeneration and reducing regeneration from seeds (Cierjacks et al. 2007, 2008; Toivonen et al. 2011). Long-term grazing and substantial wood harvesting ultimately lead to a decrease in forest biomass and to general forest degradation, manifested as a lack of certain age and/or size cohorts (Renison et al. 2011) and as a decrease in canopy density (Jameson & Ramsay 2007).

Figure 3. Anthropogenically disturbed *Polylepis* forests in Cuzco area, southeastern Peru. a) *P. racemosa* forests at 4300 m near a village and an old copper mine in Mantanay, Urubamba. b) Burnt *P. sericea* forests at 3800 m near Abra Malaga. c) Grazed *P. racemosa* forest with impeded regeneration at 4000 m at the border of Lake Yanacocha, Urubamba. d) An alpaca browsing in *Polylepis racemosa* forest stand at 4100 m in Cancha Cancha valley, Calca. Photographs by J.M. Toivonen.

1.4. The aims of the thesis

Andean *Polylepis* forests are among the highest mountain forest ecosystems worldwide, having a fragmented and often disconnected distribution from the lower elevation montane forests. There has been ample discussion as to the causes of the fragmented distribution of *Polylepis* forests (Ellenberg 1979; Kessler 1995, 2000, 2002; Gosling et al. 2009; Urrego et al. 2011). In this thesis, my purpose is to clarify the role of functional, environmental and anthropogenic factors determining *Polylepis* forest distribution in the Central and Southern Andes. First, I assess, which functional traits enabling *Polylepis* species to grow at high elevations are genetically determined and have been potentially crucial to the species' evolution and adaptation to low temperatures and drought (article **I**). Secondly, I address the question of the causes of the current fragmented distribution of *Polylepis* forests, by searching for a consensus on the importance of natural versus anthropogenic causes determining *Polylepis* forest distribution (articles **II-IV**).

In response to decreased temperature and humidity conditions at high elevations, trees are expected to manifest genetically determined adaptations and phenotypically plastic acclimations in their functional traits. In article **I**, my purpose was to determine whether there is evidence of climatic adaptations regarding these traits, by assessing the degree of genetic determinism in the functional traits of nine *Polylepis* tree species among fourteen important traits that enable trees to withstand cold and dry conditions. The degree of genetic determinism was defined by relating interspecific variation in a functional trait to the climatic niche optima of the species. The assumption was that if this relationship was similar to the expected climate-trait relationship, based on empirical observations in previous studies and on theoretical predictions of climate-trait relationships, any variation observed in the trait must be genetically determined. Another purpose was to determine whether variation in physiological traits is genetically more strongly controlled than that in morphological traits. Finally, I wanted to find out whether the selected functional traits show a phylogenetic signal, i.e. whether closely related species are functionally more similar than distantly related ones.

For high elevation trees, the importance of the micro-climate in defining suitable conditions for tree growth and seedling establishment is expected to increase with elevation as a result of increasing environmental harshness; the anthropogenic impact, conversely, is expected to decrease with elevation because of reduced human accessibility and human population density (Toivonen et al. 2011). Following this principle, my purpose in article **II** was to determine whether *Polylepis* forests are associated with specific topographic positions in the landscape, and whether the potential associations between terrain features and *Polylepis* forest distribution change with elevation.

Polylepis forests form one of the highest treelines in the world. Their growth conditions, and the factors that ultimately constrain tree growth, are nevertheless still poorly known. My purpose in article **III** was to ascertain how tree height changes with elevation among stands of five species of *Polylepis* under different humidity conditions and under human impact versus natural conditions, and whether air or soil temperatures are the crucial determinants of tree height and treeline formation.

Due to the long history of human settlements in the Andes, human influence was expected to strongly affect *Polylepis* forest structure and distributions. In article **IV**, I investigated whether the structural variation of *Polylepis* forest stands can be explained by human disturbance; the latter was quantified in terms of indices of accessibility, such as the geographical distance between a forest stand and the nearest human settlement, road and market center.

2. MATERIAL AND METHODS

2.1. Study area and species

The Andes are the longest continental mountain chain in the world (ca. 7000 km in a north-south direction), ranging from Venezuela to Argentina. The highest peak is Mount Aconcagua (6962 m) in Argentina, but several other volcanoes also exceed 6000 m in elevation. On an evolutionary time-scale, the Andes are a relatively young mountain chain. The uplift of the mountain chain started about 20 million years ago (Burnham & Graham 1999), but the emergence of the majority of the current alpine habitats dates back only a few million years or even less (Gregory-Wodzicki 20000). These new high elevation habitats were inhabited by taxa originating, at least in part, by extensive adaptive radiations of several lowland ancestors (Hooghiemstra & Van der Hammen 2004). The genus *Polylepis* is one of these taxa (Simpson 1986; Kerr 2003; Schmidt-Lebuhn et al. 2006). The current taxonomical classification of *Polylepis* genus suggests ca. 30 ecologically and/or biogeographically distinct species (Schmidt-Lebuhn et al. 2006). The species show a gradual change in their morphological characters: from tall trees with thin leaves, multiple leaflets and multi-flowered inflorescences at the upper parts of humid cloud forests to small-sized trees with small and coriaceous leaves and small inflorescences in high mountain habitats (Simpson 1979, 1986; Kessler 1995; Kerr 2003; Schmidt-Lebuhn et al. 2006).

Article **I** dealt with the climatic adaptations of nine *Polylepis* species originating from different geographical regions in the central and southern Andes, from a wide range of elevation and climatic conditions: from humid montane forests to dry high elevation habitats (Table 1, Fig. 4).

In articles **II-IV**, I studied the natural and anthropogenic constraints determining the *Polylepis* forest distribution in the Cordilleras Vilcanota and Vilcabamba in the Cuzco region, Southeast Peru. The area has been subject to human influence for thousands of years, due to its close proximity to ancient centers of human settlement by the Urubamba River (Chepstow-Lusty et al. 1996; Chepstow-Lusty & Winfield 2000). Despite this long human history, the area is known to have fairly extensive *Polylepis* forests at elevations between 3300 m and 4950 m (Lloyd & Marsden 2011; Toivonen et al. 2011). The climate of the region varies from a semi-dry to a sub-humid tropical alpine climate, with a pronounced wet season from October to March. Diurnal temperature fluctuations are strong, especially in the dry season. Salient differences in humidity and temperature within the region have enabled the evolution, diversification and specialization of a number of plant and animal taxa, including the genus *Polylepis* (Fjeldså 1992; Fjeldså and Kessler 1996). Seven species of the genus are found within a radius of ca. 30 km around the town of Urubamba. This is the highest concentration of *Polylepis* species found anywhere (Fjeldså and Kessler 1996). In article **II** I focused on monospecific, elevationally segregated forest stands of *P. racemosa* and *P. subsericans* on the

semi-dry slopes of the Cordillera Urubamba, part of the Vilcanota mountain chain. The study area is characterized by several steep glacial valleys, with smaller ravines connected to them. The highest snow peak of the Cordillera, Nevado Chicon, reaches 5400 m of elevation. In articles **III-IV** I studied the semi-dry and sub-humid forest stands of the Cordilleras Urubamba and Vilcabamba, with the highest snow peak, Salcantay, reaching ca. 6300 m. In this area species are segregated not only by elevation but also by humidity. (Table 1, Fig. 4).

During recent decades the human population has increased greatly in the area, mainly in the valley bottom of the Urubamba River (the Sacred Valley of the Incas), while high elevations have remained sparsely populated. At elevations above 3800 m only a few villages are found, but cattle and sheep grazing are still intensively practiced there.

Table 1. Geographical regions (A-E), species and elevation ranges for all 11 species used in the four articles. Asterisks indicate a treeline species.

| Geographical region	Species	Elevation (m)	Article
A. Sub-humid eastern Andes of South Peru	*P. pauta*	2700-3600	I, III-IV
	P. sericea	3700-4200	III-IV
	P. pepei*	4100-4600	III-IV
B. Semi-dry eastern Andes of South Peru	*P. microphylla*	3300-4000	I
	P. racemosa	3200-4200	I-IV
	P. subsericans*	4200-4900	I-IV
C. Humid eastern Andes of central Bolivia	*P. hieronymi*	1900-3300	I
	P. neglecta	2400-3500	I
	P. tomentella*	3200-4500	I
D. Dry western Andes of central Bolivia	*P. tarapacana**	4000-4800	I
E. Semi-dry eastern Andes of Argentina	*P. australis**	1800-3800	I
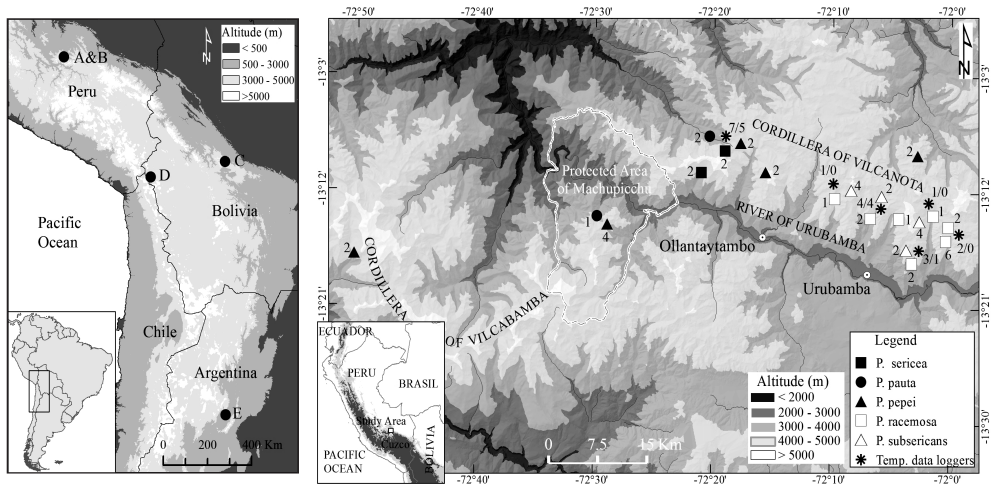
Figure 4. Maps of study areas. Left side: Five regions (A-E) showing provenances of different *Polylepis* species used in article **I**. A) Sub-humid eastern Andes of southern Peru, B) Semi-dry eastern Andes of southern Peru, C) Humid eastern Andes of central Bolivia, D) Dry western Andes of central Bolivia, E) Semi-dry eastern Andes of Argentina. Right side: Study area in Cordilleras Vilcanota and Vilcabamba, Cuzco, South Peru (articles **II-IV**). Black symbols indicate study sites at sub-humid areas and white symbols at semi-dry areas. Number of study plots at each site is indicated close to symbols. Asterisks indicate temperature data loggers (air/soil).

2.2. Common garden experiment

Genetically determined traits are typically unresponsive to environmental variation, whereas plastic traits respond to varying environmental conditions (e.g. Clausen *et al.* 1940; Bradshaw 1965; Schlichting 1986; Sultan 2000). Genetic determinism in a given trait can be studied by growing individuals of different species in the same environment and observing whether they show interspecific variation in the trait. If they do, the trait must be genetically determined. In article **I**, I carried out a common garden experiment at the greenhouses of the Experimental Botanical Garden of the University of Göttingen in 2008, to assess the degree of genetic determinism in the important functional traits of nine *Polylepis* species originating from different climatic conditions and geographic regions in the Andes. I grew individuals of different *Polylepis* species from seeds, seedlings or root suckers under constant greenhouse conditions for 18 months and measured several functional traits of the species, including above- and belowground morphology and photosynthetic performance, measured as light response curves of photosynthesis (Meir et al. 2007). The traits measured were selected according to their expected importance for the species' ability to withstand cold and dry conditions (Table 2).

Table 2. Functional traits measured

Trait	Unit
Single leaf area	cm²
Specific leaf area	cm² g^{-1}
Specific root area	cm² g^{-1}
Specific root length	m g^{-1}
Root tip abundance	n mg^{-1}
Leaf-area–based maximum net photosynthesis rate	μmol CO$_2$ m^{-2} s^{-1}
Leaf-mass–based maximum net photosynthesis rate	nmol CO$_2$ g^{-2} s^{-1}
Stomatal conductance to water vapor in maximum light conditions	mol H$_2$O m^{-2} s^{-1}
Dark respiration rate	μmol CO$_2$ m^{-2} s^{-1}
Leaf transpiration rate	mol H$_2$O m^{-2} s^{-1}
Ratio of intercellular to ambient CO$_2$ concentration	mol CO$_2$ mol CO$_2$$^{-1}$
Quantum use efficiency [1]	unitless
Light saturation point [2]	μmol photons m^{-2} s^{-1}
Light compensation point [3]	μmol photons m^{-2} s^{-1}

[1] Coefficient of initial slope of light response curve of photosynthesis, indicating efficiency of light use in CO$_2$ assimilation
[2] PAR (photosynthetically active radiation) value at which 90 % of maximum net photosynthesis is reached and the carbon assimilation rate can no longer increase because of limited carboxylation
[3] PAR value at which photosynthesis and respiration are balanced, so that the rate of CO$_2$ assimilation matches the rate of CO$_2$ released from respiration

2.3. Determination of species climatic niche optima

In this work, I used a two dimensional approximation of the multidimensional niche space (Hutchinson 1957), determined by two relevant and readily interpretable climatic variables: mean annual temperature and annual precipitation (**I**). Toward this end, I compiled climate data of species occurrence localities, using information from several scientific publications documenting *Polylepis* species locations, my own field excursions, and georeferenced occurrence information from specimen location data in the GBIF (http://www.gbif.org/) and Tropicos (http://www.tropicos.org/) databases. I extracted the climate data for the species occurrence localities from WorldClim global modeled climate data (http://www.worldclim.org) at a spatial resolution of ~1 km^2 (Hijmans *et al.* 2005). Before using all this legacy data, I manually cleaned it. For species with a large distribution range I only included climate records near the areas of the provenances, that I used in the experiment to ensure a correspondence between the climate data and the species ecophysiological data. For species with a narrow distribution range, I used all climatic records. WorldClim climate data includes 19 bioclimatic variables; of these, I used mean annual temperature and total annual precipitation, two easily interpretable and statistically uncorrelated variables. Based on Principal Component Analysis (PCA), these two variables also captured a large part of the variation in climatic niche space based on all 19 bioclimatic variables. Species climatic niche optima were defined as species-specific means for mean annual temperature and total annual precipitation. The number of climatic records used in calculating the species-specific means varied from 10 to 49, except for one

species (*P. tomentella*), represented by 139 records. The determination of the climatic niche optima was based on climatic records from the current distribution range of the species. The current distribution is almost certainly reduced by human activities; thus the estimated niche optima may not reflect the whole ecological potential of the species.

2.4. GIS and remote sensing methods

To study the associations between micro-scale terrain features and *Polylepis* forest distribution, I used a remote sensing -based approach (**II**). I mapped *Polylepis* forest patches in the Cordillera Urubamba using a high-resolution aerial photograph from the year 2010, with a pixel size of 2 m x 2 m (available in Bing Map web mapping service). The image was largely cloud-free, allowing accurate digitizing of *Polylepis* forest stands on a GIS (Geographic Information Systems) platform. Parts that were covered by clouds were mapped with the help of Google Earth satellite images (Google Earth Quickbird image of August 2012 with a pixel size of 2.4 m x 2.4 m, accessed in September 2013). Extensive ground truthing was carried out during several field excursions since 2006. This mapping exercise resulted in much higher resolution data than in previous studies examining associations between topography and *Polylepis* forest distribution (e.g. Braun 1997; Bader et al. 2007; Bader & Ruijten 2008; Coblentz & Keating 2008) (Fig. 5).
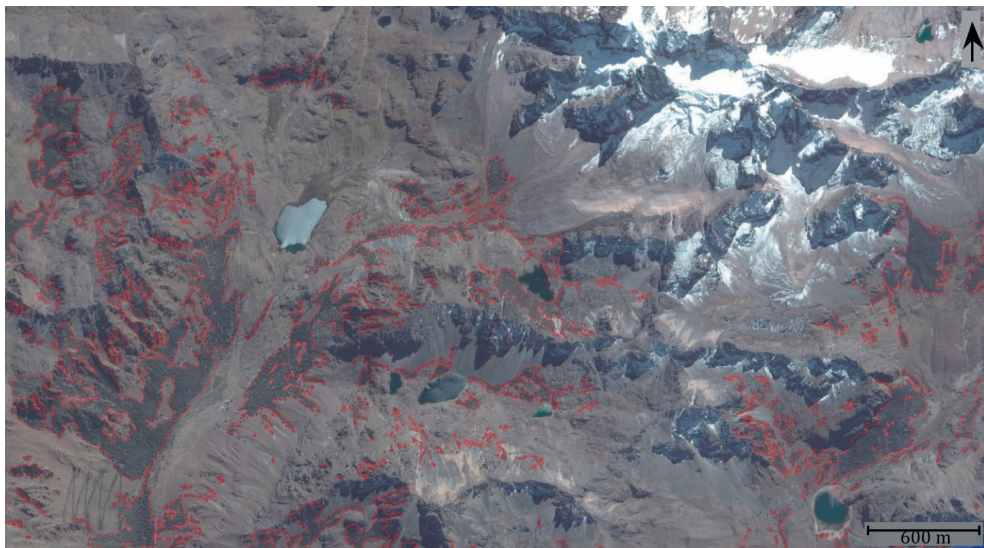

Figure 5. An example of the digitized *Polylepis* forest stands (red outline) in the Cordillera Urubamba. The image is an aerial photograph from the year 2010 with a pixel size of 2 m x 2 m (Bing Map web mapping service).

I selected ten terrain features and indices, based on their expected importance for tree growth and seedling establishment and survival at tropical high elevations

(Table 3). Terrain features and indices were calculated using the Aster Global Digital Elevation Model (version 2), with 8m of vertical resolution and 30 m x 30 m of pixel size with algorithms available in SAGA GIS and ArcGIS.

Table 3. Selected terrain features and indices based on Aster Global Digital Elevation model (version 2).

Terrain feature / index	Unit	Description
1. Aspect	Categorical variable	Exposition towards slope is facing
2. Morphometric protection index	Unitless	Topographic sheltering; calculation based on pixel values within 300 m radius
3. Overland distance to the nearest river	Meters	Overland distance to the nearest river measured using DTM-based potential river network
4. Plan curvature	Unitless	Terrain surface curvature described perpendicularly to slope steepness. May be convex, linear or concave.
5. Profile curvature	Unitless	Terrain surface curvature described parallel to slope steepness. May be convex, linear or concave.
6. Slope steepness	°	Slope angle in degrees
7. Solar radiation	Mwh m^{-2} year^{-1}	Potential annual incoming solar radiation (insolation); quantitative equivalent of exposure
8. Direct solar radiation hours	h year^{-1}	Duration of potential annual direct incoming solar radiation
9. Topographic wetness index	Unitless	Soil moisture and surface saturation index; calculation based on control of local topography on hydrological processes
10. Vertical distance to the nearest river	Meters	Vertical distance to nearest river, measured using the DTM-based potential river network

2.5. Measurements of forest structure and microclimate

The fieldwork for forest structure and microclimate measurements was carried out in two campaigns (**III-IV**). In 2006, I established 28 plots of 10 m x 10 m in the Cordilleras Urubamba and Vilcabamba, Cuzco, Peru, with the aim of covering the distribution of the five *Polylepis* species found in the sub-humid and semi-dry areas of the cordilleras. Plots ranged from 3070 m to 4450 m of elevation. Averaging the data between plots established within the same forest stand and differing only slightly in elevation resulted in a total of 24 plots, of which eleven were in semi-dry areas (six in *P. racemosa* stands and five in *P. subsericans* stands) and thirteen in sub-humid areas (four in *P. pauta* stands, four in *P. sericea* stands, five in *P. pepei* stands). In each plot, I measured tree circumference at breast height and estimated the height of all *Polylepis* trees ($\geq$10 cm of circumference), and counted

the number of seedlings and root suckers. I also installed temperature dataloggers (DS 1922 Thermochron iButtons, Hubbart et al. 2005) to measure air temperature in the shaded canopy and soil temperature in the root zone at 10 cm depth in eleven plots. In 2011, nineteen extra plots were established by my collaborators, with the aim of covering the widest possible elevational range per species. In these plots, the tree height and circumference of *Polylepis* trees ($\geqslant$10 cm of circumference) were measured and seven extra dataloggers were installed to measure air temperature. In total, air temperature data were successfully recorded in eighteen and soil temperature in ten plots during one, two or three years (between June 2006 and April 2012), depending on the accessibility of the stand. The measurement readings were mostly taken at four hours intervals.

2.6. Numerical analyses

To find out whether inter-specific variation in a given trait had evolved as a response to the environment, I related species-specific mean values in the trait to the preferred environmental conditions (niche optima) of the species (**I**). If they are correlated, the evolutionary adaptation of the species along the gradient of the environmental factor can be expected to include genetically determined modifications in the trait. To relate the species-specific means of functional traits to the estimated climatic niche optima of the species, I used ordinary linear regressions. To illustrate the relationships among all functional traits and between functional traits and climate, I conducted a redundancy analysis (RDA), with species-specific means of all fourteen functional traits as response variables and species-specific means for climatic niche variables as explanatory variables. To study the phylogenetic signal in functional traits, I calculated phylogenetic distances between the species based on the phylogenetic tree presented by Schmidt-Lebuhn et al. (2006). Since the tree is not time-calibrated, I calculated a phylogenetic distance matrix based on the number of bifurcations between species. I also calculated dissimilarity matrices for each functional trait based on Euclidean distances. I compared the matrices using a Mantel test of matrix correspondence (Smouse et al. 1986).

To study the associations between terrain features and *Polylepis* forest distribution, as well as possible elevational changes in these associations (**II**), I divided the data into three elevation belts (3800-4199 m, 4200-4599 m, 4600-4950 m). To detect differences in mean values and frequency distributions of terrain features between the *Polylepis* stands and the landscape, I calculated marginality and specialization indices. Marginality indices describe a relative difference in a terrain feature between the mean for forest sites and for the landscape in relation to the total range or standard deviation of the terrain feature in the landscape (Hirzel et al. 2002). The specialization index was calculated as the ratio of the standard deviation of variation in a landscape terrain feature to the standard deviation of variation in that terrain feature at the *Polylepis* forest sites. A randomly chosen set of cells is expected to have a specialization value of one. Values higher than one indicate

some form of specialization. The specific values for this index depend on the reference set (Hirzel et al. 2002). To illustrate differences in the frequency distributions of terrain features between the landscape and *Polylepis* forest stands, I classified slope exposition (aspect) into eight categories (north, northeast, east etc.) and the other nine terrain variables into twenty categories at equal intervals. I also used the variable contribution and Jackknife tests of Maxent species distribution modeling (Phillips et al. 2006) to test the importance of each terrain feature in the prediction of *Polylepis* forest cover by elevation belts.

To study how *Polylepis* tree height changes with elevation with respect to variation in temperatures, humidity and human impact (**III**), a) tree height-dbh (diameter at breast height) relationship was compared among five species of *Polylepis* at natural and disturbed sites, b) temperature conditions based on micro-climatic measurements were compared between sub-humid and semi-dry sites, and c) tree height was compared between sub-humid and semi-dry sites and between natural and disturbed sites. Due to the small number of trees per plot, data from the plots of the same species were combined within 200 m wide elevation belts. In six of the belts signs of human impact were observed; the other six were considered unaffected. Tree height was plotted against dbh and a fit between linear and non-linear models was compared with R^2 and AIC-values (Burnham & Anderson 2002). Slenderness, calculated as tree height divided by dbh (Wang et al. 1998) and mean maximum tree height, calculated as the mean of 10 % of the tallest trees, were also quantified. Air and soil temperatures were compared between sub-humid and semi-dry sites after taking into account a possible elevation trend in temperatures. If a significant elevation trend was observed, residual variations were compared rather than raw values.

To study the association between forest structure and accessibility (**IV**), I related forest structural variables to indices of accessibility using ordinary linear regressions. As a measure of accessibility of the forest stand, I measured the geographical distance between each study plot and the nearest human settlement, road and market center, using the satellite images of Google Earth. Because of the commonly documented elevational dependence of forest structural variables (e.g., Wilson et al. 1987; Young 1993; Paulsen et al. 2000; Kessler et al. 2007), before relating these variables to the indices of accessibility I first removed the effect of elevation. This was done by relating the variables to elevation in a linear regression and using the residual variation in a regression with accessibility indices. Human influence has historically been stronger in the inner and drier parts of the Andes, where the centers of ancient pre-Hispanic cultures were located, than in the more remote and inaccessible humid Amazonian side of the Andes. I therefore analyzed the data from dry and humid slopes separately. Sites close to each other are typically more similar than sites lying far apart, i.e. they are spatially autocorrelated (Dale et al. 2002), which can complicate the interpretation of the results. I tested the spatial structure of the data comparing the dissimilarity matrices of Euclidean distances calculated for each residual variable of forest structure and matrices of geographical distances between the plots with a Mantel test of matrix correspondence (Smouse et al. 1986).

3. RESULTS AND DISCUSSION

I found that the ability of *Polylepis* species to inhabit Andean high elevations appear to be based on certain genetically determined functional adaptations to cold and dry conditions (**I**), and that *Polylepis* forest distribution is constrained by a number of natural and anthropogenic factors (**II-IV**). More specifically, I found that topographic features play an important role in determining the current spatial pattern of *Polylepis* forest distribution, through the formation of refugia from human activities at lower elevations and of favorable micro-climatic conditions at higher ones (**II**). We also found remarkably low treeline temperatures and high tree statures near treelines in comparison to global means, and air temperatures rather than soil temperatures are suggested as the crucial aspect of temperature conditions in limiting tree growth at high elevation treelines (**III**). I also found that human influence, measured in terms of forest stand accessibility, predicted stand structure and regeneration: more accessible stands were more degraded in terms of structural variables and regeneration than less accessible ones (**IV**).

3.1. Climatic adaptations in functional traits of *Polylepis* species

In article **I,** I assessed the genetic determinism of important functional traits of *Polylepis* species, traits which enable the species to inhabit the cold and dry conditions of the high Andes, and found some significant relationships between interspecific variation in functional traits and the climatic niche optima of *Polylepis* species. Species-specific means of specific leaf area increased and root tip abundance decreased with increasing mean annual temperature optima. This is in line with the well-known size reduction in above-ground tree biomass (e.g. Cordell et al. 1998; Moser et al. 2007; Hertel & Wesche 2008; Macek et al. 2009) and the reduction in below-ground biomass (e.g. Hertel et al. 2008; Hertel & Schöling 2011; Moser et al. 2011) with decreasing temperature. I also found a negative relationship between the mass-based maximum photosynthesis rate and mean annual temperature optima, suggesting that tree growth is limited by carbon acquisition (photosynthesis) at high elevations and not only by metabolic constraints related to carbon investment (Körner 1998; Hoch & Körner 2005). This finding, supporting the carbon source limitation hypothesis, is in line with recent findings on tree ecophysiology *in situ* at high elevation treelines (Wieser et al. 2010; Wittich et al. 2012). Species-specific means of light saturation and light compensation points were also negatively related, and quantum use efficiency positively related, to mean annual precipitation optima. This may indirectly reflect a response by these photosynthetic traits to light conditions, which are largely determined by cloud cover and thus also by precipitation. In general, the relationships between the species-specific means of functional traits and species climatic niche optima can be interpreted as evidence of genetically determined climatic adaptations to cold and/or dry conditions, which have enabled species of *Polylepis* to colonize Andean high elevations.

However, some of the climate-trait relationships that we expected based on existing theories and previous empirical evidence were not manifested (**I**). For example, neither specific leaf area nor specific root area or root length were related to climatic niche variables, suggesting a possible acclimation of these traits. It thus appears that the functional traits that are crucial in enabling *Polylepis* species to inhabit high elevations involve both genetic and phenotypic components.

I also found that among the traits and species studied physiological traits were not more strongly related to climatic niche optima than morphological ones, indicating that the former are not genetically more strongly controlled than the latter (**I**). Thus the hypothesis of the conservative inheritance of physiological traits was not supported.

Single leaf area was the only trait showing a significant phylogenetic signal; in other words, closely related species were more similar with regard to single leaf area than distantly related species (**I**). This suggests that most of the manifested climate-trait relationships are indeed not caused purely by phylogeny, but are mainly a result of ecological specialization along an environmental gradient. An adaptive trend towards dry environments has also earlier been found within the genus *Polylepis* (Simpson 1986; Schmidt-Lebuhn et al. 2006, 2010); adaptations to cold environments, on the other hand, may have occurred several times independently, shown as a fairly even and dispersed distribution of cold climate species in the phylogenetic tree of the genus.

3.2. Terrain features and *Polylepis* forest distribution

In article **II**, I studied the association between terrain features and *Polylepis* forest distribution. Human influence plays an important role in determining the natural distribution and growth conditions of *Polylepis* forests (Kessler 1995, 2000, 2002; Purcell & Brelsford 2004; Renison et al. 2006; Coblentz & Keating 2008). The associations that I found are therefore interpreted taking this into account. My principal finding was an elevational shift in the preferences of *Polylepis* forest stands in relation to terrain features. Stands were more frequently found in humid, sheltered, concave positions at lower and middle elevations (3800-4199 m and 4200-4599 m), and at sunnier and drier convex positions in western and northwestern exposures at high elevations (>4600 m). Stands at lower elevations were also close to rivers measured in overland distance, but high above the level of the rivers in terms of vertical distance, while at high elevations the pattern was the opposite. The associations observed at low elevations may be caused by human land use, especially by fire regimes and grazing. Topographically sheltered and humid sites near rivers at low and middle elevations may be better protected from grassland burning for pasture than the landscape in general. A strong difference in the vertical distance from the nearest river between *Polylepis* stands and the landscape mean at low elevations may also be a consequence of human activities, areas with difficult access (higher vertical distance from rivers) being better

protected. However, there may also exist a natural preference, *Polylepis* stands avoiding valley bottoms due to an accumulation of cold air masses at night (Sarmiento 1986; Young 1993; Kessler 2002; Fjeldså & Kessler 1996). The topographic associations that we observed at high elevations were interpreted as better reflecting the natural preferences of *Polylepis* than the associations that we observed at lower elevations. This is due to greater environmental harshness with increasing elevation, in particular temperature constraints for tree growth (Kessler et al. 2007; Körner 2012); the human impact had also been expected to decrease with increasing elevation (Toivonen et al. 2011). Sunnier and drier convex positions at west and northwest exposures seemed to be suitable for *Polylepis* at high elevations. The elevational pattern of the associations between terrain features and *Polylepis* forest distribution was similar to the pattern of the proportional contribution of each terrain feature to the performance of the predictive model of forest stand distribution.

3.3. *Polylepis* tree height, elevation, climate and human impact

Article **III** dealt with the associations between *Polylepis* tree height, elevation, climate conditions and human impact. The relationship between tree height and diameter at breast height (dbh) showed a linear relationship in elevation belts that were affected by human impact, whereas at four of the six undisturbed elevational belts maximum tree height leveled off at a certain dbh. The lack of tree height saturation at disturbed sites supports the earlier findings of lower maximum tree height at disturbed sites due to logging of the biggest trees (Toivonen et al. 2011).

In natural stands, maximum tree height decreased gradually with elevation at humid sites, but at dry sites tree height peaked at middle elevations (**III**). This may be caused by increasing drought towards low elevations at dry sites. Drought-related treelines have also been documented in a forest-steppe ecotone in Patagonia (Hertel et al. 2008) and in rain-shadowed mountain valleys (Holtmeier 2009).

Maximum tree height differed considerably between dry and humid areas. Especially near the treeline, trees grow taller in dry areas (**III**). This is a well-known phenomenon (Kessler et al. 2007; Miehe et al. 2007; Körner 2012), most likely resulting from the difference in solar radiation (Lauer 1982). Dry and humid areas differed in air temperatures but not in soil temperatures, air temperatures being higher in dry areas. This confirms the importance of solar radiation in determining tree height, and indicates that tree height in our study area is more closely related to air temperatures than to soil temperatures. This can be explained by a strong atmospheric coupling of high tree stature; it has been shown that the above-ground parts of high stature vegetation, apical meristems in particular, are faced with much lower temperatures than those of lower stature vegetation (e.g. Hadley & Smith 1987; Wilson et al. 1987; Grace et al. 1989; Körner 2003).

Remarkably tall trees were documented near treelines: 9 m tall at 4530 m in humid areas and 13 m tall at 4650 m in dry areas (**III**). Such tall trees at corresponding elevations have not been documented in any previous studies worldwide (Hoch & Körner 2005; Kessler et al. 2007; Miehe et al. 2007; Bader & Ruijten 2008). Based on satellite images, the highest elevation forest stands are located at 4700 m in humid areas and at 4950 m in dry areas. This suggests an abrupt decrease in tree height just below 4700 m, also found for *Polylepis* stands in Bolivia (Hertel & Wesche 2008) as well as for certain other treeline species in tropical mountains (Miehe & Miehe 2000; Miehe et al. 2007).

We also found substantially low air and soil temperatures for high elevation *Polylepis* forest stands (**III**). Mean growing season soil temperatures were 5.2 °C for *P. pepei* at 4530 m and 4.6 °C for P. *subsericans* at 4650 m, whereas the global treeline mean is 6-7.5 °C (Körner & Paulsen 2004; Körner 2012). Low mean soil temperatures in the growing season have also been documented for *Polylepis* elsewhere in the Andes: 4.5-6.0 °C at 4000-4100 in Ecuador (Lauer & Rafiqpoor 2000, 2002) and 4.7-5.4 °C at 4810 m in western Bolivia (Hoch & Körner 2005). Thus there is increasing evidence that *Polylepis* treeline forests grow under lower temperature conditions, especially soil temperatures, than other treeline forests worldwide. This may be due to specific physiological adaptations, such as decreased leaf size and increased root tip abundance (Toivonen et al. 2013), that enable the species of *Polylepis* to withstand especially demanding environmental conditions. It may also be possible that soil temperatures are in fact not limiting for *Polylepis*, but rather air temperatures, which were also shown to be related to tree height differences between dry and humid areas. Further research is needed to confirm the crucial aspects of temperature conditions and to clarify the physiological basis of the specific adaptations, to better understand the limitations of tree growth at high elevations.

3.4. Accessibility and structural variation of *Polylepis* forests

In article **IV** I studied the structural variation of *Polylepis* forest stands in relation to indices of accessibility, as a proxy for the degree of human disturbance, calculated as the geographical distance between forest stands and the nearest human settlement, road and market center. *Polylepis* forest structure was explained by indices of accessibility in both dry and humid areas, but the relationships differed between areas. In general, forest stands with easy access (near human settlements, roads and market centers) were more degraded than those with difficult access (far from settlements, roads and market centers). In humid areas the distance from the nearest road was clearly the most important factor explaining the forest structure, whereas in dry areas the most important factor was the distance from the nearest market center. In both areas, distance from the nearest human settlement was negatively related to the proportion of vegetative regeneration. The success of vegetative regeneration near villages was presumably caused by a positive effect of moderate disturbance, related to trampling and grazing by

domestic animals, also found by Cierjacks et al. (2007, 2008). Likewise Hagaman (2006) found that *Polylepis* stands near villages were more impacted by grazing in particular than stands far from villages. *Polylepis* forest canopy cover and soil loss have also been documented to relate similar distance based indirect measures of human impact (Cingolani et al. 2008; Renison et al. 2010). Forest structure was not more closely related to indices of accessibility for drier valleys than humid ones, except the stronger historical human influence in drier valleys. This, however, does not necessarily mean that there is no difference in the degree of degradation between dry and humid areas in absolute terms. In general, my study shows that simple measures of geographical distances can predict the variation in biomass and regeneration patterns of *Polylepis* forests. Thus these measures can be used to identify areas where *Polylepis* forests are most degraded, or at the greatest risk of degradation, and thus in urgent need of protection and sustainable management.

4.   CONCLUSIONS

Species of the high Andean tree genus *Polylepis* form special high elevation treeline habitats, at up to 5000 m of elevation in the Central Andes. These habitats are of considerable importance for a number of other endemic plant and animal species (Fjeldså 1992; Servat et al. 2002; Lloyd and Marsden 2011). The current distribution of *Polylepis* forests is fragmented and disconnected from that of other, lower-elevation montane forests. There has been ample discussion as to the causes of the fragmented distribution of the forests. In this thesis, my purpose was to identify the functional traits that have been crucial for *Polylepis* in its adaptation to cold and dry conditions, and to examine the role of natural factors versus human influence in determining the current distribution of *Polylepis* forests.

In answer to these questions, I present four new findings concerning the functional, environmental and anthropogenic factors determining Andean *Polylepis* forest distribution and treeline formation in the Andes. First, I show that *Polylepis* species have certain specific genetically determined functional adaptations, such as reduced leaf size, increased root tip abundance, and reduced mass-based photosynthetic rate (**I**). The first two are advantageous in colonizing cold and dry high elevation habitats, while the last one, the reduced photosynthetic rate, supports the carbon source limitation hypothesis for tree growth at high elevations. These findings add to our scientific knowledge concerning high elevation adaptations in trees, and have significant implications for the discussion as to the factors constraining tree growth at high-elevation treelines globally. They can also be applied as important base line information predicting the responses of high-elevation tree species to global climate change. Due to the complexity of interactions and trade-offs between functional traits and climate, however, such inferences must be drawn with caution. In future, it would be interesting to relate phylogeny, climatic niches and functional traits between all species of the genus, as well to carry out *in situ* measurements of functional traits.

Second, I show that terrain features play an important role in determining the current distribution of *Polylepis* forests through the formation of refugia from human activities at lower elevations and of favorable micro-climatic conditions at higher ones (**II**). This result confirms the importance of human influence in studying associations between vegetation and the environment. Even more interestingly, it evokes several new questions as to the role of natural factors constraining *Polylepis* forest distribution. Noteworthy topics for future research would include for example the role of the last glaciation and current processes of glacial erosion in preventing tree colonization, and aspects related to soils and nutrient uptake.

Third, remarkably low air and soil temperatures and high tree statures at *Polylepis* treelines were found out compared to the global means, and some new evidence was presented supporting the role of air temperatures rather than soil temperatures

to constrain tree growth at high elevations (**III**). These findings have important implications for the discussion concerning high elevation treeline formation worldwide. However, the specific functional mechanisms behind the link between tree growth and air and/or soil temperatures remain to be studied.

Fourth, I showed that indices of accessibility, used as indirect measures of the human impact on forest stands, predict stand structure and regeneration: stands of higher accessibility (near human settlements, roads and market centers) are more degraded regarding structural variables and regeneration than stands of lower accessibility (**IV**). This information can be used for the rapid identification of areas where *Polylepis* forests are most degraded or at the greatest risk of degradation, thus having important practical applications for conservation and sustainable forest management.

With these four findings, I conclude that the success of *Polylepis* species in inhabiting the high Andes is based on specific climatic adaptation, in particular in leaf and root morphology. On the other hand, the absence of *Polylepis* forests in large areas of the Andes is the result of several environmental and anthropogenic constraints. The role of environmental constraints determining *Polylepis* forest distribution becomes greater towards high elevations, while at low elevation the distribution is largely defined by human influence. This information has important implications for our understanding of the causes of the current distribution of *Polylepis* forests, as well as for the conservation and restoration of *Polylepis* forests in the Andes.

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6. REFERENCES

Azócar, A., Rada, F. & García-Núñez 2007. Functional characteristics of the arborescent genus *Polylepis* along a latitudinal gradient in the high Andes. *Interciencia* 32: 663-668.

Bader, M.Y. & Ruijten, J.J.A. 2008. A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography* 35: 711-723.

Bader, M.Y., van Geloof, I. & Rietkerk, M. 2007. High solar radiation hinders tree establishment above the alpine treeline in northern Ecuador. *Plant Ecology* 191: 33–45.

Baied, C.A. & Wheeler, J.C. 1993. Evolution of high Andean puna ecosystems: environment, climate, and culture change over the last 12 000 years in the central Andes. *Mountain Research and Development* 13: 145–156.

Ball, M.C., Hodges, V.S. & Laughlin, G.P. 1991. Cold-induced photoinhibition limits regeneration of snow gum at tree- line. *Functional Ecology* 5: 663–668.

Barry, R.G. 1981. Mountain weather and climate. Methuen, London.

Berry, J.A. & Björkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* 31: 491-543.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155.

Braun, G. 1997. The use of digital methods in assessing forest patterns in an Andean environment: the *Polylepis* example. *Mountain Research and Development* 17: 253–262.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burnham, R.J. & Graham, A. 1999. The history of Neotropical vegetation: new developments and status. *Annals of the Missouri Botanical Garden* 86(2): 546–589.

Cabrera, H.M., Rada, F. & Cavieres, L. 1998. Effects of temperature on photosynthesis of two morphologically contrasting plant species along an altitudinal gradient in the tropical high Andes. *Oecologia* 114: 145-152.

Caldwell, M.M. 1968. Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecological Monographs* 38: 243-268.

Caldwell, M.M., Teramura, A.H. & Tevini, M. 1989. The changing solar ultraviolet climate and the ecological consequences for higher plants. *Tree* 4: 363-367.

Chepstow-Lusty, A.J., Bennett, K.D., Switsur, V.R. & Kendall, A. 1996. 4000 years of human impact and vegetation change in the central Peruvian Andes—with events paralleling the Maya record? *Antiquity* 70: 824–833.

Chepstow-Lusty, A.J. & Winfield, M. 2000. Inca agroforestry: lessons from the past. *Ambio* 29(6): 322–328.

Cierjacks, A., Rühr, N.K., Wesche, K. & Hensen, I. 2008. Effects of altitude and livestock on the regeneration of two tree line forming *Polylepis* species in Ecuador. *Plant Ecology* 194: 207-221.

Cierjacks, A., Wesche, K. & Hensen, I. 2007. Potential lateral expansion of *Polylepis* forest fragments in central Ecuador. *Forest Ecology and Management* 242: 477–486.

Cingolani, A.M., Renison, D., Tecco, P.A., Gurvich, D.E. & Cabido, M. 2008. Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. *Journal of Biogeography* 35: 538–551.

Clausen, J., Keck, D.D. & Hiesey, W.M. 1940. Experimental studies on the nature of species. 1. Effect of varied environments on western North American plants. Carnegie Institution of Washington Publication 520, Washington DC.

Coblentz, D. & Keating, P.L. 2008. Topographic controls on the distribution of tree islands in the high Andes of south-western Ecuador. *Journal of Biogeography* 35: 2026–2038.

Cordell, S., Goldstein, G., Mueller-Dombois, D. & Vitousek, P.M. 1998. Physiological and morphological variation in *Metrosideros polymorphy*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* 113: 188–196.

Dale, M.R.T., Dixon, P., Fortin, M-J., Legendre, P., Myers, D.E. & Rosenberg, M.S. 2002. Conceptual and mathematical relationships among methods for spatial analysis. *Ecography* 25(5): 558–577.

di Pasquale, G., Marziano, M., Impagliazzo, S., Lubritto, C., de Natale, A. & Bader, M.Y. 2008. The Holocene treeline in the northern Andes (Ecuador): first evidence from soil charcoal. *Palaeogeography, Palaeoclimatology, Palaeoecology* 259: 17–34.

Ellenberg, H. 1958. Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. Umschau 1958: 645–681.

Ellenberg, H. 1979. Man's influence on tropical mountain ecosystems in South America. *Journal of Ecology* 67: 401–416.

Fjeldså, J. 1992. Biogeography of the birds of the Polylepis woodlands of the Andes. In: Balslev, H. & Luteyn, J.L. (eds) *Páramo*. An Andean ecosystem under human influence. Academic Press, Padstow, Great Britain.

Fjeldså, J. & Kessler, M. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highlands of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes. NORDECO, Copenhagen.

Gaul, D., Hertel, D., Borken, W., Matzner, E. & Leuschner, C. 2008. Effects of experimental drought on the fine root system of mature Norway spruce. *Forest Ecology and Management* 256: 1151-1159.

Germino, M.J. & Smith, W.K. 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant, Cell and Environment* 22: 407–415.

Gareca, E.E., Breyne, P., Vandepitte, K., Cahill, J.R.A., Fernandez, M. & Honnay, O. 2013. Genetic diversity of Andean *Polylepis* (Rosaceae) woodlands and inferences regarding their fragmentation history. *Botanical Journal of the Linnean Society* 172: 544–554.

Grace, J., Allen, S.J. & Wilson C. 1989. Climate and the meristem temperatures of plant communities near the tree-line. *Oecologia* 79: 198-204.

Gregory-Wodzicki, K.M. 2000. Uplift history of the Central and Northern Andes: a review. *Geological Society of America Bulletin* 112(7): 1091–1105.

Gosling, W.D., Hanselman, J.A., Knox, C., Valencia, B.G. & Bush, M.B. 2009. Long-term drivers of change in *Polylepis* woodland distribution in the central Andes. *Journal of Vegetation Science* 20: 1041-1052.

Hadley, J.L. & Smith, W.K. 1987. Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 73: 82-90.

Hagaman, D.J. 2006. Conservation and use of *Polylepis pepei* woodlands in the Apolobamba mountains of Bolivia. MSc thesis, University of Wisconsin-Madison.

Hensen, I., Cierjacks, A., Hirsch, H., Kessler, M., Romoleroux, K., Renison, D. & Wesche, K. 2012. Historic and recent fragmentation coupled with altitude affect the genetic population structure of one of the world's highest tropical tree line species. *Global Ecology and Biogeography* 21: 455-464.

Hertel, D. & Schöling, D. 2011. Norway spruce shows contrasting changes in below- versus above-ground carbon partitioning towards the alpine treeline: evidence from a Central European case study. *Arctic, Antarctic, and Alpine Research* 43: 46-55.

Hertel, D., Therburg, A. & Villalba, R. 2008. Above- and belowground response by *Nothofagus pumilio* to climatic conditions at the transition from the steppe-forest boundary to the alpine treeline in southern Patagonia, Argentina. *Plant Ecology & Diversity* 1: 21-33.

Hertel, D. & Wesche, K. 2008. Tropical moist *Polylepis* stands at the treeline in East Bolivia: the effect of elevation on stand microclimate, above- and below-ground structure, and regeneration. *Trees* 22: 303-315.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83(7): 2027–2036.

Hoch, G. & Körner, C. 2005. Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology* 19: 941-951.

Holtmeier, F.K. 2009. Mountain timberlines: Ecology, patchiness and dynamics. Springer, Berlin.

Hooghiemstra H. & Van der Hammen, T. 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. Philosophical Transactions of the Royal Society London B, 359: 173–181.

Hubbart, J., Link, T., Campbell, C. & Cobis, D. 2005. Evaluation of a low-cost temperature measurement system for environmental applications. *Hydrological Processes* 19: 1517-1523.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbour Symposium* on *Quantitative Biology* 22: 415-427.

IUCN 2013. The IUCN Red List of Threatened Species. Version 2013.2. <http://www.iucnredlist.org>. Downloaded on 21 December 2013.

Jameson, J.S. & Ramsay, P.M. 2007. Changes in high-altitude *Polylepis* forest cover and quality in the Cordillera de Vilcanota, Perú, 1956–2005. *Biological Conservation* 138: 38-46.

Jobbagy, E.G. & Jackson, R.B. 2000. Global controls of forest line elevation in the northern and southern hemisphere. *Global Ecology & Biogeography* 9: 253-268.

Julio, N.B., Sobral, A., Rondan Dueñas, J., Di Rienzo, J., Renison, D. & Hensen, I. 2008. RAPD and ISSR markers indicate diminished gene flow due to recent fragmentation of Polylepis australis woodlands in central Argentina. Biochemical Systematics and Ecology 36: 329–335.

Kerr, M.S. 2003. A phylogenetic and biogeographic analysis of Sanguisorbeae (Rosaceae) with emphasis on the Pleistocene radiation of the high Andean genus *Polylepis*. Ph.D. thesis, University of Maryland.

Kessler, M. 1995. Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia. In: Churchill, S.P. Balslev, H., Forero, E. and Luteyn, J.L. (eds), *Biodiversity and conservation of neotropical montane forests,* pp. 281-294. New York Botanical Garden, Bronx.

Kessler, M. 2000. Observations on a human-induced fire event at a humid timberline in the Bolivian Andes. *Ecotropica* 6:89–93.

Kessler, M. 2002. The "*Polylepis* problem": Where do we stand? *Ecotropica* 8: 97-110.

Kessler, M., Böhner, J. & Kluge, J. 2007. Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling* 207: 223-233.

Kessler M. & Driesch, P. 1993. Causas e historia de la destrucción de bosques altoandinos en Bolivia. *Ecología en Bolivia* 21: 1–18.

Kessler, M. & Hohnwald, S. 1998. Bodentemperaturen innerhalb und außerhalb bewaldeter und unbewaldeter Blockhalden in den bolivianischen Hochanden. Ein Test der Hypothese von Walter und Medina (1967). *Erdkunde* 52: 54-62.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445-459.

Körner, C. 2003. Alpine plant life, functional plant ecology of high mountain ecosystems. Springer, Berlin.

Körner, C. 2007. Climatic treelines: conventions, global patterns, causes. *Erdkunde* 61: 315-324.

Körner, C. 2012. Alpine treelines: Functional ecology of the global high elevation tree limits. Springer, Basel.

Körner, C. & Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713-732.

Larigauderie, A. & Körner, C. 1995. Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany* 76: 245-252.

Lauer, W. 1982. Zur Ökoklimatologie der Kallawaya-Region (Bolivien). *Erdkunde* 36: 223-247.

Lauer, W. & Rafiqpoor, M.D. 2000. Paramo de Papallacta – a physiogeographical map 1:50.000 of the area around the Antisana (Eastern Cordillera of Ecuador). Franz Steiner Verlag, Stuttgart.

Lauer, W. & Rafiqpoor, M.D. 2002. Die Klimate de Erde. Eine Klassifikation of Grundlage der ökophysiologischen Merkmale der Vegetation. Franz Steiner Verlag, Stuttgart.

Laegaard, S. 1992. Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. & Luteyn, J.L. (eds) *Páramo*. *An Andean ecosystem under human influence*, pp 151–170. Academic Press, Padstow, Great Britain.

Leuschner, C. 2000. Are high elevations in tropical mountains arid environments for plants? *Ecology* 81(5): 1425-1436.

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M. & Hertel, D. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology* 8: 219-230.

Lloyd, H. & Marsden, S.J. 2011. Between-Patch Bird Movements within a High-Andean *Polylepis* Woodland/Matrix Landscape: Implications for Habitat Restoration. *Restoration Ecology* 19: 74-82.

Macek, P., Macková, J. & De Bello, F. 2009. Morphological and ecophysiological traits shaping altitudinal distribution of three species in the dry tropical Andes. *Acta Oecologica* 35: 778-785.

Mayr, S. 2007. Limits in water relations. In: Wieser, G. & Tausz, M. (eds.) *Trees at their upper limit*, pp. 145-162. Springer, Dordrecht, The Netherland.

Meir, P., Levy, P.E., Grace, J. & Jarvis, P.G. 2007. Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology* 192: 277-287.

Miehe, G. & Miehe, S. 1994. Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia* 24: 53-110.

Miehe, G. & Miehe, S. 2000. The forest boundary in tropical mountains. *Phytocoenologia* 24: 53-110.

Miehe, G., Miehe, S., Vogel, J., Co, S. & Duo, L. 2007. Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research And Development* 27: 169-173.

Moser, G., Hertel, D. & Leuschner, C. 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems* 10: 924–935.

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N. & Iost, S. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology* 17: 2211–2226.

Rada, F., Azócar, A., Briceno, B., Gonzalez, J. & García-Núñez, C. 1996. Carbon and water balance in *Polylepis sericea*, a tropical treeline species. Trees: Structure and Function 10: 218–222.

Paulsen, J., Weber, U.M. & Körner, C. 2000. Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic. Antarctic, and Alpine Research* 32:14-20.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions**.** *Ecological Modelling* 190: 231-259.

Purcell, J. & Brelsford, A. 2004. Reassessing the causes of decline of *Polylepis* a tropical subalpine forest. *Ecotropica* 10:155–158.

Rada, F., García-Núñez, C., Boero, C., Gallardo, M., Hilal, M., González, J., Prado, M., Liberman-Cruz, M. & Azócar, A. 2001. Low-temperature resistance in *Polylepis tarapacana*, a tree growing at the highest altitudes in the world. *Plant, Cell & Environment 24*: 377-381.

Renison, D., Hensen, I. & Suarez, R. 2011. Landscape structural complexity of high-mountain *Polylepis australis* forests: a new aspect of restoration goals. *Restoration Ecology* 19(3): 390-398.

Renison, D., Hensen, I., Suarez, R. & Cingolani, A.M. 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? *Journal of Biogeography* 33: 876-887.

Renison, D., Hensen, I., Suarez, R., Cingolani, A.M., Marcora, P. & Giorgis, M.A. 2010. Soil conservation in *Polylepis* mountain forests of Central Argentina: is livestock reducing our natural capital? *Austral Ecology* 35: 435.

Sarmiento, G. 1986. Ecological features of climate in high tropical mountains. In: Vuilleumier, F. & Monasterio, M. (eds), *High altitude tropical biogeography*, pp. 11–45. Oxford Univ. Press.

Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology Evolution and Systematics* 17: 667–693.

Schmidt-Lebuhn, A.N., Fuchs, J., Hertel, D., Hirsch, H., Toivonen, J. & Kessler, M. 2010. An Andean radiation: polyploidy in the tree genus *Polylepis* (Rosaceae, Sanguisorbeae). *Plant Biology* 12: 917–926.

Schmidt-Lebuhn A.N., Kessler M., Kumar M. 2006. Promiscuity in the Andes: species relationships in *Polylepis* (Rosaceae, Sanguisorbeae) based on AFLP and morphology. *Systematic Botany* 31(3): 547–559.

Schröter, C. 1908. Das Pflanzenleben der Alpen: Eine Schilderung der Hochgebirgsflora. Raustein, Zürich.

Servat GP, Mendoza W, Ochoa JA (2002) Flora y fauna de cuatro bosques de *Polylepis* (Rosaceae) en la cordillera del Vilcanota (Cusco, Peru). *Ecología Aplicada* 1(1): 25–35.

Simpson, B.B. 1979. A revision of the genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany* 43: 1-62.

Simpson, B.B. 1986. Speciation and specialization of *Polylepis* in the Andes. In: Vuilleumier, F. & Monasterio, M. (eds.) *High altitude tropical biogeography*. pp. 304–316. Oxford University Press, NY, US.

Smith, W., Germino, M. J., Hancock, T. E. & Johnson, D.M. 2003 Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology* 23: 1101-1112.

Smouse, P.E., Long, J.C. & Sokal, R.R. 1986. Multiple regression and correlation extensions of the Mantel test of Matrix correspondence. *Systematic Zoology* 35: 627–632.

Sultan, S.E. 2000. Phenotypic plasticity for plant development, function and lifehistory. *Trends in Plant Science* 5: 537–542.

Sveinbjörnsson, B., Nordell, O. & Kauhanen, H. 1992. Nutrient relations of mountain birch growth at and below the elevational tree-line in Swedish Lapland. *Functional Ecology* 6: 213-220.

Tanner, E.V.J., Vitousek, P.M. & Cuevas, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79: 10-22.

Toivonen, J.M., Horna, V., Kessler, M., Ruokolainen, K. & Hertel, D. 2014. Interspecific variation in functional traits in relation to species climatic niche optima in Andean *Polylepis* (Rosaceae) tree species: evidence for climatic adaptations. *Functional Plant Biology* 41: 301-312.

Toivonen, J.M., Kessler, M., Ruokolainen, K. & Hertel, D. 2011. Accessibility predicts structural variation of Andean *Polylepis* forests. *Biodiversity and Conservation* 20: 1789-1802.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. *Ecological Studies* 31: 1-137.

Troll, C. 1961. Klima und Pflanzenkleid der Erde in dreidimensionaler Sicht. Naturwissenschaften 9: 332-348.

Troll, C. 1973. The upper timberlines in different climatic zones. *Arctic, Antarctic, and Alpine Research* 5: A3-A18.

UNEP-WCMC. 2004. United Nations Environment Programme. World Conservation Monitoring Center. http://www.unep-wcmc.org

Urrego, D.H., Niccum, B.A., La Drew, C.F., Silman, M.R. & Bush, M.B. 2011. Fire and drought as drivers of early Holocene tree line changes in the Peruvian Andes. *Journal of Quaternary Science* 26: 28-36.

Wang, Y., Titus, S.J. & LeMay, V.M. 1998. Relationships between tree slenderness coefficients and tree or stand characteristics for major species in boreal mixedwood forests. *Canadian Journal of Forest Research* 28: 1171–1183.

Wieser, G. 2007. Limitation by an insufficient carbon assimilation and allocation. In: Wieser, G. & Tausz, M. (eds.) *Trees at their upper limit*, pp. 79-129. Springer, Dordrecht, The Netherland.

Wieser, G., Oberhuber, W., Walder, L., Spieler, D. & Gruber, A. 2010. Photosynthetic temperature adaptation of *Pinus cembra* within the timberline ecotone of the Central Austrian Alps. *Annals of Forest Science* 67: 201.

Wieser, G. & Tausz, M. 2007. Current concepts for treelife limitation at the upper timberline. In: Wieser, G. & Tausz, M. (eds.) *Trees at their upper limit*, pp. 1-18. Springer, Dordrecht, The Netherland.

Wilson, C., Grace, J., Allen, S., & Slack, F., 1987. Temperature and stature, a study of temperatures in montane vegetation. *Functional Ecology* 1: 405-414.

Wittich, B., Horna, V., Homeier, J. & Leuschner, C. 2012. Altitudinal Change in the Photosynthetic Capacity of Tropical Trees: A Case Study from Ecuador and a Pantropical Literature Analysis. *Ecosystems* 15: 958-973.

Wright, I.J., Reich, P.B., Atkin, O.K., Lusk, C.H., Tjoelker, M.G. & Westoby, M. 2006. Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *New Phytologist* 169: 309-319.

Yamori, W., Noguchi, K. & Terashima, I. 2005. Temperature acclimation of photosynthesis in spinach leaves: analyses of photosynthetic components and temperature dependencies of photosynthetic partial reactions. *Plant Cell and Environment* 28: 536-547.

Young, K.R. 1993. Tropical timberlines: changes in forest structure and regeneration between two Peruvian timberline margins. *Arctic and Alpine Research* 25:167-174.

Zhang, S.B., Zhou, Z.K., Hu, H., Xu, K., Yan, N. & Li, S.Y. 2005. Photosynthetic performances of *Quercus pannosa* vary with altitude in the Hengduan Mountains, southwest China. *Forest Ecology and Management* 212: 291-301.