Tropical alpine treelines

how ecological processes control vegetation patterning and dynamics

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Tropical alpine treelines

how ecological processes control vegetation patterning and dynamics

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al oso Andino

habitante ilustre
de los límites de bosque

Contents

Photo previous page: fruit of *Clusia flaviflora* or 'guandera'

CHAPTER 1

General introduction

Photo previous page: young leaf of a *Blechnum* fern

General introduction

Alpine treeline dynamics

Climatic changes may have tremendous effects on species distributions and the functioning of ecosystems. We are not and will not be able to predict these effects with certainty, but a better understanding of the ecosystems concerned may help to increase the realism of our predictions. The effects of climate change are expected to be particularly pronounced in both mountain areas and ecotonal systems (McCarthy *et al.* 2001, Price 2005). The alpine treeline is the most conspicuous ecotone in mountains worldwide and is to a great extent controlled by climate. Alpine treelines have therefore been proposed as potential indicators for the response of ecosystems to climatic change (Slayter & Noble 1992, Kimball & Weihrauch 2000), and as indicators of past and present climatic trends (Griggs 1937, van der Hammen & Cleef 1986, Kupfer & Cairns 1996, Didier & Brun 1998, Kullman 1998, Van't Veer *et al.* 2000).

Temperature is an important determinant of treeline position (Tranquillini 1979, Körner & Paulsen 2004), and forest cover is therefore expected to shift upwards when temperatures increase and downwards when temperatures decrease. However, there are several reasons to expect that treelines will not change 'in parallel to the shift of any isotherm' (Holtmeier & Broll 2005), or synchronously with changes in climate (Slayter & Noble 1992). An important reason is that at local and regional scales treelines do not coincide with single isotherms, but are controlled by compound factors, including climate, substrate, disturbances, and land use (Holtmeier & Broll 2005). Another important reason is that treeline vegetation can control its own dynamics through modifications of the local growth conditions (Armand 1992, Wilson & Agnew 1992).

These external and internal controls determine not only the dynamics, but also the spatial patterns of the vegetation at the treeline. These spatial patterns may therefore serve to reveal these controls and to indicate the most likely response of a treeline to environmental changes. However, different controls can result in the same spatial or temporal patterns, so in order to interpret and relate these patterns, the underlying ecological processes need to be well understood (Levin 1992, Malanson 1997, Wiegand *et al.* 2006).

Defining the treeline

The terminology and definitions regarding treelines and related concepts such as timberlines, forest lines, treeline ecotones and tree species lines are subject to regional and personal preferences, and no common naming convention has been agreed upon so far (Körner 1998). I have therefore chosen to use the term ‘treeline’ and add to it my own definition: *the existent transition between continuous upper montane forest and continuous alpine vegetation.*

I use ‘treeline’ as an abbreviation for ‘treeline ecotone’, because in reality the treeline is a transition zone (ecotone) and not a crisp line. The upper boundary of this ecotone is defined by the lower boundary of continuous low alpine vegetation, and the lower boundary of the ecotone is defined by the upper boundary of continuous forest. The latter is the 'forest line' in the terminology of Troll for tropical mountains (Troll 1959). The uppermost single trees, which define the 'treeline' or 'tree limit' in the literal sense of the term, can be situated anywhere in this ecotone or in the uppermost forest. In the latter case, this literal treeline and the forest line coincide.

'Continuous' in my definition refers to a clear dominance of either vegetation type; a mosaic of forest and alpine vegetation is part of the treeline ecotone, while single forest patches in the alpine vegetation are not, because such patches may be extra-zonal, i.e. they may depend on locally more favorable conditions. Likewise, patches of alpine-like vegetation in gaps in the forest also do not extend the treeline. My definition of treeline thereby differs from that used in several classical treeline studies in the Alps, which regard the treeline as the line connecting the highest forest patches (Brockmann-Jerosch 1919, Däniker 1932, Körner 1998). The addition 'existent' indicates that my definition of treeline is independent of whether the treeline is natural, climatic, or anthropogenically lowered.

Even though it does not confirm strictly to previous definitions, my definition of treeline is well suited to the purpose of this thesis, because rather than referring to an imaginary line it refers to an existent transition zone with identifiable spatial and dynamic properties.

Causes of treeline

Temperature plays an important role in treeline formation, but it is not known in what way low temperature limits tree growth, at what time of the year or day low temperatures are most problematic, or how low temperatures interact with other climatic factors (Tranquillini 1979, Körner 1998). Contemporary research on the causes of treeline focuses mainly on limitations for tree establishment (Ball *et al.* 1991, Germino & Smith 1999, Cuevas 2000, Smith *et al.* 2003, Maher & Germino 2006, Piper *et al.* 2006) and on the question whether trees at treeline are source- or sink-limited, i.e. whether photosynthesis (carbon source) or growth processes (carbon sink) are more restricted by low temperatures and hence limiting for tree growth (Hoch & Körner 2003, Handa *et al.* 2005, Hoch & Körner 2005, Piper *et al.* 2006, Shi *et al.* 2006).

A number of publications summarizes the hypotheses about treeline formation, which are many and which generally are applicable at treelines in a limited range of environments (Tranquillini 1979, Grace 1989, Stevens & Fox 1991, Wardle 1993, Körner 1998, Smith *et al.* 2003). For example, hypotheses related to the length of the growing season, wind, or snow may be applicable at many treelines in the temperate and boreal zones, but not at treelines in the tropics. Still, even if not universally applicable, such hypotheses may well describe the most important mechanisms of treeline formation at the treelines concerned. Although global patterns of treeline altitude may suggest that there is one control mechanism that determines all treelines in the world (Körner & Paulsen 2004), additional processes with local or regional prevalence may be of higher interest in the light of treeline dynamics (Holtmeier & Broll 2005) and may better explain the treeline's spatial patterns and its position in the landscape. Such processes can be related to the local climate, but also to substrate, topography, disturbances, land use, and species composition (Wardle 1993, Holtmeier & Broll 2005).

Tropical alpine treelines

The climatic conditions at tropical alpine treelines differ in several important ways from those at temperate and boreal alpine treelines. The tropical environment is characterized by relatively constant mean monthly temperatures and day lengths throughout the year (Sarmiento 1986, Rundel 1994). This implies that the growing season comprises the whole year. In contrast to this low annual seasonality are the typically strong daily temperature fluctuations, which have provoked the phrase "winter every night, summer every day" to characterize tropical alpine environments (Hedberg 1964).

Solar radiation can reach very high intensities at tropical alpine treelines year-round, due to the low latitude and high treeline altitude (around 3700 m above sea level (asl)). At the same time, night frosts can also occur year-round. In contrast to the climate at many temperate and boreal alpine treelines, at tropical alpine treelines winds are generally gentle and snowfall is rare, while snow accumulation does not occur (Troll 1959, Sarmiento 1986, Smith & Young 1987).

Figure 1 Cloud forest interior, Guandera Biological Station, northern Ecuador. This forest is situated ca. 100 m below the treeline. Note the high abundance of epiphytic Bromeliads and bryophytes; towards the treeline bryophyte cover generally increases even more, to nearly full cover of both the forest floor and the trees.

Apart from the climatic differences, tropical alpine treelines also differ from high-latitude treelines in terms of species composition and land use. Tropical treeline forests are generally upper montane cloud forests with a high diversity of trees and other plant species, which are mostly broadleaved evergreens. Other characteristic features of these forests are the low stature of the trees and the high bryophyte cover and thick organic soils (Hamilton *et al.* 1995) (fig. 1).

The alpine vegetation above the treeline is called páramo in the northern Andes. It is a low but generally dense vegetation of tussock grasses or dwarf shrubs (Hofstede *et al.* 2003). From northern Ecuador northwards páramos are characterized by the presence of *Espeletia* stem rosettes or 'frailejones' (fig. 2).

Landuse at treeline altitudes in the Andes generally consists of potato farming or livestock grazing (Verweij 1992, Llambi *et al.* 2003). Livestock grazing is common in alpine vegetation worldwide, but the use of fire for pasture management is especially important in tropical mountains and may strongly affect treeline position, spatial patterns, and dynamics (Miehe & Miehe 1994, Hofstede 1995). Inadequate management of these landuse systems can result in severe land degradation, including biodiversity loss, erosion and disturbed ecological and hydrological functioning, as well as a loss of useful resources for the local population, such as firewood and non-timber forest and non-forest products (Mena Vásconez *et al.* 2001, Harden 2006). Land use practices will often affect the treeline spatial patterns, and these patterns may therefore also serve as a quickly assessable indicator of human disturbances.

Distinct forest patches in the páramo above the closed forest are not included in my definition of the treeline, because it is usually unclear whether these are naturally occurring extra-zonal islands or representatives of a climatic treeline that has been lowered by landuse. This issue, which has been called the '*Polylepis* problem' because in the Andes these patches often consist of trees from the genus *Polylepis*, is described extensively by Miehe and Miehe (1994) and by Kessler (2002). The main controversy is whether these patches are remnants of formerly more extensive forests, or whether they are restricted to locally favorable sites. Both types of patches probably exist (Wille *et al.* 2002), but the status of most patches is difficult to assess without information about the long-term vegetation history.

Mosaics of (shrub) páramo and dwarf forest patches may also be the natural pattern of many tropical treeline ecotones (Dickinson *et al.* in prep). The 'subpáramo', as recognized in Colombia (Cuatrecasas 1958, van der Hammen & Cleef 1986), can probably be considered such an ecotone. According to some authors, natural tropical treelines should be wide transition zones of gradually decreasing tree height (Ellenberg 1966) or tree cover (Miehe & Miehe 2000). Abrupt treelines are often interpreted as being the result of human land use, in particular burning of the alpine vegetation (Lægaard 1992, Miehe & Miehe 1994). However, naturally abrupt treelines occur in various parts of the world (Wardle 1965, Tranquillini 1979, Armand 1992, Slayter & Noble 1992, Cullen *et al.* 2001), and there is no reason to assume that they could not occur in the tropics as well. This, however, is difficult to verify, because natural tropical treelines hardly exist anymore (Miehe & Miehe 1994). The question what a natural tropical treeline might look like is unresolved until now.

As a result of the different conditions at treelines in the tropics or at higher latitudes, the processes that control vegetation dynamics and patterning will also differ (Miehe & Miehe 1994). Some efforts have been made to use spatial simulation models to better understand vegetation patterning and dynamics at temperate treelines (Noble 1993, Malanson 1997, Malanson 2001, Alftine & Malanson 2004, Wiegand *et al.* 2006, Zeng & Malanson 2006). For tropical treelines this thesis provides the first explicit attempt at such a modeling approach.

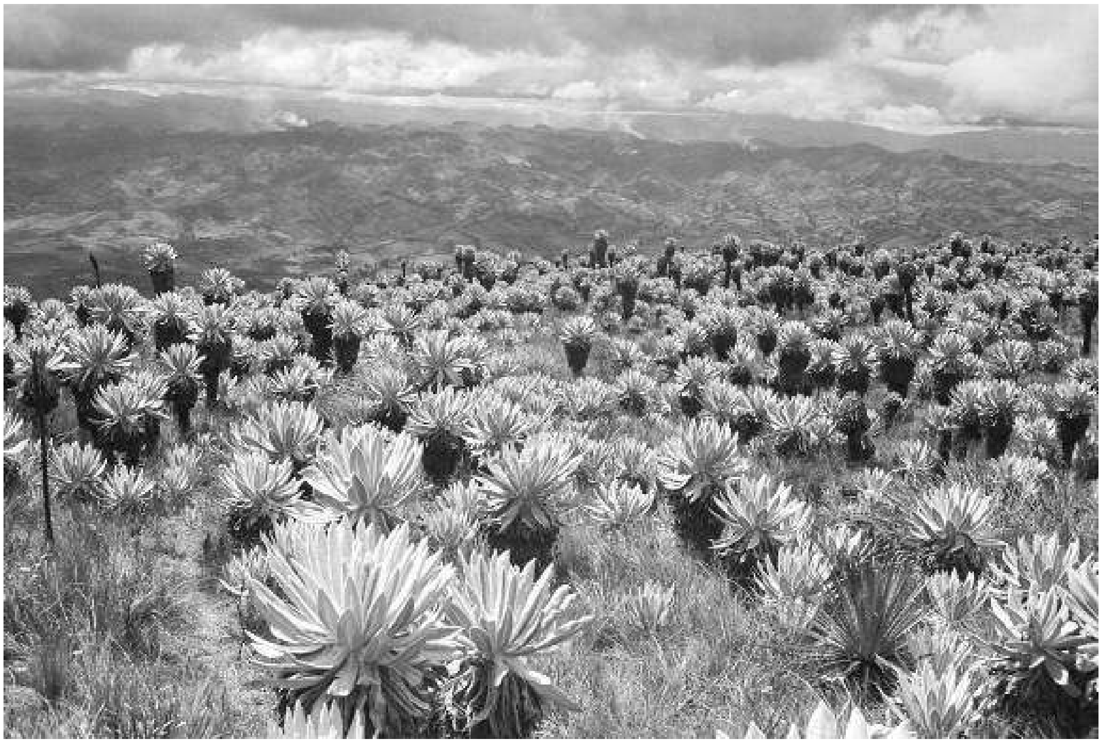

Figure 2 Tussock grass páramo with abundant *Espeletia pycnophylla* stem rosettes (Asteraceae), Guandera Biological Station, northern Ecuador. In the background the lower lying agricultural area can be seen (a patchwork of mainly potato fields and pasture for cattle) and at the horizon the páramo of El Angel situated towards the west.

Research questions and approach

The main research question in this thesis is: *What processes control spatial patterning and dynamics of the vegetation at tropical alpine treelines?* To answer this main question, the following questions were addressed:

A. What spatial vegetation patterns can be found at tropical alpine treelines?
B. What dynamics have treelines exhibited in the past?
C. What ecological processes control tree regeneration at the treeline?
D. What are the implications of these processes for treeline position, spatial patterns and dynamics, including its response to climatic warming?
E. Is the expected effect of these processes on treeline position reflected in treeline positions in a real landscape?

My approach to these questions starts with descriptive studies of vegetation patterns and dynamics, microclimate, and tree regeneration patterns (A,B), followed by an experimental testing of hypotheses about the causes for these patterns (C). The results are incorporated in a mechanistic spatial model of treeline dynamics (D), the results of which are then evaluated against the observed treeline patterns (A) and dynamics (B) and treeline position in the landscape (E).

I hypothesize that feedback processes between the vegetation and the local environment play an important role in shaping treelines. Positive feedback would cause a treeline of abruptly ending closed forest, or stable forest patches, while negative feedback would cause a treeline of increasingly open forest (Armand 1992, Wilson & Agnew 1992). Feedback loops can be used as a conceptual framework to describe the functioning of different types of processes. The general loop is: a vegetation type alters an environmental condition, and this altered condition affects the success of this vegetation type relative to other vegetation types. Examples of such a loop are: the forest moderates the microclimate, and a moderated microclimate favors tree establishment and growth (a positive feedback loop); trees cause lower average temperatures, which might decrease tree growth (negative feedback loop); the páramo promotes fires that kill young trees and hence favor páramo relative to forest (positive feedback loop).

I also hypothesize that spatial and temporal patterns are caused by the same processes and can have similar characteristics, such as abruptness (Armand 1985). Spatial patterns may reveal underlying ecological processes (Wiegand *et al.* 2006) and can then indicate the dynamics that can be expected at a given treeline, including its response to climatic changes.

Outline of this thesis

The aim of this thesis is to understand the processes that shape alpine treelines in the tropics, and the effects of these processes on vegetation patterning and dynamics.

Chapter 2 describes the vegetation structure and temperature conditions found at a wide range of tropical treelines in the Andes and on Hawaii at a local scale (transects <100 m). These descriptions provide an overview of the variety of treeline structures that can be found and the factors that may influence these structures (Question A).

In **Chapter 3** historical treeline shifts in northern Ecuador are described using soil charcoal as a proxy for past vegetation cover. This study covers a period of about 13,000 years and a vertical distance of about 350 m (Question B).

Chapter 4 explores the ecological processes that may cause spatial treeline patterns and dynamics as described in the previous two chapters. Natural tree seedling establishment around the treeline is described, and the influence of local conditions on the success of tree seedling establishment is assessed by experimentally transplanting seedlings to the páramo and the forest. Based on the results, hypotheses are formulated regarding the processes that control tree establishment and treeline dynamics (Question C).

In **Chapter 5** the hypotheses formulated in Chapter 4 are elaborated in a mechanistic spatial simulation model of tree growth on an environmental gradient. This model demonstrates the implications of these hypotheses for emergent spatial patterns and the treeline's reaction to warming. The model results are evaluated using the observed vegetation patterns and dynamics of Chapters 2 and 3 (Question D).

In **Chapter 6** the position of the treeline in an Andean landscape is quantified using remote sensing, GIS techniques and logistic regression. This large-scale pattern (90 m resolution, 25x25 km areas) is then linked to the expectations that emerged from the mechanistic spatial model (Question E).

Finally, in **Chapter 7** the results from all the previous chapters are synthesized, some general conclusions are drawn, and directions for further research are suggested.

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CHAPTER 2

Vegetation structure and temperature regimes of tropical alpine treelines

Maaike Y. Bader, Max Rietkerk and Arnold K. Bregt

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Photo previous page: upper montane cloud forest near Atillo, Ecuador

Vegetation structure and temperature regimes of tropical alpine treelines

Maaike Y. Bader[1,*], Max Rietkerk[2] and Arnold K. Bregt[1]

Abstract

Alpine treeline ecotones can be gradual transitions, abrupt boundaries, or patchy mosaics, and these different patterns may indicate important processes and dynamic properties. We present observed spatial patterns of a wide range of tropical treelines and try to explain these patterns. Treelines were studied at seven sites in the tropical and sub-tropical Andes (Argentina, Bolivia, Ecuador and Venezuela) and on a Hawaiian volcano (Haleakala, Maui). Treeline vegetation structure was described using transects perpendicular to the treeline, and air and soil temperatures were measured above and below the forest boundary. Temperature fluctuations were much larger and the average temperature was higher in alpine vegetation than in forest. Most treelines were abrupt, with surprisingly similar patterns across a wide geographical range. This abruptness could result from positive feedback processes mediated by the differences in microclimate between forest and páramo. Our data is not conclusive about the relative importance of microclimate as opposed to fire in mediating such feedbacks. However, our extensive set of comparable data from different sites in a large geographical region is an important step towards a better understanding of the nature and dynamics of tropical alpine treelines.

Keywords: microclimate, fire, boundary description, positive feedback, páramo, cloud forest, Andes, geographical comparison

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Introduction

The transition between upper montane forest and low-stature alpine vegetation is a conspicuous landscape element on mountains worldwide. These alpine treelines have been the subject of scientific investigation for well over a century (Bühler 1897/1898, Weberbauer 1911). With the current concern about climatic change, alpine treelines have attracted attention as potential indicators of vegetation response to changes in temperature and precipitation (Noble 1993, Kupfer & Cairns 1996, Didier & Brun 1998, Kullman 1998, Kimball & Weihrauch 2000), or at least as ecotones that are likely to be affected (Grace *et al.* 2002). However, the controls of treeline dynamics are still poorly understood (Tranquillini 1979, Körner 1998, Grace *et al.* 2002, Smith *et al.* 2003, Handa *et al.* 2005, Körner & Hoch 2006). Therefore detailed predictions about the effects of global warming cannot be made (Malanson 2001, Graumlich *et al.* 2004). This is true not only for the relatively well-studied alpine treelines in temperate regions, but even more so for those in the tropics.

Tropical alpine treelines differ from temperate alpine treelines mainly because they lack snow and have strong diurnal and weak annual temperature fluctuations (Monasterio 1980, Smith & Young 1987). Treeline forests in the wet tropics are usually cloud forests; a stunted, mossy and perpetually moist forest type (Hamilton *et al.* 1995). The tropical alpine vegetation most often consists of tussock grasses, although microphyllous shrubs are also common and may form shrublands. These alpine areas are often used for livestock grazing, combined with periodical burning of the vegetation. In the mesic northern Andes these alpine vegetation types are called páramo, which is the term we adopt for the alpine vegetation of all our study areas (see table 1 for a distinction between páramo types and e.g. Smith & Young 1987, Hofstede *et al.* 2003 for a discussion about tropical alpine vegetation types and names).

In this paper we use the term ‘treeline’ to denote the actual upper boundary of contiguous closed-canopy forest, irrespective of whether or not this represents the potential climatic upper limit for tree growth. Depending on the scale of observation, this boundary can be considered as a line or an ecotone of varying width.

Treelines have different spatial patterns in different parts of the world, including wide ecotones, mosaics of patches, and abrupt boundaries (Wardle 1965, Miehe & Miehe 1994, Malanson 1997, Körner 1998, Cairns & Waldron 2003). These patterns may reveal underlying processes and may therefore help us to predict vegetation response to environmental changes (Armand

1992, Wiegand *et al.* 2006). However, these underlying processes of the different patterns are not yet well understood.

A variety of hypotheses has been brought forward to explain specific treeline patterns. For instance, a transition from forest to scattered trees, as found at some coniferous treelines (Lauer 1978, Stützer 2000), can be explained by competition between trees (Tranquillini 1979) or other negative neighbor interactions, e.g. shading causing a colder root-zone (Körner 1998). In contrast, clustering of trees into patches or a closed forest can be explained by positive neighbor interactions (Tranquillini 1979, Wilson & Agnew 1992, Smith *et al.* 2003). The typical patches of upright trees or 'Krummholz' (stunted and deformed trees), as well as forest 'fingers' extending up from the closed forest, at windy temperate treelines have been attributed to the sheltering effect of established trees (Smith *et al.* 2003, Alftine & Malanson 2004, Bekker 2005). Abrupt closed forest treelines are often attributed to fire, grazing, or other disturbances (Ellenberg 1966, Norton & Schönenberger 1984, Miehe & Miehe 1994), but species interactions have also been proposed as an explanation for the abruptness of treelines (Wardle 1965, Armand 1992), in particular interactions through positive feedback between plant species and their environment (Armand 1985, Wilson & Agnew 1992, Bader *et al.* in review). Additionally, abrupt treelines can emerge if seedling establishment decreases strongly with altitude while tree growth does not (Wiegand *et al.* 2006); such a situation may emerge due to species-specific demographic factors or again due to positive feedback (Bader *et al.* in review).

Low temperature is probably an important determinant of treeline position, but it is not clear how temperature limits tree establishment or growth (Tranquillini 1979, Körner 1998). Questions that remain are whether soil or air temperature is most important, whether average or extreme temperatures or temperature sums are most important, and whether carbon gain, carbon use, or regeneration processes are most limiting (Körner 1998, Hoch & Körner 2003, Körner & Hoch 2006, Piper *et al.* 2006). A worldwide survey of soil temperatures at treeline (Körner & Paulsen 2004) revealed that most treelines had average growing season soil temperatures around 7 °C, while the three tropical treelines included in the survey had lower temperatures, around 5 °C. Average temperatures at treeline are generally higher outside than inside the forest (Azócar & Monasterio 1980, Bendix & Rafiqpoor 2001, Körner & Paulsen 2004), which appears to present a paradox, because it would imply that the conditions for tree growth are better above treeline than below. However, a seasonal or even daily average temperature is unlikely to control physiological processes. Daily temperature extremes probably have a much more pronounced direct effect on plant performance and hence treeline patterning and dynamics, especially in the tropical alpine zone (Cavieres *et al.* 2000).

Wardle (1965, Wardle *et al.* 2001) has presented comparative studies of treelines and their patterns in different parts of the world, and Miehe and Miehe (1994, 2000) and Leuschner (1996) provide reviews of (sub-)tropical treelines. However, to date no comparison of quantified spatial patterns and their causes has been made between regions, with the exception of Armand (1992), who compared the floristic abruptness of two Russian treelines. In this paper we present observed spatial patterns of a range of tropical treelines, as well as air and soil temperature data from below and above these treelines, in order to contribute to a better understanding of patterns in a large geographical region.

Methods

Study area

Treelines were selected in a wide range of geographical locations, with the purpose of including most of the variation in tropical treeline types. The location of sites is depicted in figure 1. General descriptions of the study areas can be found in table 1. Most study areas are located in the mesic tropical Andes, with the exception of Tafi del Valle, which lies in a seasonally dry subtropical valley in northern Argentina, and Haleakala, on the tropical oceanic island of Maui (Hawaii). Appendix 1 shows some photographs of study areas.

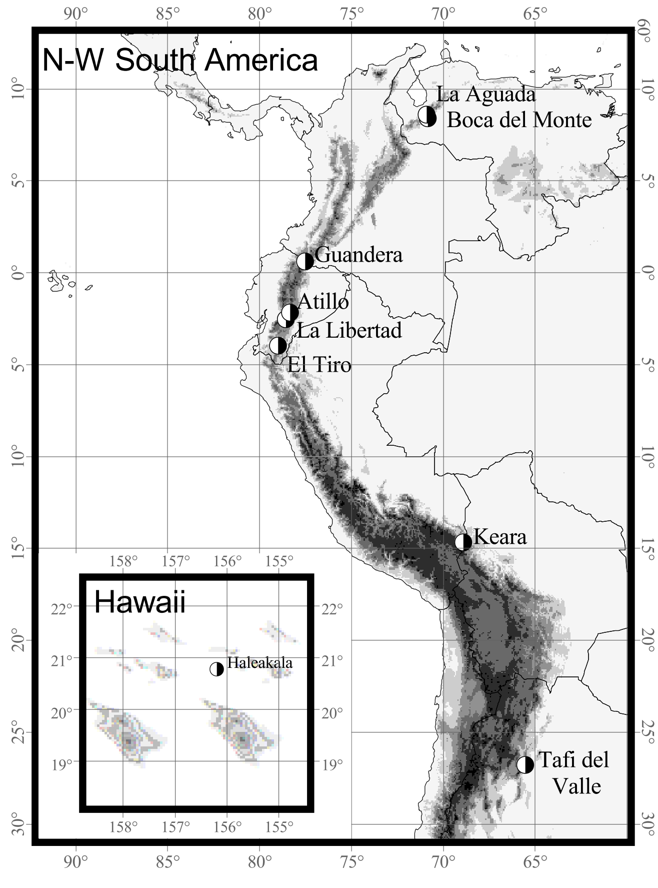

Figure 1 Map showing location of the study areas. Elevation data: GTOPO30 (USGS, 1996).

Treeline structure

Treelines were described using representative tran-

Table 1 Summary of the characteristics of each study

area.

Study area	**Position**	**Latitude Longitude**	**Altitude (m)**	**Vegetation [a]**	**Most common trees & large shrubs**
Boca del Monte (Venezuela)	Outer-Andean S-facing slopes	8° 23′ 35″ -71° 01′ 30″	3100	CF-TP	*Weinmannia pubescens*, *Myrsine dependens*, *Diplostephium* sp., *Miconia* spp., *Espeletia* sp., *Chaetolepis lindeniana*, Ericaceae
La Aguada (Venezuela)	Inter-Andean N-facing slopes	8° 34′ 10″ -71° 05′ 18″	3300	CF-TP SF-TP	*Myrsine* spp., *Clusia* sp., *Polylepis* sp., *Espeletia* sp., *Gynoxis* sp., *Chaetolepis lindeniana*, Ericaceae
Guandera (N Ecuador)	Inter-Andean W-facing slopes	0° 36′ 00″ -77° 41′ 47″	3600	CF-TP	*Weinmannia cochensis*, *Ilex colombiana*, *Clusia* spp., *Myrsine dependens*, *Gaiadendron punctatum*, *Miconia* spp., *Diplostephium* spp., Ericaceae
Atillo (C Ecuador)	Outer-Andean E-facing slopes	-2° 11′ 30″ -78° 29′ 48″	3500	EF-TP	*Escallonia myrtilloides*, *Gynoxys* sp., Ericaceae
La Libertad (C Ecuador)	Inter-Andean valley	-2° 33′ 21″ -78° 43′ 40″	3400	CF-TP	*Weinmannia cochensis*, *W. pubescens,* *Brachyotum microdon*, *Miconia* spp., *Hedyosmum* sp., Ericaceae
El Tiro (S Ecuador)	Outer-Andean E-facing slopes	-3° 59′ 40″ -79° 08′ 50"	2800	CF-SP	*Weinmannia pubescens*, *Brachyotum microdon*, *Clethra revoluta*, *Myrsine dependens*, *Hesperomeles* sp., *Symplocos* sp., *Clusia* sp., *Miconia* spp., Ericaceae
Keara (N Bolivia)	Outer-Andean E-facing slopes	-14° 41′ 54″ -69° 04′ 44″	3300	CF-TP SF-TP	S-facing: *Weinmannia microphylla*, *Vallea stipularis*, *Myrsine dependens*, *M. coriacea*, *Miconia* spp., *Oreopanax* sp., *Gynoxys* sp., N-facing: *Hesperomeles lanuguinosa*, *Baccharis* spp., *Lepechinia graveolens*, Ericaceae
Tafi del Valle (N Argentina)	Inter-Andean valley	-26° 49′ 22″ -65° 42′ 15″	2800	AF-TG	*Alnus acuminata*
Haleakala (Maui, Hawaii)	Outer volcano N-facing slope	20° 46′ 21″ -156° 13‘ 16″	1900	CF-TP	*Metrosideros polymorpha*, *Acacia koa*, *Coprosma* spp., *Cheirodendron* sp., *Vaccinium* spp.

[a] CF = upper montane cloud forest, SF = probably secondary, relatively dry forest, EF = elfin forest, AF = deciduous *Alnus* forest, TP = tussock páramo, SP = shrub páramo, TG = dry tussock grassland

sects perpendicular to the forest boundary, with sample points every 2 m. At each sample point the vertical structure and composition of the vegetation was described, with a record of species presence in intervals of 25 cm along a vertical axis. At each sample point we also registered the altitude relative to a reference altitude.

Table 1 (continued) Summary of the characteristics of each study area.

Study area	Climate	Soil & geology	Land use
Boca del Monte (Venezuela)	Rainy warm & dry cold season. Influenced by Los Llanos air.	Shallow stony soils from metamorphic rocks. Thick peaty humus layer in forest.	Extensive cattle grazing & fire.
La Aguada (Venezuela)	Rainy warm & dry cold season. Influenced by Maracaibo air.	Shallow stony soils from metamorphic rocks. Thick peaty humus layer in forest.	Previously grazing & fire, now tourism.
Guandera (N Ecuador)	High rainfall all year, small seasonal variation.	Deep dark humic Andosols in old volcanic ashes. Thick peaty humus layer in forest.	No present or previous grazing, but fire every 3-6 years.
Atillo (C Ecuador)	Wet & dry season, but rainfall even in dry season.	Deep dark humic Andosols in old & more recent volcanic ashes. Thick peaty humus layer in forest.	Extensive cattle grazing & fire.
La Libertad (C Ecuador)	Wet & dry season, but rainfall even in dry season.	Deep dark humic Andosols in old & more recent volcanic ashes. Thick peaty humus layer in forest.	Previously cattle, now alpaca grazing, no fire at treeline > 14 years.
El Tiro (S Ecuador)	Very wet and windy, 2 months dryer season.	Rather deep soils in soft claystone. Area is not volcanic. Thick peaty humus layer in forest.	No landuse due to weather conditions.
Keara (N Bolivia)	Wet & dry season, but rainfall even in dry season.	Dark humic (S-facing) / shallow stony (N-facing) soils from metamorphic rocks. Thick peaty humus layer in forest.	Cattle grazing & fire.
Tafi del Valle (N Argentina)	Rainy warm & dry cold season. In rain-shadow in inter-Andean valley.	Sandy/loamy soils from granitic rocks. No humus layer in forest.	Sheep, cattle and horses grazing & fire.
Haleakala (Maui, Hawaii)	Windward side of island, wet.	Deep, brown young volcanic soils. Some humus layer in forest.	No present landuse, but feral pigs and deer. Previously some cattle grazing.

The length of each transect depended on the nature of the forest boundary and the variation in vegetation cover. Transects were relatively short (40 to 50 m) if boundaries were abrupt and páramo and forest were relatively homogenous. More gradual boundaries and heterogeneous vegetation on either side required longer transects (up to 80 m). A total number of 50 transects was sampled, divided over seven study areas.

Several methods were tested to characterize vegetation boundaries with our data, using different variables and quantitative methods. First we tested whether we could characterize the boundaries based on vegetation height alone, or whether we needed to use species composition as an additional parameter. The species composition was summarized as the first axis from a principle component analysis (PCA), performed per study area, including all species. This axis represented only 14 to 39 % of the variation in the species composition, but it corresponded with the distinction between páramo and forest in all areas. Along the transects, changes in vegetation height co-occurred with changes in species composition, so the spatial patterns of the two parameters coincided strongly. Correlation coefficients (Spearman's rho) of vegetation height with the first PCA axis ranged from 0.63 to 0.86 ($p < 0.01$ in all cases) in the different study areas. Because of the coincidence of patterns and these strong correlations, we could characterize the boundaries based on vegetation height alone, which is the simplest parameter and therefore preferred.

We then tested several quantitative boundary detection methods based on changes in vegetation height along transects. Such methods have been successfully used for detecting boundary locations (Ludwig & Cornelius 1987, Johnston *et al.* 1992, Fortin 1994, Camarero *et al.* 2000), and we assessed their usefulness to also characterize boundary shapes. The changes in vegetation height were quantified using windows of variance and moving split windows of different sizes (2 to 5+5 cells) and with various difference metrics (variance, squared Euclidean distance, T-test) (Ludwig & Cornelius 1987, Johnston *et al.* 1992). The different methods and window sizes frequently resulted in different locations being pointed out as the boundary, and different boundary widths and shapes. Gaps in the forest canopy also caused confusion. In practice, the original plots of canopy height were always needed to clarify and validate what was seen in the plots of the changes.

We also tested a boundary description method based on curve fitting, assuming that the transition in vegetation height should show a sigmoidal pattern (Timoney *et al.* 1993, Cairns & Waldron 2003). Although this method has previously been used for vegetation cover rather than height, we tested the applicability of the method for our data. We expected that the parameter that indicates the steepness of the function would differ according to the abruptness of the treeline. We used a logistic function, expressing vegetation height as a function of distance along the transect. Most treelines could be described by such a function ($R^2 > 0.5$ for 35/52 transects). However, the steepness of the fitted function was affected more by gaps in the forest than by the abruptness of the actual treeline: forest gaps or highly irregular forest canopies lowered the steepness of the function as well as the R^2 values. The least steep functions, which also had the lowest R^2 values (≤0.3), were found at treelines characterized by forest patches above the closed forest, where the height transition showed no sigmoidal pattern. This was a meaningful result, but in other cases forest gaps confused the signal of the actual páramo-forest transition. Once again, the original plots of canopy height contained more information than the results of the curve fitting exercise.

Therefore, even though quantitative methods may work well for boundary detection and description for certain types of transitions and data, the treelines we studied could be characterized most efficiently using the most straightforward method of visually interpreting plots of the 'raw data'. We therefore classified the patterns visually using vegetation height and vertical structure as parameters. We arbitrarily set the minimum vegetation height for forest at 4 m, and the maximum height for páramo at 1 m. A change in vegetation height was considered 'abrupt' if the transition from páramo to forest over 4 m high was 4 m long or less. It was considered 'medium abrupt' if this transition was between 4 and 10 m long, and 'gradual' if the transition was more than 10 m long. The class of 'abrupt' transitions was sub-divided in transitions with an overhanging tree canopy over páramo ('overhanging canopy'), and transitions with a fringe of shrubs between the páramo and the forest ('fringed'). The transitions in the classes 'medium abrupt' and 'gradual' were always fringed. If many small patches of forest occurred above the continuous treeline, the treeline was considered to be 'patchy'. However, large single forest patches above an abrupt treeline were not considered part of the treeline structure. These patches may be extra-zonal islands in favorable microsites or may be remnants of a previously more extensive forest (Miehe & Miehe 1994, Kessler 2002); this issue is unresolved for most areas and is not part of this research.

Temperatures

Air and topsoil temperatures were measured using HOBO H8 Outdoor 4-Channel External Data Loggers (Onset Corporation) with external temperature probes. Temperature probes were installed in sets of four, placed together at 15, 35 and 150 cm above the ground and at 3 cm below the ground. Those above the ground were protected from direct sunlight by small roofs made from disposable aluminum muffin tins lined with Styrofoam. Temperature was always measured inside and outside the forest simultaneously at three locations both inside and outside, but due to equipment failure the number of

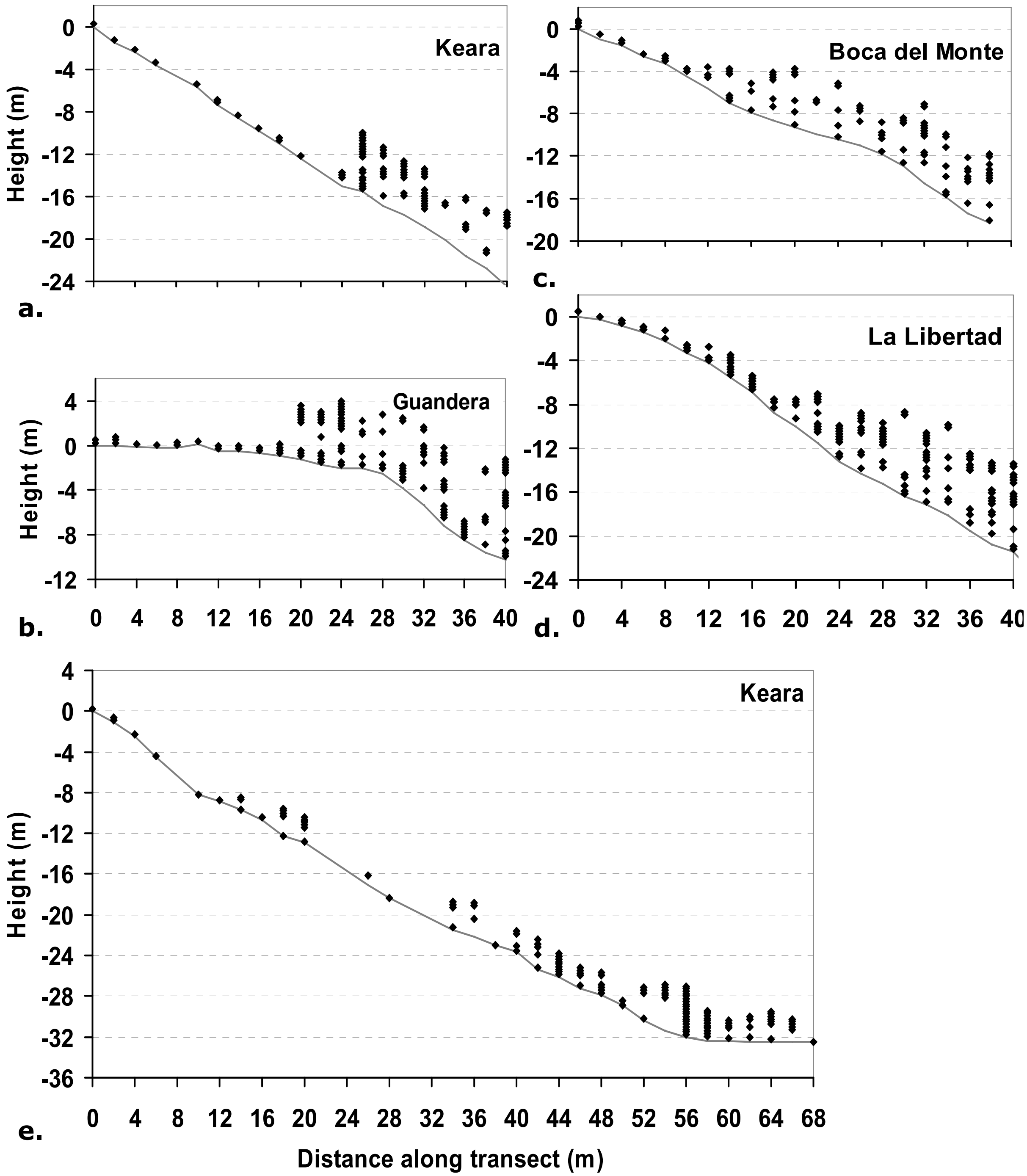

Figure 2 Examples of transect where the treeline is: a) abrupt and fringed; b) abrupt with overhanging canopy; c) medium abrupt; d) gradual; and e) patchy. The height of the underlying surface (grey line) and that of the vegetation (black diamonds) is plotted relative to the first plotted ground surface (set at distance 0). The x-axis is identical for the first four graphs.

repetitions was sometimes smaller. The temperature probes were placed so that they had no direct influence from nearby branches or leaves, but reflected the general microclimate. Temperatures were measured during three to eight days in six of the study areas where vegetation transects were made, and during one or two days in two additional study areas, where no transects were made (table 3). Temperature was logged every two minutes.

Soil temperatures were measured once at each sample point along each transect, at -12 cm and at -28 cm, provided that the soil layer was deep enough. A bi-metal steel soil thermometer (Reotemp, 1 °C accuracy) was used for the measurements at -28 cm, and a digital steel thermometer (1 °C accuracy, 0.1 °C resolution) was used for the measurements at -12 cm. Average soil temperatures of sample points with high (≥2 m) and low (<2 m) vegetation, to distinguish between forest and páramo, were compared using Student's T-test. The difference between 'high' and low' vegetation is set at 2 m, because this is half the minimum height of forest as used in the classification of boundaries.

Results

Treeline structure

In most areas treelines were abrupt in most transects (table 2). Of these abrupt treelines most were 'fringed' (fig. 2a & 3a). The fringe usually consisted of tall shrubs, *Blechnum* ferns, tall *Neurolepis* grass (Northern Andes), or trees with canopies down to ground level (Tafi del Valle). Treelines with overhanging canopies (fig. 2b) were found mostly in Guandera and Tafi del Valle. Medium and gradual treelines (fig. 2c-d & 3b-c) were principally found in La Libertad and in El Tiro, and some in Boca del Monte. Patchy treelines (fig. 2e) were found in Keara on the north-

Table 2 Frequency of treeline types in each study area, based on the abruptness of the change in vegetation height and in vegetation structure at the boundary (A-oh = abrupt & overhanging canopy, A-fr = abrupt & fringed, M =medium abrupt, G = gradual, P = patchy). Medium and gradual treelines are always fringed. Shading indicates treeline types that can be considered typical for each area.

	A-oh	A-fr	M	G	P	total
Boca del Monte	0	6	2	1	0	9
Guandera	5	7	0	0	0	12
La Libertad	0	1	2	2	0	5
El Tiro	0	0	2	1	0	3
Keara	1	4	1	0	2	8
Tafi del Valle	5	4	0	0	0	9
Haleakala	0	0	0	0	4	4
total	11	22	7	4	6	50

facing, sunny slope, and on Haleakala. In both cases the forest patches themselves had abrupt to medium abrupt boundaries, with either overhanging canopies or fringes, and occupied areas of about 4 to 25 m².

Structure classes were based on vegetation height from the ground, and they were largely confirmed when looking at the absolute vegetation altitude (relative to a horizontal plane). The more gradual transects sometimes hardly showed any rise in absolute canopy altitude in spite of the increased vegetation height (fig. 2c-d).

Figure 3 Photos show: a) an abrupt treeline in Guandera; b) (facing page) a medium abrupt treeline on Pasochoa (Ecuador, not a study site); and c) (facing page) a gradual treeline at El Tiro. Arrows show approximate scale.

Temperatures

Average air and topsoil temperatures and temperature variation in time (expressed in the standard deviation) were generally higher in the páramo than in the forest (table 3). Exceptions were temperatures in the topsoil at Boca del Monte, which was heavily shaded by the páramo vegetation; air temperatures at La Aguada, where very low night-time temperatures caused the average to be lower outside the forest; and air temperatures at Atillo, which were measured during a very cloudy and rainy period, resulting in homogenous temperatures in both space and time. Differences between páramo and forest were generally largest in the topsoil and close to the ground (table 3).

Figure 3, continued: b) Pasochoa and c) El Tiro; see caption previous page.

Area Start date	Weather	Start time	Duration d:h:m	Vegetation	T at -3 cm (°C)		T at 15 cm (°C)		T at 150 cm (°C)	
					mean (sd)	min-max	mean (sd)	min-max	mean (sd)	min-max
Boca del Monte 23-01-04	Clear nights, 2.5 d cloudy, 2.5 d sunny	12:30	4:03:05	Moist mossy cloud forest	8.4 (0.9)	7.0 - 9.8	8.1 (3.8)	2.0 - 20.2	8.3 (3.1)	2.9 - 19.0
		12:15	4:03:15	Dense shrub - tussock grass páramo	8.0 (2.3)	5.0 - 13.3	8.9 (7.7)	-4.3 - 29.9	9.0 (3.2)	2.5 - 19.0
		11:10	4:05:10	Burned open tussock grass páramo	13.0 (7.5)	2.9 - 34.9	9.2 (6.9)	-1.5 - 27.5	no data	
La Aguada 5-02-04	Clear nights & mornings, clouds from ca. 15 to 20 h	19:00	1:12:45	Relatively dry páramo forest	6.3 (1.7)	3.7 - 9.0	6.0 (4.3)	0.7 - 16.4	6.6 (4.1)	1.2 - 16.4
		18:05	1:13:50	Medium open shrub - tussock páramo	7.3 (5.7)	0.7 - 21.7	2.2(11.7)	-10.6- 28.3	5.5 (4.2)	-1.5 - 14.1
Guandera 13-11-03	Alternately clear / cloudy / rainy	11:30	7:04:30	Moist mossy cloud forest	7.1 (1.5)	3.7 - 12.6	7.0 (2.3)	2.5 - 15.2	7.0 (2.3)	2.0 - 13.7
		12:00	7:03:00	Dense tussock grass páramo	9.7 (1.4)	6.6 - 14.1	8.5 (6.4)	-2.4 - 31.9	7.7 (2.9)	2.0 - 19.0
Atillo 18-12-03	Continuous clouds / fog, rain & wind	13:30	1:21:30	Moist Escallonia forest	6.3 (0.2)	5.8 - 6.6	6.1 (0.5)	5.0 - 7.8	5.9 (0.4)	5.0 - 7.4
		12:30	1:22:30	Dense tussock grass páramo	7.0 (0.4)	6.6 - 7.8	6.0 (0.8)	5.0 - 8.6	5.9 (0.4)	5.0 - 7.4
La Libertad 6-12-03	Alternately clear / cloudy, some rain	14:15	5:23:45	Dry mossy forest	8.8 (1.0)	6.6 - 11.4	8.5 (2.3)	3.7 - 16.0	8.7 (2.2)	4.6 - 17.1
		13:45	6:00:45	Transition: young trees, 3-4 m	9.4 (1.4)	7.0 - 15.2	9.4 (3.3)	3.3 - 21.7	9.6 (3.4)	5.0 - 22.1
		13:05	6:01:25	Dense tussock grass páramo	12.1 (2.3)	8.6 - 21.0	11.2 (6.6)	1.2 - 36.1	9.0 (3.0)	4.2 - 19.8
El Tiro 30-11-03	Alternately clear / cloudy / misty, no rain	15:30	3:00:30	Moist mossy cloud forest	11.2 (0.8)	10.2 - 13.3	10.9 (1.6)	8.6 - 16.0	11.0 (2.1)	8.2 - 17.9
		13:35	3:02:25	Low (<30cm) shrub páramo	13.2 (1.9)	11.4 - 18.7	13.1 (5.1)	8.6 - 31.5	11.5 (2.9)	7.8 - 21.3
Keara 7-09-03	1.5 d clear , 1.5 d cloudy& rainy	17:00	2:16:45	Moist mossy cloud forest	6.8 (1.2)	4.6 - 10.2	6.8 (2.1)	3.3 - 12.6	7.0 (2.1)	3.3 - 12.9
		17:00	2:16:45	Medium open tussock grass páramo	10.5 (3.2)	5.8 - 18.7	8.3 (5.2)	2.0 - 24.4	7.8 (3.0)	3.7 - 16.4
Tafi del Valle 28-09-03	Alternately clear / light cloud cover	15:00	3:01:30	Dense tussock grass	17.0 (8.0)	5.8 - 35.3	17.3 (9.4)	0.7 - 38.3	15.2 (6.6)	0.7 - 27.9

Previous page: Table 3 Summary of temperature data from a representative selection of sensors at -3 cm (in topsoil), 15 cm and 150 cm above the soil surface, in forest (shaded) and in alpine vegetation in different study areas. Temperature is registered by shaded sensors and stored in dataloggers every 2 minutes for several days.

Temperature differences between night and day were most pronounced close to the ground (at 15 cm), especially in the páramo (fig. 4a). Temperatures in the upper soil layer were usually dampened compared to air temperature (fig. 4). However, these temperatures could become much more extreme in dry and exposed soil, like the dry granitic sand soils in Tafi del Valle, and the soil under the open burnt páramo on the dry west-facing slope at Boca del Monte (table 3). In all cases the topsoil temperature had a smoother course through the day, and was delayed by a couple of hours compared to the air temperature (fig. 4).

Soil temperatures at both -12 and -28 cm were significantly higher under páramo than under forest in all areas, except in Tafi del Valle at both depths and in Haleakala at -28 cm (table 4). The standard deviation (here a measure for variation in space) was either the same in forest and páramo (equal variance according to Levene's test), or higher in páramo, reflecting a more heterogeneous shading of the soil in the páramo than in the forest.

Average soil temperatures at -28 cm under forest, which should best reflect the average seasonal temperature, were highest in Haleakala and lowest in Keara and Guandera (table 4). Co-incidentally, Haleakala also has the treeline at the lowest altitude, followed by El Tiro and Tafi del Valle, while Guandera has the highest treeline (table 1).

Discussion

Most areas had abrupt treelines, and the vertical structures of forest and páramo were surprisingly similar across a wide geographical range. The tropical Andes treelines, from Bolivia to Venezuela, coincided not only in structure, but also to a surprising extent in floristic composition (often to genus level, data not shown). Vertical structures of forest and páramo in Hawaii were again quite similar to those in most Andes sites, despite the different species composition. Only the monospecific and simply structured Alnus forest in Tafi del Valle differed markedly from the diverse and complex cloud forests at the other sites, yet the alpine vegetation, though drier than the tropical páramos, consisted of high tussock grasses and the treeline was abrupt, like at most of the tropical sites.

Air and soil temperatures were generally lower under forest than under páramo. Temperature differences between day and night were much more

Table 4 Mean soil temperatures in forest (vegetation height ≥ 2 m) and in páramo (vegetation height < 2 m) at -12 cm and at -28 cm, per study area; mean (bold), standard deviation and number of sample points (n). Also shown are the differences between mean temperatures in páramo and forest (Tpáramo - Tforest) and their significance according to Student's t-tests.

		-12 cm		-28 cm [a]	
		mean T (°C)	$T_{\text{páramo}} - T_{\text{forest}}$ t-statistic [b]	mean T (°C)	$T_{\text{páramo}} - T_{\text{forest}}$ t-statistic [b]
Boca del Monte	forest	**9.4** sd= 1.3 n= 98		**9.5** sd= 1.1 n= 75	
	páramo	**10.9** sd= 2.7 n= 78	**1.5** 4.48** NE	**9.7** sd= 1.3 n= 33	**0.2** 1.02 E
Guandera	forest	**8.7** sd= 0.8 n= 108		**9.0** sd= 0.7 n= 108	
	páramo	**10.0** sd= 1.1 n= 134	**1.3** 10.13** NE	**10.1** sd= 0.9 n= 134	**1.1** 11.44** NE
La Libertad	forest	**10.3** sd= 1.0 n= 64		**9.9** sd= 0.6 n= 60	
	páramo	**11.3** sd= 0.8 n= 63	**1.0** 5.69** E	**11.0** sd= 0.6 n= 39	**1.1** 8.70** E
El Tiro	forest	**11.9** sd= 0.7 n= 22		**11.3** sd= 0.5 n= 22	
	páramo	**13.0** sd= 1.1 n= 31	**1.1** 4.11** E	**11.8** sd= 0.7 n= 32	**0.5** 3.22* E
Keara	forest	**9.1** sd= 1.4 n= 76		**8.9** sd= 0.8 n= 63	
	páramo	**10.9** sd= 2.1 n= 127	**1.8** 7.24** NE	**9.7** sd= 0.7 n= 73	**0.8** 6.56** E
Tafi del Valle	forest	**11.5** sd= 2.5 n= 104		**9.9** sd= 1.4 n= 77	
	páramo	**12.1** sd= 3.2 n= 96	**0.6** 1.59 NE	**10.3** sd= 1.5 n= 65	**0.4** 1.55 E
Haleakala	forest	**14.8** sd= 1.9 n= 69		**14.5** sd= 0.5 n= 18	
	páramo	**15.7** sd= 0.8 n= 113	**0.9** 4.30** E	**14.8** sd= 0.4 n= 36	**0.3** 1.88 NE

[a] Excluded are points where the thermometer probe could not enter the soil more than 24 cm

[b] Difference between mean temperature in forest and in páramo per area and t-statistic (independent sample student's t-test). NE and E refer to the equality of the variances according to a Levene's test. If variances are not equal (NE), the reported t values are those of an adjusted t-test. This adjusted test gave the same conclusion of significance as an unadjusted test in all cases. Significance of t-statistic: * p<0.05, ** p < 0.001

pronounced in the páramo than in the forest, as were differences between clear and cloudy days, and between air close to the ground and air higher up. These differences are all related to the radiation regime. Irradiance can be strong year-round at tropical treelines, due to the high altitude combined with the low latitude. On clear days, the páramo surface and the air just above it warm up strongly during the day and cool down strongly during the night due to radiation. In contrast, the forest interior is protected by the canopy and therefore maintains a relatively constant and low temperature. The similarity

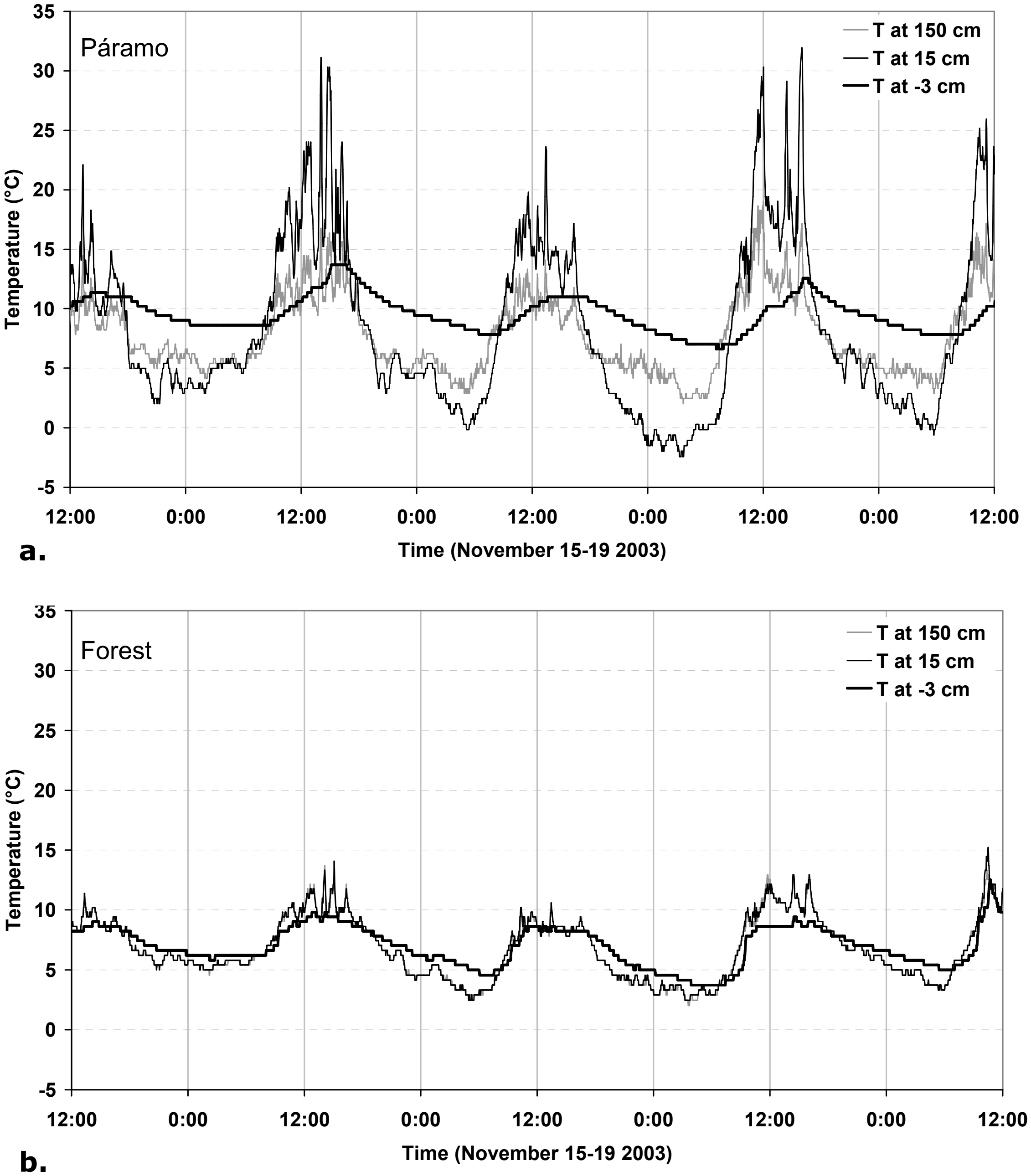

Figure 4 Temperatures in Guandera during 4 days. a) In the páramo, and b) in the forest (the temperature at 15 cm and at 150 cm coincide strongly, which is the reason why only 2 lines can be seen in most of the graph). The weather during these days: 15-11 sunny in the early morning (not shown), then cloudy with drizzly rain; 16-11 cloudy morning, sunny afternoon, rain at night; 17-11 cloudy all day; 18-11 sunny morning, thick clouds from just before midday, some light rain in the afternoon; 19-11 sunny morning with some clouds.

in soil temperatures in and outside the forest in Tafi del Valle, in contrast to the differences found in other areas, is almost certainly due to lack of shade under this forest, which is composed of deciduous *Alnus* trees that were without leaves during the measurements.

Soil temperatures were measured only once at each point along the transects, and the different points in a study area were measured within a few days. The measured soil temperatures may therefore not accurately represent the average yearly temperature. However, thermal seasonality is low in most of our study areas, and there is no seasonal bias in the timing of our measurements. It is therefore remarkable that the soil temperatures in all study areas were higher than the average growing season temperatures measured recently at 30 treelines worldwide (at -10 cm and in the shade of trees) (Körner & Paulsen 2004), which were mostly between 6 and 8 °C. In contrast to our data, the three tropical sites included in the global comparison (Körner & Paulsen 2004) had relatively low growing season means (4.5 - 6.7 °C), the growing season being year-round or nearly so. This is in accordance with other studies at tropical treelines (Winiger 1979, Ohsawa 1990, Miehe & Miehe 1994, Bendix & Rafiqpoor 2001).

The fact that we measured higher soil temperatures could indicate that the treelines in our study areas are situated below their potential climatic altitude, which would be in accordance with the dominant view that actual tropical treelines are to a great extent anthropogenic features (Ellenberg 1966, Lægaard 1992, Miehe & Miehe 1994, Ellenberg 1996, Young & Keating 2001, Kessler 2002). However, the fact that other studies found lower soil temperatures could also indicate a bias of these studies towards the uppermost forest patches above treeline, which some consider representatives of the natural treeline (Lægaard 1992, Sarmiento & Frolich 2002), but which others consider extra-zonal islands in locally favorable sites (Troll 1959, Walter & Medina 1969, Lauer 1988). In many cases the climatic treeline is probably situated somewhere in between the present treeline and the uppermost forest patches (Miehe & Miehe 1994, Kessler 2002, Wille *et al.* 2002), and the mean annual temperature at this climatic treeline would be somewhere between 5 °C and 9 °C, which is in accordance with the global pattern (Körner & Paulsen 2004). However, too few temperature data from 'natural' tropical treelines are available as a reference to be conclusive about this issue. The treeline on Haleakala (Hawaii) is a special case. This treeline is relatively low, and soil temperatures were higher than those at the Andean treelines, because the native tree species are less adapted to the high altitude environment than species on the continents. This is clear from the fact that a full grown exotic pine plantation grows above the native treeline.

In spite of the global coincidence of treelines at similar average growing season temperatures (Körner & Paulsen 2004), these average temperatures can hardly be expected to directly control treeline position. In fact, we found that average temperatures were higher above the treeline than in the forest, a finding that is confirmed in several other tropical (Azócar & Monasterio 1980, Miehe & Miehe 1994, Kessler & Hohnwald 1998, Bendix & Rafiqpoor 2001) and worldwide (Körner & Paulsen 2004) treeline temperature studies. Low soil temperatures probably also do not limit tree regeneration, because these were also higher in the páramo and higher than the lower threshold of 5-7 °C for the growth of most tree species (Körner & Hoch 2006). More likely, the mechanisms restricting tree growth above the treeline are related to the extreme temperatures that occur here, especially the low night temperatures followed by strong solar radiation during the day, causing photoinhibition or more serious damage to unprotected plants (Wardle 1965, Ball *et al.* 1991, Germino & Smith 1999, Bader *et al.* online first). The highest standard deviation and most extreme minimum and maximum air temperatures are almost always found in the páramo at 15 cm above the ground. This implies that this air layer close to the ground has the most stressful temperature conditions for plants, including sub-freezing temperatures at night. Páramo plants are well adapted to these conditions (Rundel *et al.* 1994), but this may not be true for young trees, which consequently cannot establish outside the forest (Bader *et al.* online first). The different temperature regimes in forest and páramo may therefore be an important factor in the stabilization and shaping of treelines, especially where fire is not an overriding factor.

If the climate above the treeline is too harsh for tree establishment, while the climate inside the forest allows tree establishment and growth, a positive feedback is operating. Positive feedback occurs when plant communities modify their environment in such a way, that they favor themselves relative to other communities. This causes a sharpening of boundaries (Wilson & Agnew 1992). Additionally, positive feedback can cause non-linear reactions to changes in climate (Kupfer & Cairns 1996, Malanson 2001, Smith *et al.* 2003). Knowing the origin of the abruptness of treelines is therefore also relevant for predictions of the vegetation response to climatic changes.

Of the studied tropical treelines even the relatively gradual ones were more abrupt than the 'sharp' Russian treelines described by Armand (1992), where the transition from forest to alpine vegetation was about 20 m long. It is assumed by many authors, that the abruptness of treelines in the tropics indicates an anthropogenic origin (Miehe & Miehe 1994). Unfortunately, in the Andes, and maybe everywhere in the tropics, it is almost if not totally impossible to find a treeline that with certainty has not suffered human influence in the past (Miehe & Miehe 2000). Therefore, no good reference sites are available that would help us to separate the influence of anthropogenic and natural processes on treeline structure. To study these processes in detail, experimental research would be necessary, for instance the exclusion of each of the processes that are expected to be important (Bader *et al.* online first).

The La Libertad area has consciously not been burnt for over a decade, providing us with a natural fire-exclusion experiment. The treeline here is more gradual because of regenerating trees in the páramo close to the former treeline, indicating the strong control that fire had previously on the position and probably the structure of this treeline. Fire can cause abrupt treelines due to a positive feedback between fuel (páramo, relatively flammable due to dry dead biomass) and fire (preventing forest growth and thus maintaining the páramo) (Vilà *et al.* 2001, van Langevelde *et al.* 2003). This control may be important in many of the study areas, as fire is a common phenomenon in all areas except El Tiro and Haleakala. In El Tiro fire does not or rarely occur because of the very wet circumstances, and the most gradual treelines were found here. However, it cannot be concluded from this that treelines without fire should always be gradual, because the circumstances at El Tiro are quite exceptional, with strong winds shearing the vegetation. In the Haleakala site, where fire is also uncommon, there were more forest patches above treeline than at most other study sites, but these had abrupt boundaries. So although fires occur in many areas, we have no information about the actual effect of fires on treelines. Therefore the possibility that other mechanisms such as alterations of the temperature regime can also produce abrupt treelines should not be excluded.

We found patchy treelines in two sites, where the reason for the observed patchiness is probably very different. In Keara the patchy treeline was located on a steep north-facing slope. This relatively dry and warm slope was favored for agriculture, and old fields were located close to the transects. In the forest cattle paths were evident. It seems likely that this part of the forest has been opened up by cattle and farmers, and it may even be secondary forest. Grazing might thus break up a treeline (Tranquillini 1979), which is in contrast to the dominant view that grazing makes treelines more abrupt (Cairns & Moen 2004), like fire does. Cattle was observed to enter the forest also in Boca del Monte, but here the effect was restricted to the undergrowth, while trees remained intact and the treeline remained closed. In contrast, the patchy treeline on Haleakala was little disturbed, except by some feral pigs and deer, and here the patchiness may well be the natural treeline pattern. In the Andes natural treelines may also have a patchy character, as seen in the sub-páramo zone recognized in Colombia (Cuatrecasas 1958, van der Hammen & Cleef 1986), and recently at a unique pristine and very wet treeline in Ecuador (Dickinson *et al.* in prep). However, this cannot be confirmed or refuted based on direct evidence, because natural treelines are so rare.

Although different positive feedback processes may result in similar spatial patterns, knowing which is dominant at a given treeline is essential for predicting its reaction to changes in climate or land use. To distinguish between the various anthropogenic and natural processes involved in shaping treelines, further field experiments are recommended. In these experiments each of the potentially important processes should be excluded in a factorial design, and vegetation development should be monitored. A first experiment, addressing solar radiation, neighbor interactions, and soil limitations, was conducted at a treeline in northern Ecuador recently and supports the hypothesis that the harsh microclimate outside the forest hinders tree regeneration (Bader *et al.* online first). Additionally, spatially explicit simulation models can be used to study the potential effects of the relevant processes on spatial vegetation patterns and dynamics, including the reaction of treelines to environmental changes (e.g. Noble 1993, Alftine & Malanson 2004, Dullinger *et al.* 2004, Wiegand *et al.* 2006, Bader *et al.* in review).

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Appendix 1: Photographs of the study areas

Keara, Bolivia ↥ **Boca del Monte, Venezuela** ↴

Tafi del Valle, Argentina ↵

Haleakala, Maui, Hawaii ↴

La Libertad, Ecuador ⮥ **El Tiro, Ecuador** ⮧

CHAPTER 3

The Holocene treeline in the northern Andes (Ecuador): first evidence from soil charcoal

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Photo previous page: partially charred wood

The Holocene treeline in the northern Andes (Ecuador): first evidence from soil charcoal

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Abstract

Indications for the speed and timing of past altitudinal treeline shifts are often contradictory. Partly, this may be due to interpretation difficulties of pollen records, which are generally regional rather than local proxies. We used pedoanthracology, the identification and dating of macroscopic soil charcoal, to study vegetation history around the treeline in the northern Ecuadorian Andes. Pedoanthracology offers a complementary method to pollen-based vegetation reconstructions by providing records with high spatial detail on a local scale. The modern vegetation is tussock grass páramo (tropical alpine vegetation) and upper montane cloud forest, and the treeline is located at ca. 3600 m. Charcoal was collected from soils in the páramo (at 3890 and 3810 m) and in the forest (at 3540 m), and represents a sequence for the entire Holocene. The presence of páramo taxa throughout all three soil profiles, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only late in the Holocene (after 5000 ^{14}C yr BP). The treeline may have been situated between 3600 m and 3800 m at some time after 4400 ^{14}C yr BP, or it may never have been higher than it is today. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the beginning of the Holocene. These results contradict interpretations of palaeological data from Colombia, which suggest a rapid treeline rise at the Pleistocene-Holocene transition. They also contradict the hypothesis that man-made fires have destroyed large extents of forest above the modern treeline. Instead, páramo fires have probably contributed to the slowness of treeline rise during the Holocene.

Keywords: pedoanthracology, páramo, cloud forest, wood anatomy, human impact

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Introduction

The present position of alpine treelines is to a large extent the result of historical ecological processes, influenced by past climates and land use. Knowing the vegetation history is therefore essential for understanding treeline positions. The present position of tropical treelines is thought to be lower than their potential position, yet it is unknown what this potential position is, due to a lack of both ecological and historical information about tropical treeline ecosystems.

According to some authors, the potential treeline altitude is indicated by the uppermost forest patches found above the actual treeline. These are interpreted as remnants of high altitude forests now destroyed by man-made fires and forest clearing (Ellenberg 1958, Lægaard 1992, Sarmiento & Frolich 2002). However, there is no evidence that these highest patches have ever been surrounded by forests (Islebe & Hooghiemstra 1997, Wille *et al.* 2002), and present patches are mostly restricted to special microsites such as ravines and boulder slopes (Troll 1959, Walter & Medina 1969). The situation for forest patches at lower altitudes, close to the actual treeline, is less clear. These may also rely on locally favorable conditions, or may be remnants of formerly more extensive forests (Miehe & Miehe 1994, Kessler 2002).

In the northern Andes, the alpine vegetation above the treeline is called 'páramo' (Monasterio 1980, Balslev & Luteyn 1992, Hofstede *et al.* 2003). The most common type of páramo in Ecuador is tussock grass páramo, dominated by large tussock grasses interspersed with various shrubs and herbs (Ramsay & Oxley 1997, Mena Vásconez & Medina 2001). Classifications of the páramos of Colombia distinguish three altitudinal zones: a subpáramo, dominated by shrubs; a 'páramo proper', dominated by tussock grasses; and a sparsely vegetated superpáramo (Cuatrecasas 1958, van der Hammen & Cleef 1986). In Ecuador, however, the shrubby subpáramo zone is usually absent (Mena Vásconez & Medina 2001). Most páramos in Ecuador are burned regularly, especially where they are used for livestock grazing (Lægaard 1992). These fires may have increased the dominance of tussock grasses at the expense of shrubs, especially in the lower parts of the páramo (van der Hammen & Cleef 1986, Ramsay & Oxley 1997, Suarez R. & Medina 2001).

Below the treeline we find upper montane forest, comprising several forest types, including dwarf forests (Cleef & Hooghiemstra 1984). Some synonyms or sub-classifications of these forests are sub-alpine rain forest, andean cloud forest, elfin forest, mossy forest, dwarf cloud forest, 'bosque alto-andino' or 'ceja andina' (see e.g. Webster 1995, Jørgensen *et al.* 1999). These forests are characterized by low stature trees with small sclerophyllous leaves, and abundant moss cover on both the trees and the forest floor. They are species-poor compared to tropical rain forests at lower altitudes (Gentry 1995), but very species-rich compared to upper montane forests in temperate regions. Common tree genera are *Weinmannia, Ilex, Ocotea, Oreopanax, Hedyosmum, Clusia, Clethra, Miconia, Podocarpus, Rapanaea, Brunellia, Hesperomeles, Gaiadendron, Polylepis, Escallonia, Gynoxys* etc. (Cleef & Hooghiemstra 1984, van der Hammen & Cleef 1986, Gentry 1995).

The Holocene history of treeline dynamics in the northern Andes has been addressed by an increasing number of palynological studies since the 1960s (e.g. van der Hammen & Gonzalez 1960, van Geel & van der Hammen 1973, Hooghiemstra 1984, Colinvaux *et al.* 1997, Hansen *et al.* 2003). There is, however, no general consensus about what happened in the different periods of the Holocene, as pollen data or their interpretations are frequently contradictory, and the timing of events is rather uncertain (Markgraf 1989, Van't Veer *et al.* 2000, Marchant *et al.* 2001).

In the late Pleistocene, several warm and colder periods occurred between the end of the last glacial and the early Holocene (van der Hammen & Cleef 1986). In the last cold period, a Younger Dryas equivalent (sensu van der Hammen & Hooghiemstra 1995) referred to as the ‘El Abra stadial’ (ca. 11,000 to 9,500 ^{14}C* yr BP), treelines were strongly lowered, down to altitudes 600-800 m lower than today (van der Hammen & Hooghiemstra 1995). After this cold and arid period treelines are thought to have risen rapidly in response to the climatic warming in the early Holocene (van Geel & van der Hammen 1973, van der Hammen 1974, Flenley 1979, Bush *et al.* 2005), though other studies show a later rise due to the continuation of arid conditions until ca. 8500 ^{14}C yr BP (Islebe & Hooghiemstra 1997, Van't Veer *et al.* 2000, Berrío *et al.* 2002).

In the middle Holocene, between ca. 7000 and 5000 ^{14}C yr BP, the climate is thought to have been warmer (‘hypsothermal’), as shown by high treeline altitudes (van der Hammen 1974, van der Hammen & Cleef 1986) and δ^{18}O data (Thompson *et al.* 1995). However, other studies find indications for a drier climate, resulting in lowered treelines {Marchant, 2001 #5496; Marchant, 2002 #5750; Hansen, 1995 #5506; Vélez, 2003 #5488; Berrío, 2002 #5610}. Records for this period are particularly heterogeneous (Marchant *et al.* 2001). ambiguity

For the late Holocene, studies show an increase in humid forest taxa between 4000 and 3000 ^{14}C yr BP, indicating a return to more humid

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* The length of ^{14}C years differs through time relative to real years, or 'calibrated' years. Different models can be used to calibrate ^{14}C years, and therefore calibrated years have an extra source of error or ambiguity. We therefore reported ^{14}C years in the text.
E.g. 11,000 ^{14}C yr ≈ 13,000 cal yr, see also table 2.

conditions (Marchant *et al.* 2001, Marchant *et al.* 2002b, Hansen *et al.* 2003). Meanwhile the appearance of crop and disturbance taxa suggests the beginnings of regional agriculture and possible forest clearance (Hansen & Rodbell 1995, Wille *et al.* 2002, Hansen *et al.* 2003, Vélez *et al.* 2003). A lowering of treelines after 3000 ^{14}C yr BP is generally interpreted as an effect of human disturbance, masking the climatic signal (Hansen & Rodbell 1995, Wille *et al.* 2002, Vélez *et al.* 2003, Bush *et al.* 2005).

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Although pollen records provide valuable information about past vegetation cover, pollen-based reconstructions of treeline shifts are rarely spatially precise, because pollen can be transported long distances by wind. Also, pollen records hardly ever allow for an unambiguous interpretation, because the pollen signal depends not only on vegetation distribution, but also on other variable factors like wind direction (Hansen *et al.* 2003) and lake size (Markgraf 1989). This may partly explain the contradictory results of different palynological studies in the Andes, although regional differences in climate and vegetation history are probably also important.

The usual method for reconstructing the fire history of the vegetation is counting charcoal particles on pollen slides (Patterson III *et al.* 1987, Clark 1988, Haberle & Ledru 2001). However, like pollen, this microscopic charcoal is easily transported by wind (Clark 1988) and the palaeofires can therefore not be precisely located. Another disadvantage is that the type of vegetation burned is derived indirectly, from the pollen spectrum. A more local signal of past fires and vegetation cover is offered by macroscopic charcoal fragments in the soil.

Soil charcoal analysis (pedoanthracology) was first developed in France (Thinon 1978), and is based on anatomical identification and ^{14}C dating of charcoal fragments (≥ 0.4 mm) from the soil. Charcoal is composed of inorganic carbon and therefore does not decompose in the soil. In contrast to pollen, charcoal is conserved in all types of soil. Botanical identification of charcoal fragments is possible because the wood structure is conserved during carbonization (fig. 1). The charcoal fragments are not very mobile, because of their relatively large size (Clark *et al.* 1998, Ohlson & Tryterud 2000), and provide a proxy for the local species composition with high spatial precision.

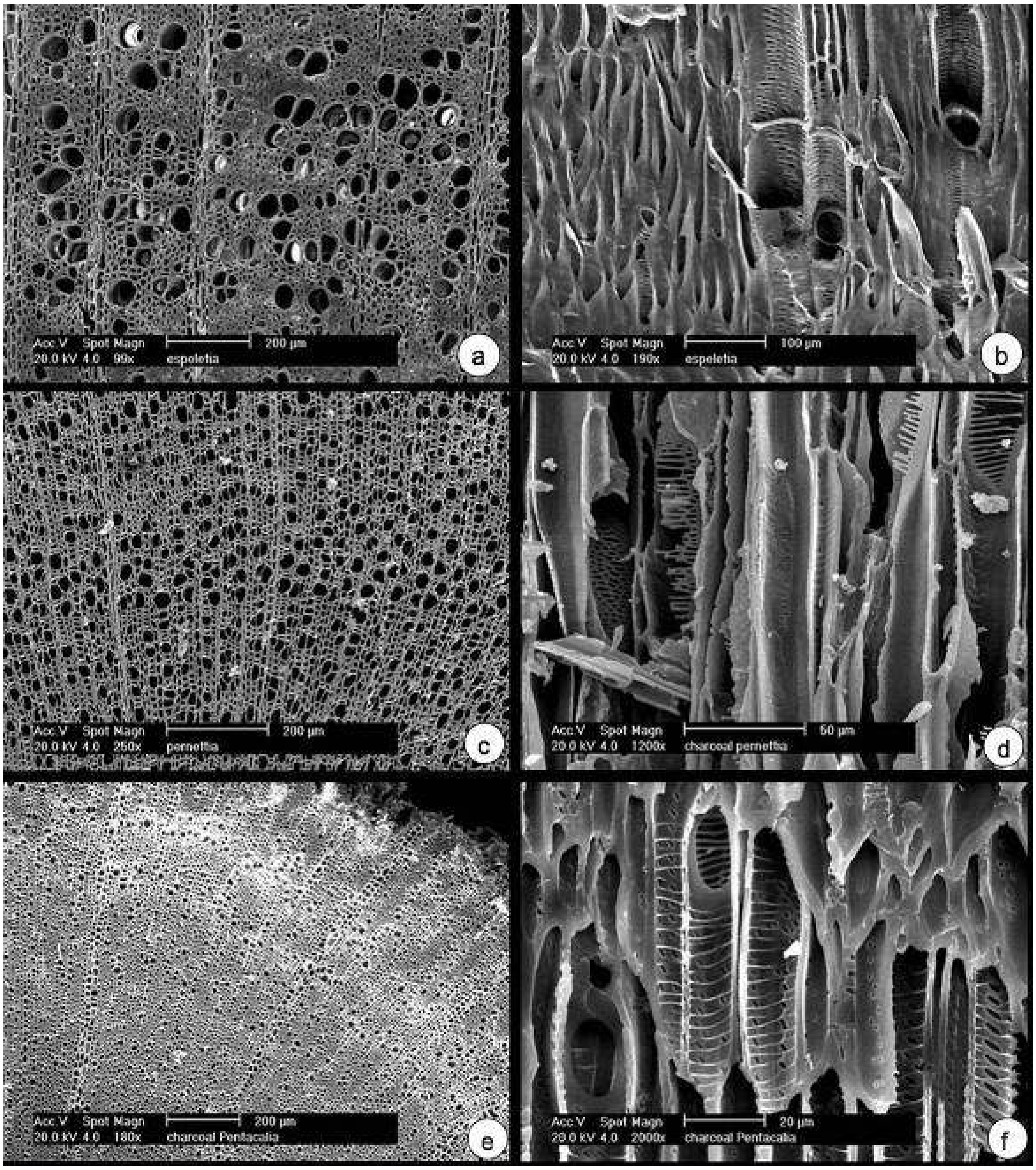

Figure 1 Microscopic features of the wood of the indicator species for forest and páramo, from Guandera Biological Station. Selected electron microscope photographs of wood anatomy: a-b Espeletia pycnophylla, transverse and radial (wood) section; c-d Pernettia prostrata, transverse (wood) and radial (charcoal) section; e-f Pentacalia vaccinoides, transverse and radial (charcoal) section. See Appendix 1 for a description of the wood features.

In spite of these advantages, pedoanthracology is still not widely applied. Most pedoanthracological studies have been carried out in the French Alps to reconstruct altitudinal changes in treeline location (Carcaillet & Thinon 1996, Talon *et al.* 1998). In these studies evidence could be found for the presence of forest above the actual treeline (Carcaillet & Brun 2000), but the presence of alpine vegetation, and hence the absence of forest, was impossible to infer from the data, because the alpine meadows contain few or no woody species and leave no charcoal. In contrast, in the tropics the vegetation above treeline contains various woody species whose presence in the charcoal record can indicate the absence of forest. The only pedoanthracological studies in the tropics so far have been located in lowland areas in Brazil (Scheel-Ybert *et al.* 2003) and French Guyana (Tardy 1998). Ours is the first pedoanthracological study in tropical mountains.

In this paper we show how macroscopic charcoal from the soil allowed the reconstruction of vegetation cover and treeline position since the late Pleistocene in northern Ecuador. Our objective was to verify whether the treeline has been higher in the past, and what has been the role of fire in its dynamics. We compare our results with those from several palynological studies in the northern Andes and present our view on the dynamics of tropical alpine treelines. In order to be able to identify the historical soil charcoal, we have also created the first reference database of wood anatomy for tropical Andean species.

Study area

The study area is situated on the western flanks of the eastern Cordillera in northern Ecuador (N 0° 36′, E -77° 42′, fig. 2), at the treeline in the protected area of Guandera Biological Station. The station conserves one of the last extensive upper montane cloud forests on the inner slopes of the Ecuadorian Andes, and the best conserved stand of montane *Clusia* forest known in Ecuador (H. Navarette, Universidad Católica Quito pers. comm. 2005). The cloud forest occurs in a band

Figure 2 Map showing the location of the study area in the Andes in northern Ecuador.

between the agricultural area (mainly potato cultivation) below and the páramo above.

The area has a typical humid tropical alpine climate with low temperatures and high precipitation all year round, and strong diurnal, but weak annual temperature fluctuations. Climate data from a forest clearing at 3370 m asl, ca. 2 km from our transect, indicate an annual precipitation sum of ca. 1700 mm for 2002, and daily temperatures at between 4 °C and 15 °C in most months (average not recorded) (Bader *et al.* online first). One-week measurements in the páramo showed temperatures between 2 °C and 19 °C at 1.50 m (Bader *et al.* accepted). The soil of the páramo is a deep and well developed Andosol (Soil Survey Staff 1999). The soil of the forest has an organic upper horizon of 30-100 cm consisting principally of roots.

The upper montane cloud forest at the treeline has a mixed canopy composed mainly of the tree species *Ilex colombiana* Cuatrec. (Aquifoliaceae), *Weinmannia cochensis* Hieron. (Cunoniaceae), *Miconia tinifolia* Naudin (Melastomataceae), *Clusia flaviflora* Engl. (Clusiaceae) and *Gaiadendron punctatum* (Ruiz & Pavón) G. Don. (Loranthaceae). The most common shrub species in the forest understory are various Ericaceae, *Miconia chlorocarpa*

Figure 3 Photo of the lower part of the study area. In the foreground and on the right tussock grass páramo, on the left upper montane cloud forest. Two patches of forest can be seen in the páramo.

Cogn. (Melastomataceae), and *Desfontainia spinosa* Ruiz & Pav. (Loganiaceae). At the forest edge large *Diplostephium* shrubs (Asteraceae) and caulescent *Blechnum* ferns (Blechnaceae) are the most common elements. Down from ca. 100 m below the treeline, stands of *Clusia*-dominated forest are found. The treeline is an abrupt boundary between forest and tussock grass páramo. It is located at ca. 3600 m above sea level (asl), and judging from historical aerial photographs it has been at this position for at least 40 years. Up to ca. 100 m from the treeline in topographical depressions and valleys there are several small patches of forest with the same species composition as the continuous mixed forest (fig. 3).

The páramo vegetation consists mostly of large tussock grasses (*Festuca* sp., *Calamagrostis* sp.) interspersed with the terrestrial Bromeliad *Puya hamata* L.B.Smith, with the tall (up to 4 m) stem rosette *Espeletia pycnophylla* Cuatrec. (Asteraceae), and with small shrubs like *Pernettya prostrata* (Cav.) DC. (Ericaceae), *Pentacalia vaccinoides* (Kunth) Cuatrec. (Asteraceae), *Brachyotum alpinum* Cogn. (Melastomataceae) and *Hypericum laricifolium* Kunth. (Clusiaceae). Only three forest tree species were found regenerating in the páramo: seedlings and saplings of *Weinmannia cochensis* and *Diplostephium* sp., and clonal shoots of *Gaiadendron punctatum* were abundant close to the treeline, but no adult plants of these species were found in the páramo (Bader *et al.* online first).

At the present time, the páramo vegetation is burned approximately every 3-6 years. There are no records of naturally induced fires. In other regions fire is often used as a pasture management tool, but in Guandera there are no indications of present or past livestock grazing. Here, the main reason for burning the páramo is the local belief that these fires will induce rainfall. The páramo dries rapidly under the strong solar radiation and it then burns well because of the abundance of dead plant material in the tussocks. In contrast, the cloud forest maintains a moist microclimate because of the abundance of mosses, and it is not affected by fire except sometimes at the very edges, where trees may get scorched (pers. obs.). After a fire the páramo vegetation, especially the tussock grass, recovers rapidly. In contrast, shrubs and any small trees that may have appeared in the páramo (always of the species *W. cochensis*, *G. punctatum*, and *Diplostephium* sp.) die or recover much more slowly (pers. obs.).

Methodology

Soil sampling

Three pits were dug in an altitudinal transect: in the páramo at 3890 m asl (GUA1) and at 3810 m asl (GUA2), and in a *Clusia*–dominated part of the forest at 3540 m asl (GUA3) (fig. 4). In the selection of pit locations we avoided steep slopes and areas with signs of past disturbances or erosional features (Carcaillet & Thinon 1996). Pits were ca. 1 m wide, 2 m long, and 1.25 to 2 m deep. The depth was determined by the depth of a 2-3 cm impermeable layer consisting of iron oxides, below which there was a horizon of volcanic ash and pumice. The soil horizons and their colors and structure were concisely described in the field (Soil Survey Staff 1999). The actual vegetation was described around each sampling point, in plots of 5x5 m in the páramo and 20x20 m in the forest, estimating ground cover and height of the different vegetation layers and species.

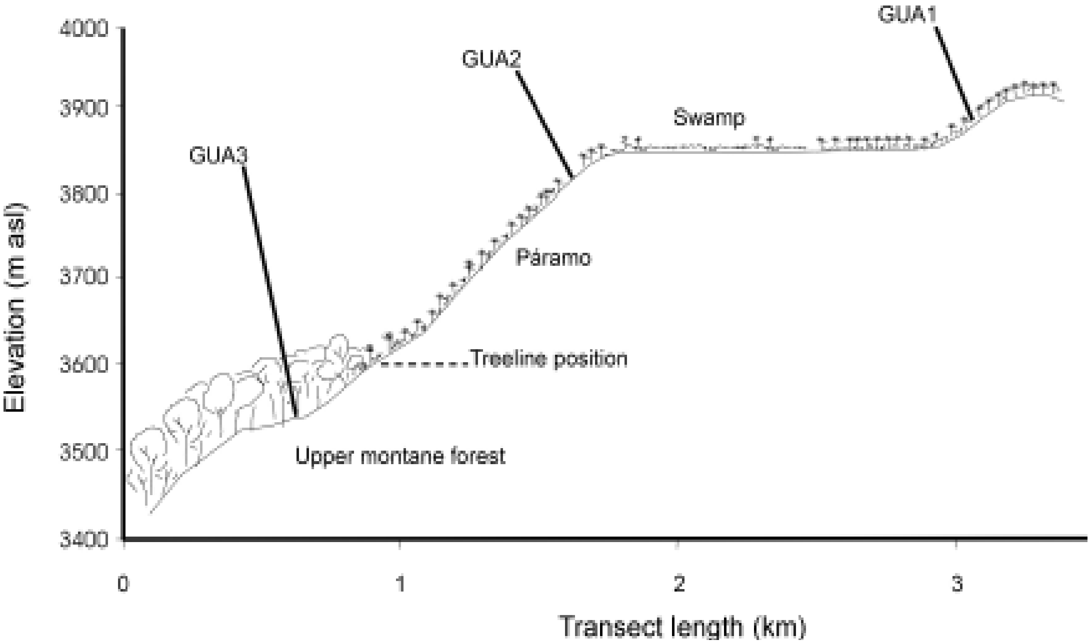

Figure 4 Location of the sampling points along an altitudinal transect in Guandera Biological Station.

Samples were taken from the base of the pit first and then upwards in levels of ca. 25 cm thickness. The levels did not cross pedological horizons, and were sampled discontinuously (ca. 5 cm vertical distance between samples) in order to avoid mixing of samples. From each level 7 to 10 kg of soil was collected. Collecting this large amount of soil is necessary when the bulk of charcoal in the soil is unknown a priori, in order to be sure to extract enough charcoal fragments for identification and dating (Thinon 1992, Carcaillet & Thinon 1996).

Charcoal extraction

The soil samples were air dried before sieving to harden the charcoal, which was weakened by the long presence in humid soil. Once dried, the samples were left to soak in ca. 25 l of water for a few hours, in order to dissolve the soil aggregates to facilitate the sieving. We sieved the soil with running water through a column of two sieves with mesh sizes of 2 and 0.4 mm. A sieve with a 5 mm mesh size, as used in this procedure by Carcaillet & Thinon (1996), was not necessary, because there were no stones present in the soil. The 2 mm sieve retains the largest charcoal fragments, plus organic material, mostly root fragments. The 0.4 mm sieve retains the rest of the charcoal fragments that are large enough for identification, plus the sand fraction of the soil. After drying, the charcoal was manually separated from the sand and the organic material under a dissection microscope.

Wood sampling and construction of charcoal reference collection

Generally, the identification of soil charcoal fragments is based on comparison with wood anatomy atlases and reference collections of wood (xilotheca) and charcoal (anthracotheca). For the species in our study area, the wood anatomy was unknown (P. Gasson of Kew Royal Botanical Gardens, pers. comm. 2006); for South America the only available references are a wood anatomy atlas for Amazonian species (Détienne & Jacquet 1983), and some material from specific studies in south eastern Brazil (Scheel-Ybert *et al.* 1998). We therefore created the reference material for the species of our study area ourselves. To this end we collected wood samples of all woody species that were encountered in our floristic survey (table 1). Stems or branches (15-20 cm long, min. 10 cm diameter if possible) of five individuals of each species were sampled. Species were identified at the QCA herbarium of the Pontificia Universidad Católica del Ecuador in Quito. Nomenclature (incl. authors and families) is according to Jørgensen et al. (1999).

The wood samples were used to create the xilotheca and the anthracotheca, and a database of anatomical features (Box 1). The wood samples were observed and described on the three fundamental wood plains (transverse, longitudinal tangential and longitudinal radial) using an electron microscope. The anatomical descriptions were based on the IAWA list of microscopic features for hardwood identification (Wheeler *et al.* 1989). The procedure was repeated with modern charcoal samples, because the identification is based on comparison directly with charcoal rather than wood. Charcoal was observed using an incident light microscope (100×, 200×, 500× and 1,000×). To create charcoal from the wood samples, the air-dried samples were covered by sand to restrict the oxygen supply to avoid total combustion, and heated in a muffle furnace at 350 ºC for 20 minutes (Machado Yanes 1992). The woody structures of the caulescent fern Blechnum were studied, but they were not included in the database, because the database is based on the wood anatomy of angiosperms.

Charcoal identification

For taxonomical identification, all soil charcoal fragments were observed through an incident light microscope and compared to the reference collections and database. Our database did not yet include all the collected species, and some species previously present in the study area may be absent in the modern vegetation. However, to reconstruct treeline position we only needed a few species that could be confidently identified and that could serve as indicators to distinguish forest and páramo.

The selection of indicator species was based primarily on their unique occurrence in either forest or páramo, in combination with their abundance in the actual vegetation, and the identifiability of their wood anatomy. We based the assignment of species to forest or páramo on their distribution in our study area and on information available in the literature (Cleef & Hooghiemstra 1984, Kuhry 1988, Gentry 1995, Mora G. 1998, Marchant *et al.* 2002a) (table 1). Much of the latter information referred to genera and not to individual species. Also, species of the same genus may have similar wood structures and their charcoal might be confused. Therefore indicator species were preferred that had a strong habitat preference on the genus level. The indicator species for forest were *Ilex colombiana*, *Clusia flaviflora*, *Oreopanax confusus*, and *Ocotea infrafoveolata*. The indicator species for páramo were *Espeletia pycnophylla*, *Pernettya prostrata*, and *Pentacalia vaccinoides*. The presence of these species in the charcoal record was considered a dominant indication of the vegetation physiognomy at the time of charcoal formation. If we consider that present-day vegetation associations may differ from the associations that existed in the past, the use of indicator taxa may pose some problems. Still, trees and heliophilous shrubs should provide quite good indicators for forest and lower páramo-like vegetation respectively.

Charcoal quantification and dating

The amount of charcoal in the soil was expressed as the soil charcoal concentration (mg charcoal/ kg dry soil: ppm), which includes only charcoal particles ≥ 0.4 mm. This quantity was calculated per level and for the whole profile.

Nine charcoal samples from different pits and levels were radiocarbon (^{14}C) dated by accelerator mass spectroscopy (AMS). Where possible, the dating was performed on single identified charcoal fragments (Carcaillet 2001). However, to collect the minimum quantity of charcoal necessary for dating (1 mg), it was often necessary to use two or more fragments. Where possible, we used identified charcoal fragments of the same species, but in two cases we used a bulk sample of unidentified charcoal (table 2). In the organic layer of the forest soil charcoal was absent, so macro remains of roots were dated instead.

As a pre-treatment for AMS dating, each sample was mechanically cleaned with tweezers under a dissection microscope, and chemically cleaned from absorbed mineral carbonates and organic matter with cycles of hydrochloric acid (HCl 3%) and sodium hydroxide (NaOH 3.2%) alternated by neutralization with de-ionized water. For further purification, samples were submitted to a pyrolysis process by heating them in a glass tube with a Bunsen burner for ca. 10 minutes under nitrogen flow.

Some samples were dated at the Dynamitron Tandem Laboratory in Bochum, Germany (Lubritto *et al.* 2004). Other samples were dated at the Center for Isotopic Research on Cultural and Environmental Heritage (CIRCE) in Caserta, Italy (Terrasi *et al.* in press) (table 2). All samples were pre-treated at the latter facility, and labeled DSA. The ^{14}C ages were calibrated with Calib 4.4 (Stuiver *et al.* 1998), using 1σ probability distributions.

Results

Modern vegetation

The modern vegetation around the upper páramo pit (GUA1) was tussock grass páramo. The tussock grasses (*Festuca* and *Calamagrostis*) had a ground cover of ca. 80% and an average height of 15 cm. *Espeletia pycnophylla* and *Puya hamata* were abundant, and shrubs had a ground cover of only 5% and an average height of 25 cm. Shrub species found were *Loricalia ferruginea*, *Pentacalia vaccinoides*, *Hypericum laricifolium* and *Diplostephium* sp. There was abundant regeneration of *E. pycnophylla*.

The modern vegetation around the lower páramo pit (GUA2) was also tussock grass páramo. The tussock grasses had a ground cover of ca. 60% and an average height of 35 cm. Compared to GUA1, shrubs had a higher ground cover (15%) and were higher (50 cm), and *H. laricifolium* was more abundant.

Table 1 Woody species in the present vegetation (upper montane cloud forest and tussock grass páramo) of Guandera Biological Station, collected for the charcoal reference collection. Species marked with * are our indicator species. The columns 'Forest' and 'Páramo' indicate whether species occur in the forest and/or in the páramo in our study area, and column 'Abundance' indicates their abundance in the upper 100 m of the forest (3500-3600 m asl). These data are a summary of our vegetation transects in the forest and in the páramo (unpublished data), and for forest species we also used a floristic inventory of four 50x50 m forest plots in our study area (Mora G. 1998). The columns 'Veg type' shows the occurrence of the genus in different types of vegetation, according to summaries of survey data in other parts of the Andes (see table footnotes).

Species	Family	Forest	Páramo	Abundance[b]	Growth form[c]	Veg type[d]	Veg type[e]	Veg type[f]	Ecology of the species/genus according to Marchant et al. (2002)
* *Ilex colombiana* Cuatrec.	Aquifoliaceae	X		++	Tr	f,d	f	f	Species: Tree, up to 3600 m in Colombia, particularly in humid sites
* *Clusia flaviflora* Engl. and *Clusia multiflora* Kunth	Clusiaceae	X		++	Tr	f	f	f	Genus: Trees and shrubs, wide distribution in forests up to 3200 m
Miconia chlorocarpa Cogn.	Melastomataceae	X		++	Sh	d,s	f	f,d,s	Genus: Dwarf shrubs and small trees, in moist and wet early successional forest up to 4800 m, frequent in páramo-forest transition and sub-Andean forest.
Miconia tinifolia Naudin	Melastomataceae	X		++	Tr	d,s	f	f,d,s	
Gaiadendron punctatum (Ruiz & Pavón) G.Don.	Loranthaceae	X	X[a]	++	Tr	f,d	f	d	Species: Parasitic tree, comon in forest-páramo ecotone, subalpine dwarf forest and shrub páramo
Weinmannia cochensis Hieron.	Cunoniaceae	X	X[a]	++	Tr	f,d	f	f	Genus: Trees, common in Andean forests
Weinmannia pinnata L.	Cunoniaceae	X		+	Tr	f,d	f	f	Genus: Trees, common in Andean forests
* *Oreopanax confusus* Marschal.	Araliaceae	X		+	Tr	f,d	f	f,d	Genus: Hairy trees and shrubs common in Andean forests, especially in secondary forests and from 3500 to 3700 m
Desfontainia spinosa Ruiz & Pav.	Loganiaceae	X		+	Sh				-

Myrsine dependens (Ruiz & Pav.) Spreng.	Myrsinaceae	X	+	Tr		f		Species: Small tree, present in upper Andean humid dwarf forest (3200-3500), most common genus in upper montane rainforest
Escallonia myrtilloides L.F.	Escalloniaceae	X	+	Tr	f,d	f	f,d	Species: Tree, in páramo, dominant at 3000-3400 m, esp. at wet upper forest line, forms high altitude forests (3800-4100)
Macleania cocoloboides A.C. Sm.	Ericaceae	X	+	Sh	f,s			-
* *Ocotea infrafoveolata* van der Werff	Lauraceae	X	+	Tr		f		Genus: Trees and shrubs, lowland to upper montane rainforests
Gaultheria sclerophyllia Cuatrec.	Ericaceae	X	-	Sh	s,d			Genus: Shrubs, pioneer in montane areas, in forest (2800-3200 m), extending to subpáramo and páramo
Symplocos sp.	Symplocaceae	X	-	Tr		f	d	Genus: Trees and shrubs, in mature Andean forests and about the forest line, including shrub-páramo
Freziera microphylla Sandwith	Theaceae	X	-	Tr				-
Brunellia pauciflora Cuatrec. & C.I.Orozco	Brunelliaceae	X	-	Tr	f	f	f	Genus: Trees of secondary forest/light gaps, usually found in mesic montane rainforest
Clethra ovalifolia Turcz.	Clethraceae	X	-	Tr	f,d	f	d	Genus: Trees and shrubs, montane forest (2800-3300 m in Colombia), 3250-3500 m in Costa Rica, exending to páramo
Weinmannia dzieduszyckii Szyszyl.	Cunoniaceae	X	-	Tr	f,d	f	f	Genus: Trees, common in Andean forests
Weinmannia auriculifera Hieron.	Cunoniaceae	X	-	Tr	f,d	f	f	Genus: Trees, common in Andean forests
Weinmannia rollotii Killip	Cunoniaceae	X	-	Tr	f,d	f	f	Genus: Trees, common in Andean forests
Tristerix longibracteatus (Desr.) Barlow & Wiens	Loranthaceae	X	-	Ep				-
Hesperomeles obtusifolia (Pers.) Lindl.	Rosaceae	X	-	Tr	f,d	f	f	Genus: Trees and shrubs prominent about Colombian upper forest line, monospecific stands in sub-Andean rain forest

Blechnum sp.	Blechnaceae	X	X	++	Ca	d,s	f,d,s	Genus: Mostly herbaceous ferns, occasionally trees, in lower páramo and sub-Andean and Andean forests (1500-3200 m)
Thibaudia parviflora (Benth.) Hoerold	Ericaceae	X	X	-	Sh			-
Diplostephium spp.	Asteraceae	X	X[a]	++	Sh	s	f,s,p	-
* *Espeletia pycnophylla* Cuatrec.	Asteraceae		X	++	Ca	p	p	Genus: Stem rosette growth form found from Venezuela to Ecuador, exclusive in páramo and subpáramo (3000-4400 m)
Hypericum laricifolium Juss.	Clusiaceae		X	++	Sh	d,s,p	f,d,s, p	Genus: Shrubs and dwarf shrubs in high Andes. Common in grasspáramo and some forest-types from 2800-4150 m. Heliophytic[ref.f]. Species: common in páramo at ca. 3500 m
Brachyotum alpinum Cogn.	Melastomataceae		X	++	Sh	d,s	f,p	-
* *Pentacalia vaccinioides* (Kunth) Cuatrec.	Asteraceae		X	+	Sh	d	d,p	Genus: Heliophytic[ref.f]
* *Pernettya prostrata* (Cav.) DC.	Ericaceae		X	+	Sh	p	s,p[g]	Genus: Dominant Puna genus, but also montane rainforest plant. Species: typical in tussock grass páramo[ref.f]
Disterigma alaternoides (Kuth) Nied.	Ericaceae		X	-	Sh	s		-

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[a] Only young regeneration in the páramo, no adult plants

[b] Abundance in the upper 100 altitudinal m of the forest in Guandera: ++ = very abundant, + = common, - = rare

[c] Growth form of the species: Tr = tree, Sh = shrub, Ca = caulescent rosette, Ep = epiphyte

[d] Occurrence of the **genus** in different vegetation types: p = páramo, s = subpáramo dwarf shrub, d = subpáramo dwarf forest, f = forest. Based on vegetation classifications from Colombia (Kuhry, 1988).

[e] Occurrence of **genus** in important quantity in forests, based on data from all along the Andes (Gentry et al., 1995)

[f] Occurrence of the **genus** in different vegetation types: p = páramo, s = subpáramo dwarf shrub, d = subpáramo dwarf forest, f = forest (including some dwarf forest types). Based on vegetation classifications from Colombia (Cleef and Hooghiemstra, 1984).

[g] *P. prostrata* is a tussock grass páramo element at species level

The modern vegetation around the forest pit (GUA3) was *Clusia* forest. The 20-m high canopy layer had a cover of ca. 70% and was dominated almost completely by *C. flaviflora*, although *Weinmannia cochensis* also occurred. The sparse lower canopy layer (8-10 m) was composed of *Oreopanax confusus* and *Miconia tinifolia*. Caulescent *Blechnum* ferns (0.5-1.5 m high) covered ca. 15%, and Bromeliaceae dominated the herb layer, which had 40% ground cover, and were abundant as epiphytes. Moss cover was low (15%) compared to mixed forests in the area, and litter cover was high (35%). No tree seedlings or saplings were observed in the plot, and they also appeared to be rare in other parts of the *Clusia*-dominated forest.

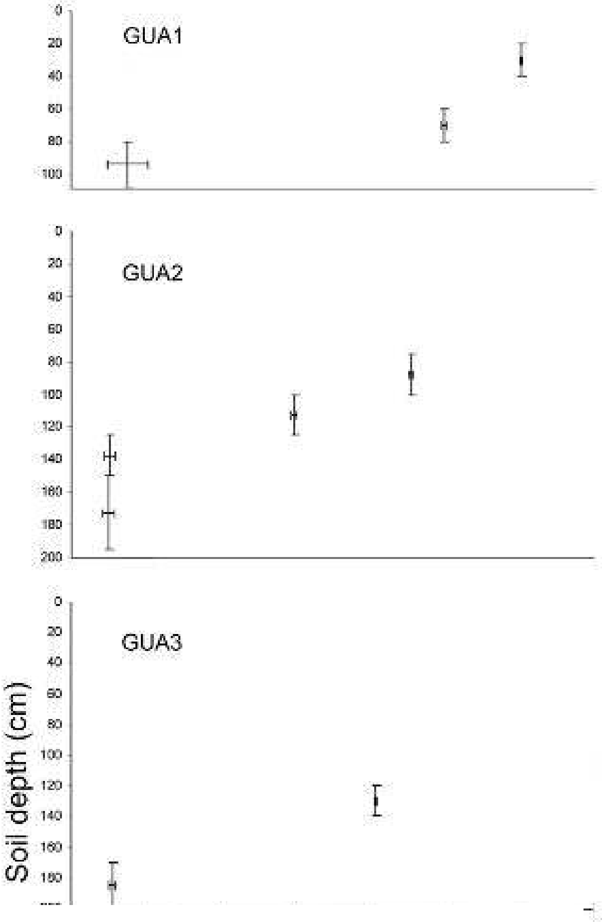

Figure 5 Depth-age relationships for the three profiles. Horizontal bars indicate the range of the calibrated dates at 1 σ, while vertical bars indicate the thickness of the sampling level to which the dates are applied.

Charcoal age and concentration

The age of the charcoal from the deepest soil levels was similar in all pits, at ca. 11,000 ^{14}C yr BP, corresponding to the Pleistocene-Holocene transition (table 2). So the profiles represent a sequence for the entire Holocene, although there is a hiatus between ca. 10,600 and 3700 ^{14}C yr BP in GUA1 (fig. 5). Charcoal ages decreased with decreasing depth in the soil, with no inversions of charcoal age with depth, indicating an ordered stratification of the charcoal in the soil (fig. 5).

Charcoal was present at all depths in all soil profiles, except in the organic layer in the forest (level I, II and III of GUA3) (fig. 5). The charcoal concentration was highest at 125-150 cm in the lower páramo (level VI, GUA2), corresponding to ca. 11,000 ^{14}C yr BP. A second peak is seen in the higher páramo at 25-50 cm (level II, GUA1), corresponding to ca. 2000 ^{14}C yr BP. Very little charcoal was present in the organic soil immediately underlying the organic layer in the forest (level IV, GUA3).

Table 2 Radiocarbon dates of soil charcoal fragments from Guandera Biological Station, northern Ecuador. Charcoal was dated by AMS either at the Dynamitron Tandem Laboratory (Bochum Universität, D, #) or at the Center for Isotopic Research on Cultural and Environmental Heritage (Seconda Università di Napoli, I, *). The AMS ^{14}C measurements were calibrated using the CALIB 4.4 software (Stuiver *et al.* 1998).

Lab. code	Profile level	Depth (cm)	^{14}C yr BP	Cal yr BP (1σ)	Taxa dated (number of fragments)
DSA345	GUA1 - II	20-40	* 2026 ± 39	2006 – 1924	Unidentified (3)
DSA342	GUA1 - IV	60-80	# 3692 ± 47	4091 – 3972	*Blechnum* sp.(7) + Unid. (5)
DSA341	GUA1 - V	80-108	# 10596 ± 367	13033 – 11944	*Pentacalia vaccinioides* (1)
DSA322	GUA2 - IV	75-100	# 4364 ± 51	4975 – 4860	*Diplostephium* sp. (1)
DSA754	GUA2 - V	100-125	* 7236 ± 32	8110 – 7976	*Pentacalia vaccinioides* (1)
DSA313	GUA2 - VI	125-150	# 10886 ± 158	13133 – 12823	Unidentified (2)
DSA312	GUA2 - VII	150-195	# 10964 ± 167	13158 – 12854	*Pentacalia vaccinioides* (7)
DSA575	GUA3 - III	60-100	* modern	-----	*Clusia flaviflora*, root (1)
DSA549	GUA3 - V	120-140	* 5050 ± 30	5889 – 5807	*Pernettya prostrata* (1)
DSA551	GUA3 - VII	170-200	* 10842 ± 46	12994 – 12825	*Pentacalia vaccinioides* (1)

Charcoal identities

Identification of soil charcoal fragments was possible to the genus level, and often even to the species level (fig. 6). Páramo indicator taxa were found in all profiles from 11,000 ^{14}C yr BP until present (in the páramo, GUA1 & GUA2) or until 5000 ^{14}C yr BP (in the forest, GUA3). No forest indicator taxa were found in any charcoal sample. Several taxa were found that, in combination with the páramo indicator taxa, may indicate the presence of a shrubby páramo or subpáramo type vegetation (*Diplostephium, Miconia*). The uppermost level (level I) of both páramo profiles contained charcoal of *Espeletia*, a species now very abundant in the tussock grass páramo.

Discussion

The presence of páramo taxa throughout all three soil profiles, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only very late in the Holocene (after 5000 ^{14}C yr BP). A treeline ecotone or sub-páramo may have reached up to 3810 m asl after 4400 ^{14}C yr BP. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the

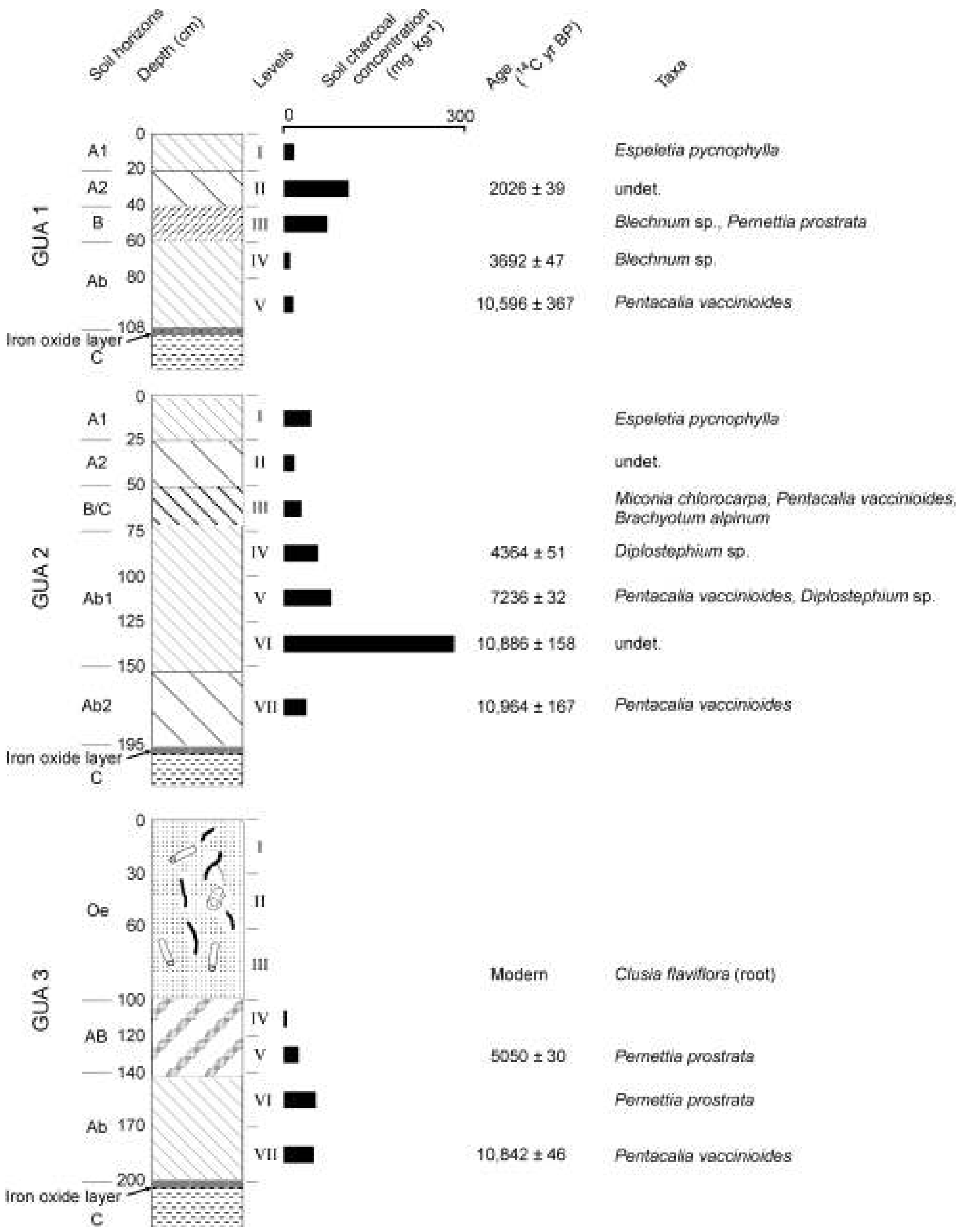

Figure 6 Soil profiles from the páramo (GUA1 and GUA2) and from the forest (GUA3) in Guandera Biological Station, northern Ecuador. The black bars represent the charcoal concentration per level (mg charcoal × kg dry soil $^{-1}$). Dates are expressed in uncalibrated ^{14}C years BP. Taxa of identified charcoal are reported for each level.

Pleistocene-Holocene transition 11,000 ^{14}C yr BP. These fires have not turned forest into páramo, but they have possibly prevented forest extension into the páramo.

The presence of *Pentacalia* charcoal in the deepest level of each profile, aged ca. 11,000 ^{14}C yr BP, confirms the findings of Hooghiemstra and Cleef (pers. comm. 2006), who interpret abundant *Pentacalia* pollen in samples of the same age in combination with abundant grass pollen as a grass páramo interspersed with patches of *Pentacalia* shrubs. It is not surprising that we find this type of cold-climate vegetation in the coldest period of the El Abra stadial (Van't Veer *et al.* 2000). However, at 5000 ^{14}C yr BP there was still páramo vegetation even at the lowest sampling point, where we now find forest (level V of GUA3, at 3540 m asl). This is evidenced by the presence of charcoal from Pernettya prostrata, which is a typical tussock grass páramo species (Kuhry 1988), plus the absence of charcoal from forest species. This is in contradiction with palynological studies from Colombia and Ecuador which show a rise of the treeline to its present altitude already at the beginning of the Holocene (van der Hammen 1974, Flenley 1979).

After 5000 ^{14}C yr BP there is only very little charcoal present in the forest profile (GUA3, at 3540 m asl), which may indicate that fires were less frequent. The absence of fires apparently allowed the actual forest to develop, while in turn the moisture of the forest would have suppressed further fires. So the actual forest is certainly <5000 years old (the age of level V) and could be <4000 years old (the extrapolated age of level IV). The dating of the lowest layer of organic forest soil revealed an age of 100 ^{14}C years. However, the dated material was a root - most of the organic layer consists of roots - and we cannot exclude that this root has penetrated this deepest level long after forest formation. Considering the large size of the *Clusia* trees, the forest must certainly be well over 100 years old. Moreover, observations on the floristic composition and structure of the *Clusia* forest suggest that this is a late-successional forest type. The time of first forest establishment may therefore be even much earlier than the age of the actual *Clusia* forest would suggest.

At the highest altitude (GUA1, at 3890 m asl), páramo taxa were present throughout the profile, so we conclude that at this altitude there has been páramo vegetation during the entire Holocene, even if the hiatus between ca. 10,600 and 3700 ^{14}C yr BP do not allow for very definite conclusions based on this profile alone.

In the middle pit (GUA2, at 3810 m asl), some species are present from 7200 ^{14}C yr BP (level V) that indicate a more shrubby vegetation, possibly similar to some contemporary subpáramo shrub types. This shrubby vegetation lasted for a considerable period, at least to 4400 ^{14}C yr BP, but due to a lack of identifiable charcoal and a lack of datings, it is not yet possible to deduce when tussock grass become dominant again, like it is today. The presence of a páramo indicator (*Pentacalia*) shows that there was no closed forest at 3810 m. However, the presence of the genera *Miconia* and *Diplostephium*, which comprise shrubs characteristic for treeline ecotones (Marchant *et al.* 2002a) and for dwarf forest and dwarf shrub páramo (Cleef & Hooghiemstra 1984), may indicate that the treeline was situated not far below this altitude, although the site may also have been part of an extensive zone of shrub-páramo. If the treeline ever rose above its present altitude at 3600 m asl, this must have happened only after 5000 ^{14}C yr BP, as forest did not establish before this time at 3540 m. Whether the treeline has really been higher than the present 3600 m asl in the late Holocene remains to be investigated with additional sampling points closer to the treeline.

The increased importance of shrubs during the middle Holocene indicates a relatively moist or warm climate, perhaps combined with a decreased fire frequency as a result of increased moisture or decreased land use. Warmer conditions favorable for forest growth were also suggested for the middle Holocene in Colombia by van der Hammen (1974), who states that treelines moved up to above their present position during this 'hypsothermal' period. Other palynological studies in Colombia found depressed treelines during this period, which they attribute to a drier climate (Marchant *et al.* 2001). The increase in forest pollen that van der Hammen et al. (1974) found, has also been interpreted as a decline in páramo flora (leading to an overrepresentation of long-distance forest pollen), suggesting a dryer or colder climate (Markgraf 1989, Horn 1993). The original interpretation appears to be supported by δ^{18}O data from Peruvian glaciers, which indicate a warm period from 8400 to 5200 ^{14}C yr BP (Thompson *et al.* 1995). The higher temperatures would have caused a rise of the treeline where temperature was limiting, while at the same time, if this period was also drier, this would have caused a lowering of the treeline where moisture was locally limiting. This may explain part of the contradictions in different treeline reconstructions for this period. Still, the contrasting conclusions that can be drawn from the same data (van der Hammen 1974, Markgraf 1989) also show the inherent uncertainty in palynological interpretations.

The presence of charcoal from 11,000 ^{14}C yr BP indicates that fires have been part of this ecosystem for a long time. However, we did not find indications that fire has destroyed forests and thus created páramo. Rather, fires may have inhibited or slowed down forest expansion, possibly together with other inhibiting factors such as excess solar radiation and extreme daily temperature fluctuations in the páramo (Bader *et al.* online first). Similarly, Horn (1993) concluded that although fires had occurred during all of the Holocene in a Costa Rican páramo area, 'these fires have not carved páramo from forest'. This is in contrast with the view that forest patches in the páramo are remnants of formerly more extensive forests (Ellenberg 1958, Lægaard 1992, Sarmiento & Frolich 2002).

Regarding the uncertain status of forest patches above the treeline, the most likely hypothesis offered so far is that the highest of these patches are restricted to favorable microsites, while the lower patches may be remnants of formerly more extensive zonal forests (Miehe & Miehe 1994, Kessler 2002, Wille *et al.* 2002). However, based on our results it appears more likely that many patches are neither remnants nor extra-zonal islands, but foreposts of an expanding forest that has been stopped by frequent páramo fires. Both the special microclimatic or edaphic conditions and the protection from fire that are typical of the common locations of forest patches (boulder slopes, ravines, topographical hollows) would contribute to such a scenario: trees may establish earlier and grow faster in such locations, and because of their size be less susceptible to fire, and by competition reduce the biomass (=fuel load) of surrounding tussock grasses. If, on top of that, the fire frequency or the fire intensity is lower because of a protected position, forest patches can develop while the surrounding areas remain páramo.

At present, natural fires are unlikely to occur, because the vegetation is always wet during thunderstorms, and there is no volcanic activity nearby that might ignite fires. In the beginning of the Holocene, as well as during several later periods, the climate appears to have been drier (Van't Veer *et al.* 2000, Marchant *et al.* 2001, Marchant *et al.* 2002a, Vélez *et al.* 2003), and fires may have occurred naturally. For the Andes, the presence of charcoal at the Pleistocene-Holocene transition is generally explained by this dryer climate, and this type of interpretation is applied until the middle Holocene. Only when the first direct evidence of anthropogenic disturbance is found in the pollen record (pollen from agricultural and disturbance species), are fires generally attributed to man (Hansen & Rodbell 1995, Marchant *et al.* 2001, Wille *et al.* 2002, Hansen *et al.* 2003, Bush *et al.* 2005).

The first appearance of humans in South America is dated at the Pleistocene-Holocene transition (Fiedel 1999, Gnecco 2003). These first inhabitants did not practice agriculture, so no pollen of disturbance vegetation or agricultural species witness their presence, but they could leave traces of fire (Piperno *et al.* 1990). They were hunter-gatherers, and just like is still happening on the mountains of East-Africa (Wesche *et al.* 2000), mountain grasslands or shrublands may have been burned to facilitate hunting. Also, fires may reflect the use of the areas with open vegetation above the treeline for traveling (Hermes 1955). In this way early human populations may have already influenced the high-altitude vegetation in the beginning of the Holocene, possibly preventing forest expansion into the páramo. However, the distinction between natural and anthropogenic fires can not be made, so we are restricted to speculations as to the origin of the palaeofires, and hence as to the 'naturalness' (as opposed to man-made origin) of the lower parts of the modern páramo.

Charcoal particles ≥ 0.4 mm provide information about local fires (Patterson III *et al.* 1987, Ohlson & Tryterud 2000). The charcoal concentration found in the soil depends on the type and quantity of the burned biomass (Carcaillet 1998) and on the time since burning (di Pasquale 1998). This concentration is therefore not a simple measure for the fire frequency. Still, the strong correspondence in the timing of the charcoal peak in level VI of GUA2 and that found on a continental scale by Haberle & Ledru (2001) may indicate an increased fire frequency during this period, and asks for further investigation.

The pedoanthracological methods used here have some clear advantages over the more traditional palynological methods, most importantly the high spatial resolution that can be obtained thanks to the local nature of the charcoal proxy. A disadvantage is the large amount of soil needed to extract sufficient identifiable charcoal, which implies that the levels from which soil is collected are relatively thick, resulting in a low temporal resolution. This coarse sampling may partly explain the hiatuses in our chronologies, but these discontinuities may also be due to erosion. The origin of the hiatuses will be addressed in further analysis of the soil profile.

Soil charcoal data from a small number of pits is sufficient to provoke many interesting hypotheses about vegetation history, and falsify others. Still, a more detailed spatial analysis of past vegetation cover requires a larger number of sampling points. Considerable improvement can also be made by the extension of the charcoal reference collection, which is in fact being extended continuously. Based on the results described here, additional sampling points were located at optimal positions for detailing the speed and timing of treeline movements. Data from these additional profiles are being investigated at present.

Conclusions

The charcoal records in the studied soils represent the entire Holocene, starting at ca. 11,000 ^{14}C yr BP. The presence of páramo taxa throughout all three records, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only recently (after 5000 ^{14}C yr BP). During the middle Holocene (7200-4400 ^{14}C yr BP) there was a period favorable for shrub and tree growth, and the treeline may have risen most during this period. However, the treeline has never reached 3890 m asl, and we have no strong indication that it ever reached 3810 m asl. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the beginning of the Holocene. These fires have not caused a downward movement of the treeline, but they have possibly slowed down forest extension into the páramo. Further research will focus on detailing the speed and timing of treeline rise.

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		Key features of wood anatomy		
Species	Family	Transverse section	Tangential section	Radial section
Ilex colombiana	Aquifoliaceae	growth ring boundaries indistinct or absent; wood diffuse-porous; vessels partly solitary, partly in clusters and with arrangement in radial pattern; mean tangential diameter of vessel lumina 50-100 µm	ray width 1 to 3 cells; intervessel pits scalariform	simple perforation plates
Oreopanax confusus	Araliaceae	growth ring boundaries indistinct or absent; wood diffuse-porous; vessels in dendritic and radial pattern; vessel cluster common; mean tangential diameter of vessel lumina <50 µm; intervessel pits scalariform	ray width 1 to 3 cells; intervessel pits scalariform	simple perforation plates; rays with procumbent, square and upright cells mixed throughout the ray
Espeletia pycnophylla	Asteraceae	growth ring boundaries indistinct or absent; wood from diffuse to semi-ring-porous; vessel solitary or in clusters; mean tangential diameter of vessel lumina 50-100 µm; axial parenchyma vasicentric and confluent	rays of two distinct sizes; rays width 1 to 3 cells and larger rays commonly >10-seriate; intervessel pits scalariform and opposite	simple perforation plates; ray with procumbent, square and upright cells mixed
Pentacalia vaccinioides	Asteraceae	growth ring boundaries distinct; wood diffuse-porous; vessels in radial pattern and exclusively solitary; mean tangential diameter of vessel lumina <50 µm; axial parenchyma diffuse in aggregates; axial parenchyma scanty paratracheal and vasicentric	ray width 1 to 3 cells; intervessel pits alternate; helical thickenings in vessel elements present	scalariform perforation plates; all ray cells upright and/or square
Clusia flaviflora	Clusiaceae	growth ring boundaries indistinct or absent; wood diffuse-porous; vessels partly solitary, partly and with arrangement in radial pattern; mean tangential diameter of vessel lumina <50 µm; parenchyma vasicentric and diffuse	ray width 1 to 3 cells; intervessel pits scalariform; helical thickenings in vessel elements present	reticulate and scalariform perforation plates with 20-40 bars; body ray cells procumbent with one row of upright and/or square marginal cells
Pernettia prostrata	Ericaceae	growth ring boundaries distinct; wood diffuse-porous; wood diffuse-porous; vessels exclusively solitary; mean tangential diameter of vessel lumina <50 µm	ray width 1 to 3 cells; intervessel pits alternate; helical thickenings in ground tissue fibres	scalariform; reticulate and/or other types of multiple perforation plates; all ray cells upright and/or square
Ocotea infrafoveolata	Lauraceae	growth ring boundaries indistinct or absent; wood diffuse-porous; vessels partly solitary, partly in clusters; axial parenchyma vasicentric; mean tangential diameter of vessel lumina <50 µm	ray width 1 to 3 cells; intervessel pits alternate; ray width multiseriate portions as wide as uniseriate portions	simple perforation plates; body ray cells procumbent with one row of upright and/or square marginal cells

CHAPTER 4

High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador

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Photo previous page: seedlings of *Gaiadendron punctatum*

High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador

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Abstract

Many tropical alpine treelines lie below their climatic potential, because of natural or anthropogenic causes. Forest extension above the treeline depends on the ability of trees to establish in the alpine environment. This ability may be limited by different factors, such as low temperatures, excess solar radiation, competition, soil properties, dispersal ability and fires. In this paper we address the following two questions: Do trees regenerate above the present treeline, and what are the inhibiting factors for tree establishment? To answer these questions we described the spatial pattern of recent tree establishment below and above the present treeline in northern Ecuador. Also, we experimentally transplanted seedlings into the alpine vegetation (páramo) and the forest, and investigated the effect of shade, neighboring plants, and substrate on their survival. The number of naturally occurring tree sprouts (seedlings, saplings and ramets) was highest just outside the forest, and decreased with distance to the forest edge. However, only two species that were radiation-tolerant made up these high numbers, while other species were rare or absent in the páramo. In the forest the species diversity of sprouts was high and the abundance per species was relatively low. The transplanted seedlings survived least in experimental plots without artificial shade where neighboring plants were removed. Seedling survival was highest in artificially shaded plots and in the forest. This shade-dependence of most tree species can strongly slow down forest expansion towards the potential climatic treeline. Because of the presence of radiation-tolerant species, the complete lack of forest expansion probably needs to be ascribed to fire. However, our results show that natural processes can also explain both the low position and the abruptness of tropical treelines.

Keywords: cloud forest, cold-induced photoinhibition, fire, páramo, positive feedback switch, transplantation experiment

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Introduction

On most tropical mountains the actual treeline lies at a lower altitude than the potential climatic treeline (Miehe & Miehe 1994, Kessler 1995). In this paper we use the term treeline to refer to the actual upper boundary of closed forest. The potential climatic treeline then delimits the potential forest extent under the current climatic conditions. The altitude of this potential treeline is unknown, however, because both historical treeline dynamics and the ecological drivers of current dynamics are not well understood (Kessler 2002, Wille *et al.* 2002).

In general, two possible explanations for the positional discrepancy between the actual and the potential treeline exist. Firstly, treelines may still not have moved up to their potential altitude from previously lower positions (e.g. in the last ice-age) due to the slowness or absence of natural colonization (Slayter & Noble 1992, Wardle & Coleman 1992, Holtmeier 1994). Secondly, treelines may have been moved down from previously higher positions due to human activities, especially fire (Lægaard 1992, Miehe & Miehe 1994, Kessler 1995, Ellenberg 1996, Wesche *et al.* 2000, Hemp & Beck 2001, Wille *et al.* 2002). The latter, anthropogenic scenario now dominates the literature as the explanation for the relatively low treeline positions in the Ecuadorian Andes and in most other tropical mountain areas.

Temperature is generally considered to be the main natural determinant of treeline position (Körner & Paulsen 2004), and treelines are therefore expected to react strongly to global warming (Kupfer & Cairns 1996, Kullman 2001). However, if a treeline lies below its climatic potential, for whatever reason, the forest could extend upwards even if there is no increase in temperature. Forest extension, whether due to climatic change or not, depends on the ability of trees to establish above the present treeline. This ability may be temperature dependent for some species, but other limitations, such as excess solar radiation, competition from neighbors, unfavorable soil properties, low dispersal ability, and fire could be equally important.

Treelines in tropical mountains experience very high solar radiation levels, due to the combination of low latitude and high altitude. Excess radiation can have negative effects on plants, causing overheating, desiccation, and photoinhibition (Barber & Andersson 1992, Long *et al.* 1994). These negative effects are aggravated by low temperatures (Ball *et al.* 1991, Krause 1994, Huner *et al.* 1998, Close *et al.* 2000), especially frost, which can occur year-round at night at tropical treelines. Cold-induced photoinhibition has been recognized as a limitation for tree seedling establishment at treelines in Australia and North America (Ball *et al.* 1991, Germino & Smith 1999, Germino *et al.* 2002).

Competition from surrounding vegetation could also limit tree seedling establishment (Wardle & Coleman 1992), but facilitation tends to gain relative importance in more stressful environments such as alpine areas (Choler *et al.* 2001, Pugnaire & Luque 2001, Callaway *et al.* 2002). At least at some temperate treelines, seedlings seem to benefit rather than suffer from surrounding alpine vegetation (Germino *et al.* 2002, Smith *et al.* 2003, Maher *et al.* 2005), but for tropical treelines this balance is yet unknown. In the páramo, the alpine vegetation of the northern Andes, plant cover is often very dense and over half a meter high, and may therefore compete heavily with tree seedlings, although it could also offer protection.

In this paper we address the following two questions: do trees regenerate above the present treeline, and what factors limit tree establishment? Based on the reasons given above, we suspected that excess solar radiation is a main limitation for tree regeneration above tropical treelines. We therefore hypothesized that only radiation-tolerant tree species could naturally regenerate in the páramo, and that other species could survive here only if extra shade were provided artificially, while removing shade from neighboring plants would decrease survival. To test the first hypothesis we studied the spatial pattern of recent tree establishment below and above the present treeline in northern Ecuador. To test the latter we experimentally transplanted seedlings into the páramo, where treatments consisted of providing shade and clearing neighbors, and into the forest. We also hypothesized that tree seedlings did not depend on the organic, moss-covered forest substrate, but could establish equally well in the mineral páramo soil. To test this, one treatment in the forest consisted of removing the thick organic layer, thereby exposing the mineral soil.

Understanding the natural dynamics and the regeneration requirements of cloud forests at the treeline can have important implications for reforestation or ecological restoration in páramo areas. Our results will also help to understand different reasons why treelines can lie below their climatic potential and why they are usually abrupt, and offer insight in the treeline dynamics we can expect due to climatic change (Slayter & Noble 1992).

Study area

The studied treeline is part of the private biological reserve Guandera Biological Station, situated on the inner flanks of the eastern Cordillera in northern Ecuador (N 0° 36′, E -77° 42′, fig. 1). The area is of volcanic origin and has deep dark humic Andosols, developed in old volcanic ashes. Precipitation is high all year round. Average temperatures are low and fluctuate little through the year, but diurnal temperature fluctuations are strong (fig. 2).

The treeline in this area is an abrupt boundary between upper montane cloud forest (Hamilton *et al.* 1995) and tussock grass páramo (Hofstede *et al.* 2003) (fig. 3). It varies in altitude from ca. 3500 to 3700 m above sea level (asl), and its position has been stable for at least 40 years, as evidenced by historical aerial photographs. Patches of forest are found up to 100 m from the closed forest boundary in small topographical depressions and valleys. These patches are also at least 40 years old.

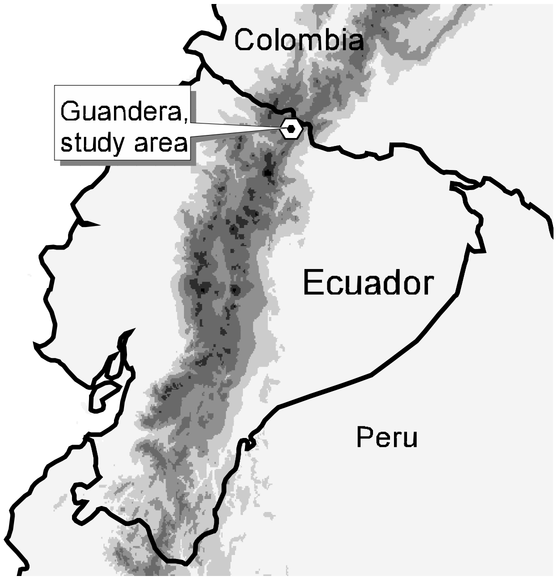

Figure 1 Map of Ecuador showing the location of the study area. Elevation data: GTOPO30 (USGS, 1996).

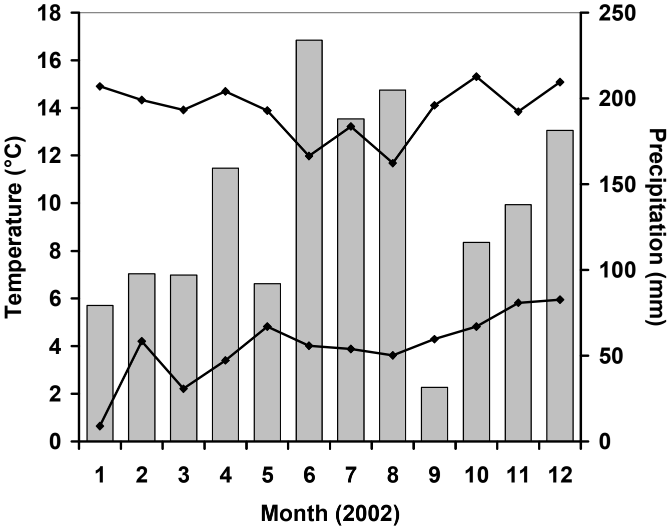

Figure 2 Climate of Guandera in 2002, a year with normal weather conditions. Mean maximum and minimum daily temperature at 2 m (lines) and total precipitation per month (bars). Data from weather station at Guandera Biological Station, in open area in cloud forest at ca. 3370 m asl.

The reserve is named after the tree species *Clusia flaviflora,* locally called guandera, a large and distinctive tree with abundant aerial roots, which dominates parts of the forest. Other parts of the forest have a mixed canopy composed mainly of the tree species *Ilex colombiana, Weinmannia cochensis, Miconia tinifolia, Clusia flaviflora* and *Gaiadendron punctatum* (authorities in table 1). The most common shrub species in the understory are various Ericaceae, *Miconia chlorocarpa* Cogn., *Desfontainia espinosa* Ruiz & Pav. and

Figure 3 Photograph of the study area in Guandera Biological Station in northern Ecuador. This part of the treeline is situated at ca. 3650 m asl. In the foreground and on the left there is tussock grass páramo with abundant Espeletia pycnophylla stem rosettes, and on the right there is upper montane cloud forest, locally known as the 'ceja andina'.

Myrsine sp. At the forest edge large *Diplostephium* shrubs and caulescent *Blechnum* ferns are the most common elements. The forest floor is totally covered with moss, including *Sphagnum* species, especially at the forest edge, and has a peaty organic layer of 30-100 cm on top of the dark mineral soil.

The páramo is dominated by large tussock grasses (*Festuca* sp., *Calamagrostis* sp.), which generally form a dense layer of about 0.5 m high. The terrestrial Bromeliad *Puya hamata* L.B.Smith and the tall (up to 4 m) stem rosette *Espeletia pycnophylla* Cuatrec. are abundantly interspersed in the grass. There is no animal husbandry in the páramo, nor has there been in the past (local people, pers. comm.), but fires are lit every 3-6 years because of the traditional belief that burning the páramo will induce rainfall, and due to carelessness or arson.

Methods

Natural regeneration pattern

To describe the pattern of natural tree regeneration 20 transects were laid out from 10 m below to 85 m above the treeline (distances along the slope). Eight plots of 5x6 m were located along each of these transects, with the lower boundaries of the plots at –10 m, -5 m, 0 m, 5 m, 12 m, 20 m, 40 m and 80 m above the treeline. Additionally, one set of five plots was located further (over 300 m) above the treeline. Within all these plots all tree seedlings, saplings and ramets up to 1.4 m in height were counted (ramets principally of *Gaiadendron punctatum*, a species with strong clonal distribution). We will use the term sprouts to refer to seedlings, saplings and ramets together. In each the forest plot we also estimated the canopy cover of each tree species.

Transplantation experiment

To test what factors may be limiting the regeneration of different tree species above the treeline, we transplanted tree seedlings to positions below and above the treeline. In the páramo seedlings were planted in 56 plots in a randomized-complete-blocks design. Each block contained four plots (ca. 1x3 m in size and 25 m apart) with a different treatment in each plot: cleared neighboring plants, shaded with a shade tent, both cleared and shaded, and control. Fourteen blocks were established at different distances from the treeline (between 3 m and 170 m), and each distance was represented by two blocks (ca. 500 m apart). The shade tents were made from black 80% shade cloth. Neighbors were cleared to approximately 0.5 m around the seedlings. Seven seedlings were planted in each páramo plot.

In the forest seedlings were planted in 12 plots in a randomized-complete-blocks design with two treatments: undisturbed forest substrate (moss), and cleared organic layer (revealing the underlying black soil). Two blocks were established (ca. 500 m apart), each block containing three plots of both treatments, and both blocks were situated between 5 m and 20 m below the treeline. Eight seedlings were planted in each forest plot.

Seedlings (3 to 50 cm tall) of eight tree species were included in the experiment, because we expected species-specific responses. Seedlings were collected in the forest near the treeline, and were generally planted the same day. They were easily pulled out of the moss and organic material of the forest floor, generally with no or little damage to the roots. Seedlings were collected in numbers roughly proportional to their occurrence in the forest, so rare species were planted in small numbers. The height and survival of the seedlings were assessed after 2, 6, 18 and 30 months. As an exception, *Gaiadendron* seedlings were assessed only once, 12 months after they were planted, because these were planted at a later date. These seedlings came from a nearby nursery (at ca. 3350 m asl), because they were too rare in the forest to be collected in sufficient numbers.

Between the 6-month and the 18-month measurements we found very little additional mortality inside the shade tents. We therefore expected little additional mortality in the last year, and to gain more information from the experiment we decided to test the effect of exposure to radiation on established seedlings. To this end some of the tents were removed. Thereby 4 of the 14 'cleared & shaded' treatments became 'cleared' treatments, and 6 of the 14 'shaded' treatments became 'control' treatments.

To assess the effect of the treatments on the microclimate, air and soil temperatures were measured. Air and topsoil temperatures were recorded every 2 minutes in forest moss and in all páramo treatments during 7 days. During these days the weather was variable, with sunny and cloudy periods, including some light rain. We used HOBO H8 Outdoor 4-Channel External Data Loggers (Onset Corporation) with external temperature probes. Temperature probes were installed at 15 cm above ground and at 3 cm below ground. Those above ground were protected from direct sunlight by small roofs made from disposable aluminum muffin tins lined with Styrofoam. Measurements were replicated (two sets of measurement series for each of the 4 treatments), but due to technical failure only one measurement series per treatment was usable. Soil temperatures at 12 cm below ground were measured once in each plot at the end of the experiment using a digital steel thermometer (1 °C accuracy, 0.1 °C resolution).

Results

Natural regeneration pattern

The number of naturally occurring sprouts was highest in páramo plots just outside the forest, and decreased with distance from the forest edge (fig. 4). The high numbers in the páramo were due to the abundance of *Gaiadendron* ramets and *Weinmannia* seedlings, which were both relatively rare in the forest. The numbers of both *Gaiadendron* and *Weinmannia* sprouts in the páramo correlated negatively with the distance from the forest edge (Spearman's correlation of rank coefficients: $R=-0.71$ and $R=-0.60$, $p< 0.01$). Other species occurred in too low numbers in the páramo to allow calculating such a correlation. Inside the forest the species diversity of sprouts was high; seven species were found, but numbers were relatively low (table 1 & fig. 4). Seedlings of *Diplostephium* (Asteraceae) were also common in the páramo, but these were not included in this part of the study because this species is

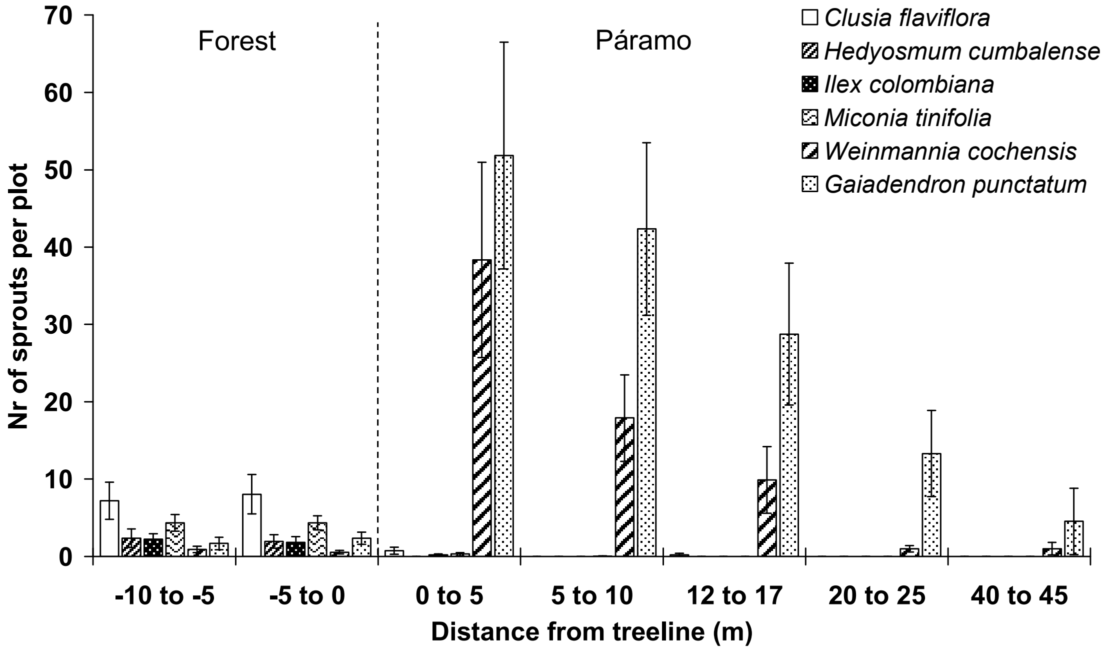

Figure 4 Mean number of naturally occurring sprouts (including seedlings and ramets) in 30 m² plots at different distances from the forest edge. Each bar represents the mean of 20 plots, error bars represent the standard error. Not shown are sprout numbers in plots at 80-85 m and at >300 m, because no sprouts occurred here.

not a tree but a large (up to 4 m) shrub. However, because of its expected insensitivity to high radiation levels, this species was included in the transplantation experiment.

The total number of plots where a species was found in the canopy correlated positively (Spearman's R=0.80; p< 0.01) with the total number of sprouts of this species (in all plots in both forest and páramo) (table 1). For most of the common species, the average canopy cover of that species correlated positively with the total number of sprouts of that species per transect (Spearman's R for *Gaiadendron*: R=0.45, p<0.05; *Clusia*: R=0.74, p<0.01; *Miconia*: R=0.60, p<0.01; *Hedyosmum*: R=0.68, p<0.01). In contrast, in only one case did canopy cover per transect for a species correlate positively with the number of sprouts of another species (*Clusia* cover with *Hedyosmum* sprouts: Spearman's R=0.63, p<0.05).

Transplantation experiment

The transplanted seedlings had the lowest overall survival rate in the cleared plots without shade, followed by the control (fig. 5). The artificially shaded plots and those in the forest all had relatively high seedling survival, and after

Table 1 Number of sprouts found in 30 m^2 plots in forest and páramo: mean number per plot and standard deviation. The last column is the number of forest plots (total 40) where the tree species was present in the canopy. Two species of *Clusia* occur in the study area, but these were not distinguished in this study.

Species	Family	Mean (sd) nr of sprouts		# plots w species in canopy
		Páramo (125 plots)	Forest (40 plots)	
Gaiadendron punctatum (Ruiz & Pavón) G.Don.	Loranthaceae	17.6 (38.1)	2.0 (3.5)	26
Weinmannia cochensis Hieron.	Cunoniaceae	8.4 (25.4)	0.7 (1.5)	35
Clusia flaviflora Engl. and *C. multiflora* Kunth	Clusiaceae	2.0 (6.2)	7.6 (10.8)	21
Miconia tinifolia Naudin	Melastomataceae	1.1 (2.8)	4.4 (4.2)	31
Hedyosmum cumbalense Swartz.	Chloranthaceae	0.5 (2.5)	2.2 (4.6)	8
Ilex colombiana Cuatrec.	Aquifoliaceae	0.5 (1.8)	2.0 (3.2)	31
Escallonia myrtilloides L.F.	Escalloniaceae	0.0 (0.2)	0.1 (0.3)	2
Clethra ovalifolia Turcz.	Clethraceae	-	-	1
Oreopanax cf. confusus Marschal.	Araliaceae	-	-	4

18 months there was no significant difference between these treatments (fig. 5). Accordingly, substrate type had no effect in the forest. At the 2-month measurement, survival did not yet differ between plots, although the health of the seedlings already predicted the differences found later. The removal of shade, 18 months after planting, had a significant negative effect on the survival of the seedlings that had survived so far both in the treatment with and without neighboring plants (two-way Anova, using the arcsine transformed survival per plot as the dependent variable, $p<0.05$). There was no correlation between the distance from the treeline and survival of the sprouts (Spearman's R=-0.05 for survival after 30 months), and treatments had the same effects at all distances from the treeline (no block effect in Anova).

The survival after transplantation differed between species (one-way Anova, $p<0.01$), and species responded differently to treatments (two-way Anova, interaction term: $p<0.01$) (fig. 6). Seedlings of *Clusia* and *Diplostephium* had the highest overall survival rates (Bonferroni post-hoc test, $p<0.01$), but *Clusia* survived much less in the treatments without shade, while *Diplostephium* indeed appeared to be rather insensitive to the different treatments.

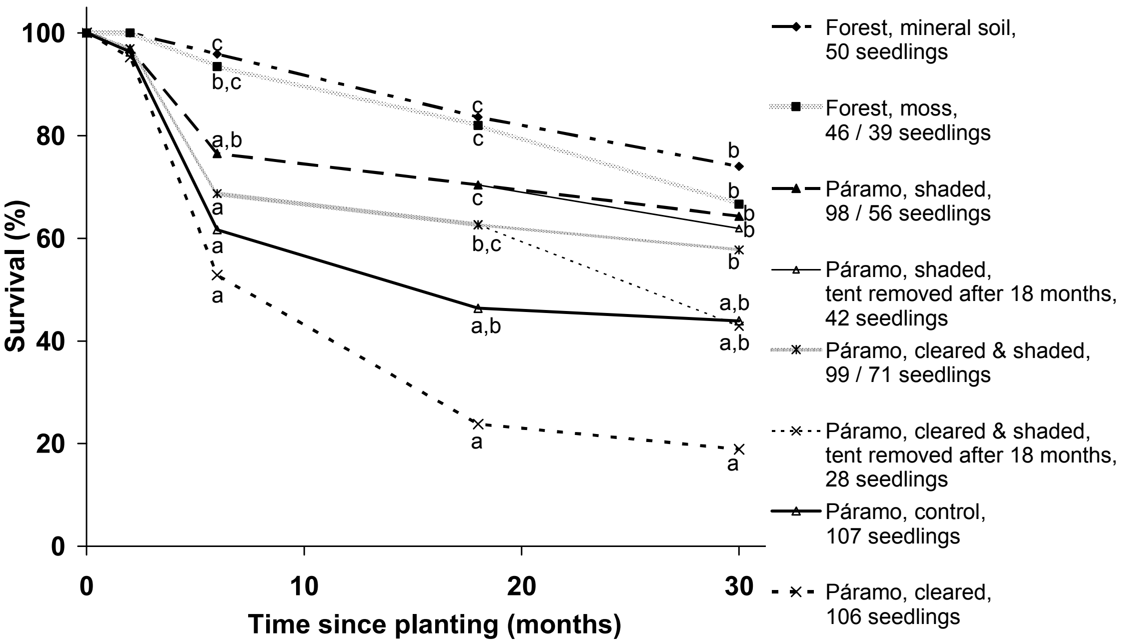

Figure 5 Survival of all transplanted seedlings through time in the different treatments. Different letters indicate significant ($p<0.05$) differences between treatments, per measuring time, according to a one-way Anova and Bonferroni post-hoc test, using the arcsine transformed survival per plot as the dependent variable. There was no block effect, i.e. there was no effect of distance from the treeline. At 18 months part of the plots with shade treatments were changed: tents were removed. Therefore the graph is split in two at this point. The number of seedlings involved in each treatment is shown in the legend, and a second number is the number of seedlings (both dead and alive) still in this treatment after 18 months (in the forest a plot in moss was lost after 18 months). The seedlings that were planted at 18 months are not included.

Seedlings of *Ilex* and *Gaiadendron* had lower overall survival rates, but while survival of *Ilex* seedlings did not differ between treatments, *Gaiadendron* seedlings survived much less in the cleared plots without shade, while in the plots where páramo neighbors were left intact they had a higher survival. Species not included in figure 6 were *Miconia chlorocarpa*, *M. tinifolia*, *Oreopanax* sp., and *Weinmannia cochensis*. These were planted in numbers too low to allow detection of a species-specific response.

Seedlings had hardly grown in 2.5 years; in fact many had decreased in size due to damage to the upper part of stems and leaves, or due to a rise in the measurement base: fast growing moss in the forest. The types of damage observed were discoloration and subsequent shedding of leaves, drying out of leaves and stems, some wilting, and occasionally some infections by fungi or other plant pathogens (rot). Often, only exposed parts of leaves showed discoloration or senescence, suggesting direct damage from radiation. No insects or traces of browsing were observed on the seedlings. The average length increase of the surviving seedlings was -3 cm, so a decrease. Of the 316 surviving seedlings, only 71 had grown more than 1 cm, 156 had "grown" less than -1 cm, and 89 had the same size as at planting (a change in size of 1 cm or less is not considered growth, because of the measurement accuracy). Only twelve of the larger seedlings had grown more than 10 cm, 8 of which were *Diplostephium*. Expressed relative to the stem size at planting, average growth of surviving seedlings was -9%, 160 seedlings had "grown" less than -10%, and only 84 seedlings had grown more than 10%. Growth differed between treatments; relative growth of surviving seedlings was

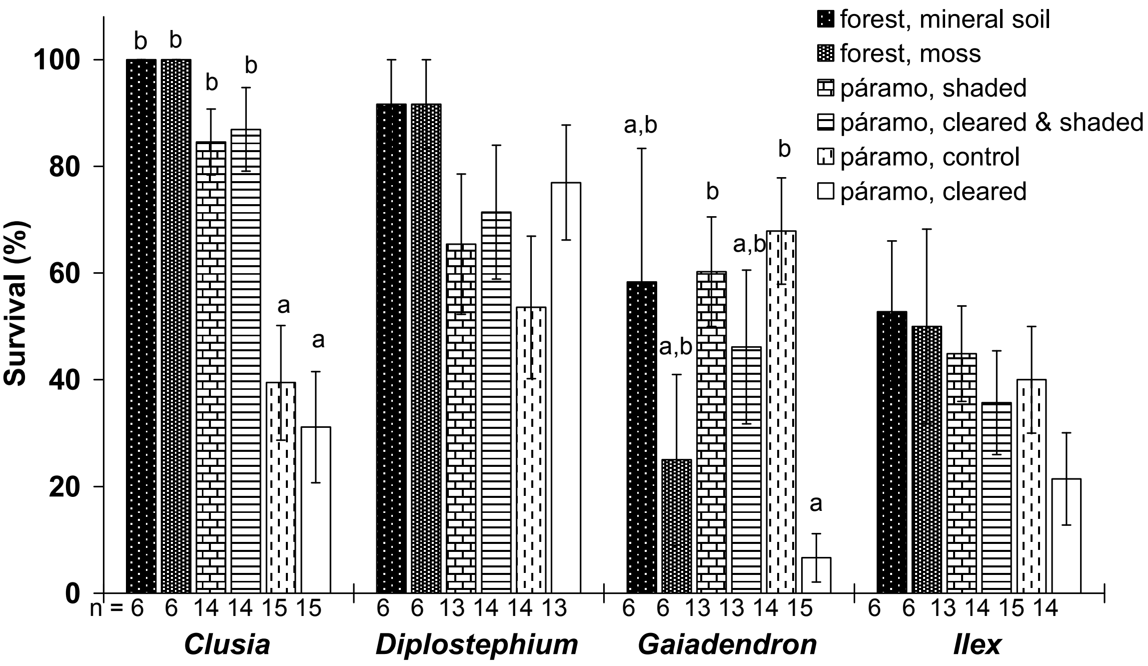

Figure 6 Survival of transplanted seedlings after 18 months (*Clusia*, *Diplostephium* and *Ilex*) or after 12 months (*Gaiadendron*). The order of the treatments reflects a decrease in the overall seedling survival (for all species together, see fig. 5). Bars represent the mean of the plots, error bars represent the standard error. Most plots contained 1 to 3 seedlings of a species and the number of plots involved is shown under each bar. *Diplostephium* sp. and *Ilex* do not react significantly to the treatments, in contrast to Clusia and *Gaiadendron*. For the latter species different letters indicate significant (p<0.05) differences between treatments, per species (one-way Anova and Bonferroni post-hoc test per species).

Table 2 Temperatures (°C) in the different treatments of the transplantation experiment. Temperatures of topsoil (-3 cm) and air (15 cm) are summaries of data recorded with dataloggers every 2 min during 7 days (13 to 20-11-2003): mean and sd of one point over time. Temperatures of the soil at 12 cm depth were measured once in each plot: mean and sd of several points at one time (n=number of points measured).

	°C	Forest, mineral soil	Forest, moss	Shaded (in tent)	Shaded & cleared	Control	Cleared
15 cm (air)	min T		2.5	-0.6	-2.0	-2.0	-2.0
	max T		15.2	30.3	31.5	35.7	29.9
	mean T (sd)		7.0 (2.3)	8.2 (5.4)	8.6 (6.1)	8.2 (6.8)	8.3 (5.5)
-3 cm (soil)	min T		3.7	5.8	5.0	7.0	5.0
	max T		12.6	11.8	13.7	12.2	19.0
	mean T (sd)		7.1 (1.5)	8.4 (1.2)	9.1 (2.0)	9.4 (1.1)	11.3 (3.4)
-12 cm (soil)	mean T (sd)	9.2 (0.3) n=5	9.9 (0.1) n=3	10.8 (0.3) n=8	11.6 (1.4) n=9	11.8 (0.5) n=19	12.7 (1.0) n=18

lowest (-25 % to -13 %) in the forest plots and in the plots without artificial shade, and highest (25 % and 3 %) in plots with artificial shade (one-way Anova and Bonferroni post-hoc test, p<0.01).

Air and topsoil temperatures were similar in the four páramo treatments, but differed between páramo and forest (table 2). Still, also the treatments in the páramo caused some differences that may have affected the performance of the seedlings. The maximum topsoil temperature was higher in the cleared plot and to a lesser extent in the cleared & shaded plot, and minimum topsoil temperatures were lower in both these treatments compared to the páramo treatments without clearing. The bare soil surface in the unshaded cleared plots was also observed to be rather dry, and there was hardly any reinvasion by herbs or tussock grasses. In contrast, beneath the shade tents a ground cover of moss indicated a moister microclimate. Another treatment effect that could have affected seedlings is the higher minimum air temperature in the shaded plot (table 2). However, in the cleared & shaded plot the minimum air temperature was the same as in the unshaded plots, and the maximum air temperature varied without any consistent relationship to the treatments. In the forest the mean temperatures were consistently lower and air temperatures were less variable and less extreme than those in any of the páramo treatments. Here, moss is also abundant, because of and contributing to the high humidity. So the main aspects of the forest microclimate that the shade tents reproduce are the protection from radiation, as intended, the higher humidity, a side-effect, but not the lower and more constant temperatures. The clearing of neighbors also did not affect air temperatures, but it increased soil temperature fluctuations through increased exposition to solar radiation during the day and to radiative cooling at night.

Discussion

Most tree species did not regenerate naturally above the studied treeline. Seedlings that were transplanted into the páramo survived and grew most under artificially provided shade. Natural shade from the páramo vegetation also had a positive effect on survival, outweighing competitive effects. The effect of substrate type on seedling survival was negligible. So according to our results excess solar radiation indeed hinders tree regeneration above this tropical treeline, similar to what has been found at several temperate treelines (Wardle 1985, Ball *et al.* 1991, Germino & Smith 1999, Kitzberger *et al.* 2000, Germino *et al.* 2002, Maher *et al.* 2005).

The species that are naturally regenerating in the páramo all have adaptations to protect themselves from the direct effects of excess radiation, such as photoinhibition and overheating. *Diplostephium* has whitish pubescent leaves that reflect sunlight, *Weinmannia* rapidly turns red in sunlight due to the production of protective pigments, and *Gaiadendron* is orange in high light situations (pers. obs.). The preference of *Gaiadendron* for high-light environments is also reflected by its usual habitus: in closed forest it grows epiphytically while in open habitats it grows terrestrially (Kuijt 1963, Beyer 1993). So indeed we found that only sprouts of radiation-tolerant tree species occurred in the páramo.

Damage by excess solar radiation can occur in several forms (Valladares & Pearcy 1997). Direct damage related to over-excitation of the photosynthesis apparatus (photoinhibition, photooxidation) is aggravated by low temperatures. Plants that cool down strongly during the night are therefore particularly vulnerable to the negative effects of solar radiation in the morning (Lundmark & Hällgren 1987, Ball *et al.* 1991), so that exposed plants are dually affected (Germino & Smith 1999). However, the shade tents did not affect minimum soil temperatures, and minimum air temperature was higher in the shaded but not in the cleared & shaded plot. Still, seedlings showed a strong positive reaction to both shade treatments. We therefore conclude that high radiation is a more important limitation for tree seedling establishment than extreme temperatures *per se*. Nightly frosts certainly contribute to the adverse conditions for tree regeneration in the páramo, but mainly when they are followed by strong sunlight during the day (Ball *et al.* 1991, Krause 1994, Close *et al.* 2000).

Direct radiation damage was evident in the patterns of leaf discoloration of some of the species. This damaged appeared more serious than just photoinhibition, as it caused shedding of the leaves and in most cases the death of the whole seedling. Both photooxidation and UV damage may play a role. In other species the cause of the damage appeared to be more related to overheating and desiccation, which are also caused by excess radiation. The topsoil of cleared plots warmed up more than that of other plots, but because of the good water retention capacity the páramo soil dried out only superficially. Still, because of the high water demand for transpirational cooling of exposed leaves, and because of the dryer air in the exposed plots, water stress and subsequent overheating may have negatively affected seedling performance (Valladares & Pearcy 1997, Smith *et al.* 2003). Although our results clearly demonstrate that radiation causes damage and hinders tree regeneration, the exact mechanisms of radiation damage in the studied species definitely need further investigation.

Most tree species regenerated naturally only in the shade of the forest. Dependence of seedlings on shade is common in many natural ecosystems (Callaway 1995, Pugnaire *et al.* 1996, Weltzin & McPherson 1999), yet it is important to realize that it also affects tropical treelines, because this intolerance to radiation can influence treeline dynamics and spatial patterns (Slayter & Noble 1992, Kupfer & Cairns 1996). It can for instance be one of the reasons why the treeline in this area is so stable, even though the potential climatic treeline may lie at a higher altitude. Such stability could involve a positive feedback between vegetation and environment, causing a 'switch' (Wilson & Agnew 1992). Shade-dependence can create a positive feedback switch because the forest provides shade, so that tree growth is favored and the forest is maintained, while the lack of shade in the páramo inhibits tree establishment so that the páramo is maintained. Such positive feedback can not only stabilize the treeline, but can also make it more abrupt (Armand 1992, Wardle & Coleman 1992, Wilson & Agnew 1992, Camarero & Gutiérrez 2004). Shade-dependence of tree seedlings could therefore be an alternative or additional explanation for the abruptness of tropical treelines (Tranquillini 1979, Bader *et al.* accepted), which is usually attributed to fire alone (Miehe & Miehe 1994).

However, in our study area tree species are present that are not shade-dependent and that could therefore stop a positive feedback based on radiation. Yet no recently established adult trees were observed in the páramo, and the treeline had not advanced for at least 40 years. This is probably due to the fires that occur regularly in the páramo. After a páramo fire the tussock grasses re-grow rapidly (Beck *et al.* 1986, Lægaard 1992, Hofstede *et al.* 1995, Wesche *et al.* 2000), but tree seedlings are killed or recover slowly after having been set back to ground level (pers. obs., (Wesche *et al.* 2000). In this way frequent fires prevent the trees' emergence from the fire trap, the flame zone of páramo fires (Bond & Keeley 2005). Seedlings can therefore not develop into adult trees, which are less vulnerable to fire, and which could provide shade for further forest development. Fire can therefore create a positive feedback switch (van Langevelde *et al.* 2003), just like shade-dependence can, because the moist cloud forest provides young trees with protection from fire (Kessler 2000), while the páramo provides good fuel for the fires that prevent trees from establishing (Vilà *et al.* 2001). The positive feedbacks resulting from shade and fire may re-enforce each other, shade-dependence slowing down forest expansion between fires, and cause a treeline to be even more stable and abrupt.

In addition to radiation and fire, there are other natural factors that might be expected to limit tree establishment above the treeline. We will discuss the role of dispersal, competition, and substrate.

Natural tree establishment strongly decreased with distance from the forest edge, yet the survival of transplanted seedlings did not decrease with this distance. Seedlings were also more abundant under the canopy of trees of the same species. Also, the most common sprouts in the páramo were *Gaiadendron* ramets, which do not depend on seed dispersal. The importance of clonal growth for this species can be easily observed in the field, because of its strongly clustered distribution. This all indicates that dispersal is an additional limiting factor for forest extension, as has been suggested for some temperate treelines (Wardle & Coleman 1992, Cuevas 2000).

Competition for space or other resources with páramo vegetation may take place, but at the same time seedlings depend on the facilitative effect of shading. This is true especially for transplanted *Gaiadendron* seedlings, even though this species was earlier concluded to be radiation-tolerant. Once again, this can probably be explained by the clonal growth of this species, because ramets may only be radiation-tolerant if they have parental support, while seedlings such as those we planted may still be shade-dependent. Also the other species showed no positive effect of the removal of neighbors, so competition is not an important limitation for tree seedling establishment.

The mineral páramo soil does not appear to be a problem for tree seedlings, because seedlings did well in the páramo soil, providing they were sufficiently shaded. Also, seedlings planted in the forest did equally well in mineral soil and in the natural forest substrate. In fact, seedlings planted in this moss were sometimes almost overgrown by it, which probably explains partly why we measured negative growth in seedlings in the forest. This probably did not benefit them, even if it did not kill them. Seedlings in the forest therefore appear to grow in moss simply because that is the only substrate available in the forest, and not because they are favored by it.

Treelines in other parts of the tropics often have similar forest and alpine vegetation types and environmental conditions as those found in our study area (Bader *et al.* accepted). We can therefore expect that also at other tropical treelines tree regeneration is naturally hindered by excess radiation, again in combination with low night-temperatures and limited dispersal. Anthropogenic páramo fires are also common at most treelines, and probably further hinder tree regeneration. If we assume that warmer temperatures would cause a rise in the potential treeline, three scenarios of the effects of climatic warming on actual tropical treelines are possible. First, where fires continue to be lit in the páramo, treelines will not shift upwards. Second, where fires are suppressed but no radiation-tolerant tree species are present, treelines will also not shift upwards. And third, even where fires are suppressed and some radiation-tolerant tree species are present, treelines will shift upwards only slowly. In the latter case, treelines may shift upwards even without climatic warming if they are not in equilibrium with the current climate. It is then quite plausible that (some) tropical treelines are still on their way up from their position in the last ice age, and that the use of fire in the páramo has stopped the upwards movement, rather than having caused a downward displacement of the treeline. This scenario is also suggested by recent palaeological findings in our study area (di Pasquale *et al.* accepted).

The proposed effects of positive feedback switches on treeline dynamics, patterns, and historical reconstruction are largely hypothetical, and the relative importance of anthropogenic influences and natural processes will depend strongly on the local climate, species pool and land use history. However, the existence of natural processes that can, at least in theory, explain the low position, stability, and abruptness of tropical treelines, stresses the need to remain critical of the fire-dominated view most authors adopt nowadays. It also stresses the need for more research on this issue, especially fire-exclusion experiments and replications of the experiment presented here in other tropical treeline environments with different tree species.

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CHAPTER 5

Climate change in a simple spatial model of treeline dynamics influenced by excess solar radiation and fire

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Photo previous page: cloud forest canopy, Guandera, Ecuador

Climate change in a simple spatial model of treeline dynamics influenced by excess solar radiation and fire

Maaike Y. Bader[1,*], Max Rietkerk[2] and Arnold K. Bregt[1]

Abstract

Climate change could cause alpine treelines to shift in altitude or to change their spatial pattern, but little is known about the drivers of treeline dynamics and patterning. The position and patterns of tropical alpine treelines are generally attributed to landuse, especially burning of the alpine vegetation. Species interactions, in particular facilitation through shading, have been suggested also to be important for treeline patterning and dynamics. We studied how fire in the alpine vegetation and shade dependence of trees may affect the position and spatial pattern of tropical alpine treelines and their response to climatic warming. We developed a spatially explicit mechanistic model of tree growth on a gradient of minimum temperature under conditions of excess solar radiation and periodic fires. We changed the effects of neighbours by varying the shade produced by trees or the radiation tolerance of trees and by adding páramo fires. The positive feedback that resulted from the neighbour interactions strongly affected the emergent treelines. Treeline position was elevated by stronger shade and lowered by lower radiation tolerance and by fire. Stronger shade and fire made the treeline less dissected and more abrupt, while lower radiation tolerance also made the treeline less dissected, but not more abrupt. The distance and speed of treeline advance after a temperature increase were reduced by all forms of positive feedback. Our model demonstrated that next to fire, shade dependence of trees can also lead to abrupt treelines and relatively low treeline positions. This implies that these patterns do not necessarily indicate human disturbance, but that they may indicate that the forest consists of shade-dependent tree species. Strong abruptness of a treeline may also indicate that it will respond slowly to climatic changes.

Keywords: positive feedback switch; photoinhibition; páramo; cloud forest; neighbor interactions; shade dependence

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Introduction

Alpine treelines are largely climate dependent, so climatic changes could cause changes in treeline altitude or spatial patterns. Various properties of treelines make the rate and direction of such changes difficult to predict. These include the presence of land use and other disturbances, interactive effects of different climatic factors, topographic complexity, slow reactions due to slow demographic processes, and complex dynamics due to positive feedbacks between vegetation and microclimate (Slayter & Noble 1992, Noble 1993, Kupfer & Cairns 1996, Malanson 2001, Graumlich *et al.* 2004, Holtmeier & Broll 2005). None of these properties are well understood, not in temperate regions and even less so in the tropics.

We will focus here on the complex dynamics that may arise from positive feedback. Positive feedback does not only affect treeline dynamics, but also the spatial pattern of the treeline ecotone (Wilson & Agnew 1992, Smith *et al.* 2003, Resler 2006). Existing treeline patterns include abrupt boundaries, gradual transitions, and vegetation mosaics (Wardle 1965, Körner 1998b, Camarero *et al.* 2000). These patterns are often not related to patterns in substrate or topography, but can be brought about by plant interactions alone (Armand 1992, Wilson & Agnew 1992). Being able to interpret these patterns in terms of underlying processes is important both for understanding treeline ecology and for predicting the response of treelines to climatic changes (Wiegand *et al.* 2006).

Simple mechanistic spatial models have an important potential for studying the effect of local interactions on emergent spatio-temporal patterns (Rietkerk *et al.* 2002). Previous treeline models of this type have focused on coniferous species in temperate regions (Malanson 1997, Malanson 2001, Alftine & Malanson 2004, Wiegand *et al.* 2006), and the results can probably not be extrapolated to tropical treelines, or even to many other temperate treelines. For instance, in the model by Alftine & Malanson (2004) wind and snow are important factors, while at tropical treelines they do not play significant roles (Sarmiento 1986). In the model by Wiegand *et al* (2006) the trees are shade intolerant, while tropical treeline species are often shade dependent (Bader *et al.* online first). Positive feedback has also been modeled generically as a positive effect of neighbors on site conditions (Malanson 1997, Malanson 2001).

The occurrence of alpine treelines is traditionally attributed to low temperatures (e.g. Brockmann-Jerosch 1919, Griggs 1946, Körner 1998a). Recently, this idea was given new impulse by a global comparison of treeline altitudes, which showed that these altitudes correlate best with the average growing season temperature (Körner & Paulsen 2004). This correlation of treeline position with average temperature does not, however, offer a mechanistic explanation for treeline occurrence. In fact, we come across a proper paradox, because average soil and air temperatures are higher above the treeline than in the shade of the forest (Bendix & Rafiqpoor 2001, Körner & Paulsen 2004, Bader *et al.* accepted). If low average temperatures limit tree growth, then conditions for tree growth are more favorable above treeline than in the forest. Yet trees do not establish above the treeline, and it is still unclear why not (Grace 1989, Stevens & Fox 1991, Wardle 1993, Körner 1998a, Sveinbjörnsson 2000, Smith *et al.* 2003, Körner & Hoch 2006).

Our study focuses on the vegetation dynamics and spatial patterns of tropical alpine treelines, defined as the transition between upper montane cloud forest and páramo, the latter in the broad sense of tropical alpine vegetation (Hofstede *et al.* 2003). In tropical mountains solar radiation can reach very high intensities, due to the high sun angle and thin atmosphere layer (Caldwell *et al.* 1980). Although sunlight is a resource for plants, excess radiation can cause a decrease of photosynthetic potential and damage to plant tissues (Barber & Andersson 1992, Long *et al.* 1994). This photoinhibition, the negative effect of excess radiation, is stronger at low temperatures (Ball *et al.* 1991, Krause 1994, Huner *et al.* 1998, Close *et al.* 2000), especially if there is a frost. Frosts can occur nightly in tropical alpine areas, which are characterized by strong diurnal, rather than seasonal temperature fluctuations (Sarmiento 1986, Rundel 1994). Tree seedlings at several treelines, both tropical and temperate, have been found to be shade dependent and sensitive to cold-induced photoinhibition (Wardle 1965, 1985, Ball *et al.* 1991, Germino & Smith 1999, Bader *et al.* online first).

Natural treelines are largely climate controlled, but natural treelines are rare, especially in the tropics (Miehe & Miehe 1994). Here, most areas above the actual treeline are used for livestock grazing in combination with fire management, and these fires commonly play an important role in the vegetation dynamics (Hofstede *et al.* 1995, Suarez R. & Medina 2001). Although fire usually does not spread into the moist cloud forest, it can strongly influence treeline patterns and dynamics, especially by removing young trees that may emerge in the páramo above the actual treeline. Many tropical treelines may have been lowered by fire and may continue to be influenced by it (Lægaard 1992, Miehe & Miehe 1994).

We present a model of tree growth at tropical alpine treelines, addressing the effects of shade dependence of trees and the effects of fire in the páramo. In the model solar radiation and fire are drivers of positive feedback switches (Wilson & Agnew 1992). Such a switch occurs when a vegetation type alters the environmental conditions such that it favors itself relative to other vegetation types, which can cause a sharpening of boundaries and the emergence of stable vegetation mosaics. The model is explicitly spatial; trees receive shade and protection from fire from neighboring trees. The model is used to study the effect of these local interactions on treeline spatial patterns, dynamics, and the response to warming.

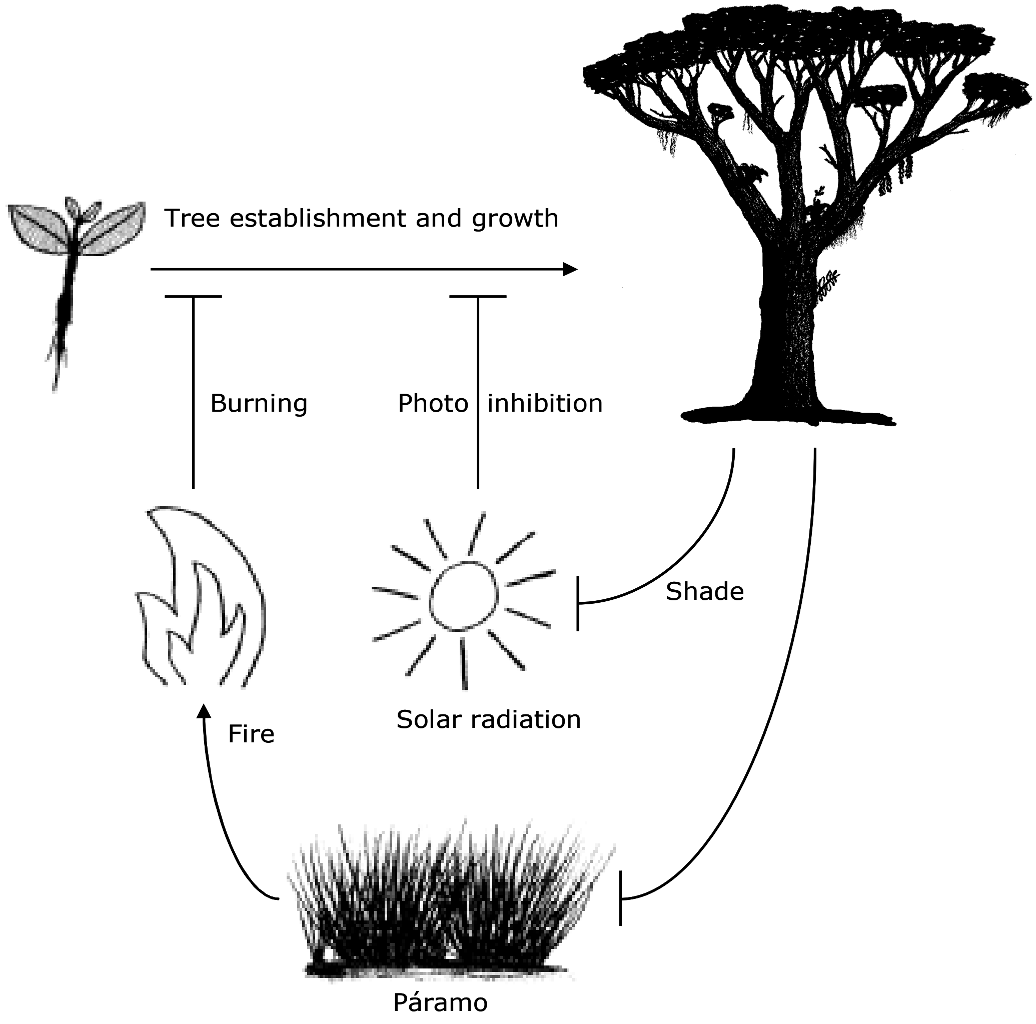

Figure 1 Positive feedback loops present in the model. Stopping symbols (┬) indicate inhibitory effects, arrows indicate promotory effects. The inner loop shows positive feedback mediated by excess radiation; the outer loop shows positive feedback mediated by fire. Trees positively influence tree growth and establishment by providing shade, thereby lowering the intensity of solar radiation and thereby limiting photoinhibition. In the model the presence of a tree also implies the absence of páramo tussock grasses, so that trees restrict fire and hence positively influence tree growth and establishment.

Methods

We developed a spatially explicit model with the aim of demonstrating the effects of neighbor interactions on the spatial pattern and position of the treeline and on possible treeline shifts in response to climatic warming. Neighbor interactions cause two positive feedback loops, one involving radiation and the other involving fire. Radiation hinders tree growth, but trees provide shade and shade allows the establishment and growth of more trees, thereby assuring their persistence and spread. Fire also hinders tree growth, and páramo tussock grasses promote fire, which eliminates trees, thereby assuring the persistence and spread of páramo vegetation (fig. 1).

Model structure

The model represents the growth of trees in a 2-dimensional grid. Each grid cell represents an area of about 2x2 m, and the state variable of each grid cell is tree height. This simplifies trees to square columns, which in this paper we will refer to as 'trees'. Tree growth follows a logistic function and is reduced at high radiation with low minimum temperature by reduction factor p.

$$\frac{dH}{dt} = p \cdot r \cdot H \cdot \frac{H_{max} - H}{H_{max}} - d \cdot H \qquad (1)$$

Where t = time (months); H = tree height (m); p = growth reduction factor (≤1), which is a function of radiation (R) (equation 2); r = specific growth rate (month^{-1}); H_{max} = the maximum tree height (m) if d = 0; and d = loss rate (month^{-1})

Reduction factor p represents the fraction of the maximum carbon assimilation (photosynthesis - respiration) that is being reached and is calculated by a hyperbolic photosynthetic response curve (Landsberg 1986, Spitters 1986), as follows:

$$p = \frac{q \cdot R \cdot mp}{q \cdot R + mp} - resp \qquad (2)$$

Where mp = maximum photosynthesis level (0-1), which is less than 1 under photoinhibition, as a function of radiation (equation 3); q = the quantum yield (efficiency) or initial slope of the photosynthetic response curve ($\text{Watt}^{-1}\ m^{2}$); R = radiation level received by the tree ($\text{Watt}\ m^{-2}$); and resp = respiration (0-1).

The maximum photosynthesis level (mp) decreases linearly under high radiation levels due to photoinhibition. The following equation is based on graphs sketched in Falowski *et al.* (1994) and Huisman (1997):

$$\mathrm{mp} = 1 - \frac{\mathrm{R} - (\mathrm{R_s} - \mathrm{rt} \cdot \mathrm{T})}{\mathrm{R_m} - \mathrm{R_s}} \tag{3}$$

Where R_s = radiation level at which photoinhibition starts (Watt m^{-2}); rt = lowering of R_s for each degree of lower minimum air temperature (Watt m^{-2} $°C^{-1}$), T = minimum air temperature (°C), and R_m = radiation level above which photoinhibition is maximal (so photosynthesis is 0) (Watt m^{-2}). Shade dependence is expressed as the relative advantage of trees in the shade compared to trees exposed to radiation. It can be increased by lowering the radiation tolerance of the trees by lowering R_m, or by increasing the amount of shade provided by neighbors.

Radiation is decreased as a function of the size of the trees in the eight neighbor cells. For simplicity, we assume that temperature is not affected by neighbors. The radiation strength in the shade of neighbors is calculated using Lambert-Beer's law:

$$\mathrm{R} = \mathrm{R_{ext}} \cdot \exp(-\mathrm{k} \cdot \sum \mathrm{w_{ij}} \cdot \frac{\mathrm{H_{ij}}}{\mathrm{H_m}}) \qquad \mathrm{i}, \mathrm{j} = -1,0,1 \tag{4}$$

Where R_{ext} = external radiation (radiation in the absence of neighbors) (Watt m^{-2}), k = extinction coefficient for radiation in the canopy (-), H_m = maximum tree height actually reached in the model ($< H_{max}$ if $d>0$) (m), H_{ij} = height of neighbor trees (direct and diagonal) (m), w_{ij} = weight factor (0-1), and i and j indicate the positions of neighboring cells.

It is explicitly assumed that all space not occupied by trees is occupied by tussock grass páramo and that small tree seedlings are omnipresent in the grass layer. Dispersal limitation may occur at real treelines (Dullinger *et al.* 2004), but the purpose of our model was specifically to explore the effects of radiation and fire only. Tree seedlings emerge from the grass layer when the conditions of radiation and minimum temperature, are more favorable than a fixed threshold: $R-(R_s - rt \cdot T) < R_e$, where R_e = radiation threshold for seedling establishment (Watt m^{-2}). This threshold is lower than the equilibrium threshold for tree growth based on the model equations, i.e. seedling emergence is more sensitive to radiation than tree growth. Trees get established with a starting size of 0.5 m, which is the assumed height of the grass layer.

Table 1 Elements of the model.

Symbol	Description	Units	Values used	References
t	time	months	variable	
T	minimum temperature	°C	-6 to 2	Rundel 1994
R_{ext}	external radiation	Watt m^{-2}	1300 (var in fig 1)	Körner 1999
R	radiation received by tree	Watt m^{-2}	variable	
H	tree height	m	variable	
H_{max}	maximum tree height if d = 0	m	30	pers obs.
r	tree growth rate	m $m^{-1}month^{-1}$	0.03	calibrated
d	tree death rate	m $m^{-1}month^{-1}$	0.006	calibrated
p	growth reduction factor	≤1	variable	
q	initial slope photosynthetic response curve	0-1	0.02	calibrated
Resp	Respiration	0-1	0.1	calibrated
R_s	radiation level start of photoinhibition	Watt m^{-2}	100 (800 in fig 2)	Egerton *et al.* 2000
R_m	radiation level maximum photoinhibition	Watt m^{-2}	2000 (var in fig 2)	calibrated
R_e	upper radiation threshold for establishment	Watt m^{-2}	1300	calibrated
rt	change in R_m for each degree T < 2 °C	Watt m^{-2} °C^{-1}	-25	calibrated
k	extinction coefficient radiation in canopy	-	0 to 0.8	Landsberg 1986
w	weight factor for shading from neighbors	-	1 or 0.7 *	

* weighted by distance: 1 for direct neighbors, 0.7 for diagonal neighbors

The páramo grass tussocks, which contain a high fraction of dead standing biomass, are good fuel, and fire periodically damages trees that have too many grass neighbors (>4). Trees less than 2 m tall are removed completely by fire, while larger trees are reduced by 1/H at each fire event. The model is fully deterministic.

Simulations

The model was run on a 100*100 cell grid. Minimum temperature decreased linearly from the bottom to the top of the grid, while external radiation was uniform in space. This imitates the relatively small rates of increase of radiation with altitude compared to the lapse rate of temperature. The initial tree pattern was a linear gradient from 0% cover at the lowest minimum temperature (top row of the grid) to 100% cover at the highest minimum temperature (bottom row of the grid). The initial pattern was identical for sets of model runs that are presented together for comparison. As boundary conditions we assumed that there were no trees above the top end of the grid and a full cover of 10-m tall trees below the bottom end, while the left and the right ends were connected, so that the grid was cylindrical.

The parameter values used for constants and inputs are given in table 1. These values were based on realistic values from literature when possible, while others were calibrated to make the model run within realistic bounds. The exact values of these parameters did not affect the qualitative effects of each of the different feedback scenarios, so they were of limited relevance to the purpose of our study. Other parameters were varied; this constituted the different feedback scenarios.

To study the effect of climatic warming on our modeled treeline, we increased the minimum temperature by 3.6 °C over one year or over 100 years. The one-year scenario was added to facilitate the interpretation of the dynamics after change; there was no qualitative difference in the response to this abrupt change or to the more gradual change. The 100-year scenario is in the range of estimates for global temperature increase over the next 100 years (IPCC 2001, Stainforth *et al.* 2005). The aim of these simulations was not a quantitative prediction of treeline advance, but a qualitative assessment of the type of dynamics that can be expected at treelines where positive feedback processes are important. The model was run for 800 years, to allow a stabilization of the treeline before and after the rise in temperature.

The result of the modeled interactions with neighbors is a positive feedback: trees locally promote the establishment and growth of trees, while páramo (or the absence of trees) locally inhibits the survival and growth of trees and thereby promotes páramo. The strength of the feedback is determined by the relative advantage of trees neighboring other trees compared to trees neighboring páramo.

We varied the strength of the positive feedback in three ways: 1) through the amount of shade produced by trees (varying k); 2) through the radiation tolerance of trees (varying R_m); and 3) through the addition of fire events (every 5 years). The first two parameters both affect the feedback loop driven by excess radiation, while fire adds a new feedback loop (fig. 1).

To emphasize that the temperature gradient represents a gradient related to altitude, we refer to positions on this gradient in terms of altitude: a lower temperature corresponds to a higher altitude. The 'altitudinal' boundary zone between continuous areas of trees (forest) and continuous areas where trees are absent (páramo) represents the treeline. Treeline dissectedness is the length of boundary between trees and non-trees, and includes patchiness. Treeline abruptness is the rate of increase in tree height along the slope at

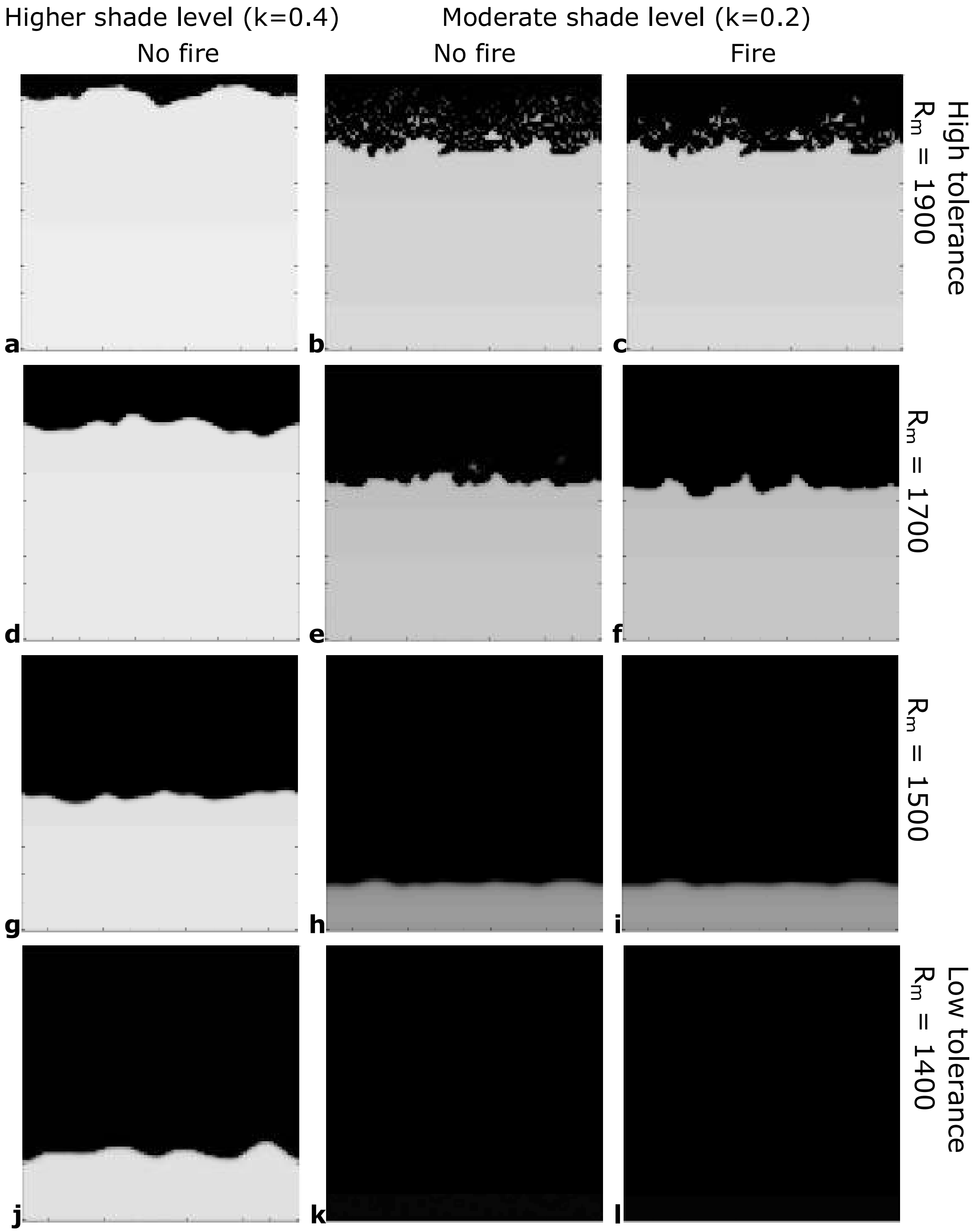

Figure 2 Effects of radiation tolerance, shade from neighboring trees, and fire on the position and the pattern of the treeline. Shown are spatial patterns of tree height after running the model for 800 years. Radiation tolerance decreases from the top to the bottom row: R_m = 1900, 1700, 1500 and 1400 Wm^{-2} (decreasing tolerance), R_s = 800 Wm^{-2}, R_{ext} = 1300 Wm^{-2}. Trees provided more shade in the left column (k = 0.4) than in the middle and right

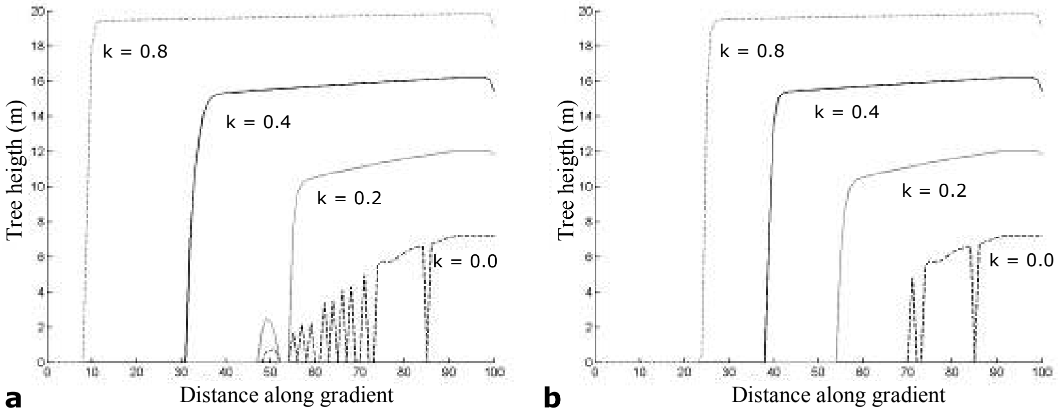

Figure 3 The effect of shade and fire on the abruptness of the treeline transition: Tree height along a transect from the top to the bottom of the grid after running the model for 800 years. The transect is the 50th column of the grids shown in the left columns of figures 6 (a) and 7 (b). a) Scenarios without fire. b) Scenarios with fire occurring every 5 years. In both graphs the lines represent different shade levels: no shade (k = 0), intermediate shade (k = 0.2 k = 0.4), and strong shade (k = 0.8). Note how both shade and fire increase the abruptness of the transition.

the treeline, scaled between zero and the maximum attained tree height.

Results

Running the model on a temperature gradient resulted in the emergence of a treeline, unless the settings for shade, radiation tolerance and fire frequency were such that the treeline was situated outside the range of the gradient (fig. 2). This was the case, for instance, if the radiation tolerance was too low relative to the external radiation and the strength of shade provided by neighbors (fig. 2k&l). The position, spatial pattern and dynamics of the treeline were strongly altered by positive feedback and varied according to the settings for shade, radiation tolerance and fire.

Figure 2 (caption continued from previous page) columns (k = 0.2). In the left and middle columns there was no fire, while in the right column there were fires every 5 years. Temperature did not change through time. The grid size is 100x100. The initial pattern was exactly the same for each run, and was a randomly assigned linearly decreasing cover of 10 m high trees, from 100% cover (bottom of grid) to 0% cover (top of grid). Gray shades indicate tree height, ranging from 0 (black) to 24 m (white).

Treeline position and pattern

With increasing shade from neighbors, the treeline was situated at higher altitudes and the spatial pattern of treeline was less dissected (fig. 2). If trees were less tolerant to radiation, the treeline was situated at lower altitudes and its spatial pattern was again less dissected. Finally, fire caused a slight depression of treeline altitude and lower dissectedness. The effect of fire on treeline dissectedness was especially evident at low shade levels, where fire removed single trees and small patches (fig. 2c,f). At higher shade levels treeline dissectedness was low anyway, due to the effects of shade. The abruptness of the treeline is also affected by fire mainly at the lowest shade levels (compare fig. 3b to fig. 3a), where it makes the treeline more abrupt by removing the smallest (single) trees.

Shade increased the abruptness of the treeline, especially when we compared low levels of shade to no shade (fig. 3). In line with this, if there was shade, treelines were abrupt at all levels of radiation tolerance (fig. 4). At low shade levels, decreased radiation tolerance resulted in smaller trees (fig.

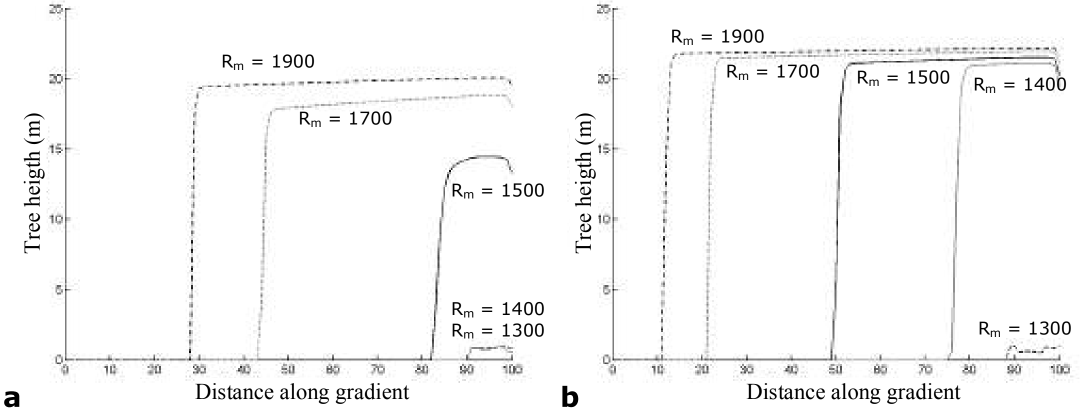

Figure 4 The effect of radiation tolerance and shade on the abruptness of the treeline transition: Cross-sections of tree height along transect from the top (0) to the bottom (100) of the grid after running the model for 800 years. The transects are the 50th column of the grids shown in the middle (a) and left (b) columns of figure 2. a) Scenarios with k = 0.2. b) Scenarios with k = 0.4. In both graphs the lines represent different radiation tolerance levels, from high (Rm = 1900 Wm-2) to low (Rm = 1300 Wm-2) tolerance. Other parameter settings: R_s = 800 Wm-2 and R_{ext} = 1300 Wm-2. The lowest tolerance did not allow any tree growth, only the continuous replacement of emerging seedlings. The height decrease at the right of each graph (position 100) is due to the boundary condition: 10-m high trees below the bottom row of the grid. This condition did not affect treeline properties.

4a) and a slightly more gradual treeline, but at higher shade levels (fig. 4b) this effect largely disappeared.

When the model was run without neighbor interactions (no shade) and without fire, so without positive feedback, tree height gradually decreased with altitude, reflecting the temperature gradient (figs. 3a and 6a). The patchiness of this treeline reflects the initial pattern used for the model run and the impossibility of new tree establishment above the externally determined threshold altitude.

Treeline dynamics

In scenarios without warming, treeline positions moved slowly towards an asymptote after the quick cover increase or decrease in the period following initialization of the model (fig. 5). All lines in figure 5 originate at 50% cover. In the first time step of the simulation (the first month), tree cover increased rapidly in the runs with the most radiation tolerant trees (5a) and in those with shade (5b), because seedlings could establish in all locations favorable enough at that time. These favorable locations included all open sites below the altitudinal establishment limit plus all open sites with enough tree neighbors. Such fast seedling establishment also caused the jump in cover at

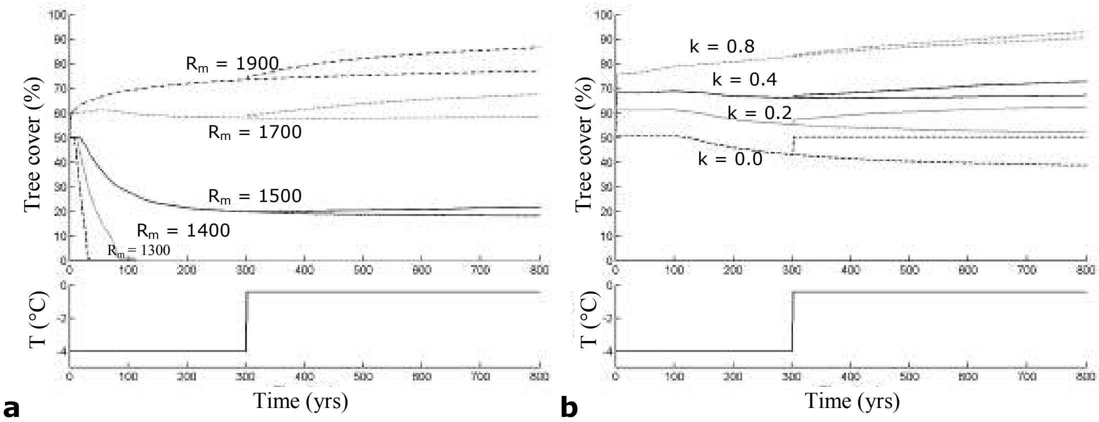

Figure 5 Tree cover with constant and with abruptly increased temperature. Temperature change of the central cell of the grid is shown in the bottom graphs. All are scenarios without fire. Starting cover is 50% in all cases – quick cover increase in the first year is due to quick establishment in all sufficiently favored sites. a) Effect of radiation tolerance, from high to low tolerance. Same runs as in the middle column of figure 2 (k = 0.2). b) Effect of the shade level. Same runs as those in figure 6. Note how both stronger shade and low radiation tolerance decrease the reaction to temperature increase.

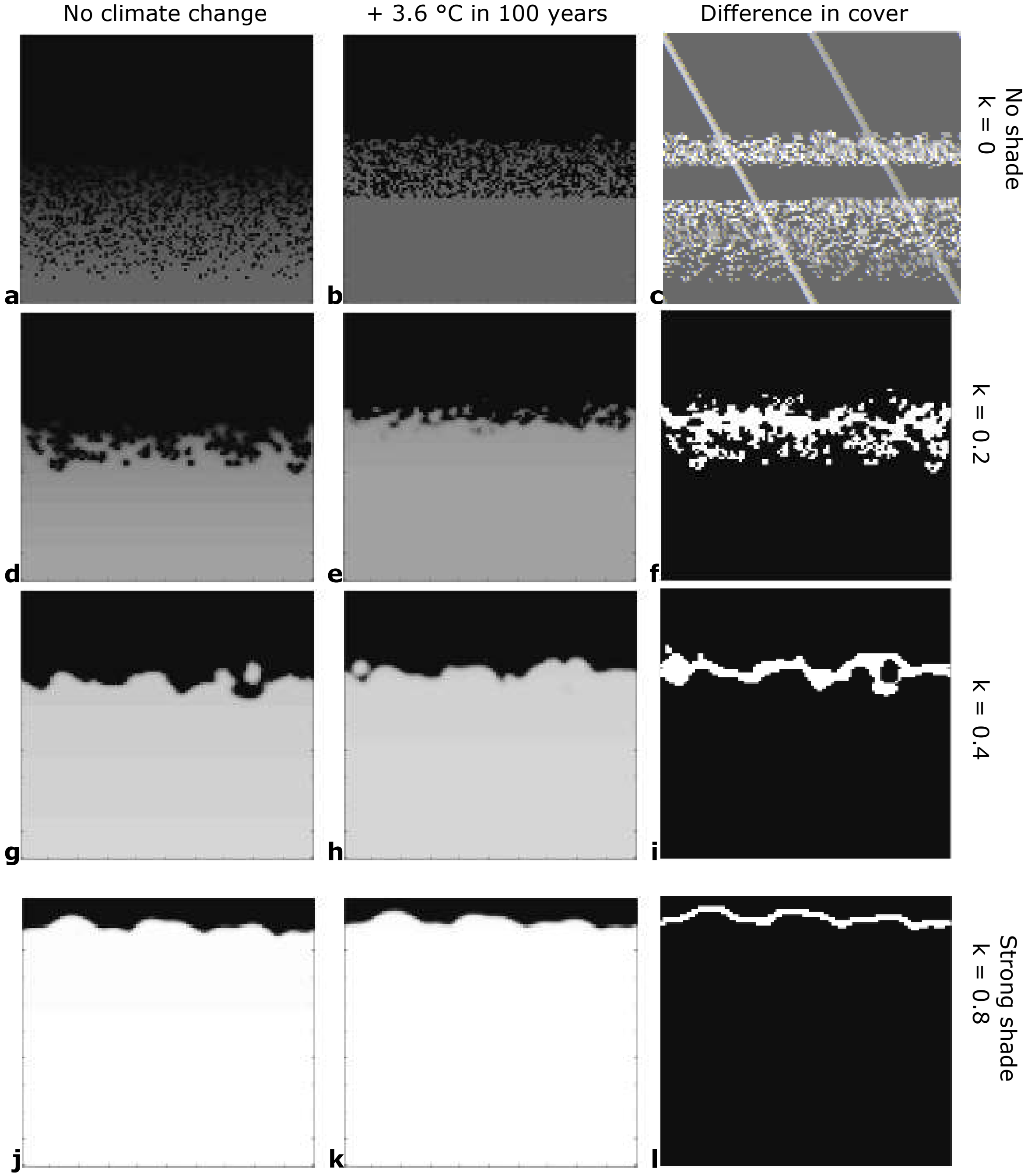

Figure 6 Effects of climate change on final pattern of treelines without fire. Each row of images represents a different level of shade from neighboring trees, which has a positive effect on tree growth. Shown are spatial patterns of tree height after running the model for 800 years. The grid size is 100x100. The initial pattern was exactly the same for each run and was a randomly assigned linearly decreasing cover of 10 m high trees, from 100% cover (bottom of grid) to 0% cover (top of grid). In each figure the left column shows the result if the temperature gradient is kept constant

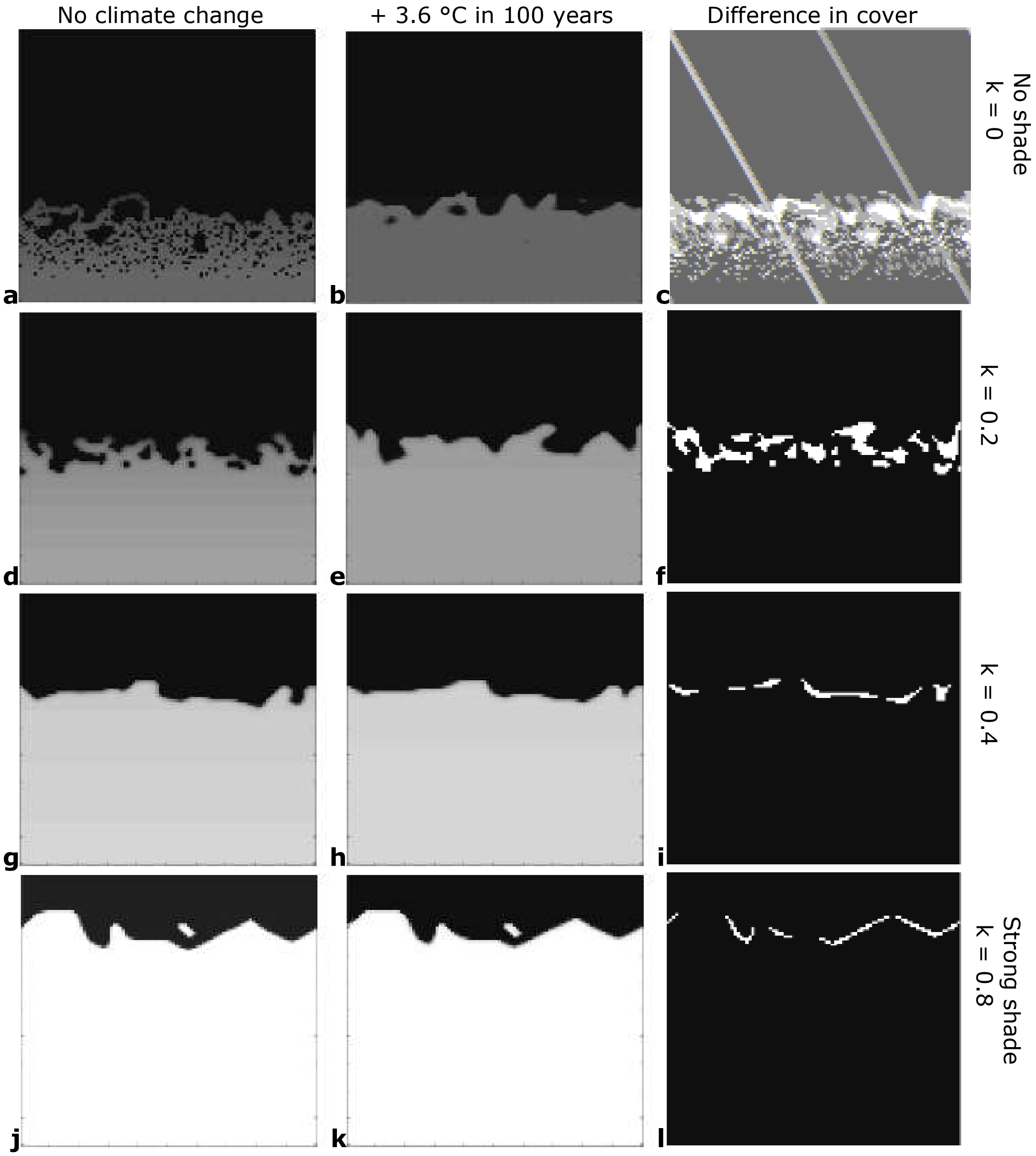

Figure 7 Effects of climate change on final pattern of treelines with fire occurring every 5 years. For further details see caption figure 6.

Figure 6 (continued) throughout the 800 years. The middle column shows the result if temperature is increased by 3.6 °C over 100 years (between year 300 and 400), and the right column shows the increase in tree cover (in white) due to this increase in temperature. The black band in figure 6c represents a zone where trees have persisted both with and without warming. In the first two columns gray shades indicate tree height, ranging from 0 (black) to 20 m (white).

the time of warming; at this time a number of sites suddenly became just favorable enough for establishment.

Treeline advance after warming was slowed down and limited in extent by lower radiation tolerance (fig. 5a). However, this effect was only found if the shade level was low, like in figure 5a. At higher shade levels the radiation tolerance no longer caused differences in treeline advance (not shown). The jump in cover that occurred at the time of warming was largest in the runs with the most tolerant trees, because the number of sites that became favorable after warming was higher if external climate had more influence, which was the case if trees depended less on shade from neighbors. After the initial jump, lower radiation tolerance still slowed down cover increase, because of the slower growth under conditions of high radiation and, feeding back, the slower growth of shading trees. The lowest two levels of radiation tolerance (R_m = 1300 and R_m = 1400) did not allow for the maintenance of any trees, or any recovery after warming at this low shade level.

Treeline advance after warming was also slowed down and limited in extent by stronger shade (figs. 5b and 6). The jump in cover at the time of warming was especially large in the scenario without shade, because in this scenario trees were solely dependent on the external climate, and a rise in temperature caused a rise in the establishment limit and subsequent quick seedling establishment. If shade played a role, the treeline could be situated above the external establishment limit, and a rise in temperature only increased establishment in some shaded sites. After the initial jump, cover increase was highest with light shade; without any shade new establishments above the external limit were impossible and further advance depended on the recovery of suppressed trees, while stronger shade allowed the treeline to be situated at higher altitudes even under the pre-warming conditions, and rendered it increasingly insensitive to changes in the external temperature gradient.

Figures 6 and 7 show the increase in tree cover (independent of tree height) due to warming. The strange pattern of change in figure 6c can be explained as follows: the bottom patterned area reflects the filling in of gaps due to a rise of the establishment limit, the black band is where trees persisted both with and without a rise in temperature, and the top patterned area shows trees that persisted only if there was a rise in temperature.

Fire strongly slowed down and limited the upward shift of the treeline after warming (compare figs. 6 and 7). This was due to the fact that isolated trees or small patches of trees above treeline had been removed (burned), and due to continued burning of seedlings emerging above the treeline. Without fire and with no or weak shade, patches and single trees had remained, more or less suppressed in stature, above the closed treeline (fig. 6a,d). These suppressed trees could react quickly to warming through increased growth. Where fire had removed these isolated trees and patches, establishment was only possible in the shaded cells just above the existing closed treeline, and treeline advance was slower and limited in extent.

Discussion

The position, spatial patterns, and dynamics of the treeline were all affected by positive feedback, but the effects differed depending on which parameters were used to strengthen the positive feedback switch. If the switch resulted from stronger shade, treelines were positioned at higher elevations, while if the switch resulted from lower radiation tolerance or from fire, treelines were positioned at lower elevations. Stronger shade or fire made the treeline less dissected and more abrupt, while lower radiation tolerance also made the treeline less dissected, but not more abrupt. The advance of the treeline after a temperature increase was always reduced in speed and extent by a stronger positive feedback switch, whether it be brought about by stronger shade, lower radiation tolerance, or fire.

So the overall negative effects of lower radiation tolerance and fire caused lower treelines and slowed down and limited treeline advance after the temperature increase. However, the overall positive effect of stronger shade caused higher treelines but also slowed down and limited treeline advance. It is clear that the observed effects on the reaction of the treeline to climate change are not the result of an overall positive or negative effect on tree growth, but of a positive feedback switch that stabilizes the treeline. The strongest stabilization is achieved by the combination of shade and fire, causing a two-factor switch (Wilson & Agnew 1992).

Malanson (1997, 2001) increased positive feedback in his treeline model by increasing the positive effect of neighbors on a compound 'site quality'. Similar to our results, positive feedback resulted in more abrupt treelines (Malanson 1997). However, in contrast to our results, positive feedback resulted in a quicker forest cover increase after climatic change (Malanson 2001). This was the result of the overall positive effect of the presence of trees. We also found that a stronger positive effect, i.e. stronger shade, caused quicker forest cover increase, but only at the initiation of the model runs, so starting from a situation far from equilibrium. If the temperature was increased when the treeline was in a more or less stable position, stronger shade (positive effect) as well as lower radiation tolerance and fire (negative effects) slowed down and limited forest extension. This shows the importance of understanding the history and current dynamics of a treeline in order to predict its reaction to climatic change.

For a quantitative prediction of a treeline's response to climatic change, a model should include several additional processes, especially dispersal (vegetative or through seeds) and interactions with the alpine vegetation (Malanson 1997, Dullinger *et al.* 2004). Dispersal limitation and competition from alpine vegetation could strongly slow down forest expansion and would, for instance, limit the fast forest cover increase observed at the initiation of our model and after warming. However, our model was not aimed at quantitative predictions; for such predictions a different model structure is needed, as well as extensive field research for obtaining realistic estimations for all parameters (Dullinger *et al.* 2004). More importantly, the importance and functioning of all relevant processes needs to be well understood, which they are not for tropical alpine treelines, or indeed alpine treelines in general.

The reason that a positive feedback switch limits and slows down forest extension is that it makes trees depend more on neighbor interaction and less on the external climate. If feedback plays no or a small role, a treeline will be located more or less where the external environment dictates it to be, and under these circumstances a change in this external environment can have a direct effect on treeline position. However, protection by neighbors allows trees to grow where the external environment is unsuitable for growth. Even if this external environment improves by a rise in temperature, growth outside the protection of neighbors is still impossible, so that treeline advance is limited. In contrast, if the external environment deteriorates, growth may still be possible within the protection of neighbors, so treeline retreat will also be limited. Positive feedback thus buffers the treeline against external changes and causes hysteresis: a change from forest to páramo will occur at lower external temperatures than a change from páramo to forest (Armand 1985, 1992).

Increasing the positive effect of trees on neighbors, in our case by increasing the amount of shade, is the easiest way of strengthening the positive feedback switch in a model such as ours or that of Malanson (1997, 2001). However, differences in switch strengths between different treelines in the field will more likely be related to the radiation tolerance of the tree species rather than the amount of shade produced. Our results show that stronger shade and lower radiation tolerance have opposite effects on treeline position, though both result in a stronger switch. Stronger shade increases the positive effect of having tree neighbors so that patches expand and merge and the treeline will lie above the climatic boundary for individual trees. In contrast, lower radiation tolerance causes a lowering of the climatic boundary for individual trees, which increases the negative effect of having non-tree neighbors so that single trees and small patches disappear. The effect of fire is different: a higher fire frequency also increases the negative effect of having non-tree neighbors, but the result is that the treeline lies below the climatic boundary for individual trees. Therefore a treeline that is affected by fire may move upwards at cessation of burning, while it reacts little to a change in climate.

Positive feedback can cause abrupt treelines, but a recent treeline model by Wiegand *et al* (2006) shows that treelines with abrupt height transitions can emerge without positive feedback due to certain combinations of demographic parameters. However, the necessary parameters (seedling mortality rising rapidly with altitude, mortality dropping rapidly with age, and little growth inhibition) do actually imply a positive feedback: once a tree is established it grows well and its chance of mortality drops fast, while if no tree is established it is unlikely that it will, due to high seedling mortality. In our model a similar effect occurs, because seedling establishment is more sensitive to radiation than tree growth, so once a seedling has established, a tree will be able to grow. However, this growth is possible only if there is sufficient shade of neighbors. So in our model growth inhibition and mortality are lowered by the presence of neighbors. In the Wiegand *et al* (2006) model the reason for the low growth inhibition and rapidly dropping mortality with age are not specified, but are in fact positive feedbacks between tree age and survival.

Increasing shade and decreasing radiation tolerance are two ways of increasing the relative advantage of being shaded. This relative advantage is also greater under high external radiation, which indeed caused a lowering of the treeline in our model (not shown). Consequently, slopes that receive high solar radiation can be expected to have treelines at lower altitudes compared to slopes that receive less radiation. Especially slopes that receive radiation in the early morning, when plants are still cold from the preceding night and therefore more susceptible to cold-induced photoinhibition, can be expected to have low treelines. This pattern is indeed found at treelines in central Ecuador (Bader & Ruijten in review).

The inhibiting effect of shade dependence and fire on treeline advance may explain why many tropical alpine treelines are located at altitudes below what may be the temperature limit for trees. Many treelines may not have kept up with the climatic warming since the late glacial. In fact, such slow advance during the Holocene is evident from palaeo-ecological field data from a treeline in northern Ecuador (di Pasquale *et al.* accepted), although palaeo-ecological data from other tropical treelines may indicate faster treeline fluctuations (van der Hammen 1974, Flenley 1979, Wille *et al.* 2002).

Most tropical treelines are very abrupt boundaries (Bader *et al.* accepted). Fire is usually a common phenomenon in the alpine vegetation, and as shown by our model it may explain the abruptness of these treelines as well as their apparent stability. This is in accordance with the dominant explanation for the abruptness of treelines in tropical mountains (Lægaard 1992, Miehe & Miehe 1994). However, we have shown that this abruptness and stability can also be explained by shade dependence of treeline forest trees. An abrupt treeline does therefore not necessarily indicate that it is shaped by fire, but may indicate that the tree species in the treeline forest are shade dependent. The abruptness of a treeline can also indicate the type of response that can be expected after climatic warming (Armand 1985, 1992). Treelines may then be naturally inclined to shift, but shade dependence of the trees would strongly slow down such a shift, as would fire in the páramo. At treelines where fire plays an important role, a cessation of páramo burning would have a far greater effect on treeline patterns and dynamics than a rise in temperature.

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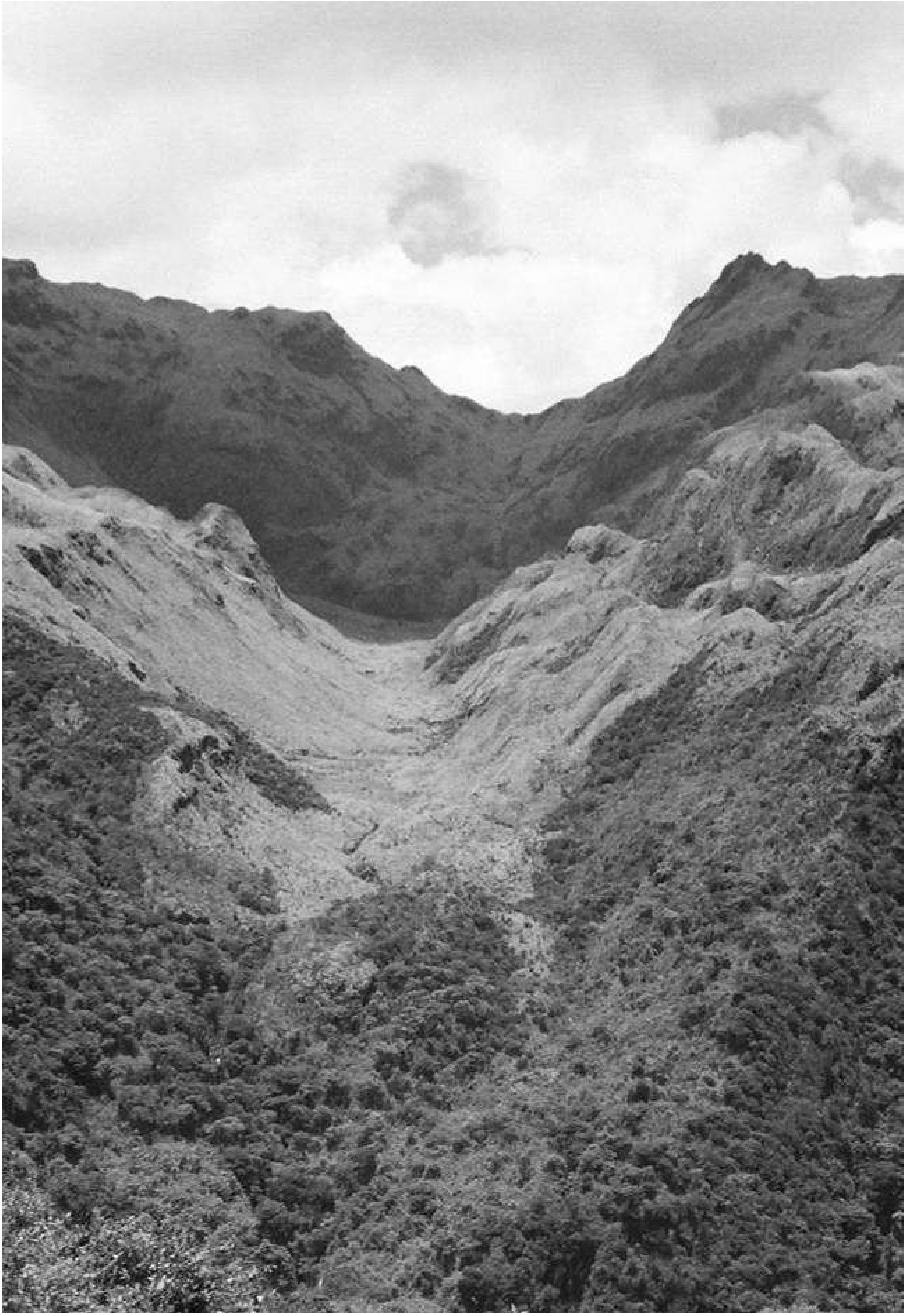

CHAPTER 6

A topography-based model of forest cover at the alpine treeline in the tropical Andes

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Photo previous page: treeline near Atillo, Ecuador

A topography-based model of forest cover at the alpine treeline in the tropical Andes

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Abstract

The position of alpine treelines in tropical mountains is influenced by climate, substrate and anthropogenic disturbances, but the effects and relative importance of these factors are hardly known. We present a method to assess the influence of topography-related environmental conditions on the forest distribution at the treeline and to compare this forest distribution between areas. We developed this method with data from Sangay National Park, situated on the eastern slopes of the Andes in central Ecuador. A logistic regression model was built using topographical variables and environmental indices, derived from a digital elevation model, to explain forest cover, derived from a Landsat ETM image, in a zone around the average treeline altitude. The model shows that after altitude, which can explain about 80% of forest cover, wetness has the next strongest effect (areas accumulating water, but also cold air, were devoid of forest, resulting in *inverted* treelines), followed by eastness (western slopes had forest to higher altitudes). Application of the model in two nearby areas showed that the treeline was lower in both areas, probably due mainly to macroclimatic differences in one area, and due partly also to human land use in the other. The locations with the largest deviations could be the focus of further research concerning human impacts on treeline vegetation. The fact that treelines are located at lower altitudes on east-facing slopes may be due to the high radiation received by east-facing slopes in the clear mornings, photoinhibiting tree seedlings in the páramo. In spite of the limitations of the quality and resolution of the remote sensing data, the presented method provided indications for important ecological factors at the treeline. The method also allowed detecting differences in treeline position between areas, which may reflect climatic differences or the location of anthropogenic disturbances.

Keywords: logistic regression model; DEM; remote sensing; topography; cloud forest; páramo; Andes; Ecuador; Sangay National Park

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Introduction

The causes of alpine treeline are not well understood, nor are the factors that determine its position in the landscape. We use the term treeline to denote the transition from the uppermost closed forest to low alpine vegetation. Available warmth is generally assumed to be the main limitation for forest growth at the treeline (Körner 1998), but locally other factors may determine the forest distribution, e.g. moisture availability, solar radiation, wind, snow cover, geomorphic processes, and human influence (Holtmeier & Broll 2005). The spatial pattern of forest distribution should reflect the important factors at a particular treeline and can therefore help to understand what ecological processes are taking place. It can therefore also contribute indirectly to our understanding of the effects of changes in climate or landuse.

Most tropical mountains have long been inhabited by people, who may have affected forest distribution at treelines by clearing the forest or by preventing forest expansion by burning the alpine vegetation. Because of the widespread and long-standing human influence it is hard to determine which treelines have been affected and which have not and what the natural treeline position would be. This results in controversies regarding the status of present treelines and forest patches in the alpine zone (Ellenberg 1979, Miehe & Miehe 1994, Kessler 2002) and regarding practical issues such as whether and where páramo areas should be (re-)forested (Fehse *et al.* 2002).

In mountain regions the topography is an important determinant of local conditions, including microclimate, soil properties, and disturbances (Brown 1994). The use of topographic variables derived from a digital elevation model (DEM) as substitutes for field-measured environmental variables is becoming common practice in the modeling of mountain vegetation (Brown 1994, del Barrio *et al.* 1997, Hoersch *et al.* 2002, Dirnböck *et al.* 2003, Hörsch 2003, van Niel *et al.* 2004). The advantage of using topography derived from a DEM as a substitute is that, especially in tropical mountains, climatic and other environmental data are generally scarce and difficult to obtain, and that these are usually point-data. In contrast, spatially continuous elevation data are available for free for the entire world (USGS 2003), albeit not always at the required spatial scale.

Most studies that relate mountain vegetation to topography are located in the European Alps (Guisan & Theurillat 2000, Hoersch *et al.* 2002, Dirnböck *et al.* 2003, Hörsch 2003) or in the Rocky Mountains (Brown 1994, Allen & Walsh 1996, Cairns 2001). No such efforts in tropical mountains have been published so far, although landslide hazards have been predicted based on topography in southern Ecuador (Brenning 2005). Important climatic factors for forests at the treeline are temperature and solar radiation (Körner 1998). These factors are strongly influenced by the topography, but in the tropics the effect of topography is different than it is in temperate regions. For instance, in the tropics north-south differences are less pronounced, while east-west differences may be larger (Smith 1977, Sarmiento 1986), and patterns related to snow accumulation and movement are absent.

Logistic regression models have been frequently used to predict vegetation types (Brown 1994, Augustin *et al.* 2001, Virtanen *et al.* 2004, Calef *et al.* 2005, Maggini *et al.* 2006), species distributions (Robertson *et al.* 2003), animal habitats (Augustin *et al.* 1996), and landslide hazards (Brenning 2005) based on topography and other environmental factors. Other methods that have been used for the prediction of vegetation or land-units based on topography are Binary Discriminant Analysis (del Barrio *et al.* 1997), Principal Component Analysis (Robertson *et al.* 2003), and multinomial logit models (Augustin *et al.* 2001). However, in several comparative studies the results of logistic regression compare favorably with other methods (Robertson *et al.* 2003, Brenning 2005), although the performance of different methods may depend on the type of landscape studied (Cairns 2001).

We used a logistic regression approach to describe the relationship between forest distribution at the treeline, and hence the position of the treeline itself, and mountain topography. The purpose of the model is twofold: 1) The identification of topographic variables and related environmental conditions and processes that are important for forest distribution; and 2) The comparison of forest distributions in areas that differ in terms of human disturbance, climate or other factors. We show how a model developed for a natural treeline in central Ecuador helped to identify important factors affecting forest distribution and treeline position. This model was then applied in two nearby treeline areas, one that is presumably undisturbed and another that is known to experience more human influence.

Methods

Study area

The three study areas (one for model development and cross-validation and two for model application) are situated in central Ecuador on the eastern Cordillera of the Andes in Sangay National Park (fig. 1). On this Cordillera, the west-oriented, inter-Andean watersheds are mostly devoid of forest, due to human land use, and are not included in the study areas. The east-oriented watersheds have forested slopes, stretching from the treeline down to the Amazonian lowland forests. Generally, the vegetation belts on the Amazonian side occur at lower elevations than those on the inter-Andean side, because of

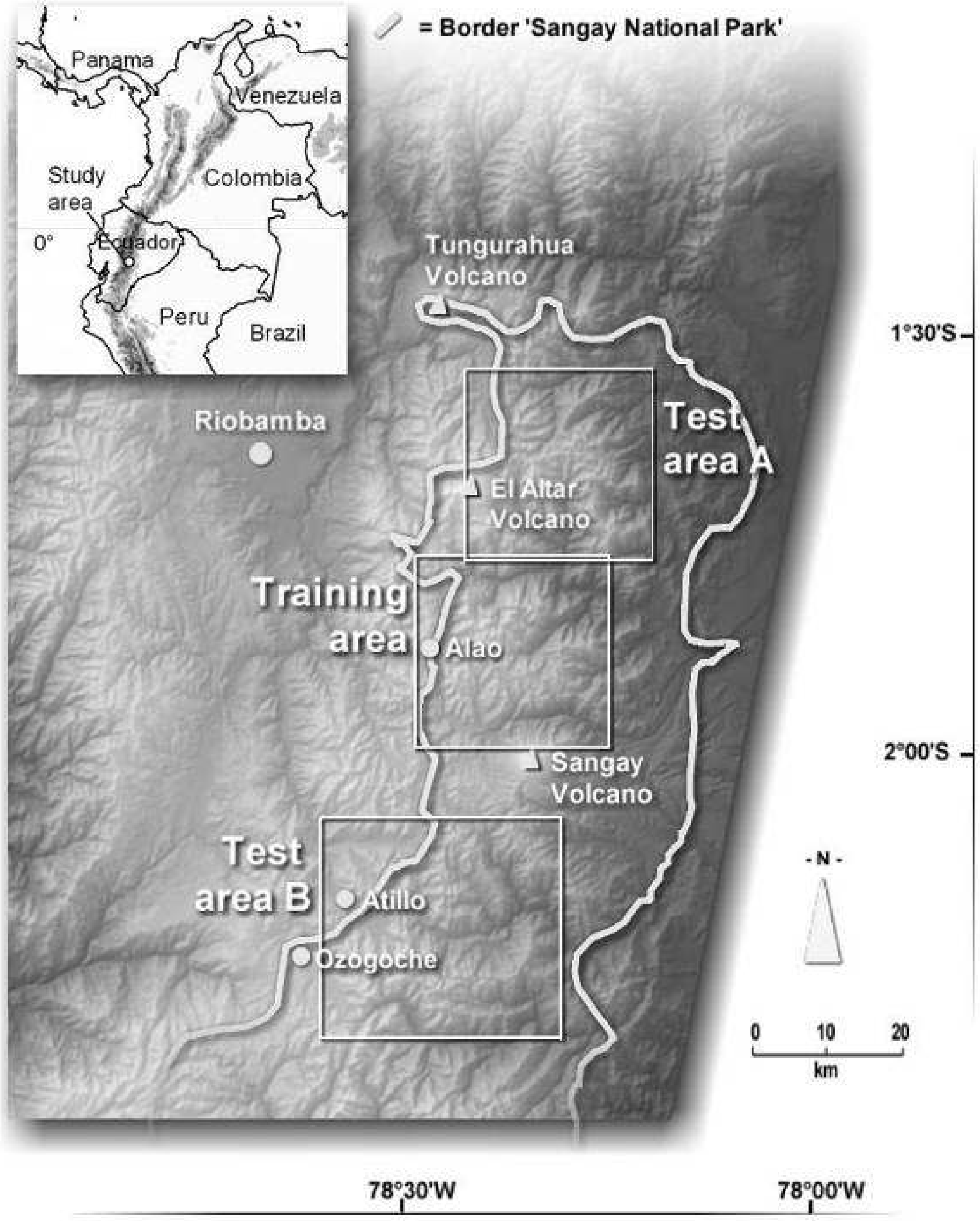


Figure 1 Location of the study areas in Ecuador and in Sangay National Park. Grayshades indicate altitude: on the inset map of NW South America darker shades represent higher altitudes, on the main map darker shades represent lower altitudes. Elevation data: inset: GTOPO30 (USGS, 1996); main map: SRTM (USGS, 2000).

the higher cloudiness and resulting lower temperatures on the Amazonian side (Bendix & Rafiqpoor 2001, Sklenář & Lægaard 2003, Bendix *et al.* 2006a). The following description is based on our field observations in the area near Atillo and existing literature about this park (Armstrong & Macey 1979, Mena *et al.* 1997, Downer 2001, UNEP-WCMC 2003).

The study areas have a typical tropical alpine climate with low average temperatures and little annual variation, but strong diurnal fluctuations (Sarmiento 1986). Precipitation is high year round. There is a relatively dry season from October to February in nearby Atillo (fig. 1), but this seasonality varies between locations and is expected to be less pronounced on the Amazonian side, where the study areas are located (Bendix & Lauer 1992, Mena *et al.* 1997). Soils are deep humic Andosols that have developed in volcanic ashes of different ages. The topography is generally steep, with U-shaped glacial valleys above ca. 3000 m, and V-shaped river valleys in the lower parts.

The alpine vegetation (páramo) is dominated by tussock grasses (*Calamagrostis* sp., *Festuca* sp.) interspersed with various shrubs and herbs. Some wetter and undisturbed páramos are dominated by a tall reed-like bamboo (*Neurolepis aristata*). The forest is an upper montane cloud forest, which is characterized by low stature trees with small sclerophyllous leaves and high epiphyte cover, especially bryophytes. Species richness is low compared to that of tropical lowland forests (Gentry 1995), but high compared to that of temperate montane forests. The highest parts of the cloud forests are dwarf forests dominated by the tree species *Escallonia myrtilloides* and *Gynoxys buxifolia*, in association with various Ericaceae and *Neurolepis aristata*, and possibly other trees or shrubs like *Diplostephium*, *Brachyotum*, *Hesperomeles*, *Buddleja*, and *Miconia* (fig. 2).

The three study areas were selected based on the quality of the data (cloud-free images needed) and the level of human influence expected. Within the square areas shown in figure 1, the forest distribution was modeled only in an altitudinal zone around the treeline in the east-oriented watersheds (Figs 5 & 6). The first area, used for the development of the model (*training* and *cross-validation area*), is located north of Sangay volcano and is about 25 x 25 km in size (NW corner: 78º29' W, 01º46' S). This area is located at about six hours walk from the nearest village (Alao, ca. 5000 inhabitants) to the closest point. Human influence is restricted to extensive cattle grazing and some hunting. Burning is a commonly associated practice, but no evidence of widespread fires was identified.

The second area, used for application of the model (*test area A*), is located north of the training area, east of El Altar volcano, and is about 25 x 25 km in

Figure 2 Photo of the treeline in test area B, in Sangay National Park near Atillo. The new Guamote-Macas gravel road can be seen on the left, as well as the National Park ranger cabin. On the right in the foreground a typically shaped upper montane *Escallonia myrtilloides* tree is shown.

size (NW corner: 78º27' W, 01º33' S). This area is very remote and is expected to experience little to no human influence. The Landsat image of this area had some cloud cover, so that some parts of the treeline are excluded from the application.

The third area, also used for application of the model (*test area B*), is located south of the training area, at one hour walk from the village of Atillo (ca. 400 inhabitants in 1986 (UNEP-WCMC 2003)) to the closest point, and is about 30 x 30 km in size (NW corner: 78º35' W, 02º04' S). The people of Atillo cultivate potatoes and graze cattle and sheep in a broad glacial valley that is part of a west-oriented watershed (not included in the study area). Cattle grazing and the associated burning of the páramo vegetation are extended to the mountains around, including parts of the National Park. Another, similar village (Ozogoche) is also situated close to the study area. Human influence is expected to decrease with distance to these villages. A gravel road connecting Guamote in the inter-Andean valley to Macas in the Amazon lowlands, via Atillo, has recently been established here and is expected to have a strong environmental impact in the region (UNESCO 1999) (fig. 2).

Data

The data used were a Landsat Enhanced Thematic Mapper (ETM) image from NASA's Global Orthorectified Landsat Data Set (Tucker *et al.* 2004), and a digital elevation model (DEM) produced by the Shuttle Radar Topography Mission (SRTM)(USGS 2003). The Landsat image had a resolution of 28.5 m; the DEM had a resolution of 90 m. These spatial resolutions determined the scale at which the analysis was done, and the type of patterns and processes that could be distinguished.

Both the Landsat image and the DEM were geo-referenced by the supplier. The elevation values of the DEM were also rounded to integers, resulting in 1-meter intervals (USGS 2003, GLCF 2006). The reported spatial accuracies of the orthorectified data are <50 m root mean square error for the Landsat data (Tucker *et al.* 2004), and < 9 m geolocation error and <6 m height error for 90% of the SRTM DEM (Rodriguez *et al.* 2005). However, because of the strong relief, errors can be much larger for our study areas than is apparent from these global quality assessments (Jarvis *et al.* 2004, Falorni *et al.* 2005). These inaccuracies will affect the predictive power of the logistic regression model negatively (van Niel *et al.* 2004).

Data preparation

The DEM had some missing values over land and negative values over water bodies, and it contained terraces, probably caused by the rounding of elevation values in the pre-processing by the provider (Wood 2003). These 'bad values' and terraces were removed by creating elevation contour lines from the DEM and subsequently creating a hydrologically correct DEM from these contour lines (Hutchinson 1989). This method is preferred over simpler filtering methods because the hydrologically correct DEM is more useful for the topographical analysis.

The DEM was used to derive the following topographic variables and environmental indices: slope angle, aspect (eastness and northness), plan curvature, profile curvature, wetness index (CTI), solar radiation index (PRR), and erosion index (STCI) (table 1, fig. 3). The variables were derived at the original resolution of the DEM (90 m), and then resampled to 28.5 m to match the resolution of the Landsat image.

The position of the treeline was extracted from the Landsat image and used to define a *treeline zone*, within which the model was developed. This zone was used in order to exclude altitudes outside the range of the treeline. The forest area was identified using supervised classification with a flexible probability threshold. Small clusters of forest and non-forest pixels (≤4 pixels: covering less than half a SRTM pixel) were considered noise and were removed, because

Table 1 Topographic variables and environmental indices used as independent variables in the logistic regression.

Variable	Description	Calculation	Ecological meaning
Altitude	altitude above sea level (m)		temperature, moisture, CO_2 pressure
Slope	slope angle (degrees)		solar radiation, stability, erosion, moisture
Eastness	aspect east-west (1 to -1)	sin(aspect)	solar radiation in morning or afternoon, wind
Northness	aspect north-south (1 to -1)	cos(aspect)	solar radiation in summer or winter
Plan curvature	curvature perpendicular to slope direction	-1 = concave 1 = convex	solar radiation, wind, moisture, erosion/deposition
Profile curvature	curvature in slope direction	-1 = convex 1 = concave	moisture, erosion/deposition
CTI	Compound Topographic Index (or Wetness Index)	$\ln(A_s / \tan \beta)$ *	moisture, water logging, cold air ponding
PRR	Potential Relative Radiation	hourly shaded relief	solar radiation potential
STCI	Sediment Transport Capacity Index	$(A_s/22.13)^{0.6}$ / $(\sin \beta/0.0896)^{1.3}$ *	erosion potential

* A_s= contributing area, derived with D∞ algorithm (Tarboton 1997)
β = local slope angle
[1,2,3] References: 1. (Schmidt & Persson 2003) 2. (Pierce *et al.* 2005) 3. (Moore *et al.* 1993)

their classification is more likely to be incorrect and because in any case such small features could not be related to the coarser-scaled SRTM DEM. The classified image was converted to a vector format, where the boundaries between forest and non-forest were represented as lines. These lines were converted back to a grid format with the original pixel size (28.5 m). The overlay of this gridded line with the DEM (resampled to 28.5 m) gave us the altitude of all forest boundaries. To exclude forest boundaries not related to the altitudinal treeline, we excluded altitudes below 3300 m. From the remaining boundaries the average altitude was calculated, as well as the standard deviation. We then defined the *treeline zone* as the average treeline altitude ± two standard deviations (this was 3634 ± 2*185 m). This implies that approximately 95% of the treeline is included in the zone. Within this zone, the distribution of forest/non-forest was the subject of investigation. We used a combination of IDL ENVI (RSI/ITT, Boulder, CO, USA) and ArcGIS 9 (ESRI, Redlands, CA USA) for the preparation of the data.

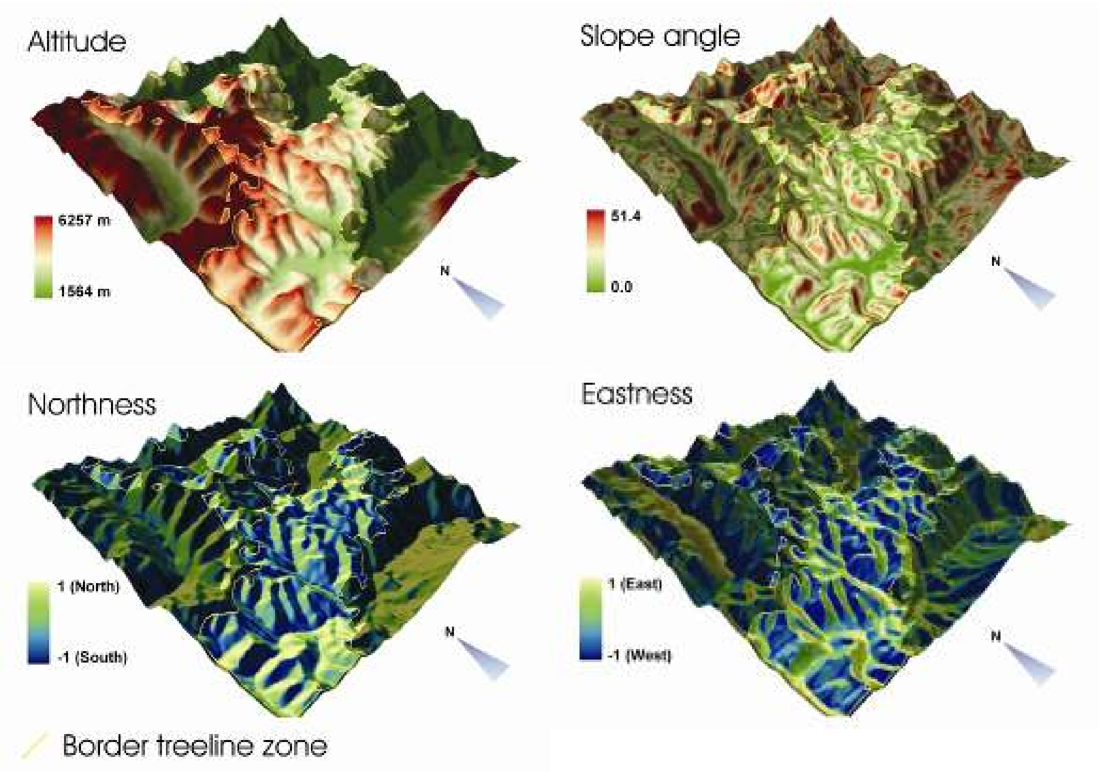


Figure 3 Distribution of the topographic variables and environmental indices in the training and cross-validation area. The legends refer to the lighter area within the border of the treeline zone.

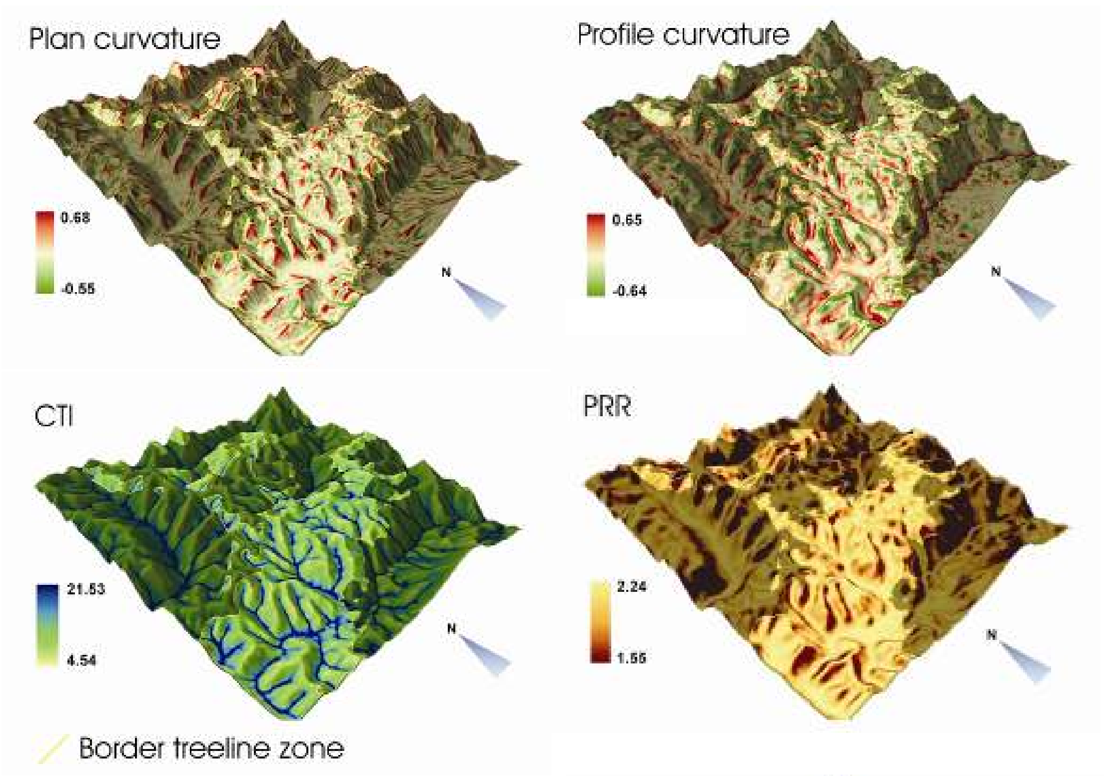
Logistic regression

A logistic regression model was built to predict the forest/non-forest distribution based on the topographic variables and environmental indices (Brenning 2005). A logistic regression model predicts the probability that a pixel is covered by forest as follows:

$$P(\text{forest}) = \frac{e^{(a+b_1 \cdot X_1 + b_2 \cdot X_2 + \ldots + b_n \cdot X_n)}}{1 + e^{(a+b_1 \cdot X_1 + b_2 \cdot X_2 + \ldots + b_n \cdot X_n)}}$$

Where a and $b_{1\ldots n}$ are the model coefficients (B) for the constant and the topographic variables $X_{1\ldots n}$.

Only half of the first study area was used for building the model (*training area*), while the other half was used for cross-validation (*cross-validation area*). The area was divided into these two halves following a checkerboard pattern with 1-km squares (fig. 5a). For the regression, the SPSS (SPSS Inc., Chicago, IL, USA) procedure binary logistic regression was used with the



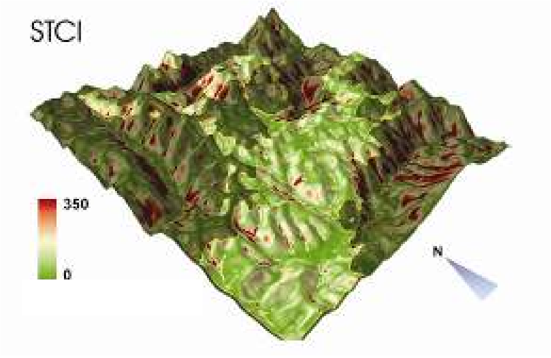


Figure 3 (continued) Note that the scales of plan and profile curvature have opposite meanings (see table 1). CTI = Compound Topographic Index, PRR = Potential Relative Radiation, STCI = Sediment Transport Capacity Index.

forward stepwise algorithm based on a maximum likelihood ratio test (Hosmer & Lemeshow 1989).

There was multicollinearity (bivariate or multivariate correlation) between some of the explanatory variables, as shown by high Variance Inflation Factors for slope (10.0), PRR (6.0), CTI (4.5) and STCI (2.5). Multicollinearity complicates the assessment of the effects of the correlated variables in the model, but it does not affect the model's predictive power (Garson 1998). Multicollinearity can be handled either by leaving out the most correlated variables, or by combining variables into principal components (Brown 1994, Baker & Weisberg 1997, Garson 1998, Cairns 2001, SSTARS 2005). However, when variables are combined into principal components the role of the individual variables becomes unclear, so we chose not to apply this method. Instead, we constructed separate models including only one of the correlated variables in each, and interpreted the ecological effects of these variables from these *stripped models*.

Spatial autocorrelation can be included in regression models to account for patterns that are due to purely spatial processes such as seed dispersal or herding behavior (Augustin *et al.* 1996). However, at the scale of our data we expected similarity between neighbors to be due mainly to the similar topographical position, and not to purely spatial processes. We therefore chose not to include a spatial autocorrelation term in our model.

However, spatial autocorrelation also implies that the data are not independent. Spatial dependence between data points will cause a false increase in the statistical significance of the model coefficients (Garson 1998, Dalthorp 2004, Brenning 2005, Maggini *et al.* 2006). A possible solution to this problem is to build the model with a subsample of points, thereby increasing the distance and decreasing the correlation between points (Brown 1994, Brenning 2005). However, with this solution a lot of information is not used. We therefore chose to use all data points and to treat the reported significance of the model and model coefficients with extra caution.

The model was applied to the held-back half of the checkerboard for cross-validation. The overall predictive accuracy of the model was determined by

Table 2 Results of a forward stepwise logistic regression including all the independent variables (the *complete model*). Significance of all variables: p<0.001. The only variable not included in the model is profile curvature. The variables that have considerable effects on the models are printed bold. The last column is the change in -2 Log Likelihood if the variable is removed from the model.

Complete model in training area	**Variable**	**Model Coefficient (B)**	**S.E.**	**Wald**	**Change in -2 Log Likelihood**
Total Chi-Square: **79699**	**altitude**	-0.01312	0.00007	**33185.48**	**75950.79**
	eastness	-0.75409	0.01332	**3207.19**	**3401.21**
	CTI	-0.50856	0.00978	**2701.91**	**3001.21**
Nagelkerke's R2: **0.633**	slope	0.06243	0.00281	494.70	498.68
	northness	-0.24279	0.01311	343.06	345.18
	STCI	0.00701	0.00041	290.06	328.65
Predictive accuracy: **84.0 %**	PRR	3.19912	0.20847	235.49	237.19
	plan	-0.95959	0.10560	82.57	82.78
	Constant	42.69393	0.56869	5636.22	

comparing the predicted forest cover, using threshold P(forest) > 0.5, with the actual cover as derived from the Landsat image. The number of correctly predicted pixels for each class, as shown in a classification table, is used to calculate the overall predictive accuracy.

Model application

The model was applied to test areas A and B, in a treeline zone with the same altitudinal limits as that in the training area (3264 to 4044 m a.s.l.). Apart from calculating the overall predictive accuracy for each area, we visually inspected the shape and locations of the deviations between the actual and predicted cover. We also trained logistic regression models on the test areas, using the methodology as described above, to see if the same topographic factors were important here.

Results

Importance of variables in the model

Eight of the nine topographic variables contributed significantly to the logistic regression model (the *complete model*); only profile curvature was excluded (table 2). The included variables contributed significantly to the model according to all statistics (Wald, Change in -2 Log Likelihood, Akaike Information Criterion). However, the predictive accuracy of the model was

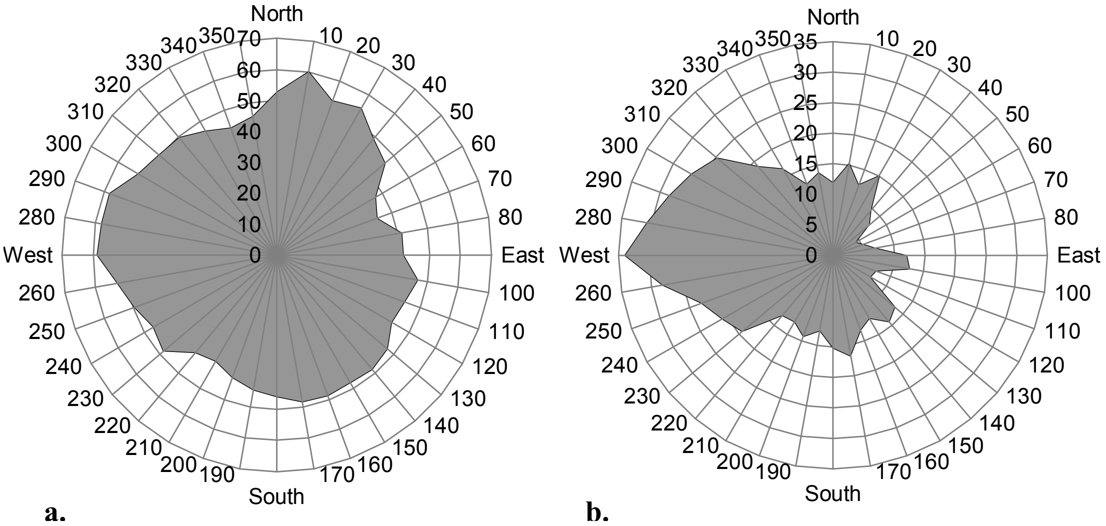


Figure 4 Aspect ecograms of the presence of forest on slopes below (a) and above (b) the average treeline altitude (3634 m). Shown is the percentage of the total number of pixels with a certain aspect where forest is present. Note the different scales on the radial axes.

Table 3 Classification tables showing the predictive accuracies of the models of each of the steps of the forward stepwise logistic regression in the training area. Shown are the numbers of pixels that were observed and predicted in the two classes. The correct predictions are underlined. For each step, the first percentage in the last column represents the specificity of the model, the second percentage the sensitivity, the third the overall accuracy (=number of correctly predicted pixels divided by the total number of pixels).

Step	**Predicted**	Non-Forest	Forest	**Correctly predicted (%)**
	Observed			
Step 1 (**+altitude**)	Non-Forest	52915	11461	82.2
	Forest	12606	46795	78.8
			Overall accuracy	**80.6**
Step 2 (**+CTI**)	Non-Forest	54589	9787	84.8
	Forest	11491	47910	80.7
			Overall accuracy	**82.8**
Step 3 (**+eastness**)	Non-Forest	54941	9435	85.3
	Forest	11139	48262	81.2
			Overall accuracy	**83.4**
Step 4 (**+slope**)	Non-Forest	54891	9485	85.3
	Forest	10668	48733	82.0
			Overall accuracy	**83.7**
Step 5 (**+STCI**)	Non-Forest	55007	9369	85.4
	Forest	10584	48817	82.2
			Overall accuracy	**83.9**
Step 6 (**+northness**)	Non-Forest	55032	9344	85.5
	Forest	10499	48902	82.3
			Overall accuracy	**84.0**
Step 7 (**+PRR**)	Non-Forest	55030	9346	85.5
	Forest	10448	48953	82.4
			Overall accuracy	**84.0**
Step 8 (**+plan curvature**)	Non-Forest	55019	9357	85.5
	Forest	10429	48972	82.4
			Overall accuracy	**84.0**

increased very little (<0.05%) by the inclusion of the last two variables (table 3). The significance of these variables was probably inflated because of the spatial dependence of the data points. We therefore used the complete model (last step of the stepwise regression) for prediction, but not for the assessment of the importance of the variables.

The importance of the individual variables could be derived from the complete model only for uncorrelated and strongly contributing variables. Altitude was clearly the main factor determining treeline position; a model including only altitude correctly predicted forest cover in 80% of the training pixels (table 3). Exposition differences between west and east slopes (eastness) were more important than those between north and south (northness); forest cover was higher on western slopes. This was due mainly

Table 4 Results of forward stepwise regressions including only one of the correlated variables per regression (the stripped models). Significance of all variables in all models: p<0.001. The single correlated variable is underlined, the variables that have cons

Model	Variable	Model Coefficient (B)	S.E.	Change in -2 Log Likelihood
CTI	**altitude**	-0.01294	0.00007	**76238.58**
	CTI	-0.68647	0.00740	**10522.35**
Total Chi-Square:	**eastness**	-0.69105	0.01253	**3207.61**
77526.64	plan	-2.79590	0.09761	837.78
	northness	-0.12069	0.01200	101.35
Predictive accuracy: **83.6 %**	profile	0.51165	0.08572	35.72
	Constant	51.68671	0.28626	
Slope	**altitude**	-0.01242	0.00007	**73975.32**
	slope	0.09609	0.00105	**9678.62**
Total Chi-Square:	**eastness**	-0.81767	0.01288	**4343.49**
76682.92	profile	-2.12126	0.08408	641.31
	plan	1.23750	0.08504	212.10
Predictive accuracy: **83.5 %**	northness	-0.17255	0.01201	207.30
	Constant	42.93493	0.23667	
PRR	**altitude**	-0.01167	0.00006	**70759.06**
	PRR	-6.74224	0.09315	**5717.82**
Total Chi-Square:	**eastness**	-0.80607	0.01278	**4254.13**
72722.11	profile	-1.87158	0.08162	528.35
	plan	1.58804	0.08264	370.46
Predictive accuracy: **82.7 %**	northness	0.02964	0.01170	6.42
	Constant	56.44628	0.35429	
STCI	**altitude**	-0.01087	0.00006	**66404.95**
	STCI	0.01701	0.00032	**3231.53**
Total Chi-Square:	**eastness**	-0.62693	0.01205	**2830.62**
70235.83	**plan**	3.93679	0.08976	**1985.04**
	profile	-1.13367	0.08092	196.19
Predictive accuracy: **82.2 %**	northness	-0.09474	0.01159	66.88
	Constant	38.52169	0.21142	

to the higher position of the upper treeline on these western slopes, as demonstrated by the fact that western slopes had higher forest cover only above the average treeline altitude (fig. 4).

The importance of the correlated variables (Slope, CTI, PRR and STCI) was derived from the stripped models, which included only one correlated variable at a time (table 4). Of these correlated variables, wetness (CTI) best predicted forest cover, high wetness indicating low forest cover. This reflected the absence of forest in broad valley bottoms. The model reproduced these forest-free valley bottoms, but these modeled areas were less in extent than the real (classified) forest-free areas (fig. 5b).

Although multicollinearity is not supposed to affect the non-correlated variables, we saw a reversal of the importance and the direction of some variables when including different correlated variables (table 4). In particular, the roles of plan and profile curvature were reversed when including slope, PRR

Table 5 Results of forward stepwise regressions for test areas A and B. Significance of all variables: p<0.001. The variables that have considerable effects on the models are printed bold.

Area	**Variable**	**Model Coefficient (B)**	**S.E.**	**Change in -2 Log Likelihood**
Test area A	**altitude**	-0.01372	0.00008	**63210.98**
	eastness	-0.83946	0.01161	**5588.71**
Total Chi-Square: **71151**	**CTI**	-0.62653	0.01334	**2442.34**
	STCI	0.04523	0.00132	1204.94
Nagelkerke's R2: **0.545**	northness	-0.38291	0.01174	1078.47
	PRR	3.30456	0.15074	479.72
Predictive accuracy: **80.0 %**	profile	0.88804	0.09308	91.62
	slope	0.01967	0.00303	42.18
	Constant	43.71905	0.45502	
	altitude	-0.00781	0.00004	**76301.02**
Test area B	profile	-1.91420	0.05759	1105.63
Total Chi-Square: **79228**	eastness	0.22069	0.00823	721.04
	CTI	-0.18100	0.00822	498.13
	northness	-0.19992	0.00915	479.18
Nagelkerke's R2: **0.416**	PRR	-1.80495	0.12007	226.39
	STCI	0.00377	0.00027	207.04
Predictive accuracy: **78.8 %**	plan	0.79113	0.05735	190.73
	slope	-0.01579	0.00178	79.29
	Constant	32.77744	0.33207	

or STCI instead of CTI. With CTI convex curvatures (ridges) had low forest cover, while with the other variables they had high forest cover. We interpreted this as follows: CTI was generally low on ridges, so based only on CTI forest cover should always be high on ridges, but this effect of CTI was counteracted by the plan and profile curvature variables. In contrast, when slope, PRR or STCI replaced CTI, the absence of forest in valley bottoms was accounted for by lower forest cover at concave curvatures.

So the topographic variables that appeared to have a real effect on forest distribution were altitude, CTI, and eastness, in that order. In the model trained on test area A the same variables were indicated to be most important (table 5), but in the model trained on test area B altitude had a more dominant effect, and the next most important variable was profile curvature. However, multicollinearity was strong in both test areas for the same variables as in the training area (slope, PRR, CTI, STCI), so the importance of these correlated variables cannot be derived with certainty from these models. Again we explored the effect of including only one correlated variable at a time in

Table 6 Classification tables showing the predictive accuracies of the *complete model* in the training and cross-validation areas and in test areas A and B. Shown are the numbers of pixels that were observed and predicted in the two classes. The correct predictions are underlined. For each area, the first percentage in the last column represents the specificity of the model, the second percentage the sensitivity, the third the overall accuracy (=number of correctly predicted pixels divided by the total number of pixels).

Area	**Predicted**	Non-Forest	Forest	**Correctly predicted (%)**
	Observed			
Training	Non-Forest	55019	9357	85.5
	Forest	10429	48972	82.4
		Overall accuracy		**84.0**
Cross-validation	Non-Forest	55970	11056	83.5
	Forest	9704	47602	83.1
		Overall accuracy		**83.3**
Test A	Non-Forest	57520	39854	59.1
	Forest	1524	37646	96.1
		Overall accuracy		**69.7**
Test B	Non-Forest	66503	45031	59.6
	Forest	15037	90720	85.8
		Overall accuracy		**72.4**

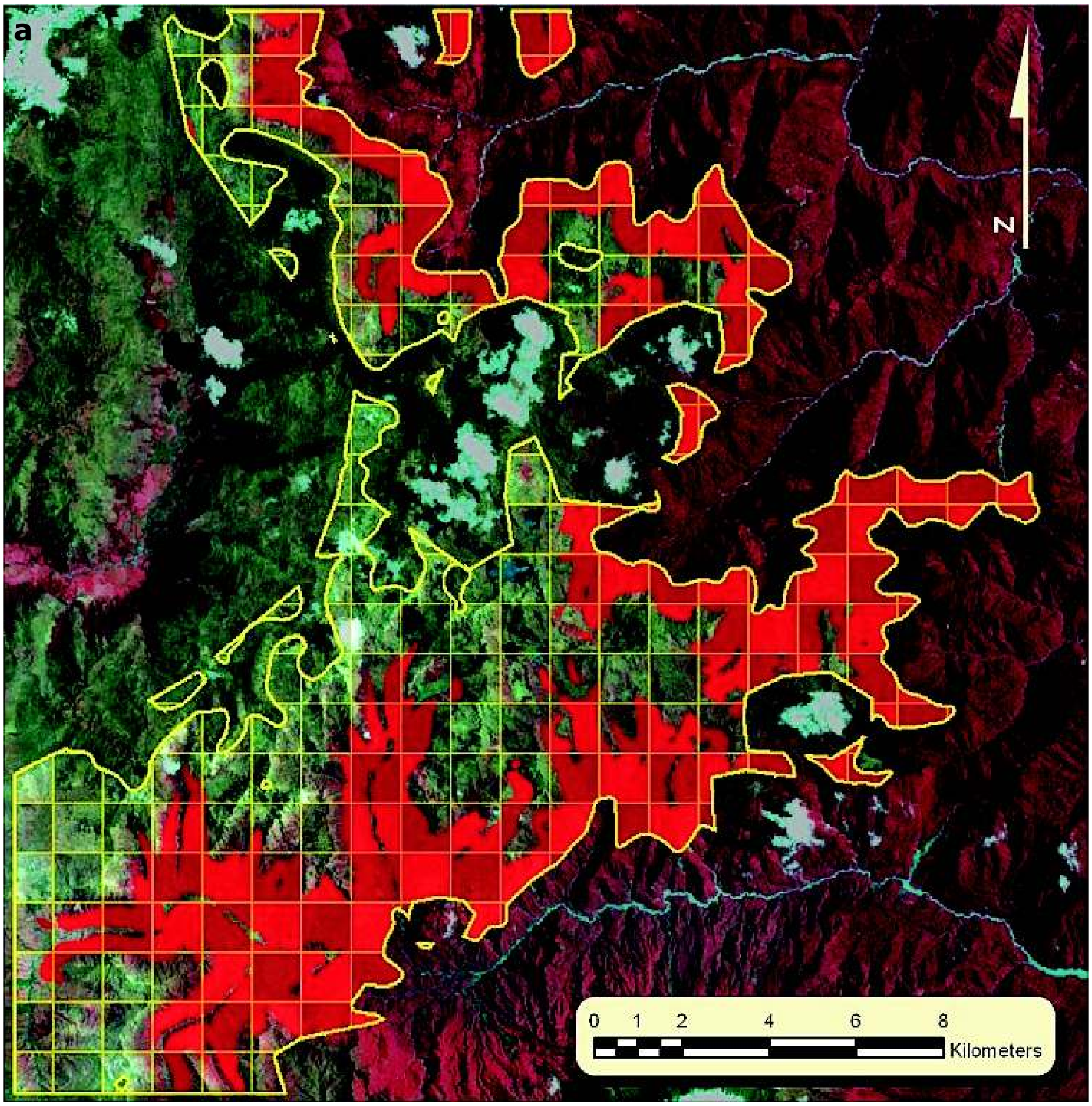


Figure 5a Predicted forest cover in the training and cross-validation area. Light-er squares of the checkerboard pattern are the training area, darker squares are the cross-validation area.

stripped models (not shown), which confirmed the likeness of the pattern in test area A with the training area, and the dominance of altitude relative to all other variables in test area B.

Model application

The predictive accuracy of the complete model was high both in the training area (84.0%) and in the cross-validation area (83.3%) (table 6). The specificity (percentage correctly predicted non-forest pixels) was somewhat

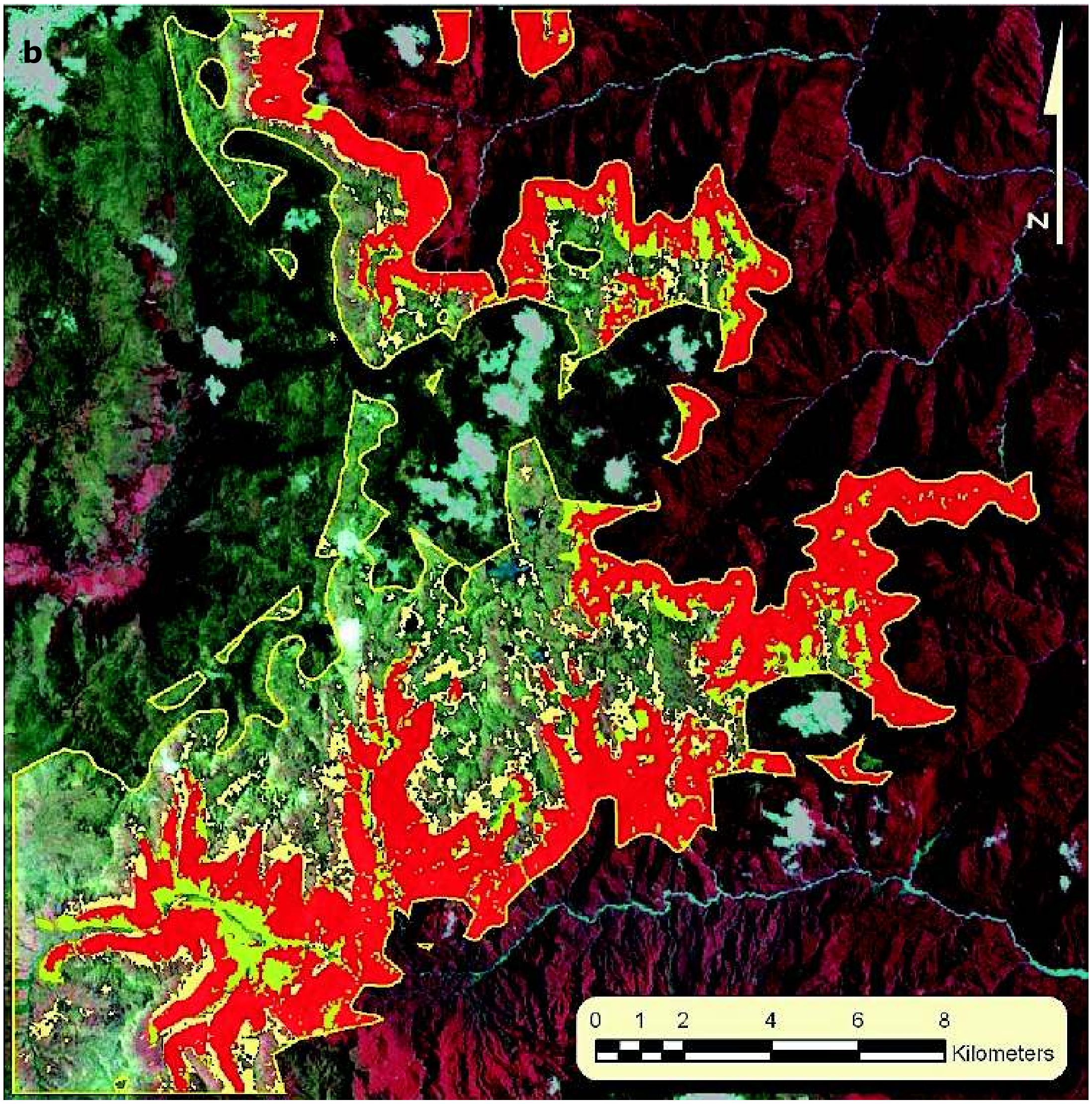


Figure 5b Difference between predicted forest cover and the real forest cover (classified from the Landsat image) in the training and cross-validation area. Green indicates areas where forest is predicted where in fact forest was not present. Yellow indicates areas where no-forest is predicted where in fact forest was present. Red indicates correctly predicted forest. Overall classification accuracy in training area: 84.0 %; in cross-validation area: 83.3 %.

higher than the sensitivity (percentage correctly predicted forest pixels).

In test area A the predictive accuracy of the model was lower (69.7%), which was due to an over-estimation of forest cover throughout the area (fig. 6a). So in this area, the specificity was very low, while the sensitivity was very high (table 6). In test area B the predictive accuracy was also lower (72.4%)

but in this area the over-estimation was more concentrated in certain locations, while in other locations forest cover was under-estimated (fig. 6b).

Discussion

Forest distribution pattern

Treeline position does not fluctuate randomly around an elevational contour line but depends on other topographic variables in a predictable way. After altitude, the most important variables were CTI (wetness index) and eastness.

The strong effect of the wetness index in the model is mainly due to the absence of forest on the flat bottoms of glacial valleys, where water tends to stagnate. This pattern, resulting in 'inverted' treelines, is common in U-shaped valleys in mountains worldwide (Wardle 1985, Miehe & Miehe 1994). Apart from accumulating water, such valley bottoms also accumulate cold air at night, which drains from the higher slopes and stagnates in these flat areas (Wardle 1985, Sarmiento 1986). Water and frost accumulation patterns in a landscape are in fact often very similar (Blennow 1998). The reason for the absence of trees in these valley bottoms may therefore be either waterlogging or low night temperatures, or a combination of both.

The strong effect of eastness in the model is due to the higher position of treelines on western slopes than on eastern slopes. This difference may be caused by the difference in solar radiation received. Like in many tropical mountains, a typical day in our study area has a clear morning and a cloudy and often rainy afternoon, followed by a clear evening (Smith & Young 1987, Luteyn *et al.* 1999, Poveda *et al.* 2005). As a result, eastern slopes tend to receive more solar radiation (Sarmiento 1986). Excess radiation, especially when preceded by low night temperatures, can cause photinhibition in maladapted plants (Ball *et al.* 1991, Germino & Smith 1999). Eastern slopes do not only receive more radiation, they also receive this radiation in the morning, directly after the cold night, when plants are most vulnerable. Seedlings of most cloud forest tree species appear to be sensitive to such cold-induced radiation damage (Bader *et al.* online first), which may explain why these trees have difficulties establishing outside the forest, particularly on eastern slopes. Slowness of forest extension due to excess radiation may therefore have caused the observed lower treelines on these slopes.

Other conditions that may differ between eastern and western slopes are wind, moisture and temperature. The higher radiation received by eastern slopes may result in dryer conditions and higher temperatures (Smith 1977, Azócar & Monasterio 1980). On the other hand, although cloudiness is not expected to differ significantly between slopes at this scale, the eastern slopes are exposed to the prevailing winds coming up from the Amazon basin and may receive more wind-driven moisture, resulting in windier and wetter conditions (Cavelier & Goldstein 1989). We do not know balance between these factors and unfortunately no supporting climatic field measurements are available for this region. In our study area an excess of moisture is more likely than a lack of moisture, but in well-drained positions this should not impair forest growth. Wind may be strong during storms, but is generally gentle, like in most tropical mountains (Bruijnzeel & Veneklaas 1998). Temperatures may be higher because more radiation is received (Azócar & Monasterio 1980, Sarmiento 1986), but higher temperatures would not depress the treeline (Körner & Paulsen 2004). We therefore maintain that the most important reason for the lower treelines on eastern slopes is probably radiation damage to young trees, but this issue needs further research.

The small effect of northness on forest distribution was to be expected in this tropical region. The small effect of and PRR is probably due to the difference between this *potential* radiation and the actual radiation when cloudiness is accounted for. Clouds are especially frequent on the eastern slopes of the Andes, and the changes in cloudiness through the day strongly affect the actual distribution of radiation (Bendix *et al.* 2006b) and hence the distribution of forest.

Model application

Whether the position of a treeline is climatic, natural or anthropogenically lowered is often unclear for a particular location. In many tropical mountain ranges it may be impossible to find an undisturbed training area to compare potentially disturbed areas against (Miehe & Miehe 1994, Dickinson *et al.* in prep). In such cases, a pragmatic solution is to train the model in the least-disturbed area known in the region, and use this best-we-have pattern as the standard to detect differences. These differences may indicate anthropogenic disturbances, but they could also point to variations in other environmental conditions. Because of the rather remote situation, our training area is presumed to experience limited human influence. However, we have no certainty about this, so it is safer to consider forest distribution in this area a best-we-have pattern, rather than a natural pattern.

In test area A, which we presumed also to be little disturbed, the model over-estimated forest cover all along the treeline. Still, a model trained in this area showed the same importance of variables as the models from the training area, which agrees with the even distribution of the over-prediction. If disturbances were responsible for the relative lack of forest, we would expect more localized effects and an alteration of the relationship with the topography. It therefore seems that these treelines are lower because of

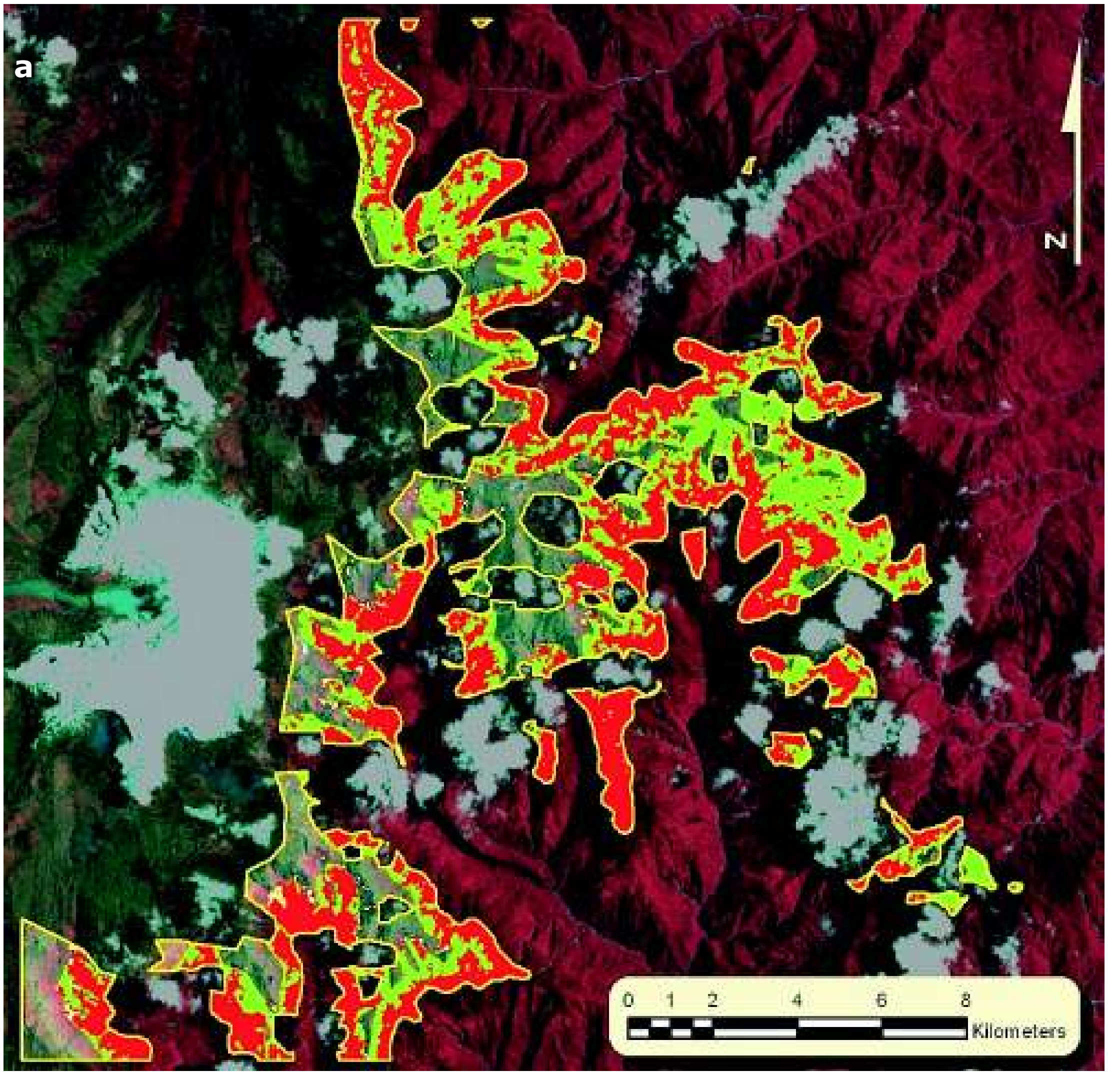


Figure 6a Difference between predicted forest cover and the real forest cover (classified from the Landsat image) in test area A (a). Green indicates areas where forest is predicted where in fact forest was not present. Yellow indicates areas where no-forest is predicted where in fact forest was present. Red indicates correctly predicted forest. Overall classification accuracy in test area A: 69.7 %.

climatic factors rather than human disturbances. The valleys in this area mostly start on the slopes of the snow capped El Altar volcano (5319 m). Temperatures may therefore be lower due to downslope movement of cold air during the nights. Also, cloudiness may be higher here, causing lower temperatures, but according to the three-year NOAA-AVHRR data presented by Bendix *et al.* (2006a), cloud frequency does not differ notably between our three study areas.

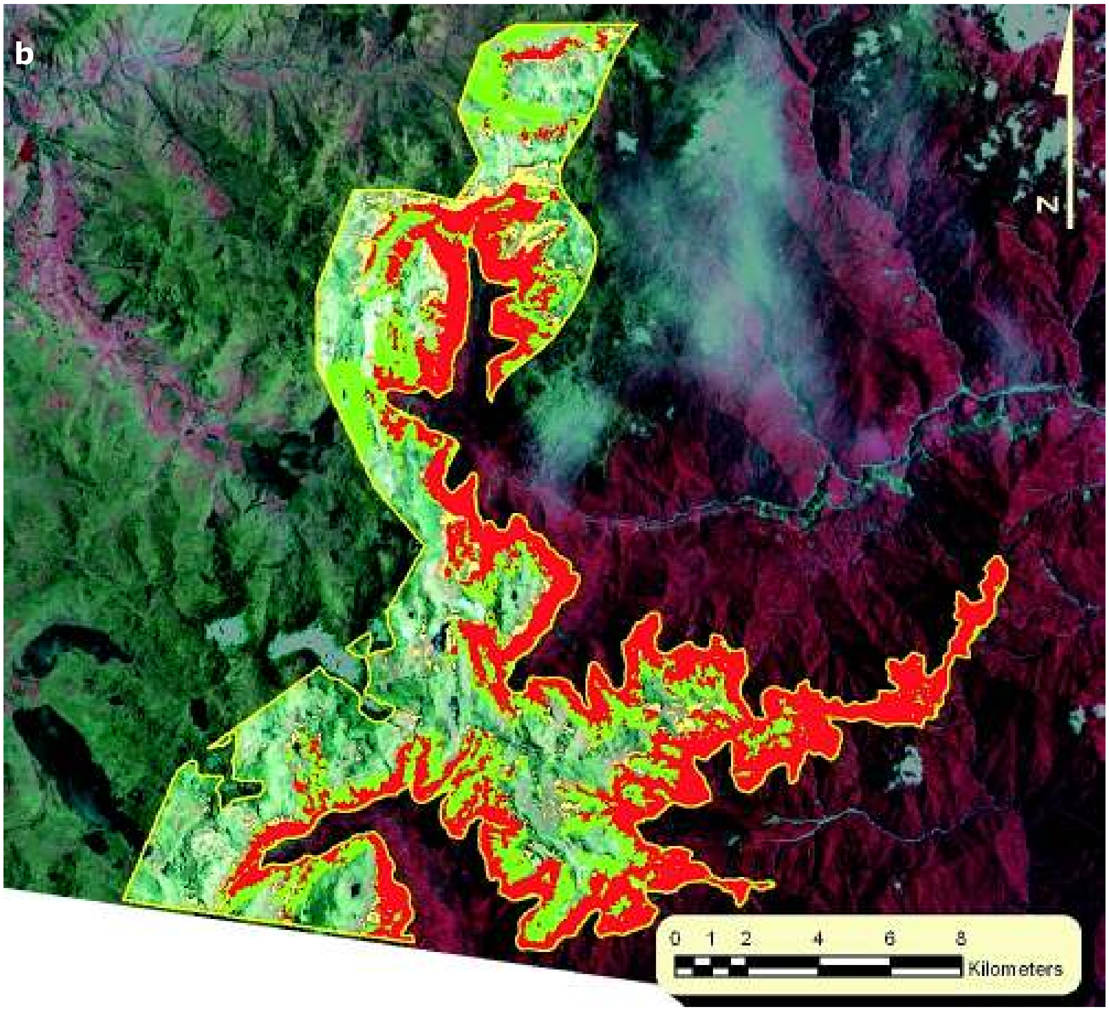


Figure 6b Difference between predicted forest cover and the real forest cover (classified from the Landsat image) in test area B (b). Color legend as in fig 6a. Overall classification accuracy in test area B: 72.4 %.

Test area B, which we presumed to be more disturbed, at least locally in the proximity of Atillo and Ozogoche, also had a lower treeline than the training area, as seen in the over-estimation of forest cover by the model. In this case the over-estimation was less evenly distributed in the area. Moreover, the model trained on this area indicated a different relationship with the topographic variables than in the training area. Here we can also not exclude climatic reasons for the lower treeline. Still, the location of the largest over-estimations might indicate an unnatural lowering that warrants further investigation.

The type of patterns of forest distribution caused by human land use can be very similar to the patterns caused by natural processes, and may therefore be hard to distinguish. For instance, the lack of forest valley floors could theoretically also be caused by preferential human settlement in flat areas (Wardle 1985), and treelines could be lowered on eastern slopes due to stronger fires if theses slopes are dryer, or due to agricultural benefits if they are warmer (Smith 1977). After identifying interesting locations, the real history of these sites can therefore only be studied in the field, for instance by determining the local land-use or by reconstructing vegetation history based on local proxies, such as macroscopic charcoal (di Pasquale *et al.* in press).

It should be mentioned that this modeling approach is not the most appropriate approach if changes due to contemporary disturbances are studied, for instance the effects of the new Guamote-Macas road through Atillo and test area B. In such a case it is much more accurate and simple to compare the actual forest distribution on remotely sensed images from before and after road construction.

Methodological issues

Classification: At the local scale, treelines are ecotones of varying width, having spatial patterns ranging from abrupt boundaries, gradual transitions in tree height or density, or mosaics of vegetation patches (Wardle 1965, Körner 1998, Bader *et al.* accepted). Zooming out, the treeline starts to look more and more like a crisp boundary. In the section of the study area that we visited, the transition zone was narrow, less than 30 meters, so at the scale of a Landsat image (30-m pixels) this treeline was abrupt and could be considered a line. Still, we cannot exclude that in other parts of the study areas broader transition zones were present, like in some remote areas of nearby Llanganates National Park (Dickinson *et al.* in prep). With our method such zones of shrubs and forest patches are classified as forest, so that the treeline is defined as the upper boundary of the treeline ecotone. For an analysis of the spatial pattern within the ecotone, which can indicate land use effects or natural vegetation processes, a classification with more classes and data with a higher spatial detail are needed (Wiegand *et al.* 2006, Bader *et al.* accepted, Dickinson *et al.* in prep).

Spatial resolution: Small forest patches in the páramo, even when discernable on the Landsat image, cannot be explained by the topography due to the lower DEM resolution (90 m). These small patches were therefore excluded from the analysis. A model based on this DEM can only describe large-scale patterns and indicate prevailing environmental conditions, even if in the field there can be considerable variability due to smaller topographic features. This problem occurs at all scales, and the most suitable scale of investigation should ideally be based on the goals of the study, although availability of data is also an important criterion in practice. If the main goal of the model is to detect human disturbances, the current scale is sufficient if large-scale impacts are of concern. If the main goal is to understand the processes that cause the treeline, the current scale is sufficient to reveal some important limitations for forest growth, as shown in this study. Still, patterns caused by other limitations may only be discernable at a more detailed scale.

Spatial accuracy: The DEM as well as the Landsat image had limited spatial accuracy, resulting in some displacements of forest cover relative to the topography. As long as the errors in both datasets are randomly distributed, they will weaken the effect of topographic variables in the logistic model, but they will not lead to any false positive conclusions. However, systematic errors may cause relationships in the model that are not related to relationships in the terrain. In the Americas the SRTM DEM appears to contain an over-estimation of the altitude of northern to eastern slopes (Jarvis *et al.* 2004, Rodriguez *et al.* 2005). This could lead to a model falsely indicating that treelines are higher on these slopes. However, our models indicated that treelines were higher on western slopes, and we can therefore be confident that this relationship is no artifact of systematic errors in our data.

The 16% forest cover that could not be explained by topographic variables may be attributable to random natural variation or to the effects of processes not related to the topography or not captured in the topographic variables used, for instance rock type and disturbances. Also, the model includes only linear relationships and no interactions between variables, simplifications that have probably resulted in a lower fit of the model. Additionally, the model fit will be lower because of the spatial inaccuracies in the data and the low resolution of the DEM. However, the fact that we found strong relationships of forest cover with topography in spite of the simple nature of the model and the low accuracy of the data in fact increases our confidence that these statistical relationships describe real and meaningful vegetation patterns.

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CHAPTER 7

Synthesis

Photo previous page: treeline to the west of Boca del Monte, Venezuela

Synthesis

Each of the chapters in this thesis is a step towards answering the main research question: *What processes control spatial patterning and dynamics of the vegetation at tropical alpine treelines?* The main conclusion is that both páramo fires and excess solar radiation combined with low night temperatures can limit tree establishment above the treeline and thereby control the patterning and dynamics of the vegetation. These processes cause positive feedbacks, which can explain the observed abruptness, landscape-scale patterns, and slow dynamics of tropical alpine treelines.

Existent vegetation patterns and past dynamics

In order to determine what spatial vegetation patterns can be found at tropical alpine treelines, the vegetation structure of seven treelines was studied (Chapter 2). In spite of the large geographical distances between these treelines (from Venezuela to Argentina to Hawaii) their structure was remarkably similar and generally consisted of an abrupt transition in vegetation height and species composition. The diversity of treeline structures worldwide is quite large, including gradual transitions in tree height or canopy closure, vegetation mosaics with patches of either upright trees or 'Krummholz' (stunted, deformed trees), and abrupt forest boundaries. The studied tropical treelines only exhibited a small subset of these possible structures. This is probably due to the similar climate and type of species present at the studied treelines. At all treelines, except that in Tafi del Valle (northern Argentina), the climate can be characterized as cool humid tropical and the species composition of the forest as evergreen broadleaved shade-loving cloud forest species. The key word here is shade-loving, as will be discussed below. The studied treelines have also all experienced human influence to some extent, either in the past or continuing today, mainly in the form of livestock grazing and the associated use of fire. This landuse is often assumed to have caused the existent treeline patterns, but, as is argued in this thesis, the possible causes of the observed patterns are not restricted to landuse influences.

We studied the historical dynamics of the treeline in northern Ecuador, where we reconstructed past vegetation cover by identifying and radiocarbon dating soil charcoal (Chapter 3). The charcoal indicated that fires already occurred in this area 13,000 years ago, before the beginning of the Holocene, and that the forest has moved up to its present altitude only in the second half of the Holocene. This implies a slow treeline advance after the climatic warming at the beginning of the Holocene.

So the studied tropical treelines were mostly abrupt, while the palaeo-ecological data indicated a lagged response of the treeline to climatic warming. These non-linear spatial and temporal patterns point at a role of positive feedback between the vegetation and the environment in controlling vegetation patterning and dynamics at the treeline (Armand 1985, Wilson & Agnew 1992). Ultimately, the emerging patterns and dynamics of the vegetation depend on regeneration processes, which determine the persistence and spread of forest and páramo.

Vegetation-environment feedbacks

In the páramo average daily temperatures are higher and temperature extremes are stronger than in the forest (Chapter 2). These microclimatic differences may play an important role in determining tree regeneration at the studied treelines, although when fires occur in the páramo their effect may overrule that of the microclimate. Both the microclimate and fire can mediate a positive feedback switch (Wilson & Agnew 1992) (Chapter 5), where tree regeneration is promoted in the forest and/or inhibited in the páramo.

Important aspects of the microclimate for tree establishment are the high solar radiation levels in the páramo and the low temperatures that occur here during the night. In the forest, the canopy cover protects young trees from solar radiation during the day and from radiative cooling during the night, and most tree species were found to regenerate naturally only in the forest (Chapter 4). When tree seedlings were experimentally transplanted into the páramo or into the forest, their survival was also significantly higher in the forest and in artificial shade in the páramo than in the páramo without shade (Chapter 4). Facilitation from the surrounding páramo vegetation was stronger than competition and probably consisted of the provision of shade. The positive effect of neighbors and the artificial shade treatment may also be related to a dampening of temperature fluctuations under this protective cover, although temperature measurements were ambiguous and did not confirm this supposition.

The importance of excess radiation in limiting tree regeneration was clear from this experiment, which extends similar findings from Australian (Ball *et al.* 1991) and North American (Germino & Smith 1999, Smith *et al.* 2003, Maher & Germino 2006) treelines to the tropics. Additionally, tree regeneration above the treeline may be limited by the recurrent páramo fires. Fire is commonly considered the main cause of abrupt treeline patterns and relatively low treeline positions (Lægaard 1992, Miehe & Miehe 1994), but it is important to recognize that processes other than fire, in particular damage to young trees from strong solar radiation combined with low night temperatures, may have similar effects on vegetation patterns and dynamics. To my knowledge, this has not been recognized for tropical treelines before, in spite of the potentially strong effects on the reaction of treelines to environmental changes.

Predicted treeline position, patterns and dynamics

If shade dependence does indeed control treeline dynamics, this predicts a lower treeline position on slopes that receive stronger radiation, an intuitive prediction confirmed by the spatial simulation model (Chapter 5). Especially radiation in the morning would prevent treeline advance, because radiation damage is worsened by low temperatures, such as when plants are still cold from the preceding night (Ball *et al.* 1991). This hypothesis is confirmed by the pattern of treeline position in the landscape, which includes lower treelines on eastern slopes (Chapter 6).

The local treeline pattern, or treeline structure, was abrupt in all model runs with positive feedback (Chapter 5), which agrees with the treeline structures observed in the field (Chapter 2). This does not prove that positive feedback has caused the observed abrupt treelines, but it shows that it can cause such treelines. Likewise, the model does not prove that fire or cold-induced photoinhibition are important determinants of treeline patterns, but it shows that if they are, abrupt treelines may emerge as a result.

In the model, patchy treelines occurred only at low feedback strengths, because strong positive feedback caused a closing of the treeline. This happened either because fire and shade dependence caused single trees and forest patches to disappear, or because strong shade allowed forest gaps and treeless areas between patches to be filled in. This may seem in contradiction with the results of simple spatial vegetation models where positive feedback resulted in the emergence of patches (Alftine & Malanson 2004, Rietkerk *et al.* 2004). However, for patches to persist, local positive feedback needs to be complemented by some density-dependent constraint on the expansion of tree cover. This may occur if a limiting resource is depleted (Rietkerk *et al.* 2002), or if a disturbance factor is promoted (Alftine & Malanson 2004). At tropical alpine treelines there are no indications that such density-dependent constraints occur, and they were therefore not included in the model. Patchiness at tropical treelines is probably transient and emerges due to environmental heterogeneity and chance establishment rather than self-organizing mechanisms.

None of the studied treelines is probably a climatic treeline; not because they have necessarily been lowered by human landuse, but because they have not kept up with past climatic changes. Likewise, treelines on eastern slopes may be lower because they are lagged behind relative to those on western slopes (Chapter 6). It appears that generally treeline shifts are very slow, as evidenced from the dynamics of our northern Ecuadorian treeline during the Holocene (Chapter 3). This slow reaction to warming also occurred in the model due to positive feedback (Chapter 5).

As a result of the positive feedback through the favorable forest microclimate, an established forest can rejuvenate and persist even if the external climate deteriorates, but forest establishment can only occur in protected microsites or after amelioration of the external climate. Vegetation shifts will therefore not only be very slow, but they will also exhibit hysteresis (Armand 1985): a change from forest to páramo occurs at a lower temperature and at higher radiation levels than a change from páramo to forest (fig. 1). This implies a strong dependence of treeline position on its own

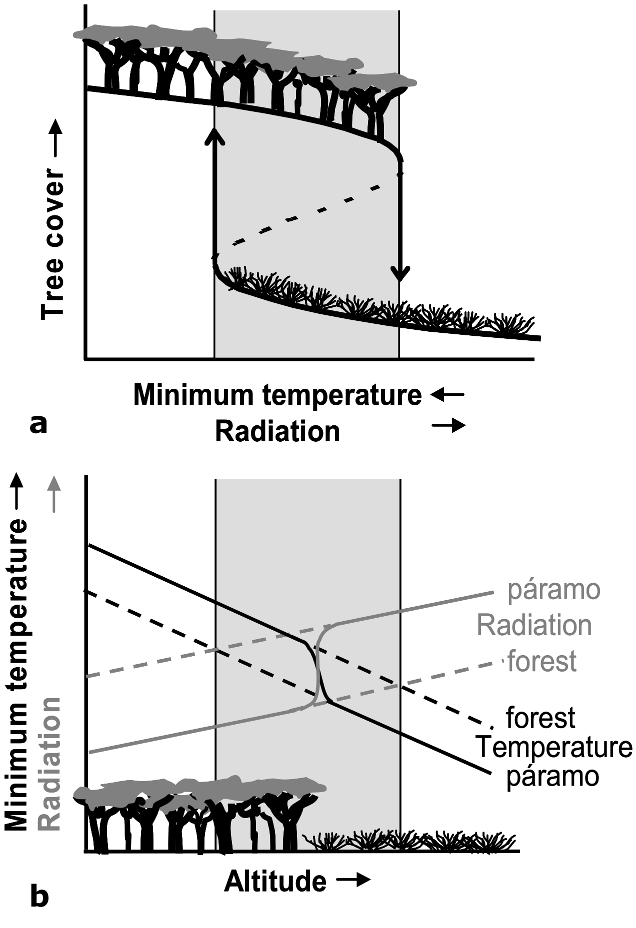

Figure 1 Hysteresis and alternative vegetation states. a) Catastrophe fold; the arrows show catastrophic state shifts at environmental thresholds. b) Changes in minimum temperature and radiation gradients at the treeline. In both figure a and b, the gray area indicates the boundaries of the alternative states zone. To the left of this zone, minimum temperature is high enough and solar radiation is weak enough for tree growth even if forest is absent, so that a forest will always develop. To the right minimum temperature is too low and/or solar radiation is too high for tree growth even if forest is present, so that only páramo can develop. With the given vegetation distribution, favorable conditions for tree growth are created by the forest itself (solid lines).

history. In the model (Chapter 5) this was reflected by the effect of the initial pattern of trees on the final position of the treeline (not shown); a higher initial tree density led to treelines at higher altitudes if positive feedback occurred. Due to this hysteresis, treelines can be situated at different altitudes in spite of equal climatic conditions. The 'climatic' treeline is therefore a difficult concept and does not relate to the actual position of existent treelines, including natural treelines.

So in tropical mountains there is an altitudinal zone, which may be several hundreds of meters wide, where both forest and páramo are natural vegetation types, representing alternative system states (fig. 1). The existence of such alternative states implies that shifts from one state to the other occur 'catastrophically', as an accelerated change once a threshold in external conditions is reached or due to a disturbance (Rietkerk & van de Koppel 1997, Scheffer *et al.* 2001, Scheffer & Carpenter 2003, Rietkerk *et al.* 2004).

Abrupt treelines and 'catastrophic' treeline shifts can be considered spatial and temporal equivalents, controlled by the same feedback mechanisms, as suggested by Armand (Armand 1985, 1992). In our model (Chapter 5) such accelerated shifts did not occur, because the threshold temperature for tree establishment without the shade of neighbors was not reached in the warming scenarios. The limited advance due to positive feedback can be considered as pre-catastrophic inertness to change. The model predicted abrupt treelines in combination with little and slow advance after warming, while gradual patterns were predicted in combination with a stronger response to warming, the latter in treelines not affected by positive feedback. This confirms that there is a link between spatial patterns and temporal dynamics, and opens up possibilities to use spatial treeline patterns as an indicator for the response of the treeline to changes in landuse and climate. For example, when an abrupt treeline experiences warming, I would expect little response until some threshold (minimum) temperature is reached. Once such a threshold is reached and forest expansion sets off, the treeline shift would be accelerated through positive feedback.

Recommendations for further research

The shade-dependence of treeline trees suggested in this thesis was inferred from experimental evidence and could explain the observed spatial and temporal patterns: the abruptness of most treelines, the slowness of treeline advance after the warming at the beginning of the Holocene, and the lower treelines on eastern slopes. However, the mechanisms of solar radiation damage to plants were not studied at a physiological level, and the tolerance limits of different plant species were not quantified. Based on my results and on general physiological principles and research at other treelines it appears likely that the combination of high radiation and low night temperatures is most damaging to young trees, causing cold-induced photoinhibition (Ball *et al.* 1991, Baker & Bowyer 1994, Germino & Smith 1999). Still, we can not exclude that other types of damage, such as freezing, desiccation, and overheating, are equally or more important. For tropical treelines we have no conclusive evidence that radiation and low temperatures combine to cause physiological damage. It is also unknown what the tolerance limits are of different plant species for radiation, low temperature, and their interactive effects. Understanding these tolerance limits will be essential for future attempts to model and predict treeline dynamics in a changing climate, and ecophysiological studies addressing these issues are therefore recommended.

Also, the tolerance limits of different species will determine their role in the succession of forest expansion (Llambi *et al.* 2003, Maher & Germino 2006). Radiation tolerant species are essential for the establishment of an initial tree or shrub cover, in the shade of which more shade dependent species can establish. The mechanisms and pathways of such succession also warrant further investigation. This is important not only for understanding natural vegetation dynamics, but also for designing restoration strategies for upper montane forest (Renison *et al.* 2002, Byers *et al.* 2006).

Our mechanistic model is a strong simplification of real tree growth and vegetation dynamics, and the parameter values are based on general literature sources that do not refer to tropical treeline plant species. Still, this model could demonstrate the qualitative effects of different feedback mechanisms. More elaborate models may be constructed to quantify treeline dynamics, but as long as we do not understand all relevant processes, or have realistic values for model parameters, such efforts are unlikely to yield quantitatively useful results. Moreover, the higher complexity of such models would decrease their transparency and hence the probability that they would further our understanding of how ecological processes affect the treeline.

At this stage the most critical task in tropical treeline research, and in tropical mountain research in general, is still gaining a qualitative understanding of the processes controlling ecosystem functioning and dynamics. As shown in this thesis, simple simulation models can provide a useful tool for advancing this understanding. Field experiments addressing specific ecological processes are perhaps even more useful at this stage, where much pioneering work has already been done, but many ecological mechanisms are still to be unraveled.

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Summary

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Photo previous page: ***Espeletia pycnophylla*** **stem rosettes in páramo island in the forest, unburnt with full leaf cover, Guandera, Ecuador**

Summary

The alpine treeline, defined as the transition between upper montane forest and alpine vegetation, can be a gradual transition, an abrupt boundary, or a patchy mosaic. The position of the treeline in the landscape also varies between regions. These different spatial patterns are caused by processes that also determine the dynamic properties of the treeline, such as its response to changes in climate or landuse. Spatial patterns may therefore serve to indicate the temporal dynamics that a treeline is likely to exhibit, if the underlying processes are well understood.

The reasons why treelines exist are still not fully known. The same goes for the causes of the various spatial treeline patterns and for the dynamics that treelines have exhibited in the past or that they will exhibit as a result of the currently accelerated changes in global climate. For tropical alpine treelines, human landuse and burning of the páramo (i.e. the tropical alpine vegetation) are often cited as determinants of treeline position and pattern. The role of other ecological processes is unknown, however, even though this role may be very important. The tropical alpine environment differs in some important ways from that in the alpine zone at higher latitudes. At tropical alpine treelines there is no or little thermal seasonality through the year, while daily temperature fluctuations can be extreme; wind and snow are generally unimportant; and species richness is much higher than at temperate and boreal treelines.

This research aimed at understanding how ecological processes control the spatial patterning and dynamics of the vegetation at tropical alpine treelines. I used a research approach starting with descriptive studies of vegetation patterns and dynamics, microclimate, and tree regeneration, followed by experimental testing of hypotheses about the causes for these patterns. This lead to a mechanistic spatial model of treeline dynamics, whose results were evaluated against the observed treeline patterns and dynamics and treeline position in the landscape.

The spatial structure of different treelines was studied in Argentina, Bolivia, Ecuador, Venezuela and Hawaii. Most of these treelines were abrupt, with transitions from páramo to forest of less than 4 m. Soil temperatures and mean daily air temperatures were higher above the treeline than in the forest, and temperature extremes were more pronounced above the treeline. The measured differences in microclimate between forest and páramo, in particular the low night temperatures in the páramo, may hinder tree regeneration outside the forest. This would cause a positive feedback: where there is forest the climate is improved for forest regeneration. This

microclimate-mediated feedback offers an alternative explanation for treeline abruptness next to the more commonly recognized effect of fire. Fire also causes positive feedback, because it burns the páramo but not the moist cloud forest.

Treeline history during the Holocene was studied in northern Ecuador. Soil charcoal analysis (anthracology), including taxonomical identification and ^{14}C dating of charcoal fragments, showed that treeline advance after the climatic warming at the start of the Holocene has been slow. The treeline reached its present-day altitude at ca. 3600 m only in the second half of the Holocene. Fires have been part of this ecosystem for at least 13,000 years, but it is unsure whether the early fires occurred naturally or whether they were lit by the early human inhabitants. Fire may be one of the causes of the slow treeline advance, while dispersal limitations and microclimatic establishment limitations may be additional causes.

Patterns of tree establishment and their controls were studied at the same treeline in northern Ecuador. Seedlings of most tree species occurred naturally only in the forest. Seedlings and vegetative ramets of only two tree species, *Gaiadendron punctatum* and *Weinmannia cochensis*, occurred naturally in the páramo. Tree seedlings experimentally transplanted to the páramo had low survival after 2.5 years when exposed to full sunlight (19%), with the exception of seedlings of *Diplostephium* sp. (ca. 80 %). Seedlings transplanted to the forest had high survival both in the thick organic, moss-covered forest soil (67%) and in the artificially exposed mineral soil (74%). In the páramo, artificial shade increased survival to levels similar to survival in the forest (64%; 58% with neighbors removed), while neighbor removal in unshaded plots decreased survival from 44% to 19%. So tree establishment above treeline is hindered by strong solar radiation. I hypothesize that the low night temperatures in the páramo worsen this effect, leading to cold-induced photoinhibition.

This negative effect of radiation was incorporated in a mechanistic spatial model of tree growth, which had the aim of demonstrating how shade dependence and páramo fires can influence treeline position, spatial patterns and dynamics. The model was run on a gradient of minimum temperature under conditions of excess radiation. Additionally, periodic páramo fires could be added and the minimum temperature could be increased through time to simulate climatic warming. Trees positively influenced tree establishment and growth in neighboring sites by providing shade and by protecting them from páramo fires. Both fire and shade dependence of the trees therefore caused positive feedback. If positive feedback occurred, the emergent treelines were more abrupt and shifted more slowly and over smaller distances after warming. This agrees with the observed abruptness in real tropical treelines and with the slow treeline advance during the Holocene. Treelines were positioned at higher altitudes if strong shade was provided and at lower altitudes if trees were less radiation tolerant and if fires occurred.

Finally, forest distribution at the treeline was related to topography in a remote sensing based study using logistic regression. East-facing slopes had lower treelines than west-facing slopes. Eastern slopes also receive high radiation in the morning, when tree seedlings are still cold from the preceding night and hence more sensitive to photoinhibition. This pattern therefore confirms the expectation and model prediction that strong radiation combined with low night temperatures would result in a lower position of the treeline.

In conclusion, the ecological processes that control spatial pattern formation and vegetation dynamics at tropical alpine treelines appear to function through positive feedbacks between vegetation and environment. These feedbacks can be mediated through páramo fires or through the microclimate, in particular through solar radiation and night temperatures. Excess solar radiation after cold nights hinders tree establishment and treeline advance into the páramo. As a consequence, even in the absence of fire, treelines can be abrupt transitions and will respond slowly to climatic changes.

Samenvatting

De alpiene boomgrens, gedefinieerd als de overgangszone tussen bergbos en alpiene vegetatie, kan een geleidelijke overgang zijn, een abrupte grens, of een mozaïek van plantengemeenschappen. De positie van de boomgrens in het landschap verschilt ook per regio. Deze verschillende ruimtelijke patronen worden veroorzaakt door processen die ook bepalend zijn voor de dynamische eigenschappen van de boomgrens, zoals de reactie op klimaat- of landgebruikveranderingen. Ruimtelijke patronen kunnen daarom een aanwijzing geven voor de te verwachten temporele dynamiek van een boomgrens, mits de onderliggende processen goed begrepen worden.

De reden dat boomgrenzen bestaan is nog niet volledig bekend. Hetzelfde geldt voor de oorzaken van de verschillende ruimtelijke patronen, en voor de dynamiek die boomgrenzen in het verleden hebben laten zien of die zij zullen laten zien als gevolg van de huidige versnelde klimaatsveranderingen. Voor tropische alpiene boomgrenzen worden landgebruik en het branden van de páramo (de tropische alpiene vegetatie) vaak als bepalend gezien voor de positie en het patroon van de boomgrens. De rol van andere ecologische processen is daarentegen onbekend, hoewel deze rol erg belangrijk zou kunnen zijn. Het tropische alpiene milieu verschilt op een aantal belangrijke punten van het alpiene milieu op hogere breedtegraden. Aan tropische alpiene boomgrenzen zijn de temperaturen het hele jaar door ongeveer hetzelfde, terwijl de dagelijkse temperatuurschommelingen zeer extreem kunnen zijn; wind en sneeuw spelen meestal geen belangrijke rol; en de soortenrijkdom is veel groter dan die van boomgrenzen in gematigde en boreale streken.

Het doel van dit onderzoek is te begrijpen hoe ecologische processen de ruimtelijke patroonvorming en de vegetatiedynamiek van tropische alpiene boomgrenzen bepalen. Mijn onderzoeksaanpak begint met beschrijvende studies van vegetatiepatronen en -dynamiek, microklimaat en bosverjonging, gevolgd door een experimentele toetsing van hypotheses over de oorzaken van deze patronen. Dit leidde tot een mechanistisch ruimtelijk model van boomgrensdynamiek, waarvan ik de uitkomsten heb vergeleken met de waargenomen boomgrenspatronen en dynamiek, en met de positie van de boomgrens in het landschap.

Ik heb de ruimtelijke structuur van verschillende boomgrenzen bestudeerd in Argentinië, Bolivia, Ecuador en Venezuela, en op Hawaï. De meeste van deze boomgrenzen waren abrupt, met overgangen van páramo naar bos van minder dan 4 meter lang. De bodemtemperatuur en de gemiddelde dagelijkse luchttemperatuur waren hoger boven de boomgrens dan in het bos, en de uiterste temperaturen waren extremer boven de boomgrens. Deze verschillen tussen het microklimaat van het bos en dat van de páramo, en in het bijzonder de lage temperaturen 's nachts in de páramo, zouden een beperking kunnen vormen voor de bosverjonging buiten het bos. Dit zou een positieve terugkoppeling tot gevolg hebben: waar bos staat wordt en gunstig klimaat geschapen voor bosverjonging. Deze door het microklimaat veroorzaakte terugkoppeling is een alternatieve verklaring voor abrupte boomgrenzen, naast het vaker herkende effect van vuur. Vuur veroorzaakt ook een positieve terugkoppeling, doordat het wel in de páramo woedt, maar niet het vochtige mistbos.

De geschiedenis van de boomgrens gedurende het Holoceen hebben we bestudeerd in het noorden van Ecuador. Een analyse van houtskool uit de bodem, namelijk het taxonomisch op naam brengen en ^{14}C dateren van houtskoolfragmenten (anthracologie), liet zien dat de boomgrens na de klimaatopwarming aan het begin van het Holoceen slechts langzaam omhoog is geschoven. De boomgrens heeft zijn huidige hoogte op ca. 3600 m pas bereikt in de tweede helft van het Holoceen. Vuur komt al voor in dit ecosysteem sinds minstens 13,000 jaar, maar het is onbekend of deze vroege vuren een natuurlijke oorzaak hadden of dat ze door mensen werden aangestoken. Vuur kan één van de oorzaken zijn voor het langzame opschuiven van de boomgrens, naast beperkingen in de zaadverspreiding of beperkingen ten gevolge van het microklimaat.

Patronen van bosverjonging en de bepalende factoren hiervoor hebben we bestudeerd aan dezelfde boomgrens in het noorden van Ecuador. Zaailingen van de meeste boomsoorten kwamen van nature alleen voor in het bos. Zaailingen en vegetatieve scheuten van slechts twee boomsoorten, *Gaiadendron punctatum* en *Weinmannia cochensis*, kwamen van nature voor in de páramo. Van de boomzaailingen die experimenteel naar de páramo werden overgeplant leefden er na 2.5 jaar nog maar weinig (19%) als ze bloot stonden aan de volle zon, behalve zaailingen van *Diplostephium* sp. (ca. 80 % overleving). De boomzaailingen die naar het bos waren overgeplant overleefden grotendeels, zowel in de dikke organische, met mos bedekte bosbodem (67%), als in de kunstmatig vrijgemaakt minerale bodem (74%). In de páramo zorgde kunstmatige schaduw voor overlevingspercentages vergelijkbaar met die in het bos (64%; 58% als buurplanten waren verwijderd), terwijl het verwijderen van buurplanten in onbeschaduwde percelen de overleving deed afnemen van 44% tot 19%. Bosverjonging boven de boomgrens wordt dus gehinderd door sterke zonnestraling. Waarschijnlijk wordt dit effect verergerd door de lage nachttemperaturen in de páramo, welke bijdragen aan kougeïnduceerde foto-inhibitie.

Dit negatieve effect van zonnestraling heb ik verwerkt in een mechanistisch ruimtelijk boomgroeimodel, met als doel te laten zien hoe schaduwafhankelijkheid van bomen, en ook branden in de páramo, de positie, het ruimtelijk patroon en de dynamiek van boomgrenzen kan beïnvloeden. Het model werd gerund op een gradiënt van minimum temperatuur, onder condities van zeer hoge zonnestraling. Daarbij konden periodieke branden in de páramo toegevoegd worden, en de minimum temperatuur kon worden verhoogd om opwarming van het klimaat na te bootsen. Bomen hadden een positieve invloed op de vestiging en groei van buurbomen, doordat ze schaduw leverden en bescherming tegen vuur. Zowel vuur als schaduwafhankelijkheid van bomen resulteerden daarom in een positieve terugkoppeling. Als positieve terugkoppeling optrad, waren boomgrenzen abrupter en verschoven ze langzamer en minder ver omhoog na de opwarming. Dit komt overeen met de waargenomen abruptheid van echte tropische boomgrenzen, en met het langzame opschuiven van de boomgrens tijdens het Holoceen. Als bomen veel schaduw gaven lagen boomgrenzen op hogere hoogte, en als bomen minder tolerant waren voor zonnestraling of als er vuur optrad, lagen boomgrenzen op lagere hoogte.

Als laatste hebben we de bosverspreiding aan de boomgrens gerelateerd aan de topografie, met behulp van remote sensing en logistische regressie. oosthellingen hadden lagere boomgrenzen dan westhellingen. Oosthellingen ontvangen vooral ’s ochtends, wanneer planten nog koud zijn van de voorafgaande nacht, sterke zonnestraling, met bijbehorende schade voor eventuele boomzaailingen in de páramo. Dit patroon bevestigt daarom de verwachting en modelvoorspelling dat sterke zonnestraling gecombineerd met lage nachttemperaturen een lagere boomgrens tot gevolg zouden hebben.

Concluderend, de ecologische processen die de ruimtelijke patroonvorming and vegetatiedynamiek aan tropische alpiene boomgrenzen bepalen, lijken te functioneren via positieve terugkoppelingen tussen de vegetatie en haar omgeving. Deze terugkoppeling kan plaatsvinden via páramobranden of via het microklimaat, in het bijzonder via sterke zonnestraling en lage nachttemperaturen. Te veel zonnestraling na een koude nacht hindert de vestiging van jonge bomen en het opschuiven van de boomgrens de páramo in. Als gevolg hiervan kunnen boomgrenzen, zelfs als de páramo niet gebrand wordt, abrupte overgangen zijn, en zullen zij langzaam reageren op klimaatsveranderingen.

Resumen

La transición entre el bosque montano alto y la vegetación alpina puede ser una transición gradual, un límite abrupto, o un mosaico de parches de vegetación. La posición de este límite de bosque en el paisaje también varía según la región. Estos diferentes patrones espaciales son causados por procesos que también determinan las propiedades dinámicas del límite de bosque, como por ejemplo su reacción frente a cambios climáticos o cambios en el uso de tierra. Por lo tanto, los patrones espaciales pueden servir para indicar la dinámica temporal que un límite de bosque pueda mostrar, si es que se comprenden bien los procesos que causan estos patrones.

Las razones por las cuales el bosque tiene un límite altitudinal no se conocen completamente todavía. Tampoco se conocen bien las causas de los diferentes patrones espaciales, o la dinámica que hayan mostrado los límites de bosque en el pasado o que mostrarán como resultado de los actuales cambios climáticos acelerados. Para límites de bosque en montañas tropicales el uso de la tierra por el hombre y las quemas de los páramos (la vegetación alpina tropical) se nombran frecuentemente como determinantes de la posición y de los patrones espaciales de los límites de bosque. Por otra parte, el papel de otros procesos ecológicos no se conoce, a pesar de que este papel puede ser importante. El ambiente alpino en el trópico se distingue de algunas maneras importantes del ambiente alpino en latitudes más altas. En el límite de bosque tropical no existe casi la estacionalidad térmica durante el año, mientras que las fluctuaciones diurnas de la temperatura pueden ser extremas; el viento y la nieve generalmente no son importantes; y la riqueza de especies es mucho más elevada que en los límites de bosque templados o boreales.

Esta investigación tiene como objetivo entender como los procesos ecológicos controlan la formación de patrones espaciales y la dinámica de la vegetación en límites de bosque en montañas tropicales. El método utilizado comenzó con estudios descriptivos de los patrones y la dinámica de la vegetación, del microclima y de la regeneración de árboles, seguido por una prueba experimental de las hipótesis sobre las causas de estos patrones. De ello surgió un modelo mecanístico espacial de la dinámica del límite de bosque, el cual se evaluó con los patrones y con la dinámica observados, y con la posición del límite de bosque en el paisaje.

La estructura espacial de varios límites de bosque se investigó en Argentina, Bolivia, Ecuador, Venezuela y Hawai. La mayor parte de estos límites fue muy abrupta, las transiciones de páramo a bosque fueron menores de 4 m. Las temperaturas del suelo y las temperaturas medias diarias del aire

fueron más altas encima del límite que en el bosque, y las temperaturas extremas fueron más pronunciadas encima del límite. Las diferencias entre el microclima del bosque y él del páramo, y en particular las bajas temperaturas nocturnas en el páramo, pueden constituir una restricción para la regeneración de los árboles fuera del bosque. Esto causaría una retroalimentación positiva: donde hay bosque el microclima es mejorado para la regeneración del bosque mismo. Esta retroalimentación mediada por el microclima ofrece una explicación alternativa para el patrón abrupto de los límites de bosque, además que el más reconocido efecto del fuego. El fuego causa otra retroalimentación positiva, porque quema el páramo, pero no el bosque de niebla húmedo.

La historia del límite de bosque durante el Holoceno se investigó en el norte de Ecuador. Un análisis de carbón recuperado del suelo (anthracología), incluyendo la identificación taxonómica y una datación ^{14}C de fragmentos de carbón, mostró que el avance del límite de bosque durante el Holoceno ha sido lento. El límite alcanzó su altitud actual a aprox. 3600 m sólo en la segunda mitad del Holoceno. El fuego ha sido parte de este ecosistema desde hace por lo menos 13,000 años, pero no se sabe si las quemas tempranas se han dado naturalmente o si han sido provocados por los habitantes. Las quemas pueden ser una de las causas del lento avance del límite de bosque, mientras que limitaciones en la dispersión también que limitaciones microclimáticas para el establecimiento de árboles pueden ser causas adicionales.

Se estudiaron los patrones de establecimiento de renuevos y sus causas en el mismo límite de bosque en el norte de Ecuador. Renuevos de la mayoría de las especies se dieron naturalmente sólo en el bosque. Renuevos y retoños vegetativos de sólo dos especies, *Gaiadendron punctatum* y *Weinmannia cochensis*, se dieron naturalmente en el páramo. De los renuevos transplantados experimentalmente al páramo pocos (19%) sobrevivieron después de 2.5 años cuando estaban expuestos plenamente a la radiación del sol, con la excepción de *Diplostephium* sp. (c. 80 %). De los renuevos transplantados al bosque la mayoría sobrevivió, tanto en el suelo orgánico grueso y cubierto con musgo del boque (67%) como en el suelo mineral artificialmente descubierto (74%). En el páramo, la sombra artificial aumentó la supervivencia hasta niveles parecidos a los del bosque (64%; 58% cuando se quitó la vegetación vecina), mientras la eliminación de la vegetación vecina en rodales sin sombra disminuyó la supervivencia de 44% a 19%. Entonces el establecimiento de árboles encima del límite de bosque se limita a causa de la fuerte radiación solar. Mi hipótesis es que este efecto se empeora con el frío de las noches en el páramo, causando fotoinhibición por baja temperatura.

Este efecto negativo de la radiación fue incorporado en un modelo mecanístico espacial del crecimiento de árboles, con el objetivo de demostrar cómo la dependencia de la sombra y quemas en el páramo pueden influir en la posición, los patrones espaciales y la dinámica de los límites de bosque. Se corrió el modelo en un gradiente de temperatura mínima, bajo condiciones de radiación excesiva. Además, se podrían añadir quemas en el páramo, y la temperatura mínima se podía aumentar para simular un calentamiento climático. Los árboles tenían una influencia positiva sobre el establecimiento y el crecimiento de árboles vecinos, porque ofrecieron sombra y protección de las quemas del páramo. Por eso las quemas así como la dependencia de la sombra de los árboles causaron una retroalimentación positiva. Si se dio una retroalimentación positiva, los límites de bosque que surgieron eran más abruptos, y avanzaron menos y más lentamente después del calentamiento. Esto está de acuerdo con las observaciones que la mayoría de los límites de bosque tropicales son abruptos y que el avance del límite durante el Holoceno ha sido lento. La posición de los límites era más alta si hubo sombra fuerte, y más bajo si los árboles fueron menos tolerante a la radiación y cuando hubo quemas.

Finalmente, se relacionó la distribución de bosque alrededor de su límite con la topografía, en un estudio en base de sensores remotos y usando una regresión logística. Las laderas dando al Oriente tenían límites de bosque más bajos que las laderas dando al Occidente. Laderas dando al Oriente también reciben una alta radiación en las mañanas, cuando las plantas están todavía fríos de la noche anterior y cuando están entonces más sensibles a la fotoinhibición. Este patrón entonces confirma la expectativa y la predicción del modelo que la radiación fuerte combinado con bajas temperaturas nocturnas resultaría en una posición del límite de bosque más bajo.

En conclusión, los procesos ecológicos que controlan la formación de patrones espaciales y la dinámica de la vegetación en límites de bosque en montañas tropicales parecen funcionar por medio de retroalimentaciones positivas entre la vegetación y su ambiente. Estas retroalimentaciones pueden ser mediadas por las quemas en el páramo o por el microclima, sobre todo por radiación solar y temperaturas nocturnas. Radiación solar excesiva después de una noche fría restringe el establecimiento de árboles y el avance del límite de bosque hacia el páramo. Como consecuencia, aún cuando no se quema el páramo, los límites de bosque pueden ser abruptos y responderán lentamente a cambios climáticos.

Acknowledgements

Curriculum Vitae

Publication list

PE&RC Education certificate

Photo previous page: wonderful accomodation, Guandera, Ecuador

Photo: Rolando and his nephew Bernardino packing up camp, Keara, Bolivia

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Photo: Me at the treeline in Boca del Monte, Venezuela.

Curriculum Vitae

I was born in The Netherlands on April 13th 1975 and named Maaike Bader[1], and I lived in the flower-growing village of Kudelstaart until I was 18. After leaving highschool (VWO, Alkwin Kollege, Uithoorn) in 1993 I spent one year traveling and working on various farms in New Zealand and Australia before starting to study Biology at the then Wageningen Agricultural University. After receiving my 'propedeuse' (first year) diploma in 1995, I left for New Zealand for another year and worked on a farm. From when I continued studying Biology in 1996 untill now I have been a student, doing Biology (Ir. degree, equivalent to MSc) and Geo-information Science (MSc), graduating *cum laude* for both in November 2001, and continuing shortly afterwards writing the proposal for this PhD, all at Wageningen University.

During my MSc studies I wrote four research theses and I did a short internship. During the internship I assisted in a research on ant gardens (arboreal ant nests with epiphytic plants growing on them) in the Amazon rain forest in Colombia. My first thesis dealt with the ecology and spatial distribution of vascular epiphytes in a secondary cloud forest in the Colombian Andes. I extended this thesis with a study into the use of GIS for analyzing epiphyte data, which lead to my first scientific publication. I then wrote a thesis in central Australia, with the CSIRO Centre for Arid Zone Research, about the possibility of using spatial and temporal variability in vegetation productivity, derived from satellite images, to predict biodiversity in the semi-arid ecosystem around Alice Springs. My last MSc thesis, at the Instituto Manantlán de Ecología y Conservación de la Biodiversidad, Universidad de Guadalajara, was a ethno-ecological study about people's use and perceptions of riverside vegetation in an indigenous community in central Mexico.

From 2002 to 2006 I worked on this PhD thesis at the Centre for Geo-information of Wageningen University and Research Centre. In this research on tropical alpine treelines I have used a variety of methods, including vegetation descriptions in the field, field experiments with tree seedlings, microclimatological measurements, mechanistic spatial modeling, remote sensing, GIS, statistical modeling, and the palaeo-ecological interpretation of soil charcoal. I did fieldwork for about a year altogether in the Andes (Ecuador, Bolivia, Argentina, Venezuela) and for a few weeks in Hawaii (Maui). I also twice visited the Laboratorio de Ecologia Applicata of the University 'Federico II' in Naples (Italy), to learn modeling using the software 'Simile' and to write Chapter 3 of this thesis.

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[1] I added the Y. in 'Maaike Y. Bader' so that my publications will be distinguishable in the databases; it turns out there are a lot of other M. Baders in science.

Publication list (updated March 2008)

Bader, M., H.J.F. van Dunné & H.J. Stuiver 2000. Epiphyte distribution in a secondary cloud forest vegetation; a case study of the application of GIS in epiphyte ecology. *Ecotropica* 6: 181-195.

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

Bader, M.Y., M. Rietkerk & A.K. Bregt 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic, Antarctic, and Alpine Research* 39: 353-364.

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

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

Bader, M.Y., M. Rietkerk & A.K. Bregt. A simple spatial model exploring positive feedbacks at tropical alpine treelines. *Arctic, Antarctic, and Alpine Research* (in press 2008)

Zotz, G. & M.Y. Bader. Epiphytic plants in a changing world; Global change effects on vascular and non-vascular epiphytes. *Progress in Botany* (in press 2008)

PE&RC PhD Education Statement Form

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities).

Review of Literature (4 credits)
- Spatio-temporal modelling of treeline dynamics (2002)

Writing of Project Proposal (5 credits)
- Spatio-temporal modelling of treeline dynamics (2002)

Post-Graduate Courses (4 credits)
- The art of modelling. PE&RC-SENSE (2004)
- Theoretical ecology. SENSE (2005)
- Plant ecophysiology. Functional Ecology (2005)

Deficiency, Refresh, Brush-up and General Courses (3 credits)
- Ecosystem modelling. Utrecht University (2004)
- Scientific writing. PE&RC (2005)
- Writing a grant proposal. Functional Ecology (2006)

PhD Discussion Groups (3 credits)
- Forest and conservation ecology (2002-2006)
- Statistics, maths and modelling in production ecology and resource conservation (2004-2006)

PE&RC Annual Meetings, Seminars and Introduction Days (1 credit)
- Introduction weekend. PE&RC (2003)
- PE&RC days (2002 and 2005)

International Symposia, Workshops and Conferences (4 credits)
- RMA World conference on natural resource modelling. (Lesbos, Greece, 2002)

- Second GMBA symposium on ‘Linking mountain diversity with fire, grazing and erosion’ (La Paz, Bolivia, 2003)
- Second international symposium, ‘Mountains in the mist: science for conserving and managing tropical montane cloud forest’ (Waimea, Hawaii, 2005)
- Open science conference: Global change in mountain regions (Perth, Scotland, 2005)

Laboratory Training and Working Visits (3 credits)

- Modelling and writing paper: Laboratorio di Ecologia Applicata, Dipartimento di Arboricoltura, Botanica e Patologia Vegetale, Università degli Studi di Napoli ‘Federico II’. (2003 and 2006)

Photo: Traditional transportation by llama train on the road to Keara, Bolivia.

Cover photo: treeline at Boca del Monte, view north towards the Sierra Nevada de Mérida, Venezuela
Cover design: Maaike Y. Bader
Photo Andean bear (p. -3): James Clare, Cuenca, Ecuador
Photo wood structure (p. 50): Stefania Impagliazzo, Portici, Italy
All other photos: Maaike Y. Bader