

Treeline and vegetation dynamics in response to environmental changes in Nepal, the central Himalaya

Krishna Babu Shrestha

Dissertation for the degree of philosophiae doctor (PhD)
at the University of Bergen, Norway
2013



UNIVERSITET I BERGEN

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Prof. Ole Reidar Vetaas, University of Bergen, Norway



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In memory of my
Late father: Youbak Lal Shrestha
&
Late mother: Yob Kumari Shrestha



Treeline at Ngawal, Manang



Pinus wallichiana tree



Treeline at Lauribinayak, Rasuwa



Abies spectabilis tree



Quercus semecarpifolia forest at Ghorepani



Quercus semecarpifolia tree

Cover photos showing forests studied (left panels) and the corresponding individual trees (right panels). Top four photos by Krishna Shrestha, bottom two photos by Inger Måren

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Abstract

Shrestha, K. B. 2013. Treeline and vegetation dynamics in response to environmental changes in Nepal, the central Himalaya. Ph.D. Thesis, Faculty of Science, University of Bergen, Norway.

Aims: To describe and evaluate patterns of vegetation response to ongoing environmental changes across climate-limited (alpine treeline ecotone) and human-modified (temperate Himalayan oak forests) ecosystems in Nepal, central Himalaya.

Methods: I used dendroclimatological techniques to examine spatial and temporal changes in tree growth responses (paper I) and recruitment patterns (paper II) to climatic variability across a dry *Pinus wallichiana* and a mesic *Abies spectabilis* treeline ecotone. Trees from various ecological elevations (forest line, treeline and krummholz line) were cored, annual growth was measured and site chronology was developed for analysing climate-growth relationships. Transects were laid out between the forest line and tree species line, crossing the treeline. Seedlings, saplings and trees were sampled in each transect for age analysis.

Alpha, beta and gamma diversity were studied across a forest border from a forested to open landscape in a subalpine-alpine region (paper III) and an anthropogenic disturbance gradient (paper IV). Vascular plant species richness and environmental variables were recorded in each plot (10 m × 10 m). Alpha diversity was estimated as average species richness per plot. Beta diversity was based on gradient length estimated by Detrended Correspondence Analysis (DCA). Gamma diversity was estimated as total species number present in the landscape.

Main results: At the dry locality, tree growth at the forest line responded positively to warm summers and after cold winters: possibly a response to early onset of growing season. At the mesic locality, growth at lower altitudes (forest line) showed signals of drought limitation, whereas at higher altitudes, decreased growth was associated with an early onset of the monsoon. Reduced growth at the treeline was related to the high winter snow fall and delayed onset of growing season.

The current treelines in both areas have remained stationary over the decades. Climate and land-use are both important factors for treeline structuring processes.

Number of trees and saplings in the dry area is higher compared to the mesic area suggesting that tree establishment rate is higher in the dry area giving a higher potential for treeline advance.

In a set of vertical transects sampled across the forest line, a positive correlation between canopy and temperature gradients was found. Detrended Correspondence Analysis revealed low species turnover and a continuum in species composition across the forest border ecotone. The low species turnover and minor differences in alpha diversity could be attributed to human influence. Furthermore, in differently disturbed *Quercus semecarpifolia* forest at Phulchoki and Ghorepani, alpha and gamma diversity show a unimodal response to disturbance gradient. Linear relationships were observed between beta diversities (β_{SD} and β_A) and disturbance gradient.

Conclusion: Climate signals in the pattern of tree growth responses and recruitment are site-specific. Both growing season as well as non-growing season climate factors are important drivers for vegetation changes, but they vary between study areas, with altitude and with time scale (whole time-periods vs. decadal periods). Species diversity changes along environmental gradients with spatial as well as temporal scales.

Further perspective: The Himalaya are under-represented in studies of vegetation-climate relationships. The main reason is logistic challenges and lack of reliable climate data from desired locations. Future research of a similar nature to the present study should include more than one species sharing the same environment, and investigate these same species in various geographic regions and ecological settings. Impacts on the ecosystem level can be investigated by quantifying and examining species diversity and other ecosystem level responses (e.g. carbon sequestration).

Keywords: Alpha-diversity, beta-diversity, climate change, dendrochronology, dendroclimatology, disturbance, diversity, ecotone, environmental change, forest line, gamma-diversity, land-use, mass effect, species richness, tree-ring, treeline

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Last but not least, I would like to dedicate this thesis to my late parents who raised and educated me; but especially my wife Kalpana Shrestha for her constant and untiring support. She became outstandingly able to hold all the family responsibility during this work. Finally, acknowledgement is due to my son Dibas, who always felt proud of me for pursuing this study.

List of papers

*My thesis is based on the following four scientific research papers; hereafter referred to by their roman numerals (Papers I-IV). Papers III & IV are reproduced with the kind permission of **Folia Geobotanica** and **International Journal of Biodiversity Science, Ecosystem Services & Management** respectively.*

Paper I

Shrestha, K. B., Hofgaard, A. and Vandvik, V. Tree growth response to climatic variability in two climatically contrasting treeline ecotone areas, central Himalaya, Nepal. *Canadian Journal of Forest Research* (submitted)

Paper II

Shrestha, K. B., Hofgaard, A. and Vandvik, V. Treeline dynamics in dry and mesic areas of Nepal, central Himalaya. *Journal of Plant Ecology* (to be submitted)

Paper III

Shrestha, K. B. and Vetaas, O. R. (2009): The forest ecotone effect on species richness in an arid trans-Himalayan landscape of Nepal. *Folia Geobotanica* **44**, 247-262.

Paper IV

Shrestha, K. B., Måren, I. E., Arneberg, E., Sah, J. P. and Vetaas, O. R. (2013): Effect of anthropogenic disturbance on plant species richness in oak forests in Nepal, central Himalaya. *International Journal of Biodiversity Science, Ecosystem Services & Management* **9**, 21-29.

Declaration

Paper I

Shrestha, K. B., Hofgaard, A. and Vandvik, V. Tree growth response to climatic variability in two climatically contrasting treeline ecotone areas, central Himalaya, Nepal. *Canadian Journal of Forest Research* (submitted)

Krishna B. Shrestha	Experimental design, field work, data processing, statistical analysis, wrote the paper
Annika Hofgaard	Experimental design, discussion on data, interpretation, co-writing, editing
Vigdis Vandvik	Discussion on data, interpretation, co-writing, editing

Paper II

Shrestha, K. B., Hofgaard, A. and Vandvik, V. Treeline dynamics in dry and mesic areas of Nepal, central Himalaya. *Journal of Plant Ecology* (to be submitted)

Krishna B. Shrestha	Experimental design, field work, data processing, statistical analysis, wrote the paper
Annika Hofgaard	Experimental design, discussion on data, interpretation, co-writing, editing
Vigdis Vandvik	Discussion on data, interpretation, editing

Paper III

Shrestha, K. B. and Vetaas, O. R. (2009): The forest ecotone effect on species richness in an arid trans-Himalayan landscape of Nepal. *Folia Geobotanica* **44**, 247-262.

Krishna B. Shrestha	Field work, data processing, statistical analysis, wrote the paper
Ole R. Vetaas	Experimental design, editing

Paper IV

Shrestha, K. B., Måren, I. E., Arneberg, E., Sah, J. P. and Vetaas, O. R. (2013): Effect of anthropogenic disturbance on plant species richness in oak forests in Nepal, central Himalaya. *International Journal of Biodiversity Science, Ecosystem Services & Management* **9**, 21-29.

Krishna B. Shrestha	Field work, data processing, statistical analysis, wrote the paper
Inger E. Måren	Field work, data processing, editing
Ellen Arneberg	Field work, data processing
Jay P. Sah	Experimental design, editing
Ole R. Vetaas	Experimental design, editing

Introduction

A major concern of present-day vegetation ecology is to explore the impact of ongoing global environmental changes on various ecosystem structures and functions. Climate change and human land-use change are two important global change drivers, and there are feedbacks and links between these two forcings (Bonan 2002; Huntley & Baxter 2005). A central aspect of climate change is the warming of Earth's surface with a reported increase in global mean surface air temperature of 0.74°C over the 20th century. This trend is predicted to continue for the 21st century and one ecologically important aspect of this change is high inter-annual as well as inter-decadal variability (IPCC 2007). Societal, technological and economical changes of human civilization have influenced human activities over the millennia, and is now a major forcing of changes in the world's biota (Bonan 2002; Körner *et al.* 2006).

Vegetation shows changes at all organizational levels (from individuals to ecosystems) in response to climate change; but responses vary according to spatial (local, regional, global) and temporal scale (decadal to millennial) (see Huntley & Baxter 2005). At the individual level, species respond through changes in growth and life-cycle characteristics, whereas at the population level they respond through recruitment and mortality patterns. The response at a community level is observed in changes in the density and distribution range of constituent species and also in species diversity (Pickett & White 1985). Depending upon the sensitivity and ability of species to respond to climate change, novel communities may evolve (Thomas *et al.* 2004; Araújo & Pearson 2005).

The main part of this Ph.D. is a study of an alpine treeline ecotone, characterized as a conspicuous and highly temperature-sensitive boundary between the subalpine forest and alpine vegetation zones (Körner 1998; Körner 2003; Körner & Paulsen 2004). Ecosystems in this zone are relatively natural, hence any recent or past changes in environment are reflected conspicuously in terms of vegetation responses (Germino *et al.* 2002; Dullinger *et al.* 2004; Holtmeier & Broll 2005; McDonald *et al.* 2006). The sensitivity of plant species to changes in temperature is high across this ecotone but species also respond to changes in other abiotic factors (e.g. radiation,

moisture, wind, slope exposure, topography) (Holtmeier & Broll 2005; Wang *et al.* 2005; Wang *et al.* 2006; Li *et al.* 2008; Aune *et al.* 2011).

Long-lived tree species preserve records of past changes in their environment in the form of tree-rings, but different species may respond to different specific environmental cues, and the response of trees of the same species may vary among populations growing under different environmental settings (Bekker 2005; Carrer *et al.* 2007). Change in population structure in response to altered environmental conditions can also be observed, for example, in the upward shift of the treeline or forest encroachment into the open alpine area (Danby & Hik 2007; Batllori & Gutiérrez 2008; Harsch *et al.* 2009). Increased seedling and sapling density with increased temperature gives potential ground for such vegetation changes (Luckman & Kavanagh 2000; Daniels & Veblen 2004; Hofgaard *et al.* 2009). However, the upward shift of the treeline is not a universal phenomenon, since stationary as well as recessing treelines have also been documented (Harsch *et al.* 2009). If the treeline shifts upward or forest expands towards open (alpine) area, it is often assumed that community composition is altered either by loss of habitat area or change of habitat location (Keller *et al.* 2000; Grace *et al.* 2002; Dirnböck *et al.* 2003; Kullman 2004; Walther *et al.* 2005). Scherrer & Körner (2010) point out that changes in some climate factors (e.g. precipitation regime) may influence plant species distribution, and certain habitat types may become reduced, although biodiversity as such may be less endangered by climate change in an alpine landscape. Thus, in general, it is uncertain whether an upward shift of the treeline ecotone will have negative impacts on plant species diversity.

The Himalaya, climate and vegetation changes

The monsoon-dominated climate of the greater Himalayan region shows great spatial and temporal variability due to the extreme topography and high folded mountains. In this region, mountains act as barriers against the atmospheric circulation of the summer monsoon, and the distribution of rainfall shows high variability with elevation and slope. Inner valleys receive much lower rainfall than the outer mountain slopes (Chalise & Khanal 2001). At high altitudes (>3000 m.a.s.l.) a major portion of annual precipitation falls as snow. In Nepal, the summer monsoon brings down-pours from

June to September (Chalise & Khanal 2001). The Himalaya are experiencing a noticeable warming this century and the rate is higher than the global average (Hingane *et al.* 1985; Shrestha *et al.* 1999; New *et al.* 2002; Gao *et al.* 2004; IPCC 2007). The average temperature in Nepal has increased by 0.6°C from 1976 to 2005 which corresponds to an annual average increase of 0.02°C (Practical Action 2009). The rate of warming in Nepal is progressively greater with elevation (New *et al.* 2002).

This climatic complexity provides opportunities for studying variability in the relationships between the processes of climate and vegetation changes in climatically contrasting treeline ecotones within the same geographical region. Tests of hypotheses explicitly linking vegetation response to climatic variability are underrepresented in studies from the high elevation areas of the Himalaya (but see; Sano *et al.* 2005; Bhattacharyya *et al.* 2006; Singh *et al.* 2006; Shah *et al.* 2009; Tenca & Carrer 2010; Borgaonkar *et al.* 2011). Practices such as summer grazing in subalpine pastures of this region may also influence the original treeline ecotone (Beug & Miede 1999; Schickhoff 2005). Furthermore, a typical pattern of agriculture in the Middle Hills area of Nepal Himalaya is the extensive use of forests for timber, fodder, and litter, which can largely modify the forest ecosystem (Singh & Singh 1987; Måren & Vetaas 2007). Given this context, a study focusing on vegetation response to climate and land-use change will contribute to our understanding of how species and biological systems respond to ongoing environmental changes in these areas.

Objectives

This research aims to contribute to our understanding of vegetation responses to a changing environment across two ecosystems; one from a climate-sensitive semi-natural ecosystem across two alpine treeline ecotones representing a dry and a mesic environment, and another from a human-modified ecosystem across disturbed oak forests in the Middle Hills area of Nepal, central Himalaya. The broad topic underlies the specific questions raised in papers I-IV.

(a) Climatic variability over the past decades as a driving force for vegetation changes across space and time

Paper I: Growth dynamics

- Evaluate response patterns of tree growth to climatic variability along the elevation gradient across an alpine treeline ecotone, and between climatically different areas (dry vs. mesic environments).
- Understand patterns of variation in tree growth responses over time (e.g., between decadal periods), and evaluate driving forces for such variability.

Paper II: Population dynamics

- Assess establishment time of the current treeline in two study areas, and examine area-specific treeline development processes.
- Evaluate recruitment patterns, age structures, and height growth as indicators of treeline advance as predicted for the region.

(b) Environment and human land-use as a driving force of community changes in space and time

Paper III: Community dynamics

- Test if species richness declines with increasing elevation across a treeline ecotone as predicted from coarse-scale data.
- Evaluate if species richness is enhanced in the middle of the ecotone as an ecotone effect.

Paper IV: Community dynamics along a disturbance gradient

- Assess the effect of anthropogenic disturbance on different measures of plant species diversity.
- Evaluate variations in relationships between disturbance gradient and different diversity measures.

Treeline: pattern, processes and terminologies

The treeline is generally considered to be the highest elevation at which a single upright tree with height greater than 2 m can be found within a landscape (Hofgaard 1997; Körner 2003), although there is no one conventional definition available. The causal factors for treeline formation are also uncertain although various theories and explanations have been proposed. Generally, the treeline is believed to be set by heat deficiency (Körner 2003). Insufficient air and soil temperatures during the growing season adversely affect growth, regeneration, and survival and thus limit the establishment of trees. Several thermal indicators have been proposed as a global driver of treeline elevation: the 10°C isotherm of mean monthly temperature of the warmest month (see Daubenmire 1954; Troll 1973), growing season length of approximately 100 days (Ellenberg 1963), and mean growing season temperature of 5.5–7.5°C (Körner & Paulsen 2004). On a regional scale, aspect and topography along with other climatic and biotic factors (altitudinal temperature gradient, climate variability, diseases, insect infestations etc.) act as treeline determinants (Holtmeier & Broll 2005). However, determining the exact location of, and the factors that determine, the treeline on a local scale is rather difficult since various micro-climatic factors entangle with regional and global drivers (Körner 1998; Körner 2003). Various types of treelines have been proposed, such as climatic (temperature), orographic and edaphic (soil), and anthropogenic (human) (Holtmeier & Broll 2005).

Various bioclimatic border zones can be defined (not an exact ‘line’; see Körner 2003) in a forest alpine transition zone of the Nepal Himalaya. I use the term ‘forest line’ as a synonym for timberline (Körner 2003) for the border zone between closed forest and open landscape beyond the uppermost elevations of closed stands of trees (> 2 m height; Hofgaard 1997). In paper III, I refer to this border zone as a ‘forest ecotone’ or ‘forest line ecotone’. In this study, the forest patch of 0.1 ha with > 50 % canopy cover was considered as forest (Shrestha & Vetaas 2009).

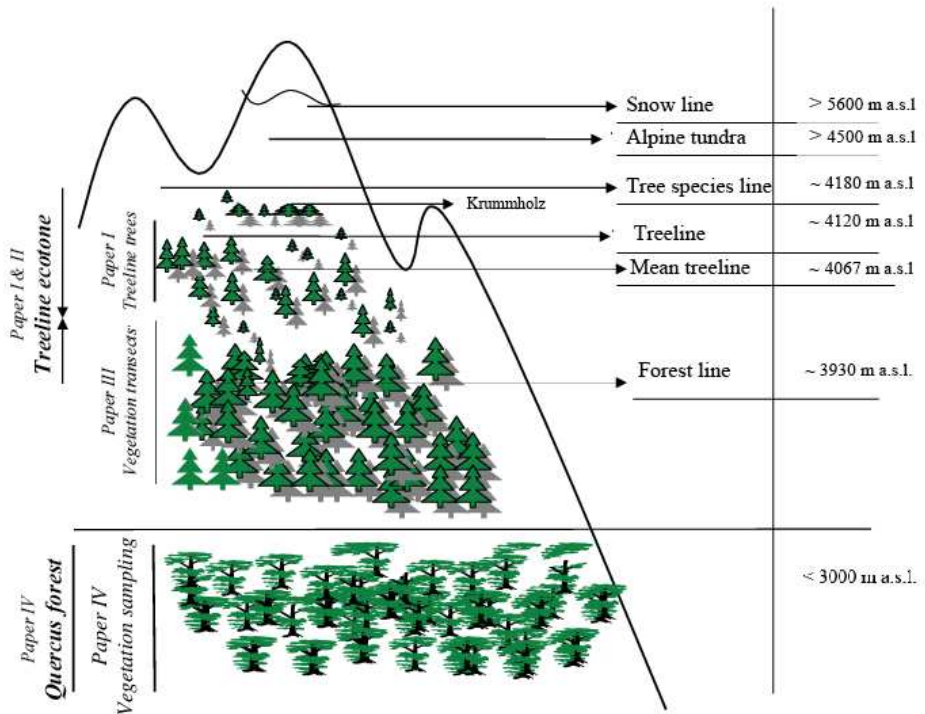


Figure 1. Schematic representation of the study design (after Körner & Paulsen 2004). Approximate elevational positions from the study area at Ngawal (dry area) are shown for the different eco-regions across the treeline ecotone.

As mentioned above (also see Fig. 1), the elevation of the uppermost occurring tree individual (>2 m; Daubenmire 1954; Hofgaard 1997); was set as the treeline in this study. Above the treeline, is a zone where tree species individuals do exist but they do not reach upright stature and are present in a stunted and twisted form less than 2 m in height. These forms of trees are known as krummholz and their structure is considered to be an adaptive feature under the harsh weather and severe winds of an alpine environment (Körner 2003). The uppermost individual of a tree species, regardless of its growth form (normally it is a seedling), defines the tree species line (Körner & Paulsen 2004). This is the border line beyond which alpine area starts. Thus, the treeline ecotone covers a whole transition zone from closed forest to alpine areas; this is a well known temperature limited ecotone (Gosz & Sharpe 1989).

Alpine treeline in Nepal Himalaya

The Himalayas, the highest mountain chain of the world, passes through Nepal. The vast chain extends from north-west to south-east in a massive arc for about 2500 km covering an area of 612,021 km² (Singh & Singh 1992) along the northern fringes of the Indian sub-continent bracketed by the Indus River in the west and the Brahmaputra River in the east. The Tibetan plateau lies north of this mountain belt. As well as Nepal, the Himalaya cover parts of Bhutan and the Indian states of Sikkim, Himachal Pradesh, and Jammu–Kashmir.

Nepal has a bioclimatic elevation ranging between the tropical zone at lowland Terai (60 m) and the alpine zone above 4500 m. It is one of the longest bioclimatic elevation gradients in the world (see also; Vetaas & Grytnes 2002). The subalpine vegetation zone in Nepal generally starts at elevations around 3000 m and extends up to around 4500 m.a.s.l., depending upon aspect and geographic regions. Treeline elevations in the Nepal Himalaya vary between ~3600 m and ~4500 m and increase by 130 m per degree decrease of latitude (Körner 2003; Schickhoff 2005). Increase of treeline elevation with the decrease of latitude is a global phenomenon (Salisbury & Ross 1992; Körner 2003) but variations in treeline elevations within Nepal follow particular Himalayan patterns (Schickhoff 2005). Many drivers that cause variations in the treeline such as aspect, prevailing winds, and soil quality (Daubenmire 1954) vary extremely over short geographical distances in the Himalayan mountain system.

Furthermore, treeline elevations in the Himalayas are likely to be affected by the increase in continentality and large mountain mass effect (Daubenmire 1954; Schickhoff 2005; Richardson & Friedland 2009). The high mountain chains often act as topographic barriers against moist air masses causing decrease of annual precipitation and cloudiness which is coupled with more sunshine leading to higher summer temperatures. This phenomenon causes the treeline to be found at higher elevations and is known as Massenerhebungseffekt (Körner 2003; Schickhoff 2005). The monsoon-dominated climate creates an east to west precipitation gradient maintaining a drier environment in the west. The monsoon brings moisture-laden southerly winds and causes heavy precipitation between May/June and September across the country. However, mountain barriers create high local variation in precipitation patterns over a short geographical range with the rain-shadow effect causing limited rainfall in many places of the country (viz, dry Ngawal).

Generally, the treeline ecotone on moist northern slopes is dominated by shade-tolerant tree species such as *Abies spectabilis*, *Betula utilis*, and *Rhododendron campanulatum* but on dry southern slopes, light-demanding species such as *Pinus wallichiana* and *Juniperus* spp. are dominant (Vetaas & Grytnes 2002; Schickhoff 2005). The treeline on southern slopes reaches higher elevations compared to that on northern slopes indicating a higher climatic limit as well as higher snowline elevations on the southern slopes. Above the treeline, a harsh alpine climate allows only scrub vegetation. This zone, however, has been used as summer pasture land in Nepal which might modify the treeline elevations (Miehe 1997; Beug & Miehe 1999; Schickhoff 2005).

Anthropogenic disturbance and effect on plant species diversity

Just below the subalpine area of the Himalayas, we find the Middle Hills ranging between 2000 m and 3000 m.a.s.l. *Quercus semecarpifolia* trees from this belt are heavily lopped for green fodder during the dry season (November-March). This practice severely affects the morphology, health, and regeneration ability of trees and alters the forest ecosystem (Mahat *et al.* 1986; Thadani & Ashton 1995; Måren & Vetaas 2007). In this human-modified ecosystem, I examined impacts of land-use on plant species diversity by evaluating different measures of diversity. Species richness

was estimated in terms of alpha (α ; within habitat) and gamma (γ ; total number of species in the landscape) diversity. Species turnover in the changing landscape (different levels of disturbance) was estimated in terms of beta (β ; between habitat) diversity.

The study areas and their climate

The four study areas included in this thesis are from central Nepal (Fig. 2). Ngawal (DRY, paper I & II) is a part of the trans-Himalayan arid zone and is located in the upper part of the U-shaped Manang valley (28°41'N and 84°00'E) in north-central Nepal (Stainton 1972). The valley is situated south of the Tibetan plateau and is surrounded by many mountain ridges and steep slopes. The climate is characterized by warm dry summers with frequent strong winds, which produce xeric conditions. The annual mean temperature and annual precipitation of Chame (2680 m.a.s.l.; ~17 km from Ngawal) averaged for 1985-2005 are 10.7°C and 934.4 mm, respectively.

Lauribinayak (MES, paper I & II) is situated in the Langtang valley in Rasuwa district (28°07'N, 85°21'E), near the Tibetan border (Ono & Sadakane 1986). This is a valley drained by Langtang Khola river (a tributary of Bhotekoshi-Trishuli Gandaki river). Climate data available from Dhunche (1982 m.a.s.l.; ~ 5 km from Lauribinayak) show that the annual mean temperature and annual precipitation are 15.4°C (1995-2005) and 1491 mm (1985-2005), respectively. Lauribinayak is more mesic than Ngawal with greater precipitation and cooler temperatures. Snow is common in the winter and lasts for about five months (November-March) in both study areas.

Phulchoki (27°35'N, 85°24'E) and Ghorepani (28°25'N, 83°45'E) (paper IV) represent the Middle Hills region in Nepal and are situated in the temperate monsoonal climatic zone of the Indian subcontinent. In these areas, a major part of the annual precipitation falls during the monsoon period. Phulchoki is warmer (summer; 26.3°C) than Ghorepani (summer; 20.5°C), whereas Ghorepani receives much higher rainfall than Phulchoki (2860 vs. 1870 mm; Shakya 1985; Practical Action 2009).

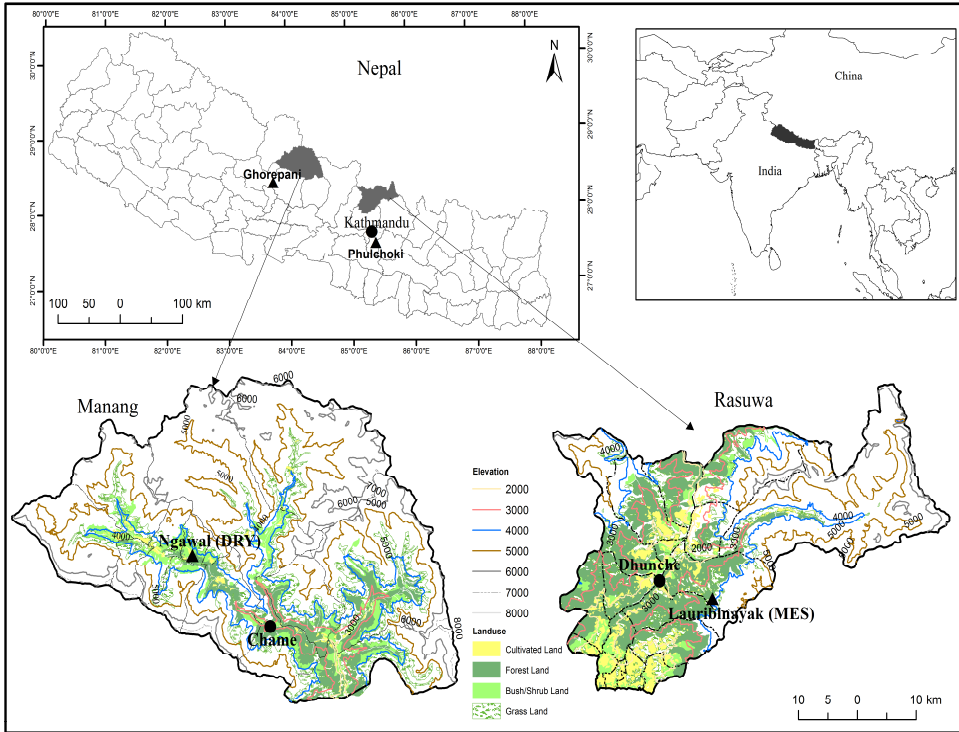


Figure 2. Maps showing the study locations and climate stations used in this thesis in Nepal: Ngawal (DRY; papers I, II & III) in the Manang district; Lauribinyak (MES; papers I & II) in the Rasuwa district; Phulchoki and Ghorepani in Kathmandu and Myagdi districts, respectively (paper IV). ▲ indicates sampling areas, and ● indicates climate stations.

Methodology

Theoretical settings and scale

This thesis includes four scientific papers (I-IV) based on research carried out in alpine, subalpine, and temperate zones of the Himalayan landscape. Alpine and subalpine ecosystems are generally characterized as semi-natural as well as climate (temperature) sensitive. The ecosystems in the forests of the Middle Hills temperate zone are more heavily modified by anthropogenic disturbance. The first three studies (papers I-III) encompass elevational gradients parallel to climatic (temperature) and other environmental gradients (viz. area). In this thesis, the treeline ecotone studies (papers I and II) cover an elevation range of 3930-4180 m.a.s.l. (252 m) in dry areas and 3770-3950 m.a.s.l. (180 m) in mesic areas. In the dry area, species diversity pattern was studied across the forest line in the elevation range of 3850-4040 m.a.s.l. (190 m). Paper IV examines community changes along a disturbance (canopy) gradient in temperate Himalayan forests and covers a total elevation range of 2275-2800 m.a.s.l.

In papers I & II, two coniferous tree species (*Pinus wallichiana* and *Abies spectabilis*) representing dry and mesic environments, respectively, were selected to assess individualistic responses to spatial (forest line, treeline, and krummholz) and temporal (annual and decadal) variations of climatic factors (temperature and precipitation). The relationships were analyzed over a spatial extent of 252 m in the dry and 180 m in the mesic areas. The temporal extent covered 21 years (1985-2005). Climate-growth relationships were explored over the whole analytical period, and in two decadal windows (1985-1994; 1995-2005). The species' responses were also analyzed at the population level through age structure analyses. The temporal window of age analyses was 28 years (1978-2005). Age analysis provides a picture of response in mortality and recruitment patterns. Paper II is based on sample sizes of 195 (181 included for age analysis) at Ngawal and 163 at Lauribinayak, in areas of 3.2 and 4 ha, respectively. The small area of the transects are indicative of short spatial distances between transect end points due to the steep mountain slopes and rugged topography of the Himalayan region, whereas the short time-scale reflects a relatively newly-

established treeline forest, and methodological constraints of common-window analysis across the space.

In papers III & IV, community-level responses to the changing environment are examined on a local spatial scale (*sensu* Lomolino 2001). Various ecological attributes of scales (sample unit, grain, focus, extent) were considered during the study, since scale (spatial and temporal) drives the changing pattern of species diversity (Rosenzweig 1995; Scheiner *et al.* 2000). In both papers (III & IV), a same-sized quadrat (10 m x 10 m = 100 m²) was used as a sampling unit. The grain size for alpha diversity (100 m²) is also the same in both studies, since alpha diversity is measured as average species richness per plot. However, the grain size for gamma diversity is different in the two studies, as gamma diversity is defined as the total number of species present in the designated landscape (Lomolino 2001). Detrended Correspondence Analysis (DCA) was used to estimate beta diversity, which indicates compositional change of species across the landscape (Hill & Gauch 1980). Thus, alpha, gamma, and beta diversity are based on the ‘focus’ or designated landscape. For example, in paper III, the ‘focus’ is the forested or open landscape, each of which includes 66 quadrats and hence encompasses a total sample area of 6600 m² (66 x 10 x 10 m²). On the other hand, in paper IV, the ‘focus’ refers to the disturbance class, which is characterized by lopping intensity. The total area sampled in each disturbance class varies from 1000 m² (10 quadrats) to 1500 m² (15 quadrats). In total, 63 and 65 quadrats were sampled in Phulchoki and Ghorepani, respectively, which lie within an extent of 200 km.

In papers III & IV, the same sampling procedures were applied (see Methods in paper IV for details). Paper III compares alpha diversity between forested and open landscapes, and explores whether temperature or land-use show an overriding influence on species richness. Paper IV examines how alpha, gamma, and beta diversity are affected at different levels of anthropogenic disturbance in the forests.

Focal species and their distribution

***Pinus wallichiana*, Ngawal (DRY; in papers I, II & III)**

Himalayan blue pine (*P. wallichiana*) dominates the subalpine area of dry south-facing slopes at Ngawal. This western Himalayan element is native to species in Afghanistan, India, Pakistan, and Bhutan, and grows between 1800 m and 4300 m a.s.l. (Ohsawa *et al.* 1986). It is a light-demanding evergreen tree that grows on well-drained sandy soil and can tolerate drought as well as frost. Tree height of this species ranges from 10 to 15 m. *Juniperus indica* is the main associated component of this forest. At high elevations, *Juniperus* species appear in Krummholz form.

***Abies spectabilis*, Lauribinayak (MES; paper I & II)**

Himalayan fir (*A. spectabilis*) is native of an area extending from Afghanistan through Kashmir and the Himalaya, east to Bhutan and south-eastern Tibet, and grows between 2700 m and 3900 m a.s.l. (Stainton 1972). This evergreen tree species normally grows on acidic clay soil on shady slopes and is susceptible to late spring frost. Growth rate of this tree species is relatively slow and tree height ranges from 20 to 30 m. *Betula utilis* and *Rhododendron campanulatum* are the main associated species. A shrub species, *Rhododendron anthopogan*, largely occupies the understorey layer.

***Quercus semecarpifolia* (Phulchoki, Ghorepani, paper IV)**

Quercus semecarpifolia belongs to the western Himalayan element and is distributed from Afghanistan to south-west China within an altitudinal range of 2100 to 3800 m a.s.l. (Polunin & Stainton 1984). It is predominantly found in the dry western part of Nepal, but also in the eastern part on dry south-facing slopes (Ohsawa *et al.* 1986). The species has high variation in morphology depending upon the degree of human impact, climatic variability, and tree age. Tree height generally ranges from 25 to 30 m. An aggregated leaf drop normally occurs during late spring (May) and new leaves emerge within a couple of weeks (June). Trees are nearly evergreen because old leaves do not entirely fall until the new leaves appear (see paper IV). This oak species is dominant in the forests at Phulchoki and Ghorepani between the elevations of 2300 to 2850 m.a.s.l. These forests are characteristic of the Middle Hills in the central Himalaya (Dobremez 1976).

Climate complexity, temperature loggers and verification of station data

Regional and local characteristics of climate are affected by topography, movement of air masses and latitude (Barry 1992; Pepin 2001). Temperature decreases with increasing elevation with characteristic environmental lapse rates (Huntley *et al.* 1989; Ohsawa 1990). Lapse rates are not constant, however, and may vary between sites, regions, and different times of year (Dodson & Marks 1997; Rolland 2003). In rugged terrains like the Himalayan mountain system, temperature and precipitation can vary remarkably over short geographic distances due to the effect of topography. Hence, the regional distribution of temperature and precipitation is very complex. The lack of precise climate data for desired locations and for desired time periods is a common problem in the high elevation mountain areas of Nepal (Shrestha *et al.* 1999; Friedland *et al.* 2003). One way to circumvent such problem is to extrapolate data from nearby climate stations, often situated at lower elevations by using regional lapse rates. However, it is currently an open question as to what extent these extrapolated data really represent the climate of the areas of interest?

The closest climate station to one of my study areas (*viz.*, Dhunche; see method, paper I for details) had insufficient data points and many missing records. I used estimated temperature data based on Kathmandu data (having longest and the most reliable data) for the study's temperature-growth analyses. During estimation, using global lapse rate could be problematic, since lapse rate shows significant spatial variability (Dodson & Marks 1997; Pepin 2001; Rolland 2003). Thus, the precision of estimated temperature data was optimised by first using monthly lapse rates calculated on basis climate stations from high-elevation areas within central Nepal. The applicability of the estimated temperature data was then tested by correlating the estimated temperatures with temperature data recorded by loggers installed locally in the study areas during this study. The applicability of using precipitation data available from Kathmandu was also tested by correlating with the data available from Dhunche (nearest station to Lauribinayak). This was done because a positive correlation over time between precipitation data from these two locations would indicate that the Kathmandu station captures the temporal variability in precipitation over years in the surrounding areas even if the exact precipitation levels may not be identical.

Climate loggers (Gemini Data loggers version 2.3; Type Tiny tag +12; -40/85°C; reading capacity; 16238) were set up in different elevational locations (forest, forest line, treeline, tree species line) across the whole range of treeline ecotones (both southern and northern slopes of Lauribinayak, Rasuwa and southern slope of Ngawal). They were installed at 2 m above the ground and at ground surface. Care was taken to avoid placing the loggers in direct sunlight. The loggers are waterproof, have high reading accuracy, large memories, and designed for use in harsh outdoor conditions. The logger data are available for 4 years (2008-2012) for Lauribinayak, and for 3 years (2009-2012) for Ngawal (see Appendix 1). Data were checked obviously erroneous recordings (unrealistically high or low recordings in one single logger; not paralleled by other loggers at the site) and trustable data only were used for testing within- and between-year correlations with the climate-station data (see Methods, paper I for details). Here, I present a brief overview of air temperature variation across two treeline ecotone areas is presented based on the data available from the temperature loggers installed at 2 m above the ground (see Appendix I).

Lapse rate, annual mean and diurnal variation of temperature

Annual mean air temperature (AMT) for the treeline areas in central Nepal based on the logger data is around 5°C (4.64 ± 0.28) with Lauribinayak in the north having the lowest (4.25°C) and Ngawal to the south having the highest (5.19°C) values (Fig. 3, Appendix I). The mean temperature change along our treeline ecotones is similar to the lapse rate value calculated based on climatic stations for central Nepal (0.57°C/100 m). The lapse rates were calculated as 0.37°C, 0.53°C and 0.58°C for Ngawal south, Lauribinayak south and Lauribinayak north, respectively, although we note that estimating and testing lapse rate values for individual slopes based on the limited available logger points (average 3 per slope) is not statistically valid.

Temperature is a very important aspect of climate elsewhere and acts as a main driving force of many environmental processes. Diurnal and seasonal variations in temperatures were estimated for the different ecological elevations (forest line and tree species line) for both slopes at Lauribinayak and the south slope only at Ngawal. The diurnal temperature range (hereafter DTR) is the difference between the maximum and minimum temperatures in a 24-hour period.

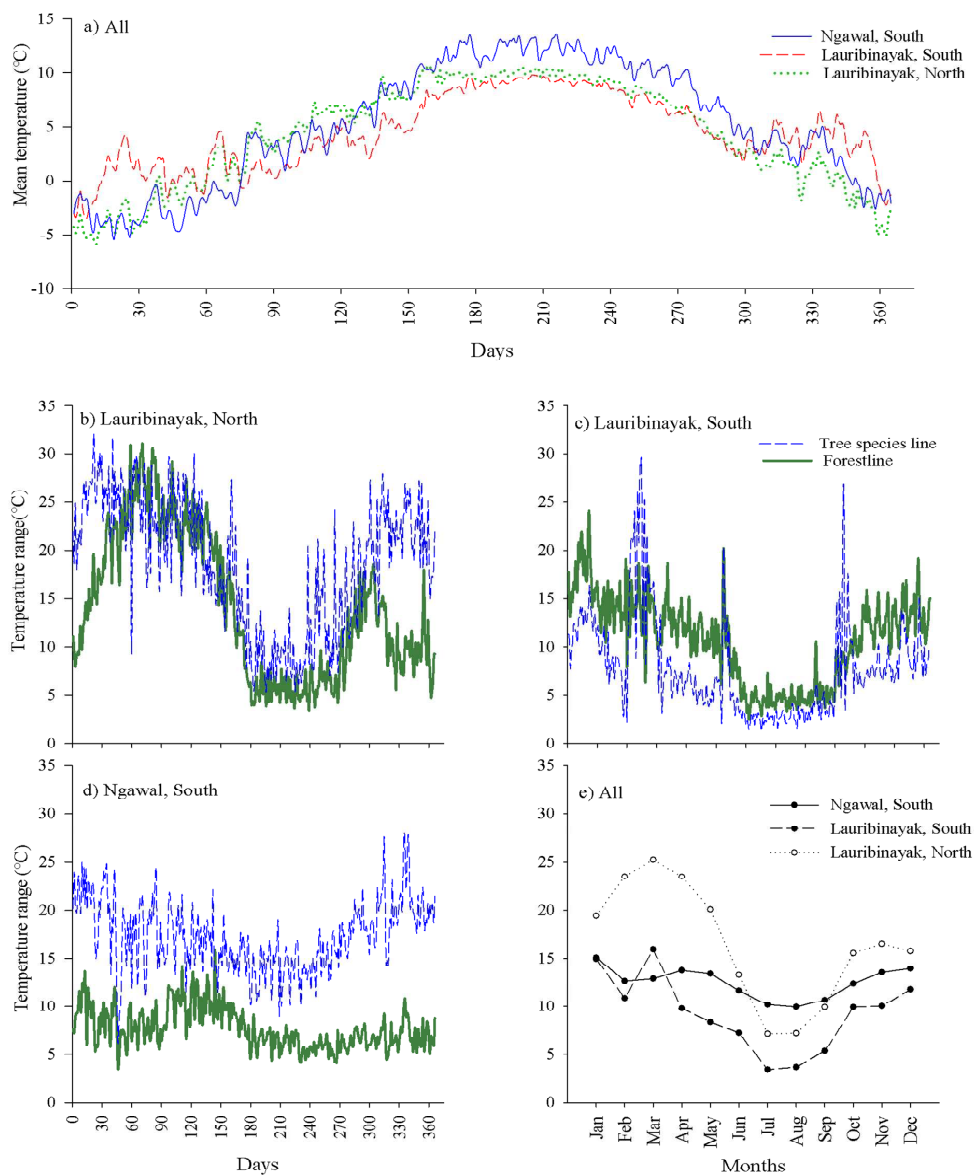


Figure 3. Mean daily temperature for three slopes (a) and diurnal temperature ranges at the forest line (solid green line) and tree species line (dotted blue line) for the North and South slopes of Lauribinayak, Rasuwa (b and c) and the South slope of Ngawal, Manang (d). The bottom right panel (e) shows mean monthly diurnal temperature ranges (MMDTR). Temperatures were recorded at 2 hourly intervals by temperature loggers, installed 2 m above the ground.

DTR values can be averaged to give a monthly mean diurnal temperature range (hereafter MMDTR). The annual diurnal temperature range (hereafter ADTR) is an average of MMDTR. In this study, ADTR fluctuated between 7.9°C and 25.2°C for Lauribinayak north, between 3.4°C and 15.9°C for Lauribinayak south and between 9.9°C and 15.1°C for Ngawal south (Fig. 3). MMDTR during winter and spring was larger than during summer on the south slopes in both areas (Appendix I, Fig. 3). A similar pattern was observed for the northern slope of Lauribinayak. Higher ADTR on the north slope suggests that the climate of this slope is more continental than the southern slope (Barry 1992). However, temperature amplitudes do not necessarily correlate with seasonal means, hence the area with a high diurnal range is not necessarily warmer than an area with a low diurnal range, or vice versa (Körner & Paulsen 2004).

Sampling design

Dendrochronology (papers I & II)

Dendrochronological techniques (Fritts 1976) were applied to address the research questions raised in papers I & II. Dendrochronology is a scientific method used for dating past events with the help of annual growth rings observed in cores extracted from tree trunks. In this technique, each annual ring is dated and its correlative feature with climate variables of the corresponding, or previous, year is analyzed (known as dendroclimatology).

Sufficient numbers of healthy and dominant trees were cored from three elevational locations (forest line, treeline, and krummholz (only in Lauribinayak)). After measuring the ring widths, five residual site chronologies were constructed from two study areas (one for each elevational location). Statistical software such as COFECHA (Holmes 1983) and ARSTAN (Cook 1985) were used during cross dating and chronology development processes (see Methods in paper I for details).

Dendrochronological methods were also used to analyze age structure and tree establishment patterns (paper II). In each study area, three altitudinal transects were laid out which extended from the forest line up to the tree species line crossing the treeline. Age of each individual was estimated by counting annual rings and branch whorls (see Methods in paper II). All individuals of trees, saplings and seedlings were sampled for height and stem DBH (Diameter at Breast Height). Geographical coordinates and elevation were recorded for each individual (GPS). Each treeline tree was cored at two levels; 2 m and 0 m (Gamache & Payette 2005) and data were used for estimating treeline establishment period (see Methods in paper II).

Vegetation sampling and analysis (papers III & IV)

Paper III is based on data sampled in vertical and horizontal transects placed across forested and open landscape in Ngawal (see Methods in paper III). Each transect comprised eleven systematically sampled plots (quadrats). Five plots were placed on either side of a subjectively located central plot (representing transition from forest to open landscape) along elevation and canopy gradient. Each plot was divided into four sub plots, each of 5 x 5 m². All vascular plant species were recorded from each sub-plot and abundance of each species within a plot was estimated in terms of frequency on a scale of 0 to 4. Various environmental variables (canopy cover, altitude, aspect, slope, RRI and grazing) were recorded for each plot. The same sampling procedure was followed in paper IV, where sample plots were placed in six disturbance classes distinguished on the basis of percentage of canopy cover which represents the intensity of land-use.

Results and discussion

Response to climatic and ecological attributes

Among the four papers included in this thesis, climate change (variability in temperature and precipitation) effects are primarily discussed in papers I & II. Paper III also sheds light upon the role of temperature for understory species distributions across the treeline ecotone. The effects of other ecological drivers and land-use systems are touched in paper II and extensively discussed in papers III & IV.

Climate (Papers I, II & III)

This thesis reveals clear climatic signals with noticeable spatial and temporal variability in both tree growth (paper I) and population structure (paper II) in two study areas. Primary climatic drivers include both growing-season as well as non-growing-season factors, and they vary between the study areas, elevational locations, and analytical windows (whole time-periods vs. decadal periods). There is only limited consistency in terms of specific climatic factors or temporal patterns. Tree growth in two areas shows different response patterns with a strong response to winter climate in the dry area, and to spring climate in the mesic area, thus highlighting the importance of non-growing-season climate. The timing of the onset of the monsoon is important only in the mesic area.

Tree growth behaved differently with respect to summer temperature in the two study areas, with varying responses between the elevational locations and decadal periods (1985-1994; 1995-2005). For example, the radial growth of pine showed a significant positive response to summer temperature (June), but only at the forest line; while in the mesic *Abies spectabilis* area, tree growth showed a negative response to early summer temperature that is consistently observed across all analytical time periods (full and decadal) and at all elevations. Increased tree growth in the dry *Pinus* area could be attributed to cold winters producing higher snow-fall and more persistent snow cover. Heavy accumulation of snow becomes a stable moisture source in such a dry area as it initiates an early onset of the growing season (Vaganov *et al.* 1999; Bekker 2005). However, there are inconsistencies in the relationship between growth and winter temperature across the two decades. The negative growth response to

winter temperature is only detected in the later analytical period, when winter temperatures are more variable and generally warmer than in the earlier analytical period. Warm winter is associated with reduced snow-cover duration affecting moisture availability (Beniston 2005). Such climate conditions are restrictive not only to tree growth but also for survival of seedlings and hence might be responsible for the limited numbers of pine seedlings in the dry area. Furthermore, these conditions might be responsible for trees becoming established at lower elevations only during the latest analyzed decade (1990-1999). Poor growth years at the forest line were associated with high spring temperatures and low spring precipitation suggesting the possibility of spring drought as a growth-limiting factor.

Reduced growth in warm summers in the mesic *Abies spectabilis* area, contradicts the commonly-observed positive growth response to summer temperature reported from many treeline ecotone regions world-wide, including the Himalaya (Esper *et al.* 2003; Wang *et al.* 2005; Wang *et al.* 2006; Dang *et al.* 2009; Shah *et al.* 2009). Growth reductions under above-average growing-season temperatures in temperature-limited systems (including many alpine and arctic treeline ecotones) have been observed elsewhere, and are often attributed to drought events or drought periods (Barber *et al.* 2000; Kirchhefer 2001; Lloyd & Fastie 2002; Wilmking *et al.* 2004). Such relationships could potentially explain the negative growth response to temperature in our *Abies spectabilis* area. Further, this negative growth response to temperature also implies that factors other than temperature *per se* might have driven the climate-growth relationship pattern in the area. For example, the date of cambial initiation, an important climate-linked process related to tree-ring growth, is known to be affected by date of snow melt, winter precipitation and soil warming (Worrall 1983; Kirilyanov *et al.* 2003). In the Himalaya, part of the early monsoon (May) precipitation may fall as snow which delays snowmelt and the onset of the growing season. During periods of high winter precipitation, the growth response is negative for the same reasons, i.e., delay of snowmelt and late onset of growing season (Peterson *et al.* 2002).

A characteristic of the Himalayan climate is the sharply rising temperatures from March through May, with the monsoonal precipitation lagging behind by some

months, resulting in potential for spring water deficit (Sano *et al.* 2005). At the forest line of our mesic area, the potential importance of drought in explaining the negative relationship between tree growth and spring temperature is supported by a coincident positive relationship with spring precipitation, which is especially prominent during the earlier drier decade. In contrast, the relationship between tree growth and both winter and spring precipitation is negative in the later, wetter decade suggesting a shift in limiting factors for growth as that spring drought is not limiting tree growth at the higher elevations of the mesic area during this period. High precipitation implies increased cloudiness, leading to a significant reduction of soil temperature through reduced radiation input or high cloud albedo (Takahashi *et al.* 2005), which may delay soil-warming in spring and hence contribute to reduced tree growth.

The role of temperature in the distribution of understorey species across a treeline ecotone is not well known. Paper III tests whether there is significant variation in species richness between an open alpine landscape and a forested landscape just below the forest line. Slightly higher species richness was found in the open alpine landscape, which may be attributed to greater solar radiation and large diurnal temperature fluctuations. These temperature attributes favour dwarf plant species such as herbs and cushion plants (Germino *et al.* 2002; Körner 2003). However, insignificant differences in species richness between two landscapes suggest that temperature does not have an overriding role in determining the local species richness (alpha-diversity) patterns in the area.

Land-use (Papers II, III & IV)

Papers II, III & IV discuss vegetation responses to land-use changes. In the Himalaya, the semi-natural environment near the upper treeline ecotone has been under human influence for millennia, exposed to land-use practices such as fire (burning of shrubs) and grazing (Paper III; Schmidt & Stubbendieck 1993; Schickhoff 2005). Changes in local people's occupation and livelihoods, and the implementation of conservation areas or national parks, has decreased the pressure upon these forests; significantly so during recent decades (Beug & Miede 1999; Schickhoff 2005). Paper II discusses the influence of human and herbivore activities on treeline establishment and forest structure. For example, the larger numbers of trees and saplings in Ngawal suggests

that this area has a lower impact of human activities and herbivory, and fewer saplings at Lauribinayak indicate higher grazing pressure, which may be restricting upslope treeline advance in this area. The presence of bushes (viz. *Rhododendron anthopogan* in the mesic area and *Juniperus* spp. in the dry area) in both study areas provides some protection for seedlings and saplings from browsing.

Paper III reports slightly higher species richness in open alpine areas compared to the adjacent forested subalpine areas. Paper III also argues that the prostrate growth-form of junipers, and a dominance of grasses and sedges (e.g. *Stipa* sp.; *Carex* sp.) indicates that the pine treeline is influenced by grazing (Kitayama 1992; Armand 1992; Auerbach & Shmida 1993). This argument implies that the climatic / potential forest line in this area could be at a higher elevation (Miehe 1997) and this is supported by the presence of both alpine and forest species in our open area, such as the forest-specialist species that find a forest-like environment under krummholz-formed junipers, which provide shelter and protection from browsing (Fuentes *et al.* 1984). Furthermore, higher species richness in the open area might be due to grazing which can facilitate the introduction of new species by creating small gaps and increasing environmental heterogeneity (Vandvik *et al.* 2005; Alados *et al.* 2007).

Paper IV highlights relationships between changes in species diversity and anthropogenic activities in the Middle Hill mountain forests. These forests are under serious threat because the economy in this area is heavily dependent upon timber, fodder and fuelwood available from these forests (Måren & Vetaas 2007). The study emphasizes the importance of moderate levels of disturbance in the forests, which allows enhancement of all measures of species diversity as well as sustains the livelihood of local farmers.

Ecotone effect (Paper III)

An ecotone is a transition zone between two adjacent ecological systems and hence possesses a mixture of floristic and faunistic characteristics from both of the community types (di Castri 1990; Holland *et al.* 1991; Risser 1995). Within the ecotone many species fall at the margin of their physiologically determined range (Curtis 1959). This is the reason why ecotones are sensitive to climate change (Gosz & Sharpe 1989). Any ecotone is a dynamic zone—a peak in species turnover is

assumed—and the ecotones created and maintained by human activities tend to be spatially abrupt.

In Paper III, we hypothesised that species richness may be enhanced in the middle of the transects; i.e. at the border between forest and open landscape where species assemblages from the both forest and the open landscapes meet. This is a local edge effect and also termed the (forest) ecotone effect. The finding in this study is comparable to the results presented by Camarero *et al.* (2006) from a Pyrenean *Pinus* forest where greater light availability was described as a probable cause of the upslope increase of plant richness. Grytnes (2003) and Grytnes *et al.* (2006) found a unimodal pattern in species richness across the sub-alpine forest ecotone. They used a considerably longer transects than ours which may explain why we found no significant pattern in richness with altitude across our forested to open landscapes. Our transects extended 120 m above the forest line, and if there was a local edge effect we would expect the highest plots to have lower richness compared to those around the centre of the transects. The distribution of the samples shown in the DCA diagram (Paper III) indicates a continuum of species along the transects from forest to open alpine landscapes.

Mass effect (Paper III)

Mass effect is the process of species establishment by propagules at sites where they cannot maintain viable populations due to a failure to reproduce (Shmida & Wilson 1985). The mass effect can temporarily enhance species richness in a landscape by species migration from a source population. However, this effect does not create a self-maintaining population in sink locations. In this study (paper III), the higher species richness found in the open alpine areas can be attributed to an asymmetric mass effect as discussed by Grytnes (2003) to explain a peak in species richness observed in his study. According to this concept, seed dispersal from the forest to the open alpine landscape is possible, but reverse dispersal might be prohibited by the canopy cover. Thus, although higher species richness in the alpine landscape could indicate an asymmetric mass effect in my study (paper III), higher total species number in the forested patches obscure the possible imprints of mass effects on local species diversity patterns.

Concluding remarks

This thesis aimed to shed light upon the vegetation responses to recent environmental changes, in climate-sensitive (treeline ecotone areas) and human-modified (disturbed Middle Hill forest) ecosystems in the Nepal Himalaya. Individualistic (paper I), population (paper II) and community (papers III & IV) level responses to the ambient environmental conditions were evaluated over various spatial and temporal scales.

An important finding from, is the contribution of non-growing season climate factors to variability in tree growth, and I argue that these factors operate mainly by altering growing season length. For example, in the dry environment, cold winters promote pine tree growth by causing a relatively early onset of the growing season through increased moisture facilitation from the melting snow in the pre-monsoon period, relative warmer winter years. In the mesic area, on the other hand, high snow accumulation during cold winters results in late melt-out and retards growth of fir tree species by limiting the growing period.

This thesis also highlights the contributions of site-specific factors in treeline structuring processes in both study areas. The low number of pine seedlings in the dry area could be due to climatic stress caused by the more variable climate with some very warm winters and some very cold summers of recent years. In the same area, a relatively high density of saplings and trees indicates low pressure of biotic activities and high potential for treeline advance. Fewer saplings and trees in the mesic area suggest high biotic pressures (herbivores) which may restrict the potential for treeline advance. The pattern of community composition across forest to open ecotone suggests that grazing pressure is sufficient to override the climate ecotone effect in the pine area. Small differences in alpha diversity and small turnover along altitude in species composition support this argument.

Finally, this thesis recommends allowing low intensity forest use by local people in the Middle Hills area as intermediate-level and spatially variable prescribed forest disturbances by enhancing all measures of species diversity and can thus mitigate biodiversity loss in these landscapes.

Future perspectives

This study contributes to the under-represented central Himalayan treeline literature. In two treeline papers (papers I & II), I considered two tree species (*Pinus* and *Abies*) representing two contrasting environments (dry and mesic). This could be elaborated by adding more species sharing the same environments (Juniper in dry; Birch in mesic) in order to compare species-specific patterns of tree growth responses. Furthermore, by considering more than one locality or region, the study can be given a multi-scale approach. The study of growth response of a species with various growth-forms in the same environment may also be very interesting. For example, the growth response of the climate-sensitive treeline shrub *Cassiope fastigiata*, which is regarded as an important indicator of vegetation-climate relationships.

One of the main shortcomings for climate-growth studies from the Nepal Himalaya is the limitation of climate data: the longest available station data temperature and precipitation series are only 50 years (Kathmandu airport). The data of sufficient quality (i.e., time series covering both temperature and precipitation over ecologically interesting time periods, with few missing data points) from treeline elevations are nearly impossible to obtain. For more reliable climate-growth studies from high elevation areas of the Himalaya, resourceful and long-term plans for data collection and quality are necessary.

In paper II, I considered evaluating tree-establishment patterns at treeline elevations over the decades, but the small data set I have available makes it hard to assert anything about the treeline patterns of the study areas. However, contributions of climate vs. land-use have been discussed. Quantitative land-use and geomorphological data will give a stronger basis for saying something about treeline dynamics in the areas. Further, to examine patterns of land cover (specifically tree cover) and their changes across the sub-alpine transition zone, the use of spatial information technology (remote sensing and GIS) could be highly effective.

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References

- Alados, C.L., Aich, A.E., Komac, B., Pueyo, Y. & García-Gonzalez, R. (2007) Self-organized spatial patterns of vegetation in alpine grasslands. *Ecological Modelling* **201**, 233-242.
- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography* **28**, 693-695.
- Armand, A. (1992) Sharp and gradual mountain timberlines as result of species interaction, In: A.J. Hansen, F. di Castri. (eds.) *Landscape boundaries: Consequences for biotic diversity and ecological flows*. Springer: New York. pp. 360–378.
- Auerbach, M. & Shmida, A. (1993) Vegetation change along an altitudinal gradient on Mt. Hermon, Israel: no evidence for discrete communities. *Journal of Ecology* **81**, 25-33.
- Aune, S., Hofgaard, A. & Söderström, L. (2011) Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research* **41**, 437-449.
- Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **405**, 668-673.
- Barry, R.G. (1992) *Mountain, weather and climate*. Routledge: London.
- Batllori, E. & Gutiérrez, E. (2008) Regional treeline dynamics in response to global change in the Pyrenees. *Journal of Ecology* **96**, 1275-1288.
- Bekker, M.F. (2005) Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arctic Antarctic and Alpine Research* **37**, 97-107.
- Beniston, M. (2005) Warm winter spells in the Swiss Alps: Strong heat waves in a cold season? A study focusing on climate observations at the Saentis high mountain site. *Geophysical Research Letters* **32**, L01812.
- Beug, H.J. & Miehe, G. (1999) *Vegetation history and human impact in the eastern central Himalaya (Langtang and Helambu), Nepal*. Stuttgart University: Germany.
- Bhattacharyya, A., Shah, S.K. & Chaudhary, V. (2006) Would tree-ring data of *Betula utilis* be potential for the analysis of Himalayan glacial fluctuations? *Current Science* **91**, 754-761.
- Bonan, G. (2002) *Ecological climatology: Concepts and applications*. Cambridge University Press: Cambridge.
- Borgaonkar, H.P., Sikder, A.B. & Ram, S. (2011) High-altitude forest sensitivity to the recent warming: A tree-ring analysis of conifers from Western Himalaya, India. *Quaternary International* **236**, 158-166.
- Camarero, J.J., Gutiérrez, E. & Fortin, M.J. (2006) Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries. *Global Ecology and Biogeography* **15**, 182-191.
- Carrer, M., Nola, P., Eduard, J.L., Motta, R. & Urbinati, C. (2007) Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. *Journal of Ecology* **95**, 1072-1083.

- Chalise, S. & Khanal, N. (2001) An introduction to climate, hydrology and landslide hazards in the Hindu Kush-Himalayan region, In: L. Tianchi, S. Chalise, B. Upreti. (eds.) *Landslide Hazard Mitigation in the Hindu Kush-Himalayas*. ICIMOD: Kathmandu. pp. 51-62.
- Cook, E.R. (1985) *A time-series analysis approach to tree rings standardization*. University of Arizona: Arizona.
- Curtis, J.T. (1959) *The vegetation of Wisconsin: an ordination of plant communities*. University of Wisconsin Press
- Danby, R.K. & Hik, D.S. (2007) Variability, contingency and rapid change in recent subarctic alpine treeline dynamics. *Journal of Ecology* **95**, 352-363.
- Dang, H.S., Zhang, K.R., Zhang, Y.J., Tan, S.D., Jiang, M.X. & Zhang, Q.F. (2009) Treeline dynamics in relation to climate variability in the Shennongjia Mountains, central China. *Canadian Journal of Forest Research* **39**, 1848-1858.
- Daniels, L.D. & Veblen, T.T. (2004) Spatiotemporal influences of climate on altitudinal treeline northern Patagonia. *Ecology* **85**, 1284-1296.
- Daubenmire, R. (1954) Alpine timberlines in the Americas and their interpretation. *Butler University Botanical Studies* **11**, 119-136.
- di Castri, F. (1990) On invading species and invaded ecosystems: the interplay of historical chance and biological necessity, In: F. di Castri, A.J. Hansen, M. Debussche. (eds.) *Biological invasions in Europe and the Mediterranean basin*. Springer: The Netherland.
- Dirnböck, T., Dullinger, S. & Grabherr, G. (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography* **30**, 401-417.
- Dobremez, J.F. (1976) *Le Népal: Ecologie et biogéographie*. Centre National de la Recherche Scientifique.
- Dodson, R. & Marks, D. (1997) Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Climate Research* **8**, 1-20.
- Dullinger, S., Dirnböck, T. & Grabherr, G. (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* **92**, 241-252.
- Ellenberg, H. (1963) *Vegetation Mitteleuropas mit den Alpen in kausaler, dynamischer und historischer Sicht*. Sicht: Ulmer, Stuttgart.
- Esper, J., Shiyatov, S.G., Mazepa, V.S., Wilson, R.J.S., Graybill, D.A. & Funkhouser, G. (2003) Temperature-sensitive Tien Shan tree-ring chronologies show multi-centennial growth trends. *Climate Dynamics* **21**, 699-706.
- Friedland, A.J., Boyce, R.L., Vostral, C.B. & Herrick, G.T. (2003) Winter and early spring microclimate within a mid-elevation conifer forest canopy. *Agricultural and Forest Meteorology* **115**, 195-200.
- Fritts, H.C. (1976) *Tree rings and climate*. San Francisco Academic Press: New York.
- Fuentes, E.R., Otaiza, R.D., Alliende, M.C., Hoffmann, A. & Poiani, A. (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* **62**, 405-411.
- Gamache, I. & Payette, S. (2005) Latitudinal response of subarctic treelines to recent climate change in eastern Canada. *Journal of Biogeography* **32**, 849-862.

- Gao, Z., Chae, N., Kim, J., Hong, J., Choi, T. & Lee, H. (2004) Modeling of surface energy partitioning, surface temperature, and soil wetness in the Tibetan prairie using the Simple Biosphere Model 2 (SiB2). *Journal of Geophysical Research* **109**, D06102.
- Germino, M.J., Smith, W.K. & Resor, A.C. (2002) Conifer seedling distribution and survival in an alpine treeline ecotone. *Plant Ecology* **162**, 157-168.
- Gosz, J.R. & Sharpe, P.J.H. (1989) Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landscape Ecology* **3**, 229-243.
- Grace, J., Berninger, F. & Nagy, L. (2002) Impacts of climate change on the treeline. *Annals of Botany* **90**, 537-544.
- Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* **26**, 291-300.
- Grytnes, J.A., Heegaard, E. & Ihlen, P.G. (2006) Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecologica* **29**, 241-246.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* **12**, 1040-1049.
- Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: An improved ordination technique. *Vegetatio* **42**, 47-58.
- Hingane, L.S., Rupa Kumar, K. & Ramana Murty, B.V. (1985) Long-term trends of surface air temperature in India. *International Journal of Climatology* **5**, 521-528.
- Hofgaard, A. (1997) Inter-relationships between treeline position, species diversity, land-use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography* **6**, 419-429.
- Hofgaard, A., Dalen, L. & Hytteborn, H. (2009) Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science* **20**, 1133-1144.
- Holland, M., Risser, P.G. & Naiman, R.J. (1991) *Ecotones: the role of landscape boundaries in the management and restoration of changing environments*. Chapman and Hall: New York, USA
- Holmes, R.L. (1983) Computer assisted quality control in tree ring dating and measurement. *Tree Ring Bulletin* **43**, 69-78.
- Holtmeier, F.K. & Broll, G. (2005) Sensitivity and response of Northern Hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* **14**, 395-410.
- Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989) Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography* **16**, 551-560.
- Huntley, B. & Baxter, R. (2005) Vegetation ecology and global change, In: E. van der Maarel. (eds.) *Vegetation ecology*. Blackwell Publishing: Oxford. pp. 357-372.
- IPCC (2007) *Climate Change 2007 - The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC*.

- Keller, F., Kienast, F. & Beniston, M. (2000) Evidence of response of vegetation to environmental change on high-elevation sites in the Swiss Alps. *Regional Environmental Change* **1**, 70-77.
- Kirchhefer, A.J. (2001) Reconstruction of summer temperatures from tree-rings of Scots pine (*Pinus sylvestris* L.) in coastal northern Norway. *The Holocene* **11**, 41-52.
- Kiralyanov, A., Hughes, M., Vaganov, E., Schweingruber, F. & Silkin, P. (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees* **17**, 61-69.
- Kitayama, K. (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Plant Ecology* **102**, 149-171.
- Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**, 445-459.
- Körner, C. (2003) *Alpine Plant Life: functional plant ecology of high mountain ecosystems* Springer-Verlag: Berlin.
- Körner, C., Nakhutsrishvili, G. & Spehn, E. (2006) High elevation land-use, biodiversity, and ecosystem functioning, In: E.M. Spehn, M. Liberman, C. Körner.(eds.) *Land-use change and Mountain Biodiversity*. Taylor & Francis Group: New York.
- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* **31**, 713-732.
- Kullman, L. (2004) The changing face of the Alpine world. *Global Change NewsLetter* **57**, 12-14.
- Li, J.B., Cook, E.R., D'Arrigo, R., Chen, F.H., Gou, X.H., Peng, J.F. & Huang, J.G. (2008) Common tree growth anomalies over the northeastern Tibetan Plateau during the last six centuries: implications for regional moisture change. *Global Change Biology* **14**, 2096-2107.
- Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* **52**, 481-509.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**, 3-13.
- Luckman, B. & Kavanagh, T. (2000) Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* **29**, 371-380.
- Mahat, T.B.S., Griffin, D.M. & Shepherd, K.R. (1986) Human impact on some forests of the Middle Hills of Nepal I. Forestry in the context of the traditional resources of the state. *Mountain Research and Development* **6**, 223-232.
- Måren, I.E. & Vetaas, O.R. (2007) Does regulated land-use allow regeneration of Keystone forest species in the Annapurna Conservation Area, Central Himalaya. *Mountain Research and Development* **27**, 345-351.
- McDonald, R.I., Motzkin, G., Bank, M.S., Kittredge, D.B., Burk, J. & Foster, D.R. (2006) Forest harvesting and land-use conversion over two decades in Massachusetts. *Forest Ecology and Management* **227**, 31-41.
- Miehe, G. (1997) Alpine vegetation types of the central Himalaya, In: F.E. Wielgolaski. (eds.) *Ecosystems of the World – Polar and Alpine Tundra*. Elsevier. pp. 161-184.

- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research* **21**, 1-25.
- Ohsawa, M. (1990) An interpretation of latitudinal patterns of forest limits in south and east-Asian Mountains. *Journal of Ecology* **78**, 326-339.
- Ohsawa, M., Shakya, P.R. & Numata, M. (1986) Distribution and succession of west Himalayan forest types in the eastern part of the Nepal Himalaya. *Mountain Research and Development* **6**, 143-157.
- Ono, Y. & Sadakane, A. (1986) *Natural background of the yak transhumance in the Langtang valley, Nepal Himalaya*. Tokyo Metropolitan University
- Pepin, N. (2001) Lapse rate changes in northern England. *Theoretical and Applied Climatology* **68**, 1-16.
- Peterson, D.W., Peterson, D.L. & Ettl, G.J. (2002) Growth responses of subalpine fir to climatic variability in the Pacific Northwest. *Canadian Journal of Forest Research* **32**, 1503-1517.
- Pickett, S.T.A. & White, P.S. eds. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.
- Polunin, O. & Stainton, A. (1984) *Flowers of the Himalaya*. Oxford University Press: Oxford.
- Practical Action (2009) *Temporal and spatial variability of climate change over Nepal (1976-2005)*. Practical Action Nepal office
- Richardson, A.D. & Friedland, A.J. (2009) A review of the theories to explain Arctic and Alpine treelines around the World. *Journal of Sustainable Forestry* **28**, 218-242.
- Risser, P.G. (1995) The status of the science examining ecotones. *Bioscience* **45**, 318-325.
- Rolland, C. (2003) Spatial and seasonal variations of air temperature lapse rates in alpine regions. *Journal of Climate* **16**, 1032-1046.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press: Cambridge.
- Salisbury, F.B. & Ross, C.W. (1992) *Plant physiology*. Wadsworth: Belmont, California.
- Sano, M., Furuta, F., Kobayashi, O. & Sweda, T. (2005) Temperature variations since the mid-18th century for western Nepal, as reconstructed from tree-ring width and density of *Abies spectabilis*. *Dendrochronologia* **23**, 83-92.
- Scheiner, S., Cox, S.B., Wilig, M., Mittelbach, G.G., Osenberg, C. & Kaspari, M. (2000) Species richness, species-area curves and Simpson's paradox. *Evolution Ecology and Research* **2**, 791-802.
- Scherrer, D. & Körner, C. (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* **16**, 2602-2613.
- Schickhoff, U. (2005) The upper timberline in the Himalayas, Hindu Kush and Karakorum: A review of geographical and ecological aspects, In: G. Broll, B. Keplin. (eds.) *Mountain Ecosystems: Studies in Treeline Ecology*. Springer-Verlag: Berlin. pp. 275-354.
- Schmidt, T.L. & Stubbendieck, J. (1993) Factors influencing eastern red cedar seedling survival on rangeland. *Journal of Range Management* **46**, 448-451.

- Shah, S.K., Bhattacharyya, A. & Chaudhary, V. (2009) Climatic influence on radial growth of *Pinus wallichiana* in Ziro Valley, Northeast Himalaya. *Current Science* **96**, 697-702.
- Shakya, P.R. (1985) Phytogeography and ecology of Nepalese rhododendrons, In: T.C. Majpuria. (eds.) *Nepal: Nature's Paradise*. White Lotus: Bangkok. pp. 181-191.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography* **12**, 1-20.
- Shrestha, A.B., Wake, C.P., Mayewski, P.A. & Dibb, J.E. (1999) Maximum temperature trends in the Himalaya and its vicinity: An analysis based on temperature records from Nepal for the period 1971-94. *Journal of Climate* **12**, 2775-2786.
- Shrestha, K. & Vetaas, O.R. (2009) The forest ecotone effect on species richness in an arid Trans-Himalayan landscape of Nepal. *Folia Geobotanica* **44**, 247-262.
- Singh, J., Park, W.K. & Yadav, R.R. (2006) Tree-ring-based hydrological records for western Himalaya, India, since AD 1560. *Climate Dynamics* **26**, 295-303.
- Singh, J.S. & Singh, S.P. (1987) Forest vegetation of the Himalaya. *The Botanical Review* **53**, 80-192.
- Singh, S.P. & Singh, J.S. (1992) *Forests of Himalaya: Structure, functioning, and impact of man*. Gyanodaya Prakashan Nainital, India.
- Stainton, J.D.A. (1972) *Forests of Nepal*. John Murray: London.
- Takahashi, K., Tokumitsu, Y. & Yasue, K. (2005) Climatic factors affecting the tree-ring width of *Betula ermanii* at the timberline on Mount Norikura, central Japan. *Ecological Research* **20**, 445-451.
- Tenca, A. & Carrer, M. (2010) Growth climate response at high elevation: comparing Alps and Himalayas. In: T. Levanic, J. Gricar, P. Hafner, R. Krajnc, S. Jagodic, H. Gärtner, I. Heinrich, G. Helles (eds.) *Tree Rings in Archaeology, Climatology and Ecology Dendrosymposium 2009*. Postdam, Slovenia. pp. 89-97.
- Thadani, R. & Ashton, P.M.S. (1995) Regeneration of banj oak (*Quercus leucotrichophora* A. Camus) in the central Himalaya. *Forest Ecology and Management* **78**, 217-224.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature* **427**, 145-148.
- Troll, C. (1973) The upper timberlines in different climatic zones. *Arctic and Alpine Research* **5**, A3-A18.
- Vaganov, E.A., Hughes, M.K., Kirilyanov, A.V., Schweingruber, F.H. & Silkin, P.P. (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature* **400**, 149-151.
- Vandvik, V., Heegaard, E., Måren, I.E. & Aarrestad, P.A. (2005) Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology* **42**, 139-149.

- Vetaas, O.R. & Grytnes, J.A. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography* **11**, 291-301.
- Walther, G.-R., Beißner, S. & Burga, C.A. (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**, 541-548.
- Wang, T., Ren, H.B. & Ma, K.P. (2005) Climatic signals in tree ring of *Picea schrenkiana* along an altitudinal gradient in the central Tianshan Mountains, northwestern China. *Trees-Structure and Function* **19**, 735-741.
- Wang, T., Zhang, Q.B. & Ma, K. (2006) Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Global Ecology and Biogeography* **15**, 406-415.
- Wilmking, M., Juday, G.P., Barber, V.A. & Zald, H.S.J. (2004) Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* **10**, 1724-1736.
- Worrall, J. (1983) Temperature–bud-burst relationships in amabilis and subalpine fir provenance tests replicated at different elevations. *Silvae Genetica* **32**, 203-209.

Appendices

Appendix I: Overview of temperature data taken from data loggers installed at 2 m above the ground in various locations in the two study areas.

Slope	Logger location	Elevation (m.a.s.l.)	Latitude	Longitude	Mean (°C)	Mean max. (°C)	Mean min. (°C)	Absolute max. (°C)	Absolute min (°C)	Period of recordings	Data points (every 2 hours)
Lauribinayak, North	Forest	3660	28.0973	85.3797	4.6	6.3	3.1	12.1	-1.9	05.06.2008 / 05.06.2009	4481
	Forest line	3770	28.0953	85.3803	4.8	13.8	-0.4	22.3	-9.7	05.06.2009 / 05.06.2012	17508
	Tree species line	3950	28.0933	85.3880	3.7	16.2	-2.4	20.5	-11.9	05.06.2008 / 05.06.2012	17508
Lauribinayak, South	Forest	3640	28.0950	85.3742	5.1	13.5	0.1	16.7	-8.3	05.06.2008 / 05.06.2012	17504
	Forest line	3700	28.0938	85.3755	4.6	11.0	0.3	13.6	-7.9	05.06.2008 / 05.06.2012	17509
	Tree species line	4040	28.0890	85.3865	3.9	8.4	0.6	10.8	-6.9	05.06.2008 / 05.06.2012	17519
Ngawal, South	Forest	3767	28.6491	84.1098	5.9	20.4	1.4	20.7	-8.8	23.05.2009 / 23.05.2012	13152
	Forest line	3930	28.6787	84.1126	4.5	9.0	1.3	15.7	-7.7	23.05.2009 / 23.05.2012	13152
	Tree species line	4180	28.6550	84.1162	5.9	16.5	-0.8	21.8	-11.1	21.05.2009 / 21.05.2012	13152

Max. = maximum; Min. = minimum

Appendix II (Table 2 of paper I): Overview of the climate at forest line, treeline and krummholz line elevations of the study areas. Temperature data (°C) for the coldest (January), the warmest (July) and monsoon onset (May) months are extrapolated from the Chame and Kathmandu climate station data for the period 1985-2005 based on regional monthly lapse rate calculations (see Methods for their calculation). Mean min = mean of daily minimum values; Mean max = mean of daily maximum values; m.a.s.l. = metres above sea level.

Study areas/ Climate stations	Elevation (m.a.s.l.)	Temperature (°C)												Precipitation (mm)	
		January			May			July			Annual Mean	Total	summer		
		Mean min	Mean max	Mean	Min min	Mean max	Mean	Min min	Mean max						
<i>Pinus wallichiana</i> , DRY/Chame	2680	-2.5	9.2	3.4	7.8	19.9	13.8	10.5	20.3	15.4	10.7	934.4	434.8		
Forest line	3930	-10.5	1.2	-4.6	0.8	12.9	2.5	3.5	12.3	7.4	2.7				
Treeline	4120	-17.1	-3.9	-10.5	0.0	12.1	6.1	2.2	12.0	7.1	2.4				
<i>Abies spectabilis</i> , MES/Kathmandu	1336	2.5	18.9	10.7	15.5	28.7	22.1	20.0	28.2	24.1	18.8	1509.5	986.1		
Forest line	3770	-12.1	4.3	-3.9	1.9	15.1	8.5	5.4	13.6	9.5	4.2				
Treeline	3910	-12.5	4.0	-4.2	1.6*	14.8	8.2	5.1	13.3	9.2	3.9				
Krummholz line	3925	-13.1	3.4	-4.8	1.0*	14.2	7.6	4.5	12.7	8.6	3.3				

*Absolute minimum sometimes goes to below 0°C