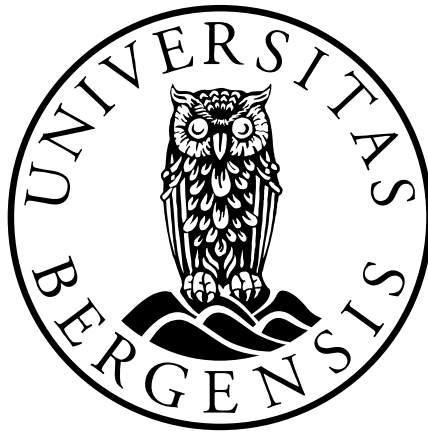


# **Species Richness Patterns in Space and Time in the Himalayan Area**

**Chitra Bahadur Baniya**



Dissertation for the degree of philosophiae doctor (PhD)

University of Bergen, Norway

2010



# Species Richness Patterns in Space and Time in the Himalayan Area

Chitra Bahadur Baniya



Dissertation for the Degree of Philosophiae Doctor (PhD)

University of Bergen, Norway, 2010



## All photographs taken by Chitra Bahadur Baniya

Photographs from left to right and first to the last rows:

1. Upper Manang, 3475 m, Nepal showing both active and abandoned fields
2. Buddha Mountain, 4985-5685 m, Tibet: Early snow fall in 2004
3. Bhraka, Upper Manang, 3175 m, Nepal showing both active and abandoned fields

1. *Pedicularis roylei*, 5010-5260 m, Buddha Mountain, Tibet
2. *Meconopsis horridula*, 5035-5360 m, Buddha Mountain, Tibet
3. *Gentiana urnula*, 5260-5460 m, Buddha Mountain, Tibet

1. *Ajania rubigena*, 5110-5385 m, Buddha Mountain, Tibet
2. *Lamiophlomis rotata*, 4985-5135 m, Buddha Mountain, Tibet
3. *Cremanthodium nanum*, 5335-5360 m, Buddha Mountain, Tibet

1. *Cremanthodium ellisii*, 5210-5435 m, Buddha Mountain, Tibet
2. *Delphinium brunonianum*, 5385-5435 m, Buddha Mountain, Tibet
3. *Saussurea tridactyla*, 5035-5310 m, Buddha Mountain, Tibet

1. *Arctocetraria nigricascens*, 5085-5585 m, Buddha Mountain, Tibet
2. *Thylacospermum caespitosum*, 5310-5510 m, Buddha Mountain, Tibet
3. *Saussurea* sp., 5210-5285 m, Buddha Mountain, Tibet

# Contents

|                           |      |
|---------------------------|------|
| DECLARATION.....          | IV   |
| ACKNOWLEDGEMENTS.....     | III  |
| ABSTRACT.....             | VIII |
| LIST OF PUBLICATIONS..... | X    |

## Synthesis

|  |    |
|--|----|
| INTRODUCTION.....  | 1  |
| <i>AIMS</i> .....  | 4  |
| <i>BUDDHA MOUNTAIN, TAR- PAPER I</i> .....   | 5  |
| <i>TIBET'S HIGHEST ALPINE ZONE- PAPER II</i> .....   | 6  |
| <i>NEPAL-PAPER III</i> .....   | 7  |
| <i>MANANG-PAPER IV</i> .....   | 9  |
| TERMINOLOGY .....  | 10 |
| SCALE .....  | 10 |
| AREA .....   | 14 |
| VARIABLES AT THE LOCAL-SCALE.....  | 14 |
| VARIABLES AT THE LANDSCAPE-TO-MACRO-SCALES.....  | 15 |
| VARIABLES AND MECHANISMS INFLUENCING SPATIO-TEMPORAL RICHNESS PATTERNS   | 17 |
| <i>SAMPLING ARTEFACTS</i> .....  | 17 |
| <i>MASS EFFECTS</i> .....  | 18 |
| <i>SPECIES-POOL</i> .....  | 18 |
| <i>HISTORICAL FACTORS AND LOCAL-SCALE COMMUNITY SUCCESSIONAL PATTERNS</i> .....                                | 19 |
| <i>CLIMATE AND ENERGY-RELATED VARIABLES TO EXPLAIN LANDSCAPE AND MACRO-SCALE ELEVATIONAL PATTERNS</i><br>..... | 20 |
| <i>MECHANISMS UNDERLYING THE UNIMODAL RICHNESS PATTERN OF LICHENS OF NEPAL AND TAR</i> .....                   | 22 |
| <i>STRESS, STABILITY, DISTURBANCE AND WATER-ENERGY DYNAMICS</i> .....  | 23 |
| CONCLUSIONS .....  | 25 |
| FUTURE PLAN .....  | 26 |
| REFERENCES.....  | 27 |

## Papers I-IV

# Declaration

This dissertation consists of an introduction, two published, and two papers submitted for publication. Three papers are co-authored and one is a single author paper. The publishers of both the published papers granted copyright permission to include them in this thesis. The nature of the contributions by the different authors is outlined below.

Paper I:

**Baniya, C.B., Solhøy, T., Gauslaa, Y. & Palmer, M.W.** Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. (*Submitted*).

Chitra Bahadur Baniya – Ideas, concept, field design/work, data processing, statistical analysis, writing, editing, and correspondence

Torstein Solhøy – Supervision, rechecked field work

Yngvar Gauslaa – Editing

Michael W. Palmer – Statistical analysis, editing

Paper II:

**Baniya, C.B.** Vascular and cryptogam richness in the world's highest alpine zone, Tibet. (*Submitted*).

Own idea, concept, data collection, processing, writing and corresponding

Paper III:

**Baniya, C.B., Solhøy, T., Gauslaa, Y. & Palmer, M.W.** 2010. The elevation gradient of lichen species richness in Nepal. *The Lichenologist*, **42** (1): 83-96.

Chitra Bahadur Baniya – Ideas and concept, literature and herbarium survey, processing, statistical analysis, writing, editing, review, correspondence to the journal

Torstein Solhøy – Supervision, editing

Yngvar Gauslaa – Editing, making graphs, guiding to correspond the journal Editor

Michael W. Palmer – Statistical analysis, editing

Paper IV:

**Baniya, C.B., Solhøy, T. & Vetaas, O.R.** 2009. Temporal changes in species diversity and composition in abandoned fields in a *trans*-Himalayan landscape, Nepal. *Plant Ecology*, **201**: 383-399.

Chitra Bahadur Baniya – Ideas, concept, field design, field work, taxonomic identification, data processing, data analysis, writing, and editing

Torstein Solhøy – Supervision

Ole Reidar Vetaas – Supervision, editing, correspondence to the journal

# Acknowledgements

This dissertation could not have reached completion without positive thoughts, significant guidance, practical help and advice. A foreign PhD student such as me who did fieldwork in outside of my own received substantial help from a number of people and organizations. I would like to acknowledge them all. Thanks to the Norwegian State Loan Fund (Lånekassen) for funding this study. I thank the Service Commission, Science Dean Office, and Central Department of Botany, Tribhuvan University, Nepal for a study leave; to the Network for University Co-operation Tibet-Norway, Oslo, and Faculty of Mathematics and Natural Science, Bergen University.

I am indebted to Torstein Solhøy for supervising me. I benefitted greatly from many aspects of his academic and social networks. I got a great help from both of my co-supervisors Yngvar Gauslaa, Norwegian University of Life Sciences, Ås and Mike W. Palmer, Oklahoma State University, Oklahoma, USA. I will never forget Yngvar, all his encouragements, and practicalities in strengthening my academic field. Many thanks to Mike, he visited me and my family from such a long distance. I got his great time and insights to be realistic on natural data than model. My sincere thanks also go to Ole Reidar Vetaas and Per Harald Salvesen for helping me to come to Bergen University as their MPhil student. I thank to Walter Obermayer, University Graz for helping me in many ways and also thank to all my co-authors for their valuable comments and time.

Academic difficulties during my PhD such as plant identification, statistical analysis, analysing software, books, literature, writing and editing were made possible and easier by John Birks. I got whatever I wanted from him. His valuable comments and remarks after each edition on my manuscripts made me optimistic. I am very much fortunate that he and Hilary invited me to several lovely dinners at their home, got nice time to watch slides and DVDs of his expeditions in High Asia, and alpine areas of the world. My sincere gratitude is always to John Birks and Hilary Birks. Without their help I would not have been able to achieve a PhD.

I got both academic and administrative help from all members of the Department of Biology, the EECRG research group, the Science Library, and Centre for Foreign Students, University of Bergen. All are highly acknowledged. Some special names are Tor Tønsberg, Per Magnus

Jørgensen, Dagfinn Moe, Torbjørg Bjelland, Dag Olav Øvstedal, Astri Boten, Solfrid Hjelmtveit, Beate Helle, Peter Emil Kaland, Einar Heegaard, John-Arvid Grytnes, Vigdis Vandvik, Richard Telford, Ingrid Solhøy, Ana Veronica Cordova, Leikny Lavik, Hege Folkestad, Late. Arvid Kleppe and Tommy Strand who helped me in many ways. Also help provided by Knut Helge, Arild Breistøl, Frode Falkenberg, Gaute Bø Grønstøl, and John Skarveit was indispensable.

I am grateful to my respected teachers Govind Prasad Sharma Ghimire and Pramod Kumar Jha from the Botany Department, Kirtipur, Nepal and Bijaya Kattel from Florida, USA. I am happy that they motivated me in the field of botany, plant ecology and lichenology. Many thanks to Ram Prasad Choudhary, Krishna Kumar Shrestha, Sanu Devi Joshi, Janak Devi Manandhar, Vimal Narayan Prasad Gupta, all teachers, staff and students of Central Department of Botany who helped me in different ways during my PhD. Many thanks for sharing all my responsibilities of teaching during the time when I was away.

I will not forget the time and life I shared with many international students at Fantoft, staffs at Fantoftgård kindergarten. I got help from many international friends. Renuka Priyantha Ilandarige, a student at UoB from SriLanka receives my special thanks for his kindness in sharing with me many aspects as well as time with his family. The Nepalese Society in Bergen (NEBERS), Nepalese students and families at Fantoft always kept me and my family in touch and alive with all things Nepalese and Nepal. All Nepalese at Bergen and particularly Krishna Babu, Keshav Paudel, Prativa, Bishnu, Kapil, Deepak, Rajiv, Buddha, Meeru, Jyoti, Chandana and Anank Bhandari were cooperative in many ways. I enjoyed the company of my colleagues Marianne Presthus Heggen, Arguitxu de la Riva Caballero, Bjørn Arild Hatteland, Brooke Wilkerson, Ingelinn Aarnes, Ronald Semyalo, and La Duo for sharing coffees and lunch with me and many invaluable discussions during my PhD life.

My fieldwork in Tibet and Manang, Nepal would not have been possible without great help provided by friends such as Tsering, La Qiong, CaiDong, PuBu, Migmar, Dronba, Joachim Schmidt, Chhong Norupa, Ram Prasad and others. Thank you all. I got time to participate in PhD courses in Sweden and Iceland. Many thank to Kristina Articus, Uppsala University, Sweden and Bjarni E. Guðleifsson, Agricultural University, Iceland for giving me valuable time. My special thanks go to Cathy Jenks for her valuable time in language correction and practical suggestions.



*Finally, I would like to dedicate this PhD to my respected parents who raised me in such a remote village with never-ending love and faith, to my dear brothers and sister who encourage me regularly, my wife Hira who is painlessly helping me with her full support, co-operating with me in my every difficulty of PhD life, especially the final year when I run out of financial support, my dear wise and lovely kids Pratima, Prabhat and Pratik who are patiently looking forward for me to finish my PhD and to rejoin their school back home, and are always eager to look at BUWA's (father) happy face when I returned home every evening from University and my brothers-in-law, Nanda Bahadur and Shiva who are helping me regularly from Nepal.*

Bergen, December, 2009

Chitra Bahadur Baniya



# Abstract

Baniya, C.B. 2010. Species Richness Patterns in Space and Time in the Himalayan Area. PhD Thesis, Faculty of Science, University of Bergen, Norway.

**Aims:** The Himalayan Mountains are highly sensitive to current global climate changes and their local impacts. Potentially more sensitive are lichens growing throughout the Himalaya and species living in the alpine zones of the world. In this synthesis I examine the variation in species composition and richness patterns at different scales of spatio-temporal gradients from mountainous areas in the Tibet Autonomous Region (TAR) and the Nepalese Himalaya.

**Methods:** This thesis is based on field-survey data as well as secondary data from published floras. The study of the temporal responses of plant species composition, richness and soil heterogeneity is based on direct field sampling in old abandoned fields forming different chronosequences in the *trans*-Himalayan zone, Nepal. Likewise, the elevational response of species composition, richness patterns and soil nutrient heterogeneity are investigated by direct field observations and sampling in Buddha Mountain, Nyenchentanglha Shan, Central Tibet, TAR. Buddha Mountain elevation gradient study is compared with similar species but based on secondary data, namely published floras over almost a similar elevational range. The elevation gradient of lichen species in Nepal has been studied based on published literature on Nepalese lichens.

**Major findings:** (i) Lichens, both in TAR, on Buddha Mountain and in the Nepalese Himalaya represent the organism group with the highest elevational occurrences and a high degree of adaptations to extreme environments. A unimodal elevational relationship is common in lichen species richness. Maximum richness for Nepalese endemic lichens coincides with the maximum elevation range for Nepalese vascular plant endemics. (ii) Landscape-level elevational species richness patterns (Buddha Mountain) show an early plateau and a sharp decline afterwards that differs from the smooth declining pattern with the interpolated macro-scale elevational ranges. This may indicate that differences in scale of the

measurement of species, averaging out of environmental heterogeneities and the influence of climatic variables increasing with increasing spatial scales are all potentially important. (iii) The general pattern for the total richness hides a variety of specific patterns for the subgroups of life-forms and substrate types considered. (iv) A divergence pattern of secondary succession is indicated after increasing beta diversity along the temporal gradient in the *trans*-Himalayan zone. But the total species richness clearly indicated a unimodal species richness pattern in the secondary succession. Decreased richness with increased beta diversity towards the oldest abandoned fields highlights the potential importance of the high intensity of grazing, and grazing-tolerant ‘nurse’ species protecting future forest species.

**Conclusions:** Species richness and composition patterns are highly scale dependent at all levels of spatio-temporal gradients. Scales at all hierarchical levels are inter-related. Some variables such as soil-related local-scale heterogeneity are highly important at the local-scale species composition and richness patterns. But that type of variables will not be significant or will be averaged out at a broader scale. Climate-related variables are highly influential at the broad-scale but can also be influential at local scales. Species richness patterns depend on the studied group of species, functional group of species, life-forms and their geography. The ecological significance of species depends on elevation. For example, in Nepal an elevation of 500 m is suitable for big wild animals, likewise 1000 m for vascular plants and 3100 to 3400 m for lichens. This indicates an important conservation strategy.

**Implications:** Further investigation on elevational and temporal species richness patterns in other landscapes of both Tibet and Nepal Himalaya will extend the findings of the present study and help to predict the local impact of broad-scale climate change on the biodiversity hotspots of the Himalaya.

**Keywords:** Species richness, lichen, elevation gradient, Nepal, Himalaya, Tibet

## List of publications

The dissertation is based on the following four publications, and they will subsequently be referred by their Roman number in the synthesis.

Paper I:

**Baniya, C.B., Solhøy, T., Gauslaa, Y. & Palmer, M.W.** Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. (*Submitted*).

Paper II:

**Baniya, C.B.** Vascular and cryptogam richness in the world's highest alpine zone, Tibet. (*Submitted*).

Paper III:

**Baniya, C.B., Solhøy, T., Gauslaa, Y. & Palmer, M.W.** 2010. The elevation gradient of lichen species richness in Nepal. *The Lichenologist*, **42** (1): 83-96.

Paper IV:

**Baniya, C.B., Solhøy, T. & Vetaas, O.R.** 2009. Temporal changes in species diversity and composition in abandoned fields in a *trans*-Himalayan landscape, Nepal. *Plant Ecology*, **201**: 383-399.



# **Synthesis**

Species Richness Patterns in Space and Time in the  
Himalayan Area

**Chitra Bahadur Baniya**





# Introduction

Every mountain has its own special meaning and symbolism at least in the culture in which I grew up. For example, people often go for pilgrimage to Mount Kailash (in western Tibet) in the belief that the mountain was the birth-place of the God Shiva. Many wonders and questions are associated with each mountain besides its beauty. Explaining differences in species composition at a particular time and space are one of the hardest problems for an ecologist. A great mystery is concerned with how species differ in their number, type and zonation within and between mountains.

It has been almost 200 years since biogeographers tried to explain scientifically the latitudinal gradient of species diversity. Willdenow (1805), von Humboldt (1849), Darwin (1859), Wallace (1878), etc. were among the early famous biogeographers, evolutionary biologists and ecologists who initiated studies of diversity gradients. Willdenow (1805) was perhaps the first to present the soil and heat-energy related hypotheses to explain species richness patterns. However, gradients in species diversity are an old concept. It may have been known to Stone Age people because they were familiar about where to find prey after fighting, burning etc. (Lomolino 2001, Lomolino *et al.* 2006). Different names are given to their daily routine nowadays, such as spatial autocorrelation and non-random distribution of resources for finding game animals after fire, etc.

The altitudinal (elevation) gradient is believed to be a mirror of the latitudinal gradient in species richness (Stevens 1992, Rahbek 1995, 1997, 2005). There are, however, some differences such as the condensation of huge latitudinal area into a short, narrow elevation band (Körner 2003, 2007). Many ecologists have strongly utilized both latitude and altitude as the main predictors for species richness in their studies (Pianka 1966, Rohde 1992, Brown 1995, Vazquez & Givnish 1998, Odland & Birks 1999, Gaston 2000, Körner 2000, Ohlemuller & Wilson 2000, Brown 2001, Heaney 2001, Lomolino 2001, Md. Nor 2001, Grytnes 2003, Bhattarai *et al.* 2004, Carpenter 2005, Herzog *et al.* 2005, Oommen & Shanker 2005, Rahbek 2005, Wilson *et al.* 2005, Bruun *et al.* 2006, Fontaneto & Ricci 2006, Harris 2006, Lomolino *et al.* 2006, Grau *et al.* 2007, Mittelbach *et al.* 2007, Qian *et al.* 2007, Romdal & Grytnes 2007, Kessler 2009). A review by Rahbek (2005) found 204 studies that concentrated on species richness patterns for different species along the macro-scales of

elevational or latitudinal gradients in different parts of the world. More than 120 different plausible hypotheses related to species richness have been compiled (Palmer 1994), and the number is increasing. However, many of them are neither mutually exclusive, nor inclusive, with more than 100 violating the assumptions of the competitive exclusion principle (Palmer 1994).

After Brown (1995) laid the foundation of macro-ecology, studies on elevational gradients became popular among ecologists to answer earlier questions related to diversity theory for both latitude and altitude. The altitudinal gradient is believed to be a natural experimental station on each mountain (Körner 2007). Studies on species richness patterns that mainly focus on area (Palmer & White 1994, Rosenzweig 1995), energy (Wright 1983, Palmer & Dixon 1990), water-energy (O'Brien 1993, Hawkins *et al.* 2003), evolutionary time (Ricklefs 1987, Begon *et al.* 1990, Mittelbach *et al.* 2007), competition and disturbance (Connell & Slatyer 1977, Grime 1977, Connell 1978, Huston 1979, Tilman 1982), fire (Auclair *et al.* 1976), and the species pool concept (Zobel 1997) have contributed much. There is now increasing consensus about that macro-scale patterns are resulting from available energy, evolutionary time, habitat heterogeneity, area and geometric constraints (Mittelbach *et al.* 2007). Despite this consensus, debates continue regarding issues on other aspects of species richness patterns.

Similarly, the foundation of the temporal gradient in species richness patterns was laid by Cowles (1899) after his study on plant colonization on the sand-dunes of Lake Michigan. It greatly influenced Fredric E. Clements who later presented a challenging holistic theory of succession (Clements 1928) and ecosystem development. This holistic view of succession is hotly debated among ecologists. The contrasting individualistic theory of succession and ecosystem development was proposed by Gleason (1926). Both theories are still critical in studies on succession and community ecology. It has been believed that both these theories may be appropriate but at different scales (e.g., Odum 1971, Horn 1974, Pickett 1976, Glenn-Lewin 1980, Christensen & Peet 1984, Carson & Barrett 1988, Inouye & Tilman 1995, Fukami *et al.* 2005, del Moral 2007). Questions of scale will be discussed below. North America became one of the highly active areas in research related to secondary succession or old-field succession study followed by work in Europe (Bazzaz 2005). The Initial Floristic Composition (IFC), and Relay Floristic Composition (RFC) models of succession (Horn 1974), and the facilitation, inhibition and tolerance mechanisms of

succession (Connell & Slatyer 1977) were well accepted in successional studies. Each theory is not free of debate. The Long Term Research (LTR) at the Park Grass Experimental Station of Rothamsted, England is a good tool to resolve some of these debates (Silvertown *et al.* 2006). In addition, long-term and chronological short-term temporal responses in species richness patterns on glacier forelands and in palaeoecological research will help to resolve some of these debates.

Surprisingly, the Himalaya, one of the global biodiversity hotspots (including its central part, Nepal) is poorly explored in term of its biodiversity. Within the Himalaya, lichens which are known to be a very sensitive group of species to environmental change have been completely ignored. There have been some taxonomic studies done on this group by foreign as well as Nepalese scientists. More than 2000 species of lichens are expected to occur in Nepal (Sharma 1995), but a critical documentation hardly exceeds 525 species (Paper III).

When I looked at the history of the botanical exploration of Nepal, it dates back to 1802 during which the first botanical exploration of Nepal was done by Francis Buchanan-Hamilton, a superintendent at the Royal Botanic Garden, Calcutta (Rajbhandari 1976). The second major exploration was done in Eastern Nepal by Sir J. D. Hooker in 1848. The first elevational species gradient paper related to forest-tree species in Nepal was published by Yoda (1967). Almost after three decades an another elevational species richness pattern on animals and mammals of Nepal was published by Hunter & Yonzon (1993). In-between, the vegetation and ecological map of Nepal was published (Dobremez & Jest 1969). Research regarding to Nepalese biodiversity is now increasing in the current decade. Unfortunately, Nepal does not have a flora, and it is thus far from knowing its real diversity status. It is the same in the Tibet Autonomous Region (TAR). Flora Xizangica was published (Cheng-yih 1983-1987) by the Chinese Academic of Sciences but it has not been revised after its initial publication. Both Nepal Himalaya as well as TAR are far from knowing the real status of biodiversity of its flora and fauna. Both areas lie in a highly sensitive and highly vulnerable zones with respect to predicted global climate changes (IPCC 2007). The high mountains of Nepal and Tibet share and store more than 85% of the water necessary for people living further down slopes or on the plains. Most of the biggest Asian rivers originate from here. IPCC (2007) says that almost 82% of the TAR's glaciers have already vanished as have glaciers in Nepal. Unfortunately, we do not know which species we already have lost, and

that we are currently losing. Loss of biodiversity is an inevitable result of change in climate that has been experimentally proved (Silvertown *et al.* 2006).

Such perspectives urged me to start biodiversity research in the Nepalese Himalaya. First I tried to understand the response of species along short chronosequences. Abandonment of agricultural and pastoral land is a common and dominant practice mostly in the high *trans*-Himalayan zone in Nepal. Thus I selected this as a main source of landscape change to study short-term temporal changes in species richness patterns in Nepal together with elevational species richness patterns. I chose one mountain in TAR to study the elevational pattern of all species including lichens. Later, I compared this local elevational species richness pattern with the species richness of the whole TAR using data from floras.

After comparing the results from different ecological approaches, contrasting spatial and temporal scales of investigations, and rigorous statistical testing, I hope to maximize the scientific soundness of my conclusions and to increase ecological understanding from my work.

## *Aims*

Climatically harsh and unstable conditions at high elevations may give a decline in species richness but this is not the case on sub-tropical mountains directly, on a macro-scale, or for functional groups. On the climatically more congenial sub-tropical mountains, the Nepalese elevation gradient shows unimodal species richness patterns for vascular plant, fern, moss, liverwort and orchid richness but is not known for one of the most sensitive organisms in nature, namely lichens. The study of species richness patterns in the short temporal change gradient in the *trans*-Himalayan zone is one of the first studies of its kind in this area.

The specific questions that this thesis addresses are as follows:

Paper I: Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet.

- How does floristic composition vary within a landscape whose elevation represents the mid- to the high-alpine zone of Buddha Mountain?

- How do the richness patterns vary in functional groups, and between a quadrat-based field survey and an interpolation study?

Paper II: Vascular and cryptogam richness in the world's highest alpine zone, Tibet.

- How does the elevational species richness pattern vary along TAR's mid- to high-elevation gradient?
- How do the functional groups behave along this elevational richness pattern, and which climate variables may influence these patterns?

Paper III: The elevation gradient of lichen species richness in Nepal.

- How does lichen species richness vary along the elevational gradient in Nepal and do their functional groups follow this overall pattern?

Paper IV: Temporal changes in species diversity and composition in abandoned fields in a *trans*-Himalayan landscape, Nepal.

- What is the successional compositional pattern of species in different aged abandoned fields?
- Do the changes in species richness and beta diversity match with the temporal gradient? Which local factors influence these successional patterns?

I made Paper I is core of this dissertation under which research questions are generated and answered by other papers. These studies are based on the following study areas:

### ***Buddha Mountain, TAR- Paper I***

Buddha Mountain (30° 11' N, 90° 29' E) lies 100 km north-west of Lhasa, the capital of TAR. The altitude of this mountain ranges from 4985 to 5700 m above sea level. According to the Meteorological Bureau of Lhasa, Damzhung is the closest climatic station (about 80 km NE, and at 4200 m asl) from the study site and has a mean annual temperature of 1.5°C, mean summer temperature of 14°C, and the mean winter temperature is -7°C. The mean annual precipitation is 442 mm. The vegetation of the studied mountain slope below 5300 m

asl represents an alpine steppe type of the mid-alpine zone and nival or desert type above 5300 m asl (Chang 1981, Miede 1988, Birks *et al.* 2007). *Kobresia* spp., *Stipa koelzi*, cushions of *Androsace tapete* and *Arenaria bryophylla*, *Astragalus donianus*, *Oxytropis* spp., *Ranunculus lobatus*, *Lancea tibetica*, and *Thalictrum alpinum* together with *Saussurea* spp. represent species common to alpine steppe vegetation. *Sedum* spp., *Rhodiola* spp., *Androsace coronata*, *A. zambalensis*, *Arenaria gerzensis*, *Thylacospermum caespitosum*, *Draba glomerata*, *Gentiana urnula*, *Ranunculus involucratus*, *Saxifraga* spp., *Koenigia islandica*, *Anomobryum concinatum* and some saxicolous lichens such as *Dimelaena oreina* and *Rhizoplaca peltata* represent alpine type species.

### ***Tibet's highest alpine zone- Paper II***

Elevation between 4900 to 6000 m asl of TAR is the study area of paper II. The Tibetan Plateau is the largest and highest and the youngest alpine plateau in the world (Chang 1981). It is surrounded by tall mountains with an average elevation between 4500 to 5000 m asl. Tibet Autonomous Region (TAR) or Xizang is the political and official designation by the government of China to represent part of the present Tibetan Plateau. TAR stretches between 78° 25' to 99° 06' E and 26° 50' to 36° 53' N with altitudinal range between 2700 to 8848 m asl. It covers an area of 1.23 million km<sup>2</sup> (Birks *et al.* 2007). It runs parallel to the main Himalayan arc, over 2500 km long. Its eastern border is with other biodiversity hotspots, such as the Yunnan and Sichuan provinces of China, whereas its north-western border meets the Karakorum Mountain and the Takla Makan desert (Dickoré & Miede 2002).

The Tibetan Plateau was believed to be uplifted over the last 120 million years due to the collision between the Asian plate and continental fragments (Molnar 1989, La Duo 2008). Later, the Himalaya was believed to be uplifted after collision between the Asian and the Indian plate about 60 million years ago (Singh & Singh 1987). Thus, the Tibetan Plateau may have a history almost twice that age of the Himalaya. Both are considered as the youngest and the most fragile mountain areas in the world.

Very tall mountains and the Plateau of TAR play a major role in the central Asian climate and its biota. The TAR has 50-60% less atmospheric pressure than sites at the sea level, lies closer to the troposphere than mountains elsewhere, causing great impacts on the

atmospheric circulation, heats up land masses more quickly, receives high solar radiation due to low interception by clouds, and receives the highest amount of UV-B radiation compared to mountains elsewhere (Chang 1981). These features made the Plateau a “Hot Island” (Birks *et al.* 2007). Life-forms adapted to this environment show an unique physiological and ecological adaptation. In addition, the Himalayan arch in the south-east acts as a strong barrier to the Indian monsoon. This creates a rain shadow in the TAR except in some narrow through-valleys in the south and east. The TAR receives an annual precipitation of 200-1000 mm during summer. It shows a spatial trend of decreasing precipitation from south-east to north-west. During the winter, cold and dry air blows out from central Asia due to the Siberian high pressure that creates winter rain towards the north-west. It also shows a spatial pattern of decreasing values towards the east. Lhasa, the capital of TAR which lies in the central part, receives 443 mm annual rainfall, and has an average annual temperature between -16.5°C and 7.7 °C to a 28.3°C extreme (Chang 1981).

The present vegetation of the TAR clearly indicates two horizontal (east-west) and vertical (north-south) gradients (Chang 1981, Miehe 1988, Ni 2000, Birks *et al.* 2007, Miehe *et al.* 2007, Miehe *et al.* 2008). TAR has a sub-tropical montane forest to high-cold desert vegetation along the horizontal gradient and sub-tropical rain forest to nival zone along the vertical gradient. Birks *et al.* (2007) classified the south-central TAR’s vegetation above 3500 m asl into 9 horizontal and 4 vertical zones based on annual precipitation. There is variation in each mountain system as elsewhere. However, TAR seems to have a more complicated vegetation zonation than elsewhere (Chang & Gauch 1986, Schaller 1998, Wang *et al.* 2007).

### ***Nepal-Paper III***

Paper III covers the whole country of Nepal. Nepal (26°22’ to 30°27’ N and 80°04’ to 88° 12’ E) lies in the central Himalayan zone. The average distance between east-west is 885 km and between north-south is between 145-248 km (Kansakar *et al.* 2004). Both eastern and western Himalayan elements are present here. The country has the highest mountain in the world, Mount Everest (8848 m asl) with TAR. The lowest elevation is at 60 m asl towards the south. The shape of the country looks like a tilted rectangle, bordered by the Indo-Gangetic plain on three sides and by TAR in the north. Eastern Nepal, the less tilted side on

the map, lies closer to the eastern Himalaya, the main entrance for the Indian Monsoon coming from the Bay of Bengal. The monsoon is the main source of precipitation that has a spatial pattern starting from eastern to western Nepal. It begins in May and ends in September. Winter precipitation is also available here but that spreads from western Nepal through westerly winds. It also shows a spatial pattern beginning from western Nepal and ends towards eastern Nepal. Some places in central Nepal, e.g. Lumle and Langtang receive the highest amounts of annual precipitation (above 6000 mm) (Kansakar *et al.* 2004). Some rain-shadow areas are also present in Nepal such as Upper Manang and Dolpo that lie behind the main mountain range. These areas hardly receive more than 400 mm annual precipitation and resemble the Tibetan Plateau.

Weather conditions in Nepal vary from place to place. During summer, the southern part of Nepal which is the flat lowland (Terai) experiences maximum temperatures between 35-40°C, while hilly regions have 22-27°C. Likewise, winter temperatures in the flat lowland ranges between 7-23°C, and the hills have around 12°C. There are places at high altitudes that are always covered by snow and have freezing temperature throughout the year.

The elevation gradient is a very strong, sharp and important ecological gradient in Nepal. Within the shortest north-south transect of about 200 km distance one can pass from the tropical to the nival zone (Dobremez 1976). The elevation gradient in Nepal is also inseparable from land-use patterns. Nepal is an agricultural country where almost 90% of the population directly dependent on subsistence agriculture and livestock (Menon 2009). All agricultural practices depend directly on the monsoon and the westerlies in the hilly mountains regions except some arable areas in the flat inner valleys, and lowlands such as Terai where irrigation is a common practice.

Nepal has been divided horizontally into five physiognomic zones: Terai, Siwalik, Mahabharat, Greater-Himalaya and Trans-Himalaya (Hagen 1969, Upreti 1999). Each zone represents a definite elevation range. Similarly, the vegetation of Nepal has been classified into 8 elevational zones: Tropical, Sub-tropical, Lower temperate, Temperate, Sub-alpine, Open low-alpine, Mid-alpine and Nival zones (Yoda 1967, Dobremez & Jest 1969, Stainton 1972, Dobremez 1976, Miehe 1982, 1989, Stainton 2001).



## ***Manang-Paper IV***

Manang (28°40'N to 84°01'E) is one of the 75 districts of Nepal that lies in the north-central part. The peculiarity for this district is its location behind the Annapurna massif of above 7000 m asl elevation. This Himalayan range creates a rain shadow in this district. Thus Manang falls in the *trans*-Himalayan zone. It receives annual rainfall of about 400 mm, the temperatures recorded at Jomsom, 30 km south of this U-shaped valley are between -1.8 and 7.9°C during winter versus 14.2 and 23°C in summer (Anonymous 1999). The monsoon begins from the south-east and decreases to the north-west. The Marshyangdi River passes all the way through this district and forms an U-valley in upper Manang and a v-shaped valley towards lower Manang. My study area lies in upper Manang. This part of Manang has two distinct slopes. Part of the landscape towards the Annapurna massif is the north-facing slope with forests of *Pinus wallichiana*, *Abies spectabilis*, and *Betula utilis*. On the drier south-facing side there are settlement areas, some agricultural fields and bushes of *Juniperus* spp.

The main agricultural fields are located on either side of the Marshyangdi River. Agricultural fields are also located near villages as well as closer to the forest far from villages. However, many agricultural fields have been abandoned. Pisang has about 150 ha agricultural land out of which 75% is abandoned. Similarly, Bhraka has about 185 ha out of which 60% is abandoned (Paper IV). Villagers left their fields in different years due to many reasons. I sampled the abandoned fields belonging to two villages, Pisang and Bhraka. Pisang is located at a lower elevation than Bhraka and approximately 12 km away. Elevational difference among all the sampled abandoned fields in Pisang is 300 m asl (3175 to 3475 m asl) and 50 m asl (3400 to 3450 m asl) in Bhraka. A total of 42 abandoned fields are available for this study (paper IV).

# Terminology

Diversity studies use terms that need to be well defined. The concept of species richness is commonly used for the number of species in a sampling unit, and species diversity to denote the species richness and evenness at local scales (Whittaker *et al.* 2001). Some ecologists apply the terminology 'species density' to represent the number of species sampled in each standardized sample unit, e.g. per unit area (Whittaker 1975, Carpenter 2005) while others retain the terms 'diversity' or 'richness' rather than 'density' (O'Brien 1993, Grytnes 2002) for such applications. Different indices of biodiversity such as Shannon-Weaver's H, Simpson's  $\lambda$ , etc. are also commonly used. Such indices can be confusing and may not be easy to understand (Peet 1974, Huston 1994).

This dissertation uses the term 'species richness', because it is self-explanatory and has comparability with other studies. Species richness is the fundamental measure of community and regional diversity (Magurran 1988, Gotelli & Colwell 2001). Thus the species richness as used in this thesis is the total number of species present within the six  $1 \times 1 \text{ m}^2$  quadrats per 25 m elevation band (Paper I), the total number of species within each 100 m elevation band (Papers II and III), and the total number of species within each  $1 \times 1 \text{ m}^2$  plot (Paper IV). The smallest sampling units of quadrats and plots are considered synonymous. This thesis focuses on species richness of plants and lichens in Papers I and II, lichens in Paper III and only vascular plants in Paper IV. Species richness also applies to specific functional group richness such as forb, graminoid, cushion, shrub, crustose lichen, foliose lichen, fruticose lichen, green algal lichen, cyanobacterial lichen, saxicolous lichen, terricolous lichen, corticolous lichen etc.

# Scale

The concepts of scale and space in biodiversity studies are highly debated among ecologists. The importance of scale was first realized by R. H. Whittaker (1960) when he documented the biodiversity of Siskiyou Mountain, Oregon, USA. He coined the Greek lettering scheme of  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\epsilon$ ,  $\delta$ , etc. to represent the diversity patterns at different scales. Among them, the first three are widely used. According to Whittaker (1960),  $\alpha$  diversity represents the diversity in an individual stand or sampled unit. His Siskiyou Mountain diversity represented the  $\gamma$  diversity, and the change in species composition along stands or gradient was

designated  $\beta$  diversity. The lack of lower and upper limits to this landscape scale of diversity created controversies and confusions among ecologists. Later, Whittaker (1977) introduced a further classification regarding the measurement scale of biodiversity study. The importance and awareness of scale in ecological studies have increased in recent years (e.g., Rahbek 1995, Rahbek 1997, Whittaker *et al.* 2001, Willis & Whittaker 2002, Rahbek 2005, Willis & Bhagwat 2009), although recognized already by Allen & Starr (1982). To minimize controversies among ecologists regarding scales, Whittaker *et al.* (2001) proposed the three following intuitive terms: local-scales, landscape scales and macro-scales in their hierarchical theory of biodiversity.

Applying the scale concept to this thesis, the species richness inside each six  $1 \times 1 \text{ m}^2$  quadrats per 25 m elevation band in Paper I represents  $\alpha$  diversity and belongs to local-scale diversity. The turnover of species between each two elevation bands represents  $\beta$  diversity. It was estimated through the DCA- I axis sample score as a function of elevation, which is a valid method (Lepš & Šmilauer 2003). The whole mountain range of Buddha Mountain represents the landscape scale ( $\gamma = 143$  species). Similarly, species richness inside each  $1 \times 1 \text{ m}^2$  plot in Paper IV represents the local-scale or  $\alpha$  diversity, and the turnover between two plots represents  $\beta$  diversity. Here  $\beta$  diversity was estimated through the length of the gradient of the DCA- I axis. If I follow the hierarchical theory of Willis & Whittaker (2002), Paper IV represents the landscape spatial scale with  $\gamma = 136$  species and the local temporal scale change between 1 to 50 years. Papers II and III belong to a macro-scale study with  $\gamma = 642$  and 525, respectively.

Scale has three aspects in ecology: spatial, temporal and organizational complexity (Levin 1981). Likewise, spatial scale also has three components: sample size (grain or focus or individual size of quadrat or plot), extent and intensity (Wiens 1989, Palmer 1994, Whittaker *et al.* 2001). The sample size defines the lowermost limit of study that directly correlates with the body size of the organism studied (Brown *et al.* 2004). Sample extent defines the maximum area (uppermost limits) of study. Sample intensity defines the number of sampling units in the study. Thus in combination these three spatial components quantify the variation in the studied system. Systems are highly hierarchical in nature, dynamics at lower scales affect the dynamics of a system at higher levels and vice versa (Allen & Starr 1982, O'Neill 1989). Thus there is a strong link between grain size and extent of study area. Smaller grain

size is used to detect variation at local scale and larger grain size is used to detect larger (regional) variation.

The six  $1 \times 1 \text{ m}^2$  quadrats (Paper I), and  $1 \times 1 \text{ m}^2$  plots (Paper IV) represent the sampling size or focus for my study. The area in each 100 m elevational band between 4900 to 6000 m of the TAR (Paper II), and 100 m between 200 to 7400 m of Nepal (Paper III) do not represent the actual sampling size. It covers a large geographical area. It is impracticable to sample both TAR and the Nepalese Himalayan gradient completely. Thus, the number of species at each 100 m elevational band was counted for each study.

Paper I covers a 2.3 km transect. Paper II studies an average north-south distance of about 950 km and an average east-west distance of about 2150 km comprising an elevational range between 4900 to 6000 m. Paper III deals with an average east-west distance of about 885 km, and an average north-south distance of about 250 km to cover the elevational range of the whole of Nepal between 200 to 7400 m. Paper IV studies approximately a 1 km long transect located in abandoned fields of each village.

With respect to sampling intensity, Paper I is based on 174 quadrats per ca.  $200 \text{ km}^2$ . However, the resolution has been reduced to  $n = 29$  to avoid pseudoreplication. Paper II is based on 12 elevation bands between 4900 to 6000 m elevations in TAR of approximately  $612\,000 \text{ km}^2$  area. Paper III is based on 73 elevation bands between 200 to 7400 m elevation in Nepal comprising  $140\,000 \text{ km}^2$ . Paper IV is based on 242 plots in ca.  $2.2 \text{ km}^2$  abandoned fields.

Temporal scale cannot always be separated from those of spatial scale. Willis and Whittaker (2002) have classified the ecological temporal scale into three levels confounded with the spatial scale in the hierarchical theory of biodiversity. According to them, the successional change in species composition and richness patterns recorded between 1 to 100 years can only be seen at the local scale, and is defined as the local temporal scale. If the dynamics occur between 100 to 1000 years, this will fall under a landscape temporal scale. Finally, pattern occurring in more than 10,000 years is defined as a regional temporal scale. Most of the community dynamics research falls under the local temporal scale regardless of study area size. Studies of chronosequences formed after abandoned agriculture, fires, volcano eruptions, sand-dune formation, deglaciated moraines or long term research studies are examples of the local temporal scale. Palaeoecological inventories comprising a time scale of

10,000 years are an example of regional temporal scale. Ecological research based on temporal scales between 100 to 1000 years is an example of the landscape temporal scale.

Paper IV represents purely the local scale temporal change in species composition and richness patterns in between 1 year to 50 years in old abandoned fields. As a short temporal gradient it is hard to separate it from the spatial scale. Thus the first axis sample scores were extracted out through an age-constrained Canonical Correspondence Analysis (CCA) and utilized as a predictor variable as was done by Lepš *et al.* (2001) and Bartolome *et al.* (2004). Other papers utilized temporal scales indirectly.

Organizational complexity scale may focus on variations within- and/or between populations. Experimental manipulations are needed to test hypotheses related to species diversity. All papers in this thesis are descriptive, dealing with spatial and temporal variation among communities. Papers I and IV are based on observational studies and Papers II and III are based on interpolation approaches. It was not possible to do any experimental manipulations in my thesis research.

Some authors such as Shmida & Wilson (1985) have suggested the minimum geographical area to measure biodiversity pattern. They suggested  $10^2$  to  $10^3$  m<sup>2</sup> area to measure terrestrial plants for  $\alpha$  diversity, and  $10^6$ - $10^8$  m<sup>2</sup> for  $\gamma$  diversity. Mittelbach *et al.* (2001) defined the scale of study based on geographical extent and ecological association. They recognized four geographical scales: local scales (0- $2 \times 10^4$  m), landscape scale ( $2 \times 10^4$  - $2 \times 10^5$  m), regional scale ( $2 \times 10^5$  - $4 \times 10^6$  m) and continental to global ( $> 4 \times 10^6$  m).

If I look at geographical distance for my samplings, Papers I and IV both cover at least 10-100 m distance between each sampling unit. This comes far below the lowest limit as set by Shmida & Wilson (1985). May be this limit applies more towards other ecological communities than sub-alpine or alpine areas which I have been studying. The geographical distance for Papers II and III are rather complicated to know as they are interpolation studies. Papers I (*ca.*  $2 \times 10^5$  m<sup>2</sup>) comes under the landscape geographical scale, both Papers II and III fall within the continental to global scales but paper IV ( $22 \times 10^2$  m<sup>2</sup>) represents the local scale of Mittelbach *et al.* (2001).

## Area

The space/geography (Area) occupied by species has been a controversial issue in diversity research. It took almost 35 years after the first publication of the Equilibrium Theory of Island Biogeography by MacArthur & Wilson (1967) to reach the general appreciation about the scale dependency of area (Palmer & White 1994, Rosenzweig 1995, Gaston 2000, Whittaker *et al.* 2001, Lomolino *et al.* 2006). Data dealing with species richness can only be compared between areas similar in size (Clinebell *et al.* 1995). This view was clearly highlighted by the differences in patterns between Papers I and II. Models at two different scales of areas of measurement (landscape in Paper I and macro-scale in Paper II) of species richness are used. Difference in patterns was thus directly connected to the scale of area. Paper III allowed a comparison of patterns shown by species richness along the same Nepalese Himalayan gradient. Based on earlier findings, I believe that the unimodal richness patterns for both total and endemic lichen richness documented in Paper III are caused by factors such as habitat diversity and environmental suitability rather than elevational band area. An area effect is also considered insignificant for the higher species diversity at the equator (Terborgh 1973, Rosenzweig 1995, Chown & Gaston 2000). All these authors believed that higher diversity at the equator is due to the larger continuous area with a similar ecoclimate that result in lower probabilities of extinction and higher probabilities of allopatric speciation.

## Variables at the local-scale

Environmental heterogeneity (Palmer 1990), disturbance (Connell & Slatyer 1977, Connell 1978, Huston 1979), fire (Auclair *et al.* 1976), and species pool (Zobel 1997) are local-scale dependent variables. Variations, tests and predictions in species-richness studies are usually done on local-scale data. Existing hypotheses are tested and theories are developed based on local-scale ecological studies.

Plant community dynamics and succession are visible phenomena at a local scale. In addition, changes in biomass and vegetation cover, as well as species richness changes after experimental treatments can also be striking processes. The long-term research at the Park Grass Experimental Station of Rothamsted, England is a good example of a local-scale

study. This experimental station, established in 1856 for other purposes than succession and competition studies, has provided a unique data source to resolve debates within local-scale plant ecology (Silvertown *et al.* 2006). The Resource Ratio Hypothesis of Tilman & Downing (1994) was developed based on this Long Term Research experiment (LTR). Successional changes that were well experimented in the 150 years LTR are still relevant in modern discussions dealing with stability and competition (Silvertown *et al.* 2006).

The first successional study started in the sand-dunes of Lake Michigan (Cowles 1899) which led Fredric E. Clements to develop his holistic view of community development and succession (Clements 1928) that was widely accepted at the time. Successional studies continued in old abandoned fields of the Piedmont Mountain of North Carolina (Oosting 1942) and the Sandhills of South Carolina (Odum 1960). Secondary succession studies resulted in the Initial Floristic Composition (IFC) and Relay Floristic Composition (RFC) models and mechanisms of succession (Horn 1974) and the facilitation, inhibition and tolerance mechanisms of succession (Connell & Slatyer 1977), and tested models of energy flow, biomass production, dominance and competitive replacement mechanisms in the succession from bare-ground in local-scale studies. Odum (1969, 1971) proposed models of succession relevant for different scales of space and time that varied among researchers. In general, a local-scale study, like the one used in Paper IV, is a useful approach to understand ecological processes at the lowest resolution. Variables such as changes in soil pH, bare ground, vegetation cover, and soil moisture index were linked with short-term temporal changes in species richness and composition. Using species cover and their richness in the regression models can be problematic because of circular reasoning (Palmer 1993), thus they do not relate to the observed effect of species richness but they illustrate changes in the field with time. Paper I utilizes change in soil-nutrient related variables such as N, C, and pH from two quadrats at each elevation band.

## **Variables at the landscape- to macro-scales**

After the foundation of macro-ecological investigation by Brown (1995), new insights resolved questions asked over 200 years ago concerning the general theory to explain latitudinal biogeographical patterns. Present research focusing on elevational gradients may partly apply to latitudinal gradients (Brown 2001). Latitudinal and altitudinal gradients are two macro-scale species richness patterns. Both have been studied in several groups of living

plants and animals as well as in fossils (Rohde 1992, Körner 2000, Ohlemuller & Wilson 2000, Lomolino 2001, Harris 2006, Lomolino *et al.* 2006, Grau *et al.* 2007, Mittelbach *et al.* 2007, Birks & Birks 2008, La Duo 2008, Kessler 2009, Miede *et al.* 2009, Willis *et al.* 2009). Elevation and latitude *per se* have no direct influence on species richness but act through environmental factors correlated with these variables (Grytnes 2002). The controlling factors towards each macro-scale variable (latitude and altitude), are to some extent, similar and yet dissimilar.

Macro-scale patterns are mainly controlled by climatic variables (Whittaker *et al.* 2001) shaping the distribution of each biome (Woodward 1987). Climate maintains as well as generates biodiversity patterns at macro-scales (Wright 1983, O' Brien 1993, Hawkins *et al.* 2003). Various climatic factors such as temperature, rainfall, moistures, day length, seasonal variation, solar radiations, UV-B radiation, atmospheric pressure, and air humidity influence species composition and species richness patterns at macro-scales (O' Brien 1993, Brown 1995, Odland & Birks 1999, Grytnes 2002, Bhattarai 2003, Birks *et al.* 2007, Grau *et al.* 2007, Körner 2007, Birks & Birks 2008).

Papers I, II and III try to link elevational macro-scale climate variables to species composition (Paper I) and species richness patterns. Paper IV also shows an indirect effect of climate change. Agricultural fields in the *trans*-Himalayan sub-alpine zone were abandoned as a result of declining production of crops, and unpredictable seasonal changes faced by local people. Due to the absence of measurements of such climatic factors in this thesis, I predicted climatic factors from similar studies done in nearby regions. For example, the mid-to high-alpine zone in the Tibet Autonomous Region (TAR) is geographically defined as a rain- shadow region in High Asia. High mountains receive more solar and UV-radiation than mountains elsewhere. Thus patterns derived after such climatic filters may have a high influence.



# Variables and mechanisms influencing spatio-temporal richness patterns

## *Sampling artefacts*

Macro-scale studies often collect data from a large grain-size in area. Thus field surveys are hardly feasible. It is a common trend to depend on secondary sources such as biological collections in museums, herbaria, published accounts in floras or faunal monographs, and distribution maps. Indeed, the importance of such information is growing in the present world's growing concern about the conservation of biodiversity (Sun ZhenHua *et al.* 2007). Interpolation of species ranges from their observed extremes of the studied gradient is common for both latitudinal and altitudinal patterns (Rahbek 1995, 1997, Patterson *et al.* 1998, Odland & Birks 1999, Heaney 2001, Md. Nor 2001, Grytnes & Vetaas 2002, Vetaas & Grytnes 2002, Hawkins *et al.* 2003, Koleff *et al.* 2003, Bhattarai *et al.* 2004, Grytnes & Beaman 2006, Grau *et al.* 2007, Sun ZhenHua *et al.* 2007). Distribution maps for species are good sources of information for a macro-ecological study, but a detailed investigation for each or at least a target species prior to the completion of a distribution map is required.

Common assumptions such as the presence of a species at all elevational bands or cells between the observed extremes and absence of occurrences of the species beyond the observed ranges are made in all interpolation studies. However, these assumptions are easily violated (Birks 1993, Whittaker *et al.* 2001). There are disjunct distributions of species, endemic species, rare and other threats to biodiversity. Species can be absent from a certain area due to different causes than interpolation and can also be present outside the observed ranges.

Papers I, II and III rely on species richness patterns from some of the least studied areas such as the Tibetan Autonomous Region (TAR) and the Nepal Himalaya. Moreover, lichens represent one of the least studied groups in biodiversity analyses. This thesis shares sampling artefacts to other similar studies. Furthermore, the thesis shares the view of Vetaas & Grytnes (2002) that the area of altitudinal bands does not account for significant variation in species-richness patterns for the Nepalese Himalaya. Epiphytic lichen species included in Paper III are dependent on vascular species for their host and on the special micro-environments

created by them. The dispersal barrier caused by certain landscape elements has been proposed in the interpolation of species range data towards their observed extremes (Colwell & Lees 2000). The generated null-models define the mid-domain effect based on the occurrence of a peak in species richness in the intermediate part of the studied gradient or domain (Whittaker *et al.* 2001). The argument arises from the consequences of placing datasets of varying species ranges randomly within a bounded domain. Part of the studies in Papers I and II are fully located towards the higher end of the elevation gradient *i.e.*, the mid-to high-alpine zone of TAR. Thus we are more concerned about the spatio-temporal dynamics of species-richness patterns. We anticipated and acknowledge potential artifacts after interpolation.

### *Mass effects*

Mass effects are important phenomena in the establishment of a species from its original distribution to a new area. This process has been given various terms such as the rescue effect (Brown & Kodric-Brown 1977, Stevens 1992), mass effect (Shmida & Wilson 1985) and the source and sink effect (Pulliam 1988). These studies propose that the mass effect has an effect on the shape of the elevational richness pattern. Kessler (2000b) found an up-slope mass effect for palm species elevational richness patterns. He also stated that high elevational species would show a down-slope mass effect and that mid-elevational species would respond to both sides (Kessler 2000b, Grytnes 2002). In an empirical study, increased species richness at ecotones may be the cause by mass effect (Shmida & Wilson 1985).

My thesis focuses mainly on the mid-to high-alpine zone (Papers I and II) in the high Himalayan Mountain area where a sharp elevation gradient will result in other ecological changes (Körner 2007). A unimodal pattern of lichen species richness could have a mass effect from both sides of the elevational gradients (Paper III).

### *Species-pool*

The species-pool hypothesis (Eriksson 1993, Zobel 1997) states that the number of species in a certain habitat is dependent upon the commonness of this habitat elsewhere. The species-pool hypothesis is connected more with historical and evolutionary explanations of species

diversity than with ecological species-richness patterns (Bhattarai 2003). The environment, size of area, and geology can all determine this relationship. The observed elevational decline in species richness with increasing altitude discussed in Papers I and II may be due to a decline in the regional species-pool of biodiversity in hotspots such as the Himalaya and the Sichuan and Yunnan provinces of China. This phenomenon may be also true for the unimodal richness pattern for lichens in Nepal (Paper III), but the elevation of maximum richness is substantial higher than the maximum richness of vascular plants and other plant types. Thus I believe that local phenomena may be more important for lichens than the species-pool as such. In Paper IV the richness towards the oldest abandoned field is apparently enriched by the species-pool from adjacent forests. Thus the oldest abandoned fields were more likely to be within surrounding vegetation that act locally as a species-pool.

### *Historical factors and local-scale community successional patterns*

Changes in species composition and in species-richness patterns in different chronosequences are influenced by historical factors and local-scale successions. Although a chronosequence study is a good source of understanding ecological succession, it has the assumption of the repetition of the youngest chronosequence via the old stages (Pickett 1989). The importance of land-use history prior to abandonment in secondary succession has been widely discussed (Odum 1960, 1969, 1971, Drury & Nisbet 1973, Horn 1974, Pickett 1976, Huston & Smith 1987, Pickett 1989, Glenn-Lewin *et al.* 1992, Pausas 1994, Bazzaz 2005, Pausas *et al.* 2006, Krebs 2008). Different colonization processes, species richness patterns, hypotheses and theories have been proposed and well established through succession studies. Historical factors often has less probability of re-occurrence and that would be eliminated by macro-scale or dynamic factors related to climate which often have a high probability to re-occur (Whittaker *et al.* 2001).

Paper IV shows that there is a general pattern among colonizing species, unimodal successional species richness patterns and divergence patterns of succession through time. General patterns are explained by scales such as differences in time since abandonment, and specific patterns are explained by differences in local factors such as soil pH, moisture, relative radiation index, and closeness to species-pool (forest). A decreasing trend in soil pH and vegetation cover with time differed from the generally expected trend, but agreed with

results from some other studies (Bonet & Pausas 2004, Arbelo *et al.* 2006) in which old fields were grazed. Grazing may create an intermediate intensity of disturbance through time and give unimodal temporal species richness patterns (Grime 1977). Unimodal species richness patterns in succession with maximum modeled richness between 15 to 25 years is also common in other studies (Horn 1974, Brown & Southwood 1987, Bazzaz 2005), although other responses have also been reported (Carson & Barrett 1988, Silvertown *et al.* 2006). A high richness in a mid-successional phase may occur when both pioneer (light-demanding) species and species of mature phase (shade-tolerant) co-exist (Bazzaz 2005).

This study shows a decreasing pattern in total richness and vegetation cover towards the oldest temporal gradient with increasing  $\beta$  diversity. The divergence of patterns of succession may be due to surrounding vegetation composition (source-pool), a high grazing pressure interaction with species, and spatial heterogeneity. Decreasing diversity during intensive grazing was observed in Papers I and II. The study sites of the two papers differ in scale and intensity of grazing. Increasing  $\beta$  diversity with decreasing total richness would be a facilitation effect of succession (Connell & Slatyer 1977) through more suitable (heterogeneous) habitats as for example, the nursery effect provided by thorny bushes (Pausas 1994, Pausas *et al.* 2006).

### *Climate and energy-related variables to explain landscape and macro-scale elevational patterns*

Climate is a main driving factor in influencing landscapes and macro-scale patterns of diversity (Whittaker *et al.* 2001). The general elevational decline in species richness for both plants and lichens at the quadrat scale for Buddha Mountain (Paper I), interpolated species ranges from the mid- to the high-alpine zone of the Tibet Autonomous Region (Paper II) and the unimodal elevational pattern for Nepalese Himalayan lichens (Paper III) may be caused by climatic variables. However, these general patterns do not apply to all functional and taxonomic subsets such as unimodal patterns for cushions, cryptogams and lichens in Buddha Mountain (Paper I), and unimodal relationship for lichens (Paper II). The shape of the decline relationship found in Paper I was quantified by the type of curve fit between the DCA-I axis sample scores and elevation. I argue that that declining patterns could have been caused by climatic factors as well as by extreme physical and environmental features at high

elevations in this geologically young mountain. Specifically, the declining pattern for the total richness with elevation in Buddha Mountain (Paper I) was hidden due to separate but contrasting patterns of individual functional groups. The shrubs start to decline at the lowest elevation, followed upwards by almost similar declining trends of vascular plants, forbs and graminoids. Cushions declined at higher elevations followed by bryophytes and finally lichens at the highest elevation. Similarly, this declining pattern for the total richness (Paper II) followed by similar elevational patterns of functional groups (non-graminoids, graminoids, Asteraceae, total moss, pleurocarpous moss and acrocarpous moss) except for a unimodal relationship found in lichens. The decline is rather gentle compared to other interpolation studies. Differences among adaptational features for each functional group against harsh and unstable environmental factors would influence the response type to the environment (Agakhanyantz & Breckle 1995, Klimes 2003, Körner 2003). Such filters include large differences in ambient temperature, precipitation, cloud formation, short growing season, differences in landscape geometry, high solar and UV-B radiation, etc. An almost similar declining pattern for most species and their functional and taxonomic group except some such as lichens points to climate as the main factor.

The initial plateau followed by the sharp decline in the elevational richness pattern in Buddha Mountain (Paper I) differed from the smoothly declining elevational pattern in interpolated species ranges of the flora-based elevational species richness pattern (Paper II) for various causes. The scale-dependency of species along the elevation gradient may be one cause. Environmental heterogeneity, which is minimized in the study of Paper I may vary as a function of elevation (Palmer 2006) and thus accentuate differences from interpolation studies. Fine-scale environmental variation in factors such as soil pH, N, C, moisture, atmospheric humidity, disturbance etc., influence the success of species which may be less important at broader floristic scales (Whittaker *et al.* 2001). Thus a smoothly declining elevational species richness pattern would have been expected. A general question can be about why there is not a plateau in richness after increasing endemism. Local endemism may increase at higher elevations which may inflate the richness for regions covering many mountains (Paper III). Specifically, in some quadrats at specific elevation bands e.g. 5500 m (Paper I) I found higher species richness for lichens than in the interpolated species ranges (Paper II). That implies that lichens may have been insufficiently studied in TAR.

## *Mechanisms underlying the unimodal richness pattern of lichens of Nepal and TAR*

A uniqueness in the elevational biodiversity pattern for lichens is confirmed after both interpolation and direct field observation along the elevation gradient in Nepal and TAR (Papers I, II and III). The highly significant unimodal richness pattern for the total lichen richness in Nepal with the highest richness between 3100-3400 m represents the highest elevation maximum compared to that of major taxonomic groups of plants. This general pattern is also evident for the endemic lichen species richness of Nepal with maximum richness between 4000-4100 m that represented the sub-alpine zone in Nepal. Maximum endemic lichen richness lies within the range of the highest endemic richness of vascular plants in Nepal (Vetaas & Grytnes 2002). A unimodal richness pattern with elevation is also commonly found among lichen life-form richness, lichen photobionts types and the main lichen substratum types.

Area accounted less for unimodal vascular richness pattern in Nepal (Vetaas & Grytnes 2002). This may also apply to lichen richness. Hot, humid and closed canopies with disturbed forest patches at lower elevation are also less congenial for lichens. The elevation zone of the highest lichen diversity is characterized by maximum variation in rainfall such as annual rainfall (> 4000 mm) in the rainy south side and lowest (< 500 mm) towards the northern, rain-shadow side, with mean summer temperature between 14-17°C in Nepal (Bhattarai *et al.* 2004). This elevation zone is represented by mixed, broad-leaved and coniferous forests with varied roughness and pH of barks. The canopies formed by these forests may give extreme local variation in the availability of water that facilitates lichen growth. These entire features may support the highest richness for lichens in general, and particularly for the more light-demanding, canopy-inhabiting fruticose form of green lichens. The lower canopy and forest floor receives less light and is suited to shade-tolerant foliose species and flat forms which may capture light from one direction only (Gauslaa *et al.* 2009). The lower temperate forest between 2400-2500 has the highest number of foliose lichens and open canopies in the sub-alpine zone appear more suitable for crustose species.

The high endemic lichen richness in Nepal at high elevations is presumably associated with the history of glaciations that causes phylogeographic isolation and further facilitated by reduced competition after periods of harsh and unstable climatic conditions, with rapid

freezing and drying water-cycles. The latter interpretation may also apply for the unimodal richness pattern of lichens in the mid-to high-alpine zones of TAR. High solar and UV-B radiation, high fluctuations in ambient temperature, rapid shifting between moist and dry conditions and frequent cloud formation may be more beneficial to lichens than to other photosynthetically active groups of organisms.

### *Stress, stability, disturbance and water-energy dynamics*

Considering the general diversity hypotheses formulated to explain macro-scale latitudinal and elevational species richness patterns (Fraser & Currie 1996, Whittaker *et al.* 2001), ecological factors like available energy (water, solar), disturbance, environmental stress and stability may shape declining elevational diversity patterns for total species richness as well as specific patterns in their functional and taxonomic subsets (Papers I and II) from the mid-to high-alpine zone of TAR, as well as the unimodal richness patterns for lichens and lichen functional groups (Paper III) from Nepal. One can easily expect a declining elevational pattern due to decreasing temperature and precipitation with increasing elevation. These factors are expected to be strongly influential for the TAR transect, as it is located in the high elevation rain-shadow side, unlike the rainy side of the Himalaya where the Nepalese elevational gradient is studied. Low precipitation is believed to be a major limiting factor for the biodiversity of Tibet (Chang 1981, Birks *et al.* 2007). Both temperature and precipitation are presumably more influencing factors in Tibet (Chang & Gauch 1986, Ni 2000, Wang *et al.* 2006) than for the Nepalese Himalayan elevation gradient. In addition to energy, other local factors may facilitate colonization of non-woody species in such harsh and unstable environments. Such hypotheses need to be tested in designed and controlled sets of experiments. Finally, one must not forget the young geological history of the Tibetan Plateau and the Nepalese Himalayas. Thus hypotheses related to disturbance (Huston 1994, Miede *et al.* 2009), stress and stability (Begon *et al.* 1990, Callaway 2002), water-energy dynamics (O'Brien 1993), and the local effect of macro-scale climate change (Birks *et al.* 2007, La Duo 2008) may be plausible explanations behind this declining pattern.

The maximum richness for lichens at 5500 m in Buddha Mountain, 5000-5500 m in the TAR, and 3100-3400 m in Nepal represent the highest elevational maxima among all biological groups studied. The capacity for lichens to survive at both simulated (de Vera *et al.* 2004) and real (Sancho *et al.* 2007) outer-space conditions documents an extreme

tolerance. A linearly increasing elevational richness pattern for lichens (Körner 2003, Grytnes *et al.* 2006), unimodal for lichens and linear for bryophytes (Bruun *et al.* 2006), and a higher and more linear richness pattern for both mosses and lichens than for other vascular plants were also reported from European Alps (Theurillat *et al.* 2003, Virtanen *et al.* 2003). Kessler (2000a) from the South America has reported a unimodal richness pattern for lichens. Since my study is confined to the mid-high alpine zones of TAR, lichens represented the main component of cryptogams on Buddha Mountain. This elevation zone may have high stress due to frequent and severe frost, fluctuating ambient and ground temperature, strong winds, snow, poor soils, periods of very low humidity, strong UV-B and solar radiation, short growing season, etc. These factors likely strongly impact and limit the distribution of vascular plants, but are not necessarily destructive to lichens. Cushion plants (e.g., *Androsace*, *Thylacospermum* spp.) exhibit more tolerance than other forms of vascular plants. Possibly this modified growth-form helps them in this extreme environment. Limited study in this part of the world limits our understanding. The highly heterogeneous microhabitats of the Tibetan Mountains are poorly known in the science of biodiversity.

The declining pattern of total species diversity in the TAR would be explained first by decreasing area with elevation. Also, this alpine zone receives strong solar radiation that warms the landscape and rapidly evaporates water (Ni 2000). Some high-alpine plants have developed special features such as silky hairs such as some *Saussurea* spp. to avoid overheating and decrease transpiration (Gauslaa 1984), or form cuticles with high transpiration resistances and high reflection of short-wave radiation (Yang *et al.* 2008). Other adaptational features such as succulent leaves for crassulacean acid metabolism (CAM) photosynthesis (*Sedum* and *Rhodiola* spp.) are common in cold deserts (Körner 2003). Particularly high doses of UV-B radiation occur in all high mountains at low latitudes (Willis *et al.* 2009), which lichens can screen due to their high concentration of melanin, and/or parietin pigments in their outer cortex (Gauslaa & Ustvedt 2003). Cloud formation, strong wind, and high moisture content of air are also common at the mountain summits. Lack of multiple layers in the vertical stratification in the alpine vegetation creates an amount of convective long-wave radiation during night which cools air far below freezing temperature (Körner 2003). Thus there will be a strong selection among species that causes a decline in species richness with increasing elevation in TAR (Paper II).



## Conclusions

From my four papers and review of the pertinent literature, I can conclude that species richness patterns are real and highly scale-dependent at all spatial and temporal scales. Scales at all hierarchical levels are inter-related. Some dominant variables important at local-scales such as soil-related heterogeneity will be averaged out at the macro-scale. Climate-related variables will be highly influential at the macro-scale but will be also influential at the local-scale. The species richness pattern depends on the studied group of species, its functional group, life-form, and their geography. Ecological significance of species differs by elevation. For example, in Nepal an elevation of 500 m has been shown suitable for the large wild animals, likewise 1000 m for vascular plants and 3100 to 3400 m for lichens. This highlights an important issue in conservation. The inclusion of the horizontal elevational zone concept in a conservation strategy will avoid species of importance compared to the vertical zonation concept in designing the conservation area.

No ecological study is free from errors, which is true for this spatio-temporal study as well. The wisest thing is to evaluate such errors and artefacts and to improve in later studies. One must be vigilant in avoiding pitfalls of earlier works. The work which I have done has been rather challenging. The study of biodiversity study in the Himalaya, especially in Nepal, is rather young compared to Europe, America and elsewhere. It is the same in TAR, with its complex geography, due to many logistical and political reasons. My field-survey data supplement interpolated data. They support theories and hypotheses of species diversity and will help to build new hypotheses. I feel that each of my studies has its own importance for a particular scale of space and time. There is the choice of variables to measure and to quantify the underlying patterns. Behind every ecological pattern there is a great role of nature and its history which we ecologists or biogeographers must simply accept and acknowledge.

I highlight the conclusions of my thesis as follows:

- Lichens are represented as one of the most stress-tolerant groups of species in the Buddha Mountain, Tibetan Autonomous Region, and the Nepalese Himalaya. A unimodal relationship-elevation relationship is common among these areas. Maximum richness for Nepalese endemic lichens coincides with the maximum

elevation range for Nepalese vascular plant endemics. But total lichen species richness in Nepal is at the highest elevation among all studied plant groups.

- Landscape-level elevational species richness patterns show an early plateau and a sharp decline afterwards that differed with no early plateau but a smooth decline afterwards at the macro-scale. That may clearly indicate the difference in scale of measurement of species, averaging out of environmental heterogeneities and the influence of climatic variables increasing with increasing scales.
- The general pattern for total richness is hidden amongst many specific patterns for their functional, life-form groups.
- An increasing trend in  $\beta$  diversity with decreasing species richness and with increasing age of abandoned fields in the *trans*-Himalaya suggests high grazing pressure and grazing-tolerant species may act as nurseries to protect seedlings for the future generation of trees on this landscape.

## Future plan

Field-based studies in a particular elevational band which has high richness and local-scale studies at a particular mountain will help to supplement this study in the Nepalese Himalaya.

Lichens are a highly sensitive form of life. Further studies on their species richness patterns in different environmental gradients will help to understand if there is a local impact of macro-scale climate change.

More studies in Buddha Mountain as well as in the mid- to high-alpine elevation zone of TAR will help to understand changes in biodiversity in the face of future climate change.

Our present knowledge of elevational and successional patterns in TAR and Nepal will help theoretical and empirical understanding of the science of biodiversity.

## References

- Agakhanyantz, O.E. & Breckle, S.W. (1995) Origin and evolution of the mountain flora in middle Asia and neighbouring mountain regions. In: Chapin III, F.S. & Körner, C.(eds) *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Ecological studies*. Springer, Berlin, Heidelberg, New York.
- Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: prospectives for ecological complexity*. University of Chicago Press, Chicago.
- Anonymous (1999) *Climatological records of Nepal 1995-1996*. Department of Hydrology and Metrology, Kathmandu, Nepal.
- Arbelo, C.D., Rodriguez-Rodriguez, A., Guerra, J.A., Mora, J.L., Notario, J.S. & Fuentes, F. (2006) Soil degradation processes and plant colonization in abandoned terraced fields overlying pumice tuffs. *Land Degradation & Development*, **17**, 571-588.
- Auclair, A.N.D., Bouchard, A. & Pajaczkowski, J. (1976) Productivity relations in a *Carex*-dominated ecosystem. *Oecologia*, **26**, 9-31.
- Bartolome, J.W., Fehmi, J.S., Jackson, R.D. & Allen-Diaz, B. (2004) Response of a native perennial grass stand to disturbance in California's Coast Range Grassland. *Restoration Ecology*, **12**, 279-289.
- Bazzaz, F.A. (2005) *Plants in changing environments: linking physiological, population, and community ecology*. (2<sup>nd</sup> ed.). Cambridge University Press, Cambridge.
- Begon, M., Harper, J.L. & Townsend, C.R. (1990) *Ecology: individuals, populations and communities*. (2nd ed.). Blackwell Scientific Publication, London.
- Bhattarai, K.R. (2003) *Variation in species richness at the fine-scale and at the broad-scale in the Himalayas, Nepal*. PhD Thesis, University of Bergen.
- Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.-A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, **31**, 389-400.
- Birks, H.J.B. (1993) Is the hypothesis of survival on glacial nunataks necessary to explain the present-day distributions of Norwegian mountain plants? *Phytocoenologia*, **23**, 399-426.
- Birks, H.J.B. & Birks, H.H. (2008) Biological responses to rapid climate change at the Younger Dryas-Holocene transition at Kråkenes, western Norway. *Holocene*, **18**, 19-30.
- Birks, H.J.B., Birks, H.H., Everson, J., Jans, H., Thorne, D. & M., T. (2007) The AGS in Tibet 2005. *The Alpine Gardener: Tibet Special Issue*. The Alpine Garden Society, AGS Centre, Avon Bank, Pershore, UK. pp. 289-349.
- Bonet, A. & Pausas, J.G. (2004) Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. *Plant Ecology*, **174**, 257-270.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology & Biogeography*, **10**, 101-109.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.
- Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445-449.
- Brown, V.K. & Southwood, T.R.E. (1987) Secondary succession: patterns and strategies. In: Gray, A.J., Crawley, M.J., & Edwards, P.J.(eds) *Colonization, Succession and Stability*. Blackwell Scientific Publications, Oxford. pp. 315-338.

- Bruun, H.H., Moen, J., Virtanen, R., Grytnes, J.A., Oksanen, L. & Angerbjörn, A. (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, **17**, 37-46.
- Callaway, R.M.R. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844.
- Carpenter, C. (2005) The environmental control of plant species density on a Himalayan elevation gradient. *Journal of Biogeography*, **32**, 999-1018.
- Carson, W.P. & Barrett, G.W. (1988) Succession in old field plant communities: effects of contrasting types of nutrient enrichment. *Ecology*, **69**, 984-994.
- Chang, D.H.S. (1981) The vegetation zonation of the Tibetan Plateau. *Mountain Research and Development*, **1**, 29-48.
- Chang, D.H.S. & Gauch, H.G., Jr. (1986) Multivariate analysis of plant communities and environmental factors in Ngari, Tibet. *Ecology*, **67**, 1568-1575.
- Cheng-yih, W., ed (1983-1987) *Flora Xizangica* (Vol. I-V). Science Press, Beijing (In Chinese).
- Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution*, **15**, 311-315.
- Christensen, N.L. & Peet, R.K. (1984) Convergence during secondary forest succession. *The Journal of Ecology*, **72**, 25-36.
- Clements, F.E. (1928) *Plant succession and indicators*. H. W. Wilson, New York.
- Clinebell, R.R., Phillips, O.L., Gentry, A.H., Stark, N. & Zuuring, H. (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56-90.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, **15**, 70-76.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reef. *Science*, **199**, 1302-1310.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119-1144.
- Cowles, H.C. (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. 1. Geographical relations of the dune flora. *Botanical Gazette*, **27**, 95-117, 167-202, 281-308, 361-391.
- Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London, UK.
- de Vera, J.P., Horneck, G., Rettberg, P. & Ott, S. (2004) The potential of the lichen symbiosis to cope with the extreme conditions of outer space II: germination capacity of lichen ascospores in response to simulated space conditions. *Advances in Space Research*, **33**, 1236-1243.
- del Moral, R. (2007) Limits to convergence of vegetation during early primary succession. *Journal of Vegetation Science*, **18**, 479-488.
- Dickoré, W.B. & Miede, G. (2002) Cold spots in the highest mountains of the world - diversity patterns and gradients in the flora of the Karakorum. In: Körner, C. & Sphen, E.M.(eds) *Mountain biodiversity a global assessment*. Parthenon, New York. pp. 129-147.
- Dobremez, J.F. (1976) *Le Népal, Écologie et biogéographie*. Centre National de la Recherche Scientifique, Paris.
- Dobremez, J.F. & Jest, C. (1969) *Carte écologique de la region Annapurna Dhaulagiri*. Centre National de la Recherche Scientifique, Paris.

- Drury, W.H. & Nisbet, I.C.T. (1973) Succession: contribution no. 90 from the scientific staff, Massachusetts Audubon Society. *Journal of the Arnold arboretum*, **54**, 331-368.
- Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371-374.
- Fontaneto, D. & Ricci, C. (2006) Spatial gradients in species diversity of microscopic animals: the case of bdelloid rotifers at high altitude. *Journal of Biogeography*, **33**, 1305-1313.
- Fraser, R.H. & Currie, D.J. (1996) The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *The American Naturalist*, **148**, 138-159.
- Fukami, T., Bezemer, T.M., Mortimer, S.R. & van der Putten, W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, **8**, 1283-1290.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227.
- Gauslaa, Y. (1984) Heat resistance and energy budget in different Scandinavian plants. *Holarctic Ecology*, **7**, 5-78.
- Gauslaa, Y., Palmqvist, K., Solhaug, K.A., Hilmo, O., Holien, H., Nybakken, L. & Ohlson, M. (2009) Size dependent growth in two old-growth associated macrolichen species. *New Phytologist*, **18**, 683-692.
- Gauslaa, Y. & Ustvedt, E.M. (2003) Is parietin a UV-B or a blue-light screening pigment in the lichen *Xanthoria parietina*? *Photochemical & Photobiological Sciences*, **2**, 424-432.
- Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7-26.
- Glenn-Lewin, D.C. (1980) The individualistic nature of plant community development. *Vegetatio*, **43**, 141-146.
- Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T., eds (1992) *Plant Succession: theory and prediction*. Chapman and Hall, London.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.
- Grau, O., Grytnes, J.-A. & Birks, H.J.B. (2007) A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography*, **34**, 1907-1915.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **11**, 1169-1194.
- Grytnes, J.-A. (2002) *Patterns of vascular plant species richness at range of spatial scales*. PhD Thesis, University of Bergen.
- Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291-300.
- Grytnes, J.A. & Beaman, J.H. (2006) Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography*, **33**, 1838-1849.
- 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.
- Grytnes, J.A. & Vetaas, O.R. (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *American Naturalist*, **159**, 294-304.

- Hagen, T. (1969) *Report on the Geological Survey of Nepal: Preliminary reconnaissance* (vol. LXXXVI). Orell Füssli Arts Graphiques, Zurich.
- Harris, N. (2006) The elevation history of the Tibetan Plateau and its implications for the Asian monsoon. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**, 4-15.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.
- Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology & Biogeography*, **10**, 15-39.
- Herzog, S.K., Kessler, M. & Bach, K. (2005) The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography*, **28**, 209-222.
- Horn, H. (1974) The ecology of secondary succession. *Annual Review of Ecology and Systematic*, **5**, 25-37.
- Hunter, M.L. & Yonzon, P. (1993) Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. *Conservation Biology*, **7**, 420-423.
- Huston, M. (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81-101.
- Huston, M. & Smith, T. (1987) Plant succession-life-history and competition. *American Naturalist*, **130**, 168-198.
- Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Inouye, R.S. & Tilman, D. (1995) Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology*, **76**, 1872-1887.
- IPCC (2007) *Climate change 2007: the physical sciences basis. In summary for policy makers*. IPCC.
- Kansakar, S., R., Hannah, D., M., Gerrard, J. & Rees, G. (2004) Spatial pattern in the precipitation regime of Nepal. *International Journal of Climatology*, **24**, 1645-1659.
- Kessler, M. (2000a) Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography*, **27**, 275-282.
- Kessler, M. (2000b) Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations? *Biotropica*, **32**, 756-759.
- Kessler, M. (2009) The impact of population processes on patterns of species richness: Lessons from elevational gradients. *Basic and Applied Ecology*, **10**, 295-299.
- Klimes, L. (2003) Life-forms and clonality of vascular plants along an altitudinal gradient in East Ladakh (NW Himalayas). *Basic and Applied Ecology*, **4**, 317-328.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367-382.
- Körner, C. (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution*, **15**, 513-514.
- Körner, C. (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems*. (2nd ed.). Springer Verlag, Berlin.
- Körner, C. (2007) The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, **22**, 569-574.
- Krebs, C. (2008) *The ecological world view*. California University Press, Berkeley and Los Angeles, California.

- La Duo (2008) *Studies in the ecology and palaeoecology of the Lhasa valley, Tibet Autonomous Region, China*. PhD Thesis, University of Bergen.
- Lepš, J., Novotný, V. & Basset, Y. (2001) Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. *Journal of Environmental Biology*, **89**, 186-199.
- Lepš, J. & Šmilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.
- Levin, S.A. (1981) Mechanism for generation and maintenance of diversity. In: Hiorns, R.H. & Cooke, D.(eds) *The mathematical theory of the dynamics of biological populations*. Academy Press, London, UK. pp. 176-194.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology & Biogeography*, **10**, 3-13.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006) *Biogeography*. (3<sup>rd</sup> ed.). Sinauer Associates, Inc. Sunderland, Massachusetts.
- MacArthur, J.W. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press., Princeton.
- Md. Nor, S. (2001) Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology & Biogeography*, **10**, 41-62.
- Menon, N. (2009) Rainfall Uncertainty and Occupational Choice in Agricultural Households of Rural Nepal. *Journal of Development Studies*, **45**, 864-888.
- Miehe, G. (1982) Vegetationsgeographische Untersuchungen im Dhaulgiri und Annapurna Himalaya, Dissertationes Botanicæ. *Journal Cramer, Vaduz*, **66.2**, 1-152.
- Miehe, G. (1988) Geocological reconnaissance in the alpine belt of southern Tibet. *Geojournal*, **17**, 635-648.
- Miehe, G. (1989) Vegetation patterns in Mount Everest as influenced by monsoon and föhn. *Vegetatio*, **79**, 21-32.
- Miehe, G., Miehe, S., Kaiser, K., Reudenbach, C., Behrendes, L., La Duo & Schlütz, F. (2009) How old is pastoralism in Tibet? An ecological approach to the making of a Tibetan landscape. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **276**, 130-147.
- Miehe, G., Miehe, S., Vogel, J., Co, S. & La Duo (2007) Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research and Development*, **27**, 169-173.
- Miehe, G., Miehe, S., Will, M., Opgenoorth, L., Duo, L., Dorgeh, T. & Liu, J. (2008) An inventory of forest relicts in the pastures of Southern Tibet (Xizang A.R., China). *Plant Ecology*, **194**, 157-177.
- Mittelbach, G., G., Douglas, W.S., Howard, V.C., Andrew, P.A., Jonathan, M.B., Mark, B.B., Susan, P.H., Allen, H.H., Nancy, K., Harilaos, A.L., Christy, M.M., Amy, R.M., Lucinda, A.M., Mark, A.M., Thomas, J.N., Trevor, D.P., Robert, E.R., Kaustuv, R., Dov, F.S., Dolph, S., James, M.S. & Michael, T. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315-331.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381-2396.
- Molnar, P. (1989) The geologic evolution of the Tibetan Plateau. *American Scientist*, **77**, 350.

- Ni, J. (2000) A simulation of biomes on the Tibetan Plateau and their responses to global climate change. *Mountain Research and Development*, **20**, 80-89.
- O' Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of Southern Africa's woody flora. *Journal of Biogeography*, **20**, 181-198.
- O'Neill, R.V. (1989) Hierarchy theory and global change. In: Rosswall, T., Woodmansee, R.G., & Risser, P.G.(eds) *Scales and global change*. John Wiley and Sons, New York. pp. 29-45.
- Odland, A. & Birks, H.J.B. (1999) The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography*, **22**, 548-566.
- Odum, E.P. (1960) Organic production and turnover in old field succession. *Ecology*, **41**, 34-49.
- Odum, E.P. (1969) The strategy of ecosystem development. *Science*, **164**, 262-270.
- Odum, E.P. (1971) *Fundamentals of ecology*. (3<sup>rd</sup> ed.). Saunders company, Philadelphia, London, Toronto.
- Ohlemuller, R. & Wilson, J.B. (2000) Vascular plant species richness along latitudinal and altitudinal gradients: a contribution from New Zealand temperate rainforests. *Ecology Letters*, **3**, 262-266.
- Oommen, M.A. & Shanker, K. (2005) Elevational species richness patterns emerge from multiple local mechanisms in Himalayan woody plants. *Ecology*, **86**, 3039-3047.
- Oosting, H.J. (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *The American Midland Naturalist*, **28**, 1-126.
- Palmer, M.W. (1990) Spatial scale and patterns of species-environment relationships in hardwood forest of North Carolina Piedmont. *Coenoses*, **5**, 79-87.
- Palmer, M.W. (1993) Putting things in even better order: the advantages of Canonical Correspondence Analysis. *Ecology*, **74**, 2215-2230.
- Palmer, M.W. (1994) Variation in species richness: towards a unification of hypothesis. *Folia Geobotanica*, **29**, 511-530.
- Palmer, M.W. (2006) Scale dependence of native and alien species richness in North American floras. *Preslia*, **78**, 427-436.
- Palmer, M.W. & Dixon, P.M. (1990) Small-scale environmental heterogeneity and the analysis of species distributions along gradients. *Journal of Vegetation Science*, **1**, 57-65.
- Palmer, M.W. & White, P.S. (1994) Scale dependence and the species-area relationship. *The American Naturalist*, **144**, 717-740.
- Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of Southeastern Peru. *Journal of Biogeography*, **25**, 593-607.
- Pausas, J.G. (1994) Species richness patterns in the understorey of Pyrenean *Pinus sylvestris* forest. *Journal of Vegetation Science*, **5**, 517-524.
- Pausas, J.G., Bonet, A., Maestre, F. & Climent, A. (2006) The role of the perch on the nucleation process in Mediterranean semi-arid oldfield. *Acta Oecologica*, **29**, 346-352.
- Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematic*, **5**, 285-307.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, **100**, 33-46.
- Pickett, S.T.A. (1976) Succession: an evolutionary interpretation. *The American Naturalist*, **110**, 107-119.



- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E.(ed) *Long-term studies in ecology: approaches and alternatives*. Springer-Verlag, New York. pp. 110-135.
- Pulliam, H.R. (1988) Sources, sinks and population regulation. *American Naturalist*, **132**, 652-661.
- Qian, H., Fridley, J.D. & Palmer, M.W. (2007) The latitudinal gradient of species-area relationships for vascular plants of North America. *American Naturalist*, **170**, 690-701.
- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200-205.
- Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist*, **149**, 875-902.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.
- Rajbhandari, K.R. (1976) History of botanical explorations in Nepal. *Journal of Bombay Natural History Society*, **73**, 468-481.
- Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167-171.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514-527.
- Romdal, T.S. & Grytnes, J.-A. (2007) An indirect area effect on elevational species richness patterns. *Ecography*, **30**, 440-448.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Sancho, L.G., de la Torre, R., Horneck, G., Ascaso, C., de los Rios, A., Pintado, A., Wierzos, J. & Schuster, M. (2007) Lichens survive in space: results from the 2005 lichen experiment. *Astrobiology*, **7**, 443-454.
- Schaller, G.B. (1998) *Wildlife of the Tibetan steppe*. University of Chicago Press, Chicago.
- Sharma, L.R. (1995) *Enumeration of Lichens of Nepal* (Publication No. 3). Nepal Government.
- Shmida, A. & Wilson, M.W. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1-20.
- Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M. & Bliss, P. (2006) The park grass experiment 1856–2006: its contribution to ecology. *Journal of Ecology*, **94**, 801–814.
- Singh, J. & Singh, S. (1987) Forest vegetation of the Himalaya. *The Botanical Review*, **53**, 80-192.
- Stainton, J.D.A. (1972) *Forest of Nepal*. John Murray Publisher, Ltd., London.
- Stainton, J.D.A. (2001) *Flowers of the Himalaya: a supplement*. Oxford University Press, Oxford.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, **140**, 893-911.
- Sun ZhenHua, Peng ShengJing & Ou XiaoKun (2007) Rapid assessment and explanation of tree species abundance along the elevation gradient in Gaoligong Mountains, Yunnan, China. *Chinese Science Bulletin*, **52**, 225-231.
- Terborgh, J. (1973) On the notion of favorableness in plant ecology. *The American Naturalist*, **107**, 481-501.
- Theurillat, J.P., Schlüssel, A., Geissler, P., Guisan, A., Velluti, C. & Wiget, L. (2003) Vascular plant and bryophyte diversity along elevational gradients in the Alps. In:

- Nagy, L., Grabherr, G., Körner, C., & Thompson, D.B.A.(eds) *Alpine Biodiversity in Europe*. Springer, Germany, Berlin. pp. 185-193.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. & Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363-365.
- Upreti, B.N. (1999) An overview of the stratigraphy and tectonics of the Nepal Himalaya. *Journal of Asian Earth Sciences*, **17**, 577-606.
- Vazquez, G.J.A. & Givnish, T.J. (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology*, **86**, 999-1020.
- 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.
- Virtanen, R., Dirnböck, T., Dullinger, S., Grabherr, G., Pauli, H., Staudinger, M. & Villar, L. (2003) Patterns in the plant species richness of European high mountain vegetation. In: Nagy, L., Grabherr, G., Körner, C., & Thompson, D.B.A.(eds) *Alpine Biodiversity in Europe. Ecological Studies 167*. Springer, Berlin. pp. 149–172.
- von Humboldt (1849) *Aspects of nature in different lands and different climates, with scientific elucidations* (Miehe, S., trans.). Longman, Brown, Green, London.
- Wallace, A.R. (1878) *Tropical nature and other essays*. (New ed.). MacMillan and Co, London.
- Wang, W.Y., Wang, Q.J., Li, S.X. & Wang, G. (2006) Distribution and species diversity of plant communities along transect on the Northeastern Tibetan plateau. *Biodiversity and Conservation*, **15**, 1811-1828.
- Wang, Z., Tang, Z. & Fang, J. (2007) Altitudinal patterns of seed plant richness in the Gaoligong Mountains, south-east Tibet, China. *Diversity and Distributions*, **13**, 845-854.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279-338.
- Whittaker, R.H. (1975) *Communities and ecosystems*. (2<sup>nd</sup> ed.). MacMillan, New York.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology*, **10**, 1-67.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.
- Willdenow, C.L. (1805) *The principles of botany, and vegetable physiology*. Blackwood, Cadell and Davies, London.
- Willis, K.J., Bennett, K.D. & Birks, H.J.B. (2009) Variability in thermal and UV-B energy fluxes through time and their influence on plant diversity and speciation. *Journal of Biogeography*, **36**, 1630-1644.
- Willis, K.J. & Bhagwat, S.A. (2009) Biodiversity and climate change. *Science*, **326**, 806-807.
- Willis, K.J. & Whittaker, R.J. (2002) Species diversity-scale matters. *Science*, **295**, 1245-1248.
- Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005) Changes to elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.

- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496-506.
- Yang, Y., Körner, C. & Sun, H. (2008) The ecological significance of pubescence in *Saussurea medusa*, a high-elevation Himalayan woolly plant. *Arctic, Antarctic, and Alpine Research*, **40**, 250-255.
- Yoda, K. (1967) A preliminary survey of the forest vegetation of eastern Nepal II. General description, structure and floristic composition of sample plots chosen from different vegetation zones. *Journal of the College of Arts and Sciences, Chiba University National Science series*, **5**, 99-140.
- Zobel, M. (1997) The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, **12**, 266-269.

