Spatiotemporal dynamics of plant assemblages under changing climate and land-use regimes in central Nepal Himalaya

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By

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Dedicated to my

Late father: Ratibhan Bhatta

&

Mother: Jayanti Devi Bhatta

Scientific Environment

Acknowledgements

Abstract

The trajectories of vegetation and landscape dynamics have been redirected globally by climate change and land-use change. The drivers and mechanisms of the spatiotemporal changes are likely scale dependent and are most probably confounded. Himalayan landscapes are under-explored and it is particularly crucial to understand the mechanisms and trajectories of the changes they are experiencing and their scale relationship for an effective management of these landscapes. This thesis synthesises four case studies that have documented spatiotemporal changes in plant assemblages driven by climate and land-use change over the last two decades, assessed the relationship between alpha diversity (plot-based species richness) and gamma diversity (regional species richness) with a focus on scale, and tested the performance of weighted averaging (WA) regression and calibration for quantifying the elevational changes of species assemblages.

Studies were conducted in temperate, subalpine, and alpine vegetation at two locations in central Nepal. Scale sensitivity of the elevational species richness was assessed by treating the alpha diversity of different plant life-forms at different grain sizes and areas used for gamma estimation as response variables in a generalised linear model [Paper I]. Systematic changes in temporally resurveyed assemblages were analysed by ordinations and attributed to climate and land-use change using regression analyses [Papers II, III]. WA regression and calibration technique was evaluated by comparing the models for different types of temporal datasets [Paper IV].

Elevational gamma diversity can significantly predict alpha diversity and the relationship is largely scale invariant, although it is slightly less so for woody species. At a regional level, climate warming is a major driver of the demonstrated spatiotemporal changes, i.e. thermophilisation of plant assemblages. However, land-use change may confound or counteract the climatic effects at a local or landscape level. WA regression and calibration predicts fairly accurately the elevation of the plot-based vegetation assemblages. Use of species incidence data may improve the accuracy, but species data processing cannot guarantee more accurate calibrations.

To conclude, the systematic spatiotemporal changes in plant assemblages over the last two decades in central Nepal are significant, are largely irrespective of spatial scale, and are most likely related to interactions and feedback mechanisms between climate change and land-use change at different spatiotemporal scales. Taxonomic, census, and sampling accuracy are crucial in the analyses of temporal changes, especially by environmental reconstructions.

Declaration

This thesis includes a synthesis, three published research articles and a manuscript. All the papers, including the manuscript, are co-authored. The co-authors' contributions in respective articles are given below.

Paper I
Kuber Prasad Bhatta: Study design, fieldwork, data analysis, writing and editing
John-Arvid Grytnes: Study design, discussion on data analysis and editing
Ole Reidar Vetaas: Study design, discussion on data analysis and editing

Paper II
Kuber Prasad Bhatta: Study design, fieldwork, data analysis, writing and editing
Ole Reidar Vetaas: Study design, discussion on data analysis and editing

Paper III
Kuber Prasad Bhatta: Study design, fieldwork, data analysis, writing and editing
John-Arvid Grytnes: Study design and discussion on data analysis
Ole Reidar Vetaas: Study design, discussion on data analysis and editing

Paper IV
Kuber Prasad Bhatta: Study design, fieldwork, data analysis, writing and editing
Harry John B Birks: Discussion on data analysis and editing
John-Arvid Grytnes: Discussion on data analysis and editing
Ole Reidar Vetaas: Study design and editing

List of publications

(They will be represented by the Roman numeral hereafter)

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Bhatta, K.P. and Vetaas, O.R. 2016. Does tree canopy closure moderate the effect of climate warming on plant species composition of temperate Himalayan oak forest? Journal of Vegetation Science 27: 948–957. DOI: https://doi.org/10.1111/jvs.12423 [Paper II].

Bhatta, K.P., Grytnes, J.-A. and Vetaas, O.R. 2018. Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. Ecosphere 9: e0208. DOI: https://doi.org/10.1002/ecs2.2084 [Paper III].

Bhatta, K.P., Birks, H.J.B, Grytnes, J.-A. and Vetaas, O.R. 2018. Weighted average regression and environmental calibration as a tool for quantifying climate-driven changes in vegetation (DRAFT) [Paper IV].

Contents

1. Introduction

1.1 Succession and disturbance

Species diversity and composition vary across space and time at different scales (MacArthur 1984; Levin 1992; Rosenzweig 1995). The directed temporal changes in vegetation in response to changes in environmental factors or removal of a pre-existing species assemblage over an ecological time scale is called secondary succession (Connell & Slatyer 1977; Miles 1979; Pickett et al. 1987). Successional changes and disturbance are major interrelated landscape processes that influence vegetation dynamics and continually interact with human activities. In addition to evolutionary processes, disturbance also has either a positive or negative effect on species composition depending on the intensity, frequency, and spatial scale over which it operates. It can be detrimental and thereby alter the natural ecological patterns and processes at a fine scale, while at the broader scale, such as at the level of regional species pool, it contributes to spatial heterogeneity and temporal niche diversity (Luken 1990; Turner et al. 1998; Walker et al. 1999). Vegetation dynamics in an area may therefore be characterised over short to intermediate temporal scales by a dynamic equilibrium between disturbance regime and the rate of succession under operation (Huston 1994).

Plant assemblages exhibit some form of temporal dynamics at all times and external disturbances can modify the trajectory of this natural variation (Preston 1960; Luken 1990). Ecological succession thus continues to remain a central theme in ecological research in this era of ever-expanding human impacts and rapid landscape changes (Pickett et al. 2009; Meiners et al. 2015). There have been complex interactions between people and natural landscapes across the globe since the origin of humans (Luken 1990). However, anthropogenic impacts on natural landscapes have intensified over the past few centuries around the world, significantly altering the natural features of most landscapes (Foley et al. 2005; MEA 2005). As well as these severe anthropogenic disturbances, there has been unprecedented climatic change at different spatial and temporal scales around the world, with an especially warmer atmosphere

and rather erratic fluctuations in precipitation over recent decades (IPCC 2013). Evidence so far reveals that rapid changes in the geographical distribution and composition of plant assemblages around the globe are driven by anthropogenic climate changes (Walther et al. 2002; MEA 2005; Parmesan 2006). Consequently, the natural mechanisms and trajectories of temporal vegetation changes in the landscapes have been significantly redirected.

In this context, landscape management interventions have been put into practice aiming to restore the direction of disturbance-modified successional changes, a practice known as succession management (Luken 1990). Its success rests largely on the proper understanding of the successional mechanisms and pathways involved. Therefore, understanding the drivers, mechanisms, and trajectories of succession is crucial for predicting the responses of species assemblages to environmental changes and their future states (Zhou et al. 2014). This is vital for formulating effective strategies for long-term successful management or restoration of the landscapes in the context of global environmental changes (Meiners et al. 2015). Today, the disturbances take place in the context of climate change, which complicates the interpretation of the successional mechanisms and pathways.

Temporal successional changes have mostly been studied by either of two methods: space-for-time substitution that uses space as a proxy for time (Pickett 1989; Johnson & Miyanishi 2008), and temporally replicated vegetation surveys (Cooper 1923 and subsequent expeditions; Peet & Christensen 1980; Buma et al. 2017). Based on numerous underlying assumptions, space-for time substitution has been applied in ecological modelling to infer past or future trajectories of ecological systems from contemporary spatial patterns. The central assumption of the approach is that the abiotic and biotic conditions remain constant over the time span of the successional change under study, but changes in the vegetation driven by the disturbance regimes and other stochastic events are not accounted for (Pickett 1989). Vegetation and environmental factors resurveyed over time can solve these shortcomings to some extent while analysing the temporal changes. However, inadequacy of the data quantity and quality as well as inconsistencies in the survey techniques may hamper

the precise quantification of the temporal trends by this technique. Nonetheless, the later approach has been applied in this research to quantify changes in species composition over time, and the observed changes have been attributed to temporally varying stochastic (land-use disturbance) as well as deterministic (climatic) factors.

Directional temporal changes in plant assemblages in response to climate and land-use changes are mostly analysed via formulation of hypotheses. Some of the widely tested postulations, as summarised by Lenoir & Svenning (2015) are: (a) A species will shift upslope in the mountains to compensate for the increased temperature; (b) A species will adapt to the increased temperature to retain its original distributional range; (c) A species from extremes of the temperature gradient will go extinct with a rise in temperature; (d) A shade-tolerant species will increase whereas an open-habitat species will decline in abundance in response to forest canopy closure.

The plant species in assemblages likely exhibit individualistic responses to environmental change (Gleason 1926). Hence, some of the species may shift upward in the mountains in response to increased temperature, whereas a few may adapt to the increased temperature in the local habitat, and others may shift downward in response to interacting land-use factors. Even if we assume static environmental conditions over time, the species composition at a place will always change temporally due to on-going evolutionary processes. As a result, none of the developed models of temporal changes would be completely consistent with the empirical data. Therefore, multiple hypotheses of temporal changes in vegetation driven by climate and land-use change have been formulated for assessing possible responses. The hypotheses are tested by developing statistical models based on theoretical principles that are then confronted with empirical data. If a model is largely consistent with the empirical data, the underlying hypothesis is accepted, otherwise it is considered invalid.

1.2 Successional mechanisms and scale relations

Realising its role in vegetation dynamics and ecosystem functioning, succession has been at the core of ecological research for over a century (Meiners et al. 2015). Debates regarding successional mechanisms are similarly rooted long back to the early

1900s (an era of Clements 1916; Gleason 1926), revealing that temporal vegetation dynamics is a complex process far from being completely assessed or predicted. The Clementsian concept (Clements 1916) views a plant community as a 'superorganism' that has emergent properties resulting from the organisation of the components into communities, and proposes that ecological succession is largely governed by deterministic factors. Following the Darwinian theory of evolution, such environmental determinism has been adopted in different fields of modern science including geography (Johnston 2016). In contrast, the Gleasonian concept (Gleason 1926) views succession as a consequence of individualistic responses of species to their changing environment and of simultaneous stochastic processes. According to this concept, the structure and processes of assemblages are viewed as summation of those of its constituent species. These two views thus make different predictions regarding vegetation composition patterns over space and time.

Although much is now known about the mechanisms shaping vegetation assemblages, uncertainties still exist regarding spatiotemporal variations in the drivers, in the underlying mechanisms and trajectories of secondary succession under different types of environmental perturbations, and in their cross-scale linkages (Zhou et al. 2014; Meiners et al. 2015; Arroyo-Rodríguez et al. 2017). A long-standing debate concerns whether the assembly and spatiotemporal dynamics of communities are governed by deterministic or stochastic processes (e.g., Hubbell 2001; Tilman 2004; Chase & Myers 2011; Bhaskar et al. 2014) or by a combination of both (e.g., Gravel et al. 2006; Leibold & McPeek 2006; Adler et al. 2007; Caruso et al. 2011; Måren et al. 2018). A recent consensus is that both deterministic and stochastic processes operate simultaneously in the assembly of local communities (Leibold & McPeek 2006; Chase 2010; Caruso et al. 2011; Chase & Myers 2011), and that the relative importance of stochastic (neutral) versus deterministic (niche-based) processes of temporal changes is a matter of scale (Fig. 1; Chase 2014; Arroyo-Rodríguez et al. 2017). At a fine scale, stochastic processes such as birth and death rates, dispersal, disturbance, and biotic interactions become prominent, which moderate the influence of coarse-scale environmental factors on species composition (Connor & McCoy 1979; Levin 1992; Crawley & Harral 2001). At broader spatial scales, the stochastic variations are

averaged out and the influence of niche-based environmental variables such as climate, water, and energy increases to shape the vegetation structure and composition (Wiens 1989; Chase 2014; Arroyo-Rodríguez et al. 2017). Hence, the ecological patterns are expected to be more predictable at a broad scale (Wiens 1989; Levin 1992) and reveal more clearly the compositional shifts when environmental conditions change.
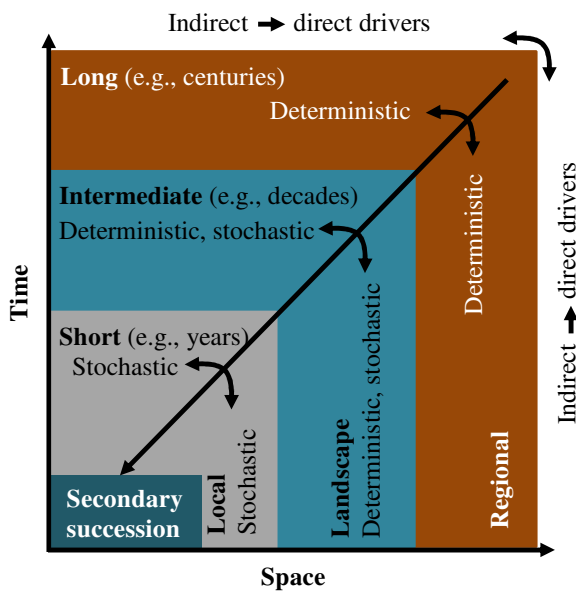
Figure 1. Concept of secondary succession and its scale relations (modified after Arroyo-Rodríguez et al. 2017). The successional process is influenced by different types of indirect and direct drivers that operate simultaneously over different scales and interact across scales. The interactions between the drivers themselves and across spatial and temporal scales are indicated by arrows.

Such a scale-dependent variation in the processes and patterns of successional changes is thoroughly investigated in this thesis with respect to species richness, and its scale sensitivity along an elevation gradient is assessed by varying spatial scale components such as grain size (size of the sampling unit), focus (total area sampled by 100 m^2 grain in each 100-m elevation band) and area for regional species richness or elevational gamma diversity estimation (extent in central Nepal in each 100-m elevation band). The correspondence between the patterns at different grain sizes and areas of gamma estimations is analysed to highlight any variation in the patterns and their potential drivers from a local to regional scale.

1.3 Scale and species diversity patterns

1.3.1 Overall scale in my research: scale in space and time

This thesis focuses on the directional temporal changes in plant species composition in central Nepal in response to climate change and land-use change along an elevation gradient. Elevation thus represents a major spatial component of the research, along which, plant species composition and environmental factors exhibit a distinct pattern. Temperature also exhibits a spatial trend, i.e. decreases linearly with elevation, in addition to a significant temporal trend. Because the sample plots are located along an elevation gradient, temporal temperature was extrapolated for the sample plots and thus exhibits the same elevational trend as that for the spatially varying temperature. Temporal variations in the land-use factors (canopy closure: Paper II, grazing reduction: Paper III) also exhibit elevational patterns, where canopy closure increases and grazing intensity decreases with elevation. Accordingly, the documented temporal changes have also been primarily manifested over space. Therefore, the study represents a typical situation of complex space-time interactions. Although attempts have been made to partial out analytically the direct effect of the elevation gradient on the observed changes [see Papers II, III], spatial and temporal patterns likely remain confounded. Depending on the specific objective of the different case studies, the overall thesis spans different spatial and temporal extents.

Spatial scale

The spatial scale covered by this thesis can be hierarchically categorised into extent, focus, and grain size. The regional area of central Nepal between 3900 m and 5000 m a.s.l. represents the largest spatial scale (extent) used to estimate the regional species richness, i.e. regional elevational gamma diversity [Paper I]. The regional area is narrowed down to a focus level by considering the cumulative area of six sample plots of 100 m^2 grain size in each 100-m elevation band and used to estimate local elevational gamma diversity in the landscape [Paper I]. Apart from this, elevational changes in the plant species assemblages have been quantified based on the species' elevational ranges in central Nepal [Paper II]. Thus, the regional area in central Nepal

in terms of species' regional elevational ranges has also been used. The temporal climatic factors (temperature and precipitation) are also at the regional scale [Papers II, III]. The regional climate was extrapolated to the plot-level climate. Sample plots of three different sizes (i.e. grain sizes of 1 m^2, 16 m^2, 100 m^2) have been used at the local level for sampling vegetation and determining explanatory factors in the landscape [Paper I]. Except for Paper I, vegetation sampled at the grain size of 100 m^2 has been used in the analyses [Papers II-IV].

Temporal scale

Vegetation and environmental data replicated over time have primarily been used in this thesis. Accordingly, different temporal scales are represented in the case studies [Papers I–IV]. Regional species richness in the subalpine–alpine belt of central Nepal [Paper I] is based on interpolation of species presences between the extremes of their elevation ranges (ranges from Press et al. 2000). Species' elevation ranges in Press et al. (2000) were estimated from herbarium specimens collected from different areas of central Nepal between the 1850s and 2000. In this regard, a temporal scale of c. 150 years is represented in the interpolated species richness. However, an empirical temporal scale of c. 2.5–3 decades has been used in the species datasets [Papers II–IV]. Climate and land-use data of the same temporal scale have been used to see if the changes in species assemblages are related to any or both of these variables.

1.3.2 Scale sensitivity of the species diversity patterns

An influence of spatial scale on biodiversity patterns has long been recognised in plant ecology and biogeography (e.g., Arrhenius 1921; Connor & McCoy 1979; Wiens 1989; Levin 1992; Palmer & White 1994; Crawley & Harral 2001; Rahbek 2005; Field et al. 2009). However, in contrast to spatial scale, the role of temporal scale remained under-documented until very recently (see Scheiner et al. 2011). The direct influence of spatial scale on species richness, i.e. species-area relationship (SAR), is one of the best-verified patterns in vegetation ecology and biogeography (Rosenzweig 1995; Lomolino 2000; Scheiner et al. 2011). Spatial scale itself, however, is a complex variable that consists of several components such as sampling unit, grain, focus, and

extent (Palmer & White 1994; Scheiner et al. 2011), and scale-related issues with one or more of these components continue to generate concerns. There have been uncertainties regarding the grain-size sensitivity of species diversity patterns along environmental gradients (e.g., Rahbek 2005; Nogués-Bravo et al. 2008; Belmaker & Jetz 2011; Rowe et al. 2015; Tuomisto et al. 2016).

In addition to the SAR, regional gamma diversity (total species present in a whole region; Lomolino 2001) may also influence the local species diversity, i.e. alpha diversity, via an indirect effect of area (Rosenzweig & Ziv 1999; Romdal & Grytnes 2007). It is unclear whether the indirect effect is dependent of spatial scale components, i.e. grain size, focus, and area from which regional gamma diversity is estimated, or whether it depends on the life-forms of the plant species. Moreover, systematic variations in the species diversity patterns among the studies of different spatial scales are also likely caused by differences in the methods of study and the nature of the quantified data (Kessler et al. 2009). These variations in the patterns due to differences in data type and study method remain confounded with those resulting from the differences in spatial scale of the studies. Therefore, a standard methodology with conceptual consistency is applied in this thesis to explore thoroughly the scale dependency of the species diversity patterns.

Biodiversity patterns are governed by a myriad of proximate (direct) and ultimate (indirect) drivers and processes operating over a range of spatial and temporal scales (Fig. 1; Levin 1992; Giladi et al. 2011; Arroyo-Rodríguez et al. 2017). At the broadest spatial scales and over the longest temporal scales, the proximate drivers such as speciation, extinction, migration, biogeographic history, evolutionary history, and regional species pool, and the ultimate drivers such as climate, energy, water, and topography are more influential (Ricklefs 1987; Hawkins et al. 2003; O'Brien 2006; Pärtel et al. 2007; Harrison & Cornell 2008; Field et al. 2009). At finer spatial scales and over shorter temporal scale, species diversity is directed by proximate drivers such as species' population dynamics, species interactions, and meso- or micro-climate, and by ultimate drivers such as disturbance regimes, soil characteristics, habitat heterogeneity, and land-use history (Grime 1973; Pacala 1996; Whittaker et al. 2001;

Michalet et al. 2006; Arroyo-Rodríguez et al. 2017). Stochasticity of local factors often dampens the strength of the richness-environment relationship at a fine scale (Connor & McCoy 1979; Crawley & Harral 2001). Therefore, reasonably different patterns of species diversity at different spatial scales might be expected. However, the species diversity and their drivers often interact across spatial and temporal scales (Fig. 1), and due to this, species diversity patterns and processes across scales are often correlated (Fig. 2a) (Zobel 1997; Harrison & Cornell 2008). Patterns at a fine scale and their drivers are hence expected to be linked with those at the regional level (Fig. 2b).

Elevational gradient in plant species richness of Nepal has been studied at regional (e.g., Grytnes & Vetaas 2002; Vetaas & Grytnes 2002; Grau et al. 2007; Zhang et al. 2015) to local scale (e.g., Bhattarai & Vetaas 2003; Carpenter 2005; Bhatta & Chaudhary 2009; Bhattarai et al. 2014). The regional patterns are based on the range interpolated species richness along an elevation gradient from tropical (60-1000 m a.s.l.) to upper alpine or nival (5000-6400 m a.s.l.) zone. However, numerous fine-scale studies have covered different portions of elevation gradient using various grain sizes of $1 m^2$ to $1000 m^2$. Broadly, majority of these studies have revealed a humped pattern of overall species richness for vascular plants that peak at different elevations, whereas a linear declining pattern for woody species along elevation gradient. Nonetheless, degree of similarity between these patterns at different scales has not been assessed. Therefore, to verify the conjecture, species diversity patterns and processes at different spatial scales have been assessed by applying precisely comparable datasets and standardised techniques, and an explicit correlation has been established between these patterns. The variation in the degree of the correspondence between the patterns with the varying grain sizes for plot-based richness and varying area for regional richness has been evaluated.
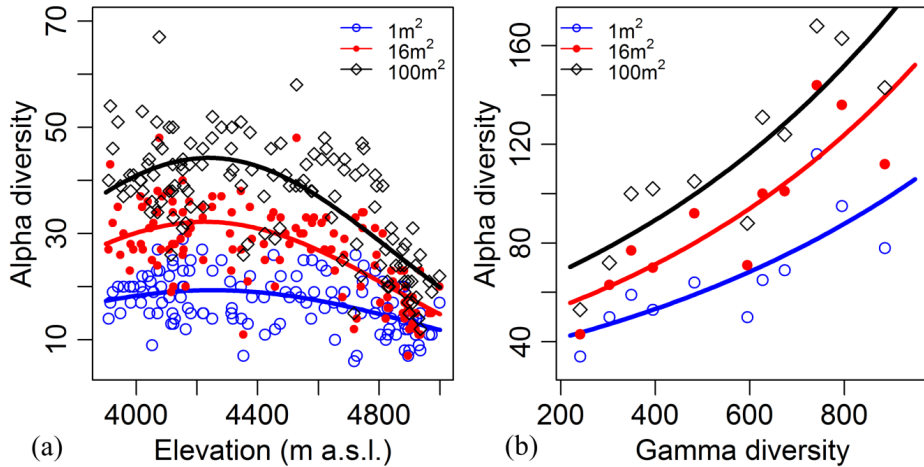
Figure 2. (a) Elevational pattern of alpha diversity at different grain sizes; (b) Relationship between alpha diversity and gamma diversity (total species richness within each 100-m elevation band in a region) of vascular plants along an alpine elevation gradient in central Nepal.

Temporal scale is as influential as spatial scale for biodiversity patterns (Preston 1960; Rosenzweig 1998; Adler & Lauenroth 2003) and, depending upon the features of the species, diversity at a place varies over a temporal scale of hours to millions of years. The successional changes in plant assemblages take place over an ecological time scale of decades to millennia (Rosenzweig 1995; Cox & Moore 2007). Following the ideas of Preston (1960), Rosenzweig (1998) argued for the first time that similar underlying mechanisms create spatial and temporal patterns, and further studies (e.g., Adler et al. 2005; White et al. 2006; Soininen 2010) proposed that the influence of spatial and temporal scale on species richness patterns is similar. This space-time relationship has been a fundamental assumption underlying the analytical approach of space-for-time substitution.

The joint influence of both types of scales on species diversity in a similar fashion has been responsible for much of the confusion surrounding the interpretation of successional patterns and processes because succession creates both patterns (Fig. 1; Huston 1994). A recent idea is that the interaction of the spatial and temporal scales affects the species diversity gradient, known as the 'time-by-area' interaction (Adler et

al. 2005; Fridley et al. 2005; Soininen 2010). This means that spatial and temporal scales of a study do not separately influence the species diversity pattern, but act in concert as two dimensions of one unified pattern (Adler et al. 2005). Consequently, the spatial and temporal patterns are frequently confounded where the temporal dataset is embedded in a spatial context or *vice versa* (Wiens 1989; Dornelas et al. 2013). Therefore, in the study of temporal changes, it is important to either assess the successional changes in a spatiotemporal context or to partial out the spatial variations and consider their contribution to the temporal patterns as measurement and process errors (Dornelas et al. 2013).

In this context, this thesis explores temporal successional trajectories in plant species assemblages along an elevation gradient resulted from changes to the environmental conditions, i.e. climate and land-use change in the central Himalayan landscape. The sample plots are distributed along an elevation gradient and the temporally varying species composition as well as explanatory factors exhibit elevational patterns. Therefore, although the direct effect of space (elevation gradient) was partialled out analytically, patterns over time and space may still be confounded to some extent.

1.4 Environmental changes and responses of mountain vegetation

Analyses of climate at different spatial and temporal scales have revealed unprecedented climatic changes across the world: in particular, a warmer atmosphere and rather erratic fluctuations in precipitation patterns over recent decades (IPCC 2013). Climate in the Himalayan region is changing at a faster rate than the global average and the more pronounced changes have been in the high-elevation regions (Shrestha & Aryal 2011; Mountain Research Initiative EDW Working Group 2015; Karki et al. 2017). As pronounced, are the anthropogenic land-use changes of different forms, such as loss, degradation, and fragmentation of natural habitats, agricultural expansion, and land conversion (Foley et al. 2005; MEA 2005). However, the temporal climate change and land-use change differ in spatial coverage, frequency, and intensity. The climatic changes span over long temporal and wide geographical extents, whereas the land-use changes are more intense at smaller spatial extents and vary frequently over spatial and temporal scale.

Following the global trend, there have been substantial impacts on the natural landscapes in the Himalayan region over the past century (Singh & Singh 1992; Khera et al. 2001; Goldewijk & Ramankutty 2004; Schlütz & Zech 2004; Miehe et al. 2009; Miehe et al. 2015). Forest clearance, expansion of agricultural lands, overexploitation of plant resources, overgrazing, and land abandonment have been the prominent forms of land-use in the Nepal Himalaya leading to habitat degradation and fragmentation (FAO 2010; GoN-MoFSC 2014). As elsewhere, the land-use drivers in Nepal vary in their nature, intensity, and frequency among the country's physiographic zones. Recent trends of forest regrowth and increase in forest cover have been observed in the Middle Hills region with the introduction of a community forestry programme (Gautam et al. 2002; Niraula et al. 2013).

In response to recent climate and land-use changes, drastic changes in the geographical distribution and composition of plant assemblages have been evident throughout the world (MEA 2005; Parmesan 2006). Upslope shifts in mountain plant species have been the most commonly observed ecological response of species to increased atmospheric temperature (Fig. 3a-3c) (e.g., Parmesan & Yohe 2003; Lenoir et al. 2008; Chen et al. 2011; Gottfried et al. 2012; Morueta-Holme et al. 2015; Dainese et al. 2017). However, climate change is multidimensional and exhibits heterogeneous patterns across the world (Garcia et al. 2014). In the mountainous regions, the degree of climate driven changes can vary significantly even within a single mountain range (Gritsch et al. 2016). This means that the nature, intensity, and frequency of climate change may be redistributed from one to the next spatial scale, and therefore, may not act uniformly across specific vegetation types and landscapes (Garcia et al. 2014). Consequently, the climate driven patterns of vegetation change at the regional scale may not necessarily reflect those at a finer scale. Moreover, the response of a species to climate change is likely to be individualistic. Therefore, it is worth analysing the climatic responses of species assemblages at different spatial scales and geographic locations to understand properly the climate directed successional trajectories in Himalayan vegetation.
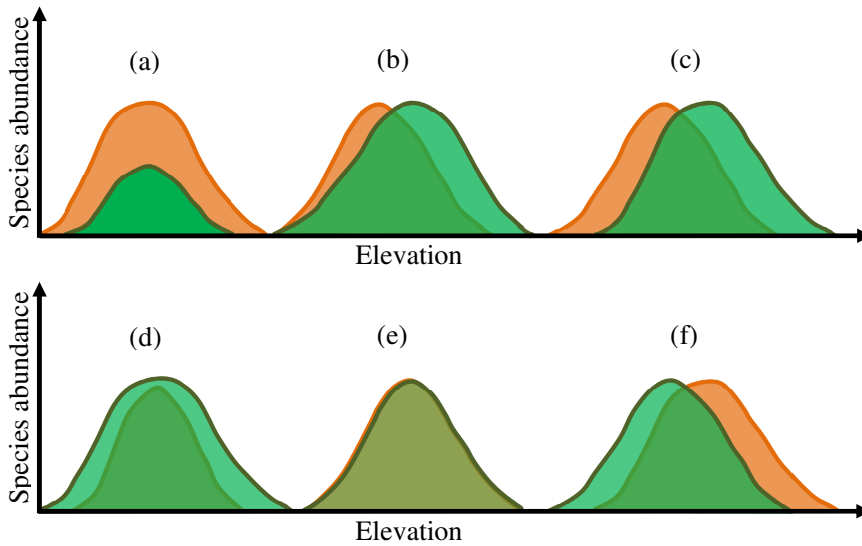
Figure 3. Concept of likely responses of species in mountains under climate warming and land-use changes (modified from Lenoir & Svenning 2015). Green represents the current and brown, the past distribution of species abundance along an elevation gradient. **(a-c)** Elevational shift of species in response to climate warming: (a) crash, (b) lean, and (c) march; **(d-f)** likely influence of simultaneous land-use change on the elevational shift in species: (d) compounding, (e) confounding, and (f) counteracting the climatic effect.

Similarly, anthropogenic land-use changes are causing global biodiversity declines with an increase in species' extinction risk and decline in population sizes at local to global levels (MEA 2005; Pimm et al. 2014; Tittensor et al. 2014; Newbold et al. 2015). However, how the species assemblages at a local level are responding to land-use change is less clear (Newbold et al. 2015). Scenarios developed by MEA (2005) reveal with high certainty that habitat loss caused by land-use change will contribute to the decline in the local and global diversity of different taxa, especially vascular plants. Like the climatic changes, the type, intensity, and frequency of land-use change differ significantly among geographic regions and vegetation types. The land-use changes and climate changes often exhibit complex confounding, compounding or counteracting interactions at different spatial and temporal scales (Goring & Williams 2017; Guo et al. 2018). (Fig. 3d-3f) Consequently, the climatic responses of the

species are often masked and modified [Papers II, III]. Such responses include upward range shifts of the species irrespective of climate warming (e.g. Grytnes et al. 2014), unexpected downslope range shifts under climate warming (see Lenoir et al. 2010a), and frequent lags in the biodiversity changes behind climate warming (e.g. Wu et al. 2015). In addition, methodological inconsistencies in analysing the climatic responses of species (e.g. Dawson et al. 2011) and a paucity of standard data (Grytnes et al. 2014) may also contribute to the obscured patterns of climate change driven responses.

Changes in the climate and land-use regimes in the Himalayan region potentially pose a serious threat to the unique biodiversity of the region (Salick et al. 2009; Singh et al. 2011; Shrestha et al. 2012b; GoN-MoFSC 2014). The effects of such environmental changes to the Himalayan biodiversity, especially in terms of species composition and geographic distribution at different spatiotemporal scales, remain seriously under-documented. This research is an attempt to address this gap and to develop a more complete and real-time understanding of how the ongoing climate changes, together with land-use changes at different scales, are driving the successional pathways of the Himalayan plant species assemblages.

1.5 Methodologies

Alongside the conceptual conjectures, methodological factors such as data sampling technique, precision and adequacy in the surveys, quantity and quality of the data, skill and expertise of the observer, and analytical techniques are also crucial in exploring the spatiotemporal patterns and processes of biodiversity (e.g., Klanderud & Birks 2003; Archaux et al. 2006; Tingley & Beissinger 2009; Ross et al. 2010; Bhatta et al. 2012; Kapfer et al. 2016). Inconsistencies or inaccuracies in these factors lead to high noise in the vegetation datasets that contribute to potentially spurious patterns being found (Jongman et al. 1995; Legendre & Legendre 1998).

Various analytical techniques, mostly in conjunction with each other, have been applied in studying the ecological responses of plant species or assemblages in mountains under climate warming. Most of these techniques have been rigorously tested and their strengths and limitations regarding the above-mentioned methodological issues are well documented. A technique of vegetation-based

environmental reconstructions has recently been introduced into modern vegetation ecology to study temporal changes in plant assemblages and their environment (e.g., Brady et al. 2010; Bertrand et al. 2011; Lenoir et al. 2013; Paper III). The technique mostly makes use of the technique of weighted averaging (WA) regression and calibration that has been extensively used in making palaeoenvironmental reconstructions (Jongman et al. 1995; Birks et al. 2010 and references therein). It is based on the principle of space-for-time substitution, where contemporary patterns of species composition in relation to their environment are used to infer environmental conditions for past vegetation. However, in modern vegetation ecology, the species composition and environment of the past are used to infer contemporary environmental conditions and any difference in the observed and inferred environment gives an estimation of the environmental change.

Performance of the technique has been tested with numerous transfer functions and with different sediment core-based training datasets (Birks et al. 1990; Birks 1994; Telford & Birks 2009; Rehfeld et al. 2016). It is perceived as a robust technique for palaeoenvironmental reconstructions, but despite being used in modern vegetation ecology for the same purpose, robustness of the technique for plot-based vegetation datasets has not been tested rigorously. Although plot-based vegetation datasets mostly fulfil the basic assumptions of the technique (as summarised by Birks et al. 2010), plot-based data differ in several ways (e.g., in spatial and temporal scale of study, the method of data collection, the nature of collected data) from the sediment core-based data used in palaeoecological studies. These differences may cause differences in the nature and degree of species-environment correspondence that ultimately might influence the estimation accuracy of the technique. Paper IV in this thesis assesses whether the technique can produce environmental estimations for plot-based vegetation data and thereby be used to reveal spatiotemporal patterns as reliably as in palaeoenvironmental reconstructions. Moreover, it explores whether the technique is useful in tackling at least some of the above-mentioned methodological issues in the vegetation datasets while analysing the spatiotemporal patterns with respect to environmental changes. It has been done thoroughly by comparing the outputs of analyses of datasets generated using different sampling techniques, with different plot-relocation accuracies, quantified on different scales, and with species of different frequencies and abundances.

2. Objectives

This research aims to assess the influence of spatial scale components on the elevational patterns of plant species richness, and to quantify the climate and land-use change driven temporal changes in the plant assemblages of central Nepal under different climatic, land-use, and physiographic settings.

The overall objective underlines the specific research questions formulated in the form of four research papers as below:

- How does scale, i.e. grain size, focus, area for gamma diversity (regional richness) estimation influence the elevational gamma–alpha diversity relationship of different plant life-forms? [**Paper I**]

- Does the elevational pattern of alpine-plant species richness vary across grain sizes? [**Paper I**]

- Are there significant changes in species composition from 1993 to 2013 that may be attributed to increased temperature and/or land-use change (increasing canopy closure)? **[Paper II]**

- Are there systematic changes in alpine species assemblages of central Nepal that have been driven by climate change and land-use change (changed grazing regime) from 1990 to 2014? **[Paper III]**

- How does the estimation accuracy of weighted averaging regression and calibration vary between species abundance and species incidence datasets, and how do species of different frequencies influence the estimation accuracy? **[Paper IV]**

3. Study area

3.1 Location, physiography, and climate

Depending on the availability of previously surveyed data, distinctiveness of the bioclimatic zonation, uniqueness of the vegetation, and evidence of changes in climate and land-use regimes, two locations in central Nepal were used for this study (Fig. 4). Central Nepal is an ideal place for testing several ecological and biogeographical hypotheses. The whole country, especially central Nepal (approximately between 26° 33′ – 29° 40′ N latitude and 83° 00′ – 86° 30′ E longitude), is the transition zone of the eastern and western Himalaya (Banerji 1963), where elevation varies from about 100 m to more than 8000 m above sea level (a.s.l.) over a relatively short south–north distance of c 200 km. The complex physiography of Nepal has been stratified into five major physiographic zones extending from east to west, namely the Tarai (below 500 m a.s.l), Siwalik (500 – 1000 m a.s.l.), Middle Hills/ Mountains (1000 – 3000 m a.s.l.), High Mountains (3000 – 5000 m a.s.l.), and High Himal (above 5000 m a.s.l.) (Fig. 4; LRMP 1986). These zones closely correspond to the seven bio-climatic zones identified by Dobremez (1976). The tropical bioclimatic zone is represented within the Tarai and Siwalik; subtropical and montane (temperate) zones are represented within the Middle Hills; subalpine and alpine bioclimatic zones are represented within the High Mountains, and nival (tundra and arctic) zones are represented within the High Himal physiographic zone. The country's complex physiography and sharp elevation gradient over a relatively short distance have resulted in a remarkable variation in its climate and vegetation (Chaudhary 1998).

Study area 1 (SA I): Phulchoki Mountain (2200 – 2700 m a.s.l.) is part of the Middle Hills (sub-Himalayan) range and is located at the south-eastern periphery of the Kathmandu valley (Fig. 4). The region falls within the zone of temperate monsoon climate, where about 80% of annual precipitation (about 1900 mm) falls during June–September and snowfall is common during winter months. Average monthly temperatures in the area range from 6.7 – 18.6 °C (winter) to 16.1 – 25.2 °C (summer). **Study area 2 (SA II)**: the Yala and Pansang Mountains within the Langtang National

Park (3800 – 5000 m a.s.l.) are part of the High Mountains zone and are located at the northern border of central Nepal adjoining the Tibetan Autonomous Region of China (Fig. 4). SA II falls within the zone of subalpine/cool to alpine/cold climate (Miehe et al. 2015), where ~650 mm precipitation falls annually and snowfall is frequent throughout the winter months (Bhatta et al. 2015). Average monthly temperatures in the area range from -6.13 – 3.63 °C (winter) to 6.44 – 11.43 °C (summer).
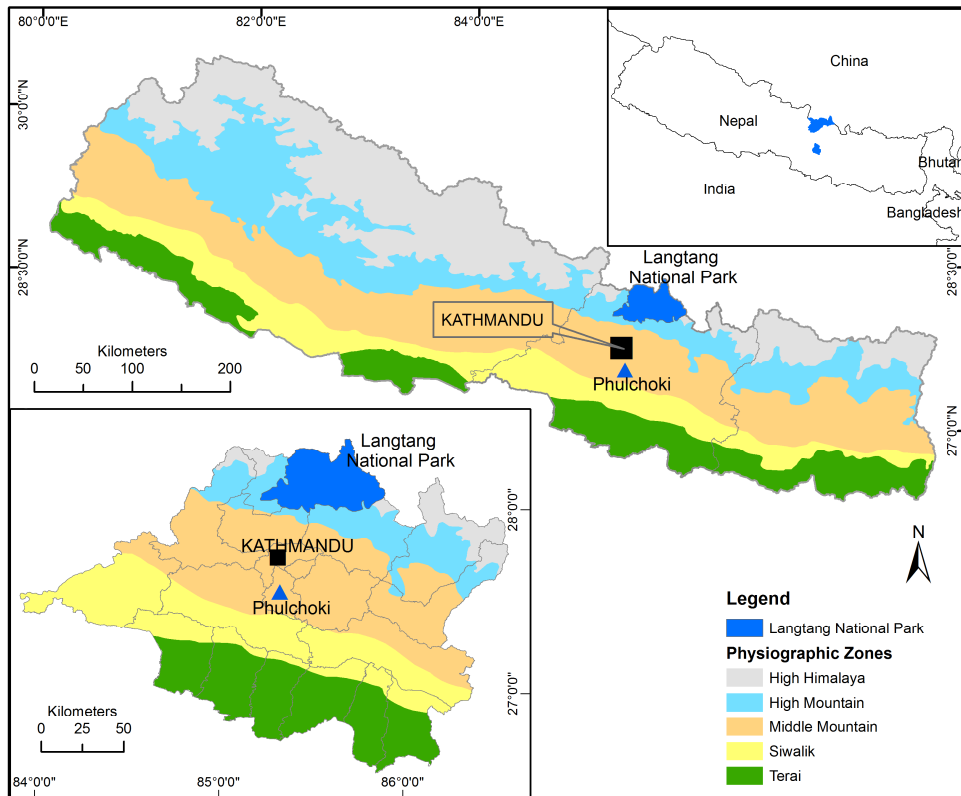
Figure 4. Location map of Nepal (top-right inset) with the study areas coloured in mid-blue; map of Nepal with physiographical zones (middle); and part of central Nepal (bottom-left insect) showing the study sites (in blue) in the different physiographical zones.

3.2 Vegetation

Nepal lies between the Holarctic and Palaeotropical phytogeographical zones, respectively to the north and south, is at the crossroads of many floristic regions (Takhtajan 1986), and also encompasses differing environments of the Eastern and Western Himalaya (Shrestha & Joshi 1996). Thus, Nepal is unique in harbouring the vegetation and flora of many phytogeographical provinces and Himalayan regions. Several phytogeographic classifications have been proposed for Nepal (e.g., Schweinfurth 1957; Banerji 1963; Stainton 1972; Dobremez 1976; Miehe et al. 2015), mainly following the vertical (south–north) physiographic and bioclimatic zonation and east–west precipitation-moisture gradient along the Himalayan axis. The detailed classifications of Stainton (1972) and Miehe (2015) describe 35 (under six phytogeographic divisions) and 30 main forest and vegetation types in Nepal, respectively, based on elevational belts, climatic zones, humidity, and major floristic composition. These are often grouped into five vegetation zones and 14 major vegetation types, mainly based on elevation and climate (Chaudhary 1998; GoN-MoFSC 2014): (1) tropical zone (below 1000 m a.s.l.; *Shorea robusta* forest, tropical deciduous riverine forest, tropical evergreen forest); (2) subtropical zone (1000–2000 m a.s.l.; *Schima–Castanopsis* forest, pine forest, alder forest); (3) temperate zone (2000–3000 m a.s.l.; lower temperate mixed broad-leaved forest, temperate mixed evergreen forest, upper temperate mixed broad-leaved forest); (4) subalpine zone (*Abies spectabilis* forest, birch–rhododendron forest); and (5) alpine zone (juniper–rhododendron association, *Caragana–Lonicera* shrub, alpine meadows).

Of these, at least seven major vegetation types (lower temperate mixed broad-leaved forest, temperate mixed evergreen forest, upper temperate mixed broad-leaved forest, Silver fir / *Abies spectabilis* forest, birch–rhododendron forest, juniper–rhododendron association, alpine meadows) of three vegetation zones (temperate, subalpine, alpine) are represented within the two study areas. The temperate forests in SA I mainly consist of oak–laurel associations, and cover an elevation belt between c. 1000 and 3000 m a.s.l. in the Himalaya (Miehe et al. 2015). The study area harbours *Quercus lanata* and *Q. semecarpifolia* at lower and higher elevations, respectively, as the

dominant canopy forming species. Sub-canopy trees such as *Ilex dipyrena, Lindera pulcherrima,* and *Rhododendron arboreum* are also associated with the oaks. Vegetation of SA II consists of subalpine (upper montane) and alpine associations (Miehe et al. 2015). The subalpine vegetation (c. 3000–4000 m a.s.l.) is characterised by the predominance of *Abies spectabilis*, *Betula utilis,* and *Rhododendron campanulatum*. However, on the drier slopes, *Juniperus recurva* is associated with the shrubby rhododendrons. Alpine vegetation between c. 4000–4300 m a.s.l. consists of dwarf shrubs such as *Ephedra gerardiana, Rhododendron lepidotum*, *R. setosum,* and herbs in the genera of *Anemone*, *Pedicularis*, and *Primula*. The upper alpine zone between c. 4300–5000 m consists of alpine meadows dominated by graminoids.

3.3 Land-use regimes

Plant resources have been an integral part of the livelihoods and culture of people in the Himalaya since ancient time; however, substantial impacts on the natural vegetation in the region have occurred only over the past century (Khera et al. 2001; Schlütz & Zech 2004; Miehe et al. 2009; Shrestha et al. 2012a; Miehe et al. 2015). Forest resources are mainly used for timber, firewood, fodder, non-timber forest products (NTFPs), livestock grazing, and for agro-forestry practices, whereas the pastures (rangelands) have been used for collection of fodder, medicinal herbs, and livestock grazing. Rapid population growth and migration, especially in the low-elevation regions over the past few decades have resulted in tremendous pressure on the forests resources leading to habitat degradation and reduction in the forest area (FAO 2010; GoN-MoFSC 2014). Similarly, overgrazing, conversion of the rangelands for other uses, overharvesting of the resources, and fire have caused degradation of the rangeland habitats. Shrinkage of the rangeland area, together with changes in socioeconomic and resource management regimes have jointly contributed to a substantial reduction in the traditional livestock grazing practice in the high Himalaya (Banjade et al. 2008; Aryal et al. 2015). At the same time, marginal agricultural lands in the rural mountainous areas have been abandoned in recent years (GoN-MoFSC 2014). The land-use disturbance drivers in Nepal vary in their nature, intensity, and frequency among the country's physiographic zones. There has also been an increase

in the forest cover over recent years, especially in the Middle Hills, with the introduction of a community forestry programme (Gautam et al. 2002; Niraula et al. 2013).

As elsewhere in the Himalayan region, substantial anthropogenic impact is evident in both the study areas. Oak (*Quercus semecarpifolia*) forest in SA I was open to the public for its use until the mid-1990s. Forest resources such as fodder, firewood, timber, and leaf litter were harvested excessively, particularly from the low-elevation areas that were relatively more accessible to settlements, and incidences of intentional forest fire were also frequent for charcoal production (Shrestha et al. 2012a). As a consequence, the forest canopy was severely disturbed (Vetaas 1997). However, with the introduction of a community forestry programme in late 1990s, the forest has been better managed leading to regrowth of the canopy cover in recent years [see Paper II].

Transhumance and agriculture have been the major livelihoods of the inhabitants of the Langtang valley (SA II) and surrounding areas. Livestock grazing was especially intense in the areas below c. 4500 m a.s.l., but there has been a significant reduction in the number of alpine grazing livestock over the recent decades. This has resulted in a significant reduction in grazing intensity mainly in the lower alpine regions (3800 – 4500 m a.s.l.), as observed elsewhere in the high Himalaya (Banjade et al. 2008; Aryal et al. 2014; Aryal et al. 2015). Decreases in livestock and crop production, restrictions imposed by the Park authorities after designation of the area as a National Park in 1986, restrictions in the community forests of the surrounding areas lying on the transhumance route, and attraction of the local people towards alternative livelihood activities such as tourism and foreign employment are the major factors behind the declining traditional transhumance practice. These temporal changes in the anthropogenic disturbance regimes in both the study areas are regarded as potential land-use factors for temporal successional changes in the vegetation of the areas.

3.4 Climate change

Climate in the Nepal Himalaya is changing at a faster rate than the global average (Shrestha & Aryal 2011; Shrestha et al. 2012b), as observed across the whole

Himalaya (IPCC 2013). A rise in atmospheric temperature has been especially evident, whereas rainfall has rather irregular temporal trends (Karki et al. 2017). Climate change in the Nepal Himalaya is rather heterogeneous spatially due to high mountain systems and complex physiography. Climate data from the weather stations nearest to the study areas have been used in this thesis. An analysis of 46 years (1968–2013) of climate data from the nearest weather station to SA I reveals a significant rise in mean annual temperature, although there is no significant temporal trend in the rainfall of the region [Paper II]. Similarly, 23 years (1988–2010) of climate data from the nearest weather station to SA II reveal a significant increasing temporal trend in mean winter minimum temperature and annual precipitation [Paper III].

4. Methods

This thesis includes four scientific papers [Paper I-IV] based on the case studies conducted in temperate, subalpine, and alpine vegetation of the central Nepal. The case studies explore the scale-sensitivity of species diversity patterns and also document the directional temporal changes in species assemblages in response to climate and land-use changes at different spatial and temporal scales.

4.1 Vegetation resurveys

A study of the changes in plant species assemblages and their potential drivers is mainly based on vegetation resurveys over a decadal temporal scale. Therefore, the vegetation data and sampling techniques of the previous studies, i.e. Vetaas (1997) in the temperate oak forest (SA I) and Miehe (1990) in the subalpine and alpine vegetation (SA II) have largely been adopted here for the resurveys in 2013 (SA I) and 2014 (SA II). The resurveys are not based on permanent plots or on exact plot relocations. Instead, previously surveyed locations were resurveyed using exactly the same sampling strategy as the previous survey (Paper II) or sampled systematically along multiple transects in the same locations using a representative number (3–5 plots in each 100-m elevation) and size of the plots (10 m x 10 m), and vegetation was recorded on a similar scale as in the previous study (Paper III). Data processing was performed prior to analyses applying very conservative criteria for the selection of sampling units and species for analyses while minimising potential sampling bias, taxonomic inaccuracies, and census biases [Papers II, III]. To avoid potential taxonomic errors, only those species that were shared between past and present surveys [Papers II, III] and had more than two occurrences in either survey [Paper II] or had more than 3% frequency in either survey [Paper III] were selected for further analyses. Furthermore, estimation bias of cover and abundance was avoided by converting the cover-abundance scores to presence (1)–absence (0) for the overall ordination analysis [Paper III]. Similarly, potential mismatches in the sampling intensity along the elevation gradient [Paper III] were minimised by matching the

sampling units of both surveys in each 50-m elevation band with respect to elevation and vegetation type.

4.2 Analytical pathway

Overall, this research considers space at local to regional scales and a time scale of decades to millennia, with complex interactions between them both. The directional temporal changes in species assemblages are expected to be confounded with those occurring across space of different scales.

In this context, first, the sensitivity of the elevational patterns of species diversity to the components of spatial scales was assessed [Paper I]. For this, the elevational patterns of empirical species richness for different plant life-forms at different grain sizes were analysed while maintaining consistent sampling strategy, proportion of the elevation gradient, and extent of sampling area for the different grain sizes. Then, elevational gamma diversity patterns from different areas (estimated by interpolation of the species' elevational ranges) were correlated with the empirical patterns at different grain sizes.

The study of the temporal variation in the composition of plant species assemblages is mainly based on the resurvey of the vegetation over a decadal scale. After partialling out the direct effects of elevation, observed directional changes in the plant assemblages were attributed to potential drivers and their possible interactions over the same temporal scale [Papers II, III]. Robustness of the observed patterns of temporal changes in response to potential drivers was tested by applying the widely used method of weighted averaging (WA) regression and calibration for environmental reconstructions [Paper III].

Finally, using temporally replicated sample datasets of different types (species abundance and species incidence datasets of total species; high-frequency species only; low-frequency species only), robustness of the WA regression and calibration technique for analysing the spatiotemporal changes in vegetation was tested [Paper IV]. Assessment of the environmental estimation accuracy is based on the comparison

of prediction errors of WA regression and the temporal trends revealed by the calibrated environment for the different datasets.

4.3 Analyses

4.3.1 Regression

Different types of regression analyses were performed based on the specific research question of the study. Generalised linear models were used to analyse the relationship between regional and local species richness patterns, and between empirical species richness and elevation gradient [Paper I]. Logistic regression was used to estimate elevational shifts in species optima [Paper III]. Linear regression analyses were performed to elucidate the change in elevation of the plant species assemblages in response to canopy gradient, time period, and locality [Paper II] and in response to time and temporal temperature gradient [Papers III, IV]. It was also used to test whether the temporal change in species abundance is related to the species' temperature adaptation, optimum elevation change, and shade tolerance [Paper II].

4.3.2 Ordination

Unconstrained as well as constrained ordination analyses were performed to show the change in species composition over spatial and temporal gradients [Papers II, III]. Correspondence analyses or redundancy analyses (when the length of the main gradient in the detrended correspondence analysis was < 2 standard deviation units) were also used to test the significance of the explanatory factors of the temporal changes [Papers II, III]. The species and site scores of the axis representing the temporal gradient were further analysed for temporal trends of compositional changes in response to temporally varying explanatory factors [Papers II, III].

4.3.3 Analysis of similarity

A one-way analysis of similarity (ANOSIM) test with Bray-Curtis distance measures (Clarke 1993) was used to analyse the extent of change in species composition between two times. This analysis is a distance-based nonparametric test of the degree of difference between two or more species groups. A similarity percentage (SIMPER)

25

procedure (Clarke 1993) was used to reveal the contribution of each species to temporal changes in species composition [Paper III].

4.3.4 Weighted averaging (WA) regression and calibration

The WA regression and calibration technique was used to estimate the current plot-based elevation (temperature) based on the past species composition and elevation, and the measured and estimated elevations of the sample plots were used to analyse the elevational shifts in the assemblages [Papers III, IV]. With this technique, WA regression first establishes a relationship between historical species composition and the environmental variable in question, and this relationship is subsequently used to predict the environment for the modern dataset (species composition). The differences between the observed and calibrated elevations of the plots of the modern dataset were considered to be the elevational shift in species composition.

5. Results and discussion

The directional temporal changes in the plant species composition of central Nepal in response to changing climate and land-use regimes have been assessed in terms of changes in species' relative abundance and elevational shifts in species assemblages. Scale always becomes an issue when one aims to investigate spatiotemporal patterns of species composition or diversity along environmental gradients (Wiens 1989; Levin 1992; Whittaker et al. 2001). As documented by earlier studies (e.g., Shmida & Wilson 1985; Ricklefs 1987; van der Maarel 1988; Wiens 1989; Levin 1992; Rosenzweig 1998), species diversity patterns and their determinants vary with spatial as well as temporal scale in a similar fashion, and the influences of spatial and temporal scales on species diversity patterns are similar (Adler et al. 2005; Soininen 2010). Consequently, the patterns and processes related to temporal and spatial scales remain confounded (Wiens 1989; Dornelas et al. 2013) and makes a causal interpretation of the observed patterns challenging.

The sample plots of both surveys are distributed along an elevation gradient and the species composition and the explanatory factors therefore exhibit distinct elevational patterns. The spatial gradients collapse into an almost single dimension when vegetation is sampled using transects along an elevation gradient (Colwell 2011; Dornelas et al. 2013), which potentially concords with the temporal gradient in this study. Moreover, the temporally replicated vegetation surveys were not based on permanent plots, but the previously sampled locations were selectively resurveyed, potentially incorporating spatial variations into the temporal data to some extent. This is a typical situation for space-time interactions, where the time series is embedded in a spatial context and *vice versa*, and consequently the spatial and temporal patterns remain confounded (Dornelas et al. 2013). Before considering the contribution of the spatial variations in the observed temporal patterns as a methodological error or endorsing these in a spatiotemporal context, it becomes crucial to assess separately the influence of spatial scale on the species diversity patterns and processes. This was done thoroughly by treating species richness as the main response variable, and various components of spatial scale, i.e. grain size, focus, and regional area, as

analytical manipulations. The degree of mismatch between elevational patterns of species richness across the nested grain sizes and across different areas used for regional richness estimation gives an estimation of the influence of spatial scale on the species richness patterns and underlying processes [Paper I].

5.1 Scale sensitivity of the elevational gradients in species diversity

Assumptions

Interpolated plant species richness for Nepal reveals a hump-shaped elevational pattern for herbs with maximum richness between 4000 and 4100 m a.s.l. and a pattern of linear decline for woody species. Therefore, the elevational gamma diversity (regional richness) pattern was *a priori* formulated as a hypothesis of alpha diversity patterns, where all the richness patterns at the regional scale would be revealed at the level of grain and focus (area of local gamma estimation). If this is true, a significant linear concordance between the local and regional richness would be revealed irrespective of grain size, area of gamma estimation, or plant life-form, verifying the scale invariance of elevational patterns of species richness.

In agreement with the hypothesis, the elevational patterns of species richness were broadly consistent from the very fine scale (1 m^2 grain size) to the regional level, implying general scale invariance in the patterns. This is partly in line with the grain size-invariant richness patterns documented by previous studies (e.g., Grytnes 2003; Nogués-Bravo et al. 2008; Rowe et al. 2015). Scale-invariance in the patterns indicates that species diversity of the local habitats adequately represents the patterns and processes of regional species richness along an elevation gradient. At all spatial scales, the rate of site-to-site species loss increases with elevation, most probably due to a decrease in land surface area and length of the growing season with increasing elevation of the alpine areas (Körner 2000, 2007). Such a generality in the climate and physiography-driven nestedness component of the beta diversity along an elevation gradient likely produces the patterns independent of spatial scale.

Minor but systematic differences are noted in the patterns across the spatial scales, especially for the woody species. The patterns become more apparent at coarse grain

sizes and with lager areas of regional richness estimation, partly in line with the patterns revealed by several coarse-scale studies (e.g., Crawley & Harral 2001; Rahbek & Graves 2001; Romdal & Grytnes 2007; Belmaker & Jetz 2011). The coarser scale represents better the regional species pool by sampling more completely the species as well as habitat diversity in a region (Romdal & Grytnes 2007). As the spatial scale decreases, the probability of a species being represented decreases due to an area effect, and the environmental conditions at such fine scales also become more exclusive (less representative) because the heterogeneity of different environmental variables is expressed at different scales (Tuomisto et al. 2016). The uniqueness of the environment of such small areas limits species colonisation. At fine scales ($1m^2$ – 16 m^2 grain sizes in this thesis), the number of individuals that can fit within each sampling unit becomes small compared to the species pool. Under such conditions, the patterns at the fine scale are mainly determined by the density of the individuals that can occupy such small areas (Oksanen 1996; Tuomisto & Ruokolainen 2012). Here, site-specific non-climatic factors such as fine-scale habitat heterogeneity, soil moisture, soil chemistry, and stochastic factors are more influential (Svenning 1999; Palmer 2006; Auestad et al. 2008). These factors jointly moderate the strength of the relationship between species richness and major environmental determinants and lead to a deviation of the local diversity pattern from that at the regional scale (Belmaker & Jetz 2011; Rowe et al. 2015). Consequently, the patterns become more stochastic as the spatial scale of the grain becomes finer (Watt 1947; Kersaw & Looney 1985).

In an apparent refutation of the hypothesis, higher scale sensitivity of woody species than herbaceous species is likely due to the life-form characteristics of the woody species and scale-sensitivity of their major driving factor, i.e. climate. The likelihood of recording woody species at a fine scale ($1 m^2$ grain) is consistently low because of their large size and low density compared with those of herbs in an alpine region (Oksanen 1996). Woody species diversity in high elevation areas is more responsive to regional climatic conditions, especially temperature (Wang et al. 2009; Qian 2013) than to fine-scale environmental factors. Therefore, the use of a larger spatial scale is particularly important for woody species diversity for two main reasons – the larger area captures better the sparse woody species density in the high elevation areas and it

represents better its driving factors, i.e. habitat diversity and abiotic environmental heterogeneity. The observed patterns thus imply that although the overall elevational patterns of species richness are largely scale invariant from the plot to regional level, they are also, to some extent, affected by variation in the relative influence of the causal factors of the spatial scale and by life-form characteristics of the plant species.

Overall scale invariance in the species richness patterns along an elevation gradient implies that species diversity in the alpine region can be reliably studied at different spatial scales ranging from 1 m^2 grain size to the regional level. Therefore, spatial inaccuracies of plot-relocations, variations in the grain sizes used in the surveys, and differences in the spatial extents of the sampling area in the landscape are unlikely to distort the basic pattern. However, the patterns for woody species are least pronounced at the fine scale. Therefore, a representative grain size of 100 m^2 has been used in the vegetation resurveys for the studies of temporal changes [Papers II, III]. The influence of the major spatial component, i.e. elevation gradient on the temporal variation in species composition was then partialled out analytically.

5.2 Temporal changes in plant species composition

An upward shift of plant species or assemblages has been the most frequently documented ecological response of species to contemporary climate change (as reviewed by Lenoir & Svenning 2015; Dainese et al. 2017). However, evidence accumulated over recent years reveals that this response may not be as pervasive and pronounced as previously expected. Several modified responses of plant assemblages under climate warming have been attributed to factors such as changed precipitation-moisture regime, land-use disturbance regime, and biotic interactions (e.g., Bertrand et al. 2011; Crimmins et al. 2011; Liang et al. 2016). The role of land-use change may be vital in modifying the trajectories of the climate warming-driven temporal changes in plant assemblages because such changes often interact with climate change and thereby compound or confound or counteract the climatic effects (Dainese et al. 2017; Goring & Williams 2017; Guo et al. 2018). Moreover, both the factors are multidimensional and heterogeneous over space, and their frequency and intensity may be redistributed from one spatial scale to the next. Consequently, their impacts may

not be uniform across geographic locations and vegetation types. The causal interpretation of the observed changes is always a challenge due to these confounding drivers, plus the relative influence of climatic versus land-use disturbance in driving the temporal vegetation changes often lacks consensus (e.g., Vittoz et al. 2009; Nowacki & Abrams 2015; Pederson et al. 2015; Zhang et al. 2015; Abrams & Nowacki 2018).

The directional temporal changes in the plant assemblages of the temperate oak forest and alpine vegetation in central Nepal have been attributed to the temporally varying climatic and land-use factors in the region [Papers II, III]. The influence of climate change has been assessed in terms of changes in species' relative abundance and shifts in the elevational distribution of species assemblages, whereas the influence of land-use factors has been interpreted from proxy variables of the ecological attributes of species such as shade tolerance and livestock palatability. Temporal change in species abundance was analysed individually for each species, while the elevational shift was analysed in terms of species assemblages, i.e. shifts in plot-elevations.

Assumptions

The null hypothesis assumes no significant systematic temporal changes in the species composition of central Nepal. In the case of the rejection of the null hypothesis, two alternative hypotheses to be tested are:

a) Climate change hypothesis: An upslope shift in the species assemblages, i.e. 'thermophilisation' will be observed, whereby an increase in those species with higher temperature optima (= lower elevation optima) and a decrease in those species with lower temperature optima (= higher elevation optima) takes place in the sample plots.

b) Land-use change hypothesis: There was a temporal canopy disturbance gradient in the temperate oak forest with an increase in canopy closure, especially in the low-elevation forest (below 2400 m a.s.l.) that was heavily disturbed (open-canopied) in the past. The land-use hypothesis therefore assumes 'mesophication' of the understorey habitat, whereby an increase in the shade-tolerant species and a decrease in the shade-intolerant species is predicted.

A temporal grazing gradient has been created by reduction in the livestock grazing in the subalpine and alpine pastures. It is especially evident in the areas below c. 4500 m a.s.l., where the density of the herbivores was high in the past. An overall increase in species abundance due to a release of grazing pressure is predicted, especially in those areas that were highly grazed in the past.

Overall, there are significant temporal changes in the species composition of both study areas, with the vast majority of species increasing in abundance, although a sizeable minority of the analysed species decreased significantly over the past two decades. The changes were statistically related to both the explanatory factors, i.e. climate warming and land-use change, and accord with the major trends of temperature and land-use driven changes across the mountainous areas of the world (e.g., Lenoir et al. 2010b; Bai et al. 2011; Gottfried et al. 2012; De Frenne et al. 2013; Rumpf et al. 2018). A closer examination of the evident changes, however, reveals rather different trends in response to the two explanatory factors and some of the patterns are potentially confounded due to interactions between climate change and land-use change.

In agreement with the climate hypothesis, changes in the temperate oak forest are explained largely by the trend of climate warming. Here, the abundance of the warm-adapted species, i.e. species with elevation optima lower than the lowest elevation of the sample plots (2200 m a.s.l) increased with a simultaneous decrease in the cold-adapted species in the plots, i.e. species with elevation optima higher than the 2600 m a.s.l. [Paper II]. Accordingly, the changes are manifest as a decrease in the weighted average elevation of the sample plots, i.e. species assemblages. Such changes are significantly more pronounced in the semi-open canopy forest than in the closed canopy forest. In the alpine vegetation, only a few species assemblages (sample plots) in the upper alpine belt reveal such an upward shift, probably in response to winter climate warming [Paper III]. In these plots, species with elevation optima lower than the elevation of sample plot increased whereas those with optima higher than the elevation of sample plot decreased. This apparent 'thermophilisation' of plant species composition in central Nepal is most likely due the species tracking their climate niche

under climate warming. This trend is broadly consistent with the patterns of warming-driven compositional changes across Asia (e.g., Bai et al. 2011; Telwala et al. 2013; Agnihotri et al. 2017), Europe, and North America (e.g., Grabherr et al. 1994; Walther et al. 2002; Klanderud & Birks 2003; Walther et al. 2005; Felde et al. 2012; Gottfried et al. 2012; Rumpf et al. 2018).

Land-use disturbance-related changes of different magnitudes are evident in the species composition of both areas and likely modified the warming-driven changes in both areas along the temporal land-use gradients. The warming-driven changes are more apparent in the oak forest with its semi-open canopy cover that was heavily disturbed and more open in the past compared to those in the closed canopy forest. This is an indication that the dense canopy in the closed-canopy forest may have moderated the process of thermophilisation by maintaining a cooler understorey microclimate (Lenoir et al. 2010b; De Frenne et al. 2013). In partial agreement with the land-use change hypothesis, there is a significant increase in shade-tolerant trees and bamboo and a decline in the shade-intolerant herbaceous and shrub species. The changes are likely driven by the mesophication of the understorey environment due to an increase in forest canopy cover. Mesophication is a process that causes structural changes to the microenvironment by developing understorey conditions that are cooler, more humid, and damp (Nowacki & Abrams 2008), and thereby influences the local abundance of species (Nowacki & Abrams 2008; Verheyen et al. 2012). The regrowth of the forest canopy most likely altered both resource quantity and heterogeneity on the forest floor thus affecting the understorey species (Bartels & Chen 2010). Among the changing species, the winners were those that were warm-adapted as well as shade-tolerant and losers were species that were cold-adapted and shade-intolerant.

The changes directed by the temporal grazing reduction are more pronounced in the alpine species composition, as evidenced by an overall increase in species abundance, alongside a downhill shift of the vast majority of the species assemblages. The changes are even more pronounced in the lower alpine areas where there was a greater decrease in livestock grazing intensity. This trend contrasts with that expected under the climate

change hypothesis and with the findings of a large number of studies that document upslope shifts in species or assemblages under climate warming (e.g., Grabherr et al. 1994; Klanderud & Birks 2003; Walther et al. 2005; Lenoir et al. 2008; Felde et al. 2012; Morueta-Holme et al. 2015). In my study, the warmer winter temperature and increased annual precipitation most likely interacted with the temporal grazing gradient to direct the compositional changes. Both the livestock palatable and unpalatable species have increased significantly after reduction of grazing pressure in the study areas and the availability of sufficient suitable space, nitrogen, and water likely minimised interspecific competition. A temporal increase in winter temperature may enhance early spring melting of snow and decrease snow cover, which strongly modifies both the physical and thermal environments in alpine areas (Kreyling 2010), and an increase in annual precipitation may enhance the water availability and potentially reduce warming-driven water stress during summer (Pfeifer-Meister et al. 2016). These factors together likely resulted in longer growing seasons with warmer and more humid conditions in the spring and summer. While these changes acted uniformly along the whole elevation gradient, more radical changes in species composition are seen towards the lower parts of the elevation gradient (below c. 4500 m a.s.l.), most likely due to significant reductions in the grazing intensity over time that potentially altered the species interactions in these areas. This facilitated the expansion of the species' populations in the lower alpine areas, signifying that the changes driven by grazing reduction prevailed over those by climate warming.

Although the directional compositional changes have been interpreted using the ecological attributes and elevational distribution of the species, the changes have been confounded to some extent. Among the increasing species in the temperate forest, not all the warm-adapted species are shade-tolerant and, *vice versa*, among the decreasing species, not all the cold-adapted species are shade-intolerant. Similarly, not all the decreasing alpine species are grazing indicators (nitrophilous) and not all the increasing species are grazing palatable species. There might be several alternative factors responsible for these variations. Some of the species may be specialised to their local microhabitats and track the fluctuations in fine-scale habitat heterogeneity and soil conditions rather than the general temperature, moisture, light, and grazing

regimes. A consistent response of all species to climate warming cannot be expected because of each species' individualistic climate niche and complex interactions with changes in land-use. Land-use change can have any of a confounding or compounding or counteracting role in the climate-driven changes of the vegetation (De Frenne et al. 2013; Goring & Williams 2017), depending largely on the life-history and eco-physiological features of the species and intensities of the drivers themselves.

In summary, climate warming at a regional level is a potential driver of changes in species composition via thermophilisation. However, the role of land-use change at a landscape scale is equally (if not more) influential in driving the temporal changes. Land-use change in the form of forest canopy closure and temporal grazing reduction may variously interact with climate warming to counteract or confound the changes driven by climate warming. Therefore, the magnitude and direction of the temporal vegetation changes in central Nepal would be dependent on the intensity as well as the frequency of both regional climate warming and land-use changes.

5.3 Weighted averaging (WA) regression and environmental calibration as a tool for quantifying climate-driven elevational shifts in vegetation

Various analytical and vegetation survey techniques were applied for analysing spatiotemporal changes in species composition under changing climate and land-use regimes [Papers I–III]. The reliability of the observed patterns and their causal interpretations depends strongly on the robustness of the methodological approach taken. The importance of the analytical techniques is paramount because each technique is based on certain underlying assumptions regarding the spatiotemporal dynamics of the species in relation to its environment and has its own strengths and limitations regarding the different methodological dimensions. Therefore, the methodological factors such as data sampling technique, precision, and adequacy in the resurveys, quantity and quality of the data, skill and expertise of the observer, and the analytical technique are of key importance (e.g., Klanderud & Birks 2003; Tingley & Beissinger 2009; Ross et al. 2010; Kopecký & Macek 2015; Kapfer et al. 2016).

Bearing this in mind, a technique of environmental reconstruction recently incorporated into modern vegetation ecology (e.g., Brady et al. 2010; Bertrand et al. 2011; Bertrand et al. 2016) was partly used in this thesis [Paper III] and its performance was rigorously tested. Prediction accuracy of the technique was assessed mainly by comparing the goodness-of-fit of the WA regression and calibration models of species abundance and incidence datasets from the two study areas that exhibited pronounced temporal trends [Paper IV].

WA regression and calibration reconstructed the environment of the plot-based vegetation datasets with a fairly high accuracy. The inferred temporal trends in the vegetation and reconstructed environment are supported by ordination analyses that reveal significant changes in species composition along the temporal gradient. However, an 'edge effect' that produces an overestimation of optima at the low end of the gradient and an underestimation at the high end was prominent with all the analysed datasets. This is most likely caused by the training sets having high compositional turnover along the dominant and long spatial gradient (ter Braak & Juggins 1993). Monotonic curvilinear deshrinking of WA regression models slightly reduced the edge-effects as recommended by previous research (ter Braak & Juggins 1993).

The accuracy of WA (average for incidence data) regression is notably higher (smaller root mean squared error of predictions (RMSEP)) with the species incidence datasets than with the abundance datasets. This difference is likely associated with methodological inaccuracies. The datasets based on vegetation surveys by different observers may be prone to inconsistencies regarding sampling design and effort, census or estimation accuracy, and individual observer's skills and experience (e.g., Archaux et al. 2006; Tingley & Beissinger 2009; Kapfer et al. 2016), ultimately contributing to spurious analyses. It is highly unlikely that two different observers with different skills and expertise will estimate the same cover-abundance for a species. Moreover, species abundance fluctuates remarkably between years due to seasonal changes in the weather conditions (Diekmann 2003). Such estimation bias in cover-abundance datasets produces higher prediction errors in WA regression because

inaccuracy in the estimated abundance is incorporated as part of the weighting that is given to a species during its WA estimation (WA calculation procedure: ter Braak & van Dam 1989). The avoidance of abundance data is therefore sometimes recommended for ecological studies that estimate the weighted average or that compare the historical and current species composition (Diekmann 1995, 2003).

Incidence datasets are devoid of such biases because the abundance of each species is standardised to 1. Also from a statistical point of view, presence-absence values are preferable over the ordinal and partly non-linear scale of cover-abundance values (Diekmann 1995). Use of incidence data for WA calculation has been recommended by many authors because the quantitative response of a species does not depend only on the environmental conditions but also on its growth form (Ellenberg 1991; Diekmann 1995 and references therein). Some species grow singly, whereas others form extensive populations. The more frequent species are weighted comparatively more in WA calculations based on abundance datasets but their higher frequency is due to growth-form characteristics rather than a better response to environmental conditions. Differences in the sampling procedure may also influence estimation accuracies of WA regression. The training set (past dataset) of study area II (Langtang region) is based on selective sampling, whereas the modern (current) dataset is based on a non-preferential sampling procedure. Such differences in the sampling design can produce several important differences in the datasets regarding the representation of frequent and infrequent species, species heterogeneity, and species-environment concordance (Diekmann et al. 2007; Michalcová et al. 2011; Bhatta et al. 2012), ultimately resulting in higher prediction errors in WA regression.

The trend of the estimation accuracy of the WA regressions with the variously processed datasets is rather inconsistent. Broadly, training sets with all species usually produced the most accurate (lowest RMSEP) estimations as assessed by the classical diagnostics of palaeoenvironmental reconstructions (Birks et al. 1990; Birks 1994); however, this was not the case for all the datasets of both study areas. Removal of the 31 most frequent species from the full training set (175 species) for study area I (Phulchoki Mountain) reduced the estimation accuracy compared to that of the total

species dataset, whereas estimation accuracy increased when the least frequent 49 species were removed from the full training set. These findings contrast with those of previous studies which find that large prediction errors occur only when the commonest and numerically most abundant taxa are included in the WA regression (Birks 1994). In the full training sets, the most frequent taxa generally have higher taxonomic precision, whereas taxonomic inaccuracy (and hence noise) is more associated with the least frequent taxa. Removal of the most frequent species from the full training set therefore causes a loss of ecological information, whereas removal of the least frequent species intuitively minimises noise within the dataset. Among the datasets of study area II, there are 113 species in the 1990 dataset and 121 species in the 2014 dataset with less than 5% frequency. Despite a high taxonomic mismatch between both datasets due to these species, removal of almost half of the species from the dataset contributed to a loss of environmental information associated with some of the correctly identified species. Moreover, low-frequency species may sometimes have a narrow environmental tolerance and may therefore be an optimal indicator species. This suggests that high accuracy in WA regression and environmental calibration requires high taxonomic accuracy, together with high spatial, temporal, and chronological precision (ter Braak & Juggins 1993; Birks 1994; Birks et al. 2010).

Accuracy of the calibrated environment was assessed qualitatively and rather indirectly by comparing the fitness of the regression models of elevational shifts in species assemblages. The models are based on the calibrated and measured elevations of the species assemblages (sample plots). The fitness of the models (indicated by adjusted r^2 of the models) mirrored the estimation accuracy of the WA regressions. This means that precise WA regression produces more accurate calibrated environmental parameters, which in turn, result in a regression model with higher adjusted r^2 for better estimating the elevational shift in plant assemblages. Thus, these trends indicate that estimation accuracy of the WA regression and environmental calibration is significantly influenced by taxonomic precision, census accuracy, and the number of taxa included or eliminated during data processing.

In summary, WA regression and environmental calibration with plot-based vegetation data perform with a fairly high accuracy, although edge-effects may be pronounced, which can be reduced to some extent by regression deshrinking procedures. Use of a species incidence matrix may improve the estimation accuracy by avoiding the estimation or census bias that is more associated with the abundance datasets. Species data processing cannot guarantee the most accurate environmental preditions: instead, the most optimal environmental reconstruction can be achieved by using the full set of species in the datasets.

6. Concluding remarks

This synthesis has assessed the scale relations of species diversity patterns, documented the directional temporal changes in plant species assemblages in response to temporally varying climate and land-use regimes along an elevation gradient in central Nepal, and tested the performance of the weighted averaging regression and and calibration technique for quantifying the temporal changes in species assemblages and their environment.

Conclusions drawn from the study are:

1. The basic elevational pattern of species richness is largely scale invariant and hence richness gradients can be reliably studied at different spatial scales from the fine grain to the regional level. Any scale sensitivity there is varies slightly according to plant life-form, most likely because the relative influence of the environmental determinants of different life-forms varies with the spatial scale. Least pronounced patterns, especially for woody species at the fine grain size, indicate that species diversity sampled using a larger grain size over a larger extent are more appropriate for the study of large-scale patterns such as elevational gradients at regional or continental scales.

2. Climate warming is a major determinant of the successional changes via thermophilisation of the plant species assemblages at the regional level. However, land-use changes may prevail over the climatic effects at the landscape and habitat level thereby confounding or counteracting the temporal changes driven by climate warming. The trajectories of the successional changes in the vegetation of central Nepal therefore depend on the intensity as well as the frequency of both factors at a particular spatial scale.

3. A large proportion of the evident temporal changes in the species composition in central Nepal are most likely driven by the complex interactions and feedback mechanisms between climate change and land-use change. Therefore, succession management in the landscape should focus on the potential interactions between both these factors in driving the temporal changes.

4. Environmental factors for plot-based vegetation datasets can be calibrated along a time scale with fairly high accuracy using weighted averaging regression and calibration, but the prediction errors may be high at the endpoints of the environmental gradient. Use of a species incidence matrix may improve the estimation accuracy of the technique. Species data processing cannot guarantee the most accurate environmental predictions: instead, most optimal calibrations can be achieved by using the full set of the species in the datasets. Taxonomic precision and census or estimation accuracy are of paramount importance in the environmental reconstructions.

7. Future perspectives

♦ Nepal Himalaya is a data-deficient region and the discrete ecological data generated by the various case studies are of different spatial resolutions and sampling schemes, which limit the use of these datasets to document the biodiversity components, patterns, and processes at different spatiotemporal extents. But because the basic spatial pattern of plant diversity is unlikely to be significantly influenced by differences in the spatial scale, these datasets can be carefully synthesised to study the spatiotemporal patterns and processes of species diversity and composition at larger scales.

♦ The potential drivers of biodiversity, especially the land-use factors in the region are severely under-documented at all scales. This thesis has used qualitative proxy variables for land-use change and used climatic variables from nearby weather stations. Quantification of the land-use factors using standard techniques is more appropriate than using subjective proxy variables. Similarly, atmospheric and soil temperatures regularly measured at different spatial and temporal scales would give a more precise picture of climate change in the region than the extrapolated climate factors.

♦ A moderating role of forest canopy closure against warmer maximum temperatures has been documented. At the same time, the densified canopy and sub-canopy layer may affect the understorey by trapping infrared radiation (enhancing the daily minimum temperature) and water vapour released from evapotranspiration, and by lowering wind speeds (reducing drying effect) thereby allowing higher understorey humidity to prevail. Research on the effect of such a modified understorey environment on the regeneration and survival of species would give a more complete picture of the compositional changes in the forests in the context of forest canopy closure and climate warming.

♦ Land-use changes interact frequently with climate change factors and thereby modify the climatic responses of the species. Studies of temporal changes focussing more on the potential interaction and feedback mechanisms between

climate change and land-use changes from landscape to regional level are warranted. This can feed the national and regional biodiversity management strategies with cutting-edge scientific information for the restoration and sustainable management of the landscapes.

♦ Testing the robustness of the observed patterns by applying different complementary analytical techniques is essential for deducing reliable conclusions. And equally important is the use of robust techniques, compatible with the nature of the datasets, which can also solve or minimise the potential errors in the datasets. Moreover, datasets with high taxonomic precision, estimation or census accuracy, and sampling adequacy are of paramount importance for elucidating the successional changes in species composition with their underpinning causation.

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