Spatial dynamics of species distributions in an anthropogenic landscape in the context of climate change

Madan Krishna Suwal

Thesis for the Degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
2018

UNIVERSITY OF BERGEN

Spatial dynamics of species distributions in an anthropogenic landscape in the context of climate change

By

Madan Krishna Suwal

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

Date and place of public defence: 8th June 2018, Bergen, Norway

Supervisor: Professor Ole R. Vetaas,
Department of Geography,
University of Bergen

First opponent: Professor Udo Schickhoff,
Biogeography and Landscape Ecology
Working Group,
University of Hamburg

Second opponent: Associate Professor Richard Field,
School of Geography,
University of Nottingham

Committee chair: Associate professor Gidske L. Andersen,
Department of Geography,
University of Bergen

Year: 2018

Title: Spatial dynamics of species distributions in an anthropogenic landscape in the context of climate change

Name: Madan Krishna Suwal

Print: Skipnes Kommunikasjon / University of Bergen

Scientific Environment

The work presented on this thesis was carried out at the Department of Geography, University of Bergen (UiB). Financial support was provided by Lånekassen fund. All the research activities were carried out at UiB. The training components of the degree were completed at UiB, Research Centre in Biodiversity and Genetic Resources – CIBIO, University of Èvora, Portugal, Institute of Marine Research, UiB and Highland Statistics Ltd. The research outputs were disseminated through different conferences as poster presentation and a talk.

Acknowledgements

I would like to express my sincere thanks to Professor Ole R. Vetaas. His regular supervision, support and constructive comments brought this work to a successful end. I also sincerely thank Krishna Babu Shrestha for his support and ideas about the research design of my first paper and comments and suggestions on other academic manuscripts. During the course, I received frequent support from Lila Nath Sharma, Kuber Prasad Bhatta and Dilli Prasad Rijal and I express my gratitude to them.

I also thank Ganga Ram Regmi and Kamal Kandel for introducing me to the field of distribution modelling and Falk Huettmann, Associate Professor at the University of Alaska Fairbanks, who trained me in distribution modelling at his lab in 2013. I thank my younger brother Radha Krishna Suwal, whose ingenuous support for a GIS training course made the foundation for my whole journey to distribution modelling.

I acknowledge many Nepalese friends, with whom I spent many days in Bergen, namely Sita Paudel Sharma and her family, Dilli Prasad Poudel and his family, Raj Kumar Adhikari and his family, Til Prasad Pangali Sharma and his family, Prakash Bhattarai, Kabita Bhatta and her family, Yog Raj Gautam, Keshav Prasad Paudel, many other friends and the Nepali Bergen Society.

I thank Tessa Bargmann, Cathy Jenks and Benjamin Robson for their help with English language editing.

I thank the staff at the Department of Geography for all administrative support, as well as the Faculty of Social Sciences, UiB and Lånekassen for supporting my studies.

I also thank my wife Rosy Makaju, who always ingenuously supported me during this course as well as in the earlier part of my life. Possibly she is not aware how her different acts kept me working. She compromised her sleep in the mornings to take care of our daughter while I left early for work; and my sweet daughter who spreads joy in my hectic academic life – both deserve and get my heartiest thanks.

Abstract

Introduction: Climate change and land-use (intensity) change are factors that force biological organisms to change their geographical distributions. These two global drivers, both alone and in combination, have a large impact on the geographical distribution of species. Explaining current distributions and predicting species' future distributions are principal activities of biogeography, but very few such studies have been undertaken in the Himalayan region. This is despite climate change being more rapid in the Himalaya than the global average. Additionally, significant out-migration (to urban areas and/or abroad) and a change from pastoralism to tourism as the main livelihood in the mountains of Nepal have caused a drastic reduction in grazing pressure from domestic animals.

Objectives: This thesis aims (i) to evaluate the spatial dynamics of a species – *Abies spectabilis* – at its upper species limit in response to recent warming and reduced land-use intensity in the central Himalayan mountains; (ii) to investigate species potential responses to climate change under future projected warming (a case study of three *Rhododendron* sister taxa) and evaluate their climatically potential current and future distribution as well as distributional overlaps; and (iii) to investigate climatic niche similarity between parapatrically disjunct subspecies of *Macaca assamensis* (Assamese macaque) and whether their climatically potential distribution areas with current and future climate overlap or not .

Methodology: To evaluate the spatial dynamics of species in current climate, an empirical study was carried out in the alpine treeline ecotone of the central Himalayan region (Paper I). The potential response of species to future projected climate was analysed based on predicted distributions from species distribution model (SDMs). The SDMs were fitted on binomial presence vs pseudo-absence and presence vs background data against associated bioclimatic variables using the Random Forest algorithm. The potential distributions were predicted for the current and future projected climate (Paper II). In a third case study (Paper III), the bioclimatic niche similarity between *Macaca assamensis* ssp. *pelops* and *M. assamensis* ssp. *assamensis* was tested with a multivariate analysis of variance. The potential distributions of both subspecies based on bioclimatic variables under current and future climate were predicted using Random Forest and MaxEnt algorithms. Their overlap was analysed with Ecological Niche Modelling Tools (*ENMTools*) software.

Main results: The upper species limit of *Abies spectabilis* is moving towards higher elevation, i.e. towards a cooler climate, in a backdrop of recent climate change and reduced land-use intensity (Paper I). The advancement of the leading edge can be interpreted as an attempt to remain within their climatic niche. The potential response under future projected warming for *Rhododendron* sister taxa is species-specific (Paper II). *Rhododendron lowndesii*, a species from a dry region of Nepal may not move to higher elevations, while predictions suggest that *R. cowanianum* may shift its leading edge along with its optimum and *R. lepidotum* may shift its whole range along with its optimum to track their climatic niches. The distribution models predicted higher overlaps of climatically suitable areas between *Rhododendron* sister taxa in the future compared to current modelled distributional overlaps.

The closely related parapatrically disjunct *Macaca assamensis* ssp. *pelops* and *M. assamensis* ssp. *assamensis* have rather different climatic niches, but with some overlap (Paper III). In geographical space, however, the subspecies are separated by a zoogeographic barrier – the river Brahmaputra. The modelled current potential geographical distributions are smaller than the predicted climatically suitable areas in the future, but it is uncertain whether the species will disperse and whether biotic interactions will allow them to occupy these areas in the future. In the projected future climate, they will lose some of their current potential geographic space and some new geographic space may become available for them.

Conclusions: Species responses to climate change are species-specific. Species maintain their spatial dynamics to remain within their climatic niches. Closely related sister taxa do not necessarily have similar climatic niches.

Key words: Climate change, Himalaya, MaxEnt, Niche, Random Forest, Spatial dynamics, Species distribution modelling

Declaration

This thesis includes a synthesis, two 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:

Madan K. Suwal: Study design, field work, data analysis, writing and editing
Krishna Babu Shrestha: Study design and editing
Laba Guragain: Data contribution for Gaurishankar Conservation Area
Rabin Shakya: Data contribution for Manaslu Conservation Area
Kalpana Shrestha: Data contribution for Manaslu Conservation Area
Dinesh Raj Bhuju: Editing
Ole R. Vetaas: Discussion on data analysis and editing

Paper II:

Madan K. Suwal: Study design, data compilation, modelling, writing and editing
Ole R. Vetaas: Discussion on model outputs, interpretation and editing

Paper III:

Madan K. Suwal: Study design, data compilation, modelling, writing and editing
Falk Huettmann: Assisted in Random Forest modelling
Ganga Ram Regmi: Data contribution
Ole R. Vetaas: Discussion on model outputs, interpretation and editing

List of publications

(They will be represented by the Roman numeral hereafter)

Suwal, M. K., K. B. Shrestha, L. Guragain, R. Shakya, K. Shrestha, D. R. Bhuju, and O. R. Vetaas (2016) Land-use change under a warming climate facilitated upslope expansion of Himalayan silver fir (*Abies spectabilis* (D. Don) Spach). Plant Ecology 217:993–1002. DOI: https://doi.org/10.1007/s1125 (Paper I)

Suwal, M. K., and O. R. Vetaas (2017) Climatic variables determining *Rhododendron* sister taxa distributions and distributional overlaps in the Himalayas. Frontiers of Biogeography 9:e34911. DOI: https://doi.org/10.21425/F59334911 (Paper II)

Suwal, M. K., F. Huettmann, G. R. Regmi, and O. R. Vetaas (2018) Parapatric subspecies of *Macaca assamensis* show a marginal overlap in climate niche (DRAFT) (Paper III)

Contents

Introduction

The distribution pattern of species has intrigued ecologists for a long time. It was first documented as early as the late 18th century by Alexander von Humboldt. A species' geographic distribution range and abundance are primarily determined by its physiological response to climate, particularly temperature (Latreille, 1819; cited by Davis *et al.*, 1998a). If climate was the only determinant of species distribution, species would have always been in equilibrium with their geographic distribution; such a scenario is not supported by empirical evidence (Vetaas, 2002; Svenning & Skov, 2004; Araújo & Pearson, 2005; Pearson *et al.*, 2006). The disequilibrium is because of different biotic and abiotic factors such as species interactions (Speed *et al.*, 2012), dispersal limitation/capability (Araújo & Pearson, 2005), species history (Svenning & Skov, 2004), and land-use (Goring & Williams, 2017; Miller & McGill, 2017). These factors prohibit species from occupying the whole of their suitable climatic ranges in geographic space (i.e. potential geography).

A major concern of current biogeography is the impact of contemporary environmental changes on species range dynamics. Empirical studies from different parts of the world have reported range and/or optimum shifts for many plant and animal species (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Crimmins *et al.*, 2011; Telwala *et al.*, 2013; Morueta-Holme *et al.*, 2015). Different scholars (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Morueta-Holme *et al.*, 2015) suggest that the ongoing climate change is one of the important drivers of these geographical range and/or optimum shifts of species. However, the causal link to climate change may be masked by disturbances like grazing (Speed *et al.*, 2012) and land-use change (Gehrig-Fasel *et al.*, 2007; Goring & Williams, 2017; Miller & McGill, 2017).

The effects on species range shift due to interactions between land-use and climate change is classified into three types by Goring and Williams (2017). These are the 'compounding effect' (both acting in the same direction), the 'confounding effect' (both act together but affects only some parts of the environmental range) and the 'counteracting effect' (climate change and land-use change act in opposite directions). The effects produced by the interaction of land-use and climate change may be synergistic (greater when combined than the sum of both), antagonistic (less when combined than the effect of each) or additive (equal to the sum of both) (Oliver & Morecroft, 2014). These effects can result in species range or optimum shifts in latitude or elevation in three different ways, namely 'march', 'lean' and 'crash' (Breshears *et al.*, 2008). 'March' is defined as a range shift with a retracting tailing edge, advancing leading edge and shifting optimum along the environmental gradient. 'Lean' is defined as a shift of only the optimum while remaining within the upper and lower range of the gradient. 'Crash' is described as a decline in population with stable edges and an optimum within the environmental gradient.

Species response to climate change is pronounced in the mountains as they have diverse climates within a short span of vertical distance (Beniston, 2003). This allows species to track their climate niche relatively easily compared to species in flat terrains (Loarie *et al.*, 2009). However, it does not guarantee their survival in the future if precipitation and temperature variables develop new interactions leading to the development of a novel climate (Williams *et al.*, 2007) or if species fail to remain within their niche due to dispersal limitation with a shifted climatic space (Thuiller *et al.*, 2005).

Studies show that species have an individualistic response to environmental change, and hence a species-specific rate of shift (Gleason, 1926; Parmesan & Yohe, 2003; Chen *et al.*, 2011). The species shift in response to climate change is also not unidirectional. Typically, species are found to move pole-wards in latitude and upwards in elevation (Parmesan & Yohe, 2003; Lenoir *et al.*, 2010; Chen *et al.*, 2011), however, some species shift downhill in the mountains (Crimmins *et al.*, 2011; Qiu, 2015) or sometimes do not shift at all (Lenoir *et al.*, 2010; Grytnes *et al.*, 2014). Such differing rates and directions of species shift may produce new species assemblages in the future (Williams & Jackson, 2007).

Future climate is projected to be warmer than now. Past climatic records show that the global mean surface air temperature has increased by 0.74°C during the last century (IPCC, 2007), and the rate of warming between 1998 and 2012 was 0.05°C per decade (Stocker *et al.*, 2014). This indicates that the most extreme future prediction (Representative Concentration Pathway (RCP) 8.5) may be a realistic scenario in the near future. The RCP8.5 projects the average surface temperature to be between 2.6°C to 4.8°C warmer by 2081 to 2100 compared to the 1986 to 2005 baseline (Collins *et al.*, 2013). If that happens, compared to current species shifts, the range and/or optimum shifts of species may become common; otherwise, species may lose their optimum climatic niche space. In the latter case, consequences can be unprecedented.

Studies on species responses to climate change in the Himalayan region are rare. In recent years, a few studies have documented the response of species to climate change (e.g. Valley, 2003; Telwala *et al.*, 2013; Shrestha *et al.*, 2014; Chhetri & Cairns, 2015; Bhatta & Vetaas, 2016; Gaire *et al.*, 2017) and a few have been carried out on the analysis of species distributions in the current climate and future projected climate (e.g. Gajurel *et al.*, 2014; Shrestha & Bawa, 2014; Kandel *et al.*, 2015; Schickhoff *et al.*, 2016; Bobrowski & Schickhoff, 2017). Given that the Himalayan region remains largely unexplored, how its species will respond to climate change is a notable knowledge gap. This thesis will contribute to our understanding about species responses to contemporary climate change as well as projected future warming. The findings of the study will be helpful in designing proactive conservation policies in the face of projected warming in the region. This synthesis compiles three different case studies based on empirical and species distribution modelling from different geographic and temporal scales.

Objectives

This thesis aims to widen our understanding of the dynamics of species spatial distributions in response to climatic changes so that they remain within their climatic niche. The spatial changes include the vertical shift of species in the mountains and horizontal shift in their distribution. The specific objectives are:

1. Recent global warming has raised the average surface temperature in the Himalayan region (Shrestha *et al.*, 1999; Shrestha *et al.*, 2012; Pachauri *et al.*, 2014), causing isotherms to move towards higher elevations in the mountains. The geographic areas that were once beyond the temperature limit of species are now within the range of species. Provided there are no other hindrances, species may shift their range towards higher elevations to stay within their temperature niche. This study will assess the change in upper species limit in the mountains of the central Himalaya.
2. The recent climate change and projected warming in the future may instigate novel climate in the Himalayan region (Williams *et al.*, 2007). In this context, this study will investigate how species may respond to such climate change by assessing the likely responses of closely related sister taxa and evaluate overlaps of their climatically potential distribution areas in current and future climate.
3. Closely related sister taxa (e.g. subspecies) are expected to have a higher degree of similarity in their niches (Losos, 2008), whereas geographically segregated (disjunct) species may have less similar niches (Garcia-Ramos *et al.*, 2000). This study aims to investigate the climatic niche overlap between parapatrically (non-overlapping distribution with geographical contact lacking interbreeding (Bull, 1991; Gutiérrez *et al.*, 2014)) disjunct subspecies and whether their climatic niche and climatically suitable geographical areas under current and future climate will overlap or not.

Conceptual framework

Species' niche

Species are characterised by living within a limited range (maximum and minimum) of an environmental gradient and are most abundant in a particular environment (optimum) (Whittaker, 1967). In the absence of any biotic (negative) interaction and migration barrier, species may occupy the whole range of the environmental gradient. Different environmental variables that are ecologically sensible to the species define a hyper-volume known as the 'fundamental niche' that supports the indefinite survival of the species. In reality, however, species tend to utilise only a portion of their fundamental niche, which is known as the 'realised niche' (Figure 1) (Hutchinson, 1957). The realised niche is smaller than the fundamental niche because of biotic (negative) interactions (e.g. competition), abiotic factors (e.g. nutrients, disturbances, land use) and dispersal limitation (e.g. migration accessibility) (Hutchinson, 1957; Soberón & Arroyo-Peña, 2017).

The biogeography of species is illustrated in relation to three components; namely **B**iotic interactions, **A**biotic factors and **M**igration accessibility (BAM diagram detail in Soberón & Peterson, 2005; Soberón & Nakamura, 2009). Species occupy geographic space that is abiotically (climate, soil, nutrients etc.) suitable, where biotic interactions (mutualism, competition, parasitism etc.) allow them to maintain non-zero positive growth rates and they are able to disperse, also known as realised distribution (Chase & Leibold, 2003; Sax *et al.*, 2013). Geographic spaces that are suitable with respect to biotic and abiotic factors, but are limited by dispersal, will not be occupied by species even though the environmental space is part of the fundamental niche of the species (Soberón & Peterson, 2005; Soberón & Nakamura, 2009); this is also referred to as an 'empty niche' (Elton, 1958).

The concept of 'empty niche' (Elton, 1958) is debated because niche is a property of species and defined by keeping species at the centre, hence there is no space for the empty niche (MacMahon *et al.*, 1981; Chase & Leibold, 2003). When a species is introduced to a new location, it fills a new (but not empty) niche (Herbold & Moyle, 1986). For example, ex-situ conservation of *Rhododendron* that is outside their realised niche has been termed a 'potential niche' (Jackson & Overpeck, 2000; Vetaas, 2002). Jackson and Overpeck (2000) also discuss that if any area where a species becomes extirpated (i.e. locally extinct due to natural or anthropogenic causes), it becomes a potential niche of the species rather than an empty niche.

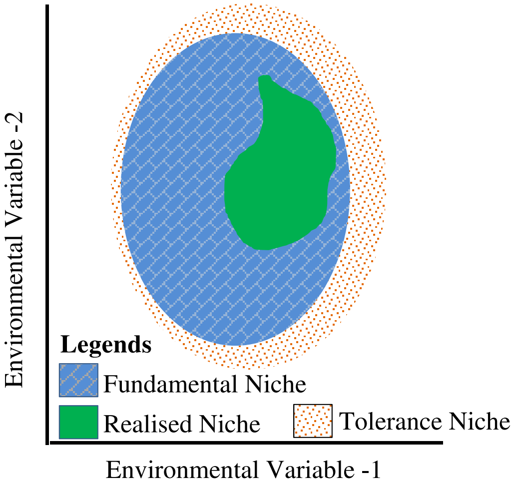


Figure 1: Illustration of different concepts of niche. The realised niche is a subset of the fundamental niche (Hutchinson, 1957) and the tolerance niche is at the periphery of the fundamental niche (Sax *et al.*, 2013).

Occasionally, species are found in areas that do not support an intrinsic positive growth rate, but allow the survival of a portion of life, known as the 'tolerance niche' (Figure 1) (Sax *et al.*, 2013) or 'sink' habitat (James *et al.*, 1984; Pulliam, 1988). These areas are outside the fundamental niche as they do not support the indefinite survival of species (Holt & Gaines, 1992; Chase & Leibold, 2003). Occupancy of those geographic spaces of tolerance niche or sink habitat is supported by a regular migration of individuals from a nearby source population (Pulliam, 1988; Holt, 1996). However, the sink remains a sink (Holt, 1996) because species niches are conserved over time (Wiens & Graham, 2005).

Species tend to retain their fundamental niche over time, known as ecological niche conservatism (Wiens & Graham, 2005). Although disagreement persists about the existence of ecological niche conservatism (Franklin, 2010), evidence of niche conservatism has been reported by different scholars (Peterson *et al.*, 1999; Ackerly, 2003; Romdal *et al.*, 2013; Anacker & Strauss, 2014). Wiens and Graham (2005) suggest it is better to concentrate on what the implications of ecological niche conservatism are instead of its existence or not. It seems that the existence of niche conservatism is more widely accepted as the use of species distribution modelling increases, as niche conservatism is a fundamental assumption of species distribution models for the prediction of species distributions across space and time.

Box 1: Glossary

Empty niche: a set of existing environmental conditions which can support indefinite survival of species provided a species arrives there

Fundamental niche: n-dimensional environmental space where species survive indefinitely in the absence of species interactions with the environment and between species

Potential niche: The intersection between realised environmental space and fundamental niche, which is larger than the realised niche and a subset of the fundamental niche

Realised niche: a subset of the fundamental niche constrained by different interactions between species and interactions of species with the environment

Sink: a set of environmental conditions occupied by species, but it does not support self-sustaining populations of species, hence it is outside the fundamental niche of the species

Tolerance niche: a set of environmental conditions where individuals of species can survive for some of their life but the establishment of a self-sustaining population is precluded. It is at the periphery of the fundamental niche. Equivalent to a *sink*.

Spatial dynamics of species in an anthropogenic landscape

Land-use has transformed a huge portion of the Earth’s surface by converting natural landscapes with human development (Foley *et al.*, 2005). Land-use change has been reported to be one of the most influential factors of change in species realised environmental range, abundance and richness, and it is projected to be the most important factor in this century (Sala *et al.*, 2000; MEA, 2005). It has direct and indirect impacts on species distribution. For instance, land-use has a direct impact on species range, tree line and optima shift (Speed *et al.*, 2012; Goring & Williams, 2017; Miller & McGill, 2017; Vitali *et al.*, 2018) and, indirectly, land-cover change affects local and regional climate (Kalnay & Cai, 2003) which ultimately affects the species in the landscape.

Land-use change is a disturbance, but a partial removal of dominant species may allow more species to occupy a geographic space. The immediate impacts of land use are mostly at a local scale. It can constrict the 'realised geographic distribution' of species prohibiting them from occupying the full range of their 'potential geographic distribution', such as range contraction of snub-nosed monkey in China (Zhao *et al.*, 2018). The release of existing land-use pressure can facilitate a range expansion of species (Gehrig-Fasel *et al.*, 2007; Vitali *et al.*, 2018). Often, land use such as grazing can mask the effect of climate change (Speed *et al.*, 2012) and sometimes the confounded effects of land use and climate change on the dynamics of species range make it hard to disentangle which factor is dominant.

Spatial dynamics of species with climate change

Habitat change and loss are the most important factors to impact species distribution, with climate change being important too. Climate change is predicted to continue to be prominent in the twenty first century (Sala *et al.*, 2000; MEA, 2005). Climate change has been reported as being responsible for range and optima shifts of both plant and animal species from different parts of world (Parmesan & Yohe, 2003; Root *et al.*, 2003; Chen *et al.*, 2011; Pauli *et al.*, 2012). The predominant shift in response to climate change is towards higher elevation or higher latitude, however, about one fourth of species are 'going against the flow' (Lenoir *et al.*, 2010 and citation therein). Lenoir *et al.* (2010) suggest this shift against the expected direction is possibly due to changes in other aspects of the climatic variables besides mean temperature, such as precipitation regime or seasonal climatic parameters. It is manifest as a downward shift of species in response to water availability (Crimmins *et al.*, 2011; Bhatta *et al.*, 2018).

The dynamics of species distributions in response to climate change occur at a broad geographical scale (i.e. regional and global scale) compared to land-use change that is (mostly) local in geographic space. Species in mountains have an advantage over flat terrain species when climate changes because the speed of spatial climate change is slower in the mountains (Loarie *et al.*, 2009) and species may only need to shift a short vertical distance to track their climatic niche space. Mountain species that have limited or no geographic space to go beyond the top of the mountain, will face geographic range contraction with their tailing edge or lower margin shifting towards higher elevations in a warming climate (Colwell *et al.*, 2008). The shift towards higher elevation or latitude may not always be distinctly due to climate change, but can also result from changes in habitat type, atmospheric carbon dioxide and nitrogen concentrations, and land use as well as species traits (Lenoir *et al.*, 2008; Forister *et al.*, 2010; Grytnes *et al.*, 2014).

Species distribution models

It is long known that a species geographic distribution is (cor)related to different bioclimatic variables and ecological processes (Grinnell, 1917; Elton, 1927; Odum & Odum, 1953; Hutchinson, 1957). Delineation of species geographic ranges has always been a challenge, particularly when species are generalist and widely distributed. It is a time- and resource-consuming process. Spatial prediction of species distributions is growing with the development of different statistical and machine-learning algorithms along with computer power (Johnson, 1980; Miller, 1986; Austin *et al.*, 1990; Austin & Meyers, 1996; Stockwell, 1999; Breiman, 2001; Drew & Perera, 2011; Phillips *et al.*, 2017). There are a number of statistical and machine-learning methods each with slightly different applications (detail in Franklin *et al.*, 2009; Araújo & Peterson, 2012) under the general term of 'species distribution modelling' that predict the range or distribution in geographic space of a species (SDM; Franklin, 2010). Guisan *et al.* (2017), however, suggest that 'habitat suitability modelling' is a better term to use.

Regardless of their names and the variety of algorithms and applications, SDMs are rooted into ecological gradient analysis, niche theory, remote sensing and geographical information science/system (Hutchinson, 1957; Whittaker, 1960; Whittaker *et al.*, 1973; Franklin, 1995). SDMs are (mostly) correlative models that use environmental and/or geographic information to explain observed patterns of species occurrences (Elith & Graham, 2009; Franklin *et al.*, 2009). Being a correlative approach, SDMs do not take account of causality or mechanisms underlying the way species have become distributed (Franklin, 2010). Franklin *et al.* (2009) suggest evaluating the 'ecological realism' of the models for consistency with ecological knowledge of limiting factors and species response curves of variables because the data rarely represent the 'true species niche'.

SDMs are useful tools to aid the understanding of abiotic and biotic environmental relationships with species for ecological inference based on observation, and to test ecological/biogeographical hypotheses about species distributions and ranges (Franklin *et al.*, 2009). In ecology, SDMs are being used to model species responses to environmental variables, species niche evaluation, niche overlap analysis between species (Nakazawa *et al.*, 2010), phylogenetic niche conservatism (Losos, 2008), discovery of new populations (Feria *et al.*, 2002) and conservation planning (Williams *et al.*, 2005; Araújo *et al.*, 2011). SMDs are also applied to predict species distributions across geographic space and time (Thuiller *et al.*, 2005; Randin *et al.*, 2006; Villemant *et al.*, 2011), although their relative success when transferred across time is debatable (Araújo & Rahbek, 2006).

Environmental space vs geographic space

Species are distributed in environmental as well as geographic space (Hutchinson's duality), and there are differences between them (Stockwell, 2006; Colwell & Rangel, 2009). The distribution of species in geographic space may be discrete over a large area; however, their environmental space may be fairly compact within an environmental gradient (Stockwell, 2006). Every location in geographic space has a point in environmental space while a point in environmental space may have more than one location in geographic space (Peterson *et al.*, 2011) or none at the present time (Jackson & Overpeck, 2000).

Ecological niche models and species distribution models are constructed with environmental variables associated with species occurrences in true geographic space (Figure 2). The environmental niche space constructed from the realised distribution of species represents the realised niche of the species, which is a portion of the fundamental niche (Austin *et al.*, 1990). Distribution models describe a species realised niche and associated realised distribution in geographic space, rather than fundamental niche (Franklin, 1995; Guisan & Zimmermann, 2000; Iverson *et al.*, 2017). It is because the fundamental niche is defined by the species' physiological responses across the full range of the environmental gradient, whilst the environmental conditions represented for the species may not be limited to the area of interest (Peterson & Soberón, 2012) unless they are endemic to that particular locality. When an area of interest is smaller than the geographical space occupied by the species, it may not cover the whole realised (and fundamental) niche of the species (Austin & Smith, 1990; Franklin, 1995; Guisan & Zimmermann, 2000). Such a situation may have a negative consequence for model prediction (Raes, 2012) when extrapolated to a new environmental space.

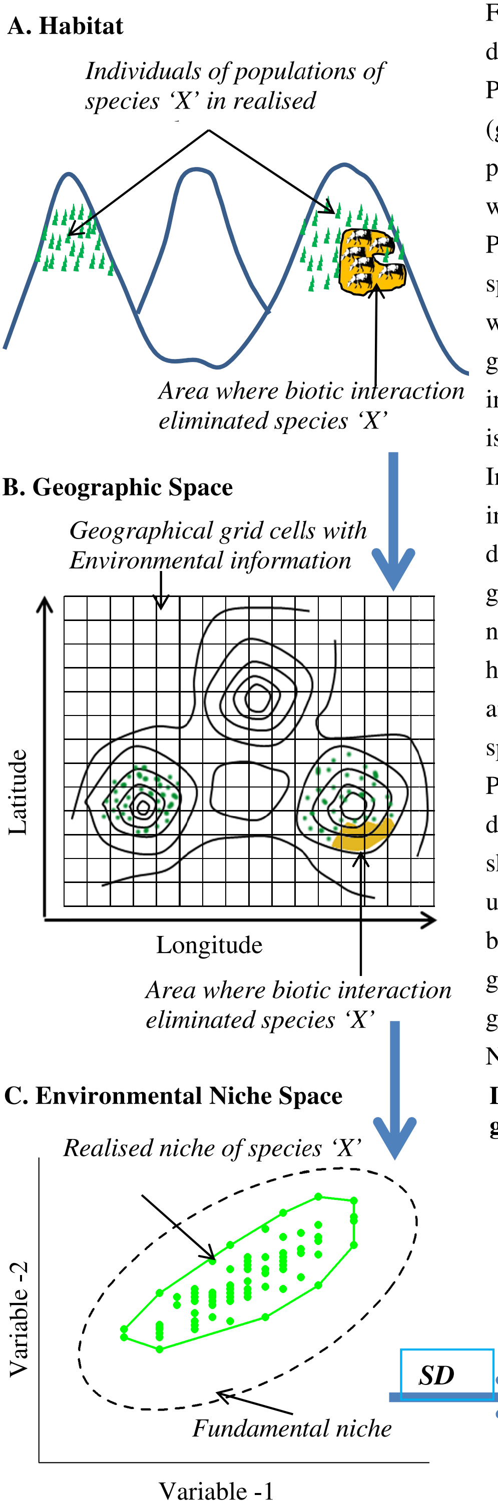


Figure 2: Schematic illustration of species distribution models (SDMs).

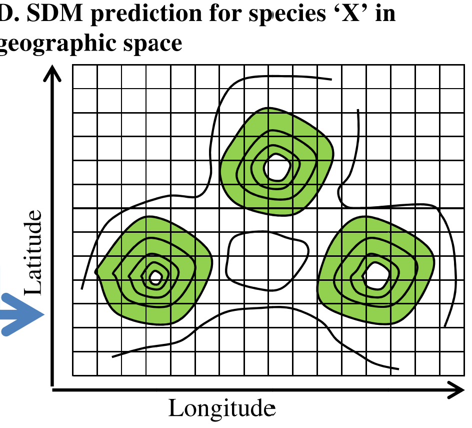
Panel A illustrates species 'X' in its habitat (green symbol). It has occupied less than its potential geographic space due to interaction with others species (herbivores, yellow area).

Panel B is a sketch map of the geographic space of the landscape in panel A overlain with an environmental variable grid. Each green dot represents the occurrence of each individual of species 'X' and the yellow area is where the species has been excluded.

In panel C, each green dot represents an individual of species 'X' in its two dimensional environmental niche space. The green (smooth line) polygon is the realised niche and the black dashed line marks the hypothetical fundamental niche. If variables 1 and 2 are climatic variables, it produces a species' climate space.

Panel D illustrates a prediction from species distribution modelling in geographic space, showing the inclusion of previously unrecorded areas and areas excluded due to biotic interactions. This is projected in geographic space and represents the potential geographic distribution of species.

Note: Illustrations do not represent real data.



Implications of niche concept in SDMs

SDMs are correlatively fitted with environmental information from true occurrence records from geographic space. It implies that SDMs are fitted from the realised distribution of species, hence they do not represent the complete fundamental niche of species (Franklin, 1995; Guisan & Zimmermann, 2000; Iverson *et al.*, 2017). Neither do they represent the true realised niche of species because they are fitted with limited (mostly climate only) environmental variables and they lack biotic interactions and other range-constraining variables (Jiménez-Valverde *et al.*, 2008). This kind of distribution model mostly predicts larger environmental space, i.e. 'potential niche' (Jackson & Overpeck, 2000), as well as geographic space compared to the realised ones. The predicted geographic space may contain new localities which the species may potentially occupy if they overcome any dispersal limitations and/or negative biotic interactions. If the models are trained with occurrences from sink habitats, the results will be misleading as the models will over predict the species ecological niche as well as its distribution in geographic space by including similar sinks as potential areas for the species.

Methodology

This thesis contains two different approaches, one is empirical based and the other is model based. The studies were conducted across three different geographic extents (Figure 3). It is hard to detect small spatial changes in response to niche variables such as temperature at a broad spatial extent; moreover, it takes many resources and much time to carry out field studies to detect spatial changes across broad geographical space. In such contexts, modelling techniques based on secondary data (e.g. published, museums and herbaria databases) are a more efficient approach. To detect spatial changes at a fine spatial scale, high-resolution data are required for modelling and empirical studies are needed.

Geographic scale and temporal scale

This thesis was carried out at three geographic scales: micro-level (Paper I), meso-level (Paper II) and macro-level (Paper III) (Barnes *et al.*, 1998). Similarly, the temporal scale of the thesis was current time (Papers I, II and III) and future time (average of 2061 to 2080) (Papers II and III).

Study area

The empirical study was carried out by sampling in two protected areas of Nepal (Paper I) and the model-based studies were carried out at the geographic extents of within Nepal (Paper II) and the regional level of southern-eastern Asia (Paper III) (Figure 3).

Micro-level (in Paper I): The first case study was carried out in two protected areas, Manslu Conservation Area (MCA) and Gaurishankar Conservation Area (GCA) in Nepal (Figure 3). Three transects in areas of reduced land-use intensity (land use does not change in the area but the intensity of the land use is reduced compared to the past) were placed in the MCA and one transect as a control with no or negligible land use was sampled from GCA. All transects sampled the treeline ecotone in the subalpine region.

Meso-level (in Paper II): The area above 900 m above sea level (a.s.l.) within Nepal was considered as the study area in the second case study (Figure 3). It includes the lower temperate, upper temperate, subalpine and alpine bioclimatic zones in Nepal.

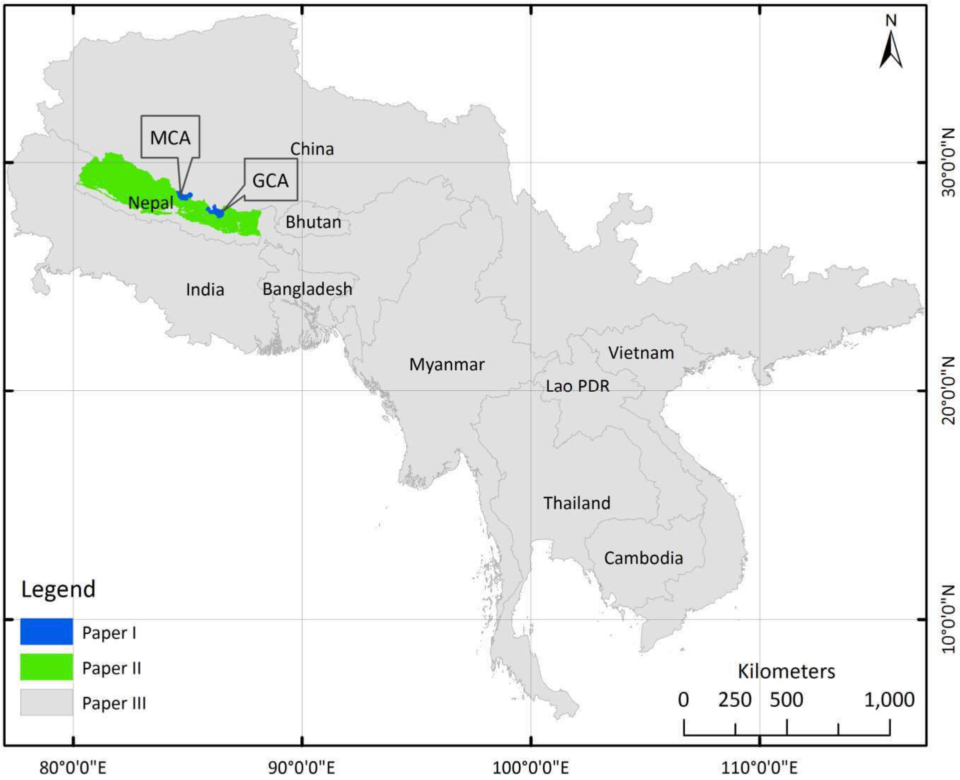


Figure 3: Study area showing the three levels of geographic extent of the three case studies. In Paper I (micro-level), three transects were surveyed in Manslu Conservation Area (MCA) and one transect in Gaurishankar Conservation Area (GCA); in Paper II (meso-level), the area above 900 m above sea level within Nepal comprises the study area; and in Paper III (macro-level), some parts of or whole countries in the Asian region comprise the study area.

Macro-level (in Paper III): The third case study was a regional study. It incorporates northern part of India, southern part of China, Nepal, Bangladesh, Myanmar, Thailand, Vietnam, Lao People's Democratic Republic (Lao PDR = Laos) and Cambodia (Figure 3).

Focal species and their distribution

In this thesis, five different species were considered for different case studies (Figure 4). Two of them have a restricted distribution and the others are comparatively widely distributed in the Himalayan region.

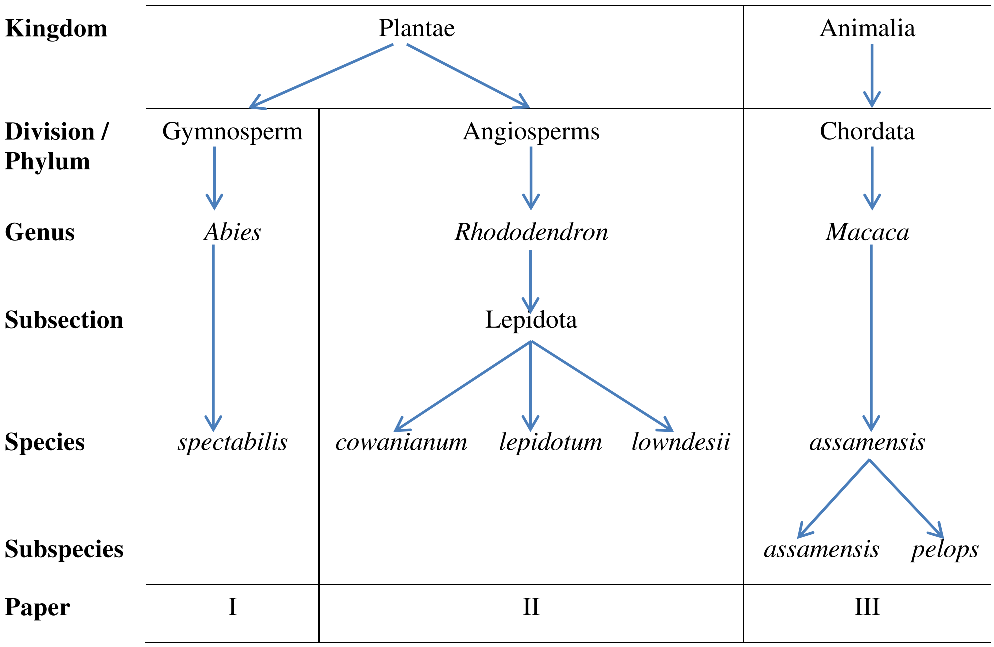


Figure 4: Schematic illustration of species, case studies and related papers. In this thesis, four plant species and one animal species were investigated in different case studies.

***Abies spectabilis* (Paper I):** The Himalayan Silver Fir (*Abies spectabilis* (D. Don) Spach) is a cool temperate and subalpine coniferous tree species. Its distributional elevation ranges between 2400 and 4400 m a.s.l.. It is distributed in the central and western Himalaya. It reaches a height of about 50 m with a trunk diameter larger than 1.5 m forming monodominant forest. Its furrowed branchlets are densely leafy with yellowish grey, brown or reddish brown colour (eFloras, 2008).

***Rhododendron* species (Paper II):** In the second case study, three species of *Rhododendron* subsection Lepidota were the focus. Two of them, *R. cowanianum* Davidian and *R. lowndesii* Davidian, are rare and endemic to Nepal. The third one, *R.*

lepidotum Wall is widely distributed in the Himalaya. The elevational range for *R. cowanianum* is between 3000 and 3900 m a.s.l., *R. lowndesii* ranges from 3200–4500 m a.s.l. and *R. lepidotum* from 2100–4700 m a.s.l. (eFloras, 2008).

***Macaca assamensis* (Paper III):** Assamese macaque (*Macaca assamensis* M'Clelland, 1840) is distributed in mountain regions of the central and eastern Himalaya and the adjoining south and southeast Asian mountain chains (Fooden, 1980, 1982; Boonratana *et al.*, 2008). Two subspecies *M. assamensis* ssp. *pelops* (western population) and *M. assamensis* ssp. *assamensis* (eastern population) are geographically isolated by the Brahmaputra river in north-eastern India (Fooden, 1982).

Data collection

This thesis is based on primary data (Paper I) and secondary (published) data (Papers II and III). The primary data were collected as part of a defined research design. Study sites for the sampling were selected and field surveys were carried out in the selected sites. A total of four transects from two protected areas were sampled to analyse the upper species limit dynamics of *A. spectabilis* in response to current climatic warming, i.e. establishing the temperature niche of the species. The effect of warming can easily be masked by land-use (or land-use intensity) changes (Gehrig-Fasel *et al.*, 2007; Speed *et al.*, 2012). To disentangle the effect of change in land-use intensity and climatic warming, a transect was sampled from an area with negligible or no land use as a control (GCA, Figure 3) as well as three transects from an area with reduced land-use intensity (MCA, Figure 3). The transects were set with reference to the uppermost individual of the species (i.e. its upper species limit, USL) in the respective landscapes. The top half of each transect extended to the treeline (highest elevation of trees at least 2 m high in a patch comprising at least three individuals (Körner, 2003)) and the lower half came downhill into the forest (Paper I).

The occurrence of *R. cowanianum, R. lepidotum, R. lowndesii* and *M. assamensis* were compiled partly from personal field records and those from colleagues, while other occurrences were compiled from published literature and herbaria (Papers II and III). The environmental data were collected from publicly available sources including WorldClim – Global Climate Data (www.worldclim.org; Hijmans *et al.*, 2005), Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) (www.chelsa-climate.org; Karger *et al.*, 2016; Karger *et al.*, 2017) and CGIAR-CSI for topographic elevation data (www.srtm.csi.cgiar.org; Jarvis *et al.*, 2008). Some variables were derived from the above collected data.

For future climate estimates, the Representative Concentration Pathway 8.5 (RCP8.5) was chosen. Based on the current warming trend, it seems to be the most realistic. RCP8.5 projects a 2.6°C to 4.8°C warming during 2081 to 2100 compared with 1986 to 2005 (Collins *et al.*, 2013). To reduce biases among different downscaling models, an average of five different General Circulation Models, namely ACCESS1-0, BCC-CSM1-1, GISS-E2-R, MIROC-ESM-CHEM and MPI-ESM-LR, was taken, as suggested by Beaumont *et al.* (2008). The future prediction was made only on a single worst case scenario and a single future period to 2070 (average of 2060 and 2080) (Hijmans *et al.*, 2005).

Variable selection

The bioclimatic variables (Appendix 1) used in the second and third case studies are derived from temperature and precipitation variables. One of the problems while working with many derived variables is multicollinearity (Alin, 2010). To reduce or avoid multicollinearity among the variables, the fewest least correlated variables were selected (Elith *et al.*, 2010; Fox & Weisberg, 2010; Petitpierre *et al.*, 2017). In the second case study (Paper II), models were fitted both using all variables and only on selected variables (selected by generalised linear model forward-backward selection). In the third case study (Paper III), the variables were selected by the combined use of cluster analysis among variables and variable inflation factor.

Data analysis and modelling

The ability of the upper species limit to dynamically track the temperature niche in response to current warming was evaluated based on elevation, which is a surrogate for the temperature variable, by estimating the difference between the historic upper species position (oldest individual along the transect) and the current upper species position. The shift in upper species limit was estimated in all transects and helped to disentangle the effect of change in land-use intensity and climate change (Paper I).

The potential response to climate change under a future projected climate RCP8.5 for 2070 was modelled for three *Rhododendron* sister species (Paper II). In this case study, the Random Forest (Breiman, 2001) algorithm was used. The models were calibrated with current bioclimatic variables and predicted with both the current and future climate. The potential response to shift in elevation for each species was evaluated along with the potential change in their climatically suitable geography from current climate to future projected climate.

Similarly, in Paper III, niche similarity between two subspecies of *Macaca assamensis* was analysed and their potential distribution based on climatically suitable areas in the current climate and future projected climate were modelled. The change in climatically suitable geography in response to projected climate was analysed. In this study, the species distribution models were fitted in by Random Forest (Breiman, 2001) and MaxEnt (Phillips *et al.*, 2006; Phillips *et al.*, 2017) (Paper III).

Modelling methods

Of the different methods to model species distributions, I used only Random Forest (Breiman, 2001) in Paper II and additionally MaxEnt (Phillips *et al.*, 2006) in Paper III, because they are good performers (Elith *et al.*, 2006; Aguirre-Gutiérrez *et al.*, 2013; Mi *et al.*, 2017).

Random Forest: Random Forest modelling was performed in *R* (R Core Team, 2017) package *randomForest* (Liaw & Wiener, 2002). In Random Forest, 2000 trees were grown as the models seemed to stabilise between 1000 and 1500 trees and Out-Of-Bag (OOB) was turned on.

MaxEnt: MaxEnt was used in the *R* through *dismo* package (Hijmans *et al.*, 2016). The optimum regularisation multiplier value was determined by developing different models with different values.

Analysing the effects of MaxEnt Regularisation Multiplier

The effect of the regularisation multiplier on different measures of MaxEnt, namely AUC, sensitivity, entropy, Kappa, and prediction of the models was assessed.

The MaxEnt models were fitted to a 29-species dataset (Appendix 2) with occurrences between 14 and 284. For better illustration of the results, the datasets were grouped into four groups: Group A (number of occurrences from 14 to < 25; total (n) = 9), Group B (25 to < 50; n = 9), Group C (50 to < 100; n = 5) and Group D (above 100, n = 6). In the models, random background data complemented the occurrence data to make the response variables binary and were fitted against the bioclimatic variables (Bio01 to Bio19; Appendix 1) from WorldClim (Hijmans *et al.*, 2005). A total of 42 regularisation multiplier values were set between 0 and 20 at different intervals (0.1 interval between 0 and 2; 0.5 interval between 2 and 5; 1.0 interval between 5 and 20). An average of 10 replications at each value was reported for the final result. The predictions from models at different regularisation multiplier values were transposed to geographic space and similarity between predictions was evaluated using *ENMTools* (Warren *et al.*, 2008).

The results concur with previous findings (Anderson & Gonzalez, 2011; Muscarella *et al.*, 2014; Radosavljevic & Anderson, 2014); the models are highly sensitive at low regularisation multiplier value and hence a higher variability of effects are observed on AUC, sensitivity, entropy, Kappa and prediction of the model, particularly with low occurrence datasets (Figure 5 and Appendix 3). Hence, the models in Paper III were tuned with optimum values of the regularisation multiplier.

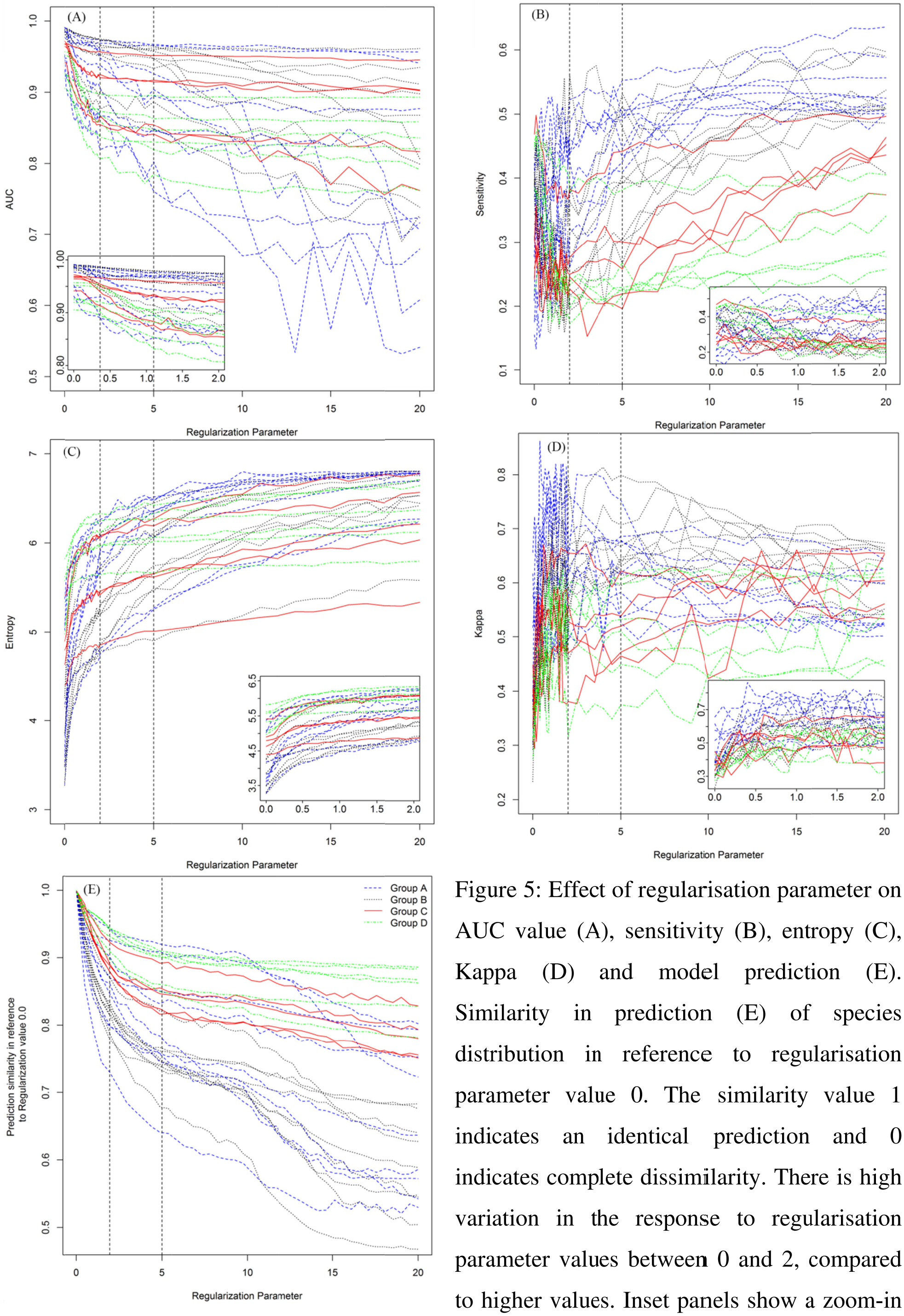


Figure 5: Effect of regularisation parameter on AUC value (A), sensitivity (B), entropy (C), Kappa (D) and model prediction (E). Similarity in prediction (E) of species distribution in reference to regularisation parameter value 0. The similarity value 1 indicates an identical prediction and 0 indicates complete dissimilarity. There is high variation in the response to regularisation parameter values between 0 and 2, compared to higher values. Inset panels show a zoom-in view of the same data from regularisation parameter 0 to 2 at an interval of 0.1.

Key assumptions in SDMs

SDMs make some ecological assumptions, which are detailed by Soberón and Nakamura (2009). Some, but not all, of the assumptions of correlative models are briefly described here.

1. **Niche conservatism**: The species distribution models rely on the fundamental assumption that ‘niches are conserved’ over time (Wiens & Graham, 2005), specifically when the niche or distribution is predicted across space and/or time. Evidence has been put forward both pro and against the concept of niche conservatism (Peterson *et al.*, 1999; Dormann *et al.*, 2010; Peterson, 2011).
2. **Equilibrium in distribution**: One of the crucial assumptions of SDMs is the expectation of equilibrium conditions of species distribution with environmental condition during the training period (Jeschke & Strayer, 2008; Booth, 2017). Empirical evidence, however, mostly does not support this assumption (Vetaas, 2002; Pearson *et al.*, 2006).
3. **Evolutionary adaptation, acclimatisation and persistence ability:** SDMs do not account for the evolutionary adaptive capacity of species genotype (but see Cotto *et al.*, 2017), phenotype, acclimatisation and persistence ability (Booth, 2017). These characteristics of species are assumed constant when models are transferred over space and time (Dormann, 2007; Jeschke & Strayer, 2008; Willis & Bhagwat, 2009).
4. **No dispersal limitation:** When the models are transferred in space, SDMs (mostly) assume unlimited dispersal of species (Jeschke & Strayer, 2008), which implies that species occupy all climatically suitable areas; this is not supported by empirical evidence (Vetaas, 2002; Pearson *et al.*, 2006).
5. **Biotic interaction and ecological traits**: Inclusion of biotic interactions and species ecological traits improves predictions of species distributions (Heikkinen *et al.*, 2007; McPherson & Jetz, 2007; Trainor *et al.*, 2014; Staniczenko *et al.*, 2017). However, data about biotic interactions between species are rare and hard to document; hence the lack of such data is often mentioned as a limitation of SDMs (Davis *et al.*, 1998b). Still, distribution

models based only on abiotic variables have proven their predictive ability (Franklin *et al.*, 2009; Nakazawa *et al.*, 2010).

Some issues and limitations of SDMs

1. **Evaluation methods**: Most of the SDMs are evaluated based on the area under the curve (AUC) of receiver operating characteristics (ROC) (Hanley & McNeil, 1982; Bradley, 1997). The AUC is indiscriminately used in almost all types of methods: presence only, presence─absence, presence─background and presence─pseudo-absence. The performance measure depends on the data input in the model, but proper attention is lacking in this aspect of distribution modelling (Soberón & Nakamura, 2009). Additionally, the exact same value of a performance measure of different methods does not guarantee an identical prediction by the models.
2. **Absence data**: Species absence data are mostly unavailable, although the use of a binomial presence-absence response in SDMs is a better predictor than presence only data (Brotons *et al.*, 2004). To overcome the dearth of absence data, background data or pseudo-absence data are commonly used in models.
3. **Background data/pseudo-absences**: To make the response variable binomial, occurrence data is complemented by pseudo-absence or background data. They are generated by different methods such as completely random, designed random (Barbet-Massin *et al.*, 2012) and environmentally or geographically stratified (VanDerWal *et al.*, 2009). Occasionally occurrence data of members of a genus of species are used as pseudo-absence data (e.g. Austin *et al.*, 1990; Vetaas, 2002).
4. **Uncertainties**: Occurrence data held in herbaria and museums (may) have geographic positional uncertainty (Naimi *et al.*, 2014). Another uncertainty relates to the resolution of predictor variables.
5. **Sources of predictor variables**: Predictions of species distribution depend on the source of the predictor variables used in the models while keeping other settings constant (Bedia *et al.*, 2013; Pliscoff *et al.*, 2014; Bobrowski & Schickhoff, 2017). Variations come from different methods that are used to

develop the predictor variables, for instance projected future climate varies from one downscaling method to another.

6. **Predictor resolution**: The prediction of models is affected by the resolution of predictor variables (Trivedi *et al.*, 2008). The commonly used 30 arc second resolution (about 1000 m) pixel may cover about 670 m (average in Nepal) in vertical distance in the Himalayan region (equivalent to about a 3.5°C temperature difference based on the interpolated lapse rate (Kattel *et al.*, 2013)).
7. **Correlative not causal:** SDMs are based on correlations between species occurrence and environmental variables. They do not represent any causal relationship (Franklin, 2010).

Dealing with the assumptions and issues

Species distribution models are an efficient and cost-effective tool to study the biogeography of species, despite the underlying assumptions and issues outlined above. Meeting all the assumptions is rarely feasible (Guisan *et al.*, 2017). However, to get the best from the models, some of the issues were tackled in this thesis by adopting different approaches, viz.:

- Multicollinearity between variables was addressed by using a subset of least correlating variables to fit the distribution models
- As a substitute for absence data in the models, I used pseudo-absence and background data in Paper II. The randomly generated background data proved to be a good solution; hence the same method was used in Paper III.
- Whenever available, a high number (>100, *R. lepidotum* in Paper II and both subspecies of *M. assamensis* in Paper III) of occurrence points were used in the distribution model preparation.
- Species occurrences as well as sister taxa constrained pseudo-absence points and were filtered out with a two-step filter to tackle geographical positional uncertainty (Paper II).

- To address the sources of variability related to predictor variables, predictor variables were selected from two different sources in Paper III, and an average of five different methods was used for future climate (Papers II and III).
- The best available resolution of the open access predictor variables was used.
- From those available, two of the better-performing modelling algorithms were used in the distribution modelling, namely Random Forest and MaxEnt.
- Different model evaluation techniques (AUC, TSS, Omission Error) were applied in Paper III.
- To extrapolate the prediction in future climate, a wide range of environmental space was covered during training the models. My study area covered the Himalayan region which encompasses different bioclimatic zones from tropical to alpine and nival (biomes), and trans-Himalayan semi-desert area. Hence, the model was trained with a wider range of environment than the species' environmental range.

Results and discussion

Species range dynamics with climate and land use (Papers I and II)

The upper species limit (USL) of *Abies spectabilis* is moving towards higher elevation where the temperature is relatively cooler. This upslope shift is caused by reduced land-use intensity in the area because of out-migration of local people (Gartaula & Niehof, 2013; CBS, 2014; Sharma *et al.*, 2014) and possibly facilitated by warming in the region (Shrestha & Aryal, 2011; Shrestha *et al.*, 2012). The upslope shift of *A. spectabilis* can be interpreted as an attempt to remain within its climatic niche space. The minimum temperature isotherm of the species has moved towards higher elevation in mountain regions due to recent warming (Shrestha & Aryal, 2011; Shrestha *et al.*, 2012).

The rate of USL shift of *A. spectabilis* differs between transects by as much as four-fold, i.e. it is site specific. Because of high levels of land-use pressure in earlier times in this region, the USL may have been controlled by human impact and hence was lower than its climatic limit (e.g. Chauchard *et al.*, 2010; Speed *et al.*, 2012), i.e. there was a 'counteracting effect' of land-use and climate change interaction (Goring & Williams, 2017). Currently though, reduced land-use intensity and global warming might synergistically influence the establishment of species at higher elevations (Morueta-Holme *et al.*, 2015; Goring & Williams, 2017).

At the control site, the annual rate of upshift of the species was less than altimeter accuracy; hence it was not possible to determine whether it was due to change in climate or an artefact. This study covered only the leading edge of *A. spectabilis*, which is advancing towards higher elevation. There is no information about whether the species is responding or not at its lower limit and optimum, but the leading edge is 'marching'.

On the basis of the findings in Paper I and the literature (Root *et al.*, 2003; Chen *et al.*, 2011; Du *et al.*, 2017), it can be assumed that some species are moving uphill in the mountains to track their climate niche with released land-use pressure and warming in the region. The response to warming is species specific (Paper II; Root *et* *al.*, 2003; Chen *et al.*, 2011) and depends on multiple variables (Pauli *et al.*, 2012). The study on *Rhododendron* sister species (Paper II) shows different potential responses to projected climate change. The model predictions show that a species from a dry region, *R. lowndesii*, may not move towards higher elevations i.e. its climatic niche is predicted to be around current geographic space. Because precipitation is typically a limiting factor for growth (Browne, 1942), which has an inverse relation with elevation in the Himalayan region (Acharya *et al.*, 2011). This means higher elevations will be drier in the future because of fewer rainy days (Collins *et al.*, 2013; Pendergrass & Hartmann, 2014). Therefore, *R. lowndesii* may not extend its distribution to higher elevations despite a warmer climate because of the reduced precipitation (Nogués-Bravo *et al.*, 2007; Lee *et al.*, 2014). Similar results have been reported from California for multiple species (Crimmins *et al.*, 2011), for *Picea crassifolia* in southern Tibet (Qiu, 2015) and different vascular plant species on a Mediterranean mountain (Pauli *et al.*, 2012).

The future climatically suitable geographic space of *R. lepidotum* and *R. cowanianum* is predicted to occur at higher elevation compared to today (Paper II). Such an upslope shift is generally expected in mountains with increasing temperature (Root *et al.*, 2003; but see Lenoir *et al.*, 2010). Evidence reveals that some other species are also expanding their range towards higher elevation in the Himalayan region (Paper I; Telwala *et al.*, 2013; Gaire *et al.*, 2014), although not all (Lenoir *et al.*, 2010; Bhatta *et al.*, 2018). The effect of warming can, however, be confounded with other variables such as grazing (Speed *et al.*, 2012), water availability (Crimmins *et al.*, 2011; Pauli *et al.*, 2012; Bhatta *et al.*, 2018) and land use (Gehrig-Fasel *et al.*, 2007, Paper I).

Under a scenario of projected future climate, three different sister species show species-specific modelled responses (Paper II). *Rhododendron lepidotum* may ‘march’, *R. cowanianum* may ‘lean’ and ‘march’, while *R. lowndesii* does not seem to follow any of the suggested approaches of ‘march’, ‘lean’ or ‘crash’. Assuming the species will follow the predicted trend, as a majority of studies suggest (Colwell *et al.*, 2008; Lenoir *et al.*, 2008; Lenoir *et al.*, 2010; Chen *et al.*, 2011), their differential rate of shift may result in a different species composition (Hobbs *et al.*, 2006;

Williams & Jackson, 2007). In such a situation, current species conservation approaches that aim to conserve representative assemblages of vegetation types may not achieve the anticipated results (Hannah *et al.*, 2002).

Climatic niche overlaps between sister taxa (Papers II and III)

The closely related *Rhododendron* species have mostly overlapping ranges of bioclimatic variables (Paper II), while two subspecies of *Macaca assamensis* have mostly non-overlapping climatic ranges and different realised climatic niches (Paper III). These studies suggest that closely related sister taxa do not always have similar climatic niches. Paper II supports the concept of phylogenetic niche conservatism while Paper III does not, implying that phylogenetic relatedness should not be treated as a signal of phylogenetic niche conservatism (Losos, 2008). There are different findings in support of (Peterson *et al.*, 1999; Peterson, 2011) as well as against niche conservatism (Losos *et al.*, 2003), hence, as suggested by Wiens and Graham (2005), the debate should not be whether phylogenetic niche conservatism exists or not, but which patterns niche conservatism may generate. The climatic niche overlap between closely related sister taxa, as demonstrated in Paper II, is common with sympatric distribution (Steinbauer *et al.*, 2016) by partitioning non-climatic niche dimensions such as micro-habitat or host species (Khelifa *et al.*, 2013; Rosser *et al.*, 2015).

Based on the current geographic distribution, *R. lepidotum* is a generalist, while *R. cowanianum* and *R. lowndesii* are restricted species; all of them have at least partial geographic overlap in their distribution (Paper II). A larger climatic niche space overlap between generalist and restricted species is estimated compared to overlap between restricted species. The differences in climatic niches mainly concern precipitation variables rather than temperature variables, which is consistent with findings for *Aeonium* and *Argyranthemum* clades by Steinbauer *et al.* (2016).

Differences in the niches of sister taxa are typically not exceptional (e.g. Dufour-Dror & Ertas, 2004; Chetan *et al.*, 2014), but are quite common when they are geographically distant or divided by a migration barrier (Garcia-Ramos *et al.*, 2000; Steinbauer *et al.*, 2016). This was the case with two subspecies of *M. assamensis*, where significantly different climatic niches of each subspecies revealed weaker phylogenetic relatedness over geographical distance. It may imply that niches have evolved over time as an adaptation to local climate.

The realised climatic niche difference between the subspecies of *M. assamensis* is related to temperature variables more than precipitation variables (Paper III). It may be due to the different elevational (a surrogate of temperature variable) distribution of the two subspecies. The western population (*M. assamensis* ssp. *pelops*) is distributed from about 1000 m to 4000 m a.s.l. (Chalise, 2003; Boonratana *et al.*, 2008), while its sister taxa *M. assamensis* ssp. *assamensis* inhabits the elevation zone below 1500 m a.s.l. (Timmins & Duckworth, 2013). This clearly suggests that they have different temperature limits and ranges. The climatic differences of their geographic space are also clearly visible on the Köppen-Geiger climate classification (Peel *et al.*, 2007).

Spatial dynamics in geographic space (Papers I, II, and III)

The spatial dynamics reported here are both vertical (up-down movement in the mountains) and horizontal (any direction). The spatial dynamics of species is reported with respect to current climate (Paper I) and predicted future climate (Papers II and III) with the assumption that species attempt to remain within their current climatic niche space. With the backdrop of contemporary climate change and reduced land-use intensity in mountain regions of Nepal, *A. spectabilis* is expanding its geographical distribution range towards higher elevations (Paper I). The land use has localised effects in the study area. The recent release of land-use pressure has facilitated the geographical range expansion of the leading edge of *A. spectabilis* on three mountain slopes. Here the climate may have either a confounding effect with land-use intensity reduction or a synergistic effect. Consistent results for the species are also reported from other mountain regions of Nepal (Gaire *et al.*, 2014; Shrestha *et al.*, 2014; Chhetri & Cairns, 2015; Gaire *et al.*, 2017). Similar spatial dynamics of the species upper limit, treeline and optima of different species are also observed from the Himalayan region (Valley, 2003; Telwala *et al.*, 2013; Bhatta & Vetaas, 2016; Schickhoff *et al.*, 2016). The spatial dynamics are attributed to land use (Shrestha *et al.*, 2014; Schickhoff *et al.*, 2016; Bhatta *et al.*, 2018) and climate change (Valley, 2003; Telwala *et al.*, 2013; Gaire *et al.*, 2014; Shrestha *et al.*, 2014;

Chhetri & Cairns, 2015; Gaire *et al.*, 2017). Most of these studies (Valley, 2003; Gaire *et al.*, 2014; Shrestha *et al.*, 2014; Chhetri & Cairns, 2015; Bhatta & Vetaas, 2016; Gaire *et al.*, 2017) are at a fine spatial scale, or based on local samples. At such a fine geographic scale, land use dominates over climate change effects. However, an interaction between land use and climate change might have contributed to the observed responses.

Under projected warming for 2070, distribution models predict an upslope shift of the climatically suitable area for *R. cowanianum* and *R. lepidotum* in the mountains of Nepal. The suitable area for *R. lowndesii*, in contrast, is predicted to be around its current distribution area (Paper II). Regardless of the elevational shift of climatically suitable geographic space in the future, the bioclimatic models predict an expansion of suitable geographic space for all the sister taxa. The entirety of the predicted areas may not necessarily be available for the species because land use will continue to shape a species' geographical range in the future and will be a stronger driver than climate change (Sala *et al.*, 2000; MEA, 2005). These *Rhododendron* species may, however, flourish across wider areas in the future because the Himalayan *Rhododendron* species can successfully establish in non-native climates (Vetaas, 2002) provided there is no migration limitation and non-climatic constraints do not limit their survival in the new localities. If they fail to shift or extend their range to new geographic space in the future, they may not fully occupy their potential climatic niche space (Pearson, 2006). Potential spatial dynamics of other species under projected future climate have been predicted by other studies in Nepal Himalaya. For example, an increase of up to 4.87% of potential area is predicted for *Ophiocordyceps sinensis* in Nepal (Shrestha & Bawa, 2014), while *Taxus wallichiana* is predicted to lose some current geographic space in the Nepal Himalaya (Gajurel *et al.*, 2014). Similar geographic shifts are also predicted outside the Himalayan region, for instance, a study of 1400 European plant species found that 32% or more of them will shift their geographic space by 2050 (Bakkenes *et al.*, 2002).

The distribution models in this study predict more climatically suitable geographic space for both *Macaca assamensis* subspecies under a projected warmer future climate compared to current climate (Paper III). Some patches of suitable geographic spaces are around and nearby the current distribution areas, while most of the predicted suitable areas are farther north and east of the current geographic spaces of the species. It suggests that the species may need to move northward (as well as other directions) to find their potential climatic in geographic space. Meta-analyses of a number of plants and animals species reveal that species geographic distributions are dynamic generally. However, some species do not exhibit any range shift in response to contemporary climate change (Parmesan & Yohe, 2003; Chen *et al.*, 2011) and sometimes the range shifts are masked by confounding effects and/or counteracting effects of land use (Speed *et al.*, 2012; Goring & Williams, 2017; Miller & McGill, 2017).

Based on the current widespread spatial dynamics of species in response to warming (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Telwala *et al.*, 2013; Gaire *et al.*, 2014; 2017; Shrestha *et al.*, 2014; Chhetri & Cairns, 2015; Suwal *et al.*, 2016), a spatial shift of species in the future may become a general trend, and is supported by the predictions here (Paper II and III) and in previous studies (Bakkenes *et al.*, 2002; Gajurel *et al.*, 2014; Shrestha & Bawa, 2014). It is because the future climate is projected to be warmer than present (Collins *et al.*, 2013; Lee *et al.*, 2014; Stocker *et al.*, 2014). Although species upshift in the mountains may become a general trend, it may not apply to all species (Lenoir *et al.*, 2010). A downhill shift in plant species, for instance, may occur because of water limitation (Crimmins *et al.*, 2011; Qiu, 2015) or no shift due to dispersal limitations or capacity, to topography (Svenning & Skov, 2004; Svenning *et al.*, 2010) or to a change in grazing intensity (Bhatta *et al.*, 2018). All possible types of effects from interactions between land use and climate change (Goring & Williams, 2017) should be taken into consideration to predict future spatial dynamics of species.

Conclusions

This thesis provided additional knowledge about responses of species to contemporary climate change and projected future warming in the Himalayan region and surroundings. It presented an upper limit shift of *Abies spectabilis* (Paper I); possible species-specific responses to future warming of three *Rhododendron* sister taxa (Paper II); and the potential distribution and distribution overlap of closely related *Rhododendron* species (Paper II) and parapatric subspecies of *Macaca assamensis* (Paper III) under current and future climate.

The thesis substantiates the fact that the spatial distribution of species is dynamic in nature. To remain within their climatic niche, species are dynamic within geographic space. However, the rates of shift as well as directions are species specific, which depends on their physiological relationships to predictor variables. *Abies spectabilis* is advancing its leading edge under a backdrop of reduced land-use intensity and warming, *R. cowanianum* and *R. lepidotum* may also advance their leading edge in future projected warmer climate, while *R. lowndesii* may not show any shift under a projected future climate with more dry days.

The two endemic species (*R. cowanianum*, *R. lowndesii*) seem to be occupying less than their climatically potential geographic space in the central Himalaya. This implies that other non-climatic biotic and abiotic factors or dispersal limitation may play a key role in their limited distribution. On this premise, it is hard to predict whether they will occupy additional climatically potential geographic space under the future projected climate.

Two parapatric subspecies of *Macaca assamensis* have different climatic niches with few range overlapping variables. The distribution models predict wider geographic spaces that are climatically suitable for them compared to their currently known distribution area. The models predict that their potential geographic space will be farther east and north compared to their current space in a future projected climate.

Future perspectives

This thesis covered studies conducted in one of the harshest and least explored geographic areas, the Himalayan region, on species niche and distribution dynamics. The empirical investigation of species' spatial dynamics under a backdrop of land-use intensity change and climate change (Paper I) covered just four sites in the central Himalayan region. Further studies with a larger number of transects covering a larger portion of the Himalayan region would broaden the picture of species dynamics. The response of species is species specific; hence more species will need to be sampled in prospective research.

The distribution models were fitted with the best openly available data. Higher resolution data may give a better picture of the distribution in areas with heterogeneous geography, like the Himalayan region. Hence, efforts and resources should also be channelled into the development and/or downscaling of high-resolution data for current climate as well future climate.

The model output varies with the source of the data because different sources have a different data policy and use different algorithms. It may be a good idea, therefore, to use an ensemble of data from different sources during model fitting, as was done with future climate data in both Paper II and Paper III.

The literature shows that distribution models with species absence, biotic interactions and other non-climatic variables improve model performance. Such data are globally rare; the Himalayan region is not just an exception. It may be worthwhile to collect such data to use in prospective studies.

References

Acharya, K.P., Vetaas, O.R. & Birks, H.J.B. (2011) Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography*, **38**, 1821–1833.

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, **164**, S165–S184.

Aguirre-Gutiérrez, J., Carvalheiro, L.G., Polce, C., van Loon, E.E., Raes, N., Reemer, M. & Biesmeijer, J.C. (2013) Fit-for-purpose: species distribution model performance depends on evaluation criteria–Dutch hoverflies as a case study. *PLoS ONE*, **8**, e63708.

Alin, A. (2010) Multicollinearity. *WIREs Computational Statistics*, **2**, 370–374.

Anacker, B.L. & Strauss, S.Y. (2014) The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20132980.

Anderson, R.P. & Gonzalez, I. (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecological Modelling*, **222**, 2796–2811.

Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.

Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity? *Science*, **313**, 1396–1397.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527-1539.

Araújo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011) Using species co-occurrence networks to assess the impacts of climate change. *Ecography*, **34**, 897–908.

Austin, M. & Smith, T. (1990) A new model for the continuum concept. *Vegetatio*, **83**, 35-47.

Austin, M. & Meyers, J. (1996) Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management*, **85**, 95–106.

Austin, M., Nicholls, A. & Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs*, **60**, 161–177.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390–407.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.

Barnes, B., Zak, D., Denton, S. & Spurr, S. (1998) *Forest Ecology*, Fourth edn. John Wiley & Sons, New York.

Beaumont, L.J., Hughes, L. & Pitman, A. (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters*, **11**, 1135–1146.

Bedia, J., Herrera, S. & Gutiérrez, J.M. (2013) Dangers of using global bioclimatic datasets for ecological niche modeling. Limitations for future climate projections. *Global and Planetary Change*, **107**, 1–12.

Beniston, M. (2003) Climatic change in mountain regions: a review of possible impacts. *Climatic change*, **59**, 5-31.

Bhatta, K.P. & 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*, 948–957.

Bhatta, K.P., Grytnes, J.-A. & Vetaas, O.R. (2018) Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere* **9**, e02084.

Bobrowski, M. & Schickhoff, U. (2017) Why input matters: Selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. *Ecological Modelling*, **359**, 92–102.

Boonratana, R., Chalise, M., Das, J., Htun, S. & Timmins, R. (2008) *Macaca assamensis*. The IUCN Red List of Threatened Species. Version 2016-3. In:

Booth, T.H. (2017) Assessing species climatic requirements beyond the realized niche: some lessons mainly from tree species distribution modelling. *Climatic Change*, **145**, 259–271.

Bradley, A.P. (1997) The use of the area under the ROC curve in the evaluation of machine learning algorithms. *Pattern Recognition*, **30**, 1145–1159.

Breiman, L. (2001) Random Forests. *Machine Learning*, **45**, 5–32.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B. & Davison, J.E. (2008) Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences USA*, **105**, 11591–11592.

Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.

Browne, C.A. (1942) Liebig and the Law of the Minimum. *Liebig and After Liebig: A Century of Progress in Agricultural Chemistry* (ed. by F.R. Moulton), pp. 71–82. American Association for the Advancement of Science, Washington, DC.

Bull, C. (1991) *Ecology of Parapatric Distributions*.

CBS (2014) National Population and Housing Census 2011: Social Characteristics Tables. In. Central Bureau of Statistics, National Planning Commission, Government of Nepal, Kathmandu, Nepal.

Chalise, M.K. (2003) Assamese macaques (*Macaca assamensis*) in Nepal. *Primate Conservation*, **19**, 99–107.

Chase, J.M. & Leibold, M.A. (2003) *Ecological Niches: linking Classical and Contemporary Approaches*. University of Chicago Press.

Chauchard, S., Beilhe, F., Denis, N. & Carcaillet, C. (2010) An increase in the upper tree-limit of silver fir *(Abies alba* Mill.) in the Alps since the mid-20th century: A land-use change phenomenon. *Forest Ecology and Management*, **259**, 1406–1415.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Chetan, N., Praveen, K.K. & Vasudeva, G.K. (2014) Delineating ecological boundaries of Hanuman langur species complex in peninsular India using MaxEnt modeling approach. *PLoS ONE*, **9**, e87804.

Chhetri, P.K. & Cairns, D.M. (2015) Contemporary and historic population structure of *Abies spectabilis* at treeline in Barun valley, eastern Nepal Himalaya. *Journal of Mountain Science*, **12**, 558–570.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J. & Wehner, M. (2013) Long-term Climate Change: Projections, Commitments and

Irreversibility. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley). Cambridge University Press, Cambridge, UK and New York, USA.

Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences USA*, **106**, 19651–19658.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. & Longino, J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *science*, **322**, 258-261.

Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S., Thuiller, W. & Guillaume, F. (2017) A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications*, **8**, 15399.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–327.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998a) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600–612.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998b) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783.

Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, **8**, 387–397.

Dormann, C.F., Gruber, B., Winter, M. & Herrmann, D. (2010) Evolution of climate niches in European mammals? *Biology Letters*, **6**, 229–232.

Drew, C.A. & Perera, A.H. (2011) Expert knowledge as a basis for landscape ecological predictive models. *Predictive Species and Habitat Modeling in Landscape Ecology: Concepts and Applications* (ed. by C.A. Drew, Y.F. Wiersma and F. Huettmann), pp. 229-248. Springer, New York.

Du, H., Liu, J., Li, M.H., Büntgen, U., Yang, Y., Wang, L., Wu, Z. & He, H.S. (2017) Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. *Global Change Biology*,

Dufour-Dror, J.M. & Ertas, A. (2004) Bioclimatic perspectives in the distribution of *Quercus ithaburensis* Decne. subspecies in Turkey and in the Levant. *Journal of Biogeography*, **31**, 461–474.

eFloras (2008) In. Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA

Elith, J. & Graham, C.H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66–77.

Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M. & E. Zimmermann, N. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Elton, C.S. (1927) *Animal Ecology*. University of Chicago Press.

Elton, C.S. (1958) *The Ecology of Invasions by Plants and Animals*, Methuen, London.

Feria, A., Patricia, T. & Peterson, A.T. (2002) Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. *Diversity and Distributions*, **8**, 49–56.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C. & Gibbs, H.K. (2005) Global consequences of land use. *science*, **309**, 570-574.

Fooden, J. (1980) Classification and distribution of living macaques (*Macaca* Lacépède, 1799). *The Macaques: Studies in Ecology, Behavior And Evolution*, pp. 1–9. Van Nostrand Reinhold, New York.

Fooden, J. (1982) *Taxonomy and Evolution of the Sinica Group of Macaques: 3. Species and subspecies accounts of Macaca assamensis*. Field Museum of Natural History, Chicago.

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. & Shapiro, A.M. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences USA*, **107**, 2088-2092.

Fox, J. & Weisberg, S. (2010) Time-Series Regression and Generalized Least Squares in R, An appendix to an R companion to applied regression. In. Sage Publications, New York

Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in physical geography*, **19**, 474–499.

Franklin, J. (2010) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press.

Franklin, J., Wejnert, K.E., Hathaway, S.A., Rochester, C.J. & Fisher, R.N. (2009) Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions*, **15**, 167–177.

Gaire, N.P., Koirala, M., Bhuju, D.R. & Borgaonkar, H.P. (2014) Treeline dynamics with climate change at the central Nepal Himalaya. *Climate of the Past*, **10**, 1277–1290.

Gaire, N.P., Koirala, M., Bhuju, D.R. & Carrer, M. (2017) Site-and species-specific treeline responses to climatic variability in eastern Nepal Himalaya. *Dendrochronologia*, **41**, 44–56.

Gajurel, J.P., Werth, S., Shrestha, K.K. & Scheidegger, C. (2014) Species distribution modeling of Taxus wallichiana (Himalayan Yew) in Nepal Himalaya. *Asian Journal of Conservation Biology*, **3**, 127–134.

Garcia-Ramos, G., Sanchez-Garduno, F. & Maini, P.K. (2000) Dispersal can sharpen parapatric boundaries on a spatially varying environment. *Ecology*, **81**, 749–760.

Gartaula, H.N. & Niehof, A. (2013) Migration to and from the Nepal terai: shifting movements and motives. *The South Asianist*, **2**, 29–51.

Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, **18**, 571–582.

Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 7–26.

Goring, S.J. & Williams, J.W. (2017) Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States. *Ecology Letters*, **20**, 461-470.

Grinnell, J. (1917) The Niche-Relationships of the California Thrasher. *The Auk*, **34**, 427–433.

Grytnes, J.A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S. & Birks, H.J.B. (2014) Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, **23**, 876-884.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.

Guisan, A., Thuiller, W. & Zimmermann, N.E. (2017) *Habitat Suitability and Distribution Models: with Applications in R.* Cambridge University Press.

Gutiérrez, E.E., Boria, R.A. & Anderson, R.P. (2014) Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums. *Ecography*, **37**, 741-753.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.

Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.H. (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, **16**, 754–763.

Herbold, B. & Moyle, P.B. (1986) Introduced species and vacant niches. *American Naturalist*, **128**, 751–760.

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

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. & Hijmans, M.R.J. (2016) Package 'dismo'. *Circles*, **9**, 1.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A. & Lugo, A.E. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holt, R. & Gaines, M. (1992) Analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. *Evolutionary Ecology*, **6**, 433–447.

Holt, R.D. (1996) Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos*, 182–192.

Hutchinson, G.E. (1957) Concluding remarks *Cold Spring Harbor Symposium on Quantitative Biology* (ed by G.E. Hutchinson), pp. 415–427.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Iverson, L.R., Thompson, F.R., Matthews, S., Peters, M., Prasad, A., Dijak, W.D., Fraser, J., Wang, W.J., Hanberry, B. & He, H. (2017) Multi-model comparison on the effects of climate change on tree species in the eastern US: results from an enhanced niche model and process-based ecosystem and landscape models. *Landscape Ecology*, **32**, 1327-1346.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

James, F.C., Johnston, R.F., Wamer, N.O., Niemi, G.J. & Boecklen, W.J. (1984) The Grinnellian niche of the wood thrush. *The American Naturalist*, **124**, 17–47.

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) Hole-filled SRTM for the globe Version 4 available from the CGIAR-CSI SRTM 90m Database (http://srtm.csi.cgiar.org). In:

Jeschke, J.M. & Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1–24.

Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65-71.

Kalnay, E. & Cai, M. (2003) Impact of urbanization and land-use change on climate. *Nature*, **423**, 528-531.

Kandel, K., Huettmann, F., Suwal, M.K., Regmi, G.R., Nijman, V., Nekaris, K.A.I., Lama, S.T., Thapa, A., Sharma, H.P. & Subedi, T.R. (2015) Rapid multi-nation distribution assessment of a charismatic conservation species using open access ensemble model GIS predictions: Red panda (*Ailurus fulgens*) in the Hindu-Kush Himalaya region. *Biological Conservation*, **181**, 150–161.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P. & Kessler, M. (2016) CHELSA climatologies at high resolution for the earth's land surface areas (Version 1.1). In. World Data Center for Climate (WDCC) at DKRZ

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P. & Kessler, M. (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, **4**, 170122.

Kattel, D., Yao, T., Yang, K., Tian, L., Yang, G. & Joswiak, D. (2013) Temperature lapse rate in complex mountain terrain on the southern slope of the central Himalayas. *Theoretical and Applied Climatology*, **113**, 671-682.

Khelifa, R., Zebsa, R., Moussaoui, A., Kahalerras, A., Bensouilah, S. & Mahdjoub, H. (2013) Niche partitioning in three sympatric congeneric species of dragonfly, Orthetrum chrysostigma, O. coerulescens anceps, and O. nitidinerve: The importance of microhabitat. *Journal of Insect Science*, **13**, 1–17.

Körner, C. (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer, Berlin.

Latreille, P.A. (1819) *Mémoires sur divers sujets de l'histoire naturelle des insectes, de géographie ancienne et de chronologie*. Deterville.

Lee, J.-W., Hong, S.-Y., Chang, E.-C., Suh, M.-S. & Kang, H.-S. (2014) Assessment of future climate change over East Asia due to the RCP scenarios downscaled by GRIMs-RMP. *Climate Dynamics*, **42**, 733–747.

Lenoir, J., Gégout, J.-C., Marquet, P., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *science*, **320**, 1768-1771.

Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W. & Svenning, J.C. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295-303.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R News*, **2**, 5.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.

Losos, J.B., Leal, M., Glor, R.E. & de Queiroz, K. (2003) Niche lability in the evolution of a Caribbean lizard community. *Nature*, **424**, 542.

MacMahon, J.A., Schimpf, D.J., Andersen, D.C., Smith, K.G. & Bayn, R.L. (1981) An organism-centered approach to some community and ecosystem concepts. *Journal of Theoretical Biology*, **88**, 287–307.

McPherson, J.M. & Jetz, W. (2007) Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30**, 135-151.

MEA (2005) Ecosystems and Human Well-being: Synthesis. In. Millennium Ecosystem Assessment, Island Press, Washington, DC.

Mi, C., Huettmann, F., Guo, Y., Han, X. & Wen, L. (2017) Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. *PeerJ*, **5**, e2849.

Miller, K.M. & McGill, B.J. (2017) Land use and life history limit migration capacity of eastern tree species. *Global Ecology and Biogeography*, **27**, 57–67.

Miller, R.I. (1986) Predicting rare plant distribution patterns in the southern Appalachians of the south-eastern USA. *Journal of Biogeography*, **13**, 293–311.

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J.D., Segnitz, R.M. & Svenning, J.-C. (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences USA*, 201509938.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M. & Anderson, R.P. (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, **5**, 1198-1205.

Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography*, **37**, 191–203.

Nakazawa, Y., Williams, R.A., Peterson, A.T., Mead, P.S., Kugeler, K.J. & Petersen, J.M. (2010) Ecological niche modeling of *Francisella tularensis* subspecies and clades in the United States. *The American Journal of Tropical Medicine and Hygiene*, **82**, 912–918.

Nogués-Bravo, D., Araújo, M.B., Errea, M. & Martinez-Rica, J. (2007) Exposure of global mountain systems to climate warming during the 21st Century. *Global Environmental Change*, **17**, 420–428.

Odum, E.P. & Odum, H. (1953) *Fundamentals of Ecology*. Saunders, Philadephia.

Oliver, T.H. & Morecroft, M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Climate Change*, **5**, 317-335.

Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N.K., Edenhofer, O., Elgizouli, I., Field, C.B., Forster, P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., Hegerl, G., Howden, M., Jiang, K., Jimenez Cisneroz, B., Kattsov, V., Lee, H., Mach, K.J., Marotzke, J., Mastrandrea, M.D., Meyer, L., Minx, J., Mulugetta, Y., O'Brien, K., Oppenheimer, M., Pereira, J.J., Pichs-Madruga, R., Plattner, G.K., Pörtner, H.O., Power, S.B., Preston, B., Ravindranath, N.H., Reisinger, A., Riahi, K., Rusticucci, M., Scholes, R., Seyboth, K., Sokona, Y., Stavins, R., Stocker, T.F., Tschakert, P., van Vuuren, D. & van Ypserle, J.P. (2014) *Climate change 2014:*

Synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B. & Calzado, R.F. (2012) Recent plant diversity changes on Europe's mountain summits. *Science*, **336**, 353–355.

Pearson, R.G. (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, **21**, 111–113.

Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of biogeography*, **33**, 1704–1711.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences Discussions*, **4**, 439–473.

Pendergrass, A.G. & Hartmann, D.L. (2014) Changes in the Distribution of Rain Frequency and Intensity in Response to Global Warming*. *Journal of Climate*, **27**, 8372–8383.

Peterson, A., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Peterson, A.T. (2011) Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson, A.T. & Soberón, J. (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. *Natureza & Conservação*, **10**, 102–107.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martìnez-Meyer, E., Nakamura, M. & Araujo, M.B. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, USA.

Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C. & Guisan, A. (2017) Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plant invasions. *Global Ecology and Biogeography*, **26**, 275-287.

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

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017) Opening the black box: an open-source release of Maxent. *Ecography*, 887–893.

Pliscoff, P., Luebert, F., Hilger, H.H. & Guisan, A. (2014) Effects of alternative sets of climatic predictors on species distribution models and associated estimates of extinction risk: A test with plants in an arid environment. *Ecological Modelling*, **288**, 166–177.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.

Qiu, J. (2015) High-altitude forests in the himalayas harder hit by droughts. In: *Scientific American*. Scientific American, Berlin.

R Core Team (2017) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Radosavljevic, A. & Anderson, R.P. (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, **41**, 629–643.

Raes, N. (2012) Partial versus full species distribution models. *Natureza & Conservacao*, **10**, 127–138.

Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.

Romdal, T.S., Araujo, M.B. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography*, **22**, 344–350.

Root, T.L., Price, J.T., Hall, K.R. & Schneider, S.H. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rosser, N., Kozak, K.M., Phillimore, A.B. & Mallet, J. (2015) Extensive range overlap between heliconiine sister species: evidence for sympatric speciation in butterflies? *BMC Evolutionary Biology*, **15**, 125.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B. & Kinzig, A. (2000) Global biodiversity scenarios for the year 2100. *science*, **287**, 1770-1774.

Sax, D.F., Early, R. & Bellemare, J. (2013) Niche syndromes, species extinction risks, and management under climate change. *Trends in Ecology & Evolution*, **28**, 517-523.

Schickhoff, U., Bobrowski, M., Böhner, J., Bürzle, B., Chaudhary, R.P., Gerlitz, L., Lange, J., Müller, M., Scholten, T. & Schwab, N. (2016) Climate change and treeline dynamics in the Himalaya. *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya* (ed. by R. Singh, U. Schickoff and S. Mal), pp. 271–306. Springer.

Sharma, L.N., Vetaas, O.R., Chaudhary, R.P. & Måren, I.E. (2014) Ecological consequences of land use change: forest structure and regeneration across the forest-grassland ecotone in mountain pastures in Nepal. *Journal of Mountain Science*, **11**, 838–849.

Shrestha, A.B. & Aryal, R. (2011) Climate change in Nepal and its impact on Himalayan glaciers. *Regional Environmental Change*, **11**, 65–77.

Shrestha, A.B., Wake, C.P., Mayewski, P.A. & Dibb, J.E. (1999) Maximum temperature trends in the Himalaya and its vicinity: An analysis based on temperature records from Nepal for the period 1971-94. *Journal of Climate*, **12**, 2775–2786.

Shrestha, K.B., Hofgaard, A. & Vandvik, V. (2014) Recent treeline dynamics are similar between dry and mesic areas of Nepal, central Himalaya. *Journal of Plant Ecology*, **8**, 347-358.

Shrestha, U.B. & Bawa, K.S. (2014) Impact of climate change on potential distribution of Chinese caterpillar fungus (Ophiocordyceps sinensis) in Nepal Himalaya. *PloS ONE*, **9**, e106405.

Shrestha, U.B., Gautam, S. & Bawa, K.S. (2012) Widespread climate change in the himalayas and associated changes in local ecosystems. *PLoS ONE*, **7**, e36741.

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* **2**, 1–10.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**, 19644–19650.

Soberón, J. & Arroyo-Peña, B. (2017) Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS ONE*, **12**, e0175138.

Speed, J.D.M., Austrheim, G., Hester, A.J. & Mysterud, A. (2012) Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science*, **23**, 617–625.

Staniczenko, P., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017) Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. *Ecology Letters*, **20**, 693-707.

Steinbauer, M.J., Field, R., Fernández-Palacios, J.M., Irl, S.D., Otto, R., Schaefer, H. & Beierkuhnlein, C. (2016) Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Global Ecology and Biogeography*, **25**, 792–804.

Stocker, T., Qin, D., Plattner, G.-K., Alexander, L.V., Allen, S.K., Bindoff, N.L., Bréon, F.-M., Church, J.A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett, N., Gregory, J.M., Hartmann, D.L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar, K., Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S., Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Talley, L.D., Vaughan, D.G. & Xie, S.-P. (2014) *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, United Kingdom and New York, NY, USA.

Stockwell, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13**, 143-158.

Stockwell, D. (2006) *Niche Modeling: Predictions from Statistical Distributions*. CRC Press.

Suwal, M.K., Shrestha, K.B., Guragain, L., Shakya, R., Shrestha, K., Bhuju, D.R. & Vetaas, O.R. (2016) Land-use change under a warming climate facilitated upslope expansion of Himalayan silver fir (*Abies spectabilis* (D. Don) Spach). *Plant Ecology*, **217**, 993–1002.

Svenning, J.C. & Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565–573.

Svenning, J.C., Fitzpatrick, M.C., Normand, S., Graham, C.H., Pearman, P.B., Iverson, L.R. & Skov, F. (2010) Geography, topography, and history affect realized-to-potential tree species richness patterns in Europe. *Ecography*, **33**, 1070–1080.

Telwala, Y., Brook, B.W., Manish, K. & Pandit, M.K. (2013) Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. *PLoS ONE*, **8**, e57103.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Timmins, R. & Duckworth, J. (2013) Distribution and habitat of Assamese macaque *Macaca assamensis* in Lao PDR, including its use of low-altitude karsts. *Primate Conservation*, **26**, 103–114.

Trainor, A.M., Schmitz, O.J., Ivan, J.S. & Shenk, T.M. (2014) Enhancing species distribution modeling by characterizing predator–prey interactions. *Ecological Applications*, **24**, 204–216.

Trivedi, M.R., Berry, P.M., Morecroft, M.D. & Dawson, T.P. (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089–1103.

Valley, H.P. (2003) Upward shift of Himalayan pine in western Himalaya, India. *Current Science*, **85**, 1135–1136.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling*, **220**, 589–594.

Vetaas, O.R. (2002) Realized and potential climate niches: a comparison of four *Rhododendron* tree species. *Journal of Biogeography*, **29**, 545–554.

Villemant, C., Barbet-Massin, M., Perrard, A., Muller, F., Gargominy, O., Jiguet, F. & Rome, Q. (2011) Predicting the invasion risk by the alien bee-hawking Yellowlegged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. *Biological Conservation*, **144**, 2142–2150.

Vitali, A., Urbinati, C., Weisberg, P.J., Urza, A.K. & Garbarino, M. (2018) Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy). *Journal of Vegetation Science*,

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.

Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Reviews*, **49**, 207–264.

Whittaker, R.H., Levin, S.A. & Root, R.B. (1973) Niche, habitat, and ecotope. *The American Naturalist*, **107**, 321–338.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Williams, J.W., Jackson, S.T. & Kutzbach, J.E. (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA*, **104**, 5738–5742.

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E. & Pearson, R. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape proteaceae. *Conservation Biology*, **19**, 1063–1074.

Willis, K.J. & Bhagwat, S.A. (2009) Biodiversity and climate change. *Science*, **326**, 806–807.

Zhao, X., Ren, B., Garber, P.A., Li, X. & Li, M. (2018) Impacts of human activity and climate change on the distribution of snub-nosed monkeys in China during the past 2000 years. *Diversity and Distributions*, **24**, 92–102.

Appendices

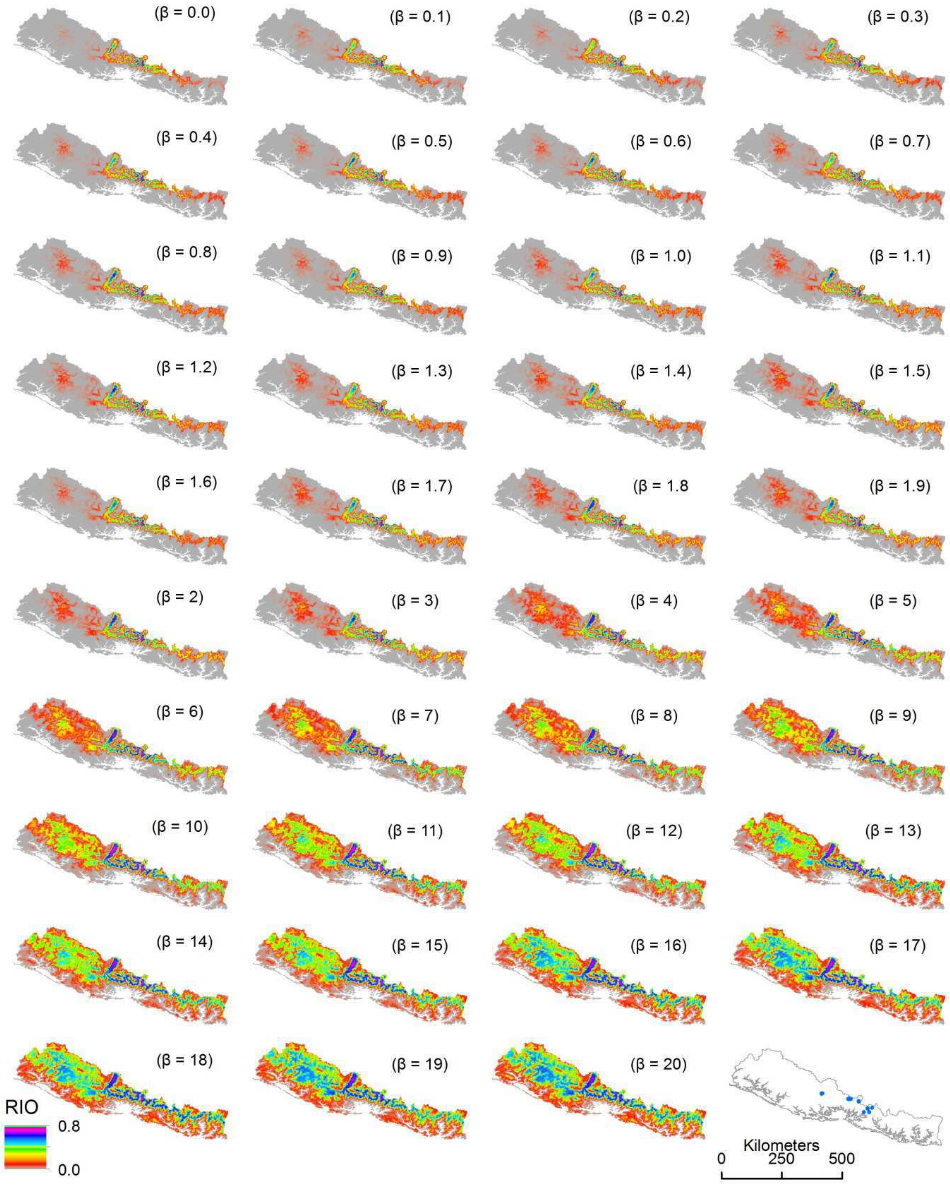
Appendix 1: List of bioclimatic, topographic and energy related predictor variables

S.N.	Abbreviation	Details	Category
1	Bio01	Annual Mean Temperature	Bioclimatic variables
2	Bio02	Mean Diurnal Range (Mean of monthly (max temp - min temp))	
3	Bio03	Isothermality (BIO2/BIO7) (* 100)	
4	Bio04	Temperature Seasonality (standard deviation *100)	
5	Bio05	Maximum Temperature of Warmest Month	
6	Bio06	Minimum Temperature of Coldest Month	
7	Bio07	Temperature Annual Range (BIO5-BIO6)	
8	Bio08	Mean Temperature of Wettest Quarter	
9	Bio09	Mean Temperature of Driest Quarter	
10	Bio10	Mean Temperature of Warmest Quarter	
11	Bio11	Mean Temperature of Coldest Quarter	
12	Bio12	Annual Precipitation	
13	Bio13	Precipitation of Wettest Month	
14	Bio14	Precipitation of Driest Month	
15	Bio15	Precipitation Seasonality (Coefficient of Variation)	
16	Bio16	Precipitation of Wettest Quarter	
17	Bio17	Precipitation of Driest Quarter	
18	Bio18	Precipitation of Warmest Quarter	
19	Bio19	Precipitation of Coldest Quarter	
20	ABT	Annual Bio-Temperature	
21	EQ	Ellenberg Climatic Quotient	
22	RRI	Relative Radiation Index	Energy
22	Elev	SRTM Digital Elevation Model	Topographic variables
23	Slope	Topographic Slope	
24	Aspect	Topographic Aspect	

Appendix 2: List of *Berberis* and *Rhododendron* species and their respective groups based on number of occurrences, Group A (number of occurrences from 14 to < 25; total (n) = 9), Group B (25 to < 50; n = 9), Group C (50 to < 100; n = 5) and Group D (above 100, n = 6). A total of four species are endemic to Nepal.

SN	Species	No. of occurrence points	Data Set	Group	Remark
1	*B. angulosa*	80	D1	C	
2	*B. aristata*	110	D2	D	
3	*B. asiatica*	92	D3	C	
4	*B. concinna*	37	D4	B	
5	*B. everestiana*	33	D5	B	
6	*B. glaucocarpa*	17	D6	A	
7	*B. hamiltoniana*	16	D7	A	Endemic
8	*B. hookeri*	16	D8	A	
9	*B. insignis*	24	D9	A	
10	*B. jaeschkeana*	21	D10	A	
11	*B. koehneana*	65	D11	C	
12	*B. mucrifolia*	36	D12	B	Endemic
13	*B. wallichiana*	22	D13	A	
14	*R. anthopogon*	285	D14	D	
15	*R. arboreum*	66	D15	C	
16	*R. barbatum*	123	D16	D	
17	*R. campanulatum*	135	D17	D	
18	*R. campylocarpum*	31	D18	B	
19	*R. cinnabarinum*	30	D19	B	
20	*R. cowanianum*	19	D20	A	Endemic
21	*R. dalhousieae*	25	D21	B	
22	*R. hodgsonii*	48	D22	B	
23	*R. lepidotum*	239	D23	D	
24	*R. lowndesii*	40	D24	B	Endemic
25	*R. nivale*	84	D25	C	
26	*R. setosum*	224	D26	D	
27	*R. thomsonii*	25	D27	B	
28	*R. triflorum*	14	D28	A	
29	*R. wightii*	16	D29	A	

Appendix 3: Effect of the regularisation multiplier in MaxEnt models, an illustration with *Rhododendron cowanianum with Relative Index of Occurrence (RIO)*. Last map (bottom-right) shows occurrence points (blue dots) of the species.



Land-use change under a warming climate facilitated upslope expansion of Himalayan silver fir (*Abies spectabilis* (D. Don) Spach)

I

Plant Ecol (2016) 217:993–1002
DOI 10.1007/s11258-016-0624-7

Land-use change under a warming climate facilitated upslope expansion of Himalayan silver fir (*Abies spectabilis* (D. Don) Spach)

Madan Krishna Suwal · Krishna Babu Shrestha · Laba Guragain · Rabin Shakya · Kalpana Shrestha · Dinesh Raj Bhuju · Ole Reidar Vetaas

Received: 14 January 2016 / Accepted: 27 May 2016 / Published online: 6 June 2016

Abstract Global warming is triggering some species to shift towards the poles or higher elevations, but spatial translocation is also influenced by land-use regime or intensity. The Himalayan climate is getting warmer and land use has changed, reducing in intensity in some areas. We estimated the upper species limit (USL) and tree limit of *Abies spectabilis* (D. Don) Spach and assessed whether these have changed over recent years. We hypothesise an upslope shift in response to enhanced temperature and changes in land-use intensity. Our four transects were located in treeline ecotones of two protected areas in Nepal, namely Manaslu Conservation Area (3 transects) and Gaurishankar Conservation Area (1 transect). Transects (20 m wide) ran from the USL of *A. spectabilis* down towards the treeline and beyond to the forest line. Length of each transect varied depending on local conditions. Co-ordinates, elevation, height and age of each *A. spectabilis* individual along the transects were recorded. We noted an upward shift of both the USL and the tree limit. The rate of shift was ca. 20 m per decade for the USL and 12 m per decade for the tree limit in the area of reduced land-use intensity and in the area with no change in land use, 5 m per decade for the USL, but almost nil for tree limit. The seedling density was higher below the treeline than above. Reduced intensity of land use was the dominant factor in upslope shift of *A. spectabilis* at both the USL and the tree limit.

Keywords *Abies spectabilis* · Central Himalaya · Climate change · Treeline ecotone · Tree limit · Regeneration · Upper species limit

Communicated by Dr. Jan Wunder.

M. K. Suwal (✉) · O. R. Vetaas
Department of Geography, University of Bergen (UiB),
PO Box 7802, 5020 Bergen, Norway
e-mail: madan.suwal@uib.no

K. B. Shrestha
UiB Global, Jekteviksbakken 31, PO Box 7800,
5020 Bergen, Norway

L. Guragain
Department of National Parks and Wildlife Reserves,
Ministry of Forests, Kathmandu, Nepal

R. Shakya
Golden Gate International College, Kathmandu, Nepal

K. Shrestha · D. R. Bhuju
Department of Environmental Science, Tribhuvan
University, Kathmandu, Nepal

Introduction

The treeline in the mountains is one of the most fundamental ecological and conspicuous physiognomic boundaries along the elevation gradient (Harsch et al. 2009; Holtmeier 2009; Schickhoff 2005). The natural alpine treelines are the result of heat deficiency that adversely affects growth, regeneration and survival of trees, and they are therefore sensitive to climate change (Körner and Paulsen 2004).

The extent and limits of the treeline ecotone are easily confounded by different factors such as the presence of herbivores (Speed et al. 2012), forms of treeline (Harsch et al. 2009), land-use dynamics (Gehrig-Fasel et al. 2007), geomorphology (Leonelli et al. 2011; Resler 2006), moisture (Crimmins et al. 2011; Qiu 2015), as well as local temperature. Several recent studies document an upslope or poleward shift of species at the treeline and suggest that this is partly as a result of recent global warming (Bhatta and Vetaas 2016; e.g. Matteodo et al. 2013; Parmesan and Yohe 2003; Sturm et al. 2001; Telwala et al. 2013).

The impact of climate change is likely to be both species specific and site specific (e.g. Chen et al. 2011; Lenoir et al. 2008; Telwala et al. 2013), making it difficult to determine the role played by climate in any changed scenario. The upslope shift for different species ranged from 586 to 787 m on the Chimborazo volcano in Ecuador over a 210-year period (Morueta-Holme et al. 2015); in the Engadine valley of Swiss Alps, more than 100 m upslope shift has been reported during the last nine decades (Frei et al. 2010) and 87 percent of 124 endemic plants species have expanded their range in Sikkim Himalaya during the last ca. 150 years (Telwala et al. 2013). The treeline has shifted upwards in Barun valley in central Himalaya in the last 130 years (Chhetri and Cairns 2015), and *A. spectabilis* has shifted upslope in Manaslu region, central Himalaya in the last ca. 160 years (Gaire et al. 2014).

Not all species, however, exhibit a range expansion or upward shift (565 species, Grytnes et al. 2014; 92 species, Zhu et al. 2012). For instance, vascular plant species were found to be tracking their environmental niche by shifting downhill because of decreased water availability in California, although average temperature increased (Crimmins et al. 2011). Climatic warming increases water stress by increasing evapotranspiration. In such cases, temperature rises without an increase in precipitation counteracts the expected effects of warming. *Picea crassifolia* was found to be translocated downhill when suffering from such a phenomenon on the southern Tibetan Plateau (Qiu 2015).

Land-use change has also been identified as a driver in species-range dynamics. For example, plant species may expand into abandoned agropastoral areas due to reduced herbivory (Sharma et al. 2014b; Speed et al. 2012). Gehrig-Fasel et al. (2007) show that the treeline is moving upwards in the Swiss Alps due to land-use change, and in the French Maurienne valley, the upper elevational limit of *Abies alba* shifted upslope by more than 300 m in 50 years after land abandonment (Chauchard et al. 2010). Herbivores suppress the growth, and kill or uproot seedlings that are thriving in the harsh treeline ecotone (Hofgaard 1997). Thus the density of herbivores affects the species range (Grytnes et al. 2014). Grazing in the treeline ecotone impacts the position of the treeline (Holtmeier and Broll 2007; Speed et al. 2010) and plant species limit (Speed et al. 2012).

The range dynamics of a treeline species under different land-use regimes can be tested in the high mountain areas of Nepal that has experienced climatic warming of 0.6 °C per decade since 1970 s (between 1971 and 1994, Shrestha et al. 1999; between 1982 and 2006, Shrestha et al. 2012). We selected sites representative of two land-use regimes: one with a history of limited land use that has not changed as a control and the other with reduced land-use intensity (RLI) to study the upper-range dynamics of *A. spectabilis* (D. Don) Spach.

The aims of this study were (i) to compare the upper species limit and the tree-limit dynamics in two contrasting land-use scenarios and (ii) to analyse regeneration within the treeline ecotone.

Methodology

Study areas

This study was carried out in two protected areas of Nepal, namely Manaslu Conservation Area (hereafter MCA; 84°39.50′E–84°41.81′E and 28°33.86′N–28°34.31′N) and Gaurishankar Conservation Area (henceforth GCA; 86°22.548′E–86°22.494′E and 27°53.865′N–27°53.914′N) (Fig. 1).

Climate

We used available climate data (1978–2009) from the nearest meteorological stations to the study areas. For the MCA, we used temperature data from Chame (2680 m a.s.l.; 28°33′N and 84°14′E; ca. 40 km west) and precipitation data from Larke Samdo (3650 m

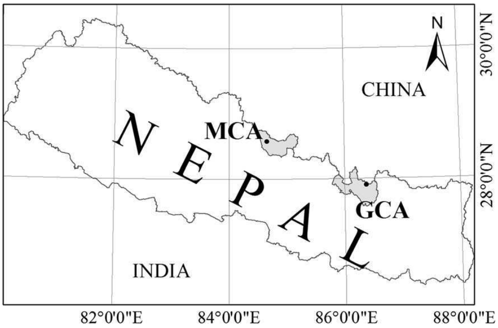


Fig. 1 *Black dots* indicate the transect locations in the two protected areas: three transects are located in MCA and one is located in GCA in Nepal

a.s.l.; 28°40′N and 84°37′E; ca. 8 km northwest). For the GCA, we used data for both precipitation and temperature from Jiri (2003 m a.s.l.; 27°38′N and 86°14′E; ca. 34 km south). Missing temperature and precipitation data were assigned the respective mean monthly values. Temperature data were extrapolated to treeline elevations assuming a mean annual lapse rate of 0.52 °C per 100 m elevation (Kattel et al. 2013). Temperature has been increasing at a rate of ca. 0.19 °C per decade in both the areas ($p < 0.05$) between 1978 and 2009. This warming rate is slower than the average warming in Nepal (between 1971 and 1994) (Shrestha et al. 1999) and in the Hindu Kush Himalayan region (between 1982 and 2006) (Shrestha et al. 2012).

Land use

In both our study areas, transhumance is still practiced, but in the GCA it does not affect the sampling area (Schickhoff et al. 2014). During summer, cattle herds are taken to the highland, while during autumn they are brought back to the lowland. In the MCA, land-use signs such as lopping, cut stumps, grazing, trampling and droppings were noticed. In the GCA, the practice of collecting dead tree branches and lopping signs were observed mainly in the dense forest at lower elevations. It is a near-natural or climatic treeline in this area (Müller et al. 2015; Schickhoff et al. 2014).

Vegetation

A. spectabilis is a coniferous tree species growing in cool temperate and subalpine regions in the central and western Himalayas. It forms monodominant forest and reaches a height of 50 m and trunk diameter of more than 1.5 m. Furrowed branchlets are densely leafy with yellowish grey, brown or reddish brown colour (eFloras 2008).

In the MCA, the lower part of the treeline ecotone is dominated by *A. spectabilis* and the upper part by *Betula utilis* and *Rhododendron* scrub. *Juniperus recurva*, *Rhododendron companulatum, R. anthopogon, R. lepidotum*, *Delphinium* spp. and *Berberis* spp. were also found in the forest of this area. In the treeline ecotone in the GCA, the lower part is dominated by *A. spectabilis* and the upper part by *Rhododendron* spp., *Betula utilis, Rhododendron campanulatum, R. anthopogon, R. lepidotum, Rosa sericea, Potentilla fruticosa* and *Berberis* spp. are found as co-occurring species.

Sampling

To be able to partially disentangle the effects of land-use intensity and climate change, we selected two study areas within the protected areas to circumvent contemporary high human disturbances. Then we filtered the areas based on the accessibility of the treeline ecotone.

One control transect was located in an area of negligible land use (transect GCA-1, control) and three transects (MCA-1, MCA-2, MCA-3) were located in an area which had undergone RLI. In all areas, we first looked for the uppermost individual (= Upper Species Limit, hereafter USL) in the treeline ecotone. Our horizontal search distance ranged from a few hundred metres to an 1800 m stretch of landscape. Transects were then drawn on the basis of the USL of *A. spectabilis* in a delimited area.

A transect of 20 m width running downhill towards the treeline [highest elevation of trees at least 2 m high in a patch comprising at least three individuals (Körner 2003)] was surveyed. From the treeline, a second half of the transect continued downhill into the forest. The second half of transect should ideally be as long as the first, but in two of the cases this was not possible due to topographical constraints.

Table 1 Elevational position of the upper species limit (USL), treeline, tree limit and calculation of the shift in upper species limit and tree limit

Transects	Transect length (m)	Position of treeline (m a.s.l.)	USL position (m a.s.l.)	Age of the oldest individual in transect	Position of the oldest individual (m a.s.l.)	Age of the uppermost individual	USL shift rate (m per decade)	Elevation of the uppermost tree (m a.s.l.)	Age of the uppermost tree	Tree-limit shift rate (m per decade)
MCA-1	265	3726	3841	51	3673	2	34	3749	15	21
MCA-2	173	3685	3753	106	3643	5	11	3727	20	10
MCA-3	570	3700	3929	237	3602	1	14	3718	35	4
GCA-1	102	3942	4001	153	3938	22	5	3951	29	1

Altogether four transects of variable lengths (see Table 1) were sampled. In each transect, trees (height ≥2 m), saplings (15–199 cm) and seedlings (≤15 cm) of *A. spectabilis* were recorded (Hofgaard and Rees 2008). Each tree was cored at the base of the tree using an increment borer (Haglöf, Sweden) to determine its age by counting the rings. The age of a sapling or seedling was estimated by the branch whorl count method (Camarero and Gutierrez 2004; Ninot et al. 2008). The height of each individual was measured. Elevation (±1 m accuracy, using a digital altimeter (Silva)), latitude and longitude (Garmin GPS) were recorded for all individuals.

Analysis

The USL shift rate (metre per decade) was calculated based on the elevation, and the age of the uppermost individual and the oldest individual occurring within the transect is given in the following equation:

$$\text{USL shift rate} = \frac{(\text{EUI} - \text{EOI})}{(\text{AOI} - \text{AUI})} \times 10, \qquad (1)$$

where EUI is the elevation of the uppermost individual; EOI the elevation of the oldest individual; AOI the age of the oldest individual and AUI is the age of the uppermost individual (modified method of Gamache and Payette 2005).

The tree-limit shift rate [the upper limit of woody plants ≥2 m tall (Wardle 1974)] (metre per decade) was calculated using the following equation:

$$\text{Tree limit shift rate} = \frac{(\text{EUT} - \text{EOI})}{(\text{AOI} - \text{AUT})} \times 10, \qquad (2)$$

where EUT is the elevation of the uppermost tree and AUT is the age of the uppermost tree.

Average shifting rate of ten individuals (metre per decade) was estimated using the following equation:

$$\text{Average shift rate} = \frac{(\text{AE}_{10}\text{UI} - \text{AE}_{10}\text{OI})}{(\text{AA}_{10}\text{OI} - \text{AA}_{10}\text{UI})} \times 10, \qquad (3)$$

where AE_{10}UI is the average elevation of 10 uppermost individuals; AE_{10}OI the average elevation of 10 oldest individuals; AA_{10}OI the average age of 10 oldest individuals and AA_{10}UI is the average age of 10 uppermost elevational individuals.

The regeneration of *A. spectabilis* was assessed with a histogram for different age groups expressed as individuals per hectare. We compared seedlings and saplings above and below the treeline in all transects in terms of density per hectare.

Results

Species limit shift

We found that the USL ranges from ca. 4000 to 3750 m a.s.l. (Table 1; Fig. 2) in our transects. The length of the transects varied from 102 to 570 m, and the number of individuals per unit area also varied between the transects. The average USL and tree-limit shift rates in the RLI area were ca. 20 and 12 m per decade, respectively. In the control area with a climatically controlled treeline, the rate of USL shift was much less, only ca. 5 m per decade, and effectively nil for the tree-limit shift. The average of ten individuals had a shift rate in the RLI area of about

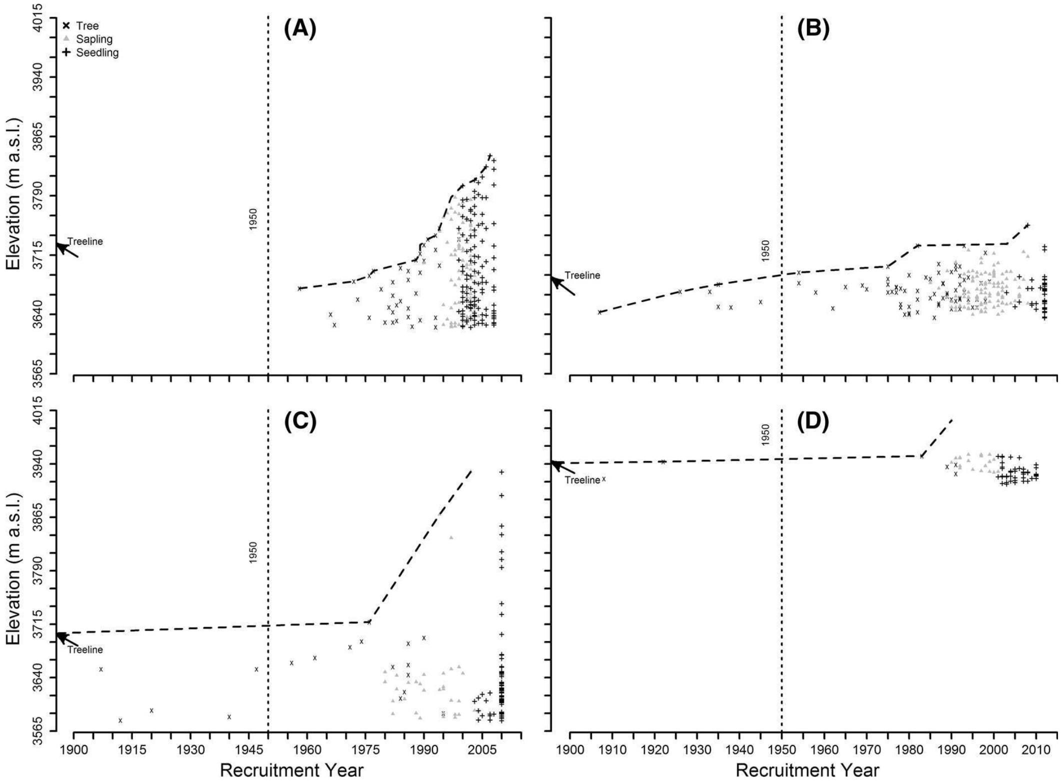


Fig. 2 *Scatter plots* of recruitment year and elevation for seedlings, saplings and trees in each of the four transects [*A* MCA-1, *B* MCA-2, *C* MCA-3 (reduced land-use intensity), *D* GCA-1 (no land-use change)]. The *dashed lines* show the upper species limit. The *arrow* indicates the position of the current treeline position and the *vertical lines* mark 1950 for comparison before and after 1950. Note: For better illustration of the plots, we hide five points in subplot *C* and two points in subplot *D* before 1900 AD

Table 2 Shift of *A. spectabilis* based on mean of 10 uppermost and oldest individuals

	Average of 10 uppermost individuals		Average of 10 oldest individuals		Vertical shift (m)	Rate of shift (m per decade)
	Elevation	Age	Elevation	Age		
MCA-1	3816	4	3660	37	156	47
MCA-2	3726	12	3665	74	60	10
MCA-3	3858	5	3624	116	235	21
GCA-1	3956	15	3945	62	11	2

26 m per decade and in the control area the shift was only ca. 2 m per decade (Table 2).

Regeneration and density in treeline ecotone

The age–frequency histogram is left skewed or inverse-J shaped (Fig. 3), except in one transect in Manaslu (MCA-1), implying a high density of seedlings and saplings. The density of seedlings and saplings was higher below the treeline (Fig. 4). The seedling density above the treeline was ca. 83 and ca. 19 individuals ha^{-1} in the RLI and control areas, respectively, while below the treeline it was ca. 301 and 800 individuals ha^{-1}. Similarly, the sapling density above the treeline was ca. 110 and 76 individuals ha^{-1}, while below the treeline it was ca. 245 and 150 individuals ha^{-1} in the RLI and control areas, respectively.

Discussion

The treeline in the eastern location (GCA) is at a higher elevation than in the western part (MCA), which matches the geographical trend in the Himalaya (Mani 1974; Miehe et al. 2015). All four treelines almost coincide with the 10 °C isotherm of the warmest month as noted by Körner (2003) and Holtmeier (2009).

We find that the USL has ascended between 63 and 327 m at the different sites, consistent with other studies in the Himalaya (Gaire et al. 2014; cf. Telwala et al. 2013). The shift rate was calculated based on two individuals in each transect and may differ from the average for the whole landscape. The USL is not static but very dynamic due to the uncertainty of lethal events at an early life stage. It records extreme events experienced by each individual rather than the average response to climate change (Kreyling et al. 2012). In an attempt to compensate for this, we used the mean measurements of 10 individuals to provide a more general expression. The mean shift rate of 10 individuals was ca. 26 m per decade in the RLI area, while it was nearly static in the control area (ca. 2 m per decade). This indicates no significant change because two metres is within the error in the estimation of elevation.

We find that the species population has expanded in the RLI area, a finding confirmed by the local people. Species are colonising new areas in the mountains and

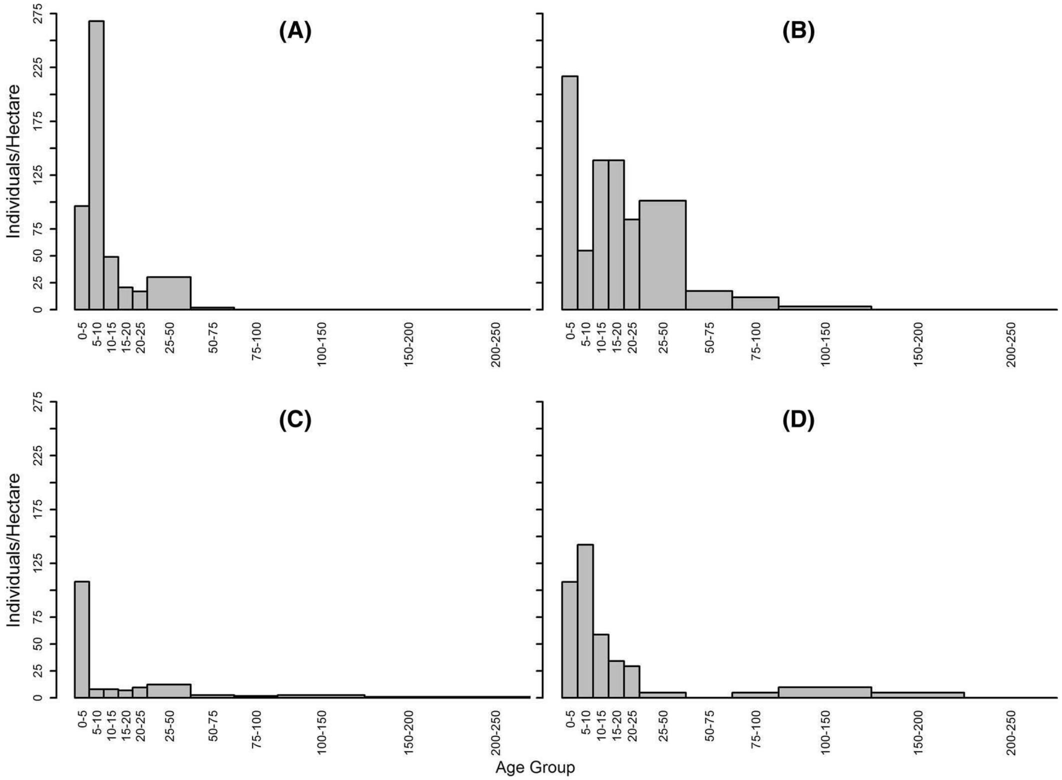
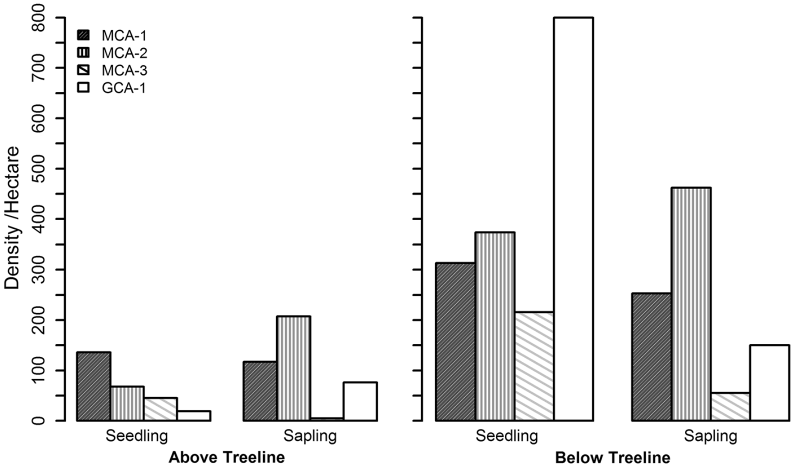


Fig. 3 Age–frequency histograms for each transect (*A* MCA-1, *B* MCA-2, *C* MCA-3 [with reduced land-use intensity), *D* GCA-1 (no land-use change)]. The *histograms* show an inverse-J shape except for MCA-1. Note: The sizes of age group class and *bar width* are increased with age

Fig. 4 Comparative illustration of seedling and sapling density (individuals ha^{-1}) above and below the treeline in all four transects (MCA transects are with reduced land-use intensity, while GCA is a control with no land-use change)



moving upslope. In the control area, however, there were only a few individuals above the treeline. The uppermost individual was recruited in 1990 and was isolated from the rest of the population. There were no other individuals of *A. spectabilis* until close to the treeline. A similar pattern was observed in the Barun valley in central Himalaya for the same species (Chhetri and Cairns 2015). Establishment of new seedlings of *A. spectabilis* in the control area may be inhibited by the monotonous thick *Rhododendron* scrub above the treeline (Baker and Van Lear 1998), and there may be an allelopathic effect (Fisher 1980; Nilsen et al. 1999) and light control (Clinton and Vose 1996) from the *Rhododendron.* The ground was almost devoid of herbaceous vegetation, indicating that it would not be easy for species to establish here.

The regeneration study clearly shows that there were many young individuals along our transects. We recorded, on an average, higher numbers of saplings along the RLI transects than along the control transect, suggesting that some level of disturbance provided opportunities for sapling growth (Vetaas 1997). The inverse-J-shaped age–frequency histograms (Fig. 3) depict that *A. spectabilis* was maintaining a sustainable population in the treeline ecotone. The density of seedlings was, as expected, higher than the density of saplings. The MCA-3 transect went through very frequent anthropogenic disturbances and only few individuals had opportunity to survive to mature age. The intense disturbances are also depicted by lower density of saplings and trees in this transect. For all our transects, we see that the densities of seedlings and saplings were higher below the treeline than above. This is in line with other studies (Ninot et al. 2008; Shrestha et al. 2007), although it contrasts with findings from Bell et al. (2014) who note an upshift of range for juveniles and from Shrestha et al. (2014) who found more seedlings of *A. spectabilis* above the treeline in Laurebinayak area in Langtang National Park, Nepal. There could be many factors to cause these patterns, such as orography, soil moisture, pH, community interaction and chance events; some are likely to be quite site specific.

Our comparison of the USL and tree-limit shift between a control area and an area of reduced land-use intensity shows that a greater shift rate occurred in the area with reduced land use. The type of land-use practice has not changed, i.e. transhumance, husbandry, agroforestry and grazing, but the intensity has reduced substantially due to outmigration of local people (CBS 2014; Bal Kumar 2003; Sharma et al. 2014a). In contrast, there has been no discernible shift of the tree limit in the control area (a change of 1 m is less than the error in the estimation of elevation). There has been a slight shift in the USL of ca. 5 m per decade, but this estimate is based on only two individuals. Reduced land-use intensity is therefore the most likely driver of range expansion in the MCA. The small increase in average atmospheric temperature has not yet impacted species distribution in this ecotone, although it has been noted in other regions (Matteodo et al. 2013; Parmesan and Yohe 2003;

Telwala et al. 2013). However, reduced intensity of land use (Müller et al. 2015) may also have synergistic effects with increased warming in the RLI area (Morueta-Holme et al. 2015).

Comparing the trends of the USL of the four transects (Fig. 2), it can be seen that the limit has increased at all sites. In the eastern Himalaya, Telwala et al. (2013) reported 87 % of endemic plants (out of 124 species) shifted upslope in response to a temperature rise in mean summer temperature of 0.76 and 3.65 °C in mean winter temperature. Over the last nine decades, an average upslope shift of 145 m was reported in Engadine valley of Swiss Alps (Frei et al. 2010) and in the last half century a 70 m elevational shift in the Montseny Mountains (Catalonia, NE Spain) was reported (Penuelas et al. 2007) as a response to global warming.

In the last 50 years the local mean annual temperature has increased by about 1 °C based on data from the nearest meteorological station. To track this warming, species are predicted to need to move upslope by about 192 m, equivalent to 38 m per decade. The analysis of our species demonstrates that it is lagging behind the recent warming. Projected climatic warming for 2081–2100 is 1.0–3.7 °C higher than the 1986–2005 normal (IPCC 2014), so a shift of between about 24–90 m per decade would be required for species to maintain their current climatic niche. However, a species' ability to respond is affected by local geomorphic processes (Macias-Fauria and Johnson 2013), grazing (Speed et al. 2012) and community interactions such as dense grassland (Rehm and Feeley 2015). Based on the predicted required shifts, it seems that the species will not be able to track the projected warming which may cause them to lose their potential habitat (Engler et al. 2011; Svenning et al. 2008) and reduce their population size (Feeley and Silman 2010).

Conclusions

In an area of reduced land-use intensity, we document the growth of *A. spectabilis* at higher elevations than the estimated upper species limit and tree limit for earlier years. The slight increase in mean annual temperature has not yet prompted a noticeable response in the species. The rate of upward shift is site specific and appears to increase after 1950.

Acknowledgments Our sincere thanks are due to Lila Nath Sharma, Kuber Prasad Bhatta, Man Kumar Dhamala, Kumar Prasad Mainali, Khem Raj Bhattarai, Raj Kumar Gautam, Mandhata Acharya, Narayan Prasad Gaire and Rosy Makaju who helped with suggestions, comments and field sampling. We acknowledge IDEA WILD, the Central Department of Botany (Tribhuvan University), the Department of National Parks and Wildlife, the National Trust for Nature Conservation, Nepal Academy of Science and Technology, Nepal Climate Change Knowledge Management Center (NAST-CDKN/NCCKMC), Norad's Programme for Master Studies and the University of Bergen for their support.

References

Baker TT, Van Lear DH (1998) Relations between density of rhododendron thickets and diversity of riparian forests. Forest Ecol Manag 109:21–32. doi:10.1016/S0378-1127(98)00259-X

Bal Kumar KC (2003) International migration in Nepal. In: Population monograph of Nepal. Central Bureau of Statistics, National Planning Commission, Kathmandu

Bell DM, Bradford JB, Lauenroth WK (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Glob Ecol Biogeogr 23:168–180

Bhatta KP, Vetaas OR (2016) Does tree canopy closure moderate the effect of climate warming on plant species composition of temperate Himalayan oak forest? J Veg Sci. doi:10.1111/jvs.12423

Camarero JJ, Gutierrez E (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Clim Change 63:181–200. doi:10.1023/B:Clim.0000018507.71343.46

CBS (2014) National Population and Housing Census 2011: social characteristics tables. Part VI, vol 5. Central Bureau of Statistics, National Planning Commission, GoN, Kathmandu

Chauchard S, Beilhe F, Denis N, Carcaillet C (2010) An increase in the upper tree-limit of silver fir (Abies alba Mill.) in the Alps since the mid-20th century: a land-use change phenomenon. For Ecol Manag 259:1406–1415

Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026. doi:10.1126/science.1206432

Chhetri PK, Cairns DM (2015) Contemporary and historic population structure of *Abies spectabilis* at treeline in Barun valley, eastern Nepal Himalaya. J Mt Sci 12:558–570

Clinton BD, Vose JM (1996) Effects of *Rhododendron maximum* L. on *Acer rubrum* L. seedling establishment. Castanea 61:38–45

Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science 331:324–327

eFloras (2008) Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA. www.efloras.org. Accessed 18 May 2016

Engler R et al (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Change Biol 17:2330–2341

Feeley KJ, Silman MR (2010) Land-use and climate change effects on population size and extinction risk of Andean plants. Glob Change Biol 16:3215–3222

Fisher RF (1980) Allelopathy: a potential cause of regeneration failure. J For 78:346–350

Frei E, Bodin J, Walther GR (2010) Plant species' range shifts in mountainous areas-all uphill from here? Bot Helv 120:117–128. doi:10.1007/s00035-010-0076-y

Gaire NP, Koirala M, Bhuju DR, Borgaonkar HP (2014) Treeline dynamics with climate change at the central Nepal Himalaya. Clim Past 10:1277–1290. doi:10.5194/cp-10-1277-2014

Gamache I, Payette S (2005) Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. J Biogeogr 32:849–862. doi:10.1111/j.1365-2699.2004.01182.x

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? J Veg Sci 18:571–582

Grytnes J-A et al (2014) Identifying the driving factors behind observed elevational range shifts on European mountains. Glob Ecol Biogeogr 23:876–884. doi:10.1111/geb.12170

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol Lett 12:1040–1049. doi:10.1111/j.1461-0248.2009.01355.x

Hofgaard A (1997) Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. Glob Ecol Biogeogr Lett 6:419–429

Hofgaard A, Rees G (2008) Common protocols for field measurements and handling of collected materials. PPS Arctic Group, Tromsø

Holtmeier F-K (2009) Mountain timberlines: ecology, patchiness, and dynamics, vol 36. Springer, New York

Holtmeier F-K, Broll G (2007) Treeline advance–driving processes and adverse factors. Landsc Online 1:1–33

IPCC (2014) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. Intergovernmental panel on climate change, Geneva

Kattel D, Yao T, Yang K, Tian L, Yang G, Joswiak D (2013) Temperature lapse rate in complex mountain terrain on the southern slope of the central Himalayas. Theor Appl Climatol 113:671–682

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

Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. J Biogeogr 31:713–732

Kreyling J et al (2012) Cold hardiness of Pinus nigra Arnold as influenced by geographic origin, warming, and extreme summer drought. Environ Exp Bot 78:99–108

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771. doi:10.1126/science.1156831

Leonelli G, Pelfini M, di Cella UM, Garavaglia V (2011) Climate warming and the recent treeline shift in the European Alps: the role of geomorphological factors in high-altitude sites. Ambio 40:264–273

Macias-Fauria M, Johnson EA (2013) Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. Proc Natl Acad Sci 110:8117–8122

Mani M (1974) Ecology and biogeography in India. Dr. W. Junk B.V., The Hague. doi:10.1007/978-94-010-2331-3

Matteodo M, Wipf S, Stöckli V, Rixen C, Vittoz P (2013) Elevation gradient of successful plant traits for colonizing alpine summits under climate change. Environ Res Lett 8:024043

Miehe G, Pendry CA, Chaudhary RP (2015) Nepla: an introduction to the natural history, ecology and human environment of the Himalayas. Royal Botanic Garden Edinburgh, Edinburgh

Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas JD, Segnitz RM, Svenning J-C (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. In: Proceedings of the National Academy of Sciences: 201509938

Müller M, Böhner J, Chaudhary R, Drollinger S, Schickhoff U, Scholten T (2015) How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal. Prog Phys Geogr

Nilsen ET, Walker JF, Miller OK, Semones SW, Lei TT, Clinton BD (1999) Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): could allelopathy be a cause? Am J Bot 86:1597–1605

Ninot JM, Batllori E, Carrillo E, Carreras J, Ferre A, Gutierrez E (2008) Timberline structure and limited tree recruitment in the Catalan Pyrenees. Plant Ecol Divers 1:47–57. doi:10.1080/17550870802260764

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. doi:10.1038/Nature01286

Penuelas J, Ogaya R, Boada M, Jump AS (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30:829–837

Qiu J (2015) High-altitude forests in the Himalayas harder hit by droughts. Why are plateau and mountain timberlines in Asia shifting downslope, despite global warming?, vol 2015. Scientific American Division of Nature America Inc, Berlin

Rehm EM, Feeley KJ (2015) The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. Ecography 38:1167–1175

Resler LM (2006) Geomorphic controls of spatial pattern and process at alpine treeline. Prof Geogr 58:124–138. doi:10.1111/j.1467-9272.2006.00520.x

Schickhoff U (2005) The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. Springer Verlag, Berlin-Heidelberg-New York

Schickhoff U et al (2014) Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators. Earth Syst Dyn Discuss 5:1407–1461

Sharma LN, Vetaas OR, Chaudhary RP, Måren IE (2014a) Ecological consequences of land use change: forest structure and regeneration across the forest-grassland ecotone in mountain pastures in Nepal. J Mt Sci 11:838–849

Sharma LN, Vetaas OR, Chaudhary RP, Måren IE (2014b) Pastoral abandonment, shrub proliferation and landscape changes: a case study from Gorkha, Nepal. Landsc Res 39:53–69

Shrestha AB, Wake CP, Mayewski PA, Dibb JE (1999) Maximum temperature trends in the Himalaya and its vicinity: an analysis based on temperature records from Nepal for the period 1971-94. J Clim 12:2775–2786. doi:10.1175/1520-0442(1999)012<2775:Mttith>2.0.Co;2

Shrestha BB, Ghimire B, Lekhak HD, Jha PK (2007) Regeneration of treeline birch (*Betula utilis* D. Don) forest in a trans-Himalayan dry valley in central Nepal. Mt Res Dev 27:259–267. doi:10.1659/mrdd.0784

Shrestha UB, Gautam S, Bawa KS (2012) Widespread climate change in the Himalayas and associated changes in local ecosystems. PLoS One 7:e36741. doi:10.1371/journal.pone.0036741

Shrestha KB, Hofgaard A, Vandvik V (2014) Recent treeline dynamics are similar between dry and mesic areas of Nepal, central Himalaya. J Plant Ecol: rtu035

Speed JD, Austrheim G, Hester AJ, Mysterud A (2010) Experimental evidence for herbivore limitation of the treeline. Ecology 91:3414–3420

Speed JDM, Austrheim G, Hester AJ, Mysterud A (2012) Elevational advance of alpine plant communities is buffered by herbivory. J Veg Sci 23:617–625. doi:10.1111/j.1654-1103.2012.01391.x

Sturm M, Racine C, Tape K (2001) Climate change—increasing shrub abundance in the Arctic. Nature 411:546–547. doi:10.1038/35079180

Svenning JC, Normand S, Skov F (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. Ecography 31:316–326

Telwala Y, Brook BW, Manish K, Pandit MK (2013) Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. PLoS One 8:e57103. doi:10.1371/journal.pone.0057103

Vetaas OR (1997) The effect of canopy disturbance on species richness in a central Himalayan oak forest. Plant Ecol 132:29–38

Wardle P (1974) Alpine timberlines. Arctic and alpine environments. Methuen, London, pp 371–402

Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. Glob Change Biol 18:1042–1052

Paper II

Climatic variables determining *Rhododendron* sister taxa distributions and distributional overlaps in the Himalayas

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F59334911

RESEARCH ARTICLE

Climatic variables determining *Rhododendron* sister taxa distributions and distributional overlaps in the Himalayas

Madan Krishna Suwal* and Ole R. Vetaas

Department of Geography, University of Bergen, Fosswinckelsgt. 6, P B 7802, N - 5020 Bergen, Norway
*Corresponding author:
madan.suwal@uib.no;
madanksuwal@gmail.com

Abstract. Endemic species in mountains are vulnerable to rapid climate change. We elucidated distributional overlaps and related climatic variables for two endemic sister taxa of *Rhododendron* and a generalist with respect to current and future climate conditions. Our research questions are: (i) Which climate factors separate the distributions of *Rhododendron cowanianum, R. lepidotum* and *R. lowndesii*? (ii) How large is the geographic overlap in current and future distributions? (iii) Is it likely that the species are able to track their niches in the future? To answer these questions, we performed species distribution modelling on binomial *Rhododendron* occurrences accompanied by random pseudo-absences and absences constrained by other *Rhododendron* taxa. We used Generalized Linear Modelling to select variables, and modelled the distribution of each species using Random Forest algorithms, predicting their potential distribution in current and future climates. We also examined range differences to identify the variables segregating the distribution of these sister taxa, and estimated current and future distributional overlap between and within species. Precipitation variables explained *R. lowndesii* distribution, whereas temperature variables explained distributions of the other two species. We found that sister taxa have similar climate niche and hence high overlap in geographic distribution in current climate (46–68%) and potentially in future climate (53–77%). Under future climate conditions, the potential distribution area of *R. lepidotum* and *R. cowanianum* is predicted to be at a higher elevation, while the prediction for *R. lowndesii* is similar to its current geography. Our models suggest that there are more potential distribution areas for these narrowly distributed endemic species than are currently occupied, which illustrates that it is rather uncertain whether the *Rhododendron* species will be able to track the geographical location of their niches in the future.

Keywords. Climate change, Himalaya, Nepal, Pseudo-absences, Random Forest, *Rhododendron*, Species Distribution Models, Species range shift

Introduction

Climate change affects species distributions (Parmesan and Yohe 2003), and species with a restricted distribution may be more vulnerable to the changes in climatic factors that determine the boundaries of their distributions (Thuiller et al. 2005, Manish et al. 2016). Understanding the extent to which a geographical range shift is needed for species to be able to track their climate niche in response to climate change is currently a crucial scientific task. Several organisms have already shifted their range margins (Parmesan and Yohe 2003, Telwala et al. 2013). These findings are underpinned by paleo-ecological data indicating that geographical range shifts were common during previous episodes of climate change (Willis and MacDonald 2011).

The magnitude of projected climatic change is large at high elevations and high latitudes (Pachauri et al. 2014). For species in the mountains, it is easier to track their climate niche than species in flat terrains because the speed of spatial climate change is slower in the mountains (Loarie et al. 2009). In addition, many species with a restricted distribution in the mountains have relatively wide climate niches compared to species with restricted distributions in flat terrains. However, both types of species have a high risk of extinction if climate change develops novel interactions between precipitation and temperature (Williams and Jackson 2007).

In general, most species are adapted to address variations in climate, but some species that are endemic to a mountain range or a mountain peak are more vulnerable to extinction (Thuiller et al. 2005, Manish et al. 2016) and are particularly vulnerable to climate change if they have dispersal limitations (Manish et al. 2016). Mountain features may increase dispersal limitations due to steeper environmental gradients, heterogeneous microhabitats and isolation mechanisms, such as sky islands, which support a large number of unique and endemic species (Steinbauer et al. 2016). In addition, the extinction of endemic species is a global process, rather than just the loss of one metapopulation (Malcolm et al. 2006).

Although the spatial distance between different climate types is short in the mountains, it is not certain that the current combination of different climatic variables will actually exist in the future. Therefore species' survival is not guaranteed if they cannot keep pace with the climate as they move (Pearson 2006). The steady increase in mean annual temperature interacts with precipitation and the timing of the growing season, which is rather short in high mountains. The species-specific responses to warming in the mountains will also pose new challenges, such as competition with new species (Williams and Jackson 2007) or a lack of essential vectors for pollination or seed dispersal (Hobbs et al. 2006, Abrol 2012).

In the Himalayan region, the disappearance of current climate conditions and the development of a novel climate is expected (Williams and Jackson 2007) including an increase in the total amount and intensity of the precipitations with a reduced number of rainy days (Pendergrass and Hartmann 2014). In such conditions, the dry season becomes drier and species are found to move downwards against the direction of warming to track their precipitation niche (Crimmins et al. 2011, Qiu 2015). The species-specific responses and pace of migration may promote novel species assemblages and interactions that can lead to uncertain consequences (Hobbs et al. 2006). In this context, the conventional conservation approaches that aim to conserve representative communities or vegetation types may be ineffective (Hannah et al. 2002). This is mainly because the idea of representative communities is rooted in plant phytosociology, which assumes that the plant community responds to climate change as a unit and not as each individual species (Gleason 1926). This view of nature will be challenged by climate change (Hobbs et al. 2006, Williams and Jackson 2007), and future dynamic conservation approaches will have to focus on individual species because each species may respond to the ongoing changes differently (Parmesan and Yohe 2003, Telwala et al. 2013).

Breshears et al. (2008) describe three possible ways of species range shifting in response to climate change; they are 'march' (defined as, range shift by colonizing leading edge, a shift in optimum and retraction at tailing edge), 'lean' (a stable range with the optimum shifting within the existing range) and 'crash' (population decline with stable edges and optimum). As such, it is important to focus on species with narrow elevational ranges and restricted geographic distributions because these specialist species will have higher risks of extinction due to their small populations and narrow ranges.

Species Distribution Models (SDMs) are being used to predict potential spatial and temporal distribution of species (Thuiller et al. 2005, Randin et al. 2006) although their relative success when transferred to future conditions is at stake (Araújo and Rahbek 2006). Species distribution shifts are mostly studied within a single taxon, between sister or descendent taxa and within communities (Thuiller et al. 2005, Mao and Wang 2011). Sister taxa are assumed to have common ancestors and are therefore expected to show some degree of niche overlap because niches are, to some extent, conserved within a clade (Wiens and Graham 2005, Losos 2008) while maintaining some distinctions among themselves (Cavender-Bares et al. 2004).

In the Himalayan region, studies on niches, distribution overlaps and shifts of sister taxa are rare (but see Vetaas 2002). We address this gap by studying *Rhododendron* sister taxa from the central Himalayas. The target sister taxa belong to the subgenus *Hymenanthes*, subsection *Lepidota*. One species has a wide distribution from the western and the eastern Himalayas to China (*R. lepidotum* Wall), whereas the two other species have restricted distributions in the central Himalayas (Nepal: *R. cowanianum* Davidian and *R. lowndesii* Davidian).

Here we seek to address: (i) Which climate factors separate the distributions of closely related *R. cowanianum, R. lepidotum* and *R. lowndesii* species? (ii) How large are the current geographic overlaps between them and what will their potential overlap under future climatic conditions? (iii) Is it likely that the species are able to track their niches in new geographic areas?

Methodology

Study area

This study was carried out within the distribution range of the genus *Rhododendron* across Nepal in the central Himalayas. The study area ranges from 80.0015°E to 88.3373°E and 26.3255°N to 30.4688°N (Fig. 1).

Taxa

Members of the genus *Rhododendron* L. (Ericaceae) are phanerophytes, i.e., shrubs or medium-sized trees. *Rhododendron* has a wide temperature range, from warm temperate zones to alpine bioclimatic zones. There are 43 lower taxa of *Rhododendron* in Nepal between approximately 900 m and 5600 m above sea level (a.s.l.) (www.efloras.org). The *Lepidota* (Hutchinson)

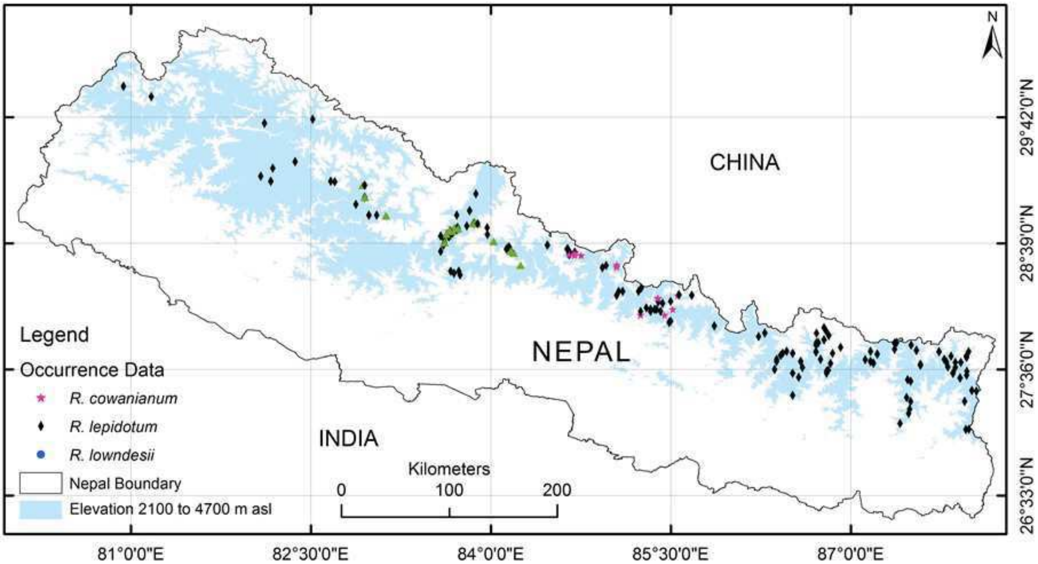


Figure 1. Study area map depicting an elevation range of three Rhododendron sister taxa (2100 to 4700 m a.s.l. with light blue colour) and their recorded presence locations with different symbols.

Sleumer subsection of the genus *Rhododendron* includes three sister taxa, *R. lepidotum* Wall, *R. cowanianum* Davidian, and *R. lowndesii* Davidian, which are distributed between approximately 2100–4700 m a.s.l. in Nepal[1]. Among these, the latter two are rare and endemic to Nepal (Rajbhandari et al. 2016).

Occurrence data

We compiled occurrence data from the National Herbarium and Plant Laboratories, Kathmandu, Nepal, the Royal Botanic Gardens Edinburgh, UK, the Tokyo Herbarium, Japan, the Global Biodiversity Information Facility[2], and from field sampling. Initially, we recorded 25, 420 and 46 presence data for *R. cowanianum*, *R. lepidotum* and *R. lowndesii* respectively. Among the collected occurrence points, we filtered out some points with high uncertainty. First, we excluded points with a very crude accuracy of the location, i.e. latitudinal and longitudinal values with less than three digits after decimal place (number of points removed: 6 points for *R. cowanianum,* 37 for *R. lepidotum*, and 6 for *R. lowndesii*). Secondly, we omitted specimens with elevation below 900 m and above 5600 m a.s.l. as they were more than 1000 m below or above the lowest and highest record of the *Rhododendron* species concerned[1]. This yielded 19 presence points for *R. cowanianum,* 271 for *R. lepidotum* and 40 for *R. lowndesii.*

Pseudo-absence data

Most SDMs and niche models are based on presence-absence data. However, species data are mostly composed only of recorded presences. In such cases, absences are complemented by pseudo-absence data for environmental information (Elith et al. 2011). There is no consensus on how to generate the best pseudo-absence data, and most studies use the random pseudo-absence method, which is equal to or better than other methods (Barbet-Massin et al. 2012). We used two different methods to generate 'pseudo-absences' to test which one would perform better. The first approach was to use the presence points for all *Rhododendron* species in Nepal except the target species as absence points combined with the presence of the target species (hereafter; "Rhododendron pseudo-absences" = "RhoPs"). The approach constrains the pseudo-absence points to be within the climatic envelope of the genus, thereby avoiding "naughty noughts" placed far outside the potential climate range (Austin and Meyers 1996). This kind of pseudo-absences has been used for *Eucalyptus* in Australia and *Rhododendron* in Nepal (e.g., Austin et al. 1990, Vetaas 2002). Among the collected occurrence points, we filtered out some points with high uncertainty using the two-step filter described in the previous section. With this method we obtained 890 *Rhododendron* pseudo-absences. The second approach was to use randomly generated equal numbers of pseudo-absences combined with presence data (hereafter; "Random pseudo-absences" = "RanPs") within the same elevational range.

Predictor variables

We used 22 water and energy related predictor variables, including 19 bioclimatic variables from the WorldClim[3] dataset (Hijmans et al. 2005), Annual BioTemperature (ABT; Holdridge 1947), Ellenberg's Climatic Quotient (EQ; Ellenberg 1963) and the Relative Radiation Index (RRI; Oke 1987). All climatic data required for preparing the ABT and EQ were taken from the WorldClim dataset (method details in Supplementary Material S1). All predictor variables were in a 30 arc-second resolution and the same coordinate system (WGS 1984), and can be made available upon request to the authors.

We prepared two groups of variables from the original set of 22. The first group was composed of all variables (hereafter the "set I" variables) and the second group was prepared by selecting a few effective variables from a Generalized Linear Model (GLM) using the bidirectional (forward and backward) selection method in R package *stats* (R Core Team 2016). Then, we

---

1 Based on http://www.efloras.org
2 http://www.gbif.org
3 http://www.worldclim.org

dropped the non-significant variables. For RanPs this yielded 9, 10 and 6 variables for *R. cowanianum, R. lepidotum* and *R. lowndesii*, respectively, and for RhoPs 12, 10 and 7 (Supplementary Material S2), (hereafter the "set II" variables). The optimum GLM models (set II variables) were partitioned to obtain the deviance explained by temperature and precipitation related variables using the R-package *ecospat* (Broennimann et al. 2016).

Future climatic scenario

We used the Intergovernmental Panel on Climate Change's (IPCC) most extreme future prediction (worst-case scenario), Representative Concentration Pathway 8.5 (RCP8.5) for our future climatic scenario because when we look at last few years, it is hard to be optimistic that the world's countries will succeed in limiting the warming to 2°C by the end of the 21st century (UNFCCC 2015), especially as recent monthly mean temperatures and annual mean temperatures have broken previous records (GISTEMP Team 2016).

The RCP8.5 projects 2.6°C to 4.8°C warming by 2081 to 2100 compared to the 1986 to 2005 baseline (Collins et al. 2013). We took the average of five different downscaled General Circulation Models, namely the ACCESS1-0, BCC-CSM1-1, GISS-E2-R, MIROC-ESM-CHEM, and MPI-ESM-LR models, to reduce model-derived biases. We predicted our results for only one worst-case scenario and for a single future period in the 2070s (average of 2060 to 2080).

The values of the predictor variables that were in raster format were extracted to the presence, rhododendron pseudo-absence, random pseudo-absence and lattice files (regular grid points of 3 km resolution above 900 m a.s.l.) for current climate and future climate in ArcGIS 10.3 (ESRI).

Distribution modelling and variable range difference analyses

To answer the first research question, which climatic factors segregate the closely related three *Rhododendron* sister taxa, Tukey's Honesty Significant Difference (HSD) post hoc test was used to identify the difference in range for all 22 variables for each species using R package *stats* (R Core Team 2016). Species distribution models were prepared to predict the potential distribution of species in current and future climate using the Random Forest method (Breiman 2001). The predictions were portrayed into geographic space to analyse the overlaps between species. The Random Forest method was used among different techniques because it can handle multiple variables regardless of their eventual multicollinearity, low numbers of presence points and different prevalence ratios (Elith et al. 2011, Barbet-Massin et al. 2012). All analyses were performed in the R package *RandomForest* (Liaw and Wiener 2002).

In the Random Forest method, we fitted models on RanPs and RhoPs with the set I and set II variables. The datasets were partitioned at 3:7 ratios for test and training datasets. We grew 2000 trees, as growth appeared to stabilize by 1000 – 1500 trees. The model was replicated five times. Each time, we evaluated the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) value. Important variables are listed based on their Mean Decrease Gini in Random Forest. Predictions of the relative index of occurrence (RIO) of species were made from each replicate of models on current climate and future climate lattice files. Then average RIO was calculated from five predictions. The predicted RIO value ranges from 0 to 1; where a higher value refers to more suitability of the location. At the end, we had a total of 24 different predictions. Then, RIO raster maps for each species were prepared by interpolating the average RIO using the Inverse Distance Weighted tool in ArcGIS 10.3 (ESRI). This raster was converted to ASCII format to be fed into the distributional overlap study.

Distribution overlap analysis

To answer the second research question, we studied the predicted distribution overlap between species using *ENMTools* (Warren et al. 2008) with three different available methods, including Schoener's *D*, *I* statistics and Relative Rank (*RR*), for both current and future climates. Then, we compared the predicted distributional overlaps based on the average of the three methods. The value ranges from 0 (no overlap at all) to 1 (complete overlap).

Geographic shift of climatic niche

To analyse the geographic shift of climatic niches of three *Rhododendron* species, i.e. the third research question, the predicted average RIO values of the lattice points were plotted against elevation for the current and future projected climate for each species, and the shift was analysed graphically as it could not be quantified because we did not convert the RIO into a binary value. We plotted the points with RIO above or equal to 0.02 for better illustration.

Effects of environmental dimension reduction analysis

The models with the set I and set II variables with RanPs and RhoPs were compared based on the AUC value and ROC curve plots in order to figure out the effect of dimension reduction in models. Then, the differences between their predictions were tested in *ENMTools*. In this analysis, the value ranges from 0 (complete dissimilarity) to 1 (total identical).

Results

Variables segregating species distributions

All but two temperature variables had similar ranges for the three species. Out of 22 variables, *R. lepidotum* had five variables' ranges that were significantly different from *R. lowndesii*, while the ranges of six variables were significantly different between *R. lepidotum* and *R. cowanianum*, and the ranges of five variables were significantly different between *R. lowndesii* and *R. cowanianum* (Fig. 2 and Supplementary Material S3). Mean temperature of the driest quarter (bio09) and precipitation of the driest quarter (bio17) were significantly different between *R. lowndesii* and both of the other species (Fig. 2). A two-dimensional niche plot of these variables (Fig. 3), showed a higher overlap of the generalist *R. lepidotum* and both endemic sister taxa, while *R. lowndesii* and *R. cowanianum* had smaller overlaps.

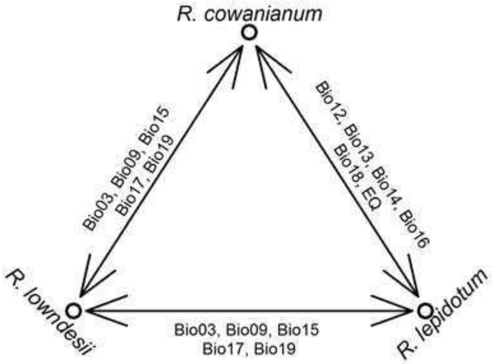


Figure 2. Climate variables that were significantly different between the realized distributions of the three species. Variable acronyms correspond to isothermality (bio03), mean temperature of the driest quarter (bio09), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (coefficient of variation) (bio15), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), precipitation of the coldest quarter (bio19) and Ellenberg Climatic Quotient (EQ).

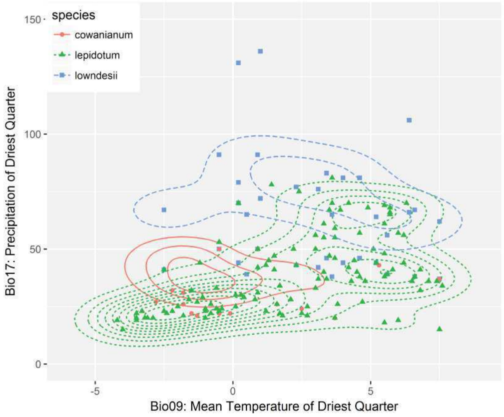


Figure 3. 2-Dimensional niche plot between mean temperature of the driest quarter (bio09) and precipitation of the driest quarter (bio17) for all three sister taxa (*R. cowanianum*, *R. lowndesii* and *R. lepidotum*). It depicts higher overlap of *R. lepidotum* climatic niche with *R. cowanianum* than with *R. lowndesii*.

Table 1. The most important variables for explaining the distributions of three *Rhododendron* species. Results from the model with presence data with random pseudo-absences using set I and set II variables.

Importance Rank Number	**All Variables (set I)**			**GLM selected variables (set II)**		
	R. cowanianum	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
1	EQ	bio03	bio13	bio15	bio03	bio13
2	bio17	bio19	bio18	ABT	bio08	bio18
3	bio16	ABT	EQ	bio19	bio01	EQ
4	bio19	bio08	bio16	bio09	bio19	bio12
5	bio18	EQ	bio15	bio06	bio10	bio09

Variable acronyms stand for: annual mean temperature (bio01), isothermality (bio03), minimum temperature of the coldest month (bio06), mean temperature of the wettest quarter (bio08), mean temperature of the driest quarter (bio09), mean temperature of the warmest quarter (bio10), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), precipitation of the coldest quarter (bio19), Annual BioTemperature (ABT) and Ellenberg Climatic Quotient (EQ)

Based on the Random Forest models of RanPs (results are not illustrated from RhoPs models as they were consistently poor, details below), the most important variables (based on mean decrease in Gini index) in both sets I and II that explained the distribution of *R. lowndesii* were precipitation of the wettest month (bio13) and precipitation of the warmest quarter (bio18). In the case of *R. lepidotum*, in set I the most important variables were isothermality (bio03) and precipitation of the coldest quarter (bio19) and in set II they were isothermality (bio03) and mean temperature of the wettest quarter (bio08). The distribution of *R. cowanianum* was mostly explained in set I by the Ellenberg Climatic Quotient and precipitation of the driest quarter (bio17) and in set II by precipitation seasonality (bio15) and Annual BioTemperature. Although there were differences in the most important variables among sister taxa (Table 1), there were only a few variable ranges that were significantly different between them (Fig. 2).

The variance partitioning analysis showed that the deviances explained by temperature and precipitation are 30% and 22.9% respectively for *R. cowanianum* in the optimal GLM (set II) for RanPs (the total explained deviance was 66.3%). For *R. lepidotum,* the total deviance explained was 51.9%, of which 37.1% was explained by temperature variables and only 6.3% by precipitation variables. For *R. lowndesii*, the deviance explained by precipitation variables was 66.5%, which was tenfold higher than the deviance explained by temperature-related variables (5.7%), and the total deviance explained was 64.0%.

Distribution overlaps under current and projected future climate

The distributional overlap analysis verified a high degree of distributional overlaps (Table 2; Fig. 4; Supplementary Material S4) for current and future climates. The average within-species predicted distribution overlap between current and future climatic condition was around 72% for all species, except for *R. cowanianum* (60% from set II variables), (Supplementary Material S5A and S5B).

Table 2. Results of the potential distribution overlap analysis between three *Rhododendron* species in current and the future climatic conditions. Values correspond to percentage of overlap.

Between species	**Current climate**		**Future climate**	
	All variables (set I)	**GLM selected variables (set II)**	**All variables (set I)**	**GLM selected variables (set II)**
R. cowanianum - R. lepidotum	63	68	77	74
R. cowanianum - R. lowndesii	57	46	72	53
R. lepidotum - R. lowndesii	55	49	68	62

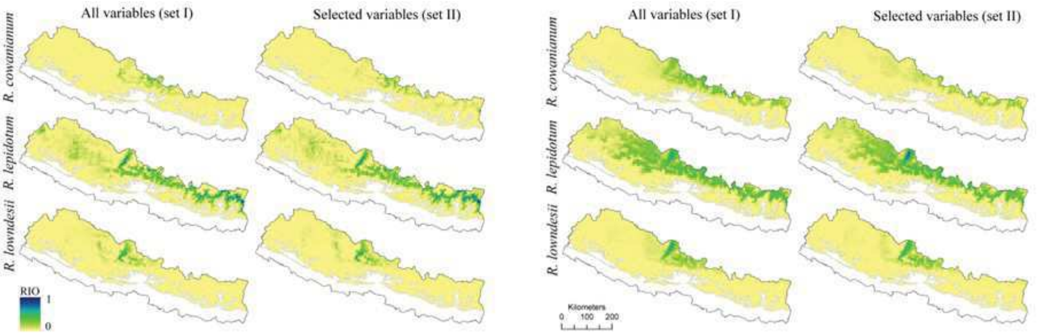


Figure 4. Maps depicting the values of the predicted relative index of occurrence (RIO) for current climate (left side panel, columns 1 and 2) and future climate (right side panel, columns 3 and 4). The predictions are for presence data with random pseudo-absences (RanPs). The white area inside the Nepal boundary is beyond the range of the study area.

Geographical shifts of climatic niche

The predictions of our Random Forest models predictions using RanPs suggested that climatic niches of *R. cowanianum* and *R. lepidotum* will move to higher elevations with projected warming. However, the climatic niche of *R. lowndesii* does not seem to move uphill in future climate projections (Fig. 5). The results were consistent across both sets of variables.

Effects of reducing environmental dimension on species distribution models

There were some differences in the predictions using set I and set II variables. The similarities are depicted in Table 3. The respective AUC values of the Random Forest models are also illustrated in the table. The ROC curves for the set I and set II variables were also close to each other (Supplementary Material S6).

Discussion

In this study, we verified that three closely related *Rhododendron* sister taxa have similar relationships to most climatic variables. As these taxa are phylogenetically highly related and geographically very close in the Himalayas, their distributions partially overlap. The distribution model suggests that the potential area of distribution of species adapted to arid environments will not move to higher elevations, whereas the potential area of distribution of the other two sister species will move to higher elevations in the future climate. Here, the potential area of distribution shift in geography is based on the 'worst-case' climatic scenario.

Climatic factors segregating species distribution

Based on the Random Forest model with the set I and set II variables on RanPs, precipitation of the wettest month and the warmest quarter are the most influential variables for the distribution of *R. lowndesii*. This aligns with empirical data that this species is mainly observed in dry regions in Nepal, where any amount of precipitation is important. The *R. lepidotum* distribution is mostly related to isothermality, a measure of how variable is temperature within each cell derived from diurnal and annual temperature ranges. Distribution of *R. cowanianum* is related to both temperature and precipitation variables as the most important variables. In other words, for *R. lepidotum* and *R. cowanianum,* water is not the main limiting factor in their distributions, in contrast with *R. lowndesii* (Fig. 3). This finding agrees with Cavender-Bares et

Table 3. Similarity in the potential area of distribution (in percentage) between models with all variables (set I) and those with GLM-selected variables (set II) under current and future climate conditions and their respective model AUC values.

	Current climate		**Future climate**	
Species	**% Similarity**	**AUC**	**% Similarity**	**AUC**
R. cowanianum	74.5	0.985	74.0	0.936
R. lepidotum	94.4	0.963	94.2	0.966
R. lowndesii	85.2	0.985	87.4	0.982

al. (2004), who found that phylogenetically close oak species share contrasting moisture preferences in North Central Florida. The most important variable lists differ between sister taxa (Table 1) and most of the variables' ranges are similar between them (Supplementary Material S3), which supports previous findings that sister taxa possess similar climatic niches on a broad scale (Hof et al. 2010) and indicates the conservation of phylogenetic niches (Losos 2008).

Range shifts and distribution overlaps under current and projected future climate

The results of Tukey's HSD tests suggest that the highest distributional overlap is found between the generalist species *R. lepidotum* and the two endemic sister taxa. On average, the sister taxa have approximately 58% (set I) and 54% (set II) overlaps in their geographical distribution (Supplementary Material S5A and S5B). This overlap is higher than the one found between descendent and parent species in the Tibetan Plateau estimated by Mao and Wang (2011). They found 32% to 36% overlap between *Pinus densata*, a descendent from the hybridization of its parent species *P. tabuliformis* and *P. yunnanensis.* However, the distributional overlap between the three *Rhododendron* species was smaller than the 80% of distributional overlap between sister taxa found on a study with 71 different species in the California Floristic Province (Anacker and Strauss 2014).

We estimated potential geographic distribution overlaps between current and future climates, assuming that the species may be able to track the geographical location of their niche, but many factors such as soil conditions, vectors for pollination, and dispersal may hamper a potential shift in geographical location therefore projected changes are always rather uncertain (Parmesan

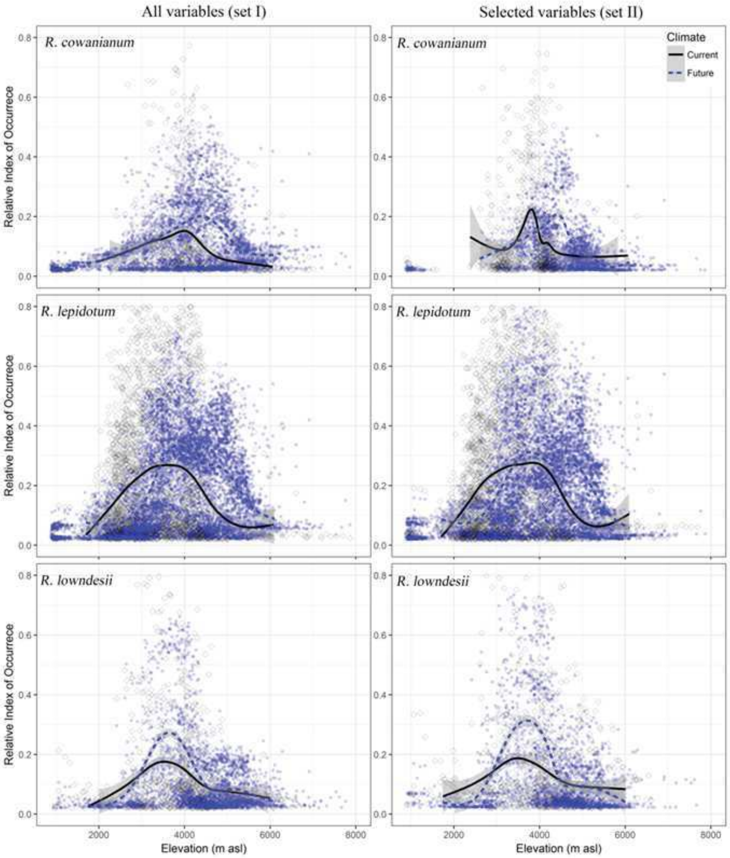


Figure 5. The optimum potential elevation for *R. cowanianum* and *R. lepidotum* show some elevational difference between current and future climates, while the optimum elevation of potential distribution of *R. lowndesii* is about the same. The peaks of the smoothing curves depict the highest occurrence probabilities of the species in the respective elevation in the x-axis (points with RIO value less than or equal to 0.02 are not depicted in plots for better illustration).

and Yohe 2003, Araújo and Rahbek 2006, Svenning et al. 2010). The degree of distributional overlap under future climate conditions is predicted to be almost the same between *R. cowanianum* and *R. lepidotum*, whereas it may increase between *R. cowanianum* and *R. lowndesii*, while the overlap between *R. lepidotum* and *R. lowndesii* is predicted to be slightly lower by set I variables and slightly higher by set II variables. This prediction agrees with the assumed niche conservatism within sister taxa (Wiens and Graham 2005). Within species, changes in the distribution of approximately 30% (set I) and 26–40% (set II) are predicted between current and future climate conditions (Supplementary Material S5A and S5B).

Based on the predictions, to be able to track their current niches *R. lepidotum* will have to 'march', and *R. cowanianum* will have to 'lean' and 'march' (Fig. 5). These species may move upslope with predicted warming as seen in other Himalayan species (Telwala et al. 2013). However, it is not necessarily true that all species require shifting upslope with warming (Crimmins et al. 2011, Qiu 2015); for instance, the potential area for *R. lowndesii* in the future climate is predicted around its current elevation. This is explained by precipitation. In the Himalayan region, the amount of precipitation has an inverse relationship with elevation, moreover, the future precipitation is predicted to be less frequent (Pendergrass and Hartmann 2014), which means that dry areas will be drier. In this situation, species may tend to stay behind the temperature niche or move downhill to track their precipitation niche. Similar instances are reported by Crimmins et al. (2011) in California, USA and Qiu (2015) in southern Tibet, China. This shows that geographical shifts along mountainsides are species-specific and more complex than just upward shifts (Gleason 1926, Halpin 1997).

Climate change may be a real threat to some endemic species if they fail to migrate due to dispersal limitations or if lack of adequate soil conditions prevent them from establishing in a new geographical location even if it is within their climate niche (Thuiller et al. 2005, Pearson 2006, Manish et al. 2016). This will in essence create large challenges for contemporary strategic biodiversity conservation (Hannah et al. 2002). Moreover, species-specific geographic shift rates (Parmesan and Yohe 2003) may involve the emergence of new community assemblages leading to novel ecosystems under future climate conditions (Hobbs et al. 2006, Williams and Jackson 2007). In this context, contemporary conservation practices may have to change from ecosystem and/or community oriented to individual species oriented (e.g., red-listed species) because conventional strategies for communities may not be suitable for rare and endemic species in a dynamic future context. Hence, conservation strategies should incorporate climate change and focus on mountains when selecting protected areas in the future (Araújo et al. 2004).

Effects of reducing environmental dimension on distribution models

Here, our strategy of dimensionality reduction provided good results. In general, the AUC has a positive relationship with the number of predictor variables (Synes and Osborne 2011). In contrast, we found a negative relationship in *R. lepidotum*. We found that the model performances with set I (including all the environmental variables) and set II (reduced set) variables are very close to each other when the prevalence ratio is higher, with low differences between the predictions. However, set I is better at low prevalence ratios. This suggests that the model can be simplified by reducing the number of predictor variables. Here, we separately selected variables for three species using GLM, which is a recognized method for selecting effective variables (Guisan et al. 2002), and generated different combinations of variables (Supplementary Material S2).

In this study, the prevalence ratio was not equal among species, as rare species had a low number of presence records. The lower number of occurrences for rare species can hinder statistical analysis. However, other studies have shown that such low occurrences of rare species data are acceptable and more accurate predictive models can be developed for rare and restricted range species

(Franklin et al. 2009). The narrow environmental range and restricted geographic distribution may have enabled the SDM to predict with higher accuracy for endemic and rare species despite the low number of occurrences. Here, our results support the previous findings. We found a higher AUC value for both the rare and endemic species (*R. cowanianum* and *R. lowndesii*) compared to the generalist species *R. lepidotum* (Table 3).

The prediction accuracy and model performance measures do not only depend on the number of presences, but are also affected by the number of pseudo-absences (VanDerWal et al. 2009). Here, we tested models wherein the numbers of pseudo-absences were set equal to the number of presences (results not included here). There are many different ways to distribute the 19 pseudo-absence points for *R. cowanianum* in the study area. We found that when the pseudo-absences were at a distance from the presence locations, the AUC was higher and the prediction was better than when the pseudo-absence points were close to the presence locations, which agrees with VanDerWal et al. (2009). This is why the RanPs models always outperformed the RhoPs models. This finding reveals that sister taxa-constrained absence values are not better than randomly generated pseudo-absences. This result is consistent with a finding by Barbet-Massin et al. (2012). The reason behind the poor performance of the sister taxa-constrained absence value is because of a low discrimination power within the model between the targeted presences and the constrained pseudo-absences as they are both within close proximity.

In conclusion, our models suggest that there is high climate niche overlap and thereby high geographical overlap for the sister species, but there are also more potential geographical areas for the two endemic species not occupied, which may relate to dispersal limitation or other environmental factors. The modes indicate that *R. lepidotum* will have to 'march', and *R. cowanianum* will have to 'lean' and 'march' to track their future climate niche, whereas *R. lowndesii* may stay behind, because its distribution is determined by precipitation. This illustrates that responses to climate change are very individual and it is also rather uncertain whether the *Rhododendron* species are able to track the geographical location of their niches in the future.

Acknowledgements

We sincerely thank our colleagues Lila Nath Sharma, Kuber Prasad Bhatta, Dilli Prasad Rijal, Khem Raj Bhattarai, Binoj Kumar Shrestha, Man Kumar Dhamala, Prakash Bhattarai, Rita Chhetri, Krishna Babu Shrestha and Falk Huettmann for sharing their ideas and data.

References

Abrol, D.P. (2012) Climate change and pollinators. In: Pollination Biology, 479–508. Springer.

Anacker, B.L. & Strauss, S.Y. (2014) The geography and ecology of plant speciation: range overlap and niche divergence in sister species. Proceedings of the Royal Society of London B: Biological Sciences, 281, 2013.2980–2013.2989.

Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity? Science, 313, 1396–1397.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology, 10, 1618–1626.

Austin, M. & Meyers, J. (1996) Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. Forest Ecology and Management, 85, 95–106.

Austin, M., Nicholls, A. & Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. Ecological Monographs, 60, 161–177.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, 3, 327–338.

Breiman, L. (2001) Random Forests. Mach. Learn., 45, 5–32.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B. & Davison, J.E. (2008) Vegetation synchronously leans upslope as climate warms. Proceedings of the National Academy of Sciences of the USA, 105, 11591–11592.

Broennimann, O., Di Cola, V. & Guisan, A. (2016). ecospat: Spatial Ecology Miscellaneous Methods. R package version 2.1.1, https://CRAN.R-project.org/package=ecospat.

Cavender-Bares, J., Ackerly, D., Baum, D. & Bazzaz, F. (2004) Phylogenetic overdispersion in Floridian oak communities. American Naturalist, 163, 823–843.

Collins, M., Knutti, R., Arblaster, J., et al. (2013) Long-term climate change: Projections, commitments and irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental

Panel on Climate Change (ed. by T.F. Stocker, D. Qin, G.-K. Plattner et al.). pp 1029–1136. Cambridge University Press, Cambridge, UK and New York, USA.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science, 331, 324–327.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions, 17, 43–57.

Ellenberg, H. (1963) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. In: Grundlagen der Vegetationsgliederung (ed. by H. Walter), 943. Eugen Ulmer, Stuttgart.

Franklin, J., Wejnert, K.E., Hathaway, S.A., Rochester, C.J. & Fisher, R.N. (2009) Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. Diversity and Distributions, 15, 167–177.

GISTEMP Team (2016) GISS surface temperature analysis (GISTEMP).– Retrieved Oct 4, 2016, from http://data.giss.nasa.gov/gistemp/.

Gleason, H.A. (1926) The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club, 7–26.

Guisan, A., Edwards, T.C. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling, 157, 89–100.

Halpin, P.N. (1997) Global climate change and natural-area protection: management responses and research directions. Ecological Applications, 7, 828–843.

Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. Global Ecology and Biogeography, 11, 485–495.

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

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A. & Lugo, A.E. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography, 15, 1–7.

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. Ecography, 33, 242–250.

Holdridge, L.H. (1947) The forests of western and central Ecuador. Forest Service, U.S.D.A. Washington.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. R News, 2, 18–22.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. Nature, 462, 1052–1055.

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, 11, 995–1003.

Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology, 20, 538–548.

Manish, K., Telwala, Y., Nautiyal, D.C. & Pandit, M.K. (2016) Modelling the impacts of future climate change on plant communities in the Himalaya: a case study from Eastern Himalaya, India. Modeling Earth Systems and Environment, 2, 1–12.

Mao, J.-F. & Wang, X.-R. (2011) Distinct niche divergence characterizes the homoploid hybrid speciation of *Pinus densata* on the Tibetan Plateau. American Naturalist, 177, 424–439.

Pachauri, R.K., Allen, M.R., Barros, V.R., et al. (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC. Geneva, Switzerland

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421, 37–42.

Pearson, R.G. (2006) Climate change and the migration capacity of species. Trends in Ecology and Evolution, 21, 111–113.

Pendergrass, A.G. & Hartmann, D.L. (2014) Changes in the distribution of rain frequency and intensity in response to global warming. Journal of Climate, 27, 8372–8383.

Qiu, J. (2015). High-altitude forests in the Himalayas hit harder by droughts. Why are plateau and mountain timberlines in Asia shifting downslope, despite global warming? Scientific American http://www.scientificamerican.com/article/high-altitude-forests-in-the-himalayas-harder-hit-by-droughts/

Oke, J. (1987) Boundary layer climates. Methuen and Company, New York.

R Core Team (2016). R: A language and environment for statistical computing. www. R-project. org. R Foundation for Statistical Computing, Vienna, Austria.

Rajbhandari, K.R., Rai, S. & Bhatt, G.D. (2016) Endemic Flowering Plants of Nepal: An Update. In: Bulletin of Department of Plant Resource (ed. by D.R. Dangol, N. Joshi, K.M. Rajkarnikar, J.J. Bhatta, U. Tandukar, S. Khadgi, L. Jha and R. Tamrakar), 38, 106–144. Department of Plant Resources, Kathmandu, Nepal.

Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? Journal of Biogeography, 33, 1689–1703.

Steinbauer, M.J., Field, R., Grytnes, J.A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A., Cardoso, P. & Chou, C.H. (2016) Topography-driven isolation, speciation and a global increase of endemism with elevation. Global Ecology and Biogeography, 25, 1097–1107.

Svenning, J.C., Fitzpatrick, M.C., Normand, S., Graham, C.H., Pearman, P.B., Iverson, L.R. & Skov, F. (2010) Geography, topography, and history affect realized-to-potential tree species richness patterns in Europe. Ecography, 33, 1070–1080.

Synes, N.W. & Osborne, P.E. (2011) Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. Global Ecology and Biogeography, 20, 904–914.

Telwala, Y., Brook, B.W., Manish, K. & Pandit, M.K. (2013) Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. PLoS ONE, 8, e57103.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the USA, 102, 8245–8250.

UNFCCC (2015). Adoption of the Paris Agreement**,** 16. United Nations Framework Convention on Climate Change, Paris.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological Modelling, 220, 589–594.

Vetaas, O.R. (2002) Realized and potential climate niches: a comparison of four *Rhododendron* tree species. Journal of Biogeography, 29, 545–554.

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution, 62, 2868–2883.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics, 519–539.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment, 5, 475–482.

Willis, K. & MacDonald, G. (2011) Long-term ecological records and their relevance to climate change predictions for a warmer world. Annual Review of Ecology, Evolution, and Systematics, 42, 267–287.

Submitted: 21 May 2017
First decision: 02 October 2017
Accepted: 16 October 2017
Edited by Joaquín Hortal

Supplementary Material S1: Methodological details of preparing ABT, EQ and RRI variables

Annual BioTemperature (ABT): It is an index for accumulated effective temperature. It is calculated from the months with mean temperature of 0 to 30^{o}C (Holdridge 1947) (as did by Fang and Lechowicz (2006))

$$ABT = \frac{\sum T}{12}\ , \qquad \text{(for months in which } 0 < \mathrm{T} < 30^{o}\mathrm{C})$$

Ellenberg Climatic Quotient (EQ): It is defined as the mean temperature of the warmest month (MTWM, in ^{o}C) divided by annual precipitation (AP, in mm per year), multiplied by 1000 (Ellenberg 1963).

$$EQ = \frac{Warmest\ month's\ mean\ temperature\ (^{o}C)}{Annual\ Precipitation\ (mm)} \times 1000$$

Relative Radiation Index (RRI): It is the relative measure of the substrate's annual exposure to solar radiation. The RRI takes account of aspect (which is measured clockwise from north and takes values from 0 to 360°), slope (in degree 0 to 90), latitude (in degree) (Oke 1987).

$$RRI = Cos(180 - Aspect) \times Sin(Slope) \times Sin(Latitude)$$
$$+ Cos\ (Slope) \times Cos\ (Latitude)$$

References

Ellenberg, H. (1963) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. In: Grundlagen der Vegetationsgliederung (ed. by H. Walter), 943. Eugen Ulmer, Stuttgart.

Fang, J. & Lechowicz, M.J. (2006) Climatic limits for the present distribution of beech (Fagus L.) species in the world. Journal of Biogeography, 33, 1804-1819.

Holdridge, L.H. (1947) The forests of western and central Ecuador

Oke, J. (1987) Boundary layer climates. Methuen and Company New York.

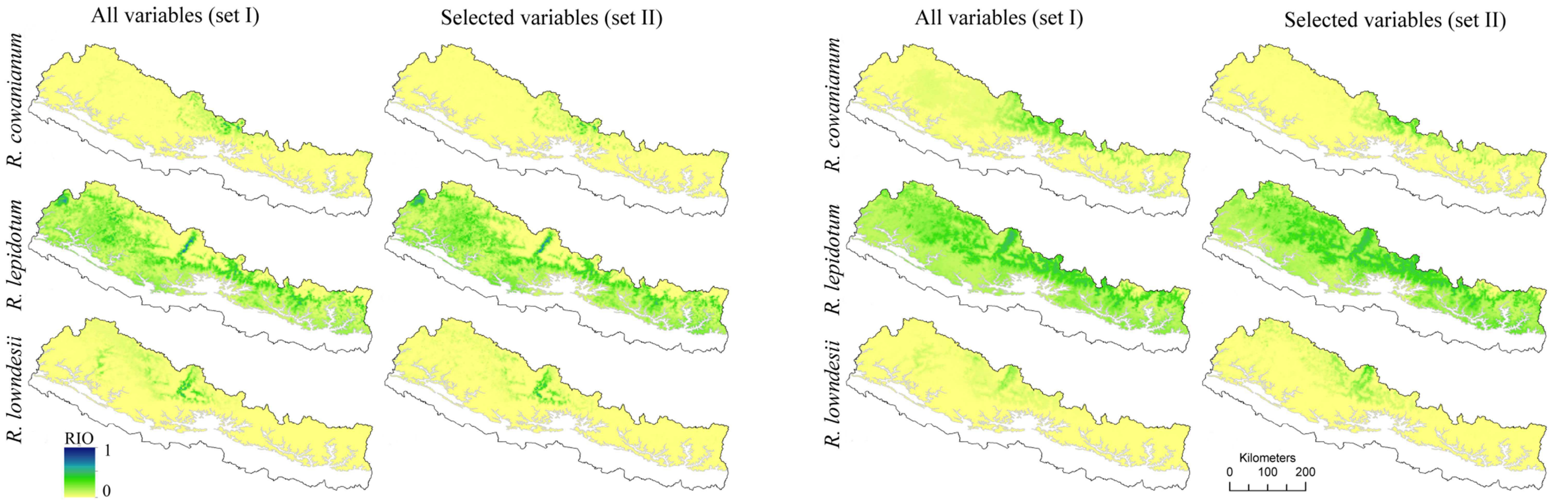
Supplementary Material S2: List of variables and GLM selected list for Random Pseudo-absence and *Rhododendron* Pseudo-absence

Variable Names	Presence with Random Pseudoabsence			Presence with Rhododendron Pseudoabsence		
	R. cowanianum	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
bio01	√	√		√	√	√
bio02				√		√
bio03		√			√	
bio04	√				√	
bio05				√		
bio06	√			√		√
bio07						
bio08	√	√				√
bio09	√		√	√		
bio10		√		√	√	
bio11		√			√	
bio12			√	√	√	
bio13		√	√	√	√	
bio14						
bio15	√	√			√	
bio16		√				√
bio17	√		√	√		√
bio18			√	√		
bio19	√	√		√	√	
RRI					√	
ABT	√			√		√
EQ		√	√			
Total Number of Variables	9	10	6	12	10	7

Supplementary Material S3: Tukey's HSD test p-value between species

SN	variables	*R. lepidotum – R. cowanianum*	*R. lowndesii – R. cowanianum*	*R. lowndesii –R. lepidotum*
1	bio01	0.147	0.64	0.64
2	bio02	0.195	0.108	0.108
3	bio03	0.735	0.004	0.004
4	bio04	0.316	0.855	0.855
5	bio05	0.311	0.326	0.326
6	bio06	0.159	0.312	0.312
7	bio07	0.171	0.611	0.611
8	bio08	0.081	0.769	0.769
9	bio09	0.105	0.025	0.025
10	bio10	0.14	0.635	0.635
11	bio11	0.125	0.607	0.607
12	bio12	0	0.989	0.989
13	bio13	0	0.722	0.722
14	bio14	0.003	0.053	0.053
15	bio15	0.536	0	0
16	bio16	0	0.749	0.749
17	bio17	0.086	0	0
18	bio18	0	0.681	0.681
19	bio19	0.405	0	0
20	ABT	0.122	0.538	0.538
21	EQ	0.031	0.696	0.696
22	RRI	1	0.993	0.993

Supplementary Material S4: Maps depicting the values of the predicted relative index of occurrence (RIO) for current climate (left side panel, columns 1 and 2) and future climate (right side panel, columns 3 and 4). The predictions are for presence data with Rhododendron pseudo-absences (RhoPs). The white area inside the Nepal boundary is beyond the range of the study area.



Supplementary Material S5A: Distribution Overlap, All variables (set I)

	SPECIES	Current Climate			Future 2070s		
	D Index	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.446	0.363	0.563	0.427	0.471
	R. lepidotum		1	0.329	0.494	0.541	0.347
	R. lowndesii			1	0.383	0.404	0.588
Future 2070s Climate	*R. cowanianum*				1	0.638	0.585
	R. lepidotum					1	0.495
	R. lowndesii						1

	I index	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.749	0.67	0.846	0.739	0.762
	R. lepidotum		1	0.625	0.746	0.813	0.62
	R. lowndesii			1	0.68	0.704	0.851
Future 2070s Climate	*R. cowanianum*				1	0.89	0.838
	R. lepidotum					1	0.79
	R. lowndesii						1

	RR Index	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.686	0.668	0.788	0.732	0.678
	R. lepidotum		1	0.687	0.649	0.734	0.61
	R. lowndesii			1	0.696	0.742	0.765
Future 2070s Climate	*R. cowanianum*				1	0.775	0.743
	R. lepidotum					1	0.757
	R. lowndesii						1

	Average	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.63	0.57	0.73	0.63	0.64
	R. lepidotum		1	0.55	0.63	0.7	0.53
	R. lowndesii			1	0.59	0.62	0.73
Future 2070s Climate	*R. cowanianum*				1	0.77	0.72
	R. lepidotum					1	0.68
	R. lowndesii						1

Supplementary Material S5B: Distribution Overlap, GLM selected variables (set II)

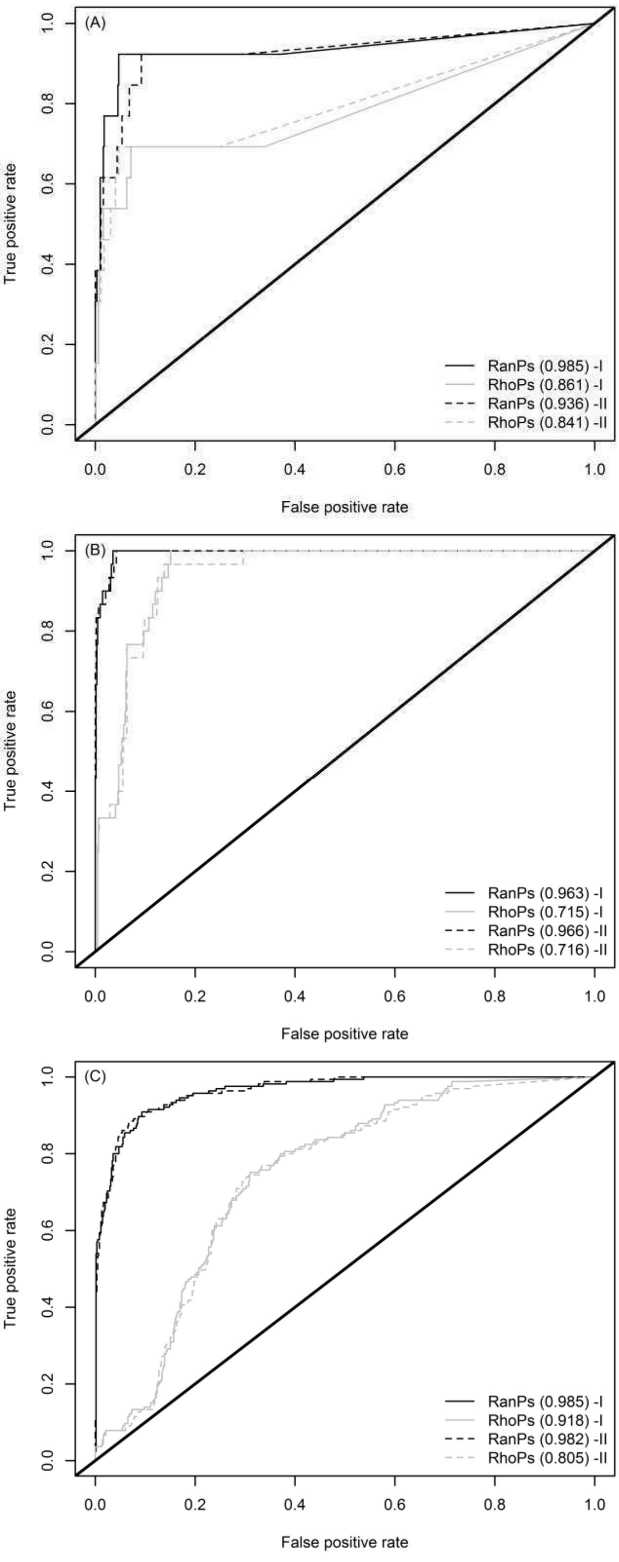
	SPECIES	Current Climate			Future 2070s		
	D Index	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.511	0.254	0.413	0.482	0.346
	R. lepidotum		1	0.293	0.387	0.552	0.342
	R. lowndesii			1	0.239	0.372	0.598
Future 2070s Climate	*R. cowanianum*				1	0.594	0.331
	R. lepidotum					1	0.438
	R. lowndesii						1

	I index	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.795	0.52	0.695	0.774	0.608
	R. lepidotum		1	0.557	0.642	0.812	0.605
	R. lowndesii			1	0.489	0.661	0.847
Future 2070s Climate	*R. cowanianum*				1	0.842	0.604
	R. lepidotum					1	0.729
	R. lowndesii						1

	RR Index	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.723	0.615	0.691	0.753	0.604
	R. lepidotum		1	0.621	0.601	0.726	0.601
	R. lowndesii			1	0.611	0.701	0.77
Future 2070s Climate	*R. cowanianum*				1	0.774	0.642
	R. lepidotum					1	0.704
	R. lowndesii						1

	Average	Current Climate			Future 2070s		
	SPECIES	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*	*R. cowanianum*	*R. lepidotum*	*R. lowndesii*
Current Climate	*R. cowanianum*	1	0.68	0.46	0.6	0.67	0.52
	R. lepidotum		1	0.49	0.54	0.7	0.52
	R. lowndesii			1	0.45	0.58	0.74
Future 2070s Climate	*R. cowanianum*				1	0.74	0.53
	R. lepidotum					1	0.62
	R. lowndesii						1

Supplementary Material S6: Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve of *R. cowanianum* (subplot “A”), *R. lepidotum* (subplot “B”) and *R. lowndesii* (subplot “C”). The values inside parenthesis are the average AUCs of the five-fold cross-validation. Inside the plot, “RanPs” is presence with random pseudo-absences, “RhoPs” is presence with Rhododendron-constrained pseudo-absences, “I” is for the all variables models (set I) and “II” represents the GLM-selected variables (set II).



Graphic design: Communication Division, UIB / Print: Skipnes Kommunikasjon AS

uib.no

ISBN: 978-82-308-3749-8