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Impacts of Climate Change on *Abies spectabilis*: An approach integrating a Species Distribution Model (MaxEnt) and a Dynamic Vegetation Model (LPJ-GUESS)

Mohan d. Joshi

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Department of Physical Geography and Ecosystem Science

Lund University

Sölvegatan 12

S-223 62 Lund

Sweden



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FACULTY OF GEO-INFORMATION SCIENCE AND EARTH OBSERVATION

Impacts of Climate Change on *Abies spectabilis*: An approach integrating a Species Distribution Model (MaxEnt) and a Dynamic Vegetation Model (LPJ-GUESS)

Mohan d. Joshi

Thesis submitted to the department of Physical Geography and Ecosystem Science, Lund University, in partial fulfilment of the requirements for the degree of Master of Science in Geo-information Science and Earth Observation for Environmental Modelling and Management

Thesis assessment Board

First Supervisor: *Dr. Paul A. Miller* (Lund University)

Co-supervisors: Nitin Chowdhary (PhD student, Lund University)

Exam committee:

Prof. Dr. Ben Smith (Lund University)

Dr. Jörgen Olofsson (Lund University)

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Abstract

Recent global warming trends, particularly in the arctic regions and Himalayas are modifying forest structure and function, notably biogeographical changes in tree species distribution. This study used future climate scenario output from the CCSM4 climate model (RCP 2.6) in two vegetation modelling approaches - the empirical MaxEnt and process-based LPJ-GUESS - to elucidate changes in the suitable habitat area, elevation shift, relative coverage, net primary production and carbon biomass for *Abies spectabilis* in Manaslu conservation area, Nepal.

Both the models are shown to be in excellent agreement with the current distribution of *Abies spectabilis* as shown by error rate and Cohen's kappa. The results under the applied climatic scenario showed decreasing suitable habitat for the species in the future with the plant expanding and moving up in the mountain. The rate of species movement is predicted to be 14 meters per decade (MaxEnt) and 30 meters of altitude per decade (LPJ-GUESS). In addition, LPJ-GUESS predicts reducing coverage of *Abies spectabilis* from the lower-temperate climatic zone (2000-2500 masl) and increasing coverage in lower-alpine climatic zone (4000-4500 masl) in the coming future. The species will respond to climate warming by increasing its Leaf Area Index, Net Primary Production and Carbon biomass. It is found that annual temperature range and precipitation seasonality (MaxEnt) influence the current distribution while in the future, mean temperature of the coldest quarter will shape the geographical distribution of *Abies spectabilis*.

Key Words: Himalaya, Manaslu conservation area, *Abies spectabilis*, Species distribution, MaxEnt, LPJ-GUESS, net primary production, leaf area index, carbon biomass

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Acronyms and Abbreviation

AUC	The Area Under ROC Curve
CCSM	Community Climate System Model
cmass	carbon biomass
DEM	Digital Elevation Model
DGVM	Dynamic Global Vegetation Model
GDD	Growing Degree Days
GeoTIFF	Geostationary Earth Orbit Tagged Image File Format
GHG	Greenhouse gas
ICIMOD	International Center for Integrated Mountain Development
IPCC	International Panel on Climate Change
KATH	National Herbarium and Plant Laboratories
KNMI	Royal Netherlands Meteorological Institute
LAI	Leaf Area Index
LPJ-GUESS	Lund-Postdam-Jena General Ecosystem Simulator
masl	meters above sea level
MaxEnt	Maximum Entropy
MCA	Manaslu Conservation Area
NDVI	Normalized Difference Vegetation Index
NPP	Net Primary Production
PFTs	Plant Functional Types
RCP	Representative Concentration pathways
ROC	The Receiver Operating Characteristic
SDM	Species Distribution Model
TUCH	Tribhuvan University Central Herbarium
WHyMe	Water Hydrology Methane

1. Introduction

1.1. Research Background

1.1.1. Climate in the Himalayas

The last few decades have witnessed alarming signals of global climate change, particularly in the Arctic region and in the Himalayas (IPCC 2007, ICIMOD 2009, Singh et al. 2011). The warming trend observed ranges from 0.01 to 0.06⁰C/yr. and the annual mean temperature is expected to increase by 2.9⁰C in the Himalayas by the middle of the century (ICIMOD 2009). Across the Himalayas, mean annual temperature has raised 0.6-1.3⁰C (1975-2006), with maximum temperatures rising between 1.1-2.0⁰C and the minimum from 0.2-0.5⁰C (Singh et al. 2011). Precipitation doesn't show any definite trend and varies from year to year, although, a distinct shift from snow to rain was apparent (Singh et al. 2011).

The Himalayan region, recognized among one of the 34 global biodiversity hotspots (Conservation International 2014) is known as highly sensitive to climate alteration and is also attributed as data-deficient region. As outlined by IPCC Fourth Assessment Report (IPCC 2007) data for the whole region were for the most part absent.

1.1.2. Dominant vegetation and distribution

Due to the extreme heterogeneity, rapid elevation changes and variable aspect and inclination, the Himalayas harbors diverse vegetation and varied microclimatic and ecological conditions (Hamilton 2002, Körner 2004). Nepal Himalaya is within the phyto-geographical transition zone between the wet eastern and the dry western Himalaya, opening thus the window for much regional diversity (Ohsawa et al., 1986).

Different authors have put forward different vegetation zones along an elevation gradient in the Nepal Himalaya. The pioneer work was done by (Dobremaz and Shakya 1975), who classified the vegetation into six zones namely; tropical, subtropical, warm temperate, temperate, cool temperate, subarctic and arctic. The principal assemblage of dominant vegetation and their natural distribution in the Nepal Himalayas is detailed in some fine scale studies (Press, Shrestha and Sutton 2000; Ohsawa, Shakya and Numata 1986). The authors documented the distribution range of 23 principal trees along the west to east gradient of Himalaya (Appendix 1).

1.1.3. Distribution and habitat of *Abies spectabilis*

Abies spectabilis (English name: silver fir, family: Pinaceae) is a densely leafy, evergreen and shade-tolerant tree up to 40 m tall with dark purple cylindrical cones. The species is distributed in the eastern Asian Himalayas from Afghanistan to Nepal. In Nepal Himalayas, it is found at an altitudinal range of 2400-4400m (Press, Shrestha and Sutton 2000). *Abies spectabilis* is generally found with *Quercus semecarpifolia* on the southern slopes whereas on the northern slopes, it is found with rhododendrons and oaks. Between 3000-3600 m, it forms an almost pure belt, dominating the forest flora. In places, it extends to the treeline; elsewhere it is succeeded by *Betula utilis* forest as the true treeline species. 'Treeline' is defined as the uppermost elevation position of an individual tree of at least three meter height (Koerner, 2003). The uppermost limit of closed forest is 'timberline' and 'ecotone' is forest-alpine transition zone near the treeline at around 3000-4000 m in Nepal Himalayas. *Abies* is a dominant ecotone species.

Abies spectabilis grows in light (sandy), medium (loamy) and heavy (clay) soils. The species prefers heavy clay (eutric regosols) and soils with a pH that is slightly acidic or neutral (<http://www.pfaf.org/user/Plant.aspx>).

1.1.4. Environmental influence on vegetation composition and distribution

1.1.4.1. Environmental and non-environmental variables

There is documentation of several environmental factors that influence plant vegetation. Temperature, humidity (precipitation and soil moisture), sunshine hours and growing degree days and winter chilling are chief among them (Austin, 2002, Prentice et al., 1992, Watt et al., 2011). Slope, aspect and inclination along with soil characteristics such as depth, temperature, water content, pH, nutrient composition and litter layer also play a major role in shaping plant survival and thus distribution (Dahlgren et al., 2007). Land use change is also one noteworthy driver towards which the sensitivity of biodiversity is immense (Sala et al., 2000). The susceptibility of plant vegetation towards environment is further enhanced by diverse anthropogenic pressures (defragmentation, deforestation, fire, harvesting etc).

1.1.4.2. Species distribution

Climatic conditions exert a strong control on the geographic distribution of species, particularly the woody plants. These species in general are more sensitive to temperature than herbaceous vegetation and their altitudinal or latitudinal limits are strongly controlled by temperature (D'Odorico et al., 2013). Consequently, changes in the range limits and increasingly skewed distributions of the species along elevation gradients has been observed in some fine scale studies (Mong and Vetaas, 2006, Kullman, 2008, Vitasse et al., 2012), indicating that plant distributions are shifting upslope in response to climate warming.

Such is the influence of environmental variables, notably temperature, that a 3⁰C increase in mean annual temperature can result in a shift in isotherms by 300-400 m in latitude and 500 m in elevation (Hughes, 2000). Vegetation responds to that by shifting their range of

distribution to compensate for the increased temperature (Thuiller et al., 2005, Kullman, 2008). Many studies have indicated that with increasing temperature, species distribution shifts to higher elevation (Parmesan, 1996, Song et al., 2004).

The last few decades have witnessed the shifting of plant species to higher elevations. The shifting rate varies with species and largely depends on species climate sensitivity. (Grabherr et al., 1994) recorded the upward migration of the alpine treeline in the European Alps at the rate of 4m per decade. In the Himalayas, the mean upward shift of the treeline is found to be of the order of 388+-80 m (Singh et al., 2012).

A study done by Tanaka et al., (2012) on the endemic *Abies* species of Japan, documented that due to the range shift the plant would gain more habitat area in the north but lose habitat in the lowlands. Another study estimated that the suitable area for Douglas fir in New Zealand would be reduced by 36-64% of the total land area by the year 2080 (Watt et al 2011).

1.1.4.3. Net primary production

Net Primary Production (hereafter 'NPP'), the net assimilation of CO₂ into organic matter by plants, is an integral component of net ecosystem exchange or net ecosystem productivity (Gower et al., 1999). In mountains, productivity is mainly determined by the distribution of precipitation, temperature and resultant effects on soil water availability and nutrients (Gao et al., 2013). Soil water availability is subsequently governed by other environmental factors as vapor pressure deficit, soil properties and CO₂ concentration (Reeves et al., 2014). Anthropogenic activities emit large quantities of CO₂ altering the climate patterns which in turn affects NPP (Greer et al., 1995).

Species respond differently to the changes in climatic factors and alteration of NPP is expected in the future as species respond to climate change through range shift or local population dynamics (Reeves et al. 2014). A study in the Tibetan plateau finds that temperature had a significantly positive effect on the mountain vegetation NPP and precipitation had a slightly negative effect (Gao et al. 2013). Changes in CO₂ concentration could also have significant effects on NPP. In fact, one study shows NPP increases by about 10% in northern and temperate ecosystems in response to a doubling of the CO₂ concentration, while changes in climate with no changes in CO₂ concentration were predicted to have almost no effect (Melillo et al., 1993). Free-air CO₂ enrichment (FACE) results confirms the enhancement of NPP by elevated CO₂ (Hickler et al. 2008).

1.1.5. Species distribution model

Species distribution models (hereafter 'SDMs') are the models that relate species geo-referenced distribution data with information on the environmental and spatial characteristics of these locations (Elith and Graham, 2009). SDMs are increasingly used to predict past, current and future geographical distribution of species (Guisan and Thuiller, 2005). SDMs are used widely in ecology and conservation biology with applications that range from, but are not limited to, quantifying the ecological niche of species (Austin 2002), assessing the impact

of climate change (Thuiller, 2004) and modeling species assemblage (Guisan and Theurillat, 2000).

The Maximum Entropy (hereafter 'MaxEnt') software package (Phillips et al., 2006) is one of the most popular tools for species distribution and ecological niche modeling. MaxEnt users are required to make a number of modeling decisions about selecting the input data, applying a threshold, random test percentage and others (Merow et al., 2013). It is to be ensured that modeling decisions are biologically motivated by specific hypotheses, study goals and species consideration.

MaxEnt takes species presence records as inputs and a set of environmental variables to predict the distribution of a species based on the theory of maximum entropy (Merow et al., 2013). MaxEnt starts by assuming the probability is perfectly uniform in geographical space and moves away from this distribution only to the extent that it is forced by the environmental variables (Phillips et al., 2006). While using presence only data, MaxEnt creates the background points which are locations without species presence record thus ensuring the most spread out or close to uniform distribution, it estimates the unknown probability distribution (Pearce and Boyce, 2006). Cells with environmental variables close to the means of the presence locations have higher probabilities (Phillips et al., 2006).

1.1.6. Dynamic global vegetation model

Dynamic global vegetation models (hereafter 'DGVM') are models that simulate shifts in potential vegetation and its associated biogeochemical and hydrological cycles as a response to climate alteration (Bonan et al., 2003). DGVMs generally incorporate group of processes; plant geography, plant physiology, vegetation dynamics, biophysics, biogeochemistry and soil hydrology. Vegetation dynamics, in a modeling framework, refers to changes in the distributions of PFTs and the PFT composition of stands (Smith et al., 2001).

The Lund-Postdam-Jena General Ecosystem Simulator (hereafter 'LPJ-GUESS') is a process-based dynamic vegetation-terrestrial ecosystem model. LPJ-GUESS simulates (a) the growth and temporal dynamics of populations of PFTs over a grid cell, integrating individual level processes and (b) growth and competition among individual plants (Smith et al., 2001).

LPJ-GUESS characterizes vegetation as patches of PFTs that occupy a portion of a grid cell. In each grid cell, each patch or PFT individual is subject to stochastic establishment, mortality and disturbance effects including fire. Given data on climate and atmospheric CO₂ concentration, it estimates the vegetation composition and cover in terms of PFTs, biomass, leaf area index and NPP (Smith et al., 2001).

1.2. Problem Description

The impacts of climate change are predicted to be most pronounced in mountain environments (IPCC 2007), where these changes are a serious threat to biodiversity. The Himalayan region has already been experiencing massive deforestation, forest fire,

overgrazing, land abandonment, and slash and burning, resulting in dramatic transformation of natural ecosystems (ICIMOD 2009).

Coupled with land use alteration, one of the most prominent impacts of climate change on vegetation might be shifting in species distributions. Species occupying lower elevation regions may migrate to higher altitude/latitude regions in the mountains to compensate for the increased temperature, resulting in divergence in the elevation range of the species. Species confined to extremes of the elevation gradient may undergo local extinction (Korner, 2004).

Since the IPCC Fourth Assessment Report (IPCC 2007) there has been a substantial increase in observations showing that hundreds of species of plants have changed functioning to some degree. However, a large source of uncertainty remains due to the unknown contribution of rising CO₂ concentration.

Very little research has been done in the Himalayan regions and even less focused on the climate change impact on phytogeography, plant physiology and vegetation dynamics. The climatic influence and its contribution to species range shifts needs to be understood to better formulate species conservation action plans.

1.3. Justification

The temperature and precipitation regimes of the Himalayan region are anticipated to change substantially during the 21st century (ICIMOD 2009), and climatic shifts are already modifying forest structure and function (Singh et al., 2011). Therefore, an accurate estimation of the performance of individual species in response to temperature and precipitation (niche estimation) is critically important to explain biogeographical changes in the tree species distributions in response to climate change in the region.

However, one of the major limitations associated with niche estimation (SDMs) is in the assumption that geographical ranges of species are determined mostly by climates (Pearson and Dawson, 2003) which is disputable. Studies have shown that distribution of species reflects both the influence of climate and other environmental factors like soil characteristics, biotic interaction, competition, dispersal, effect of CO₂ on plant productivity etc. (Austin, 2002, Bugmann, 2001, Dahlgren et al., 2007, Prentice et al., 1992, Watt et al., 2011). Inclusion of the factors which are considered to be more realistic representations of growth responses in distribution modeling is therefore, essential to effectively model the climate distribution and changes.

Mountains are biodiversity hotspots providing a range of goods and services (Reeves et al., 2014). Yet the future of goods and services derived from mountains, such as fuel wood, herbal medicines and protein is uncertain. Thus, a projection of NPP is fundamental to understanding climate change impacts on mountain ecosystems and sustainability of goods and services. Because climate change is predicted to vary from place to place, estimating the response of NPP will require the use of models that can make geographically referenced predictions.

1.4. Hypotheses and research questions

Based on empirical data sets, this study addresses the distribution response of *Abies spectabilis* to temperature, precipitation and CO₂ concentration along an elevation gradient in Central Himalaya, Nepal. The hypothesis set to define the research questions are;

"the distribution range and the suitable areas for *Abies spectabilis* will be narrowed by the year 2050 with the upward migration of the plant influenced mostly by the temperature, precipitation (climatic variables) and biotic interaction between dominant vegetation (non-climatic variables)".

I will answer the following research questions to test the hypothesis:

- Are the two models significantly different from the actual distribution of *Abies spectabilis*? Have the models been validated enough to have confidence in their projections?
- What are the current and likely future species distribution range and suitable areas for *Abies spectabilis*?
- What is the ecosystem plant species relative coverage in terms of leaf area index? How does plant species composition change in the future scenario?
- How will net primary production and carbon biomass of *Abies spectabilis* respond to the combined effect of rising temperature and atmospheric CO₂ concentration?
- Which important environmental variables determine the *Abies spectabilis* spatial distribution in Manaslu Conservation Area, Nepal?

2. Materials and Methods

2.1. Site description

Manaslu Conservation Area (hereafter 'MCA') is situated in northwest part of Gorkha district about 100 km northwest from Kathmandu, the capital of Nepal. The MCA is divided into three main valleys: Nabri (west) Kutang (middle) and Chum (east). The study area lies between 84.53⁰E to 85.09⁰E and 28.32⁰N to 28.77⁰N.

Climate: Average monthly temperatures are fairly low throughout the year. The lower temperature may drop to around -15⁰C while the annual maximum temperature rises to around 18⁰C in the year at some places. The annual rainfall varies greatly in different years. The lowest rainfall recorded in last 30 years was 530 mm in year 2001 and the wettest year recorded in last 30 years was 2007 with rainfall exceeding 1680 mm. Winter seasons witness snow fall. The altitude excluding Mt Manaslu ranges from 1338 m to 6437m a.s.l. (Figure 1a).

Soil: Soil remains dry between the periods of post monsoon till the snow fall and after the melting of snow till the monsoon rain arrives. The area mainly has Gelic leptosols (74.41%) which are shallow soils over hard rock or highly calcareous materials, followed by Humic cambisols (12.95%), Eutric regosols (11.87%) and glaciers (Figure 1c).

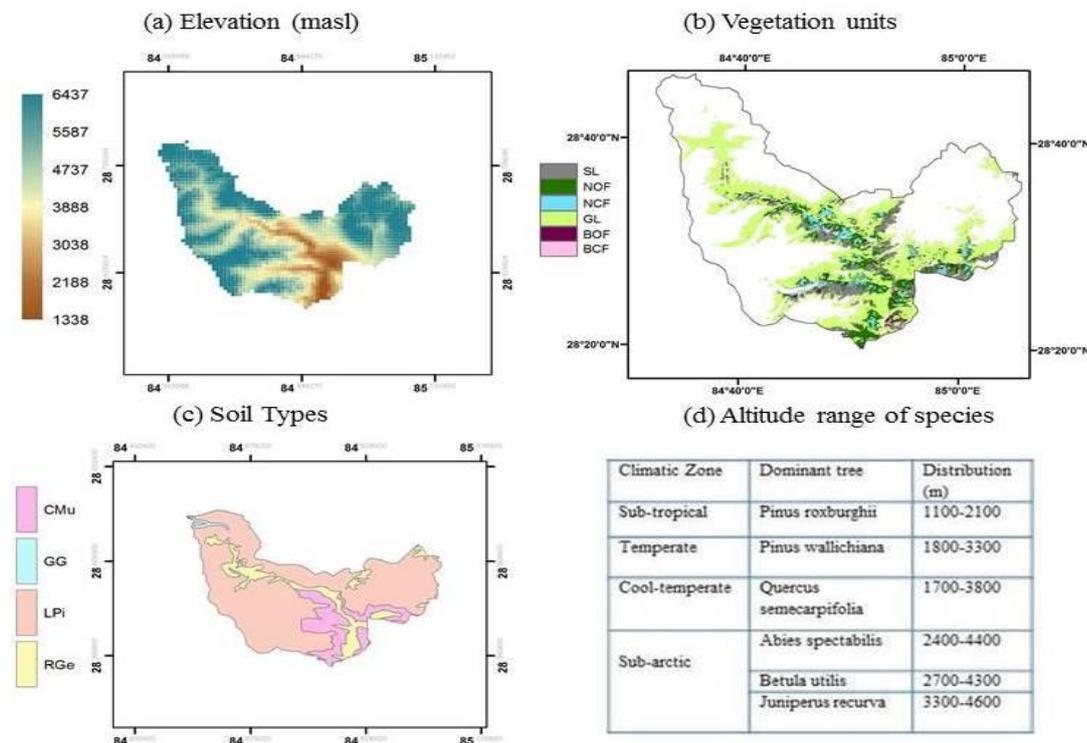


Figure 1: Environmental conditions and vegetation characteristics of the MCA- (a) surface elevation (masl), (b) vegetation units in study area [SL= Shrubland, NOF= Needleleaved Open forest, NCF= Needleleaved Closed forest, GL=Grassland, BOF=Broadleaved Open Forest, BCF=Broadleaved Closed forest], (c) soil types in MCA [CMu=Humic Cambisols, GG=Glaciers, LPI=Gelic Leptosols, RGe= Eutric Regosols (Dijkshoorn and Hunting 2009) (d) Altitudinal range of species [after (Ohsawa et al. 1986)]

Vegetation: The vegetation units are mainly dominated by grasslands followed by needleleaved open and closed forests. The needleleaved forests, depending upon the altitudinal range are dominated by *Pinus roxburghii*, *Pinus wallichiana*, *Abies spectabilis* and *Juniperus recurva*. Broadleaved forests are mainly dominated by *Quercus semecarpifolia* and *Betula utilis* (Figure 1b & Figure 1d).

2.2. Phytogeography

The south facing slope in the study area was drier compare to the north facing slope across the river owing to the direct exposure to the sun. This meso-climatic condition contributes to characteristic vegetation in both aspects of the valley. The southeast facing slope is heavily covered by shrub and herbaceous vegetation while the northeast facing slope was covered by *Betula utilis* as the dominant tree species, followed by the *Juniperus recurva*, *Abies spectabilis*, *Rhododendron campanulatum* as standing trees along with other shrub and herbaceous vegetation.

2.3. Occurrence data collection

2.3.1. Herbarium Records

All the available records of *Abies spectabilis* within the study area were collected from the National Herbarium and plant Laboratories (KATH) and Tribhuvan University Central Herbarium (TUCH) with the geographical coordinates. Encarta Atlas (2013) and Google Earth (2013) was used to geo-reference herbarium records

2.3.2. Published literatures

Data on the presence records of *Abies spectabilis* was acquired from a published study done in the same area with the permission of the author (Suwal 2010). Non-random (Purposive) sampling strategy was applied in the study area to record the species occurrence. A belt transect of 20 m width was established along the distribution range of *Abies spectabilis* which starts from the upper species limit of *Abies spectabilis* and goes down into the forests. Within this belt, geographical records (latitude, longitude, altitude) of the plant were recorded randomly.

2.3.3. Online source

Some presence coordinates of the study plant were accessed through the Global Biodiversity Information Facility (<http://www.gbif.org/>). After the removal of duplicate presence record within the same grid cell (30 arc second), the dataset altogether had 28 presence points (Figure 2).

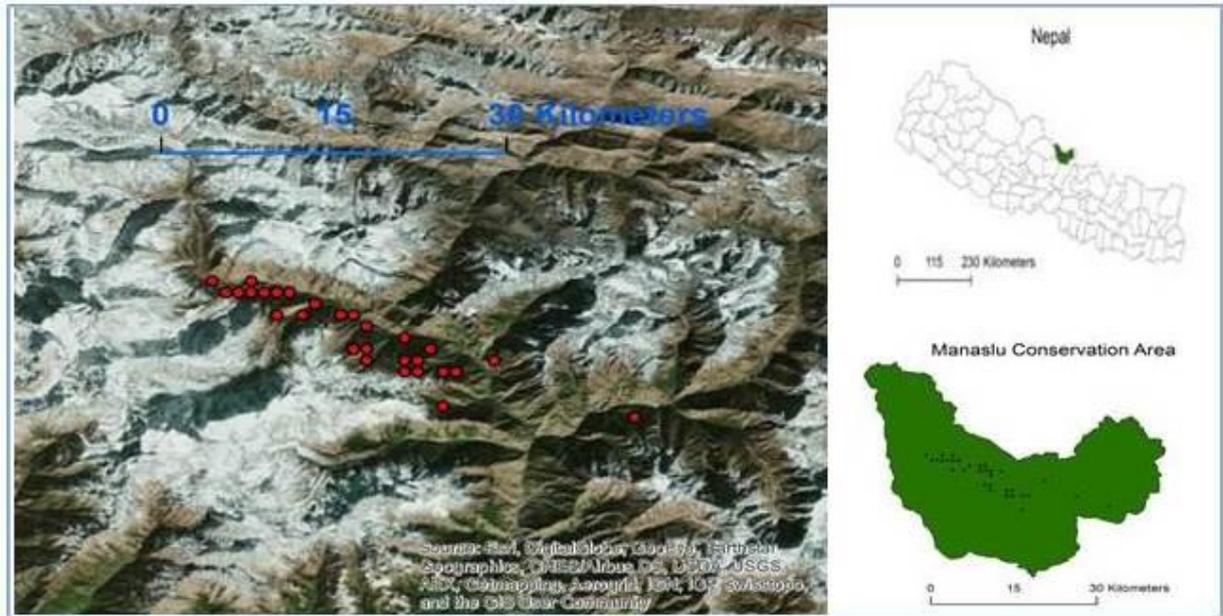


Figure 2: Study Area and the distribution of samples

2.4. Environmental driving data

For the study region, calculated average mean monthly temperature and precipitation from the years 1951-2000 at a resolution of 30 second ($0.93 \times 0.93 = 0.86 \text{ km}^2$ at the equator) were obtained from the Worldclim-Global climate data (Hijmans et al. 2005; <http://worldclim.org/>). The grid data were derived from measurements of altitude, temperature and precipitation from weather stations across the globe. These layers covers the global land areas except Antarctica in latitude/longitude coordinate reference system and WGS84 datum. Variables used to assess current climate conditions were monthly total precipitation, and monthly mean, maximum and minimum temperature and 19 derived bioclimatic variables. These variables are widely used in species distribution modeling (Austin, 2002, Khanum et al., 2013, Thuiller, 2004) .The 19 bioclimatic variables and their description is given in Table1. The outputs were obtained in GeoTIFF format which were then further processed in Arc Map 10.2 to extract the data layers for study area.

Table 1: Bioclimatic variables

Code	Description	Code	Description
BIO1	Annual Mean Temperature	BIO10	Mean Temperature of Warmest Quarter
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	BIO11	Mean Temperature of Coldest Quarter
BIO3	Isothermality (BIO2/BIO7) (* 100)	BIO12	Annual Precipitation
BIO4	Temperature Seasonality (standard deviation *100)	BIO13	Precipitation of Wettest Month
BIO5	Max Temperature of Warmest Month	BIO14	Precipitation of Driest Month
BIO6	Min Temperature of Coldest Month	BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO7	Temperature Annual Range (BIO5-BIO6)	BIO16	Precipitation of Wettest Quarter
BIO8	Mean Temperature of Wettest Quarter	BIO17	Precipitation of Driest Quarter
BIO9	Mean Temperature of Driest Quarter	BIO18	Precipitation of Warmest Quarter
		BIO19	Precipitation of Coldest Quarter

As LPJ-GUESS depends on yearly climate input to run the simulation, another dataset of yearly climate input for the year 1901-2000 was obtained from Royal Netherlands Meteorological Institute (KNMI) (<http://climexp.knmi.nl/>) on a 30 minutes resolution ($55.8 \times 55.8 = 3113.64 \text{ km}^2$ at the equator). These datasets were generated through interpolation of observed average monthly climate data.

Future climate scenario data for 2001-2100 (RCP 2.6 emission scenario) were obtained from Worldclim-Global climate data (grid data average for the year 2041-2060) and from Royal Netherlands meteorological Institute (yearly data for the year 2001-2100). These future climate projections are based on CCSM4 climate model (Community Climate System Model version 4.0) output contributed to the IPCC 5th Assessment Report (IPCC 2013) data and were statistically downscaled and calibrated using Worldclim 1.4 as baseline ‘current’ climate (the data from KNMI had not been bias-corrected). CCSM is a coupled climate model for simulating the Earth’s climate system. It is composed of four separate models simultaneously simulating the Earth's atmosphere, ocean, land surface and sea-ice, and one central coupler component (<http://www.cesm.ucar.edu/models/ccsm4.0/>).

The CMIP5 dataset of global atmospheric CO₂ concentration from 1901-2100 was used as input to LPJ-GUESS, with years 2001-2100 following the same RCP 2.6 concentration scenarios used in the CCSM4 climate projections (Paul Miller, *personal communication*).

RCP 2.6 is representative for scenarios in the literature leading to very low greenhouse gas (GHG) concentration levels. Its radiative forcing first reaches a value around 3.1 W/m^2 by mid-century and returning to 2.6 W/m^2 by 2100 (van Vuuren et al., 2007). In order to reach such radiative forcing level, GHG emissions are reduced substantially over time.

2.4.1. Data-processing to run MaxEnt and LPJ-GUESS

One large dataset containing climate parameters for each grid cell and each year was prepared to give same climate input for both the models ensuring consistency and uniformity between the models. From the yearly climatology of 1901-2000 (KNMI dataset), anomalies relative to the year 1951-2000 was calculated and applied these anomalies to each point in the Worldclim dataset. (Figure 3).

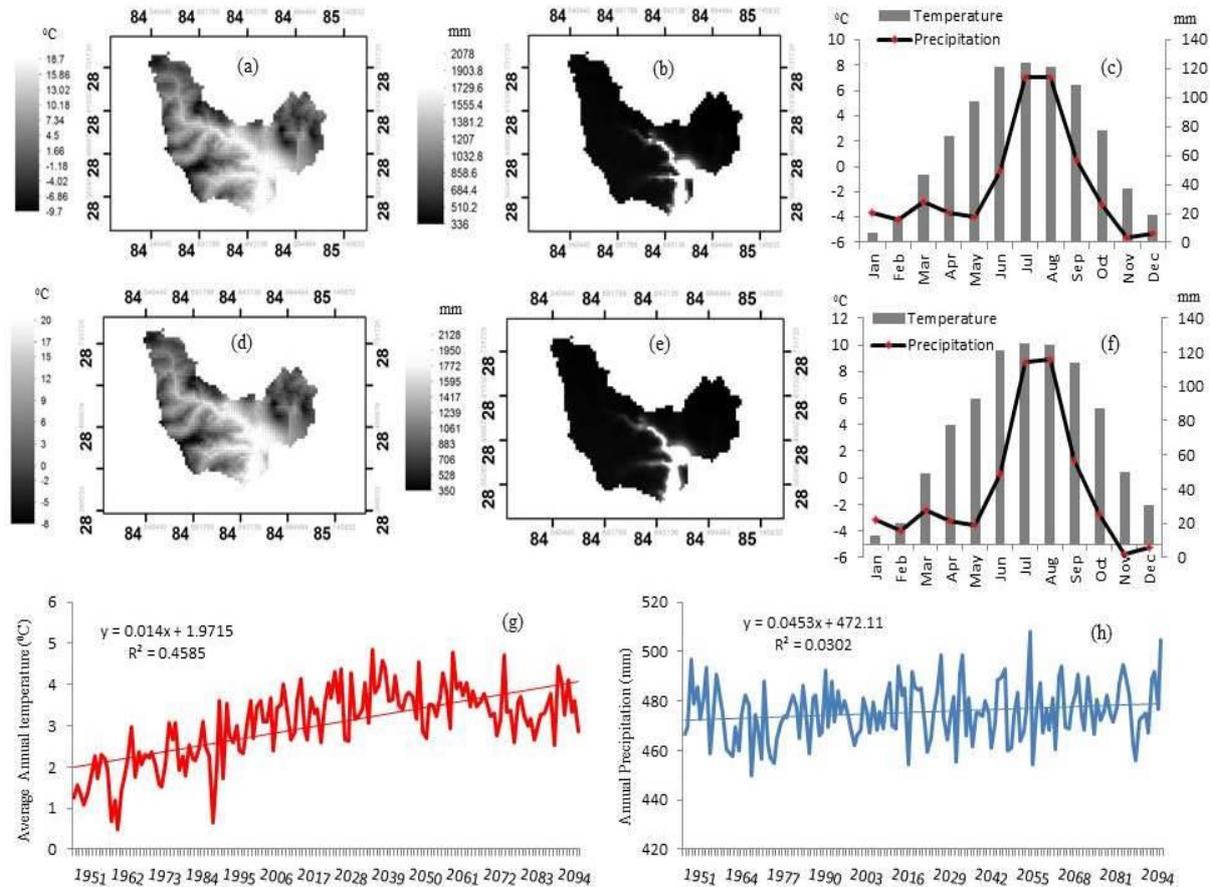


Figure 3: Climate in the Manaslu Conservation Area: (a) Annual mean temperature (1951-2000), (b) Annual mean precipitation (1951-2000), (c) mean monthly (1951-2000) precipitation and temperature, (d) Annual mean temperature (2041-2060), (e) Annual mean precipitation (2041-2060), (f) mean monthly (2041-2060) precipitation and temperature, (g) annual trend of temperature and (h) annual trend of precipitation.

2.5. Selection of Bioclimatic variables (for MaxEnt)

The selected 19 bioclimatic variables were reduced to fewer variables after examining correlation coefficient (r) among them to account for multicollinearity. Multicollinearity exists when there is correlation among the explanatory variables resulting in inaccurate model parameterization, possible exclusion of relevant variables and possible inclusion of irrelevant variables (Graham, 2003). A value of $r \leq \pm 0.90$ (Pearson correlation coefficient) was chosen as a cut-off threshold value to determine the exclusion of highly correlated values. After the exclusion, the reduced number of predictor variables was eight (Fig 4).

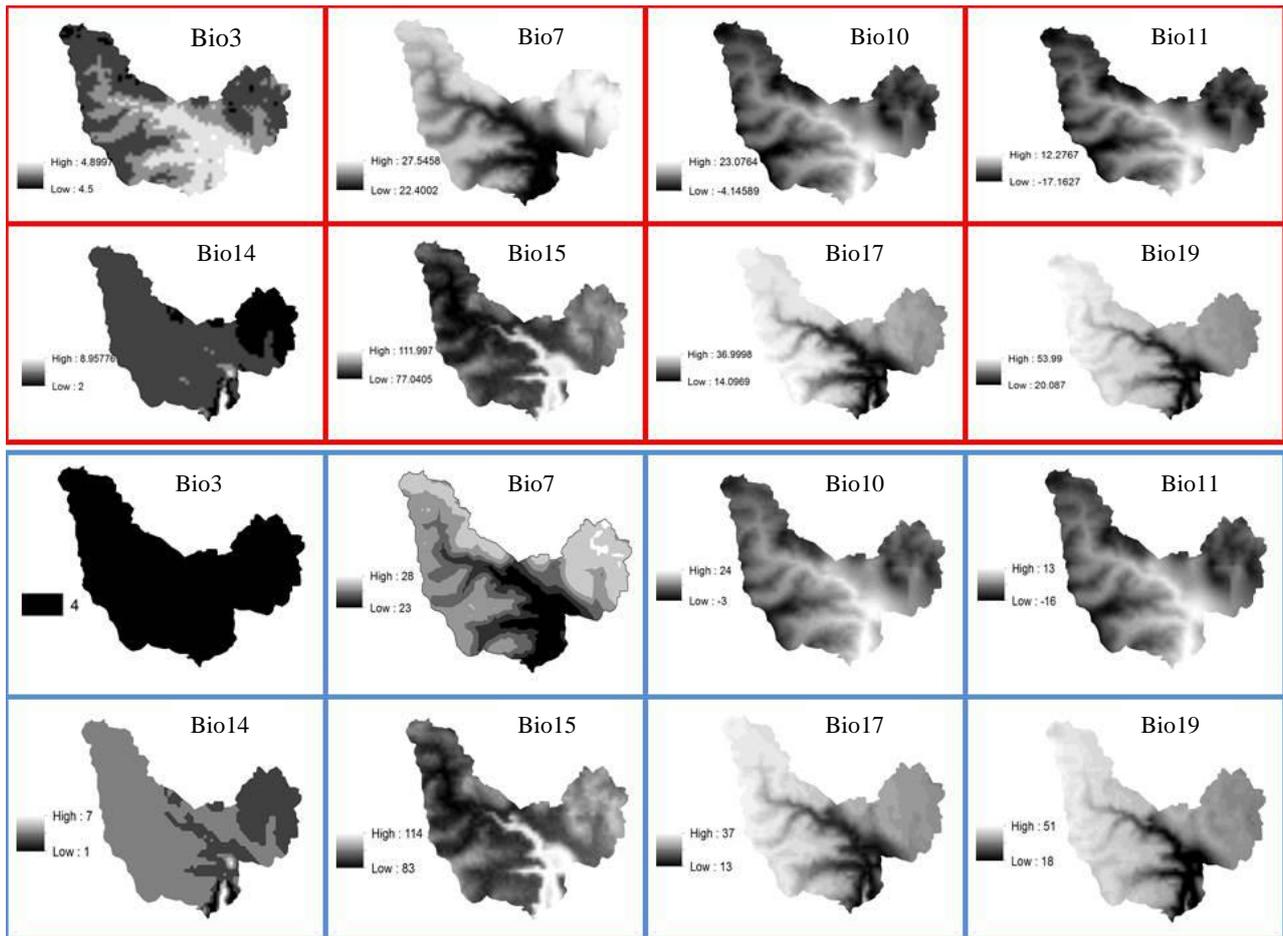


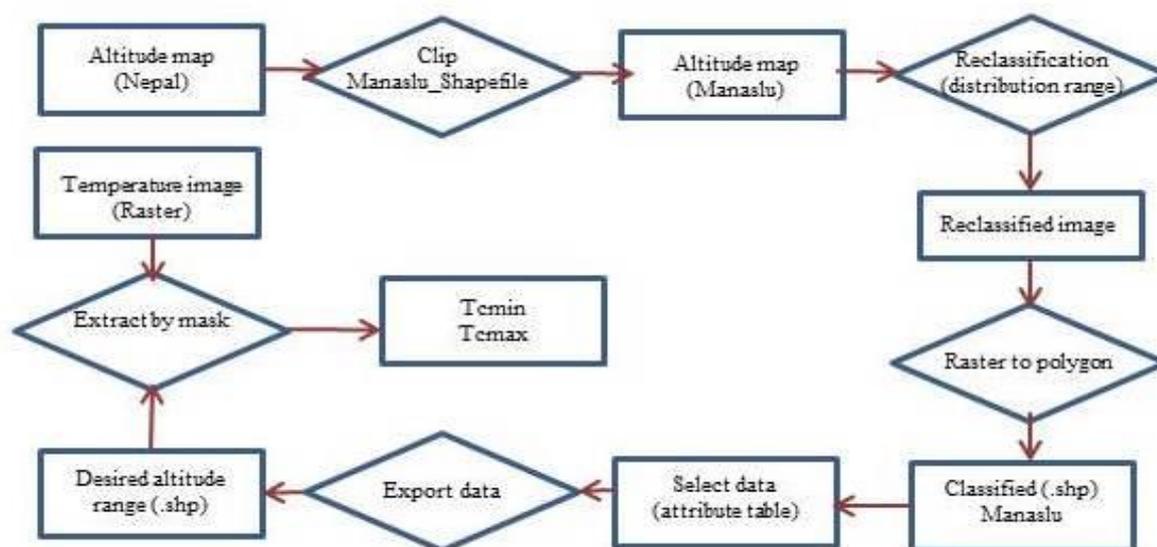
Figure 4: Predictor variables for *Abies spectabilis*

Current climate
 Future climate

2.6. Calculation of bioclimatic parameters (for LPJ-GUESS)

A minimum temperature threshold value for determining establishment and survival temperature (T_{cmin_surv}, T_{cmin_est} and T_{wmin_est}) was calculated from observed minimum monthly mean temperatures from 1950 to 2000 (<http://worldclim.org/>) and from the DEM dataset (altitude map, Nepal). Same method was applied to determine the maximum temperature (T_{cmax_est}) for coldest month (Diagram 1). No difference was made between survival and establishment temperature. Minimum growing degree days (GDD) value was obtained from related literatures in the region. Due to the unavailability of daily temperature, the value of GDD couldn't be obtained.

Diagram 1: Calculation of Bioclimatic parameters



Five dominant PFTs in the region except *Pinus roxburghii* was included in the LPJ-GUESS simulations for the simple reason that all the species except *Pinus roxburghii* falls within the suitable climatic zone for *Abies spectabilis*. Existing PFT descriptions in the guess.ins driver file were copied and renamed before their bioclimatic parameters were updated. The changed values for bioclimatic parameters are given in Table 2. Parameter values relating to growth form, allometry and phenology for PFTs are given in Appendix 2.

Table 2: Regional parameter values used for LPJ-GUESS. Tcmin_surv and Tcmin_est are the minimum coldest month mean temperature for survival and establishment. Tcmax_est is maximum coldest month mean temperature for establishment. Twmin_est is minimum warmest month mean temperature for establishment and GDD5min_est is minimum growing degree days on 5⁰C basis for establishment. * indicates the original parameters have been changed. Numbers in () are the original parameters from (Smith et al., 2001). Numbers in [] are the study in the Tibetan plateau including the study area from (Song, Zhou and Quyang 2004).

Plant Functional Types (PFTs)	Tcmin_surv	Tcmin_est	Tcmax_est	Twmin_est	Gdd5min_est
(Evergreen Conifers)					
<i>Abies spectabilis</i>	-6.0* (-31) [-7.0]	-6.0* (-30) [-7.0]	6.2*(-1) [-1.8]	8.4* (5)	330* (500) [330]
<i>Pinus wallichiana</i>	-1.7* (-2) [-5.5]	-1.7* (-2) [-5.5]	10.4* (10) [17]	12.5 *(5)	850* (2000) [850]
<i>Juniperus recurva</i>	-9.9 *(-31) [-8.0]	-9.9* (-30) [-8.0]	2.2* (-1) [-1.9]	5.4* (5)	(500)
(Deciduous Broadleaved)					
<i>Betula utilis</i>	-16.0*(-30) [-10.0]	-16.0* (-30) [-10.0]	5.4* (7)	7.7*(-1000)	600* (350) [600]
(Evergreen Broadleaved)					
<i>Quercus semecarpifolia</i>	-1.5* (-1) [-1]	-1.5* (0) [-1]	9.3* (10) [17]	11.5* (5)	780* (2000) [780]

2.7. Actual distribution

No detailed work on the distribution of *Abies spectabilis* has been done yet. Several literature studies have documented the potential distribution range but the actual scenario can be different from place to place. The best document, by far, is the one from ICIMOD. There is availability of spatial distribution of forests in Nepal at 30 m resolution (ICIMOD 2009; Uddin et al 2015). This land cover map doesn't differentiate the vegetation at species level but rather at vegetation type (coniferous, broadleaved, grass, shrub, agriculture and bare land). The actual distribution of *Abies spectabilis* at the study site thus has been extracted from the map (coniferous vegetation) intersecting with the potential range of *Abies spectabilis* (2400-4400 m) (Press, Shrestha & Sutton 2000). The limitation with the map is that, still at the potential range, though *Abies* is the dominant vegetation, there can still be presence of other coniferous like *Pinus wallichiana* and *Juniperus recurva*.

2.8. Species relative coverage per elevation zone

Vegetation coverage in terms of LAI was used to show the competition between dominant vegetation in different climatic zones. The output of LPJ-GUESS was clipped with six different climatic zones (Table 3) to extract the coordinate points which falls within these zones. Then, for each zone, LAI values were used to show species relative coverage.

Table 3: Climatic zone and Altitudinal range

Climatic zone	Altitudinal range (masl)
Sub-tropical	1398-2000
Lower-temperate	2000-2500
Upper-temperate	2500-3000
Lower-subalpine	3000-3500
Upper-subalpine	3500-4000
Lower-alpine	4000-4500
Upper-alpine	4500-4600

2.9. NPP and NDVI Value for comparison

The independent estimates for the NPP are extracted from the NASA earth observations (<http://neo.sci.gsfc.nasa.gov/>). The source provides the global NPP values map at 0.1 degrees resolution. The global map is clipped to the study area to extract the value for area of interest. NDVI values for the study area were obtained from IRI/LDEO Climate Data Library (<http://iridl.ldeo.columbia.edu/>).

2.10. Model validation

For the model validation two different approaches were used, error rate (ΔV) and Cohen's kappa (k). The distribution of *Abies spectabilis* on the MCA were simulated with two different models. $0.01^0 \times 0.01^0$ grid cells (1 arc minute) were applied on both models to simulate the distribution areas of *Abies*. The grid cells were applied using the 'create fishnet' tool in arcgis. These grid cells were assembled into continuous distribution areas with a value of 0.1 snap tolerance. Snap tolerance is a command which was used to connect the grid cells within designated distance. The command is used with the 'snapping' tool in arcgis.

The difference between the two maps (ΔV) was obtained by the ratio of the grid cells in which absent species were simulated as present (false positive) and present species were simulated as absent (false negative), to the total grid cells (Sykes et al., 1996).

N = a+b+c+d		Predicted distribution	
		Presence	Absence
Actual distribution	Presence	True positive (a)	False positive (b)
	Absence	False negative (c)	True negative (d)

$$\Delta V = (b+c) / N$$

A ΔV value of <0.15 is interpreted as a sign of excellent agreement between predicted and actual distribution, 0.15-0.30 as very good, 0.45-0.60 as fair, 0.60-0.80 as poor and >0.80 as very poor (Song, Zhou and Ouyang 2004).

Cohen's kappa (k) exclusively used for measuring the agreement between two rasters.

$$k = \frac{\text{Pr}(a) - \text{Pr}(e)}{1 - \text{Pr}(e)}$$

Where, $\text{Pr}(a)$ (relative observed agreement between rasters) = $\frac{a+d}{N}$ and

$$\text{Pr}(e) \text{ (hypothetical probability of chance agreement)} = \frac{a+b}{N} \times \frac{a+c}{N} + \frac{c+d}{N} \times \frac{b+d}{N}$$

If the rasters are in complete agreement then $k = 1$. The higher the value of k , the more is the agreement between two rasters (Smeeton, 1985).

2.11. Predictive modeling

2.11.1. MaxEnt 3.3.3

MaxEnt 3.3.3 was used as a platform to run the predictive modeling for *Abies spectabilis*. The model was run with creating response curves for each predictor variable and doing a jackknife to estimate the relative influence of individual predictors. Jackknife estimates the relative predictive power of different variables. The duplicate presence records per cell were removed. Since MaxEnt consider locations without species observation records as background, 10000 random points were created as background points.

Ten-fold cross-validations were applied to test the model performance and the result was averaged. Converting continuous suitability index map into binary maps requires a

probability threshold to determine the potential habitat changes under the future scenario. The choice of logistic threshold is critical as it influence the model results and outputs (Phillips et al., 2006). "Equal training sensitivity and specificity" was used as a threshold to define habitat and non-habitat areas. To avoid specious predictions of suitable habitat under future climate scenarios for 2050, "fade-by-clamping" option in MaxEnt was used to remove heavily clamped pixels from the final predictions.

MaxEnt supports three outputs formats: raw, cumulative and logistic. For this study, logistic output was selected which defines the logistic function as: $c \cdot r / (1 + c \cdot r)$ where c is the exponential of the entropy of the MaxEnt distribution and r is raw value. The output file type was ascii which was then further processed into arcmap10.2 to produce the final distribution maps.

2.11.2. LPJ-GUESS

An arctic-enabled version of LPJ-GUESS called LPJ-GUESS WHyMe (Miller and Smith, 2012) (Water Hydrology Methane) was used as a platform to run the simulations for all PFTs, including *Abies spectabilis*. We chose this version because it includes soil freezing processes and PFTs suited to high altitudes such as tall and low shrubs. We turned off the model's peatland and methane functionality. The simulated vegetation dynamics are the outcome of competition for light and soil water between plant individuals, each one of which belongs to a defined set of PFTs distinguished by their allometry, phenology, shade tolerance and bioclimatic limits (Miller and Smith, 2012). The model was run with the changes in some bioclimatic parameters (Table 2) and some constant values (Appendix 2). The model was run in cohort mode with 10 replicate patches in each grid cell, with simulations covering the time period from 1901 until 2100. The spin-up phase was set to 500 years. Climate forcing at a resolution of 30 arc second consisted of monthly temperature, precipitation and observed CO₂ concentration. Monthly sunshine % from the CRU TS 3.0 (Mitchell and Jones, 2005) gridcell nearest our study region was used to force the model from 1901-2001, and fixed at the 2001 level thereafter. This ensures that the future climate forcing for both MaxEnt and LPJ-GUESS is as consistent as possible. Similarly, the LPJ-GUESS soil texture class was fixed at a uniform value of 1 for each of the 1724 cells in the study area.

LPJ-GUESS produces the output in text format, which was then further processed in arcmap 10.2 to produce final distribution maps and graphs.

Diagram 2: Flowchart showing steps taken in MaxEnt. The flowchart shows the methods employed to answer the research question (RQ) number 1, 2 and 5. Note that RQ 1 and 5 are answered by both the models.

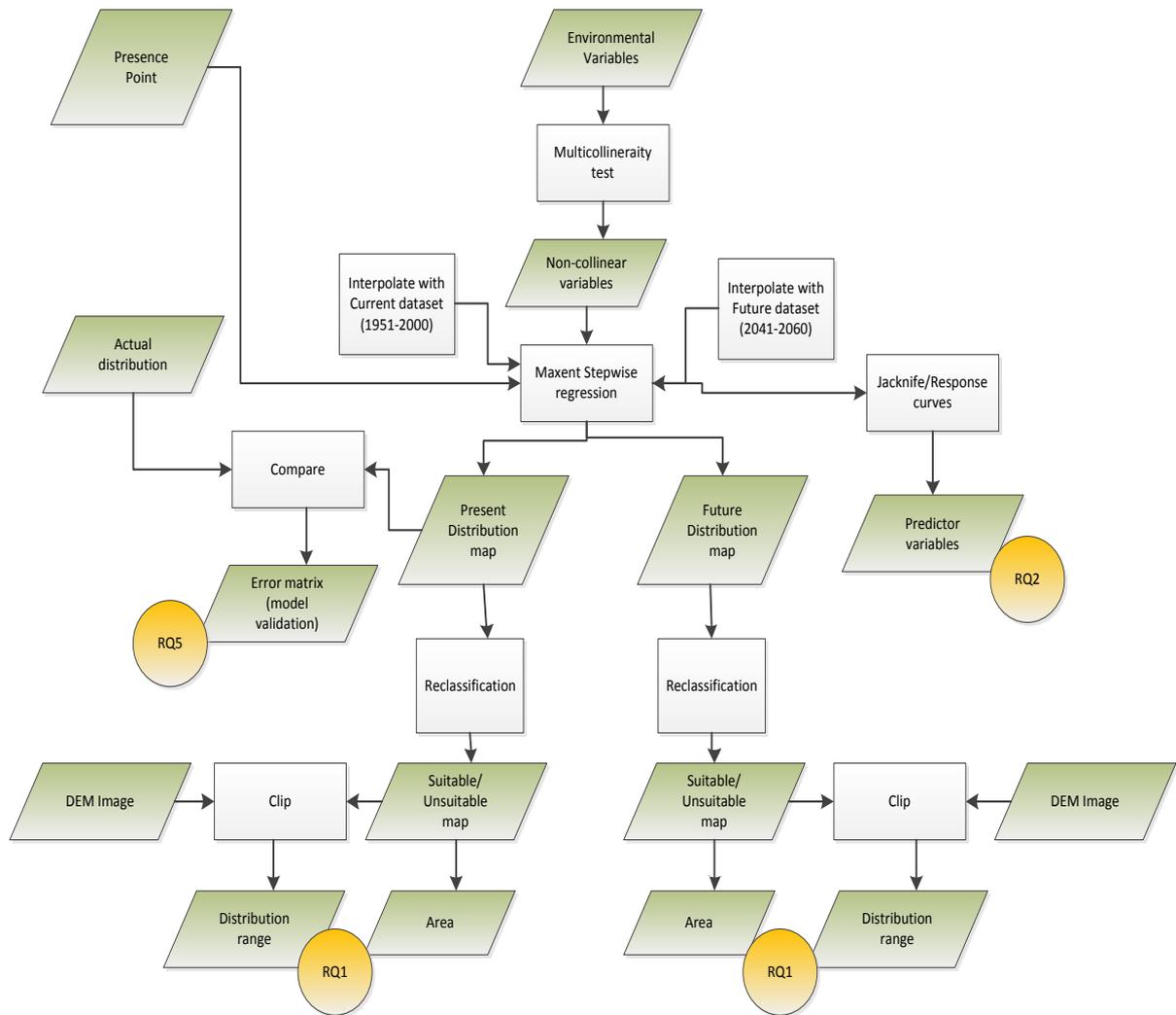
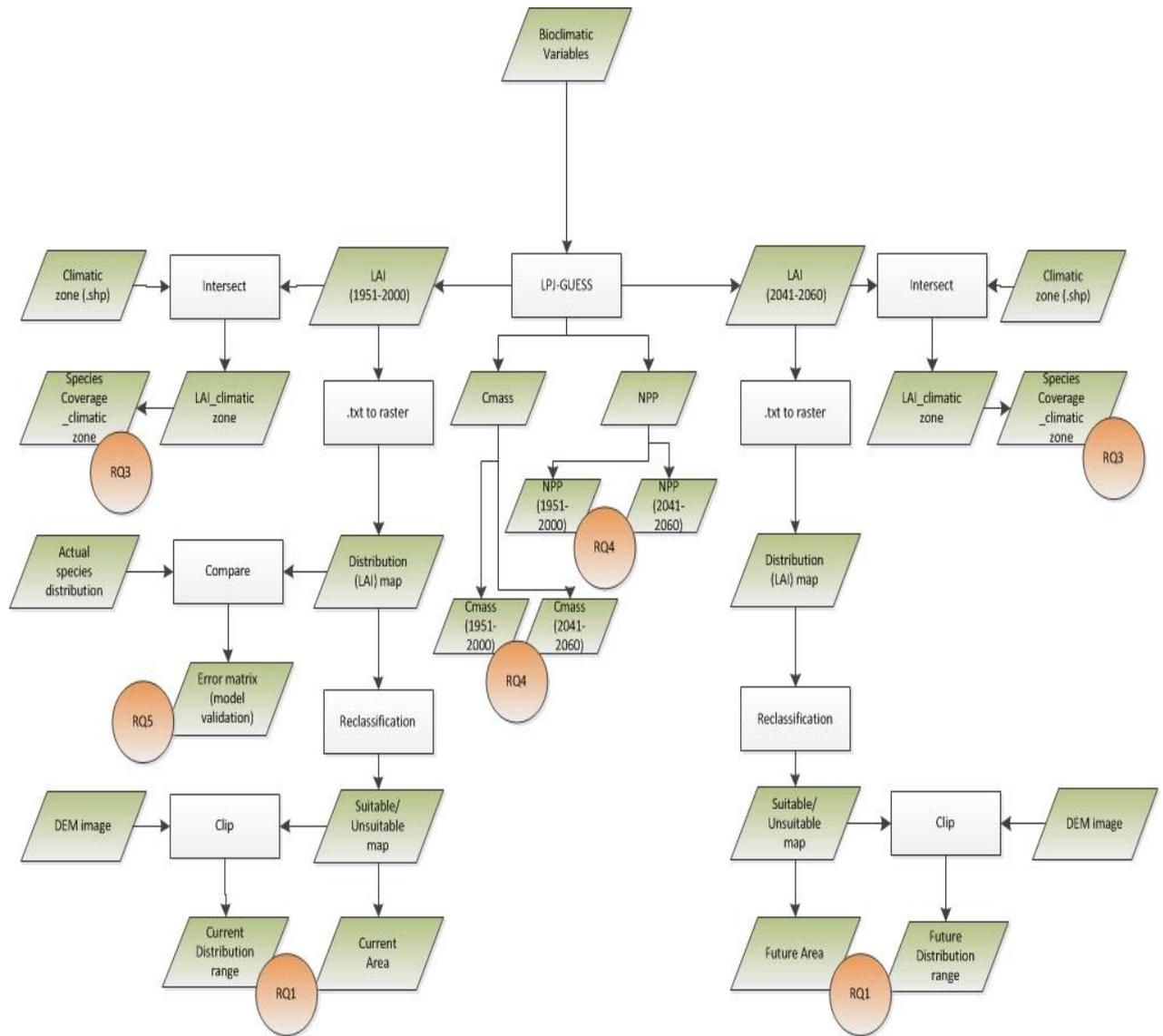


Diagram 3: Flowchart showing steps taken in LPJ-GUESS. The flowchart shows the methods employed to answer the research questions (RQ) 1, 3, 4 and 5. Note that RQ 1 and 5 are answered by both the models.



3. Results

3.1. Model comparison and validation

Visual comparison of the maps shows good agreement between simulated and modeled distribution though with some exception. The MaxEnt largely over predicts the species suitability habitat. The actual distribution shows several patches of suitable habitat whereas MaxEnt produces an almost uniform suitable area. LPJ-GUESS also over predict at some places (Fig 5).

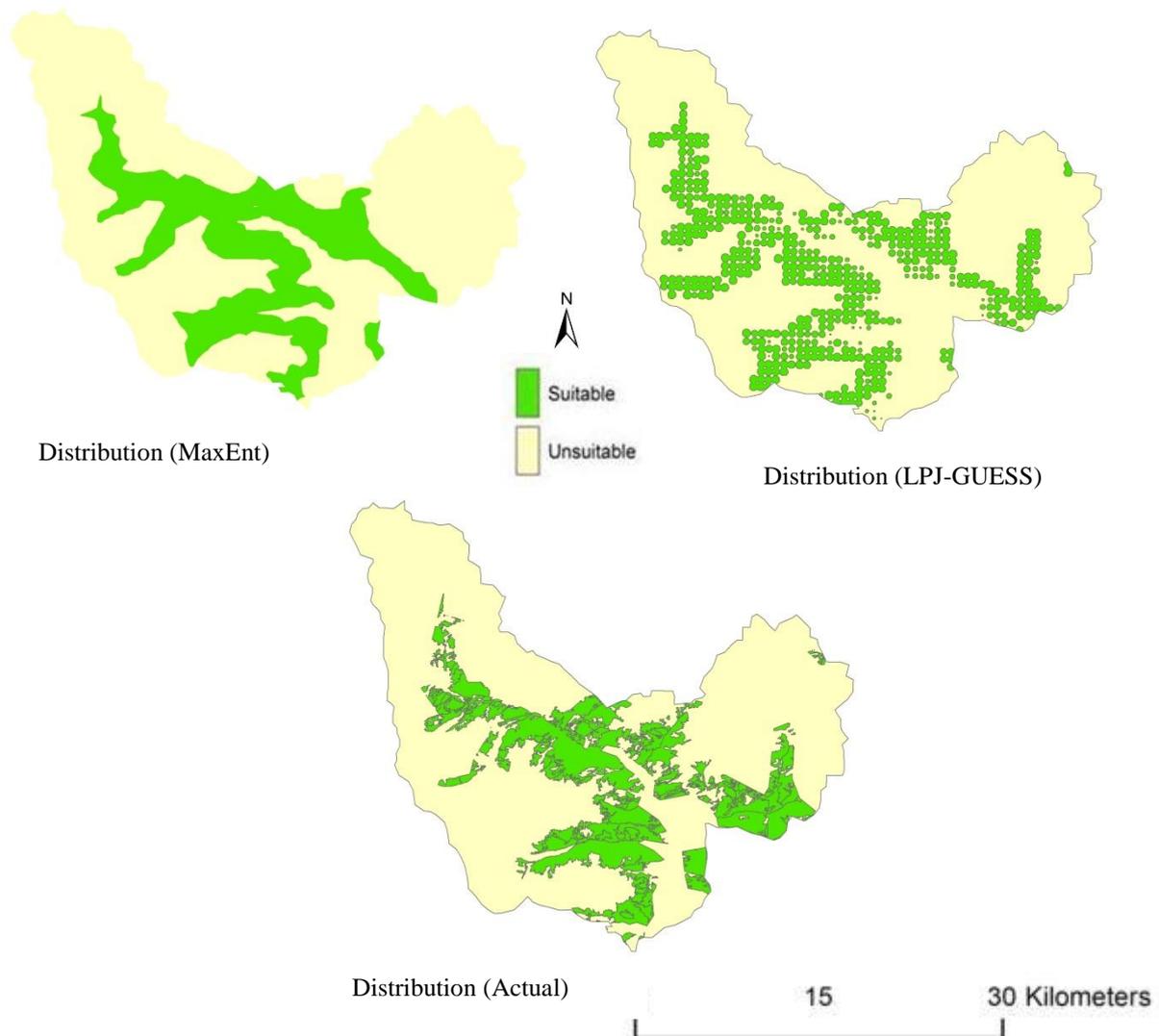


Figure 5: Comparison between model distributions and actual distribution

To compare and to validate the models requires more than just visual comparison. A confusion matrix (also called error matrix) was created to find out the accuracy between the models output and actual distribution.

Actual distribution Vs. LPJ-GUESS:

Table 4: Error matrix showing LPJ-GUESS distribution and Actual distribution

N= 524		Predicted distribution (LPJ-GUESS)	
		Presence	Absence
Actual distribution	Presence	200	22
	Absence	30	272

True Presence
True Absence
False Presence
False Absence

In the actual distribution map, there were 222 grid cells in which species were present whereas 302 grid cells were marked absent. In the LPJ-GUESS simulation, 230 grid cells had species present and 294 grid cells had no species. 22 grid cells were false and 30 grid cells were false negatives (Table 6). The error rate (ΔV) is 0.09 which classifies the model as in excellent agreement with the actual distribution.

Cohen’s kappa: there were 200 grid cells that were granted by both the maps and 272 grid cells that were rejected by both maps. Thus, the observed proportional agreement is $Pr(a) = (200+272) / 524 = 0.90$.

To calculate $Pr(e)$, actual distribution shows 222 grid cells as present and 302 grid cells as absent. Thus actual distribution map shows presence 42% (0.42). LPJ-GUESS model shows 230 grid cells as present and 294 grid cells as absent. Thus LPJ-GUESS model shows presence 44% (0.44). Therefore the probability that both the map shows presence randomly is $0.42*0.44 = 0.18$ and the probability that both of them would show absence is $0.58*0.56 = 0.32$. Thus the overall probability of random agreement is $Pr(e) = 0.18+0.32 = 0.5$.

Cohen’s kappa (k) = $Pr(a) - Pr(e) / 1-Pr(e) = 0.8$ which tells that the LPJ-GUESS model is in good agreement with the actual distribution.

Actual distribution Vs. MaxEnt:

Table 5: Error matrix showing MaxEnt distribution and Actual distribution

N= 524		Predicted distribution (MaxEnt)	
		Presence	Absence
Actual distribution	Presence	181	41
	Absence	18	284

True Presence
True Absence
False Presence
False Absence

In the actual distribution map, there were 222 grid cells in which species were present whereas 302 grid cells were marked absent. In the MaxEnt simulation, 199 grid cells had species present and 325 grid cells had no species. 41 grid cells were marked false presence and 18 grid cells were false absence (Table 7). The error rate (ΔV) is 0.11 which classify the model as in excellent agreement with the actual distribution.

Cohen's kappa: there were 181 grid cells that were granted by both the maps and 284 grid cells that were rejected by both maps. Thus, the observed proportional agreement is $\Pr(a) = 181+284/524 = 0.88$.

To calculate $\Pr(e)$, actual distribution shows 222 grid cells as present and 302 grid cells as absent. Thus actual distribution map shows presence 42% (0.42). MaxEnt model shows 199 grid cells as present and 325 grid cells as absent. Thus MaxEnt model shows presence 38% (0.38). Therefore the probability that both the map shows presence randomly is $0.42*0.38 = 0.16$ and the probability that both of them would show absence is $0.58*0.62 = 0.36$. Thus the overall probability of random agreement is $\Pr(e) = 0.16+0.36 = 0.52$

Cohen's kappa (k) = $\Pr(a) - \Pr(e) / 1-\Pr(e) = 0.75$ which tells that the MaxEnt model is in fair agreement with the actual distribution.

3.2.Species Distribution (Area)

3.2.1. MaxEnt

The species distribution of *Abies spectabilis* as predicted by MaxEnt, shows little changes between the current scenario (1951-2000) and future scenario (2041-2060) (Fig 6).

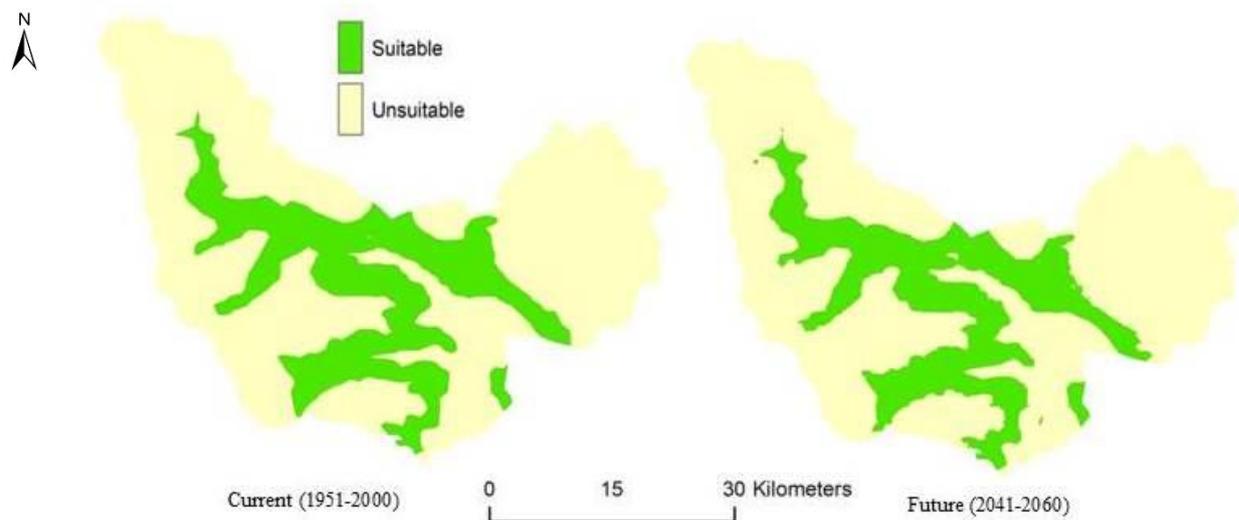


Figure 6: The current and future *Abies spectabilis* distribution as predicted by MaxEnt

There are minor changes in the potentially suitable area. Notably, all the changes that are taking place are in the forest-alpine transitional zone near the treeline (3000-4000 masl) (Fig 7).

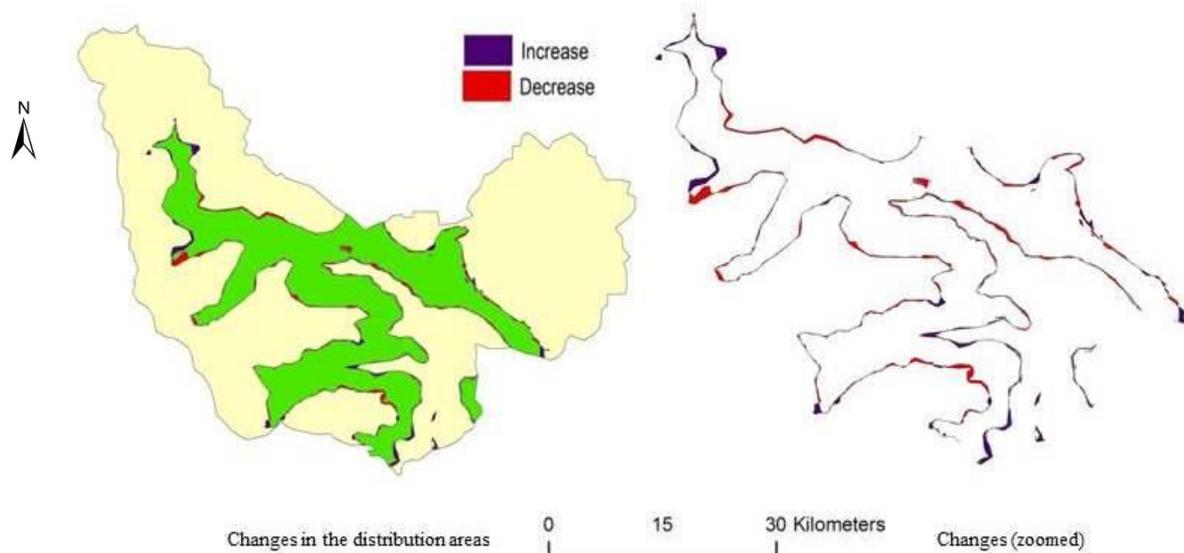


Figure 7: Changes in the distribution area for *Abies spectabilis*

3.2.2. LPJ-GUESS

LPJ-GUESS simulation showed that the species distribution in terms of LAI (LAI > 0) will change considerably in the coming years (Fig 8). Note that the smaller size indicates lower LAI and bigger size indicates higher LAI.

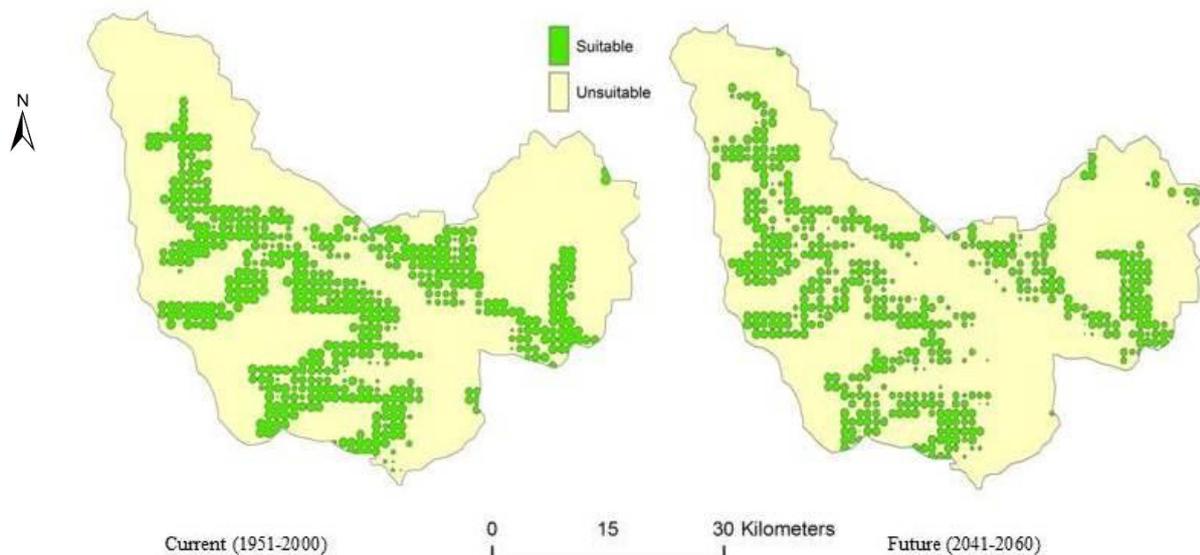


Figure 8: the current and future *Abies spectabilis* distribution as produced by LPJ-GUESS

LPJ-GUESS predicts that the suitable area will shrink by the year 2050. Notably, the habitat is decreasing more in the west than in the east. Both the models agree to the point that it is in

the forest-alpine transition zone where suitable areas are shrinking (Fig 9). Notably, the species is expanding to higher elevations.

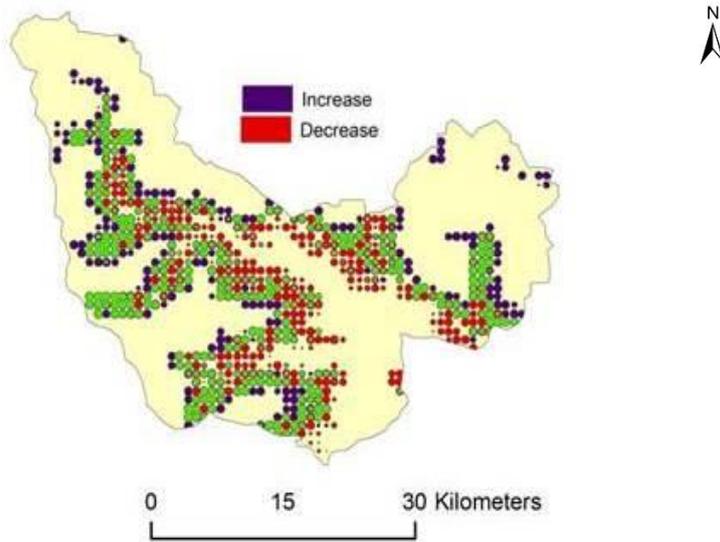


Figure 9: Changes in the distribution area for *Abies spectabilis*

The MaxEnt model predicts that, in the future scenario, only around 3% of the suitable habitat will be reduced. It calculates the unsuitable areas will be increased from 956 to 966 sq. km (increase by 1.15%) while the suitable areas will be decreased from 346 to 335 sq. km. (Table 4).

LPJ-GUESS shows considerable changes in the suitable areas, which will be reduced by 20.5% by the year 2050. The model calculates the unsuitable areas will be increased from 999 to 1063 sq.km (increase by 6.30%) while the suitable areas will decrease from 302 to 239 sq. km. (Table 4).

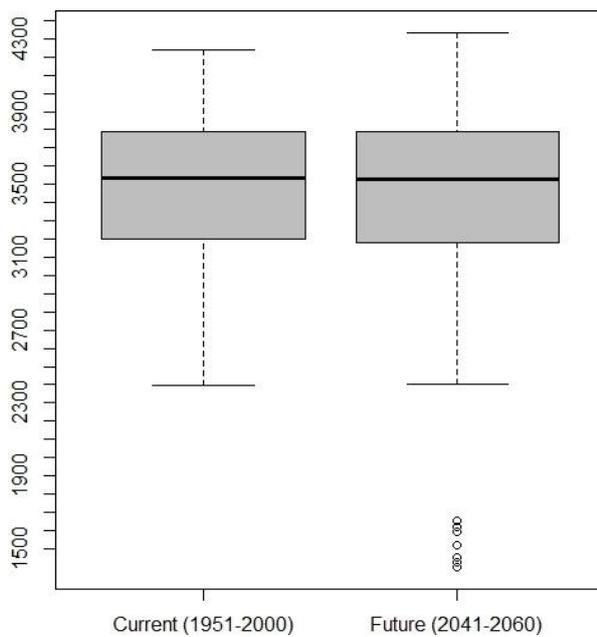
Comparison of the models in terms of suitable area shows that LPJ-GUESS is very close to the actual distribution. The actual scenario shows the area of unsuitable areas of 994 sq. km and suitable area of 307 sq. km. (Table 4).

Table 6: *Abies spectabilis* habitat: Suitable and unsuitable areas

Area (Sq. km.)	MaxEnt		LPJ-GUESS		Actual
	Current (1951-2000)	Future (2041-2060)	Current (1951-2000)	Future (2041-2060)	Current (2010)
Unsuitable	955.7	966.5	999.7	1062.8	994.8
Suitable	346.1	335.3	302.1	239	307

3.3. Species Distribution (Elevation range)

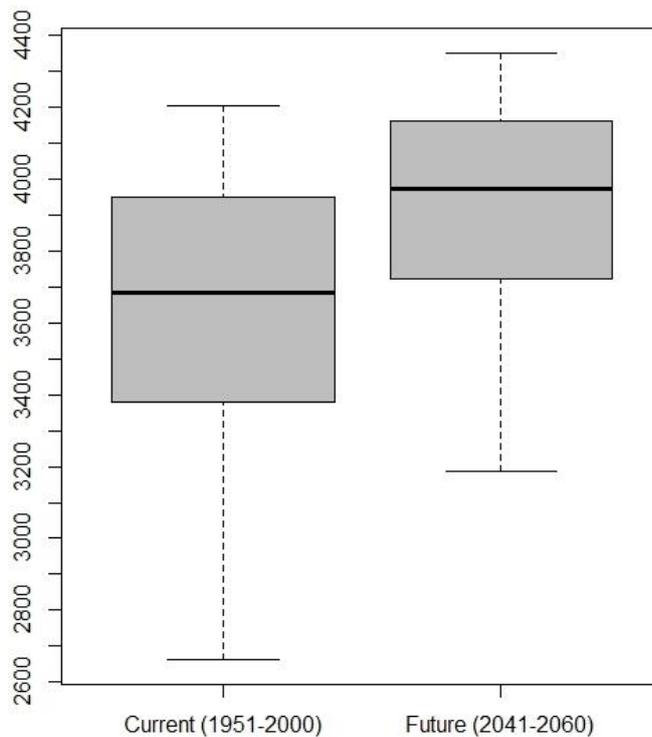
3.3.1. MaxEnt



The MaxEnt model predicts the current elevation range for the species ranges from 2400-4250 masl. In the future scenario, the species will move upwards by 70m and the upper species limit will be 4320 masl. The species will move upwards by the rate of 14m per decade (Fig 10).

Figure 10: Boxplot distribution (MaxEnt)

3.3.2. LPJ-GUESS



LPJ-GUESS predicts the current elevation range for the species ranges from 2650-4200 masl. In the future scenario, the species will move upwards by 150m. The upper species limit will be 4350 masl. The species will move upwards at the rate of 30m per decade (Fig 11). One striking dissimilarity with MaxEnt is in the lower elevation limit of the species, which does not change in MaxEnt output but LPJ-GUESS showed a shift of 550 m.

Figure 11: Boxplot distribution (LPJ-GUESS)

3.4. Species relative coverage

Species relative coverage in terms of LAI was calculated in each climatic zone. LAI values from LPJ-GUESS were used to see which species are/will present in each climatic zone. The research showed a clear horizontal and vertical transformation of vegetation patterns caused by different climatic and non-climatic factors.

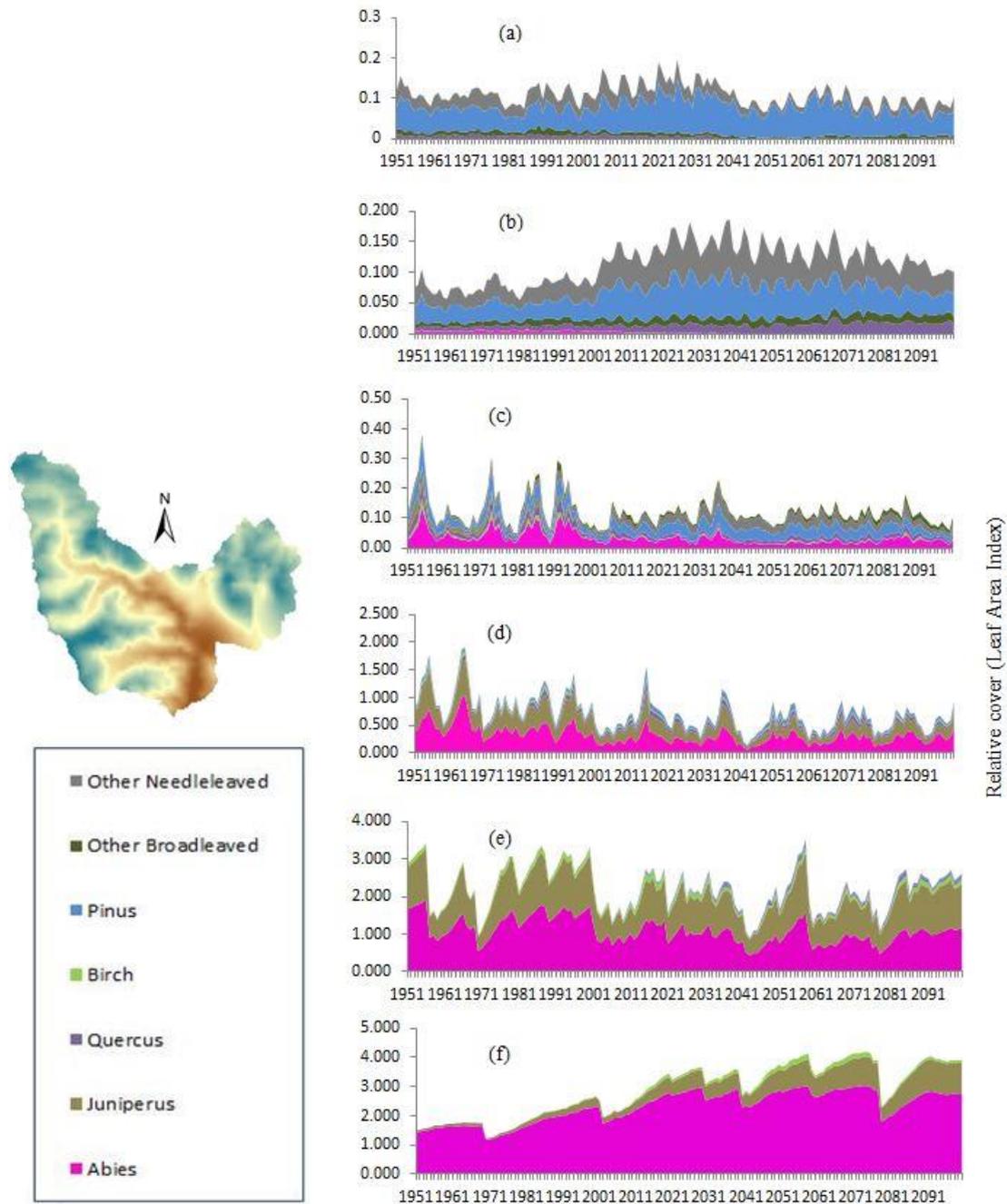


Figure 12: Potential changes in species coverage for dominant tree species in MCA as predicted by LPJ-GUESS: (a) sub-tropical climate zone, (b) lower-temperate climate zone, (c) upper-temperate climate zone, (d) lower-subalpine climate zone, (e) upper-subalpine climate zone and (f) lower-alpine climate zone

3.4.1. Sub-tropical zone (1400-2000masl)

The Sub-tropical climatic zone is observed suitable for *Pinus roxburghii*, *Pinus wallichiana* and *Quercus semecarpifolia*. Although *Pinus wallichiana* and *Quercus semecarpifolia* are not considered dominant species in this zone (refer fig 1d and Appendix 1), the distribution range falls within the potential habitat for these two species (Press, Shrestha and Sutton 2000).

The current climate scenario shows *Pinus wallichiana* has highest vegetation coverage within this zone trailed by other needeleaved, which is mainly represented by *Pinus roxburghii*. In the future, *Quercus* will have reduced coverage from this zone suggesting the possible upward range shift (Fig 12a and Fig 12a).

3.4.2. Lower-temperate zone (2000-2500 masl)

In the lower-temperate zone, *Pinus wallichiana* together with other needeleaved has the highest coverage, followed by *Quercus semecarpifolia*, other broadleaved and *Abies spectabilis*. In the current scenario, in the future, *Pinus* and *Quercus* will increase their coverage while *Abies* will be almost lost from the zone (Fig 12b and Fig 12b).

3.4.3. Upper-temperate zone (2500-3000masl)

In the Upper-temperate zone, in terms of vegetation coverage, *Abies spectabilis* face strong competition from *Pinus* and other needeleaved species. *Juniperus recurva* has sparse coverage in the current scenario and by the year 2050, the species will be absent from this zone (Fig 12c).

3.4.4. Lower-subalpine zone (3000-3500masl)

In the lower-subalpine zone, all the five tree species are present. *Pinus* and *Quercus* are advancing in this zone, considering the fact that the upper elevation limit of this zone is outside the suitable habitat for these two species. In the future scenario, *Juniperus* and *Abies* will both have reduced coverage (Fig 12d).

3.4.5. Upper-subalpine zone (3500-4000 masl)

In the upper-subalpine zone, *Abies* and *Juniperus* have highest coverage in terms of LAI trailed by *Betula*. *Quercus* has sparse vegetation in this zone. The future scenario brings an increase in coverage for *Juniperus* and *Quercus*. *Quercus* will be claiming this zone in the future while *Abies* is losing the zone (Fig 12e and Fig 12e).

3.4.6. Lower-alpine zone (4000-4500masl)

In the Lower-alpine zone, *Abies spectabilis* has highest vegetation coverage. The coverage of *Betula utilis* is sparse. In the future scenario, the zone holds good for the population of *Abies* supporting the hypothesis that plants are actually shifting upwards. *Juniperus* and *Betula utilis* subsequently increasing its coverage in the future (Fig 12f and Fig 12f).

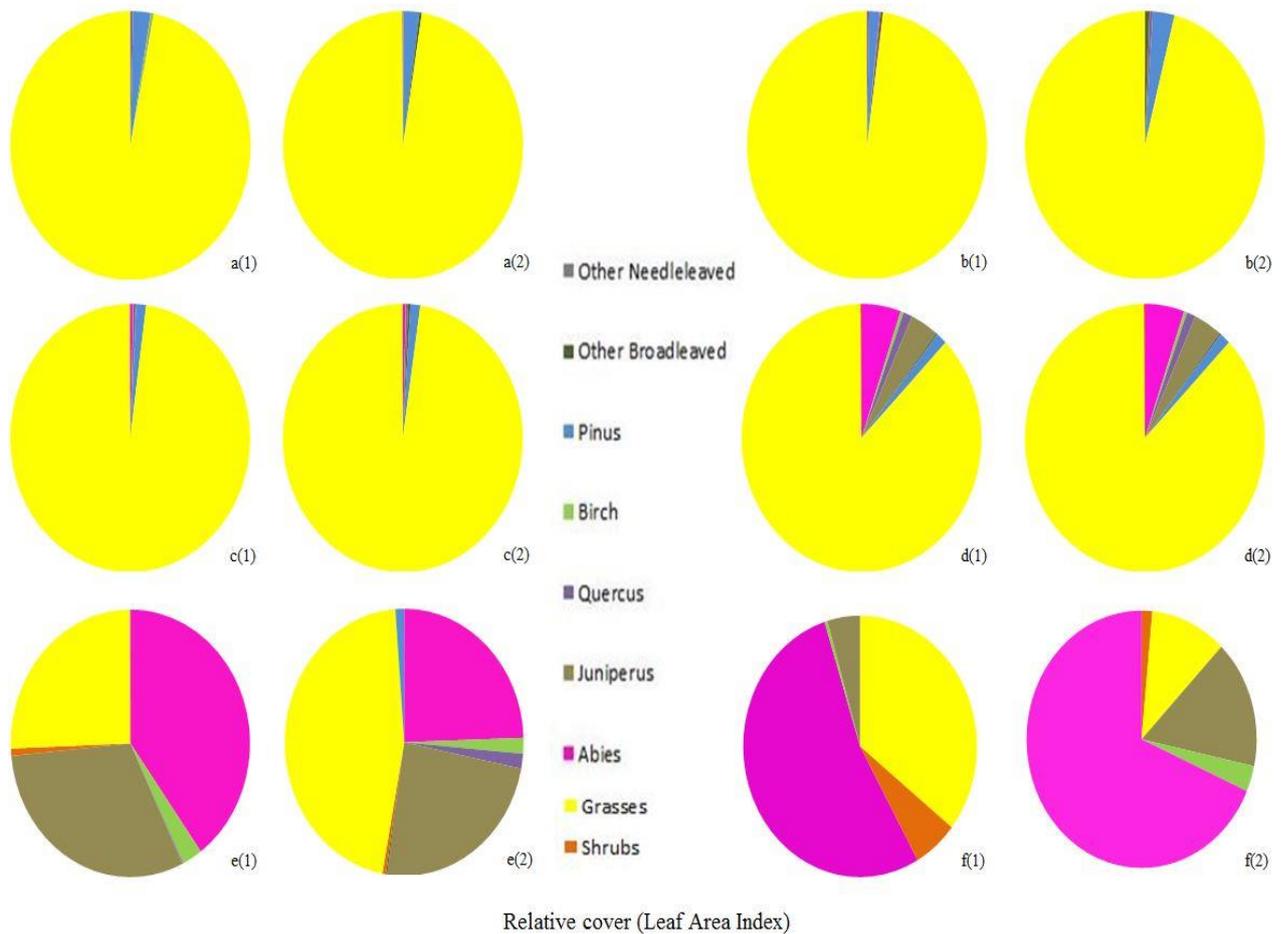


Figure 13: Proportional coverage by all vegetation including grasses and shrubs: a(1) and a(2) current and future scenario in sub-tropical zone, b(1) and b(2) current and future scenario in lower-temperate zone, c(1) and c(2) current and future scenario in upper-temperate zone, d(1) and d(2) current and future scenario in lower-subalpine zone, e(1) and e(2) current and future scenario in upper-subalpine zone and f(1) and f(2) current and future scenario in lower-alpine zone.

The Figure shows the dominance of vegetation coverage by grasses in the subtropical and temperate zone. Looking at the subalpine and alpine zone (Fig 13 d,e,f) it's clear that whenever the trees are increasing their coverage, grass coverage is decreasing. Shrubs are making their significant presence from the subalpine zone. However, the future doesn't bring good coverage for shrubs, as they will have reduced coverage from the upper-subalpine (Fig 13e) and lower alpine zone (Fig 13f). The values for all the PFTs per climatic zone are given in Appendix 3.

3.5. Response of Net Primary Productivity (NPP)

LPJ-GUESS predicts that annual average NPP for *Abies spectabilis* is increasing in the future. The time series shows NPP values in the range of 140 to 270 ($\text{gC m}^{-2} \text{yr}^{-1}$) for the current scenario with the mean value of 212. Under the future scenario, NPP is increasing with a mean value of 275.8 (Fig 14), which is characterized by increase in temperature, precipitation and CO_2 concentration (see fig 3). The NPP ranges from 240 to 310 ($\text{gC m}^{-2} \text{yr}^{-1}$). The modeled NPP values were compared with observed NDVI values for the same time period. NDVI is considered as a surrogate estimator of NPP in some cases (Xu et al., 2012). Consistent with the observed NDVI variation, LPJ-GUESS predicts almost similar variation in NPP for the period 2000-2014 (Fig 15 a) and LAI (Fig 15 b).

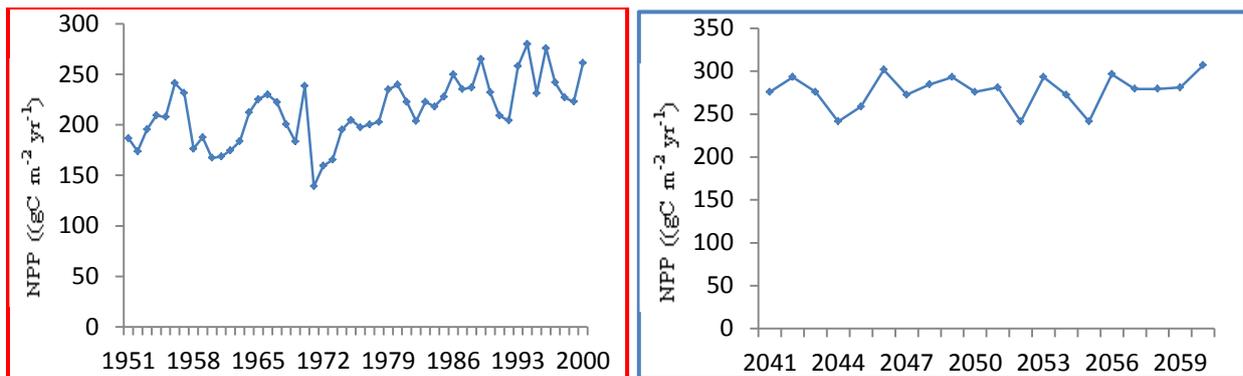


Figure 14: Time series of annual current and future NPP over the MCA as predicted by LPJ-GUESS

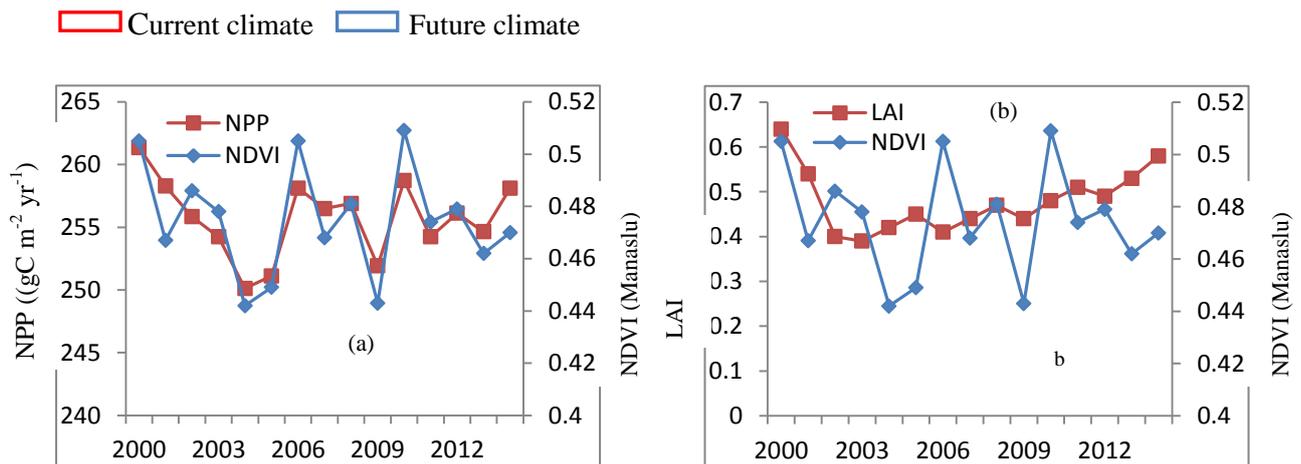


Figure 15: (a) NDVI (Manaslu) and modeled NPP ($\text{gC m}^{-2} \text{yr}^{-1}$) and (b) NDVI (Manaslu) and modelled LAI

3.6. Response of Carbon biomass (cmass)

LPJ-GUESS predicts an increase in carbon biomass with the increase in temperature,

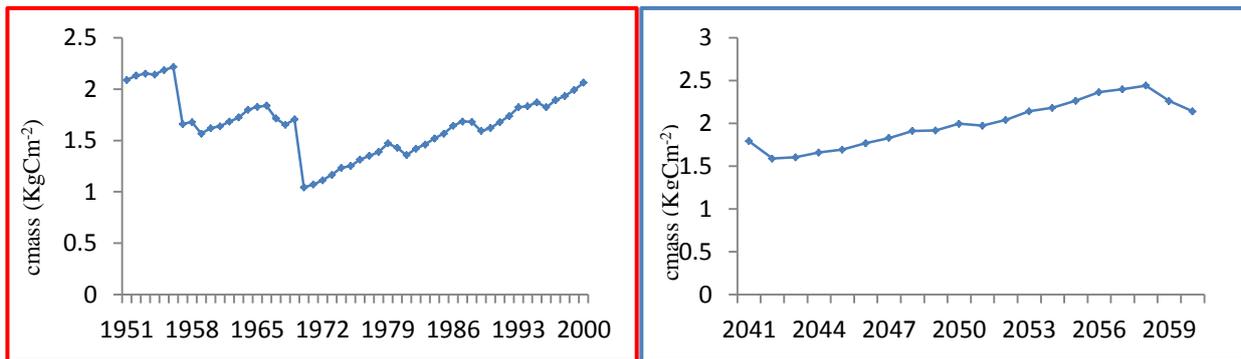


Figure 16: Time series biomass current and future

Current climate
 Future climate

precipitation and CO₂ concentration. The time series (Fig 16) shows total Cmass value for *Abies spectabilis* in the range of 1.1 to 2.2 (KgCm⁻²) under current scenario with the mean value of 1.66 (KgCm⁻²). Future scenario shows the continuous growth trend in the range of 1.5 to 2.3 (KgCm⁻²) with the mean value of 1.99 KgCm⁻² (Fig 16).

3.7. Contribution of Environmental variables

Relative predictive power: To find out, which environmental variable is most important in defining the distribution of *Abies spectabilis*, a jackknife test was done in the MaxEnt model and the results are shown in Fig 17. Jackknife shows the importance of environmental variables used in the modeling. The environmental variable with highest gain when used in isolation (blue bars) is bio7 (temperature annual range) for the current and Bio11 (Mean temperature of coldest quarter) for the future which shows the variables have the most useful information by itself. The environmental variable that decreases the gain most (light green bar) when omitted is bio15 (precipitation seasonality) for both scenario, which therefore appears to have the most information that isn't present in other variables. The values shown here are averages over 10 replicate runs (Fig 17). If MaxEnt uses only bio14 (precipitation of driest month) for the current and bio3 (isothermality) for the future, it achieves almost no gain, so that variable is not (by itself) useful for estimating the distribution of *Abies spectabilis*. Turning to the blue bars, it shows that no variable (except bio15) contains a substantial amount of useful information that is not already contained in other variables, because omitting each variable in turn did not decrease the training gain considerably (see light green bars).

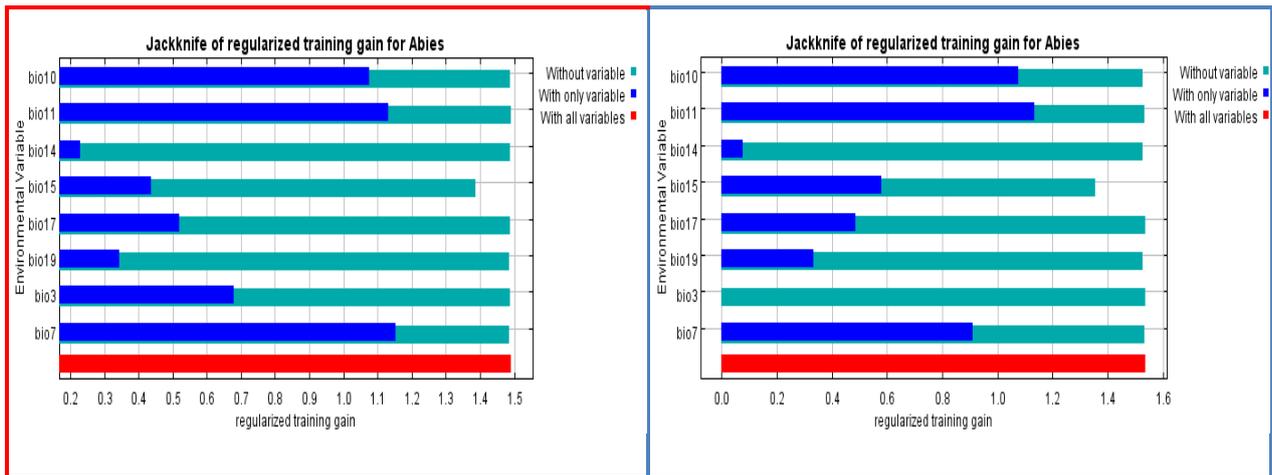


Figure 17: Relative predictive power of different bioclimatic variables

Current climate Future climate

Relative contribution: Table 4 shows the estimates of relative contributions of the environmental variables to the MaxEnt model. Percent contribution values are heuristically defined which depend on the particular path that the MaxEnt code uses to get to the optimal solution. Whereas, permutation importance is determined by randomly permuting the values of that variable among the training points (Phillips, Anderson and Schapire 2006). A large difference indicates that the model depends heavily on that variable. It shows that three variables, Bio7, Bio15 and Bio17 has most contribution and that the model depends heavily on Bio7 for the current . the future shows the added importance of Bio11.

Table 7: variable contributions

Variable	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Bio7	64.5	2.6	12.5	0.5
Bio15	21.1	51	35.6	63.2
Bio17	9.9	2.8	10.1	0
Bio10	2.1	29.6	2.5	13.3
Bio11	1.2	6.2	37.8	15
Bio19	1	6.3	1.3	6.7
Bio3	0.2	0.4	0	0
Bio14	0.1	1.1	0.2	1.2

Current climate Future climate

Prediction dependency on variable: Response curves were created in MaxEnt to show how each variable affects the MaxEnt prediction. The curve shows how the logistic prediction changes as each environmental variable is varied, keeping all other variables at their average sample value. Red margins shows the mean response of 10 replicate runs and blue margins shows the mean +/- one standard deviation (Fig 18).

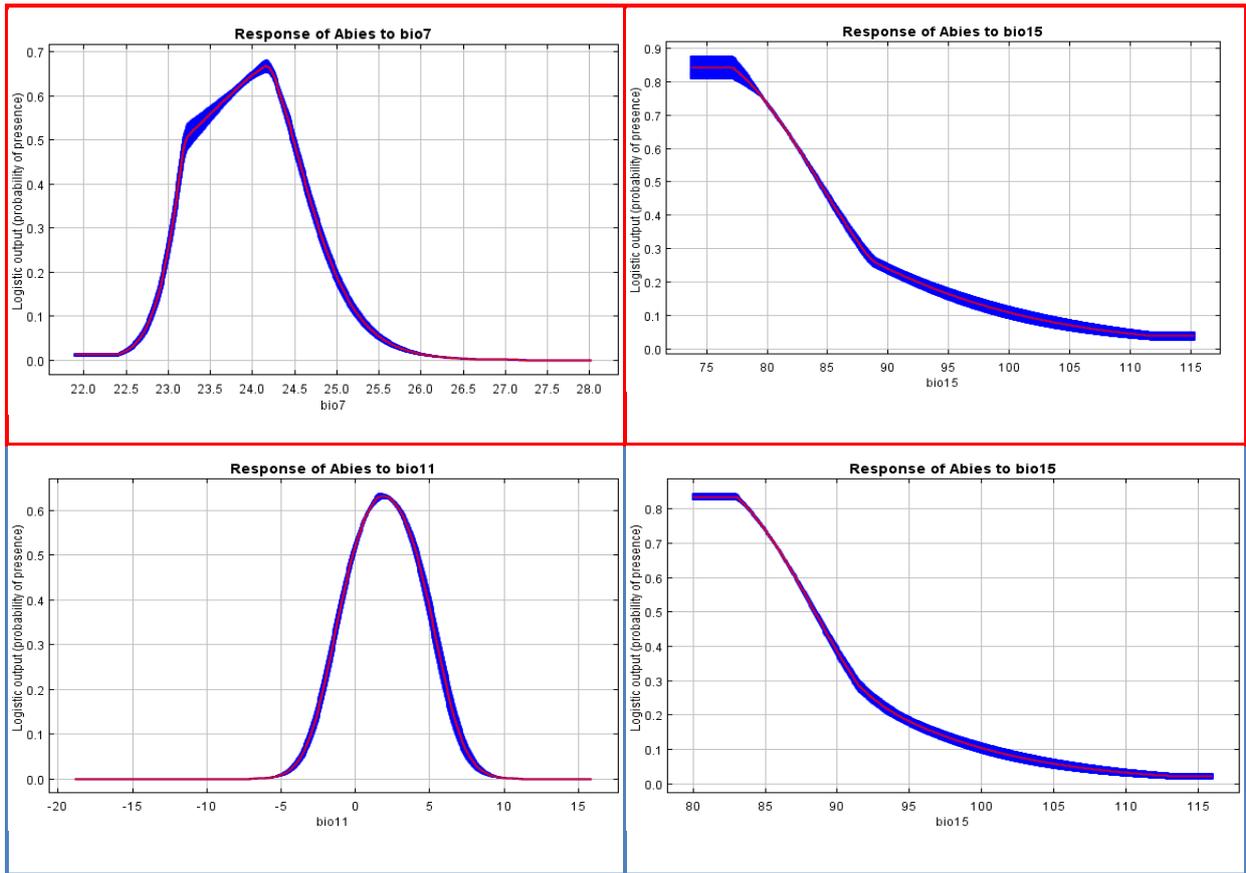


Figure 18: Response curves showing the relationship between the species probability presence and environmental predictors

▭ Current climate ▭ Future climate

The response curve explains that species probability of presence is highest in the temperature annual range (Bio7) of 23.2 to 24.2 °C. while, the habitat with the window of annual temperature range 22-22.5°C and 26-28°C is unsuitable for *Abies spectabilis*. Bio15 (precipitation seasonality or variation) of more than 80mm gradually lower the species presence probabilities. The future scenario shows slightly more resistance to precipitation variation.

Bio11 (Mean temperature of coldest quarter) is the variable which will affect the presence of *Abies* in the future. It shows a window of 0-4°C is best (at least 50% probability). If the mean temperature of coldest quarter is lower than -5°C or higher than 8°C, there is almost no probability of species occurrence.

4. Discussion

4.1. Species distribution (Area)

Plants which are adapted to mountain environments and are particularly climate sensitive could be at the risk of significant habitat losses (Millennium Ecosystem Assessment 2006). Being an ecotone species, *Abies* shows higher sensitivity towards climate changes. With a climate shift, vegetation normally responds by shifting their range of distribution to compensate for the changed climate parameters (Kullman 2008). However, species which are linked to mountain tops are more prone to significant habitat loss and ultimately extinction, because they don't have any escape place (Millennium Ecosystem Assessment 2006).

The finding of this study that, *Abies spectabilis* will bear habitat loss with the changing climate is in line with several research findings. Tanaka et al. (2012) noted large extent loss of suitable habitat for *Abies* species under future climate change in Japan. Khanum, Mumtaz and Kumar (2013) concluded that there will be moderate to high impacts of climate change on the distribution of Asclepiads and argued that plants from moderate altitude and climate will suffer more habitat loss.

However, it is improper to generalize the finding and conclude that upward shifting of species will always end with habitat loss. (Elsen and Tingley 2015) analyzed the elevational availability of surface area for global dataset and argued that in the Himalayas, lower montane species may actually receive increase in habitat area until their lower limit range surpasses high (4500 masl) elevation.

Climate change impact will vary from species to species largely depending on individuals' ability to cope with changing scenario. While considering the future prediction on habitat loss, one should also take into account the rate of dispersal, as rightly pointed out by (Skov and Svenning, 2004). They described that because of dispersal rate, the future distribution of a species might not fully correspond with the area that is suitable for it, but will be smaller. Species with poor capacity of dispersal is more likely to suffer this phenomenon. *Abies* shows weak capacity of dispersal which is 8 m for seeds and 13 m for seedlings (Wolf 2003).

4.2. Species distribution (Elevation range)

The present study showed that upper limit of *Abies spectabilis* will be moving towards the mountain top. The rate of species movement will be 14 meters per decade with total shift of 70 meters in the coming 50 years (MaxEnt) and 30 meters per decade with total shift of 150 meters as shown by LPJ-GUESS (Fig 10 and 11). The result of this study matched with the warming trend found by (Shrestha et al., 1999) indicating that climate warming has facilitated the upward movement of the plant. However, the large increase in the lower elevation range and higher upward movement shown by LPJ-GUESS emphasized on the importance of also accounting the factor other than climatic variables. The occurrence of favorable climatic conditions for seedling survival and growth when they escape the snow level and thus the microsite conditions (including the soil physiology, biotic interaction) will determine the ability of species to move upwards (Batllori et al., 2009).

The finding of this study is consistent with the study done by Suwal (2010) in the tree line advance of *Abies spectabilis* for the same study area where the rate of expansion was 34.29 meters per decade with total shift of 168 meters for the last 50 years (1958-2008). The study was based on individual age determination and historical records of the absolute altitudinal limits and is largely justifying the upward movement of species predicted by LPJ-GUESS. Similar is the finding from a study conducted by Vijayprakash and Ansari (2009) in Eastern Nepal on treeline shift of *Abies spectabilis* who observed the treeline shift by 23 meters per decade. (Gaire et al., 2014) studied the treeline dynamics with climate change at MCA and found the upward shifting of *Abies spectabilis* at the rate of 26.1 meters per decade since 1850.

Species display different rates of movement, behaving in a seemingly eccentric way in response to climate change. However species that are geographically restricted to mountains show more pronounced changes in distribution (Millennium Ecosystem Assessment 2006). Lenoir et al. (2008) depicted significant upward shift of 171 forest species by 29 meters per decade in west Europe and concluded that the shift is larger for species adapted to mountain environment.

The upward movement of a species may well be connected to its migration and biogeographical history as argued by Kullman (2008). Doing a study on some selected subalpine species in northern Sweden, he noted an upward movement of 500-800 meters since the early 20th century and concluded that the plant have reinvaded elevations where they grew during the warmest phase of the Holocene. Reconstruction of past climate in the Himalayas and modeling *Abies* distribution could shed more light on the theory, but that was beyond the scope of this research.

Climate warming within the past few decades has been sufficient to evoke substantial range limit expansion of *Abies spectabilis* (Suwal 2010, Shrestha et al. 1999, Song et al. 2004). However, it's improper to conclude that climate warming related changes are the only causal factor.

4.3. Species relative coverage

The research showed a clear horizontal and vertical transformation of vegetation patterns caused by different climatic and non-climatic factors. This vegetation pattern is attributed to the combined effect of topography and micro-climatic conditions (Ohsawa et al. 1986). The well regulated vegetation patterns along the climate gradients also indicate that climate factors controls the distribution of vegetation.

Pinus is dominant species in sub-tropical and temperate zone (see Fig 12 a and b). The plant grows in drier areas, susceptible to fire where the plant grows as an early successional species (Ohsawa et al. 1986). With the onset of increased temperature and precipitation in the coming future (see Fig 3), the plant tends to shift upwards to compensate for the changed climate. The species is also a pioneer tree in central Nepal, pioneers in the strict sense because of their adaptation to temporary bare grounds (Ohsawa et al. 1986). Because of the pioneer nature,

the plant invades into local habitat with special conditions, such as dry ridge tops giving tough competition to *Abies* populations.

Quercus spp are characterized by small, thick coarse leaves and a good ability to adapt to cold and dry habitats (Press et al., 2000). Higher elevation climatic zones receive less precipitation (see Fig 3) making it a suitable habitat for *Quercus* to proliferate. As pointed out by several studies (Ohsawa et al., 1986, Redmond et al., 2012), drier habitat prefers *Quercus* dominance because of its deep roots, xeromorphic leaves and an ability to adjust osmotically, conversing drought tolerance. The result (Fig. 12 and 12) also shows its dominance towards higher elevation climate zones, suggesting the plant might compete with *Abies* population in the future.

The alpine zone is dominated by *Juniperus recurva* along with *Abies spectabilis*. *Betula* population prefers more cold and humid conditions. Given the condition that, higher elevation climate zone receives less precipitation, the plant might seek the specific patches of habitat with cold and humid climate, thus not being a major competition to *Abies* population (Fig 12 and 13). The future climate condition doesn't hold any optimistic scenario for *Betula* population which might decline, as seen in the study done by (Song et al. 2004) where they predicted substantial loss of habitat in the coming future for *Betula* in the Tibetan plateau.

The displacement of *Abies* population completely from the lower-temperate zone in the future (see Fig 12b and 12b), indicates the role of species biotic interaction along with climatic factor. Climate change is certainly the primary factor, but it's not the only one. Had it been only due to climatic factors, the future distribution of species along the elevation, as produced by two models (see Fig 10 and 11), should not be different as they are fed with the same climatic conditions. MaxEnt (which primarily considers only climatic factor in shaping species distribution), shows the future *Abies* distribution in the range of 2400-4320 m (Fig 10), whereas LPJ-GUESS (which incorporates vegetation dynamics, plant physiology and biophysics) completely denied the species presence lower than 2600 m. the results indicates a certain role of biotic interaction in defining the future distribution of *Abies* population.

4.4. Response of Net Primary Production (NPP) and carbon biomass (cmass)

The simulation result from LPJ-GUESS suggested that the *Abies spectabilis* population would exhibit increased productivity in response to an overall warming trend over the period 1951-2060 (fig 14). This productivity increase can be partly traced to the temperature dependent advancement of the spring onset of photosynthesis, which leads to a longer growing season (Miller and Smith 2012). CO₂ further enhance the productivity. The added productivity is used by the plant for higher leaf area and for horizontal and vertical canopy growth, increasing light interception and further augmenting production (Miller and Smith 2012).

Several studies found productivity increases with the climate warming. (Miller and Smith 2012) studied tundra vegetation response to recent arctic warming and found increasing primary production and leaf area index. (Wolf et al., 2008) found the increase in biomass,

leaf area index and net primary production along with the extension of the forest northwards and upwards in the mountain in the Barents region.

With the vertical and horizontal canopy growth of the taller trees, underlying or ground vegetation receives less light, resulting in decreased productivity and coverage. This corresponds to our model simulation results where it is seen that increase in leaf area index of dominant tree species is followed by decrease in grasses and shrub coverage (Fig 13 d,e,f). (Elmendorf et al., 2012) analyzed changes in community structure of arctic tundra and observed that an increased overall abundance of shrubs and trees brings decreased coverage of bare ground.

Contrary to the understory herbs or bare ground, shrubs and trees are favored by increase in light attenuation, resulting in shrub expansion and densification. The increase in carbon biomass of *Abies spectabilis* can thus be related to the increase in its leaf area index. (Gaire et al. 2014) observed that the radial growth of *Abies spectabilis* is more responsive to temperature change. The researchers studying the treeline dynamics with climate change at Manaslu conservation area found the significant increase in *Abies* basal area as well as increment in plant density.

Although there is high degree of correlation between NDVI and NPP (Fig 15a), there can be a substantial difference in terms of both area and spatial distribution between the assessment outcomes of these two indicators (Xu et al., 2012). NDVI identify vegetated areas and used to detect live green plant canopies in multispectral remote sensing data. So even in grasslands or scrub forest, NDVI will be high but NPP will comparatively less than forests.

However, prediction of plant biomass is very sensitive to mortality rates, which determine the average longevity of individual and thus time available for the accumulation of biomass as heartwood (Smith 2001).

4.5. Contribution of environmental variables

Woody plants are generally more sensitive to the temperature than herbaceous vegetation and their altitudinal or latitudinal limits are strongly controlled by temperature (D'Odorico et al., 2013). With the gradual but continuous increase in temperature, which is even more pronounced in higher altitudes (Shrestha et al. 1999), species are redefining their habitat.

Globally, high altitude treeline species are associated with a seasonal mean ground temperature during the growing period (Koerner 2003). Our model (MaxEnt) model shows that it is annual temperature range which is defining the present *Abies spectabilis* distribution (Table 4). Species respond to the increasing temperature by shifting their elevation range, thus redefined the position of a treeline. The position of a treeline is mainly determined due to strong growth limitations by the low temperature conditions (Korner and Paulsen, 2004). This is the same result produced by MaxEnt. It shows the future distribution of *Abies* will be determined by mean temperature of coldest quarter (Fig 18 and Table 4). Mean temperature of the warmest quarter also emerges as an important predictor, suggesting a role of growing season heat sum/available energy.

LPJ-GUESS also considers the minimum and maximum temperature of the coldest month as defined bioclimatic variables. The model also chooses maximum temperature of the warmest month as a defining variable which influence the species lower limit. The influence of this extra variable (not considered by MaxEnt) can be seen in the lower species limit of the *Abies spectabilis*. LPJ-GUESS predicts the lower range for future distribution at 3200 masl whereas MaxEnt predicts it unchanged at 2400 masl (Fig 10 and 11). However, there is also likely to be competition among species which plays a major role in drawing the species lower limit. The result accord with the study done by (Gaire et al. 2014) who found that the growth and regeneration of *Abies spectabilis* is more sensitive to maximum and minimum temperature rather than average temperature. While studying the treeline dynamics of *Abies spectabilis* in the Manaslu conservation area, he concluded that the regeneration of the species is positively correlated with the monthly maximum temperature of August (which together with July is the warmest month; see fig 3c and 3f).

The precipitation for the study area, from 1951-2100 is predicted to be largely unchanged (Fig 3 h) and the MaxEnt model predicts precipitation seasonality as the environmental variable other than temperature which will redefine the species distribution (Fig 18 and Table 4). It shows that reduced variability in annual precipitation leads to a higher probability of species presence (Fig 18). This largely explains the almost unchanged habitat (area) predicted by the MaxEnt for the current and future potential distribution of the species.

The large difference between the future distributions of *Abies* produced by two models also demands an inclusion of non-environmental variables which contributes to *Abies* future distribution.

5. Conclusion and Recommendation

5.1. Conclusion

- ❖ Both the models shows valid results as the current distribution shown by the models significantly resemble the actual observed distribution of the species. The error rate for the MaxEnt distribution map is 0.11 and that of LPJ-GUESS is 0.09. Values for Cohen's kappa are 0.75 and 0.8 respectively for MaxEnt and LPJ-GUESS. The results show LPJ-GUESS is slightly better than MaxEnt in defining species distribution.
- ❖ Under the climate change scenario of RCP 2.6, the suitable habitat for *Abies spectabilis* in the future will be reduced. Both the applied models agree to the point that in the forest-alpine transition zone of 3000-4000 masl, significant changes will occur. In comparison to MaxEnt model, LPJ-GUESS model predicts a higher degree of change in the coming future. MaxEnt predicts the suitable habitat for *Abies spectabilis* population will be reduced by 11 km² whereas; LPJ-GUESS predicts the estimation at 63 km².
- ❖ Upper limit of *Abies spectabilis* will move towards the mountain top. The rate of species movement will be 14 meters per decade with total shift of 70 meters in the coming 50 years (MaxEnt) or 30 meters per decade with total shift of 150 meters as shown by LPJ-GUESS.
- ❖ There is a clear horizontal and vertical transformation of vegetation patterns caused by different climatic and non-climatic factors. The changing vegetation coverage of dominant trees from their suitable habitat indicates upward shift of dominant trees in the Manaslu conservation area. LPJ-GUESS predicts the absence of *Abies spectabilis* from the lower-temperate climatic zone in the coming future. Supporting the hypothesis that the species is moving upwards, vegetation coverage in terms of Leaf Area Index shows the species will significantly increase its coverage in the lower-alpine climatic zone (4000-4500 masl).
- ❖ *Abies spectabilis* will respond to climate warming by increasing its net primary production, carbon biomass and leaf area index. LPJ-GUESS predicts an increase of 64(gC m⁻² yr⁻¹) mean net primary production by the 2050 scenario (corresponding to a 30.18 % increase relative to modelled current NPP values). Carbon biomass will increase by the mean value of 0.33 (KgCm⁻²) (corresponding to a 19.87 % increase relative to modelled current cmass values)
- ❖ According to MaxEnt, annual temperature range and precipitation seasonality (coefficient of variation) define the current *Abies spectabilis* distribution while in the future mean temperature of coldest quarter will have the most influence upon the spatial distribution of *Abies spectabilis*, along with precipitation seasonality.

5.2. Recommendation

- ❖ The model predicts the future distribution of *Abies spectabilis* considering that there will be no anthropogenic disturbances. However, anthropogenic factors always play a major role since they contribute to shaping the distribution pattern of species by deforestation, land fragmentation, fire, harvesting etc. For a better prediction, it is recommended to take into consideration those factors. Depending upon the availability of data, land cover changes can be incorporated into models for a more realistic projection.
- ❖ Incorporation of environmental factors like slope, inclination, aspect, and radiation index could greatly improve the MaxEnt outputs. Due to data deficiency, these factors couldn't be taken into account. In future work, if the research time allows, it is suggested to include these factors.
- ❖ As outlined in the conclusion, climatic factors are not the only factors defining the future spatial distribution of vegetation. It is advisable to quantify the role of non-climatic factors in niche divergence of species at the local scale.
- ❖ The changing vegetation patterns will bring unequivocal impact on mountain livelihoods, as the people rely on nature for almost everything. It is recommended to assess the impact of climate change on people's livelihood.

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Appendix 1: Distribution range of 19 principal trees along the Nepal Himalaya. Modified after (Press, Shrestha and Sutton 2000 and Ohsawa, Shakya and Numata 1986). Note that *Pinus wallichiana* and *Juniperus recurva* are not included in this list. The species are added after the floristic composition of the study area (Suwal 2010 and the authors own observations).

	Nepal			Distribution (masl)
	West	Central	East	
Subarctic				
<i>Abies spectabilis</i>	+	+	+	2400-4400
<i>Betula utilis</i>	+	+	+	2700-4300
Cool-temperate				
<i>Quercus semecarpifolia</i>	+	+	-	1700-3800
<i>Tsuga dumosa</i>	+	+	+	2100-3600
<i>Magnolia campbellii</i>	*	+	+	2250-2700
<i>Lithocarpus pachyphylla</i>	*	*	+	2100-2800
<i>Rhododendron arboreum</i>	+	+	+	
Temperate				
<i>Pinus wallichiana</i>	+	+	-	1800-3300
<i>Quercus lamellosa</i>	*	+	+	1300-2500
<i>Castanopsis hystrix</i>	*	*	+	1000-2500
<i>Lyonia ovalifolia</i>	+	+	+	1300-3300
Warm-temperate				
<i>Castanopsis tribuloides</i>	+	+	+	450-2300
<i>Quercus lanata</i>	+	+	+	460-2600
<i>Alnus nepalensis</i>	+	+	+	500-2600
Subtropical				
<i>Pinus roxburghii</i>	+	+	-	1100-2100
<i>Castanopsis indica</i>	*	+	+	1200-2900
<i>Schima wallichii</i>	*	+	+	900-2100
Tropical				
<i>Shorea robusta</i>	+	+	+	150-1500
<i>Adina cordifolia</i>	+	+	+	150-800

+ frequent distribution, - rare distribution, * no distribution)

Appendix 2: Parameter values relating to growth form, allometry and phenology for the plant functional types simulated for LPJ-GUESS in this study. See Smith et al. (2001) and Sitch et al. (2003) for further explanation of the parameters.

PFT Simulated (abbreviation)	Phenology	Kallom ₁ / Kallom ₂ / Kallom ₃ (see Smith et al. 2001)	Leaf to sapwood cross- sectional area	Turnover Leaf/root (Yr ⁻¹)	Leaf longe vity (Yr)	Max. Crown area (m ²)	Root fraction in upper soil layer	Non- stressed longevit y (Yr)	Wood density (KgCm ⁻³)	Max. C _{Leaf} :C _{Fine Root ratio}	Fire resista nce
<i>Abies</i> Boreal, shade-tolerant needleleaved tree (BNE)	Evergreen	150/60/0.67	5000	0.33/0.7	3	50	0.6	500	200	1	0.3
Temperate,Shade- tolerant broadleaved tree (TeBS)	Summergreen	250/60/0.67	6000	1/0.7	0.5	50	0.6	400	200	1	0.1
<i>Birch</i> Boreal,shade-intolreant broadleaved tree (IBS)	Summergreen	250/60/0.67	6000	1/0.7	0.5	50	0.6	300	200	1	0.1
<i>Quercus</i> Temperate,shade- tolerant broadleaved tree (TeBE)	Evergreen	250/60/0.67	6000	1/0.7	3	50	0.6	300	200	1	0.3
<i>Juniperus</i> Boreal shade-tolerant needleleaved tree (BNE)	Evergreen	150/60/0.67	5000	0.33/0.7	3	50	0.6	500	200	1	0.3
Temperate,shade- tolerant broadleaved tree (TeBE)	Evergreen	250/60/0.67	6000	1/0.7	3	50	0.6	300	200	1	0.3

<i>Pinus</i> Temperate, shade-intolerant needleleaved tree	Evergreen	150/60/0.67	5000	0.33/0.7	3	50	0.6	300	200	1	0.3
Temperate, shade-intolerant needleleaved tree (TeNE)	Evergreen	150/60/0.67	5000	0.33/0.7	3	50	0.6	300	200	1	0.3
Tall shrub (HSE)	Evergreen	100/5/0.67	500	-/0.7	3	10	0.6	40	250	1	-
Tall shrub (HSS)	Summergreen	100/5/0.67	500	-/0.7	0.5	10	0.6	40	250	1	-
Low shrub (LSE)	Evergreen	100/5/0.67	125	-/0.7	3	10	0.6	25	250	1	-
Low shrub (LSS)	Summergreen	100/5/0.67	125	-/0.7	0.5	10	0.6	25	250	1	-
Temperate C ₃ grass (GRS)	Summergreen	-	-	1/0.7	1	-	0.9	-	-	0.2	-
Prostrate dwarf shrub tundra (PDS)	Any	-	-	1/0.7	1	-	0.9	-	-	0.2	-
Cushion forbs, lichens and moss tundra (CLM)	Any	-	-	1/0.7	1	-	0.9	-	-	0.2	-
Graminoid and forb tundra (GFT)	Any	-	-	1/0.7	1	-	0.9	-	-	0.2	-

Appendix 3: Values of LAI for different dominant PFTs per climatic zone. The LAI values for current are the average for the year 1951-2000 and values for the future are the average for the year 2041-2060. Values for grasses are sum of GRS, PDS, CLM and GFT. Values for shrubs are sum of HSE, HSS, LSE and LSS. Others includes other needleleaved and other broadleaved.

Climatic zone		<i>Quercus</i>	<i>Pinus</i>	Others	Birch	<i>Juniperus</i>	<i>Abies</i>	Grasses	Shrubs
Subtropical	Current	0.0117	0.0781	0.0142	-	-	-	3.2307	0.001
	Future	0.0014	0.0774	0.011	-	-	-	3.4780	0.0042
Lower-temperate	Current	0.0105	0.0511	0.0116	0.0003	-	0.0052	3.5922	0.0013
	Future	0.0158	0.1124	0.0218	0.000	-	0.0005	3.6675	0.0013
Upper-temperate	Current	0.0125	0.055	0.0038	0.0016	-	0.0163	4.087	0.0018
	Future	0.013	0.055	0.013	0.002	-	0.016	4.087	0.002
Lower-subalpine	Current	0.0501	0.0609	0.0086	0.0175	0.1585	0.2211	3.6510	0.0060
	Future	0.0501	0.0609	0.0086	0.0175	0.1585	0.2211	3.6510	0.0060
Upper-subalpine	Current	0.005	0.002	0.001	0.094	1.051	1.372	0.877	0.031
	Future	0.065	0.042	0.0066	0.069	0.871	0.8834	1.6575	0.065
Lower-alpine	Current	-	-	-	0.0123	0.1377	1.6253	1.0879	0.7531
	Future	-	-	-	0.1300	0.6484	2.7449	0.4296	0.2413

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