ORIGINAL ARTICLE



Modelling the impacts of future climate change on plant communities in the Himalaya: a case study from Eastern Himalaya, India

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Abstract That the Himalaya are warming at much higher rates than the global average is known. Here, we assess the future potential distribution of major plant communities in Sikkim Himalaya due to climate change using field observations and maximum entropy modelling approach. We collected data on presence and elevational distribution ranges of 584 endemic angiosperm species during field surveys at 121 sampling locations using 625 study plots and along an elevational gradient of 300-5,300 m. This field data was supplemented by already published records. Endemic species were classified into different growth forms, viz. trees, climbers, shrubs, and herbs. A total of 37,376 different species distribution models (SDMs) were built using climate projections available from 8 different general circulation models and 4 representative concentration pathways. SDMs were built for current climate (average climate for 1950-2000), 2050 (average climate for 2041-2060), and 2070 (average climate for 2061–2080). We found that about 16 and 18 % of endemic angiosperm species are likely to lose their potential habitat by 2050 and 2070, respectively. Meadows may likely lose about 1 and 3 % of their current geographical spread to shrublands by 2050 and 2070,

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respectively. Weak and insignificant values of phylogenetic signal among the growth forms indicated that climate-induced impacts were spread across the phylogenies. We report significant increase in the habitable areas of shrubs and their northward expansion, gradually replacing the herbaceous communities. This change can alter the structure and function of the Himalayan highland ecosystems besides depleting bioresource base and endangering the local livelihoods.

Keywords Alpine meadows · Climate change · Endemic plants · Himalaya · Phylogenetic signal · Species distribution models

Introduction

Climate change has affected a number of ecosystems and taxonomic groups worldwide (Parmesan and Yohe 2003; Parmesan 2006). Ecologically, most manifest effects of climate change are reflected in modifications in species assemblages (Parmesan and Yohe 2003), spatial and temporal mismatches in nutrient dynamics (Post et al. 2009), alteration of species' phenologies (Ovaskainen et al. 2013), shifts of species' ranges and niches (Bellard et al. 2012; Telwala et al. 2013), and evolutionary changes, viz. extinctions and selective adaptation of species (Hoffmann and Sgro 2011). Despite overall impacts of climate change on biota and ecosystems globally, the mountains appear to be the most vulnerable habitats to altered climate settings for having experienced continued warming, more than the global average during the last century (Diaz et al. 2003). The rate of warming in mountains across the world has been 0.13 °C/decade during the past 50 years (Pepin and Seidel 2005) and this rate is expected to increase further to

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0.25–0.48 °C/decade by 2085 (Nogués-Bravo et al. 2007). Relatively higher warming rate presents a perilous problem for the mountaintop species because they have no areas left to colonize. Described as 'summit trap phenomenon' (Pertoldi and Bach 2007), in such a scenario the warm-adapted lowland 'generalist' species migrate upwards leading to a progressive decline and extinction of mountaintop 'specialist' species (Thuiller et al. 2005).

Most of the investigations related to response of vegetation communities and plant species to climate change in the mountain ecosystems have been carried in Europe and America, namely Alps (Theurillat and Guisan 2001), Andes (Feeley and Silman 2010), Montseny mountains (Peñuelas and Boada 2003), and Rocky mountains (Inouye 2008). Despite growing interest in studying impacts of climate change in global biodiversity hot spots, there is inadequate scientific information available for the Himalaya (but see Shrestha et al. 2012; Telwala et al. 2013). As such more studies on biological responses of climate change are needed in the Himalaya than elsewhere because of its unique evolutionary history and vast diversity of its ecosystems (Pandit et al. 2014a). Also, being located in tropical latitudes, the Himalaya are exposed to relatively higher temperatures compared to other mountain systems of the world. Approximately three times higher rate of warming (0.06 °C/year) has been reported for the Himalaya than the global average (Shrestha et al. 2012). As a result of rapid warming in the Himalaya, changes in diversity and distribution of plant communities have clearly manifested in this mountain ecosystem. Telwala et al. (2013) reported a mean upward displacement of 27.53 m/decade in the endemic plant species of the Sikkim Himalayan region during the period 1849-2010. In the Tibetan plateau, Baker and Moseley (2007) reported an upward shift of tree lines by 67 m and tree limits by 45 m during 1923-2003. In addition to species range shifts to cooler higher elevations, changes in community structure and composition have also been reported due to warming. For instance, conversion of 39 % of alpine meadows into shrublands in the Tibetan plateau in <20-year period (1990–2009) has been reported (Brandt et al. 2013). These distributional changes concomitant with shuffling of species composition have been observed to result in localized or widespread extinction of endemic species in the Himalaya (Pandit et al. 2014a). Clearly, the elevated temperature profile of the Himalaya has induced a higher degree of floral flux than would be expected under an unaltered climate regime. It is, therefore, useful from ecological and conservation point of view, to assess the vegetation community dynamics in the Himalaya following climate change.

We assessed the magnitude of alterations in the spatial distribution of endemic plant species and the restructuring

of different growth forms along the Himalavan elevational gradient induced by climate change. This study is based on robust data collected from field studies and modelling approaches. To the best of our knowledge, this is a first such attempt to document the spatial dynamics of endemic plant species under various ensuing climate change scenarios in the Himalaya. We have also attempted to examine the phylogenetic context and scale of such landscape level changes due to climate change in the Himalaya. Specifically, our objectives were to: (1) document the present and future spatial habitat suitability of individual endemic plant species under different climate change scenarios, (2) investigate growth form-specific distribution patterns along the Himalayan elevational gradient under the current and future climate scenarios to trace changes, if any and (3) examine whether climate-induced diversity and distributional changes were uniformly spread across phylogenies.

Materials and methods

Study area

We carried out field ecology studies in the Sikkim state of India, located between 27°00'46" to 28°07'48"N latitude and 88°00'58" to 88°55'25"E longitude and spread over a geographical area of 7,096 km². The study area is entirely mountainous and forms a natural elevational gradient from 300 m in the south to above 8,000 m in the north. Sikkim Himalaya offers an ideal field location for investigating a variety of ecological communities ranging from tropical to alpine within a small geographic extent. The elevational gradient of our study area includes the representative forest types of the Eastern Himalaya, viz., tropical moist deciduous forests (300-900 m), sub-tropical broad leaved hill forests (900–1,800 m), montane wet temperate forests (1,800-2,700 m), sub-alpine forests (2,700-3,700 m), moist alpine scrubs (3,700-4,000 m), and dry alpine scrubs (above 4,000 m) (see Champion and Seth 1968). Sal (Shorea robusta) comprises the main dominant species of tropical moist deciduous forests with Dillenia pentagyna, Gmelina arborea, Lagerstroemia parviflora, and Toona ciliata as principal associated species. The main components of the sub-tropical broad leaved hill forests are evergreen tree species of Macaranga, Schima, Sapium, and Castanopsis intermixed with the shrubby species of Brassaiopsis, Oxyspora, Rubus, and Vitex. Montane wet temperate forests comprise broad leaved tree species such as Acer campbellii, Magnolia campbellii, Alnus nepalensis, Quercus spp., Machilus spp. at lower elevations between 1,800 and 2,700 m. The mixed coniferous forests at higher elevations, between 2,600 and 3,000 m, are dominated by Abies densa, Tsuga dumosa and Larix griffithii. The sub-alpine forests are dominated by various species of *Rhododendron* mixed with *Betula utilis*, *Cassiope fastigiata* and *Sorbus* spp. The moist alpine scrubs are characterized by stunted bushy growth forms like *Berberis umbellata*, *Cotoneaster microphyllus*, *Lonicera* spp. and *Rhododendron* spp. The dry alpine scrubs constitute alpine xerophytic vegetation with several dwarf scrub species such as *Ribes* spp., *Berberis angulosa*, *Juniperus recurva*, *Rosa sericea*, and *Rhododendron nivale*.

Species data

We included only endemic species in the present study because of their reported high vulnerability to climate change arising from limited habitat size and specificity as well as high sensitivity to altered temperature and precipitation regimes (Malcolm et al. 2006; Thuiller et al. 2006). The taxa were designated as endemic based on their description as such in Hooker's The Flora of British India (Hooker 1875–1897). Although the reference is very old, it still remains the most complete and authentic source of species' information in the region. Covered in 7 volumes, The Flora of British India includes information on nearly 120 angiosperm families from the present day Sikkim region with details of habitat, taxonomy, and elevational distribution. However, keeping in mind the various nomenclatural changes and taxonomic revisions which might have occurred over time, we augmented this source (Hooker 1875–1897) with major recent works on the Sikkim Himalayan flora (King and Pantling 1898; Hajra and Verma 1996; Srivastava 1996, 1998; Online Resource Appendix S1). For each endemic species we collected data on their growth forms (tree, shrub, climber, herb), presence and elevational distribution ranges from primary field surveys and secondary sources. Field surveys and sampling were undertaken (YT, DN, MKP) during 2005 and 2010 along an elevational gradient of 300-5,300 m (Fig. 1). We supplemented our primary sampling effort with secondary data, sourced from as many as 33 publications, documents and checklists (see Online Resource Appendix S1). Sampling in the study area was carried out in all the representative vegetation communities, ranging from tropical to alpine region to ensure a robust sampling effort. The entire elevational range of 5,000 (300-5,300) m was divided into 100 m equal elevational bands and each band was sampled using a combination of line transect and quadrat sampling methods. Quadrats were laid randomly along both sides of a 1,000 m line transect and each sampling point was mapped and geo-referenced in Universal Transverse Mercator (UTM) projection using a GPS (MagellanTM, Spor-Trak Map). A nested quadrat design of $10 \text{ m} \times 10 \text{ m}$ was used to analyze vegetation up to tree line (300-4,000 m), while nested modified Whittaker plot (MWP) design of $20 \text{ m} \times 50 \text{ m}$ was used above tree line (4,000–5,300 m) (Stohlgren et al. 1995). Two different sampling approaches were followed along the elevational gradient because the areas above tree line harbored disproportionately higher number of herbaceous species and vegetation communities as compared to the lower elevations (for details see Telwala et al. 2013). MWP design was chosen for vegetation analysis above tree line for its ability to detect even a locally rare species and the method has been successfully used in a previous regional ecological study (Telwala et al. 2013). In the nested quadrat design, trees were sampled in the main frame of 10 m \times 10 m, shrubs and climbers were sampled in the $5 \text{ m} \times 5 \text{ m}$ sub-quadrat, and herbs in $1 \text{ m} \times 1 \text{ m}$ sub-quadrat. In MWP design, shrubs and herbs were sampled both within the main plot $(20 \text{ m} \times 50 \text{ m})$ and three different nested subplots (one 5 m \times 20 m, two $2 \text{ m} \times 5 \text{ m}$, ten 0.5 m $\times 2 \text{ m}$). Trees and climbers, absent above the tree line, were not sampled in the MWP design. Sampling was carried out in the pre-monsoon (March-April), monsoon (July) and post-monsoon (October) seasons in each year to account for seasonal community fluctuations; the seasonal data was pooled for each individual sampling site. In total, 121 locations were sampled in Sikkim Himalaya using 625 plots and a comprehensive dataset of 584 endemic species was prepared. The nomenclatural validity of the species was verified using Missouri Garden's Tropicos database (http://www.tropicos. org/) and taxonomic considerations were based on observations in the field and standard literature.

Climate data

Climate data for the study area was downloaded in the form of monthly average minimum and maximum temperature, monthly total precipitation and 19 bioclimatic variables from the Worldclim database (http://www.worldclim.org/) at a resolution of 30 arc-seconds ($\sim 1 \text{ km} \times 1 \text{ km}$ grid resolution). The selected environmental variables represent the variables with the strongest links to physiology and growth of plant species (Thuiller et al. 2005; Gallagher et al. 2013). Climate data for all the 22 variables were downloaded for both 'current' and 'future' climate scenarios. Current climate conditions are represented by their averages for the period between 1950 and 2000 (Hijmans et al. 2005). Future climate scenario are represented by the projections for two time periods, 2050 (average climate conditions for 2041-2060), and 2070 (average climate conditions for 2061-2080) based on the IPCC fifth assessment report. For each climate variable, future projections were downloaded for four representative concentration pathways (RCP) (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5) available from eight different general circulation models (GCM) (BCC-CSM 1-1, CCSM4, GISS-E2-R, IPSL CM5A LR, Had GEM2-ES, MIROC-ESM-CHEM,

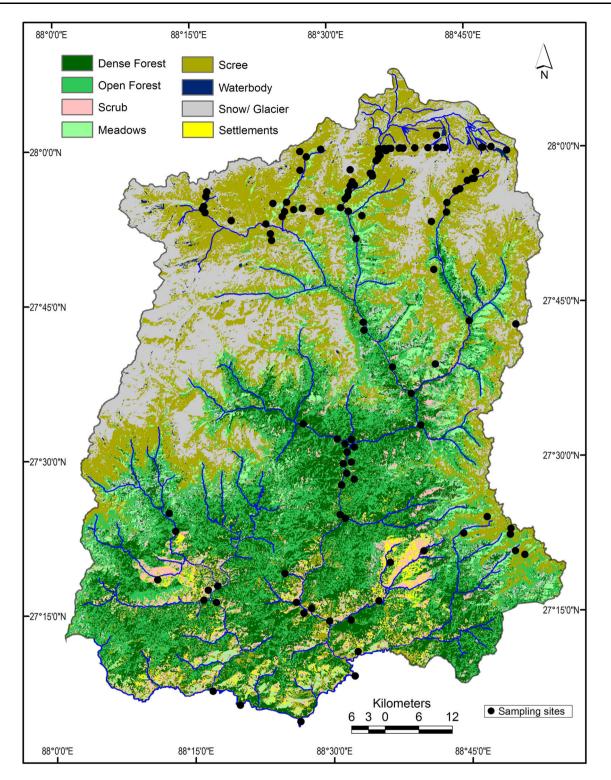


Fig. 1 Map showing the location of field survey and sampling sites in the Sikkim Himalayan region. A total of 121 locations were sampled using 625 plots in the pre-monsoon (March–April), monsoon (July), and post-monsoon (October) seasons between 2005 and 2010

MRI-CGCM3, Nor ESM 1M). As a result, for each climate variable, a total of 32 projected scenarios were downloaded separately for 2050 and 2070. Since every GCM has limitations of some statistical bias with respect to its output

(see Ehret et al. 2012), it was necessary to include all the GCMs in which the projections of the entire range of RCP scenarios were available. The RCPs correspond to the projected greenhouse gas concentration trajectories as a

result of various emissions and land use changes (Van Vuuren et al. 2011). In brief, each RCP represents the following states: (1) RCP 2.6: 490 ppm carbon dioxide equivalent (CO₂ eq.) and a radiative forcing value of 2.6 W/m², (2) RCP 4.5: 650 ppm CO₂ eq. and a radiative forcing value of 4.5 W/m², (3) RCP 6.0: 850 ppm CO₂ eq. and a radiative forcing value of 6.0 W/m^2 , (4) RCP 8.5: 1,370 ppm CO₂ eq. and a radiative forcing value of 8.5 W/ m^2 (Van Vuuren et al. 2011). In this manner we included all the current and future climate change scenarios available as of today. The data for all the 22 climate variables were first imported in Arc GIS ver. 9.3 (Esri, Redlands, CA, USA) in the form of a global dataset. Climate data of the study region was then generated from this global dataset using 'Extract by Mask' sub-tool available in the 'Spatial Analyst Tool' of Arc GIS software wherein the mask grid layer comprised the shape file of Sikkim Himalayan region in UTM projection.

Species distribution modelling

Species distribution models (SDMs) determine species distributions by relating species occurrences at known locations with environmental variables and use this relationship to extrapolate species distributions across space and time. In this way SDMs represent habitat suitability based on ecological requirement of a particular species (Elith and Leathwick 2009). Currently, two approaches to modelling species distribution are employed in literature, namely: (1) ensemble modelling wherein a number of models are used for projecting species distributions and finally a consensus view is adopted (Thuiller et al. 2009), and (2) single modelling approach in which a single SDM algorithm is used for determining species distributions (Leach et al. 2013). Use of ensemble modelling approach was not feasible in our study because different SDM algorithms have different data requirements. SDM such as maximum entropy (MaxEnt) use species presence-only data, generalized linear models and generalized additive models use species presence-absence records, while boosted regression trees uses both species presence-absence data and abundance records. Historically, endemic species have been poorly documented in the Himalaya and consistent records of their areas of distribution do not exist. Therefore, we decided to use the single presence-only modelling approach, and specifically use MaxEnt because it is one of the most dependable and useful modelling technique when majority of data are available in the form of presence-only records (as in our study) and for species such as rare and endemics, which have less number of presence records due to their localized distribution (Elith et al. 2011).

We made individual habitat suitability projections for each species using MaxEnt ver. 3.3.3k (Phillips et al. 2006) under both current and future climate scenarios. However, before running MaxEnt, we checked for the presence of collinearity between different climate variables. The climate variables which were downloaded as monthly values (minimum temperature, maximum temperature, precipitation) were first mosaiced into one layer. A correlation matrix was then prepared in Arc GIS 9.3 using Band Collection Statistics tool and the set of variables with correlation coefficient >0.6 were excluded in MaxEnt modelling exercise. Since MaxEnt requires input of species data as geo-referenced presence-only records, we interpolated species presence between the recorded minimum and maximum elevations on a reclassified 100 m digital elevation model (DEM) of the study area in Arc GIS 9.3. Interpolation method has been successfully used for documenting species richness patterns for a variety of taxa in the Himalayan region (see Bhattarai and Vetaas 2006; Grau et al. 2007; Bhatt et al. 2012).

In MaxEnt modelling exercise, the interpolated species records and uncorrelated environmental layers were first used to model potential habitat distribution of 584 endemic species individually under the current climate conditions with the following settings: calibration grid resolution of $1 \text{ km} \times 1 \text{ km}$; response curves creation; pictures of predictions; jackknife test for measuring variable importance; logistic output format; ascii output file type; linear and quadratic features; removal of duplicate presence records; 20 % random test percentage; 15 replicates; subsample replicated run type; 5,000 iterations; convergence threshold of 0.00001. The output generated by MaxEnt was a grid with probability distribution in the range of 0-1. The probability value of 0 represented the least suitable habitat while 1 represented the most suitable habitat. SDMs built using current climate scenarios were then used for projecting potential habitat distribution of each species in 2050 and 2070 using future climate data for different emission scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5) sourced from eight different GCMs. In this manner, a total of 32 projections were made for each species separately for the years 2050 and 2070. For 584 endemic species we thus developed 37,376 SDMs. For each endemic species, first the average probabilities were calculated over a range of 8 GCMs and then all the average values of 584 species were summed up to make a final species richness map. In the context of present study, we have defined species richness as the sum of all probability values in each grid cell in accordance with the protocol of Leach et al. (2013). For each growth form (trees, shrubs climbers, herbs, and total species which included all growth forms), three sets of richness maps were prepared for different climate conditions (current, 2050, and 2070) and in the latter two sets, viz., 2050 and 2070, four different subsets of richness maps were prepared for each emission scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5). The accuracy of model outputs was tested by using the area under receiver operating characteristic curve (AUC) criterion. The AUC criterion assesses the correct classification rate of presence points by the modelled function. Only those models were selected whose AUC scores were >0.7 in accordance with the standard literature (Thuiller et al. 2005; Leach et al. 2013).

After species richness maps were prepared, we calculated the geographic area occupied by various taxa of each growth form in Sikkim Himalaya at different time periods. However, it was not feasible to directly use species richness maps for calculating the geographic area occupancy of species' growth forms because richness maps represented the sum of continuous probability distributions and were prepared by using interpolation method, which assumed equal habitability over the entire elevational range. Equal habitability assumption may not reflect natural distribution of various taxa because landscape in the Sikkim Himalayan region is highly fragmented with numerous valleys, steep slopes and river divides. Therefore, it was necessary to exclude potential inhabitable areas for plant taxa between 300 and 5,300 m, such as escarpments, very steep slopes, permanent glaciated and snow covered areas, rivers, lakes and perennial water bodies from the species richness maps. To do so, we first digitized these inhabitable areas in Arc GIS 9.3 software using Survey of India topographic sheets (at 1:50,000 scale) and triangulated irregular network (TIN) models. The geographic area occupied by the inhabitable areas was calculated from the digitized regions using simple querying in Arc GIS 9.3, and then percentage relative area occupancy of each growth form community in three different time periods were calculated using the following formula:

$$PRAO = \left(\frac{G_{\rm I} - G_{\rm U}}{G_{\rm T}}\right) \times 100$$

where PRAO is the percentage relative area occupancy, $G_{\rm I}$ is the geographic area occupied by each growth form in respective species richness maps, $G_{\rm U}$ is the potentially inhabitable geographic area, and $G_{\rm T}$ is the sum of difference between $G_{\rm I}$ and $G_{\rm U}$ for all growth forms.

Phylogenetic signal

To test whether species' response to climate change was phylogenetically controlled, we analyzed the strength and significance of phylogenetic signal in our dataset. Since genetic information necessary for constructing a species level tree was not available for majority of the endemic species, we constructed a phylogenetic tree using Phylomatic ver. 4.2 (Webb et al. 2008). Phylomatic has been successfully used to generate phylogenetic trees and carrying out phylogenetically informed analyses in cases where primary gene sequences for plants are not available (see Pandit et al. 2011, 2014b). Separate phylogenetic trees were constructed for different growth forms namely trees, shrubs, climbers, herbs, and total species. Phylomatic prepares a pruned phylogenetic supertree using family level maximally resolved Angiosperm Phylogeny Group III seed plant tree (R20120829.new). The resulting supertree assumes equal branch lengths and can result in biased estimates of phylogenetic distances and phylogenetic signals (Ackerly 2000). Therefore, we calibrated branch lengths in our tree using branch length adjustment algorithm (BLADJ) in phylocom. BLADJ works by assigning branch lengths on the basis of angiosperm nodes contained in a dated tree of Wikström et al. (2001) and the undated nodes are assigned equal branch lengths between nodes which are dated. Using this calibrated node-dated tree and species trait file (prepared as the difference in average probabilities of occurrence of each species between current and future climates), we investigated phylogenetic signal for each growth form in current and future climate scenarios (2050 and 2070). Both Bloomberg's K (Blomberg et al. 2003) and Pagel's lambda (Pagel 1999) tests of phylogenetic signal were used because both provide reliable effect size measure of phylogenetic dependence (Münkemüller et al. 2012). Significance value of tests were determined by using randomizations test with 1,000 simulations in the case of Bloomberg's K, and a likelihood ratio test against the null hypothesis that $\lambda = 0$ in the case of Pagel's lambda.

Results

The endemic species dataset in our study comprised 584 plant species of which 37 were trees, 75 were climbers, 72 were shrubs, and 400 species were herbs. Under the current climate scenario, the distribution of different growth forms along elevational gradient showed that maximum endemic species rich region are concentrated at lower elevations for trees (1,900-2,800 m) and climbers (1,600-2,300 m), at middle elevations for shrub species (2,600-3,600 m), and at higher elevations for herbaceous species (3,900-4,600 m) (see Fig. 2). As a result of change in climate, these maximum endemic species regions are expected to show a prominent northward shift towards higher elevations across all the growth forms investigated. Compared to the current climate conditions, a total of 25 species (2 trees, 5 climbers, 3 shrubs, and 15 herbs) and 29 species (2 trees, 5 climbers, 3 shrubs, and 19 herbs) are likely to lose their potential habitat by 2050 and 2070, respectively (Fig. 2). This translates into loss of approximately 16 % endemic species by 2050 and 18 % loss of endemic species by 2070. However, we did not observe any change in species

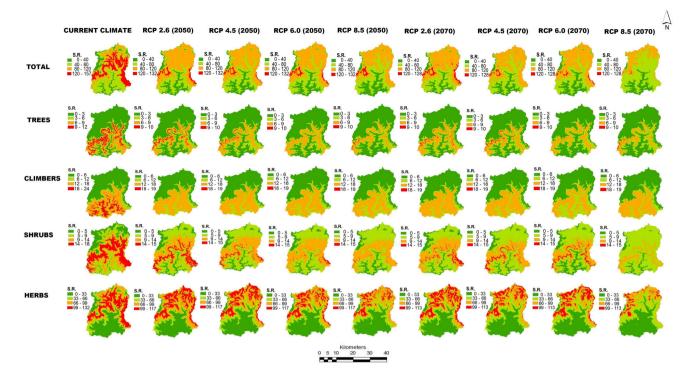


Fig. 2 Spatial distribution of different growth form communities in Sikkim Himalaya for different time periods. *RCPs* represent various representative concentration pathways according to IPCC fifth assessment report, while *S.R* represents species richness calculated

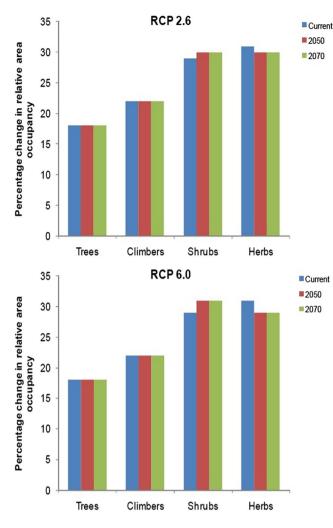
richness distribution patterns within different RCP scenarios for respective time periods.

Our MaxEnt modelling projections strongly suggested an upward/northward shift in the future distribution for all endemic species. Lowland species are likely to expand elevational ranges and habitat areas upwards, gradually displacing the upland species in the process. In particular, altered climate conditions are likely to favor the dominance of wide-range endemics such as Berberis sikkimensis, Jaeschkea microsperma, and Primula whitei, while narrow-range endemics such as Anaphalis cavei, Ranunculus sikkimensis, Saxifraga kingiana and Swertia hookeri may be obliterated from their existing habitats (see Online Resource Fig. S1). The future climate scenario is likely to exacerbate the already precarious position of species such as Arenaria melandryoides, Astragalus acaulis, Chionocharis hookeri, and Diplarche pauciflora, which occupy the northernmost limits in the study area and which have no habitable areas left for migration. These species are therefore, likely to go extinct. The most likely future scenario for the Himalayan highlands appears to be an altered landscape with preponderance of generalist species, which occupy wide range of habitats (e.g., B. sikkimensis, J. microsperma, P. whitei as mentioned earlier), while specialists such as Acronema pseudotenera, Lagotis clarkei, and Eutrema deltoideum would be marginalized to restricted localities (see Online Resource Fig. S1).

as the sum of probabilities of occurrence of all endemic species generated by MaxEnt modelling. Overall, 25 and 29 endemic species are expected to lose their potential habitats by 2050 and 2070, respectively

Our modelling projections showed that herbaceous communities currently occupy most of the geographical area (PRAO = 31 %), followed by shrubs (PRAO = 29 %), climbers (PRAO = 22 %), and trees (PRAO = 18 %) (see Fig. 3). Compared to their current one-third occupancy of geographical area, herbaceous communities are likely to lose approximately 1-3 % of their spatial occupancy by 2050 (PRAO = 30-29 %) and 2070 (PRAO = 30-28 %), respectively. In this manner, herbaceous communities are expected to lose approximately 71-213 km² of their current geographic area within a short period of 70 years. These vacated areas are likely to be occupied by shrublands and as a result the shrublands are predicted to be the communities with largest spatial occupancy in near future. Compared to 29 % geographical coverage under current climate scenario, shrublands are expected to occupy 30-31 % of geographical area in 2050 and 30-32 % in 2070 (Fig. 3). Thus, these shrublands will likely expand at the cost of present day herbaceous communities and the herbaceous community will occupy areas that are at present covered with snow but will become snow-free in future climate change scenarios (Fig. 3). Geographic extent of trees and climbers are expected to remain relatively constant with no net loss or gain (Fig. 3).

We observed extremely low and insignificant values of phylogenetic signal in our study. The values of



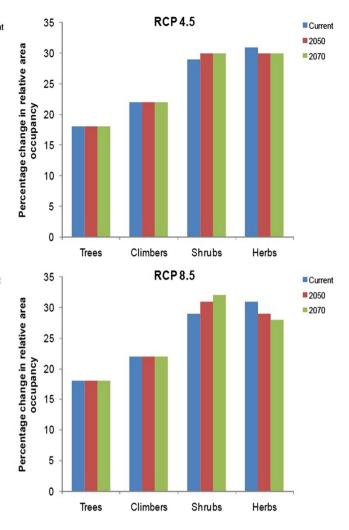


Fig. 3 Percentage change in relative geographic area occupancy of different growth form communities in Sikkim Himalaya for 2050 and 2070 compared to the current climate (\sim year 2000). In the current climate, herbaceous communities occupy maximum geographic area

while in the future shrublands emerge as the most dominant growth form community. *RCPs* represent various representative concentration pathways according to IPCC fifth assessment report

Bloomberg's K ranged between 0.05 and 0.23, while that of Pagel's lambda ranged between 0.02 and 0.27 across different growth forms (see Table 1). The low and insignificant values of phylogenetic signal in our study suggested that phylogeny had little to do with plant species responses and also indicated that these changes are climate-induced.

Discussion

Our results indicate a pronounced variability in the responses of different growth forms to climate change scenarios. Shrublands are expected to expand their existing spatial cover by acquiring additional habitats through encroachment into the herbaceous alpine meadow communities in future. A recent study conducted in the Tibetan plateau using land use/land cover changes has also indicated such a change in the Himalavan region (Brandt et al. 2013). As such, increased shrub growth has been reported to be the most conspicuous effect of climate change in various studies conducted the world over (Walker et al. 2006; Blok et al. 2011). Scientific researches show that incursion of woody shrubland vegetation into grasslands is limited by temperature and precipitation (Eldridge et al. 2011). With changing climate, increased warming and precipitation, shrubland species experience a greater physiological and demographic release due to greater availability of nutrients, and higher summer moisture deficits (Ratajczak et al. 2012). Shrubs are also known to be better competitors than grasses under conditions of increased carbon dioxide emissions (D'Odorico et al. 2012). Thus, the observed results of increased spatial cover of shrublands under future climate change scenarios are consistent with reported plant physiological responses.

Growth form	Future climate (2050)							
	RCP 2.6		RCP 4.5		RCP 6.0		RCP 8.5	
	K	λ	K	λ	K	λ	K	λ
Total	0.12 (0.51)	0.20 (0.12)	0.15 (0.14)	0.25 (0.23)	0.06 (0.87)	0.21 (1.00)	0.14 (0.31)	0.24 (0.86)
Trees	0.19 (0.23)	0.05 (0.75)	0.21 (0.23)	0.27 (1.00)	0.19 (0.16)	0.04 (0.82)	0.20 (0.16)	0.06 (0.75)
Climbers	0.18 (0.48)	0.04 (1.00)	0.18 (0.52)	0.05 (1.00)	0.18 (0.43)	0.05 (1.00)	0.19 (0.36)	0.23 (0.87)
Shrubs	0.17 (0.60)	0.16 (0.20)	0.13 (0.30)	0.10 (0.34)	0.15 (0.24)	0.16 (1.00)	0.14 (0.23)	0.08 (0.41)
Herbs	0.12 (0.15)	0.12 (0.45)	0.15 (0.60)	0.14 (0.49)	0.05 (0.90)	0.26 (0.63)	0.16 (0.90)	0.13 (0.63)
Growth form	Future climate (2070)							
	RCP 2.6		RCP 4.5		RCP 6.0		RCP 8.5	
	K	λ	K	λ	K	λ	K	λ
Total	0.14 (0.70)	0.26 (1.00)	0.13 (0.65)	0.23 (0.71)	0.11 (0.67)	0.16 (0.44)	0.13 (0.50)	0.23 (0.58)
Trees	0.19 (0.22)	0.05 (0.75)	0.18 (0.23)	0.09 (0.62)	0.19 (0.28)	0.23 (1.00)	0.20 (0.18)	0.13 (1.00)
Climbers	0.18 (0.36)	0.23 (0.86)	0.18 (0.32)	0.16 (0.23)	0.19 (0.31)	0.16 (0.69)	0.23 (0.83)	0.12 (0.38)
Shrubs	0.16 (0.11)	0.15 (0.26)	0.13 (0.33)	0.02 (0.88)	0.18 (0.43)	0.15 (0.21)	0.13 (0.36)	0.02 (0.85)
Herbs	0.15 (0.21)	0.14 (0.42)	0.15 (0.21)	0.14 (0.11)	0.12 (0.22)	0.09 (0.35)	0.13 (0.23)	0.13 (0.44)

Table 1 Measures of phylogenetic signal (Bloomberg's *K* and Pagel's lambda) for analyzing the degree of phylogenetic control in the plant species response to climate change in Sikkim Himalaya

All the growth forms showed very low and insignificant values of phylogenetic signal, indicating that climate induced responses were not limited to just a particular set of families but spread across wide phylogenies

RCP representative concentration pathways according to IPCC fifth assessment report; *Total* dataset including all growth forms viz. trees, climbers, shrubs, and herbs; the values before the brackets represent the strength of phylogenetic signal while the values inside the brackets represent the significance (*p* values) of phylogenetic signal. Significance value of tests were determined by using randomizations test with 1,000 simulations in the case of Bloomberg's *K*, and a likelihood ratio test against the null hypothesis that $\lambda = 0$ in the case of Pagel's lambda

The intrusion of shrublands into alpine grasslands may not only result in changes in species composition and decrease in species richness, but also in some large scale changes in the functional aspects of the ecosystems (see Eldridge et al. 2011 and references therein). Increased shrubland vegetation cover is known to cause an increase in the ambient air temperature through positive feedbacks between surface energy balance and microclimate conditions (D'Odorico et al. 2010). Various studies have shown that expansion of shrublands leads to increase in the intensification of erosional activities and loss of nutrient rich soil particles due to formation of bare surface areas (Li et al. 2008), and also to changes in the ecohydrological regimes with progressive desertification as woody shrubs require deeper water sources and intensifies both nutrient and water limitations (Nippert et al. 2013). Since these ecosystem-level impacts are irreversible (D'Odorico et al. 2010), the transformation of grasslands into shrublands can dramatically alter the native ecosystem state and the various associated ecosystem services (Eldridge et al. 2011).

Ecological transformation of the landscape and the associated alterations in ecosystem structure and function, following incursion of shrublands into alpine meadows in the Himalaya, are likely to impact livelihoods of resident human communities in a big way. In particular, for the communities living in the highland Himalaya, disappearance of alpine meadow communities will greatly imperil yak populations which are dependent on herbaceous plant taxa such as Heracleum sp., Kobresia sp., Juncus sp., Festuca sp., etc. (Pandit, in press). These plant communities form critical foraging pastures for the yak populations which are the most prized possessions of the Himalayan highlanders for their entire economic and socio-cultural activities (Tambe and Rawat 2009). Replacement of grassland communities by shrublands would affect the livestock herding in these areas because shrub species have lower nutritional value and are unpalatable to most grazers and ungulates compared to the grassland species (Brandt et al. 2013). The alpine meadows are also a source of vast variety of medicinal plants, which are used as critical first resource by the local communities for economic activity and as traditional medicines. About 400 plant species, mostly herbaceous endemics of high medicinal value have been reported from the high elevation grasslands (3,600-4,800 m) of Sikkim Himalaya (Rai et al. 2000). Loss of the herbaceous communities will therefore lend a serious blow to the important medicinal genetic resource besides undermining livelihoods and alternate healthcare system of human communities in these far flung areas where modern healthcare system has not reached even today.

Our results showed that climate-induced plant species responses and community changes were not limited to any specific taxa, but were spread across wide phylogenies. Clearly, the absence of any phylogenetic confounding factor in our study stems from the fact that temperature is the main driver of overall species distribution in the study area (see Telwala et al. 2013). Thus when temperature was modelled as a primary variable in SDM projections in the current study, all the species responded correspondingly with pronounced shift of their potential habitats to higher elevations.

Results of our study are based on SDM projections which are known to have limitations (see Guisan and Thuiller 2005). One limitation pertains to the fact that our SDM projections are based on the premise that climate is the sole determinant of species distribution in both current and future scenarios and all species have similar dispersal modes and abilities. These assumptions ignore traits such as phenotypic plasticity of an individual species. Species with wide phenotypic plasticity are more capable of shifting their geographic range in response to climate change (Matesanz et al. 2010). That said, in spatial situations where there is no habitat available to colonize, phenotypic plasticity can be of little use. Some other limitations of our SDM projections are non-inclusion of factors such as biotic interactions, population dynamics, functional traits, migration rates, and land use changes. But it has been shown that all these biotic and abiotic interactions are mostly manifestations of temperature and precipitation changes (Pearson and Dawson 2003) and therefore get indirectly incorporated into the model projections when climate variables are included (as in the present study). Therefore, the exclusion of abiotic and biotic interactions as such is unlikely to produce any major changes in the model results. We also understand that our results are robust enough to indicate broad scale distributional changes at species and community levels in the Himalaya because our analyses are based on an average of 37,376 simulations. So even if there was an overestimation of extinction losses and range shifts for some narrow-range endemics, the overall pattern of species and growth form responses across the spatial extent would not be hugely dissimilar to our findings.

Conclusions

To conclude, our study suggests that future vegetation communities in the Himalaya will likely comprise of more woody elements at the cost of herbaceous communities albeit areas that are presently inhabitable (glaciated and/or snow bound) are likely to become habitable in future for herbaceous flora. The higher elevations in the north of Sikkim Himalaya are expected to be particularly affected by changes in climate with 18 % loss of endemic species. Given the recent reports of increased anthropogenic pressures in Sikkim Himalaya such as intense hydropower development (Pandit and Grumbine 2012; Grumbine and Pandit 2013), coupled with ongoing deforestation (Pandit et al. 2007), urbanization and tourism (Grumbine and Pandit 2013), this study can be potentially helpful to policy makers to make informed choices about mitigation and management of climate change impacts. More importantly, human livelihoods in higher Himalaya that are likely to be threatened by the impacts of climate change, deserve immediate attention of planners and policy-makers.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No formal approval is required for this study since this article does not contain any studies with human participants or animals performed by any of the authors.

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