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Original Research Article

Modelling the potential distribution of *Betula utilis* in the HimalayaMaria Bobrowski<sup>a,\*</sup>, Lars Gerlitz<sup>a,b</sup>, Udo Schickhoff<sup>a</sup><sup>a</sup> University of Hamburg, Center for Earth System Research and Sustainability, Institute of Geography, Bundesstraße 55, 20146 Hamburg, Germany<sup>b</sup> GFZ German Research Centre for Geosciences, Helmholtz Centre Potsdam, Telegrafenberg, 14473 Potsdam, Germany

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## ABSTRACT

Developing sustainable adaptation pathways under climate change conditions in mountain regions requires accurate predictions of treeline shifts and future distribution ranges of treeline species. Here, we model for the first time the potential distribution of *Betula utilis*, a principal Himalayan treeline species, to provide a basis for the analysis of future range shifts. Our target species *Betula utilis* is widespread at alpine treelines in the Himalayan mountains, the distribution range extends across the Himalayan mountain range. Our objective is to model the potential distribution of *B. utilis* in relation to current climate conditions. We generated a dataset of 590 occurrence records and used 24 variables for ecological niche modelling. We calibrated Generalized Linear Models using the Akaike Information Criterion (AIC) and evaluated model performance using threshold-independent (AUC, Area Under the Curve) and threshold-dependent (TSS, True Skill Statistics) characteristics as well as visual assessments of projected distribution maps. We found two temperature-related (Mean Temperature of the Wettest Quarter, Temperature Annual Range) and three precipitation-related variables (Precipitation of the Coldest Quarter, Average Precipitation of March, April and May and Precipitation Seasonality) to be useful for predicting the potential distribution of *B. utilis*. All models had high predictive power ( $AUC \geq 0.98$  and  $TSS \geq 0.89$ ). The projected suitable area in the Himalayan mountains varies considerably, with most extensive distribution in the western and central Himalayan region. A substantial difference between potential and real distribution in the eastern Himalaya points to decreasing competitiveness of *B. utilis* under more oceanic conditions in the eastern part of the mountain system. A comparison between the vegetation map of Schweinfurth (1957) and our current predictions suggests that *B. utilis* does not reach the upper elevational limit in vast areas of its potential distribution range due to anthropogenically caused treeline depressions. This study underlines the significance of accuracies of current environmental niche models for species distribution modelling under climate change scenarios. Analysing and understanding the environmental factors driving the current distribution of *B. utilis* is crucial for the prediction of future range shifts of *B. utilis* and other treeline species, and for deriving appropriate climate change adaptation strategies.

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\* Corresponding author.

E-mail address: [maria.bobrowski@uni-hamburg.de](mailto:maria.bobrowski@uni-hamburg.de) (M. Bobrowski).

## 1. Introduction

Ecological niche models (ENMs) and species distribution models (SDMs) based on presence-only occurrence data are significant research tools in biogeography, ecology, evolution and conservation biology (Guisan and Thuiller, 2005 and references therein). Using modelling techniques requires the analysis of underlying climatic factors of species distributions, which is, in turn, a basic requirement for the understanding of current and future species distribution ranges. Shifts of the environmental niches of alpine treeline species under future climate change scenarios are of particular interest in this respect since high mountain environments are subjected to above-average warming rates (Schickhoff, 2011; IPCC, 2014), and treelines are expected to advance to higher elevations (Harsch et al., 2009; Wieser et al., 2014).

Linking the occurrence or abundance of a species to environmental and/or geographical variables has been shown to be a valuable tool to predict species distribution ranges or potential suitable habitats (Franklin, 1995; Austin, 2002; Barry and Elith, 2006).

In this study, we follow the principles of ecological niche modelling regarding the conditions suitable for a target species based on calibration, evaluation and interpretation (Peterson et al., 2011; Anderson, 2012). In contrast to SDMs, which intend to characterize the species' occupied distribution (*sensu stricto*), ENMs investigate relationships between known species occurrences and abiotic environmental (frequently climatic) variables in a particular region of interest (the species' abiotically suitable distribution; see Peterson and Soberón, 2012, for the distinction of ENM and SDM terminology). A variety of statistical approaches are incorporated in ENMs (for details see Guisan and Zimmermann, 2000; Thuiller et al., 2008). Basically, the model estimates the environmental conditions that a species can live in (the species' existing realized niche). Subsequently the model can be projected in geographic space, identifying consistent areas with suitable environmental conditions for the species (Araújo and Guisan, 2006; Peterson and Soberón, 2012).

Accuracies of the models under climate change scenarios (i.e. response of the species to changing climate conditions) depend on the accuracies of models of the current environmental niche of the species, the importance of which should not be underestimated. Model predictions may then be used for biodiversity conservation in order to implement appropriate ecosystem management strategies.

At local and global scales, high-elevation climatic treelines can be considered as sensitive indicators of past and recent climate change and variability (Kullman, 1998; Holtmeier, 2009; Körner, 2012). During the last decade, investigation of climate change-driven treeline dynamics has generated considerable research interest, and results have been widely reported from various treelines of the world (e.g., Randin et al., 2009; Harsch et al., 2009; Paulsen and Körner, 2014; Schibalski et al., 2014; Schickhoff et al., 2015, 2016). One widespread hypothesis is that global warming will shift the climatic ranges of treeline and subalpine/alpine species upward along altitudinal, thermally defined gradients (Gottfried et al., 2012; Pauli et al., 2012).

Modelling the distributional range of treeline species and predicting changes under future climate scenarios has become an increasingly applied component in investigations of high altitude treelines (e.g., Dullinger et al., 2004; Thuiller et al., 2005; Parolo et al., 2008). Climate-induced future range shifts have been postulated for both high-altitude and high-latitude treeline species as a consequence of rapid warming rates (Holtmeier and Broll, 2010; Dufour-Tremblay et al., 2012; Gaire et al., 2014; Shrestha et al., 2014). In contrast to other mountains of the world, the Himalayan region has been largely neglected in this respect and is clearly under-represented in scientific literature on climate change-induced species range shifts (Schickhoff, 2005; Telwala et al., 2013; Dutta et al., 2014; Schickhoff et al., 2015).

Moreover, most high altitude and high latitude treeline studies investigated coniferous tree species (e.g. *Abies*, *Picea*, *Pinus*, *Larix*), while deciduous tree species (e.g. *Betula*) remained largely out of focus. The genus *Betula* is known to be widely distributed in the Northern Hemisphere and birches are among the conspicuous broadleaved high altitude and high latitude treeline species (Truong et al., 2007; Speed et al., 2011). *Betula* spp. can be found at polar treelines (subarctic and boreal zone) as well as at alpine treelines (cool and warm temperate zones) (Holtmeier, 2009). In Europe, *Betula* species were target species in several modelling studies (e.g. Thuiller, 2003 on *B. nana*; Svenning et al., 2008 on *B. pendula* and *B. pubescens*). Our target species *Betula utilis* is widespread at alpine treelines in the Himalayan mountains (Ashburner and McAllister, 2013), and is considered to be an indicator species for climate-driven treeline dynamics (Liang et al., 2014). Presently, only few researchers have addressed the problem of modelling distribution ranges of deciduous treeline species. This applies in particular to the Himalaya. Up to date, modelling studies were either local studies on *B. utilis* (e.g. Singh et al., 2013; Indian Himalaya, Uttarakhand; Huo et al., 2010; SW China) or focused on other species (Kumar, 2012 on *Rhododendron* spp.; Ranjitkar et al., 2014 on *Oxybaphus himalaicus* and *Boerhavia diffusa*). Previous work on *B. utilis* focused mainly on dendroecology (Bhattacharyya et al., 2006; Tenca and Carrer, 2010; Dawadi et al., 2013; Gaire et al., 2013; Liang et al., 2014), remote sensing (Singh et al., 2012, 2013; Rai et al., 2013), plant physiology (Xu et al., 2012; Shi et al., 2008), and regeneration (Shrestha et al., 2007).

Thus, modelling the distribution of treeline species such as *B. utilis*, a predominant species in western and central Himalayan treeline ecotones (Schweinfurth, 1957; Schickhoff, 2005), is still a major research deficit. This study models for the first time the potential distribution of *B. utilis* in the subalpine and alpine treeline ecotone of the Himalayan mountains on a broad scale, based on underlying climatic determinants of its distribution range. We aim at assessing the performance of Generalized Linear Models (GLM), implementing a multi-step evaluation approach: i) calibration of the model, ii) evaluation of spatial prediction success and accuracy of the models, iii) projecting the distribution of *B. utilis* under current climate conditions. Using this approach, we seek to answer the following key questions:

1. Are selected climatic variables able to reflect the climatic gradient from more continental western to more oceanic eastern regions of the Himalayan mountain range?
2. What are key climatic constraints for the current distribution of *B. utilis* in the Himalayan region?
3. Which areas are predicted as potentially suitable for *B. utilis*?
4. Are there differences between the current model predictions and the distribution range delineated in the detailed vegetation map of Schweinfurth (1957)?

## 2. Materials and methods

### 2.1. Study area

The Himalayan mountain range is located between the Indian Subcontinent in the south and the Tibetan Highland in the north, and extends from Afghanistan in the northwest (c. 36°N and 70°E) to Yunnan in the southeast (c. 26°N and 100°E). It is a vast mountain region, covering an area of more than 1,000,000 km<sup>2</sup>, with a length of c. 3000 km (Pakistan to SW China) and a maximum width of 400 km.

The Himalayan mountains show a distinct three-dimensional geoecological differentiation, with a high variation of climate, rainfall, altitude, and soils (Troll, 1972; Zurick and Pacheco, 2006; Miehe et al., 2015a). The climate ranges from tropical in the Indian lowlands to permanent ice and snow at the highest elevations, and from more continental in the NW to more oceanic in the SE. The amount of annual precipitation increases with increasing monsoonal influence in the same direction along the southern front of the range (Schickhoff, 2005; Böhner et al., 2015). The small-scale heterogeneity of habitats and site conditions supports a high diversity of species and communities.

### 2.2. Target species

The distribution range of *Betula utilis* extends across the Himalayan range from Afghanistan to SW China, with the total elevational range extending from 2700 to 4500 m (Polunin and Stainton, 1984). *B. utilis* was selected as a study species due to its status as a principal broadleaved treeline species in the western and central Himalayan mountains (for photographs see Appendix A1, Fig. 1A). This species mainly grows on north-facing slopes in shady locations. In the NW Himalaya, *B. utilis* is widely distributed in the elevational range between 3100 and 3700 m, while the range shifts to higher altitudes towards the E Himalaya (mainly between 3800 and 4300 m; own database). *B. utilis* grows in mixed forests with conifers and rhododendrons and forms a narrow forest belt between coniferous forests below and a krummholz belt above (for associated tree species see Schickhoff, 2005; Miehe et al., 2015b). Pure birch stands with *Rhododendron campanulatum* and *Sorbus microphylla* in the understory are often found at the uppermost limit of subalpine forests (Schickhoff et al., 2015).

### 2.3. Species data collection

Presence-only occurrence data of *B. utilis* were accessed via the Global Biodiversity Information Facility ([gbif.org](http://gbif.org)). The database hosts 215 geo-referenced records (1980–2016) without any known coordinate issues for our study region. 202 records were added from a database compiled from a literature survey (Schickhoff, 2005; unpublished data). Additionally, we extracted 327 records from freely available satellite images (GoogleEarth™, ver. 7.1.1.1888, Google, 2015) and added them to the dataset. This method has been proven to be useful in global treeline research (Paulsen and Körner, 2014; Irl et al., 2015). These occurrence localities were validated through expert knowledge, obtained from numerous field visits in the Himalayan region. We used a total of 744 records for further analysis.

Prior to building the distribution model of a species, error sources have to be minimized, in particular those arising from spatial autocorrelation of species occurrence data. Only one occurrence point per grid cell (1 km × 1 km) was considered, furthermore only the uppermost occurrences in the treeline ecotone were used, resulting in 590 occurrence points of *B. utilis* as a basis for modelling the current distribution of this species (Fig. 1). Lowermost occurrences (e.g., in avalanche paths) were omitted since they do not represent the 'zonal' climatic conditions of the treeline birch belt.

### 2.4. Climatic variables and statistical analyses

Ecological modelling applications frequently apply simple interpolated climate data sets such as 'worldclim' (Hijmans et al., 2005), which regionalize monthly observations of precipitation and temperature based on a weighted linear regression approach, using latitude, longitude and elevation as statistical predictor variables. Despite of the high spatial resolution of approximately 1 km<sup>2</sup>, these data sets neglect local scale atmospheric processes which are crucial for the formation of site specific topo-climatic conditions in high mountain environments. Many studies show that local scale atmospheric conditions are highly influenced by the underlying terrain. Anisotropic heating at different slope positions as well as cold air drainage and pooling in mountain valleys during autochthonous weather conditions result in a complex temperature pattern, which distinctly modifies the distribution of plant communities. Likewise, the spatial pattern of precipitation is influenced by wind- and leeward slope positions, resulting in hyper-humid climate conditions at the southern declivity of the Himalayan range and semi-arid to arid conditions in the Trans-Himalayan valleys. Freely available gridded climate data sets often do not satisfy

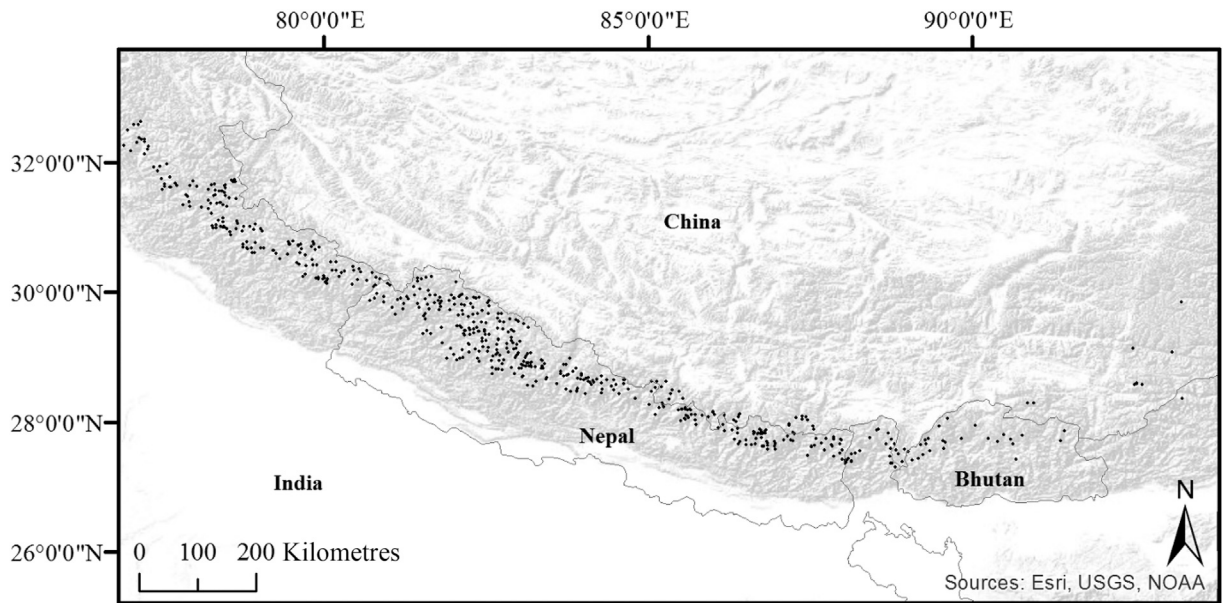


Fig. 1. Occurrences of *Betula utilis* in the Himalayan mountains (N = 590).

the requirements of ecological climate impact studies and impede the interdisciplinary investigation of climate ecosystem interactions (Soria-Auza et al., 2010).

In this study all statistical analyses were performed using the programming language R (R Core Team, 2015). All maps were created using ArcGIS (Version 10.1; Esri Inc. Redlands, CA, USA).

In order to sufficiently incorporate local scale climate variations in the framework of the presented modelling approach, we make use of two gridded long-time climate data sets (one for temperature and one for precipitation respectively), which explicitly account for important topo-climatic processes. Gridded monthly mean temperature fields with a spatial resolution of  $1 \times 1$  km were derived from the ERA-Interim reanalysis by means of an elevation and bias correction approach, which considers the climate model internal stratification of the atmosphere (Gerlitz et al., 2014). Compared with simple linear elevation adjustment techniques the approach was shown to considerably improve the quality of high resolution temperature fields in high mountain environments (Gerlitz et al., 2014).

Monthly precipitation sums with the same resolution were downloaded from the freely available 'chelsa' climate dataset (Karger et al., 2016). This climate data is based on a quasi-mechanistic statistical downscaling of the ERA-interim global circulation model with GPCC and GHCN bias correction. Precipitation amounts, which were estimated under consideration of orographic factors such as wind fields, valley exposition and boundary layer height showed high preciseness compared to precipitation data from other climate datasets (Karger et al., 2016).

Based on the gridded monthly fields of temperature and precipitation, we generated 19 climatic variables using the R-package 'dismo' (Hijmans et al., 2011). These climatic variables are widely used in species distribution modelling and represent annual characteristics (e.g., mean annual temperature), seasonality (e.g., annual range in precipitation) and extreme environmental factors (e.g., precipitation of driest month) (Nix, 1986; Hijmans et al., 2005). In addition, average precipitation of May and of March, April and May was calculated in order to account for potential pre-monsoon drought stress (Liang et al., 2014; Schickhoff et al., 2015, 2016). Furthermore, a digital elevation model was extracted from GLOBE (ngdc.noaa.gov; Global Land One-Kilometer Base Elevation). We applied ArcGIS (Version 10.1; Esri Inc. Redlands, CA, USA) to calculate slope angle and slope aspect using the 'surface' function of the Spatial Analyst toolbox. The DEM-elevation as well as its derivatives slope and aspect were utilized as additional predictor variables. The resolution of climatic raster grids and the DEM is 30 arc seconds, which equals  $1 \text{ km} \times 1 \text{ km}$ . All processing of climate data was done with R-package 'raster' (Hijmans, 2015).

Climatic and topographic predictors were chosen to reflect the species' physiological needs. Prior modelling, we examined possible correlations between all variables, since they often show high collinearity, resulting in poor model performance and misleading interpretations (Dormann et al., 2013). Spearman's rank correlations were calculated using R-package 'usdm' (Naimi, 2015) to detect multi-collinearity between environmental variables, with thresholding Spearman's rank correlation coefficient  $r_s \leq 0.7$  (Dormann et al., 2013). Correlations were visualized with R-package 'corrplot' (Wei and Simko, 2016; see Appendix A2 in Fig. A2). For all pairs of correlated variables, decisions were based on performance of univariate models and the results of hierarchical partitioning using the R-package 'hier.part' (Walsh and Mac Nally, 2013). Several test runs were calculated and out of 24 predictor variables only five predictors were included in the modelling procedure (Table 1). Only ecologically meaningful variables, which represent general pattern and annual variability of the climate, were included for modelling the potential distribution of *B. utilis*. We used variables (e.g. temperature of growing season and winter



**Table 1**  
Climatic variables used for modelling the potential distribution of *Betula utilis*.

Label	Variable	Scaling Factor	Units	Used for modelling
bio1	Annual Mean Temperature	1	Degree Celsius	
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	1	Degree Celsius	
bio3	Isothermality (bio2/bio7)	1	Dimensionless	
bio4	Temperature Seasonality (Standard Deviation)	100	Degree Celsius	
bio5	Max Temperature of Warmest Month	1	Degree Celsius	
bio6	Min Temperature of Coldest Month	1	Degree Celsius	
bio7	Temperature Annual Range (bio5-bio6)	1	Degree Celsius	X
bio8	Mean Temperature of Wettest Quarter	1	Degree Celsius	X
bio9	Mean Temperature of Driest Quarter	1	Degree Celsius	
bio10	Mean Temperature of Warmest Quarter	1	Degree Celsius	
bio11	Mean Temperature of Coldest Quarter	1	Degree Celsius	
bio12	Annual Precipitation	1	Millimetre	
bio13	Precipitation of Wettest Month	1	Millimetre	
bio14	Precipitation of Driest Month	1	Millimetre	
bio15	Precipitation Seasonality (Coefficient of Variation)	100	Percentage	X
bio16	Precipitation of Wettest Quarter	1	Millimetre	
bio17	Precipitation of Driest Quarter	1	Millimetre	
bio18	Precipitation of Warmest Quarter	1	Millimetre	
bio19	Precipitation of Coldest Quarter	1	Millimetre	X
prec_may	Average Precipitation May	1	Millimetre	
prec_mam	Average Precipitation March, April, May	1	Millimetre	X
alt	Altitude	1	Metres	
aspect	Aspect	1	Degree	
slope	Slope	1	Percentage	

temperatures) which are known to reflect prevailing climate conditions at the treeline. Some variables (e.g. Temperature of Warmest Month and Temperature of Warmest Quarter) were highly correlated, in this case we decided to use variables, which cover more than one month (i.e. quarter which equals a period of three month). In all cases usage of ‘Quarter’ variables yielded to models with higher discriminatory power and higher variable importance.

Descriptive statistics for all variables were calculated using the R-package ‘pastecs’ (Grosjean and Ibanez, 2014; see Appendix A3, Table A3a and A3b).

## 2.5. Modelling procedure

### 2.5.1. Model algorithm

Several methods are available for constructing SDMs, and they have been comprehensively compared in terms of performance (Austin et al., 2006; Tsoar et al., 2007). We used multiple regression techniques (i.e. Generalized Linear Models) as they represent a classical and robust approach to analyse presence and absence data (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989), with the function `glm()` implemented in the R-package ‘stats’ (R Core Team, 2015). GLMs were calculated with binomial distribution, logit-link function and polynomial terms of second order (Austin, 1999), but did not include terms of interactions among variables. To calculate the final GLMs step-wise variable selection in both directions (i.e. forward and backward) was applied, using the Akaike Information Criterion (AIC, Akaike, 1974), thereby the final and best model possesses the lowest value for AIC (Burnham and Anderson, 2002; Guisan et al., 2002).

### 2.5.2. Pseudo-absence selection

As GLMs need presence and absence points, pseudo-absence points were generated. For study area selection, a convex hull was used, covering the full extent of the known occurrences of *B. utilis* distribution in the Himalayan region. By limiting the study area, large regions where the species cannot occur were excluded in further statistical analyses, in order to prevent over-predicting the distribution range of the species (VanderWal et al., 2009).

For random selection of pseudo-absences, the limits were set as 5 km from the nearest occurrence, resulting in total 6000 pseudo-absences (following the pseudo-absence selection procedure for GLMs described by Barbet-Massin et al., 2012, using the ‘random points’ function of Data Management toolbox in ArcGIS, ESRI, 2012).

### 2.5.3. Model calibration and evaluation

Independent data collected from sites other than those used to train the model are essential to evaluate the predictive performance of the model. In order to obtain reliable estimates of model performance, models are tested with independent data (Araújo et al., 2005). Prior modelling, all presence and pseudo-absence points were randomly split into training and

testing subsets, using the R-package ‘caret’ (Kuhn et al., 2016), whereas training data represented 80% of the original dataset and testing data 20%. Statistical re-sampling techniques such as cross-validation (Stone, 1974) are used to decrease bias in measuring the predictive performance of the model (Pearce and Ferrier, 2000). The calibrated GLMs were validated using 10-fold cross-validation function of the R-package ‘ecospat’ (Broennimann et al., 2015). In cross-validation, all presences and pseudo-absences are divided in  $K$  equal groups. Each group consists of two subsets (i.e. training set and testing set). The predicted values are used to assess the accuracy of the prediction on the withheld test data (Pearce and Ferrier, 2000). In order to reduce variability, this procedure was repeated 5 times, resulting in 5 versions of the potential species distribution that were averaged.

The final projected distribution map only contains potential presences, predicted by all 5 model versions.

Due to the lack of a universally valid model evaluation criterion, it is essential to use more than one performance evaluation metric. We chose a multi-step evaluation approach to assess the performance of the modelling algorithms: 1) threshold-independent (AUC), 2) threshold-dependent (TSS), explained variance, Pearson’s correlation coefficient ( $r_p$ ), explained deviance, slope and intercept of the calibration curve. Finally we conducted a visual assessment of projected distribution maps.

All models were evaluated using functions and arguments incorporated in the ‘PresenceAbsence’ library (Freeman and Moisen, 2008a, b).

For threshold-independent evaluation, we used the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Fielding and Bell, 1997; Elith and Burgmann, 2002). The AUC is a non-parametric measure (i.e. no assessment of the goodness-of-fit of the model) and varies according to the suitability proportion of the study region. The AUC constitutes a measure of overall model performance (continuous discrimination between suitable and unsuitable habitat) irrespective of threshold. The AUC obtains values between 0 and 1, whereas values of  $>0.9$  are considered high, 0.7–0.9 moderate, 0.5–0.7 low and  $<0.5$  no better than random (Wiley et al., 2003; Phillips et al., 2006).

As threshold-dependent measure, we used True Skill Statistics (TSS) (Flueck, 1987; introduced to SDM by Allouche et al., 2006). In contrast to the AUC measure, the TSS is used to convert a continuous prediction into a binary one (i.e. those areas predicted as suitable versus not suitable for the species) and provides a measure of map veracity.

TSS is defined as  $1 - \text{maximum}(\text{sensitivity} + \text{specificity})$  where sensitivity and specificity are calculated on the probability threshold for which their sum is maximized (Table 2 and eqn. (1)). The TSS value can accommodate values between 0 and 1. This has been suggested as an alternative to Cohen’s Kappa (Allouche et al., 2006) when a threshold-dependent measure of performance is needed. TSS responds to species prevalence differently than Cohen’s Kappa, but nonetheless, the statistic has been shown to be negatively related to prevalence (Allouche et al., 2006). This method outperformed other techniques in recent comparisons of threshold methods (Jimenez-Valverde and Lobo, 2007). TSS was calculated using the MaxSens+Spec argument incorporated in the ‘PresenceAbsence’ library (Freeman and Moisen, 2008b). Sensitivity and Specificity are derived from the confusion matrix (Table 2, Eqn. (1)). Consequently, TSS assesses both omission and commission errors. In detail, sensitivity is the proportion of observed presences that are predicted as such, and therefore quantifies omission errors (false negative error rate). Specificity is the proportion of observed absences that are predicted as such, and therefore quantifies commission errors (false positive error rate). Sensitivity and specificity are independent of each other when compared across models, and are independent of prevalence ( $(a + c)/n$ , where  $n$  equals the total number of sites in which the species was recorded as present; Allouche et al., 2006).

For a  $2 \times 2$  confusion matrix TSS is defined as:

$$TSS = \frac{TP * TN - FP * FN}{(TP + FN)(FP + TN)} = \text{Sensitivity} + \text{Specificity} - 1 \quad (1)$$

Furthermore we calculated explained variance of the training dataset. With Pearson’s correlations the coefficient ( $r_p$ ), between the predicted and observed values for *B. utilis* were calculated. To account for the goodness-of-fit of the models, we used explained deviance, which is calculated as the quotient of the residual deviance and the deviance of the null model subtracted from 1. For models performing better than the null model, values range from 0 to 1, whereas 1 is the value of the best model. Furthermore slope and intercept of the calibration curve were calculated to examine overfitting of the models. Optimally calibrated models feature a calibration curve with intercept 0 and slope 1 (Reineking and Schröder, 2006).

All performance measures were calculated on training and testing datasets and averaged respectively. Results yielding any presumptions of the models are shown in Table 3.

**Table 2**

A confusion matrix used to evaluate the predictive performance of presence-absence models, showing the cross-tabulation of observed and predicted values as a two-by-two contingency table.

		Validation dataset	
		Presence	Absence
Model	Presence	TP (true positive)	FP (false negative)
	Absence	FN (false negative)	TN (true negative)

**Table 3**

Evaluation results for Generalized Linear Models (averaged from 5 runs) on the selected predictor variables. Following evaluation metrics were calculated: The Explained Variance on the training dataset [%], Pearson's correlation coefficient ( $r_p$ ) between observed and predicted values, the Area under the Curve (AUC), True Skill Statistics (TSS), Explained Deviance, the Slope and Intercept of the calibration curve. The results for training and test data are displayed respectively (training 80% and testing 20% of the data).

Model	Explained variance		Correlation $r_p$		AUC		TSS		Explained Deviance		Slope		Intercept	
	Train	Test	Train	Test	Train	Test	Train	Test	Train	Test	Train	Test	Train	Test
GLM	0.84		0.88	0.85	0.99	0.98	0.92	0.89	0.76	0.73	0.97	0.83	-0.01	-0.08

### 2.5.4. Model comparison

To compare the geographic extent and frequency distribution of the predictions in the GLMs, the consensus maps of the predicted probability of species presence for each raster cell of the study region were converted into binary “presence-absence”-maps, above their respective TSS threshold. Finally, we compared our current projection with the landmark work of Schweinfurth (1957), who provided the first detailed vegetation map of the Himalayan mountains (hereafter Schweinfurth map), in order to quantify differences between the current potential and previous real distribution of *B. utilis*. The Schweinfurth map summarizes the 1950s' state of knowledge of Himalayan vegetation distribution. It is based on an extensive literature survey, viz. on available published records up to 1956, complemented by all other reliable sources available such as unpublished diaries, personal communications, photographs, maps, etc. Despite showing some “white areas” it is still the most detailed vegetation map of the entire Himalayan region.

## 3. Results

### 3.1. Climatic variables

After prior-modelling examinations (i.e. multi-collinearity), five variables were selected out of twenty four potential predictor variables for modelling the potential distribution of *B. utilis*. These variables were Temperature Annual Range, Mean Temperature of the Wettest Quarter, Precipitation Seasonality, Precipitation of Coldest Quarter and Average Precipitation of March, April and May (Fig. 2).

The results of the final, averaged model revealed that variable importance varied between the predictor variables. Response curves of selected predictor variables were used to quantify the climatic niche of *B. utilis* (Fig. 3). Highest relative variable importance was found for Mean Temperature of Wettest Quarter, followed by Precipitation of Coldest Quarter. High relative variable importance was also ensued for Temperature Annual Range, followed by the Average Precipitation March–May, whereas lowest value was found for Precipitation Seasonality. Mean Temperature of Wettest Quarter showed a close-to-normal with a bell-shaped distribution. Precipitation Seasonality and Precipitation of Coldest Quarter show unimodal response curves, whereas Temperature Annual Range and Average Precipitation of March, April and May show sigmoidal response curves.

### 3.2. Model calibration and evaluation

The results of all model performance measures are given in Table 3. The calculation of explained variance revealed that our model explained 84% of the variance in the training dataset. Training and Testing models showed a clear correlation of the predicted and observed values ranging from  $r_p$  0.85 to 0.88 respectively. Explained deviance was moderately high for the subsets. Calculation of slope and intercept of the calibration curve revealed an optimal fit of the models.

The threshold-independent “Area Under the Curve” (AUC) of the receiver-operating characteristic (ROC) plot approach was very high (AUC = 0.99 AUC<sub>SD</sub> = 0.00163) for the training dataset as well as for the testing dataset (AUC = 0.98, AUC<sub>SD</sub> = 0.0041). Continuous predictions of the current distribution of *B. utilis* are displayed in Fig. 4.

In order to assess model quality, the continuous maps were converted to binary distribution maps, using the threshold-dependent measure TSS. In order to obtain binary distribution maps, continuous maps were thresholded at the averaged optimal threshold (0.088). Confusion matrices of the final model (Appendix A4, Table A4) were then used to calculate the True Skill Statistics. The calculated TSS showed high value (TSS ≥ 0.89). The binary distribution map is shown in Fig. 5.

### 3.3. Model comparison

After converting the predictions from continuous to binary, the suitable habitat area was predicted to be much larger in the western and central region of the Himalayan mountain system compared to the eastern region.

In a final step we compared the Schweinfurth map (Schweinfurth, 1957) with our current prediction to detect differences between the real distribution of *B. utilis* in the 1950s and the current potential distribution (Fig. 5). The Schweinfurth map shows patches (red) where *B. utilis* is the dominant treeline species in the uppermost subalpine forests. In the Indian western Himalaya (Himachal Pradesh, Uttarakhand), the uppermost limit of the distribution range of *B. utilis* (red) predicted by the models roughly coincides with the vegetation map. In western and central Nepal and in Bhutan, however, the predicted high



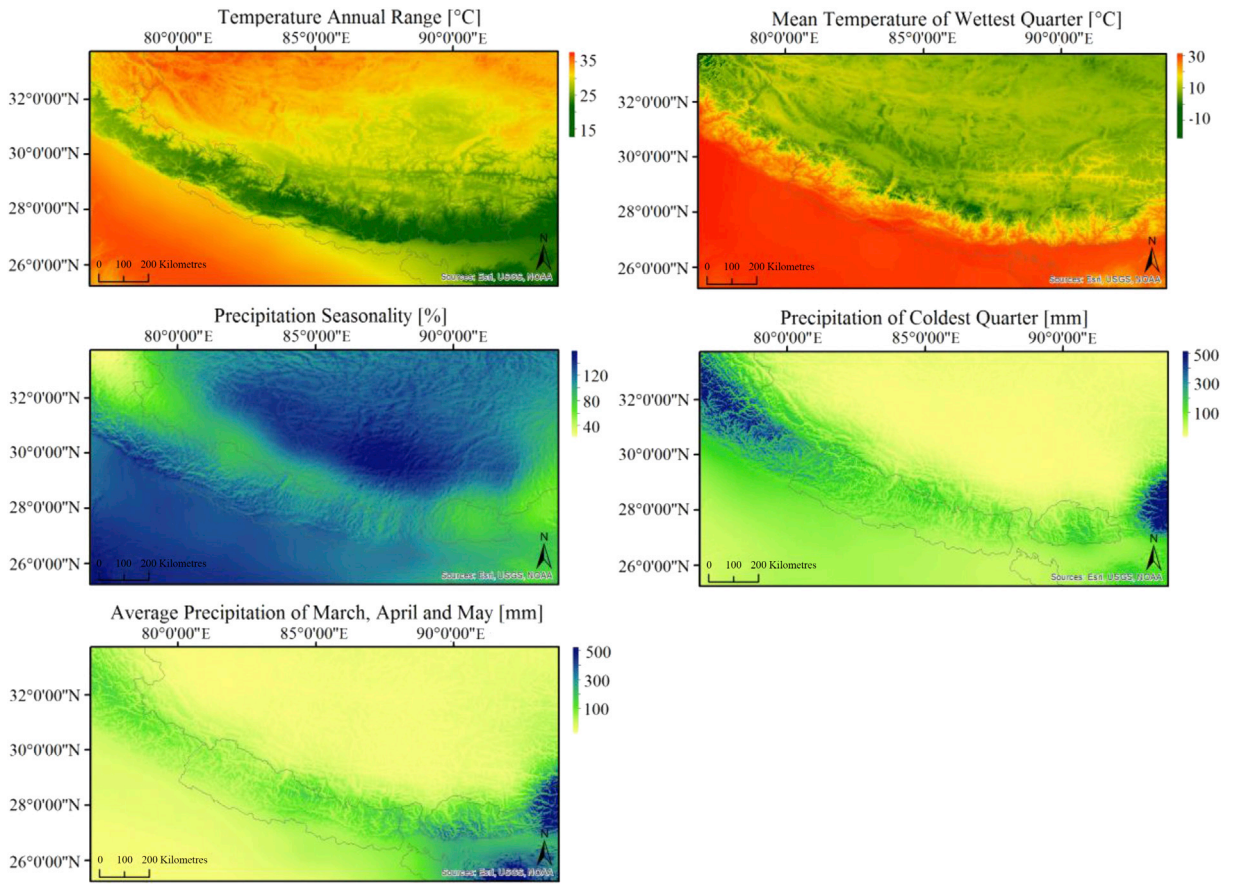


Fig. 2. Climatic variables used for modelling the potential distribution of *Betula utilis*.

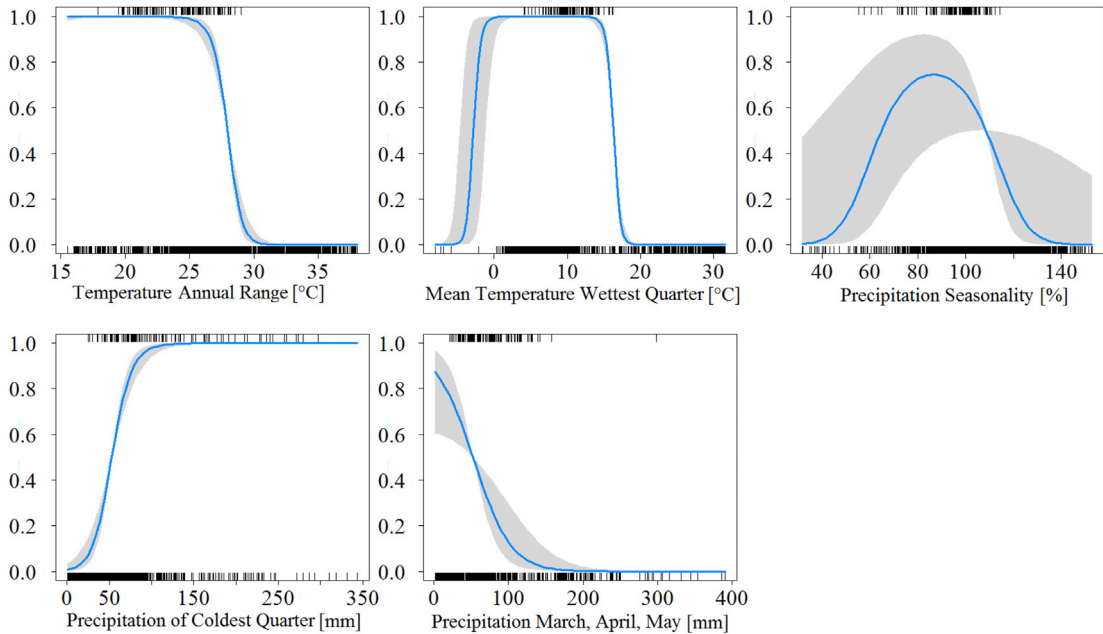


Fig. 3. Averaged response curves of the variables used in the Generalized Linear Models to model the potential distribution of *Betula utilis*. Grey-shaded areas represent the confidence interval of the predicted probabilities. Response curves do not account for interactions between the variables.

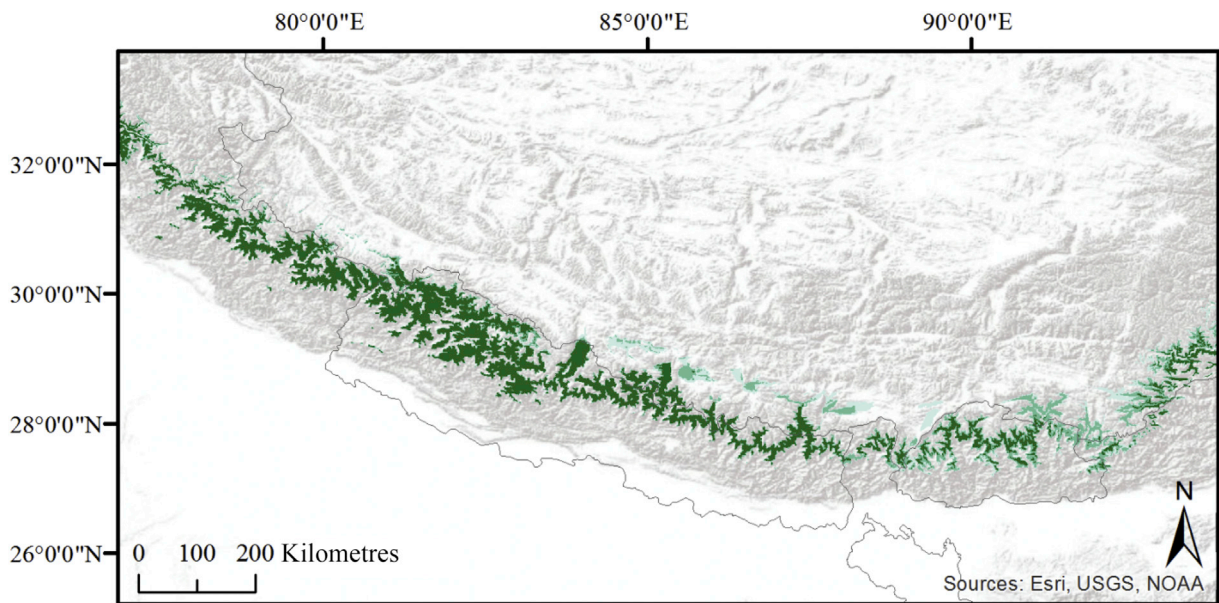


Fig. 4. Continuous predictions of the current distribution of *Betula utilis* predicted by all 5 model runs. For larger maps see [Appendix A5, Fig. A5](#).

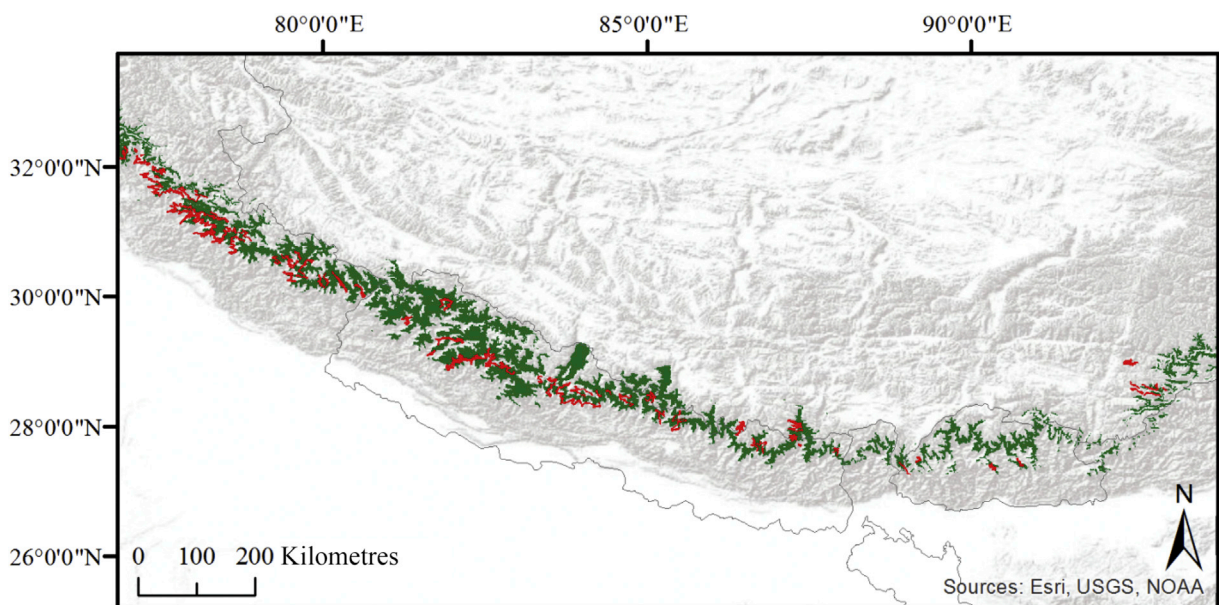


Fig. 5. Geographic extent of regions predicted as the potential distribution of *Betula utilis* (green) thresholded at True Skill Statistics ( $TSS \geq 0.89$ ) and distribution of *B. utilis* according to the Schweinfurth vegetation map (red) (Schweinfurth, 1957). For larger maps see [Appendix A6, Fig. A6](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

altitude occurrences are considerably higher than the distribution depicted in the Schweinfurth map. In the eastern Himalayan mountains (eastern Nepal and south-east Tibet), the Schweinfurth map shows patches of *B. utilis* as a prominent treeline species which are located in some instances above the predicted distribution range of the model.

#### 4. Discussion

##### 4.1. Climatic space of *B. utilis* in the Himalayan region

We found three precipitation- and two temperature-related variables most important for predicting the potential distribution of *B. utilis* (Fig. 3). Mean Temperature of the Wettest Quarter and Temperature Annual Range were most significant

among the temperature-related variables. Much lower growing season temperatures (i.e. Mean Temperature of the Wettest Quarter) in the E Himalayan mountains contribute to the lower seasonal temperature variation which favours evergreen *Rhododendron* treeline species and obviously constrains the capabilities of *B. utilis* to preoccupy its potential distribution range (Fig. 2). Notwithstanding the higher competitiveness of evergreen treeline tree species in the more oceanic E Himalaya, both evergreen and deciduous tree species are affected by direct growth limitation (sink limitation) due to low growing season temperatures at treeline elevations (Shi et al., 2008).

Furthermore, the amplitude of the highest average summer temperature (June) and the lowest average winter temperature (January) for species occurrence locations were of great importance. This reflects seasonal temperature variation having a significant effect on the occurrence of *B. utilis* (Figs. 2 and 3). The seasonal temperature amplitude decreases towards the more oceanic eastern Himalaya where we detected striking differences between the potential and real distribution of *B. utilis* (Fig. 4). In the E Himalaya, the birch becomes less competitive and is ousted by coniferous and in particular by evergreen broadleaved species (*Rhododendron* spp.) as principal treeline species (Schickhoff, 2005). Higher degree of continentality in the W and NW of the Himalayan mountain system with higher mean temperatures of warmest months and severe winter coldness at treeline elevations lowers the competitive capacity of *Rhododendron* spp. and favours the competitiveness of *B. utilis* and the realisation of its climatic niche (Fig. 2). Although mean summer temperatures are distinctly higher in the more continental W and NW Himalaya, the treeline birch belt is located at much lower elevations (3600–3800 m) compared to treelines in the E Himalaya with uppermost birch occurrences around 4500 m (Schickhoff, 2005; Schickhoff et al., 2015). This has to be attributed to very low winter temperatures ( $-13^{\circ}\text{C}$  mean temperature of coldest month at 3900 m in the Karakorum compared to  $-4$  to  $-5^{\circ}\text{C}$  at 3900 m in SE Tibet and Yunnan; Schickhoff, 2005), long duration of massive snow cover, and shorter growing seasons which more than compensate for the effects of higher summer mean temperatures.

While growing season air and soil temperatures are considered key factors controlling tree growth at treelines and elevational position of treelines at the global scale (Holtmeier, 2009; Körner, 2012), precipitation and related factors such as soil moisture and soil nutrient availability can be significant at regional and local scales (e.g., Müller et al., 2016a,b). Thus, precipitation-related variables potentially limit the climatic space of treeline tree species.

We found significant influence of three precipitation-related variables (Precipitation of the Coldest Quarter, Average Precipitation of March, April and May, and Precipitation Seasonality) for estimating the climatic space of *B. utilis*. The results of our study highlight the importance of the variable Precipitation of the Coldest Quarter for the distribution of *B. utilis*. Averaged over all occurrence locations, the period from November to January was identified as the coldest quarter. Winter precipitation in form of snow represents the annual second precipitation maximum in high elevation areas of the Himalayan mountain system (Böhner et al., 2015). Higher winter snowfall in the more continental western parts of the Himalayan region obviously contributes to increased birch occurrences compared to the eastern Himalaya (Fig. 2). The importance of snowpack as site factor for treeline birch forests was already stressed by Schweinfurth (1957), Champion and Seth (1968), Stainton (1972), Herzhoff and Schnitzler (1981), Puri et al. (1989), Dickoré and Nüsser (2000), and Eberhardt (2004). Troll (1939, 1967) highlighted the physiognomic adaptation of *B. utilis* to thick snowpack (snow-deformed trunks). Based on vegetation analyses in the W Himalaya and Karakorum, Schickhoff (1993, 2002) concluded that the distribution pattern of *B. utilis* forests is primarily controlled by thickness and duration of snow cover providing sufficient soil moisture at the beginning and at the end of the growing season, and that monsoonal summer rains, on the other hand, are of much less significance. Miehe et al. (2015b) also emphasize the association with a long-lasting snow cover, but indicate very different proportions of winter snowfall and monsoonal rainfall. *B. utilis* forests receive across their entire distribution range. Nevertheless, a higher preoccupation of the potential distribution range of *B. utilis* is obviously linked to a higher proportion of winter snowfall. Our findings suggest Average Precipitation March, April and May to be a useful predictor variable to model the potential distribution of *B. utilis*. This accentuates the results of dendroecological studies (Dawadi et al., 2013; Liang et al., 2014; Gaire et al., 2014; Schickhoff et al., 2015), which emphasized low moisture availability in the pre-monsoon season as a significant site factor restricting the growth performance of *B. utilis*. The coincidence of low precipitation, higher temperatures, and higher evaporation results in potential pre-monsoon drought stress for *B. utilis*, that will amplify in coming decades due to high temperature trends in the pre-monsoon season for most of the Himalayan regions (Gerlitz et al., 2014). Although March–April–May precipitation is low throughout the distribution range of *B. utilis*, a certain level of pre-monsoon precipitation is obviously needed to ensure sufficient soil moisture availability for the more hygrophilous birch, in particular in regions where winter snowfall is lower and less melt water is available.

The significance of higher humidity levels and sufficient soil moisture availability for the climatic space of *B. utilis* is evident from its small-scale distribution patterns. *Betula* forests thrive on humid, shady slopes with deeply weathered podzolic soils, and are more or less absent from south-facing slopes, in particular in the more continental W Himalaya (Schickhoff, 1993, 2002; Miehe et al., 2015b). Only occasionally birch individuals or patches of *Betula* trees are found in sunny exposures, most notably in the more humid E Himalaya, and when azonal site conditions (water surplus habitats) can overcompensate the effects of high irradiation and soil moisture deficits. In semi-arid to semi-humid Himalayan regions with long-lasting snow cover, north- and south-facing slopes show sharp contrasts with regard to humidity and soil moisture conditions (Schickhoff, 2005). Considerable differences in irradiation intensity may result in southern aspects below 3200 m becoming free of snow already in January, while snow cover lasts until May at same elevations on north-facing slopes (Cramer, 1997). We consider sufficient soil moisture availability to be crucial for defining the topo-climatically suitable habitat of *B. utilis*. The role of soil moisture for distribution and growth performance is often underestimated, but was shown to be



significant for other tree genera and species near the warmer edge of their suitable range (Bonan and Sirois, 1992 for *Picea mariana*; Fang and Lechowicz, 2006 for *Fagus*; Ranjitkar et al., 2014 for *Rhododendron*).

The last precipitation-related variable we found having an impact on the potential distribution of *B. utilis* is Precipitation Seasonality, which refers to the variation in monthly precipitation sums over the course of the year, expressed as percentage. Species distribution can be strongly influenced by the variability of precipitation. The median value of 97 indicates a high degree of precipitation variability due to the seasonal contrasts of a monsoon-influenced climate (Fig. 2; Appendix A3, Table A3a and A3b).

Summing up, the climatic space for *B. utilis* was well identified by our environmental niche model, and the projection to geographic space coincides closely with the current distribution of the species throughout the Himalayan mountains. Since this distribution largely represents climatic conditions in treeline ecotones, the results of our study provide insights into underlying climatic factors which might to a certain extent also delimit suitable habitats for other Himalayan treeline-forming tree species.

#### 4.2. Performance of the modelling procedure

The predictive uncertainty associated with one evaluation metric can be reduced by comparing a variety of metrics. In order to define the environmental niche of *B. utilis* we modelled the climatic space of the species and projected the results in geographic space to predict the potential species distribution. We assessed model accuracy and prediction success by threshold-independent (i.e. AUC) and threshold-dependent (i.e. TSS) model performance measures. We found very high AUC values ( $AUC \geq 0.98$ ) for continuous projections (Fig. 4). Recent research suggested AUC being a questionable measure of model performance (Lobo et al., 2008; Warren and Seifert, 2011), as it does not reflect absolute, but relative model performance. Thus, it is only valid and useful for comparison among models for a single study species in a single study region (Peterson et al., 2011). Subsequently, the maps showing the predicted probability of species presence for each raster cell were converted into binary 'presence - absence'-maps, using the threshold-dependent measure of the TSS. The TSS value for the final model was high (TSS = 0.89), assuming a high predictive performance.

#### 4.3. Geographic projection of *B. utilis*

We conducted visual inspections of the predictions of the model to observe whether the model successfully predicted the species' realized distribution throughout the entire Himalayan mountain system. According to the authors' local field knowledge, the model predictions match the actual existing distribution range of *B. utilis* to the greatest possible extent. To interpret these findings, we investigated the binary species distribution maps (Fig. 5). *B. utilis* covers a notable environmental niche width across the entire Himalayan arc. The projections of the modelling results show that the most favourable conditions are located in the upper subalpine belt in the western and central Himalayan region where climatic conditions show a comparatively higher degree of continentality. This is consistent with the distribution pattern documented in several vegetation maps showing a narrow band of birch forests forming the upper treeline in northern exposures (Troll, 1939; Schweinfurth, 1957; Miede, 1991; Schickhoff, 1994; Braun, 1996; Nüsser and Dickoré, 2002; Eberhardt et al., 2007). Towards the eastern Himalaya, where more maritime climatic conditions favour the competitiveness of evergreen *Rhododendron* spp., *B. utilis* becomes a less frequent companion in subalpine forests and at treelines (Schickhoff, 2005).

The comparison of our predictions with the Schweinfurth map showed remarkable deviations in the distribution range of *B. utilis*, especially in the central part of the Himalayan mountains (Fig. 5), where the *B. utilis* is now predicted to occur at higher elevations compared to the real occurrence in the first half of the twentieth century. As the Schweinfurth map is based on an extensive literature survey, it cannot completely ruled out that there is some noise in the underlying data due to inaccurate altimetry (in particular in the E Himalaya with high elevation *Betula* occurrences) or sampling location errors. However, a much more likely explanation is that this finding has to be attributed to land use effects. Animal husbandry, timber logging, fuelwood collection and the like have been integral parts of village economies for centuries, if not millennia. Thus, treeline ecotones have been transformed to a large extent, and the far majority of Himalayan treelines is considered to be anthropogenic (Schickhoff et al., 2015). Treeline depressions on north-facing slopes can be in the order of 300 m, with overgrazing and fire having been the main agents for lowering treelines (Schickhoff, 1995; Beug and Miede, 1999). The difference between the modelled distribution range and the Schweinfurth map occurrence of *B. utilis* reflects large-scale, long-term anthropogenic interferences in Himalayan treeline landscapes. Effects of climate warming could also play a role since the distribution range of *B. utilis* is projected to shift upslope in coming decades (Schickhoff et al., 2015). Upslope movement of anthropogenic treelines is, however, primarily a response to the cessation of land use. The few remaining near-natural krummholz treelines in the Himalaya are still relatively unresponsive to climate warming, suggesting treeline advance to higher elevation to be a medium-to long-term process (Schickhoff et al., 2016; Schwab et al., 2016).

#### 4.4. Problems/limitations of our approach

Currently, modelling studies are often based on presence-only species occurrence data instead of presence-absence data, which are always a source of uncertainty. These presence-only data are often derived from databases of natural history museums and herbaria, which contain occurrences from numerous researchers, sampled with different techniques,

intensities and periods of time (Soberon and Peterson, 2004). Sometimes, areas have been unequally sampled or occurrence data have been inaccurately georeferenced, resulting in occurrences of species with sampling bias. Such geographic sampling bias can lead to sampling bias in environmental space, which represents a major problem for modelling (Veloz, 2009; for the effects of sampling bias on model evaluation: Anderson and Gonzalez, 2011). We tried to overcome this problem by spatially filtering occurrence points (i.e. only one point per  $1 \times 1$  km grid cell). But not only presences are a source of uncertainties, also the absence points of species have to be carefully inspected. Although presence-absence data from planned surveys are highly requested, high quality presence-absence data are available only for very few species worldwide. Models using presence-absence data have proven to be of great value in predicting species distributions (Guisan et al., 2002; Thuiller et al., 2008). If true absences are not available, pseudo-absences must be generated. The selection of pseudo-absences involves a certain degree of uncertainty, which may lead to over- or underestimated predictions. Based on our results, we do stress the need for incorporating true absences in ENMs. Furthermore, biased climate data can lead to distorted models (Heikkinen et al., 2006). These geographic and environmental biases are contrary to the assumption of many modelling techniques, viz. that the localities represent a random sample from the area being modelled (Phillips et al., 2006).

Finally, it should be noted that the actual distribution range might presumably be smaller than indicated by our models, because climatic factors are not the only factors determining habitat suitability. Although not considered in this study, interactions of a whole array of site factors such as topo-climate (radiation, temperature, precipitation, length of growing season, and snow cover), topography (slope inclination, relief forms), ecology of tree species (regeneration, seed dispersal, succession stages), site history (climate oscillations, fire, human impacts, insect attacks), current biotic (browsing, trampling, diseases and insect pests) and anthropogenic influences (burning, logging, grazing, recreation and tourism) affect treeline species spatial distributions (Schickhoff, 2005; Holtmeier, 2009). In mountainous areas the resolution of climate data (i.e.  $1 \times 1$  km) is often too coarse for models to distinguish between north- and south-facing slopes. We hereby emphasise the need for fine-scale climate data in order to account for the heterogeneous terrain, leading to more precise modelling results.

## 5. Conclusions

The distributional range of *B. utilis* was found to be primarily associated with thermal (Mean Temperature of the Wettest Quarter and Temperature Annual Range) and precipitation-related factors (Precipitation of the Coldest Quarter, Average Precipitation of March, April and May, and Precipitation Seasonality).

The application of our environmental niche modelling approach with appropriate model evaluation measures for assessment of model performance provided the current distribution range of *B. utilis*. The robustness of the results increased significantly using multi-faceted approach of model performance evaluation.

The results of our study, which account for underlying climatic factors in mountain ecosystems, may serve as a baseline for the exploration of potential impacts of climate change on future treeline species distribution in regions with limited data availability. The results will enhance the quantification of altitudinal shifts and other analyses of spatial pattern dynamics in mountain ecotones, which will be of increasing significance with regard to future climate change. We expect to provide a new starting point for modelling future treeline dynamics and treeline shifts in the Himalaya under novel climate conditions.

Our results point to the need for further investigations of relevant abiotic and biotic factors for species' occurrences and range shifts such as soil parameters and anthropogenic impacts at different temporal and spatial scales. In conclusion, a better understanding of potential ranges of alpine treeline species is supported by our model results which may also provide insights for decision makers in climate change adaptation and biodiversity conservation.

## Authors contributions

M.B. and U.S. conceived the research project ideas. L.G. provided the climate data. U.S. provided the species occurrence data. M.B. compiled and analysed the data and wrote the first draft. All authors contributed to write the final manuscript.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.gecco.2017.04.003>.

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**Maria Bobrowski** performed this research as part of her PhD thesis at the Institute for Geography, University of Hamburg. Her research interests are in particular plant ecology and ecological niche modelling. The study was supervised by Udo Schickhoff, who is Professor and Head of the Biogeography and Landscape Ecology Working Group at the Institute for Geography, University of Hamburg. He is a leading expert in mountain geography and mountain ecology and has been doing research in the Himalayan mountains for over 30 years.