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# Searching for ecology in species distribution models in the Himalayas

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ABSTRACT

Modelling species across vast distributions in remote, high mountain regions like the Himalayas remains a challenging task. Challenges include, first and foremost, large-scale sampling of species occurrences and acquisition of sufficient high quality, fine-scale environmental parameters. We compiled a review of 157 Himalayan studies published between 2010 and 2021, aiming at identifying their main modelling objective in relation to the conceptualization of their methodological framework, evaluating origin of species occurrence data, taxonomic groups, spatial and temporal scale, selection of predictor variables and applied modelling algorithms. The majority of the analysed studies (40%) attempted to answer questions about potential range changes under future or past climatic conditions. The most studied organisms were trees (27%), followed by mammals (22%), herbaceous plants (20%), and birds (9%).

For almost all studies we noted that a critical investigation and evaluation of input parameters and their ability to account for the species ecological requirements were neglected. Over 87% of all studies used Worldclim climate data as predictor variables, while around 50% of these studies solely relied on Worldclim climate data. Climate data from other sources were incorporated in only 7% and an additional 6% solely used remotely sensed predictors. Only around 2% of all studies attempted to compare the influence of different climate data sources on model performance. By far, Maxent was the most used modelling algorithm with 66%, followed by ensemble approaches (16%), whereas statistical modelling techniques lagged far behind (9%). Surprisingly, we found in 37% of the studies no interpretation on the relationship between the species and the predictor variables, while 27% of all studies included brief information, and 36% provided an elaborate, detailed interpretation on species ecological needs reflected in the final model.

With this review we highlight the necessity to identify and reduce biases and uncertainty associated with species' occurrence records and environmental data a priori. Since flawed input parameters produce misleading models without ecological causality, their implementation may have detrimental consequences when the best possible adaptation to future climatic conditions is at stake.

## 1. Introduction

### 1.1. Modelling species in mountain ecosystems

Mountain ecosystems are characterized by distinct three-dimensional geo-ecological differentiation, complex topography and a pronounced small-scale variation of climatic and edaphic conditions, resulting in numerous ecological niches and often representing biodiversity hotspots (Körner et al., 2017; Körner, 2021). Compared to most lowland regions of the world, mountain regions have been less transformed by human impact (Schickhoff, 2011). However, anthropogenic interferences are ubiquitous, and, for instance, in Old World mountain regions near-natural treeline sites can hardly be found (Schickhoff et al., 2015). In the course of past climate changes, mountain ranges provided refugia for species persistence and biodiversity preservation, and even greater importance could be attached to these refugia in future (Birks & Willis, 2008; Malanson et al., 2019).

Progress in remote sensing techniques, geographic information systems and modelling techniques shaped modern scientific research on species inhabiting high mountain ecosystems. Ever since abiotic and biotic factors and processes controlling spatial and temporal species' patterns and dynamics have been investigated across mountain ecosystems worldwide (Pauli & Halloy, 2019; Körner, 2021). With the combination of results from different disciplines (i.e. ecology, vegetation science, biogeography, environmental sciences and geosciences) researchers aim to differentiate, disentangle and understand underlying

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factors controlling current distribution, species ranges and compositions to derive forecasts under climate change scenarios (Franklin, 2010).

To quantify these effects and identify the drivers, species distribution models (SDMs) have become an indispensable tool. These correlative modelling approaches are now very popular when it comes to predicting past, current and future distribution of species in mountains all over the world (e.g., Dullinger et al., 2004; Thuiller et al., 2005; Parolo et al., 2008). The growing number of publications employing SDMs can be attributed to freely accessible databases of species occurrence or abundance records and high-resolution environmental data, as well as user-friendly statistic and GIS software. To date, SDMs have become an umbrella term comprising a variety of concepts, including species distribution, ecological niche, habitat suitability, habitat preference and climatic envelope models (Guisan et al., 2017; Zurell et al., 2020). Even if this fusion initially sounds reasonable, differences between modelling aims, interpretation and associated challenges exist (Soberón & Nakamura, 2009; Peterson & Soberón, 2012; Peterson et al., 2015; Guisan et al., 2017). However, an overarching characteristic of all species distribution modelling approaches are analyses of the underlying environmental factors in relation to the species' ecology, which, in turn, constitutes a basic requirement for understanding current, past and future species distribution ranges. Most frequently climatic factors, among other abiotic and sometimes biotic parameters, are used to estimate species' niches and distributions across space and time (Elith & Leathwick, 2009). Irrespective of the model aim of inter- or extrapolation, understanding of the phenomena of the species' occurrences is a precondition to formalize a model and make predictions that hold predictive capability.

The general interest in understanding underlying factors of species ranges and dynamics as well as forecasting and hindcasting species' niches, their distribution and composition has increased during the last decades (Schickhoff, 2005; Miehe et al., 2007; Telwala et al., 2013; Dutta et al., 2014; Schickhoff et al., 2015; Holtmeier & Broll, 2019; Bobrowski, 2021). Whereas climate change impacts on European and North American mountain regions are well studied (e.g., Theurillat & Guisan, 2001; Bell et al., 2014; Braunisch et al., 2016; Halofsky et al., 2018; Scherrer et al., 2020), one of the major mountain systems of the world, the Himalayas, is still comparatively under-researched. Over the last decade, numerous modelling studies have been published, however, no review on modelling studies across taxonomic groups exists to date for the Himalayan mountain system.

### 1.2. Challenges for modelling species in the Himalayas

Modelling ecological niches and species distributions across vast areas in remote, high mountain regions like the Himalayas constitute a challenging task. The main challenges arise from large-scale sampling of species occurrences (and in rare cases absences) and acquisition of sufficient high quality, fine-scale environmental predictors. Sampling deficits can be primarily attributed to the difficult accessibility of the terrain and the geographical extent of the Himalayan mountain system. However, the quality and quantity of occurrence data determine the significance of the model. The basic assumption of the model is based on uniform or random sampling of the study area (Royle et al., 2012). The selection of an appropriate predictor variable set depends not only on the availability of high quality environmental data, but also on the spatial scale, the autecology of the species and the degree of complexity of the ecological niche (Peterson et al., 2011). The understanding of the relationship between species-specific ecological constraints and its geographic distribution is the key aspect in selecting relevant and meaningful predictor variables. If neglected, the gap between ecology and model performance could be broadened in favour of high model performance metrics with decreasing real model accuracy and limited ecological explanation of habitat requirements of the species being provided (Synes & Osborne, 2011; Thibaud et al., 2014; Petitpierre et al., 2017; Santini et al., 2021). This gap could be further widened by the unmindful usage of evaluation metrics like the AUC (Lobo et al., 2008), and when these models serve as a baseline for future projections.

Recent general modelling research focussed on quality and quantity of input data, such as the number of occurrences in relation to extent and number of generated absences (Elith et al., 2011; Barbet-Massin et al., 2012), spatial structure of occurrence data (Fithian et al., 2015), multi-collinearity of predictors and spatial autocorrelation of species distributional data (Braunisch et al., 2013; Dormann et al., 2007, 2013). A wide range of publications addressed the effect of choice of modelling algorithm on model performance (Elith et al., 2006; Franklin, 2010; Saupe et al., 2012) and compared different evaluation criteria on model performance and projection (Allouche et al., 2006; Lobo et al., 2008).

In this review we do not focus on aforementioned well-studied topics, but rather concentrate on the rarely considered challenges of high quality input data and the significance of results when modelling species in the Himalayas. This review aims at addressing key questions related to species occurrence data acquisition and reliable climate data for modelling species in the Himalayas. We highlight potential challenges, identify gaps in modelling studies, point out noteworthy trends in the field, and summarize recent modelling studies with respect to quality and quantity of input parameters, applied model methodology and consideration of the species-specific ecological characteristics. We aim at pointing out expedient avenues to integrate mechanistic understanding and empirical data for future modelling studies in the Himalayan mountain system. Overcoming the input parameter challenges synthesized in this review will support catalysing advances in ecological models in the Himalayas.

## 2. Literature Review

### 2.1. Literature search

To grasp the on-going trend of modelling studies in the Himalayas using modern SDM techniques we conducted a literature search in Web of Knowledge und applied the following search strings: "species distribution*+ model* + Himalaya*"; "ecological niche* + model* + Himalaya*"; habitat + suitability + model* + Himalaya*"; "habitat + distribution* + model* + Himalaya" and "climatic + envelope + model* + Himalaya*" to find publications of the last ten years (i.e. 2010 and today ;last access March 2021). For each publication the authors names, year of publication, study region and the following information specified below were extracted.

All figures were created using ggplot2 (Wickham, 2016) in the programming language R (R Core Team, 2020).

### 2.2. Aim of the reviewed studies

We classified each study according to their modelling aim in current distribution, range shifts under future or past climate conditions, invasion of species and species phylogeny. Additionally, we noted which modelling approach was used, and subsequently evaluated whether proposed research questions were aligned with the applied concept and terminology.

### 2.3. Extent of analyses and species occurrence data

For each study the extent of the studied region was classified as (i) micro-scale where only small spatial scales at district level were investigated, (ii) meso-scale for one country, and (iii) macro scale when the whole Himalayan mountain system was analysed. Additionally, we noted all sources of occurrence data and how many occurrences were used in the modelling procedure.

### 2.4. Source and selection of environmental data

We registered all sources of environmental data and how the

predictor variables were selected (e.g., based on statistics and ecology). Additionally, we noted whether different sources of environmental data were compared according to data quality and plausibility.

### 2.5. Modelling technique and evaluation

Because most of the studies applied correlative models, we further classified them according to the modelling algorithm (e.g., statistical, machine learning, similarity and expert rule-based). Mechanistic and process-based models were not further considered. To account for model accuracy we compiled evaluation metrics (e.g., AUC, TSS, Kappa, $R^2$).

## 3. Results & Discussion

### 3.1. Literature search

The literature search strings yielded 567 publications for the period 2010-2021. After removing duplicate publications and publications that applied other methodological frameworks (e.g., dendro ecology, genetics, regeneration and non-empirical modelling approaches), 157 publications were used for further analyses. We limited our literature search to the collections of Web of Knowledge to allow for reproducible results. All reviewed studies are listed in the Supplementary Material of this review.

### 3.2. Aim of the reviewed studies

Irrespective of taxa, modelling potential range shifts, expansion or contraction had the highest proportion with 40%. The second most frequent research aim was modelling species' current distribution (33%) followed by studies where the phylogeny of species was considered to hindcast and/or forecast their distributional region (20%). Considerably less studies attempted to model the potential of invasive species (7%). Among all analysed studies, tree species were the most popular study organism with 27%, followed by mammals (22%), herbaceous species (20%) and birds (9%) (Tab. 1). Out of all analysed studies 72% focussed on one single species and the remaining 18% addressed multiple species in single-species models.

The review on applied methodological concepts revealed diverging usage regarding the methodology and terminology between SDMs and ecological niche models (ENMs), whereas 47% used the term SDM, 33% ENM and 10% referred to both terms. An additional 4% of the reviewed studies used the terminology of habitat suitability models (HSM) and further 6% did not label their approach at all, although ENM or SDM concepts were applied. We included habitat models (n = 2) in the category SDMs and climatic envelope models (n = 2) in the category of ENMs.

**Table 1**
Overview of all analysed studies according to taxonomic group, including species richness and research aim (N = 157).

| Taxonomic group | Current distribution | Range shifts | Invasive species | Phylogeny |
|---|---|---|---|---|
| Trees | 15 | 18 | 1 | 9 |
| Shrubs | 2 | 3 | 0 | 2 |
| Herbs | 6 | 11 | 7 | 7 |
| Weeds | | 3 | 3 | |
| Plants | | | | 1 |
| Species richness | 3 | 2 | | |
| Ferns | | | | 3 |
| Fungi | | 1 | | 1 |
| Lichens | | 1 | | |
| Mammalia | 18 | 13 | | 3 |
| Birds | 4 | 6 | | 4 |
| Amphibia | 1 | 1 | | 1 |
| Fish | | 2 | | |
| Insects | 2 | 1 | | |
| Gastropoda | 1 | | | |
| Spiders | | | | 1 |

Generally, in SDMs it is attempted to model the actual distribution of species in geographic space (Peterson & Soberón, 2012), whereas ENMs can be projected in geographic space and time, identifying consistent areas with suitable environmental conditions for the species and assessing distributional changes under past or future climate conditions (Araújo & Guisan, 2006; Peterson & Soberón, 2012). It becomes obvious that whenever species potential distributional range shifts are modelled under future or past climate conditions, it refers to the conceptual framework of ENMs. However, in 73% of the analysed studies using SDM terminology potential range shifts under future or past climatic conditions were modelled. Even if studies use the collective term SDM, the underlying conceptual methodological framework of distribution estimation or niche quantification should always be taken into consideration in order to allow a clear distinction between approaches, which will in turn facilitate a consistent interpretation of the results of modelling studies in the Himalayas.

### 3.3. Extent of analyses

The extent of the study area varied greatly from local studies to studies covering the entire Himalayan arc and adjacent mountains (Fig. 1). Overall, 60% of all analysed studies modelled species at local to meso scales, whereas 40% operated at macro scales (i.e. along the Himalayan arc, Himalaya-Hengduan mountains, Hindukush-Karakorum Himalayas, Sino-Himalayas).

In particular, 31% of the studies covered the Indian Himalayas, namely Jammu and Kashmir, Ladakh, Himachal Pradesh, Uttarakhand, and Sikkim, followed by studies extending over the entire Himalayan arc (17%) and Nepal (15%).

### 3.4. Source of occurrences

Especially in vast mountain systems like the Himalayas, sampling species' presence and absence locations is limited due to time and financial constraints, therefore presence-only data was most often used. The origin of occurrence data can be separated into directly measured data in the field and collected data bundled in databases, herbaria, museums and publications (Fig. 2). We found that occurrence data used for modelling the target species were most frequently recorded directly in the field (37%) and in several studies accompanied with different sources of collections (10%). Besides other sources, field survey data were supplemented with information from databases (15%) and very frequently with data from the Global Biodiversity Information Facility (GBIF, https://gbif.org), a platform that hosts freely available species occurrence data covering the entire globe. For the Himalayan mountain system we found GBIF data and combinations with other sources in 19% of the studies. For 19% of all studies other database, mostly local databases, herbaria, museums or literature were used to gather information on species locations. It was common to combine different sources of species data when large regions were studied, whereas solely field survey data or field survey data and additional sources were chosen when local scales were targeted.

Out of 157 studies, 139 provided information on number of occurrences used in the final model with large variation in sample sizes among studies. Compared to number of occurrences sampled in the field (mean = 80), combinations of different sources resulted in higher number of occurrences, in particular when field data, literature records and databases were utilized (mean = 150). When field data were accompanied with GBIF data and additional sources, a mean of 246 occurrences records were compiled. Outstanding high average numbers were found when occurrence data was compiled from combinations of GBIF with miscellaneous databases, local and national herbaria and relevant literature (mean = 631). For other sources, local databases means of occurrences records were comparatively low, despite mean records for virtual herbaria and databases, resulting in an overall median of 128

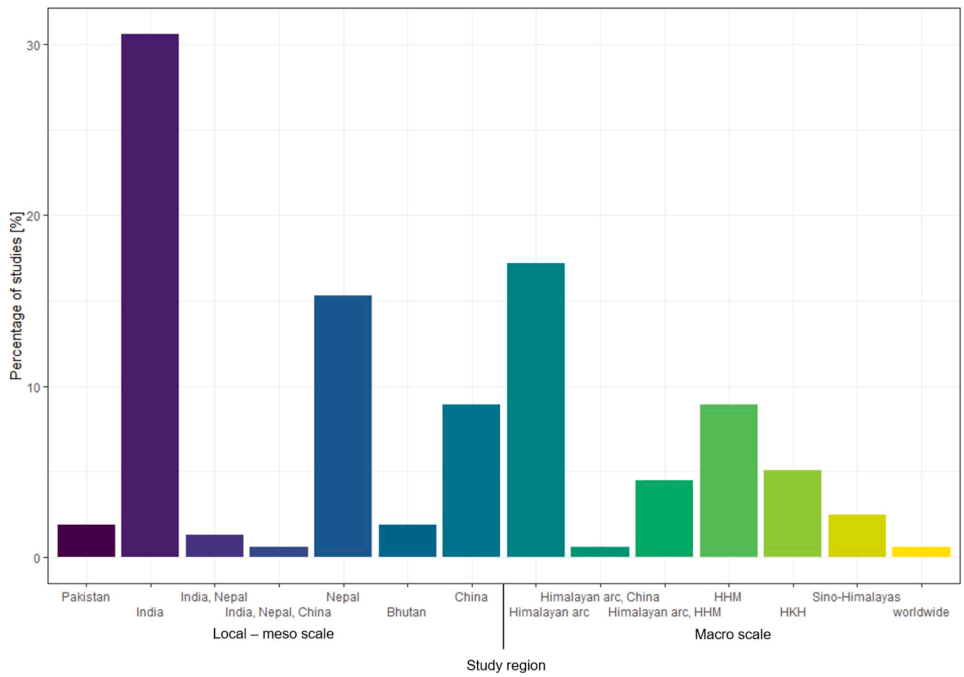


**Fig. 1.** Percentage distribution of studies according to spatial scale. Abbreviations used: HHM = Hengduan-Himalayan mountains, HKH = Hindu Kush Himalayas.

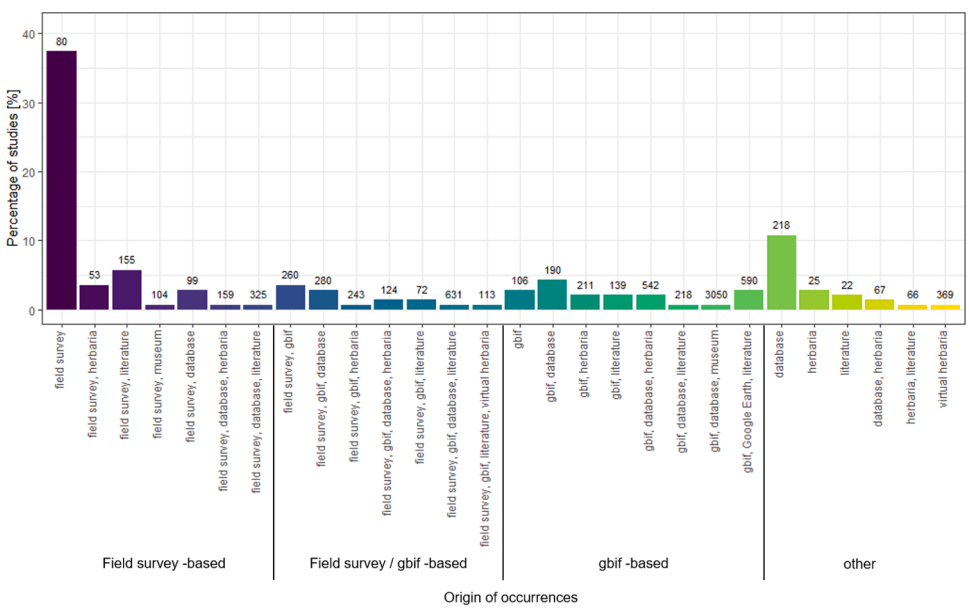


**Fig. 2.** Percentage distribution of studies according to origin of occurrence data. Numbers above each bar represent mean value of number of occurrences used in the final models obtained from respective sources.

occurrence records.

Besides data quantity, data quality plays a major role in generating a valuable occurrence data set of mountain species. One arising challenge of data derived from existing databases is the consideration of geospatial errors as a precondition to account for sampling errors (Meyer et al., 2016; Feng et al., 2019). Compared to planned, systematic field surveys, the true error measure remains unknown (Beck et al., 2013, 2014). Misidentification, duplicate records, sampling design and purpose, oversampling of certain areas and spatial clustering of species constitute possible sources of uncertainty. Especially in high elevation regions spatial bias leads to environmental bias because of the over-representation of certain environmental features of more accessible and extensively surveyed areas (Kramer-Schadt et al., 2013). Furthermore, spatial clumping may result in spatial autocorrelation and can reduce the model quality by falsely inflating measures of accuracy (Veloz, 2009), resulting in higher commission error rates (Dormann et al., 2008). Furthermore, the model may yield misleading parameter estimates (Kühn, 2007), allocating predictor variables that simply reflect the intensively studied area, further resulting in spatial extrapolation errors (Kramer-Schadt et al., 2013).

Nevertheless, in cases of large scale study areas and difficult accessibility of the terrain databases provide a cost and time effective tool. However, to obtain valuable modelling results in high mountain regions the data have to be thoroughly examined. Furthermore, the compilation of different sources such as databases, museums, herbaria and species' lists, national atlases, large-scale field surveys, regional checklists,

expert range maps, and collections from citizen science groups may be beneficial to compose a large dataset (Jetz et al., 2012).

Especially if the number of occurrences is limited, the distributional range covering the environmental gradients of the species occurrences has to be reflected in the data set (Fei & Yu, 2016), since biased occurrence data lead to biased models. Generally, studies agreed that sampling size (especially for N < 100) has significant effects on model quality, followed by the applied modelling algorithm (Thibaud et al., 2014; Soultan & Safi, 2017; Meynard et al., 2019). For example, if species records are clustered in lower, more accessible parts of the study area unlike its natural distribution, it is highly suspected that the model will show deviated results and predictions of erroneously main distribution range of the target species (Yackulic et al., 2013; Fithian et al., 2015). Furthermore, azonal observations (e.g., at both lower and higher elevations) should be removed to obtain valuable modelling results of the species niche in the target region (e.g., treeline locations) (Bobrowski et al., 2017). When the applied species prevalence is not in accordance with the actual distribution, it results in biased assumption on environmental distributional constraints (Pearson et al., 2006a). Moreover, model performance metrics are more dependent on correctly predicting absences than occurrences (Tessarolo et al., 2021). Furthermore, distortion of models under current climate conditions will subsequently lead to untrustworthy model projections under future climate conditions (Bobrowski & Schickhoff, 2017). Another major pitfall arises when spatial autocorrelation and spatial filtering are wrongly equated with each other (Sillero & Barbosa, 2021). Autocorrelation is essential for modelling as it captures relationships between locations (Dormann et al., 2007), nonetheless it causes biases when evaluating model performance (de Oliveira et al., 2014). In addition, spatial autocorrelation between training and testing data (Peterson & Soberón, 2012) and model residuals (de Oliveira et al., 2014) should be obviated. Therefore, extensive care has to be taken to filter and select the occurrence that will provide the basis for the following model procedure (Veloz, 2009). In mountain regions, applying methods like block cross-validation procedures to reduce spatial autocorrelation (Valavi et al., 2019) or using autocorrelation prone modelling algorithms provide valuable solutions (Kramer-Schadt et al., 2013).

Most modelling algorithms require presence-absence data, which were not available in most of the reviewed studies. Besides different pseudo-absence generation methods (in case of Maxent: background data, Phillips et al., 2006), the number of recommended pseudo-absences depends on the intended modelling algorithm and study sample (Barbet-Massin et al., 2012; Phillips & Dudík, 2008). However, model and sample-specific requirements are often disregarded in ensemble modelling approaches by fitting all models on the same data set (Santini et al., 2021).

### 3.5. Source of environmental data

In general, 42% of all analysed studies purely relied on one climate data source. The remaining 58% of the studies incorporated in addition to climate data mainly remotely sensed predictors, with digital elevation models (DEM) and land cover being the most prominent predictor variables. In 79% of the analysed studies, Worldclim 1.4 was utilized. In nearly half of these studies no additional predictor variables were incorporated (Fig. 3). Among freely available, relatively fine-scale (i.e. 1 × 1 km), long-term climate raster data set with global coverage, Worldclim 1.4 (Hijmans et al., 2005) is the most frequently used source of climatic variables in SDM and ENM studies with >12400 citations in Web of Knowledge Core Collection (March 2021). Especially in Europe and North America, Worldclim shows high accuracy (Hijmans et al., 2005), and is used in numerous biogeographical studies (Elith et al., 2006; Hijmans & Graham, 2006; Broennimann et al., 2012; Thibaud et al., 2014). In 2017, a new Worldclim climate data set was launched (Fick & Hijmans, 2017), which extends the former version of Worldclim 1.4 (Hijmans et al., 2005) by incorporating remotely sensed data as covariates and independent spline variables in the interpolation (Fick & Hijmans, 2017). In 6% of the studies Worldclim 2 was used and in 2% Worldclim 1.4 and 2 were combined (Fig. 3). Climond, which is based on Worldclim and CRU CL1•0 and CL2•0 data (New et al., 1999, 2002) and exhibits a spatial resolution of 50 by 50 km (Kriticos et al., 2012), was represented in 3% of all studies and used mostly without additional predictor variables.

Modellers predominantly use Worldclim, however, the recently published climate data set Chelsa (Karger et al., 2016, 2017) offers relatively fine-scale (i.e. 1 × 1 km), long-term climate raster data set with global coverage and enjoys growing popularity in the Himalayas (e.g., Bobrowski et al., 2017, 2018; Gilani et al., 2020). Studies which used Chelsa always incorporated additional predictor variables (i.e. DEM, remotely sensed land cover and land surface temperature (LST)).

Worldwide, only very few researchers attempted to compare the effect of different climate data sets on model performance (e.g.,

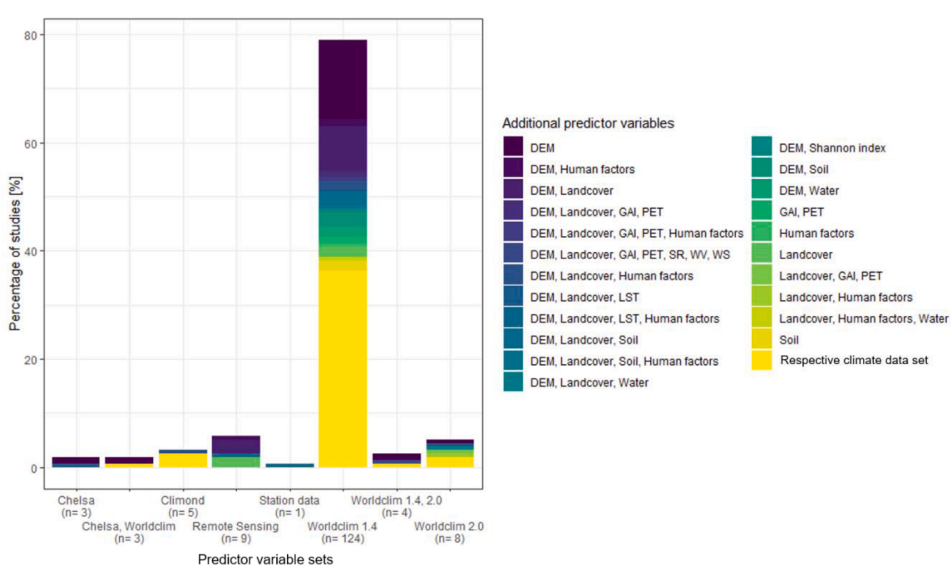


**Fig. 3.** Percentage distribution of studies according to selected predictor variables, with yellow bar sections representing the proportion of studies solely utilizing the respective climate data set. Abbreviations used: DEM = digital elevation model, GAI = global aridity index, PET = potential evapotranspiration, LST = land surface temperature.

Soria-Auza et al., 2010; Bedia et al., 2013; Fernández et al., 2013; Deblauwe et al., 2016; Bobrowski & Schickhoff, 2017; Suwal et al., 2018; Datta et al., 2020), and, only recently, first studies for Himalayan species were conducted. Our review revealed only 3 studies attempting to compare the effect of Chelsa and Worldclim climate data on model performance in the Himalayas (Bobrowski & Schickhoff, 2017; Suwal et al., 2018; Datta et al., 2020).

Predictor variables solely obtained from remote sensing products were used in 6% of the studies. Studies incorporating solely remotely sensed data (e.g., land cover and LST) provided valuable results to describe habitat suitability of mammal species (Singh & Kushwaha, 2011; Bashir et al., 2014, 2018; Qian et al., 2014; Bhattacharyya et al., 2015, 2020; Paudel et al., 2015; Khan et al., 2016; Thinley et al., 2019). Measured data from climate stations were rarely used (< 1%) in the analysed studies.

Both the temporal and the spatial resolution are highly significant to account for the environmental heterogeneity of mountain regions. In the literature reviewed here, most of the studies (93%) were based on seasonally averaged climate data, and 62% of all studies used environmental predictor variables with 1 × 1 km raster grid cells. In 18% of all studies raster at 5 × 5 km cell size were utilized, which might conceal fine scale information of the underlying terrain. Furthermore, in 8% of the studies environmental raster at 10, 18 and 340 $km^2$ resolution were used as predictor variables, respectively. In contrast, other studies (6%) resampled 1 $km^2$ grid cell of climate raster to higher resolution (e.g., 20, 30, 90, 250, 340 $m^2$), simulating artificial high resolution of climate data, while 5% of the studies incorporating predictors solely obtained from remote sensing data showed higher resolution (e.g., 30–90 $m^2$ grid cell size).

Although this misfit resolution has been widely recognized and described in many high elevation studies when capturing spatio-temporal variability in microclimate, the use of fine-scale environmental data sets (< 1 $km^2$ grid cell size) is rather the exception. Zischg et al. (2019) published a high resolution map of climatological indices with a spatial resolution of 25 × 25 m for the European Alps, emphasizing the need for expert knowledge in parameter computation. Shrestha and Bawa (2014) emphasized the need for high-resolution environmental data that capture microclimates, edaphic conditions, vegetation dynamics, and landscape heterogeneity, and Kollas et al. (2014) also emphasized the use of high-spatial-resolution temperature data for predictive modelling of temperature-based niche envelopes, with a resolution of less than 100 m. To demonstrate the mechanistic links between species occurrences and the prevailing climatic conditions, and consequently enable robust model predictions of biological responses to changing climatic conditions, estimates of climate at high spatial and temporal resolution are needed for mountain regions (Lenoir et al., 2017; Maclean, 2020).

### 3.6. Selections of predictor variables

The selection of predictor variables represents an essential step as they have to capture species' distributional constraints and reflect species eco-physiological tolerances and requirements (Guisan & Zimmermann, 2000; Austin, 2002; Jarnevich et al., 2015). Selection methods can be subdivided into ecological and statistical approaches, with predictors being chosen based either on species-specific ecological requirements or on statistical variable selection methods (Fig. 4). Overall, the majority of studies relied on statistical selection approaches (62%), while ecologically based approaches were less applied (23%). Surprisingly, 15% of all analysed studies disclosed no information on how predictor variables were selected to model the ecological niche or distribution. This in turn often leads to ambiguity when trying to interpret model predictions. In most modelling studies predictor variable selection was solely based on Pearson (30%) or Spearman (5%) correlation coefficients to remove highly correlated variables, whereas the coefficients ranged between $r = |0.6|$ and $|0.9|$. It has been generally proposed that a correlation coefficient $r \geq |0.7|$detects collinearity among variables (Dormann et al., 2013). Further statistical selection approaches comprised combinations of correlations with resampling methods like the Jackknife technique (5%), variance inflation factor analysis (VIF) (3%) or principal component analysis (PCA) (3%).

In 13% of the studies predictor variable selection were either based on the species' ecological requirements or on combinations of ecology and correlations after Pearson and Spearman, respectively. In 3% of the

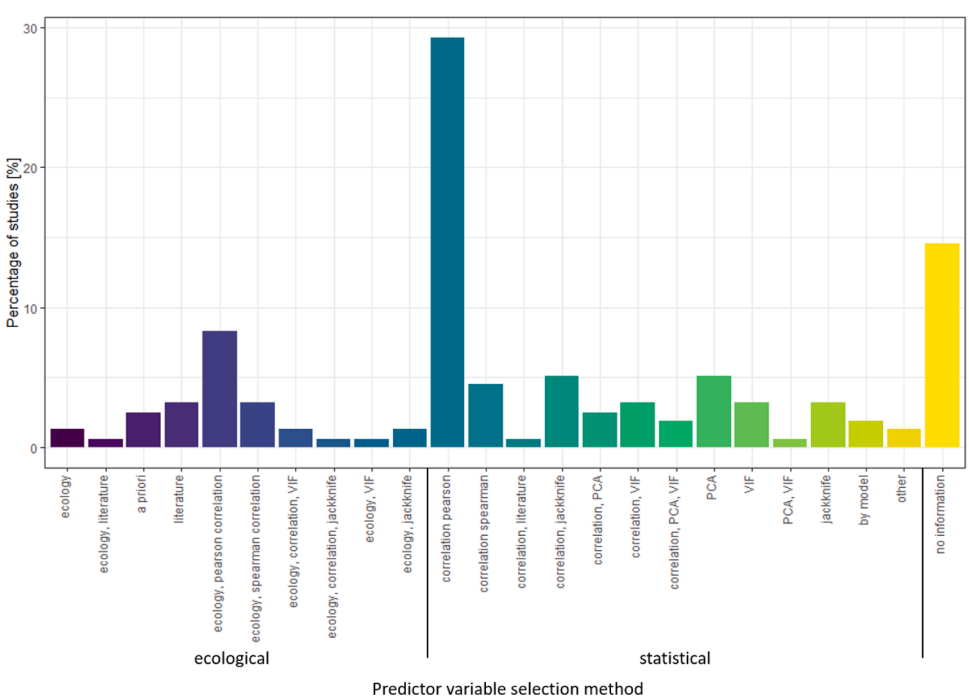


**Fig. 4.** Percentage distribution of studies according to predictor variable selection method divided in ecological and statistical approaches. Abbreviations used: VIF = variance inflation factor analysis, PCA = principal component analysis.

studies the species' ecology in the variable selection procedure was considered by information retrieved from published literature. When modelling species niches or distributions, variable selection should lead to a set of predictors that include variables which affect the species directly rather than indirectly (Guisan & Zimmermann, 2000). Furthermore, these variables can be sorted by the degree of causality of species responses to environmental factors in proximal (i.e. direct response of the species such as cold temperatures during growing season limiting plant growth) and distal responses (i.e. indirect response of the species such as mean annual temperature) (Austin, 2002; Peterson et al., 2011). Santini et al. (2021) noted the on-going trend to use automatic procedures (e.g., VIF) to exclude collinear variables irrespective of species-specific requirements (e.g., Manish & Pandit, 2019). To compile an appropriate predictor variable set, the ecology of the species should be considered, however the model assumption regarding uncorrelated predictor variables should not be violated (Dormann et al., 2013). The usage of modelling approaches handling collinearity such as BIOCLIM (Nix, 1986), ENFA (Hirzel et al., 2002) and Mahalanobis distance (Clark et al., 1993) represents another option. Recently, the robustness of Maxent in terms of collinearity based on empirical data has been discussed (see Feng et al., 2019 for a detailed discussion).

Model performance is highly dependent on input parameter quality, consisting of species data and predictor variables (e.g., Fernández et al., 2013; Syfert et al., 2013; Varela et al., 2014; Feng *et al.*, 2019). Explicit knowledge on specific ecological requirements must be available to select relevant, high qualitative environmental predictors (Austin, 2002; Baker et al., 2016, 2017; Mod et al., 2016; Descombes et al., 2020; Santini et al., 2021). Model quality could be improved by selecting relevant model variables, accounting for functional relationships among dependent and independent variables, and in parameter estimates (Houlahan et al., 2017). With predictions on anthropogenically induced climate change effects on species and their habitats (Clark et al., 2001), a shift from explanatory models to anticipatory models has been proposed (Mouquet et al., 2015; Yates et al., 2018). Anticipatory models assume that underlying hypotheses are valid, while explanatory models are based on hypotheses to be tested, with specificities often being overlooked in both prediction approaches (Mouquet et al., 2015). This circumstance may lead to a gap between solid theoretical knowledge of ecological systems and their drivers (i.e. cause-effect mechanisms) and prediction abilities may lead to vague assumptions, when not correctly interpreting the outcomes and communicating their limitations (Mouquet et al., 2015; Schuwirth et al., 2019). Modelling species niches and predicting their potential habitats should be "demonstrating" understanding of ecological drivers and not "acquiring" the ecology (Houlahan et al., 2017). A profound understanding of mechanistic processes related to the system and study organism is a precondition to develop models for mountain species with ecological significance. Although this point seems self-evident, we only found in 36% of all studies an elaborate, detailed interpretation on species ecological needs reflected in the final model and in 27% at least a brief discussion. However, in 37% of the analysed studies no interpretation on the relationship between the species and the predictor variables was given. This may be attributed to the misleading trends of models showing high discrimination accuracy and good predictive ability although they include ecologically not meaningful variables, which in turn impedes plausible interpretations (Fourcade et al., 2018; Warren et al., 2020; Santini et al., 2021).

Another explanation of the rather high proportion of analysed studies that implied no reference to species-specific requirements could be to the narrow corset of the bioclimatic predictor variables. On the one hand, they generally reflect monthly and seasonal trends in temperature and precipitation to allow direct comparison among studies, but on the other might not contain needed variables that define the ecological niche or the actual distribution of the target species. Over all analysed studies, customized variables (e.g., pre-monsoonal drought stress) were rarely used, but could easily be calculated from average monthly climate data (Bobrowski et al., 2017). Further tailored predictor variables obtained from remotely sensed topography, land cover and phenological traits may result in a more constrained predicted niche compared to solely climate-based models (Bobrowski et al., 2018). To reduce the gap between potential and actual distributions the potential of remotely sensed data to model species over vast, remote, and heterogeneous mountain regions has been emphasised (He et al., 2015). In our review we found promising applications of remotely sensed land cover products as predictor variables in studies on animals, plants and phylogeny (Ray et al., 2011; Forrest et al., 2012; Yang et al., 2013; Qian et al., 2014; Dunn et al., 2015; Paudel et al., 2015; Khan et al., 2016; Wang et al., 2016; Bobrowski et al., 2018; Chhetri et al., 2018a; Lamsal et al., 2018; He et al., 2019; Kanagaraj et al., 2019; Litvinchuk et al., 2019; Panthi et al., 2019; Rathore et al., 2019; Shankhwar et al., 2019; Bhandari et al., 2020; Bhattacharya et al., 2020; Li et al., 2020; Lu et al., 2020; Singh et al., 2020; Zhao et al., 2020).

The usage of DEMs provides another example of remotely sensed information which was included in 46% of the studies. Particularly the often utilized variable *altitude*, which serves as a proxy for the prevailing climatic conditions, constitutes the ecologically less valuable predictor variable compared to temperature derivates. This mismatch can be attributed to the fact that species do not respond directly to elevation, but to changes in temperature and other climatic parameters which are affected by elevation (Peterson et al., 2011). Furthermore, when modelling future range shifts, temperature values are likely to change, whereas elevation will not and thus contains limited ecological explanation. Additionally, when transferring modelling results to other regions (e.g., for invasive species) elevation and related temperature will vary at different latitudes (Jarnevich et al., 2015). Chhetri et al. (2018b) concluded that although elevation may not be directly associated with plant physiology, it represents a strong indicator of climatic variables that influence physiology. As a consequence, variable influence of other temperature related variables may be subsequently blurred. As an indirect variable, elevation provides a good surrogate for temperature and latitudinal ranges, but may be misleading across broader areas (Peterson et al., 2011).

### 3.7. Modelling technique and evaluation

Compared to mechanistic and process-based models, correlative models are most commonly used to model species' distributional ranges across space and time. This approach defines the niche based on the assumption that the observed current distribution of a species reflects the species' ecological requirements (Kearney & Porter, 2009, Kearney et al., 2010) and less than the full fundamental niche is captured, since biotic interactions and movement components are not distinguishable (Peterson et al., 2011). All reviewed studies applied correlative modelling techniques, which can be separated into statistical, machine learning, similarity and expert rules-based algorithms. The vast majority of studies (66%) applied the model algorithm Maxent, which is a machine-learning approach (Philips et al., 2006) (Fig. 5). The Maxent algorithm can handle presence-only data (with generated background data) to estimate target probability distribution by finding the probability distribution of maximum entropy (Phillips et al., 2006; Phillips, 2008). Another main reason for the popularity of Maxent (> 7700 citations in Web of Knowledge Core Collection, March 2021) may be traced back to the graphical user interface of the freely available Java software, that is easy to use for modelers without statistical knowledge required for detailed tuning (Phillips & Dudík, 2008). Furthermore, Maxent shows high predictive performance (Elith et al., 2006), especially with low sample sizes (Pearson et al., 2006b). Only recently it became available as a R-package "maxnet" (Phillips et al., 2017), providing options for community extensions and contributions. Despite its popularity, recent publications revealed difficult interpretability and poorly grounded ecological theory of the models (e.g., background point selection, highly complex response curves, large predictor variable sets and negligence of modelled relationships) (Halvorsen, 2013; Yackulic

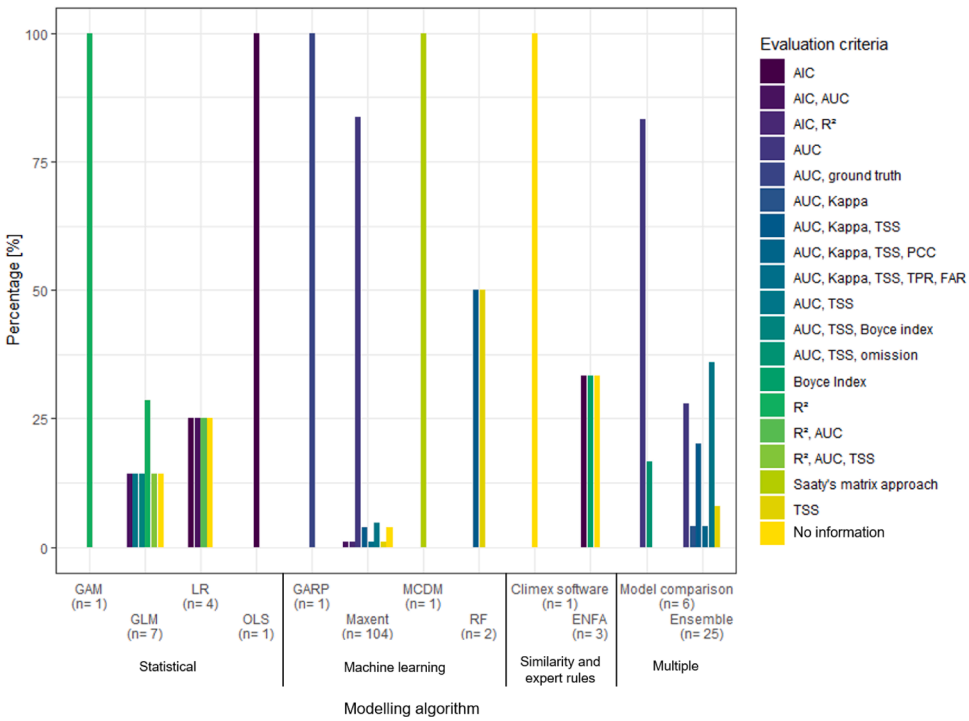


**Fig. 5.** Percentage of evaluation criteria per modelling algorithms (N = 157). Abbreviations used in the figure: GAM = General Additive Model, GLM = Generalized Linear Model, LR = Logistic Regression; GARP = Genetic Algorithm for Rule Set Production, MCDM = Multiple Criteria Decision-Making, RF = Random Forest, ENFA = Ecological Niche Factor Analysis.

et al., 2013; Vollering et al., 2019; Sillero & Barbosa, 2021). Often Maxent models are run on the default parameter setting, resulting in countless potential issues (Yackulic et al., 2013; Fourcade et al., 2018). Especially for studies claiming to model the relationship between species occurrences and the environment or projections across space and time, these circumstances can be challenging (Halvorsen, 2012; Vollering et al., 2019). Almost all studies reviewed here using the Maxent algorithm relied on the default settings without customizing according to their research target.

To combat caveats of single modelling algorithms and to create more robust predictions, ensemble modelling approaches are frequently used in ecological modelling studies. We found 16% of all analysed studies using ensembles of multiple algorithms. The rising number of publications with ensemble models may be attributable to R package "biomod2" (Thuiller et al., 2009), whereas pros and cons are discussed in the literature whether ensemble models are outperforming single algorithms (Araujo & New, 2007; Marmion et al., 2009; Dormann et al., 2018; Hao et al., 2019).

Furthermore, 4% of the analysed studies applied Generalized Linear Models (GLM), and 4% compared different modelling algorithms according to their performance.

To evaluate model performance several threshold-independent and -dependent evaluation criteria have been established (Fig. 5), however, no universal model evaluation criteria exist. In this review, most studies (63%) referred to the Area Under the Curve (AUC) to examine model performance, followed by 10% of the studies using two evaluation criteria: AUC and True Skill Statistics (TSS). Out of all studies, 6% combined AUC, TSS and Cohen's Kappa to account for model performance, whereas 6% provided no information on model evaluation.

Although the AUC as an exclusive evaluation metric for model performance has come under criticism (for an extensive discussion see Lobo et al., 2008; Warren & Seifert, 2011), it is still frequently applied without reservations to report model performance in ecological modelling studies, in particular in the Himalayas. The most severe limitation of this metric is that it is only valid and useful for comparisons among models for a single study species in a single study region (Peterson et al., 2011).

### 3.8. *Perspectives for future research in remote high elevation regions*

As most modelling algorithms require presence and absence data, wrong occurrences influence the selection of pseudo-absences regardless of selection method. Albeit numerous studies have proven the effect of presence-absence data on model accuracy and prediction quality (Brotons et al., 2004; Elith & Leathwick, 2009), presence-only data are mainly used in modelling procedures. Especially in regions with a heterogenous terrain like the Himalayas, sampling species which are distributed along the entire Himalayan arc is in most cases not feasible. However, high quality presence data sets present a valuable option, since a presence observation is the result of at least two, multi-factor processes (Peterson et al., 2011). First, the species was observed in a location which exhibits abiotically suitable conditions (i.e. the fundamental niche), and is influenced by biotic interactions (i.e. the realized niche) according to its movement abilities (e.g., dispersal over space and time). Secondly, the species was collected with certain collection intentions according to its detection abilities (i.e. the species visibility and terrain accessibility). In summary, presence-only data represent estimate indices of relative suitability (Peterson et al., 2011). For local studies, however, it may be possible to sample species with planned field surveys or even systematic field campaigns for presence-absence data sets. For macro scale studies covering the entire Himalayan mountain system, the reliability of species occurrences records obtained from databases could be validated with remotely sensed products (He *et al.*, 2015). In Singh *et al.* (2013), the current alpine treeline ecotone boundary was validated with remote sensing data, while Bobrowski *et al.* (2018) extracted *Betula utilis* occurrences from satellite images via Google Earth, which were validated by expert knowledge obtained on the basis of many field campaigns and photo documentary of *Betula* sites. This method has proven to produce large and high-quality datasets at other treeline locations (Paulsen & Körner, 2014; Irl *et al.*, 2015). The incorporation of remote sensing data allows to include locations that are

remote or hardly accessible. Such locations are often less disturbed or even undisturbed by anthropogenic influences (Irl *et al.*, 2015). One further advantage of remote sensing data, when plants are in focus, could be the generation of presence-absence data sets by using vegetation classification (He et al., 2009, 2015). In high elevation ecosystems, the distinct vegetation zonation with different spectral signals provides an ideal starting point for vegetation classifications to compile a high quality presence-absence data set. This approach is particularly promising for broadleaved deciduous tree species like *Betula*, since phenological traits from adjacent vegetation types which consist mainly of evergreen coniferous and evergreen broadleaved species in the tree layer allow a clear separation in the course of the year (Bobrowski et al., 2018).

In many publications basic information on applied climate data sets (e.g., access, meta-data, time span, versions, data type) is not sufficient to allow reproducibility and transparency (Morueta-Holme et al., 2018). Although extensive care is taken in selecting uncorrelated predictor variables, differences between available current climate datasets remain largely out of focus for the Himalayas, and most studies do not critically scrutinize the origin of climate data, computation or measurement methods, and neglect potential drawbacks and afflicted errors. Especially in topographically heterogeneous landscapes, global climate datasets often do not account for local climatic conditions due to their quantitatively limited weather station density, computation method, and relatively coarse resolution ($\geq$ 1 km) (Bobrowski et al., 2021). Often it is taken for granted that data available at global scale show equally high quality throughout all regions, however, the premature use of such data may in turn lead to erroneous models and flawed predictions, especially for projections under future climate conditions. The need for comparative studies of model performance using different climate data sets have gained interest over the last few years (e.g., Heikkinen et al., 2006; Kriticos et al., 2012; Watling et al., 2014; Stoklosa et al., 2015; Wang et al., 2016, Baker et al., 2016, 2017), however effects of different climate data sets on model performance remains largely out of focus for the Himalayan mountains (Bobrowski & Schickhoff, 2017; Suwal et al., 2018; Datta et al., 2020). Comparison and evaluation of climate data set quality is seldomly considered with potentially severe consequences for range shifts under climate change scenarios (Baker et al., 2016, 2017). Model uncertainty was found to be related to topographic heterogeneity, inter-annual variability and distance to the closest climate station (Fernández et al., 2013). Depending on spatial and temporal scales, global climate datasets like Chelsa and Worldclim lack precision of local temperature patterns and precipitation regimes of the Himalayas and thus may contain flawed climate estimates used in SDM studies (Bobrowski et al., 2021). Although climate is not the exclusive factor delimiting species distributions in the Himalayas, it is an indispensable prerequisite as species occurrences and their dynamics in high elevation habitats are governed by low temperatures and local precipitation regimes (Bobrowski et al., 2021).

New opportunities for analysing and modelling species' distributions in the Himalayas could be derived by incorporating abiotic and biotic data derived from remote sensing since they provide response and predictor variables, namely presence-absence data sets and tailored environmental data sets (e.g., solar radiation, precipitation amounts and snow cover) (Bobrowski et al., 2018; He et al., 2015; Bobrowski, 2021). Additionally, remotely sensed variables are continuous observations without interpolation and geographical bias, and therefore with less uncertainty (He et al., 2015). Recent studies have revealed how remotely sensed LST data could improve species distribution modelling studies (e.g., Buermann et al., 2008; Bisrat et al., 2012; Still et al., 2013; Bobrowski et al., 2018). As time series data of vegetation characteristics (i.e., phenological metrics) are becoming more and more readily available, changing habitat suitability can be estimated and incorporated into model approaches. Remote sensing data may lead to refined modelled distributions since they are based on real information of the Earth's surface and account for non-climatic dimensions (i.e., anthropogenic impacts), leading in turn to a more realistic actual distribution. The main advantages of high-resolution remote sensing data for mountainous areas are the acquisition of climate data at high resolution (i.e. > 1 km) for differentiation between north- and south-facing slopes, which would in turn lead to more precise modelling results.

Recently, numerous studies have been published to promote comparison, reproducibility, transparency and protocols in order to set out standard procedures for species distribution modelling studies (Rodríguez-Castañeda et al., 2012; Araújo et al., 2019; Feng et al., 2019; Merow et al., 2019; Zurell et al., 2020), which will be of extraordinary importance when conservation planning strategies or decision making procedures are targeted (Araújo et al., 2019; García-Díaz et al., 2019; Rapacciuolo, 2019; Schuwirth et al., 2019). To create a starting point for future studies, we synthesized our main findings on challenges and recommendations particularly applicable in high elevation modelling studies in Table 2. In this way, knowledge can be generated that is particularly important for modelling spatial expansion of invasive species, extinction risk assessment and potential range shifts under future climate change in remote areas like the Himalayas.

## 4. Conclusions

Modelling species in remote regions like the Himalayas faces several challenges. It is interesting to note that temporal transferability (i.e. under future or past climate conditions) studies represent the majority of recently published studies. However, problems and difficulties associated with modelling species under current climate conditions are not yet sufficiently resolved. If not mastered, severe consequences for the validity of the modelling results are to be expected, including wrong assumptions when the results serve as a baseline for projections on species potential future range shifts, expansions or contractions. The opportunity to choose ready-to-use species occurrence data sets and bioclimatic predictor variables from freely available databases might lead researchers into temptation to regard model performance more important than model quality (i.e. performance metrics *versus* ecological relevance of predictors). Additionally, the most common and user-friendly software Maxent may encourage modelling studies without statistical knowledge required for detailed tuning depending on the species' ecology. In this review, the vast majority of studies on species' potential range shifts show predictions under future climate change conditions, however, information on the ecological drivers behind the current distribution was often not the principal focus. It appears that researchers are attracted by the idea to model species distributional ranges and their dynamics under future climate conditions. Often the acquisition of sufficient numbers of species' occurrences, the evaluation of environmental data quality and their ability to account for the species ecological requirements were neglected. This in turn could lead to flawed predictions, misinterpretations and biased implications, especially when nature conservation strategies and environmental management are in focus.

Often modelling concepts and terminologies, predictor variable selection, and species-specific ecological constraints were not sufficiently taken into account, resulting in lacking transparency to comprehend modelling results and their ecological interpretations. Comprehensive understanding of underlying mechanistic processes and empirical data will reduce biases in modelling results and lead to improved predictions. In this review we highlighted possible pitfalls, revisited current research gaps and provided potential solutions for ecological models in the Himalayas in order to support reaching their full potential in future research. We emphasize the need for consistency in applied modelling concepts, terminology, methodology and ecological theory to obtain robust and expedient results in further modelling applications in the Himalayas. With this review we provide a starting point, irrespective of species group, for substantial improvements in input parameter evaluation to catalyse advances in performance and quality of modelling studies in the Himalayas.

**Table 2**
Synthesis of most common challenges detected in the modelling workflow of the reviewed studies and potential recommendations for future studies in mountain regions. This table highlights challenges which have been identified to be considered in the modelling workflow, in particular in high elevation habitats. This table does not claim to be complete, but is intended solely as an aid to orientation.

| Challenges | Modelling workflow highlights | Recommendations |
|---|---|---|
| ***Does the research aim align with target species and region extent?*** | **Research aim and target region**<br>Research scope: current distribution, range shifts, invasive species, phylogeny<br>Focal species: single or multiple singles<br>Target region: local, meso or macro scale | Alignment of **applied concepts** regarding methodology and terminology<br>Setting the target area extent in accordance to the species distribution |
| ***How to generate a high quantity and quality species data set?*** | **Occurrence data**<br>Type: presence, presence/absence, presence/background<br>Origin: field survey, gbif, other databases | Consultation of **different sources** to obtain a valuable occurrence data set<br>For database data: consideration of geospatial errors to avoid environmental biases |
| ***Are environmental data quality as well as temporal and spatial resolution appropiate?*** | **Environmental data**<br>Origin: WORLDCLIM, Remote Sensing, CHELSA, Climond, Station data<br>Spatial resolution: 1, 5, 10,18, 340km$^2$; 20, 30, 90, 250, 340m$^2$<br>Temporal resolution: current, future, past | Comparison and evaluation of **data quality** between climate data sets<br>Use of high-spatial resolution data to capture spatio-temporal variability of heterogeneous terrain |
| ***How does the modelling algorithm choice and setup influence model prediction?*** | **Model algorithm**<br>Correlative model algorithm: statistical, machine-learning, similarity and expert rules-based algorithms<br>Algorithms: Maxent, Ensemble, GLM, LR, ENFA, RF, Climex software, GAM, GARP, MCDM, OLS | Alignment of **model setup** between model algorithm and research aim<br>Customization and tuning of model settings to produce reliable/valuable model results |
| ***How to select predictor variables?*** | **Model calibration**<br>Predictor variable selection: ecological, statistical<br>Background: correlation, ecology, PCA, jackknife, VIF, literature, a priori | Combination of **ecology and statistical selection** approaches should be preferred<br>Inclusion of ecological meaningful variables to enable plausible model prediction interpretation |
| ***How to evaluate model performance?*** | **Model validation**<br>Prediction: threshold-dependent / threshold-independent<br>Evaluation criteria: AUC, TSS, Cohen's Kappa, AIC, $R^2$ | Usage of appropriate **evaluation criteria** in regard to model algorithm and prediction aim<br>Report uncertainties and limitations of model evaluation metrics |

## Declaration of Competing Interest

We state that no part of the research has been published in any form elsewhere, and that the manuscript is not being considered for publication elsewhere.

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## Supplementary materials

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