



Short communication

Distribution models for mountain plant species: The value of elevation



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ABSTRACT

The climatic conditions of mountain habitats are greatly influenced by topography. Large differences in microclimate occur with small changes in elevation, and this complex interaction is an important determinant of mountain plant distributions. In spite of this, elevation is not often considered as a relevant predictor in species distribution models (SDMs) for mountain plants. Here, we evaluated the importance of including elevation as a predictor in SDMs for mountain plant species. We generated two sets of SDMs for each of 73 plant species that occur in the Pacific Northwest of North America; one set of models included elevation as a predictor variable and the other set did not. AUC scores indicated that omitting elevation as a predictor resulted in a negligible reduction of model performance. However, further analysis revealed that the omission of elevation resulted in large over-predictions of species' niche breadths—this effect was most pronounced for species that occupy the highest elevations. In addition, the inclusion of elevation as a predictor constrained the effects of other predictors that superficially affected the outcome of the models generated without elevation. Our results demonstrate that the inclusion of elevation as a predictor variable improves the quality of SDMs for high-elevation plant species. Because of the negligible AUC score penalty for over-predicting niche breadth, our results support the notion that AUC scores alone should not be used as a measure of model quality. More generally, our results illustrate the importance of selecting biologically relevant predictor variables when constructing SDMs.

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1. Introduction

In response to climate change, mountain plants are expected to migrate to higher elevations than they currently occupy (Grabherr et al., 1994; Nilsson and Pitt, 1991). While there is empirical evidence supporting this prediction (Brusca et al., 2013; Feeley et al., 2011; Jump et al., 2012), attempts at modelling the response of mountain plants to warming have had contrasting results, with some models predicting range expansions (e.g. Gottfried et al., 1999) and others predicting contractions (e.g. Guisán and Theurillat, 2000). This inconsistency is likely due to the complex interactions between the regional macroclimate and the local geographical factors that structure mountain habitats (Beniston, 2005; Körner, 2007; Dobrowski, 2011). Such complexity may only be adequately captured by specialized modelling approaches (Randin et al., 2009) where both the climatic and geographic attributes of mountain regions are considered in the modelling procedure.

Species distribution models (SDMs) are widely used inferential tools that use climatic and geographic data associated with a

species' natural occurrence records (e.g. herbarium specimens) to predict its past, current, and future distribution (Elith et al., 2006). SDMs and their variants have frequently been used to describe and predict the distributions of mountain plant species (Guisán and Theurillat, 2000; Guisán et al., 1998; Lassueur et al., 2006; Randin et al., 2009; Zimmermann and Kienast, 1999). However, the lack of consideration for the intricacies of mountain habitats in the modelling procedures – especially the choice of predictor variables – often obscures the ecological value of their findings. For instance, nearly all the models generated by Guisán and Theurillat (2000) for alpine and subalpine plant species were driven primarily by mean annual temperature, which is often confounded with several other variables and may be especially problematic along elevation gradients (Vuille and Bradley, 2000). An ideal temperature predictor would be physiologically relevant (Körner, 2007; Platts et al., 2013). Randin et al. (2006) included physiologically relevant climatic variables in their models, but they excluded all geographic predictors with the exception of slope. The authors suggested in hindsight that their choice of predictors may not have adequately captured the complexity of the modelled mountain regions, and may be responsible for their generally weak result (Randin et al., 2006). Mountain niches are influenced by microtopography; small differences in microtopography will have significant effects on soil temperature,

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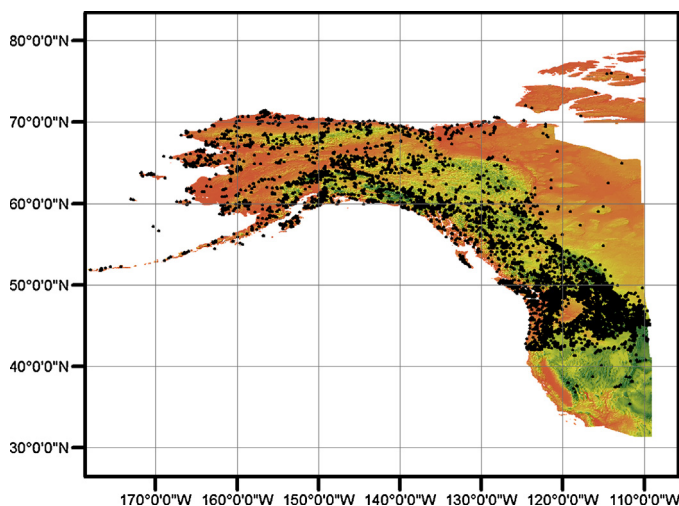


Fig. 1. Map of the study area in northwestern North America and occurrence locations (black points) for all 73 species used in the present study.

freeze-thaw cycles, snow drifting, and wind, all of which affect mountain niche properties (Gottfried et al., 1999). Thus, geographic variables likely serve as surrogates for elusive climatic factors. For this reason, it is crucial to utilize a well-constructed set of predictor variables that are relevant to the biology of species that occupy unique habitats like those of mountain regions (Elith and Leathwick, 2009).

Here, we evaluated the importance of elevation as a predictor variable in SDMs for mountain plant species. We focused on elevation because different microclimates can occur with small changes in elevation. Furthermore, elevation often connotes local precipitation and temperature features (Austin, 2002; Körner, 2007) and has long been considered an important determinant of species distributions in mountain habitats (Körner, 2004, 2007). We pursue two main objectives: first, we investigate whether elevation is important for accurately predicting the distributions of mountain plant species. Second, we explore the consequences of omitting elevation as a predictor variable in SDMs for mountain plants in terms of both model quality and the ecological relevance of predictors that influence the models.

2. Methods

2.1. Occurrence records

We retrieved occurrence records from the Consortium of Pacific Northwest Herbaria database (www.pnwherbaria.org/) for 73 vascular plant species that occupy mountainous habitats in the Pacific Northwest of North America (Fig. 1). The species included 56 herbs, 8 graminoids, 5 trees, and 4 shrubs that inhabit a range of elevations from lowlands through alpine regions (see PANGAEA data package for species list <http://doi.pangaea.de/10.1594/PANGAEA.842513>). We eliminated duplicate occurrences from the herbarium records and accounted for some potential sampling bias (see Syfert et al., 2013) by using ENMTools 1.4.3 (Warren et al., 2008) to ensure that there was a maximum of one occurrence record per 1 km² grid cell for each species—this resolution corresponds to the resolution of our environmental data (see Section 2.2). After accounting for sampling bias, the number of occurrence records for our study species ranged from 33 to 1052 and their mean elevations ranged from 683 to 2539 m (Fig. S1). We did not verify the herbarium collection data ourselves, and as such there may be some errors associated with the collections that were unaccounted for by our analyses.

2.2. Environmental data

We retrieved data for the 19 BIOCLIM variables, monthly temperature, and elevation from WorldClim (Hijmans et al., 2005). In addition, we derived 5 geographic variables from a 1 km² digital elevation model extracted from the National Geophysical Data Center (www.ngdc.noaa.gov/mgg/topo/globe.html) to supplement the climate and elevation data. We retrieved potential evapotranspiration (PET) data from the CGIAR Consortium for Spatial Information (www.cgiar-csi.org) (Trabucco et al., 2008). PET characterizes the atmospheric demand for water in a habitat. We used the PET data to calculate annual soil moisture deficit (SMD) for our study area as the difference between annual PET and annual precipitation. Lastly, we calculated growing season temperature (GST) for our study area as the mean of May–August temperatures. All data were at 30 arc second (~1 km²) resolution.

To improve model interpretability, we screened the environmental variables for correlates (Phillips, 2008) and removed one variable from each pair with correlation coefficients $> |0.7|$ (see supplemental for the screening procedure; Tables S1 and S2). Overall, we retained six climatic variables and five geographic variables. The climatic variables were: soil moisture deficit (SMD), growing season temperature (GST), mean temperature of the wettest quarter (TWQ), mean temperature of the driest quarter (TDQ), precipitation seasonality (PS), and precipitation of the warmest quarter (PWQ). We retained both GST and TDQ in spite of their correlation ($r = 0.78$) because plants actively respond to the growing season conditions, which are better represented by GST (see Section 3). Furthermore, MaxEnt is equipped with regularization procedure that to some degree is capable of diminishing the effect of correlated variables (Elith et al., 2011). The five geographic variables were: elevation, slope, eastness, northness, and topographic position index (TPI). Eastness and northness are linear components of aspect; eastness is calculated as the sine of aspect and northness is calculated as the cosine of aspect. TPI is a measure of surface undulation (see Weiss, 2001). We performed all data processing (environmental data extraction, derivation and conversion) using ArcGIS 10.1 (ESRI, Redlands, CA).

2.3. Model procedure and evaluation

We used MaxEnt 3.3.3k (Phillips and Dudík, 2008) to generate SDMs for the 73 plant species. MaxEnt requires presence-only data and has been demonstrated to be more robust than other available modelling algorithms (Hernandez et al., 2006, 2008; Pearson et al., 2007). MaxEnt computes a species' probability (from 0 to 1) of occurrence in a grid cell as a logistic function of the environmental data associated with that cell. We used cross-validation to generate 10 replicate models for each species: the data were split into k folds ($k = 10$) and $k - 1$ folds were used to train the models while 1 fold was used for testing. Cross-validation is spatially robust as it curtails model over-fitting by randomly selecting the records that are used to generate each of the 10 replicate models. We used the average of the 10 replicate models for each species in all subsequent analyses. Because the number of occurrence records ranged from 33 to 1052, we used the hinge feature for all the species to facilitate model comparisons. The hinge feature requires a minimum of 15 occurrence records, and generates non-linear models similar to that of generalized additive models that are easier to interpret than standard models (Elith et al., 2011). We separately used the default setting to construct the models and the conclusions reported here did not change (data not shown). We applied a 10th percentile training presence threshold, where suitable cells have suitability scores that are greater than the worst 10% of occurrence locations. All other settings were default.

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