

GOPEN ACCESS

Citation: Zangiabadi S, Zaremaivan H, Brotons L, Mostafavi H, Ranjbar H (2021) Using climatic variables alone overestimate climate change impacts on predicting distribution of an endemic species. PLoS ONE 16(9): e0256918. https://doi. org/10.1371/journal.pone.0256918

Editor: Ji-Zhong Wan, Qinghai University, CHINA

Received: December 15, 2020

Accepted: August 18, 2021

Published: September 2, 2021

Copyright: © 2021 Zangiabadi et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its <u>Supporting Information</u> files.

Funding: It is hereby acknowledged that authors received no financial support for the research and authorship of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

RESEARCH ARTICLE

Using climatic variables alone overestimate climate change impacts on predicting distribution of an endemic species

Somayeh Zangiabadi¹, Hassan Zaremaivan¹*, Lluis Brotons^{2,3,4}, Hossein Mostafavi⁵, Hojjatollah Ranjbar⁶

Department of Plant Biology, Faculty of Biological Sciences, Tarbiat Modares University, Tehran, Iran,
CREAF, Cerdanyola del Vallès, Spain, 3 InForest Jru (CTFC-CREAF), Solsona, Spain, 4 CSIC,
Cerdanyola del Vallès, Spain, 5 Department of Biodiversity and Ecosystem Management, Environmental
Sciences Research Institute, Shahid Beheshti University, Tehran, Iran, 6 Department of Mining Engineering,
Shahid Bahonar University of Kerman, Kerman, Iran

* zaremaih@modares.ac.ir

Abstract

Plant species distribution is constrained by both dynamic and static environmental variables. However, relative contribution of dynamic and static variables in determining species distributions is not clear and has far reaching implications for range change dynamics in a changing world. Prunus eburnea (Spach) Aitch. & Hemsl. is an endemic and medicinal plant species of Iran. It has rendered itself as ecologically important for its functions and services and is currently in need of habitat conservation measures requiring investigation of future potential distribution range. We conducted sampling of 500 points that cover most of Iran plateau and recorded the P. eburnea presence and absence during the period 2015–2017. In this study, we evaluated impacts of using only climatic variables versus combined with topographic and edaphic variables on accuracy criteria and predictive ability of current and future habitat suitability of this species under climate change (CCSM4, RCP 2.6 in 2070) by generalized linear model and generalized boosted model. Models' performances were evaluated using area under the curve, sensitivity, specificity and the true skill statistic. Then, we evaluated here, driving environmental variables determining the distribution of P. eburnea by using principal component analysis and partitioning methods. Our results indicated that prediction with high accuracy of the spatial distribution of P. eburnea requires both climate information, as dynamic primary factors, but also detailed information on soil and topography variables, as static factors. The results emphasized that environmental variable grouping influenced the modelling prediction ability strongly and the use of only climate variables would exaggerate the predicted distribution range under climate change. Results supported using both dynamic and static variables improved accuracy of the modeling and provided more realistic prediction of species distribution under influence of climate change.

Introduction

Anthropogenic climate change will affect biodiversity in different parts of world rapidly [1] and lead to large or small reductions or enhancements in species distribution areas [2]. Since, species cannot adapt as fast as environmental changes taking place, they change their distribution range and shift to new habitats or go extinct [3, 4]. Investigation on the effects of climate change on habitat suitability of species contributes greatly to the conservation of biodiversity [5]. A key issue in management of environmental resources and conservation of biodiversity is comprehension of how and how much future climate affects the species occurrences [6] especially, on endemic and endangered species [7].

Species distribution modelling (SDM) is a prominent method for predicting effects of climate change on potential distribution of species based on correlations between presence or presence and absence information of species and informative environmental predictors as driving predictors [8]. Habitat suitability maps are the output of species distribution models [9] that have been used widely for different purposes, such as predicting niche shifts of nonnative plants [10], assessment of climate change impacts on species distribution [4], testing ecological, biogeographical and evolutionary hypotheses [11, 12], predicting distributional changes at expanding range margins [13], planning future conservation [5], and also in assessing the statues of endemic and rare species under different scenarios of climate change [14]. Rare and endemic species with specialized habitat requirements represent a particular challenge for statistical analysis and valuable opportunity for predictive modelling plant species distribution [15].

Nowadays, a large number of environmental datasets are produced for different studies, such as SDM which most of them are statistically dependent [16]. Using appropriate number of variables has always been a goal to avoid prediction errors. For example, use of a large number of variables in SDM may led to collinearity problems between variables [17] and overfitting [18, 19] and deficient use led to overestimation in predictions [20]; therefore, in both cases their results are far from reality and mostly lead to under- or over-estimation in predictions [20].

One of the main reasons for credibility of modelling results is entailing (including) appropriate environmental variables into the model [9]. This is a direct consequence of the outputs of SDM are completely dependent on chosen input variables [4]. Therefore, using the most efficient and biologically relevant variables for modelling species distribution is a crucial step because it affects model performance, accuracy and reality of predictions [20, 21–26].

The species niche is affected by a number of biotic and abiotic factors at local and regional scale. However, biotic factors are often ignored in SDM because of the difficulty of task of meticulous data collection and quantification, leading to SDM most typically focusing on abiotic data instead. The main assumption of SDM is that effect of climate (dynamic, short-term, immediate) in species occurrence and distribution is a surrogate for other environmental (static, long-term) variables and therefore; climate directly or indirectly is a major constrain of species distribution [27]. For this reason and since collecting climate data is readily accessible and easily applicable in model processing [28], a common approach in many distribution modelling investigations has been to use only climatic variables [29, 30] with disregard to other environmental variables [20]. But, are these predictions solely based on climate data reliable and able to describe a realistic state of the environment capable of capturing species environmental constraints?

Environmental variables, such as soil properties and topographic profiles change only at long time scales [31] and as such, are considered as static in most SDM applications. Conversely, climatic variables are considered as dynamic variables because they change over shorter time periods. In the light of high speed of climate change in recent years and increase

in frequency and intensity of extreme events (fires, floods and landslides), these static variables (soil and topography) can become non-static in some areas [6, 31]. Knowledge on plant species distribution and its relationship with dynamic and static environmental variables is growing [20]. However, determining relative contribution of each of dynamic (climate) and static (soil and topography) variables in predicting species distribution range under changing circumstances, such as prolonged climate change needs further research.

Here, we conducted the investigation with the following objectives: (1) to assess the impacts of using static (topographic and edaphic) variables combined with climatic (dynamic) variables on the accuracy of predictive potential distribution of a restricted distribution species *Prunus eburnea* (Spach) Aitch. & Hemsl. (gray almond) using species distribution models; and (2) to evaluate the effects of using different groups of environmental variables (static vs dynamic) on the spatial prediction of future distribution of *P. eburnea* under climate change; (3) to identify the main environmental variables that define variations in *P. eburnea* habitats, and (4) to assess the independent and joint effects of each environmental variable in the potential *P. eburnea* habitats. We expect that the use of climate only variables will render different future distribution patterns from the species when compared to models in which both dynamic but also static key environmental variables are included.

Materials and methods

Study area and species

Prunus eburnea (Spach) Aitch. & Hemsl. (gray almond) is a member of the subgenus Dodecandra in the genus *Prunus*, tribe Prunoideae from Rosaceae family [32]. It is an endemic and medicinal species, widely distributed in Irano-Touranian phytogeographical region of Iran [33]. Gray almond is distributed along the eastern, southern and southwestern borders of Iran, primarily grows in rocky, sandy limestone on high mountains and lower plateaus (Fig 1). Gray almond provided important services in soil erosion prevention and deforestation [34]. However, knowledge on the occurrence and distribution of this species is limited to the locations of collection by field researchers and little is known about its distribution and niche characteristics.

Sampling

Main habitat requirements and range for *P. eburnea* were obtained from Flora of Iran [32], Flora Iranica [35] and Flora of Iran [36] studying specimens at herbariums, personal collections and scientific literature. From these sources, and the geographic information collected therein, we identified 52 areas in Iran in which the presence of *P. eburnea* was likely. In each of the areas, of roughly comparable size for which *P. eburnea* was potentially present, we placed from 4 to 5 random sampling stations, which were visited during 2015–2017. In areas outside potential species habitat, we conducted specific visits using an additional set of sampling stations in which the absence of the species was confirmed after visiting the area [37]. The minimum distance between sample stations was 10 kilometers. All sampling stations were far (10 km) from the cities and roads in order to reduce biases derived from the exploitation of the species around human settlements. Finally, a total of 500 sampling points of presence (230 N) and absence (270 N) of this species were recorded by using a portable Garmin S76, GPS model in the study area

Environmental variables

We used available climatic and topographic data obtained from www.worldclim.org [38] and edaphic layers from SOILGRIDS.ORG [39] for describing the environmental space used to identify *P. eburnea* habitats. All environmental variables were in latitude/longitude projection



Fig 1. Location and landscape of three habitats of gray almond in east (A), south (B) and west (C) of Iran on topographic map.

https://doi.org/10.1371/journal.pone.0256918.g001

and 1×1 km grid cells, which represented the minimum planning units of analysis for environmental layers for the study area. These were preprocessed, standardized and adjusted in the "Raster" library [40]. To avoid overfitting and collinearity problems between descriptor variables [41, 42], Pearson correlation test [43] was applied and finally 12 variables from different groups of environmental variables were retained (Table 1). Topographic layers were generated by using arcgeomorphometry tools [44] in ArcGIS 10.1 software [45].

Statistical analyses

Environmental layers of ecological importance for this species were selected according to available ecological knowledge about the species and expert opinions then linear correlation

Variable	Description	
Bioclimat variables (19) *	Bio 3 = Isothermality (Bio 2/ Bio 7) (* 100)	
(www.worldclim.org)	Bio 4 = Temperature seasonality (standard deviation *100) (°C)	
	Bio 11 = Mean temperature of coldest quarter (°C)	
	Bio 15 = Precipitation seasonality (coefficient of variation) (mm)	
	Bio 17 = Precipitation of driest quarter (mm)	
Гороgraphic variables (3)	Topographic variables (slope, slope aspect, elevation)	
(www.worldclim.org)	(Derived from DEM using Arc GIS 10.1 software)	
Mean solar radiation (12)	Solar radiation (kJ m ⁻² day ⁻¹) per month	
(www.worldclim.org)		
Soil	Coarse fragments (volumetric) (cm3 cm-3)	
(https://soilgrids.org)	Organic carbon content (g kg-1)	
	Silt content (gravimetric) (kg kg-1)	

Table 1. Layers of environmental variables used in this study.

https://doi.org/10.1371/journal.pone.0256918.t001

coefficient was done [46]. Layers with correlation less than 0.7 were selected. Then, variables that did not contribute significantly (p<0.005) to the explained variation were omitted [47]. PCA was used for exploring environmental patterns of data and discovering their relationship [46] as PCA considers the Euclidean distance among points when responses of species and environmental variables have linear relationship with each other [48]. We used PCA and the latent root criterion to reduce the number of variables and having uncorrelated components that accounted for most of the total variance among sampling points [49]. PCA analysis was performed by using 'pcaMethods' library [50] in R software [51] and twelve environmental variables finalized as shown in Table 1.

Partitioning methods

Next, we aimed at assessing how much of the variation in habitat selection was explained by different groups of environmental variables. Decomposition and assembling of variables was carried out for better understanding of the relative importance of each environmental variable, group of variables and their joint effects [47]. Then, we performed hierarchical partitioning (HP) and Variation partitioning (VP) analyses. For evaluating the impacts of different aspects of ecosystems on presence of species, hierarchical partitioning approach was an appropriate method here as it provided a comprehensive and flexible framework for analyzing ecological questions at different levels of studies and across temporal (years) and spatial (geography) scales [52].

We performed a series of (partial) regression analyses with redundancy analysis (RDA) and hierarchical partitioning using the 'hier.part' library [53] and 'gtools' library [54] in R software [51]. Statistical testing for each added environmental variable was performed with the Monte Carlo permutation tests (9999 permutations). Hierarchical partitioning basis on monotonic relationships between the response variable (presences and absences) and variables [47] was done. For determining the importance of each group of environmental variables, we divided all environmental variables in terms of: (1) edaphic, (2) topographic and (3) climatic groups that are not shared by the other environmental groups. This would help to understand the ecological patterns in terms of independent and joint contribution of each variable, because it quantifies variations among different aspects of environmental components more precisely [46].

Variation contribution of individual variables in species distribution can be tested and determined by using Variation partitioning (VP) [55]. VP method was done and venn diagram was constructed by using 'vegan' library [56] in R software [51]. Adjusted R2 was measured which indicates the proportion of total variation [57]. In this study, VP led to eight fractions (I) pure effect of topographic variables; (II) pure effect of climatic variables; (III) pure effect of edaphic variables; and combined variation due to the joint effects of (IV) climatic and edaphic variables; (V) climatic and topographic; (VI) topographic and edaphic; (VII) the three groups of explanatory variables and finally (VIII) unexplained variation.

Variation partitioning and decomposition of variables can be visualized by a venn diagram. By decomposition of variables, we were able to compare the extent of variables redundancy and their relative importance [52]. When the number of unexplained variation is low, it indicates that no fundamental variable is missing (number of variables was sufficient for explaining variation in data set) otherwise, it explains that nondeterministic fluctuations are in effect and more variables must be included in the analysis [48].

Distribution modelling

In this study, we used GLM (Generalized linear model) which is basically a generalization of ordinary least squares regression [8] and GBM (Gradient Boosting Machine), a boosted

decision trees method [58], as a more complicated algorithm which has good performance in SDM [59–61]. GLM and GBM were used to create potential distribution models of gray almond, using combination of different variable groups including climatic variables (C.P), climatic and edaphic variables (C.E.P), climatic and topographic variables (C.T.P) and finally climatic, edaphic and topographic variables (C.E.T.P). Weight of occurrence points were equivalent in all models [61]. Here, we used 10-fold cross-validation for each approach [7, 62]. Modelling process was performed using 'biomod2' package [63] in R platform [51].

Models were validated by calculating the area under the receiver operating curve (AUC) [64], true skill statistic (TSS) [65], sensitivity (true positive rate) and specificity (true negative rate) based on 10-fold cross-validation on the calibration data set [12, 66, 67]. AUC evaluates the ability of a model to distinguish between locations that a species is present, versus those that is not present. The performance score of the measured AUC ranged between 0–1, where 1 is a perfect score and the model is ideal, 0.5 represents a model of random selection and the results under 0.5 is reflects an unacceptable model [68]. TSS ranges between +1 (the best result) to -1 (the worst result) and calculates by (sensitivity + specificity) -1 [65]. Particularly, ROC plot has received considerable attention in SDM studies because it considered both sensitivity and specificity for all available thresholds [65] and provides a single measure of overall accuracy that is not dependent upon a particular threshold [64, 67].

We used representative concentration pathway (RCP) 2.6 of "The Community Climate System Model" (CCSM4) of future climate scenario for year 2070 (average for 2061–2080) provided by National Center for Atmospheric Research of USA widely used by researchers [69] and has strong agreement with climatic condition of Iran [70] for each SDMs.

Continuous probability of presence produced by models (GLM and GBM) transformed to binary presence/absence data using individual thresholds [71, 72]. Thresholds were calculated based on the ROC plot approach in "biomod2" library [63] in R [51] that is determined by the shortest distance of the curve to the top-left corner in the ROC plot [63].

Results

Principle analysis components

In this study, the first two PCs accounted for 41.06% of total variance of data set (PC1, 27.46% and PC2, 13.6%). The first principal components (PC1) captured more variance (27.46%) than expected by chance and is completely distinguished from the other dimensions. In PC1, solar radiation and isothermality explain the greatest proportion, and in PC2, precipitation of driest quarter and temperature seasonality explain the greatest proportion, respectively. The second to fifth components of environmental variables showed eigenvalues exceeding 1. The first six components explain 80.83% of the total variance, meaning lack of significant differentiation between components and mild differentiation between principal component 1 and others. In other words, overall combination of environmental variables affects the presence of gray almond.

In the graph of variables (Fig 2), positive correlated variables point to the same sector and negative correlated variables point to opposite section of the graph. The results showed that solar radiation and isothermality (Bio3) are strongly correlated and overlap close to axis 1. Principal-components analysis (PCA) indicated that presence of *P. eburnea* in the study area is correlated with several important environmental variables that make a suitable multidimensional niche.

Hierarchical partitioning

The independent and joint contribution of each variable in presences and absences of gray almond was determined by HP (Fig 3). Results showed coarse fragments (volumetric) of soil



Fig 2. Visualizations of environmental conditions of *P. eburnea* occurrence locations in Iran by PCA analysis, which summarize variation among the environmental variables.

https://doi.org/10.1371/journal.pone.0256918.g002



Fig 3. The independent (A), (given as the percentage of the total explained variance) and joint contributions (B), its independent contribution (dark color) and its conjoint contribution with all other variables (light color) of the variable variables for *P. eburnea*, as estimated from hierarchical partitioning.

https://doi.org/10.1371/journal.pone.0256918.g003

and slope are the most important independent environmental variables, respectively and their joint effect is amplified.

In the hierarchical partitioning analyses, the independent effects of all included environmental variables were statistically significant. The highest independent contributions belong to coarse fragments (volumetric) of soil (crfvol), slope and precipitation of driest quarter (Bio17), respectively and the lowest contributions belong to mean temperature of coldest quarter (Bio11) and organic carbon content (orcdrc), respectively (Table 2).

Variation partitioning

For determining VP, different combinations of groups of variables were performed according to equations below: (X1, X2 and X3 represent the followings: X1 = group of edaphic variables, X2 = group of topographic variables and X3 = group of climate variables).

[a+d+f+g] = X1 [b+d+e+g] = X2 [c+e+f+g] = X3 [a+b+d+e+f+g] = X1+X2 [a+c+d+e+f+g] = X1+X3 [b+c+d+e+f+g] = X2+X3[a+b+c+d+e+f+g] = All

Results of partitioning of variation using these environmental variables in RDA showed that total variation (SS) sums up to 122.7 and Variance is 0.2494. In the case of the VP results, the total explained variation in *P. eburnea* environment data was obtained by regressing with the selected statistically significant variables (p<0.05) of the three groups of environmental variables (climatic, edaphic and topographic variables) and consequently, the residual amount calculated (Fig 4). (The size of circles and overlaps in Fig 4 did not scale to their numerical values).

Variation partitioning of the data set showed that 48.94% of total variation explained by used environmental variables. The portion of each group of environmental variables in this amount of justified variance is different. that climate, explained more variance (14.17%) in *P. eburnea* occurrence than topography (2.78%), soil (12.27%), climate and soil together (8.13%),

Table 2. Results of the randomization tests for the independent contributions of separate variable variables in hierarchical partitioning for explaining variation of *P. eburnea* (Z.scores are computed as (observed—mean (randomizations))/sd(randomizations), and statistical significance (*) is based on upper 0.95 confidence limit (Z > = 1.65).

Environmental variables	Observed	Z.score
Crfvol	29.19	149.96 *
Orcdrc	8.54	41.50 *
Sltppt	9.58	35.29 *
Southness	8.98	64.15 *
Westness	8.56	44.81 *
Slope	20.20	50.54 *
Bio17	16.65	128.88 *
Bio4	8.59	60.31 *
Bio3	10.95	38.88 *
Bio11	5.50	21.36*
Bio15	15.38	99.16 *
Solar radiation	13.37	105.64 *

https://doi.org/10.1371/journal.pone.0256918.t002



Fig 4. Results of variation partitioning of *P. eburnea* **in terms of the fractions of variation is explained.** In a venn diagram, each circle shows how much of the variations of response variables is explained by each group of variables and overlap areas show the joint contribution of different variables. It must be considered the size of circles and overlaps in figure did not scale to their numerical values (variation of the environmental data is explained by three groups of explanatory variables: X1 = group of edaphic variables, X2 = group of topographic variables and X3 = group of climate variables. Residuals are undetermined variation and a, b and c represent unique effects of edaphic, topography and climate variables, respectively; while d, e, f and g are fractions indicating their joint effects).

https://doi.org/10.1371/journal.pone.0256918.g004

climate and topography together (0.54%), soil and topography together (5.07%), soil, topography and climate together (5.98%). In general, climate variables by themselves were more powerful than the other variables and groups of variables together in explaining the variations. The results showed that 51.06 percentage of variation cannot be explained by environmental variables and it is related to biotic variables, the interactions between biotic and abiotic variables.

Species distribution modelling

Results of assessing effects of different combinations of environmental variables to GLM and GBM showed that sensibility of different accuracy criteria to input variables are different. In GLM, area under the curve (AUC) scores ranged from 0.91–0.94 and specificity ranging 83.7–90.24. Also, sensitivity and true skill statistic (TSS) ranged from 83.9–92.84 and 0.67–0.75, respectively, which represented significant difference among, models accuracy. The lowest AUC score, TSS, sensitivity and specificity were observed when we used only climatic variables (Table 3).

In GBM, AUC score and TSS ranged from 0.92–0.95 and 0.86–0.89, respectively. Results indicated there are not tangible differences in AUC score and TSS using different groups of environmental variables. In all fractions, TSS and AUC score for GBM were greater than GLM. Sensitivity ranged from 86.13–93.87 that represented significant differences using different groups of environmental variables by GBM. Specificity ranged from 87.29–93.7 and it was the highest number, using only climatic variables (Table 3).

Climate change impacts

Results of using different environmental predictors combinations in predicting potential distribution of gray almond using CCSM4, RCP 2.6 in 2070 by GLM and GBM showed that using

Model	Accuracy criteria	C.P	C.E.P	C.T.P	C.E.T.P
GLM	AUC	0.91	0.93	0.94	0.94
	TSS	0.67	0.72	0.75	0.75
	Sensitivity	83.9	90.78	92.26	92.87
	Specificity	83.7	89.85	89.29	90.24
GBM	AUC	0.92	0.94	0.94	0.95
	TSS	0.85	0.86	0.88	0.89
	Sensitivity	86.13	91.3	93.69	93.87
	Specificity	87.29	89.63	91	93.7

Table 3. Comparison of area under the curve (AUC), true skill statistic (TSS), sensitivity and specificity statistics using 10 fold cross-validation for each GLM and GBM approaches using different fractions of environmental variables in modeling potential habitat suitability of gray almond in Iran (C.P: Climatic variables; C.E. P: Climatic and edaphic variables; C.T.P: Climatic and topographic variables; C.E.T.P: Climatic, edaphic and topographic variables).

https://doi.org/10.1371/journal.pone.0256918.t003

different fractions of environmental variables has a strong impact on the estimated potential of future range size. Using climatic variables alone led to predicting a major reduction of the potential distribution of gray almond but by including topographic and edaphic variables besides climatic variables, we observed a minor reduction in predicting potential distribution of gray almond in future (Table 4).

Projected effects of climate change using RCP 2.6 in 2070 on prediction distribution change of gray almond (Fig 5) shows big differences in the results between different groups. Results highlight in the margin of potential distribution especially in lower latitude, there would be more possibility for distribution by GLM and GBM.

Discussion

Our results indicated that variable selection has strong influence on predicting species distribution and model accuracy especially in case of climate change, which is commonly, used for conservation and management purposes. Here, species distribution models calibrated with climatic, topographic and edaphic variables (C.T.E.P) performed better than the others (C.P, C. E.P and C.T.P) and models were more precise (Table 3) and more realistic (Fig 5). The lowest accuracy of GLM and GBM (Table 3) was achieved using only climatic variables, which are commonly used in isolation to infer future species distributions. Since climate is not the only factor affecting distribution of species, it cannot adequately represent habitat suitability completely without considering other effective environmental variables in correlative models [22, 73]. Using only climatic variables in species modelling which their distribution is limited

Fable 4. Current and predicted future potential distribution and changes in habitat suitability under climate change condition for gray almond using different frac-
tions of environmental variables by GLM and GBM; units is km ² (C.P. Climatic variables; C.E.P. Climatic and edaphic variables; C.T.P. Climatic and topographic
variables; C.E.T.P: Climatic, edaphic and topographic variables).

Model	Group of variables	Loss (%)	Gain (%)	Range Change (%)	Current Range Size	Future Range change
GLM	C.P	84.23	3.45	-80.78	763349	616633
	C.E.P	62.86	8.6	-54.26	857789	465436
	C.T.P	63.15	6.7	-56.45	844635	476796
	C.E.T.P	46.01	9.52	-36.49	869066	317122
GBM	C.P	81.45	4.12	-77.33	740177	572378
	C.E.P	35.12	5.85	-29.27	831042	243245
	C.T.P	29.67	5.3	-24.37	839083	204484
	C.E.T.P	23.28	7.11	-16.17	852893	137912

https://doi.org/10.1371/journal.pone.0256918.t004



Fig 5. Projections using a purely dynamic model (based on climate only) versus static + climatic model by GLM and GBM. (A: Current distribution using climatic variables by GLM; B: Future distribution using climatic variables by GLM; C: Current distribution using climatic and static variables by GLM; D: Future distribution using climatic and static variables by GLM; E: Current distribution using climatic variables by GBM; F: Future distribution using climatic variables by GBM; G: Current distribution using climatic and static variables by GBM; H: Future distribution using climatic and static variables by GBM).

https://doi.org/10.1371/journal.pone.0256918.g005

by non-climatic variables leads to increasing risk of overfitting, under or over estimation of changes in potential distribution [72] and probability of extinction under climate change conditions [74, 75].

Here, our results showed static variables increased accuracy and reliability of modelling current habitat suitability (Table 3) and predicting habitat suitability of gray almond under climate change conditions (Table 4). Because, using appropriated static variables beside dynamic variables lead to more explaining niche species [61] and increasing accuracy of predictions in modelling [20, 22, 24]. Static variables play an important role in determining distribution of species. For increasing accuracy and reliability of models, it is better to include static variables, such as land cover and land use in SDM than to exclude them [31] as showed on investigations on butterflies [13].

In this study, we used principal component analysis (PCA), variation partitioning (VP) and hierarchical partitioning (HP) methods to identify relevant species-environment relationships for P. eburnea). Recognition of the proportion of each variable and group of variables in constituting a suitable habitat is helpful for better tracing and evaluating the changes in habitats. Climate information was the most important environmental group of variables for settling P. eburnea in different habitats (Figs 3 and 4). Climate characteristics are influencing factors in delimiting distribution of plants. Minimum temperatures not only have controlling roles in physiologic functions of plants [76, 77], but also affect the susceptibility of species to attack by pathogens and pests [78] and their competing and coexisting ability in interspecies interactions [79, 80]. Joint effects of environmental variables induce additive impacts on some aspects of environment. For example, combination of the effects of the solar radiation and seasonal temperature differences during winter and summer lead to different environmental conditions [81], which is especially relevant for plants which start their germination and flowering in late winter, such as species of Prunus and other rosaceae species. Results of this research indicated cumulative effects of soil depth (Crfvol) and slope on P. eburnea presence in specific habitats (Fig 3). Cumulative effects can be synergistic (amplifying) or antagonistic (decreasing) in their influence. Therefore, interactions amongst different groups of variables are important and must be taken into account when suitable habitat for species is determined. For example, temperature and precipitation are two main factors of climate that are both influenced by elevation directly. Solar radiation is dependent on latitude and affects photoperiod of plants, which controls most of physiological functions and biomass producing [82]. The high degree of overlap between climate and soil (8.13%) is at least partly because of the dependence of soil (formation, recycling, weathering and erosion) on climate [83]. In addition, results showed that soil organic carbon explained high portion of total variations in distribution of *P. eburnea* (Figs 3 and 4). Importance of soil organic carbon content (Figs 2 and 3) derived from its role in the determining accessibility of water and nutritious elements [84] and consequently to wider occurrence of plant species [85]. Similar effects result from soil texture, which facilitates nitrogen and phosphorous uptake [76, 86]. Soil properties by affecting on water and nutrients availability [87], physical support for root growth and establishment in habitats in most of plants [88, 89] play a key role in determining suitable habitats which improve accuracy of predictions [13, 90] indicated including edaphic variables, along with climatic variables led to more realistic predictions of the current distribution of shrub species. Actually, adding relevant edaphic variables to modelling by increasing probability of recognizing suitable habitats, resulted to improvement of model performance and led to more accurate mapping [90, 91]. Topographic variables by effecting on other environmental factors such as soil properties [73] play an important role in limiting species distribution [72]. Using efficient-scale topography variables in prediction of future distribution of species would help to recognize refugia (shelter) and therefore to increase the accuracy of the species range change prediction [73].

Results of this study showed that abiotic factors contributed to robustly explain the occurrence of *P. eburnea* in its native habitats and the remainder is related to biotic variables and interactions between biotic and abiotic variables that were not accounted for in our analyses. Our results indicated that regarding static variables in SDM especially in predicting impacts of climate change on species occurrences changed the predictions significantly (Fig 5). Topographic characteristics [73] and soil properties at a large scale affect plant growing conditions are key factors in predicting current and improving prediction of future potential distribution; therefore, considering only climatic variables (Table 4) (Fig 5) and ignoring topographic and edaphic heterogeneity lead to over prediction of shifts and extinction rate of species under climate change conditions [73].

When inferring and interpreting of SDM, one needs to consider that limiting factors of species distribution are far more than environmental factors and colonization and extinction dynamics may be relevant to species distributions, even though, these variables may not address those relations. It is almost impossible to measure the true niche of a species completely, because, we cannot measure and quantify all factors (biotic, abiotic and complex interactions between them) which influence presence (and absence) and distribution range of species and only we usually can get an overview on much of the conditions that make up niche. Therefore, extrapolating results from correlative modelling approaches should always be made with caution and choosing modelling variables must be prioritized [92].

Conclusion

The results of this study indicate that use of solely climatic variables would exaggerate the prediction effects of climate change on the potential distribution of species range and that non-climatic variables, such as soil and topographic characteristics are important factors that can also constrain the rate of climate-induced range expansion. This study showed the importance of including the appropriated combination of variables for habitat suitability modelling and prediction effects of climate change on it. Our results indicated using static environmental variables in addition to climatic variables to modeling, increased overall accuracy criteria of models and the results were more realistic. Although, some studies indicated that using only climatic data may provide an effective and efficient approach for primary evaluations of habitat suitability [28], our results indicated that using only climatic variables overestimate the impacts of climate change on species distributions. Disentangling of broad climatic drivers from microhabitat and soil factors in determining species distributions is of paramount importance, because, it will provide information on potential impacts of future climate change and the possible mechanisms leading to altered plant diversity (alpha, beta and gamma diversity).

Supporting information

S1 File. (RAR)

Acknowledgments

The authors thank Dr. Roozbeh Valavi from the School of BioSciences, the University of Melbourne, Australia for his valuable advices during the process of analysis.

Author Contributions

Conceptualization: LIuis Brotons.

Data curation: Somayeh Zangiabadi.

Formal analysis: Hassan Zaremaivan, Hossein Mostafavi, Hojjatollah Ranjbar.

Investigation: Somayeh Zangiabadi, Hassan Zaremaivan, Hossein Mostafavi, Hojjatollah Ranjbar.

Methodology: LIuis Brotons.

Project administration: Hassan Zaremaivan.

Software: Somayeh Zangiabadi.

Validation: LIuis Brotons.

Writing - original draft: Somayeh Zangiabadi, Hassan Zaremaivan.

Writing – review & editing: Somayeh Zangiabadi, Hassan Zaremaivan, LIuis Brotons, Hojjatollah Ranjbar.

References

- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters. 15:365–377. https://doi.org/10.1111/j.1461-0248.2011. 01736.x PMID: 22257223
- Thuiller W, Lavorel S, Arau´jo MB, Sykes MT, Prentice C. 2005. Climate change threats to plant diversity in Europe. National Academy of Sciences of the United States of America. USA 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102 PMID: 15919825
- Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA. 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22, 583–592. https://doi.org/10.1016/j.tree.2007.10.001 PMID: 17981360
- Bertelsmeier C, Luque G M, Courchamp F. 2013. The impact of climate change changes over time. Biological Conservation. 167:107–115. http://dx.doi.org/10.1016/j.biocon.2013.07.038
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters. 16:1424–1435. https://doi.org/10. 1111/ele.12189 PMID: 24134332

- Pompe S, Hanspach J, Badeck F, Klotz S, Thuiller W, Kühn I. 2008. Climate and land use change impacts on plant distributions in Germany. Biology Letters. 4, 564–567. <u>https://doi.org/10.1098/rsbl.</u> 2008.0231 PMID: 18664416
- 7. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. 2011. Ecological niches and geographic distributions. Princeton University Press, Princeton, USA.
- 8. Hijmans RG, Elith J. 2017. Species distribution modeling with R.
- 9. Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters. 8: 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x
- Chapman DS, Scalone R, Stefanic E, Bullock J. 2017. Mechanistic species distribution modeling reveals a niche shift during invasion. Ecology. pp. 1–10. <u>https://doi.org/10.1186/s12898-016-0111-y</u> PMID: 28068963
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution. 58, 1781– 1793. https://doi.org/10.1111/j.0014-3820.2004.tb00461.x PMID: 15446430
- Kirchheimer B, Wessely J, Gattringer A, Hulber K, Moser D, Schinkel CCF, et al. 2018. Reconstructing geographical parthenogenesis: effects of niche differentiation and reproductive mode on Holocene range expansion of an alpine plant. Ecology Letters. <u>https://doi.org/10.1111/ele.12908</u> PMID: 29349850
- Eskildsen A, Roux PC, Heikkinen RK, Høye TT, Kissling WD, Pöyry J, et al.2013. Testing species distribution models across space and time: high latitude butterflies and recent warming. Global Ecology and Biogeography. 22(12):1293–1303.
- 14. Vargas JH, Consiglio T, Jørgensen PM, Croat TB. 2004. Modelling distribution patterns in a speciesrich plant genus, Anthurium (Araceae), in Ecuador. Diversity and Distributions. 10:211–216.
- Forbis de Queiroz T, Baughman C, Baughman O, Gara M, Williams N. 2012. Species Distribution Modeling for Conservation of Rare, Edaphic Endemic Plants in White River Valley, Nevada. Natural Areas Journal. 32(2):149–158.
- Pérez-Rodríguez A, Fernández-González S, de la Hera I, Pérez-Tris J. 2013. Finding the appropriate variables to model the distribution of vector-borne parasites with different environmental preferences: climate is not enough. Glob Chang Biol. 2013 Nov; 19(11):3245–53. <u>https://doi.org/10.1111/gcb.12226</u> PMID: 23606561
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 36, 027e046. https://doi.org/10.1111/j.1600-0587.2012.07348.x.
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, et al. 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspect. Plant Ecology Evolutoin and Systematics. 9 (34), 137–152.
- Merow C, Smith MJ, Edwards TC, Guisan A, Mcmahon SM, Normand S, et al. 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography. 37, 1267e1281. https:// doi.org/10.1111/ecog.00845.
- Fournier A, Barbet-Massin M, Rome Q, Courchamp F. 2017. Predicting species distribution combining multi-scale drivers. Global Ecology and Conservation. 12, 215e226.
- Araujo MB, Guisan A. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography. 33:1677–1688.
- Araujo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modelling. Ecology. 93:1527–1539. https://doi.org/10.1890/11-1930.1 PMID: 22919900
- Williams KJ, Belbin L, Austin MP, Stein JL, Ferrier S. 2012. Which environmental variables should I use in my biodiversity model? International Journal of Geographical Information Science 26:2009_2047 https://doi.org/10.1080/13658816.2012.698015
- Braunisch V, Coppes J, Arlettaz R, Suchant R, Schmid H, Bollmann K. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. Ecography (Cop.) 36, 971e983. https://doi.org/10.1111/j.1600-0587.2013.00138.x.
- 25. Sheppard CS. 2013. How does selection of climate variables affect predictions of species distributions? A case study of three new weeds in New Zealand. WeedRes. 53, 259–268.
- Barbet-Massin M, Jetz W. 2014. A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. Diversity and Distribution. 20, 1285e1295. <u>https:// doi.org/10.1111/ddi.12229</u>.
- Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography. 12, 361–371.

- Bucklin DN, Basille M, Benscoter AM, Brandt LA, Mazzotti FJ, Roma~nach SS, et al. 2015. Comparing species distribution models constructed with different subsets of environmental predictors. Diversity and Distributions. 21:23–35. https://doi.org/10.1111/ddi.12247
- Carvalho SB, Brito JC, Crespo EJ, Possingham HP. 2010. From climate change predictions to actions– conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology. 16:3257– 3270.
- Hole DG, Willis SG, Pain DJ, Fishpool LD, Butchart SHM, Collingham YC, et al. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters, 12, 420–431. https://doi.org/10.1111/j.1461-0248.2009.01297.x PMID: 19379136
- Stanton JC, Pearson RG, Horning N, Ersts P. Akc akaya HR. 2012. Combining static and dynamic variables in species distribution models under climate change. Methods in Ecology and Evolution. 3, 349–357 https://doi.org/10.1111/j.2041-210X.2011.00157.x
- Khatamsaz M. 1993. Flora of Iran (Family Rosaceae). Vol. 6. Research Institute of Forest and Rangelands press, Tehran. 274315.
- Akhani H. 2004. A new spiny, cushion-like Euphorbia (Euphorbiaceae) from south-west Iran with special reference to the phytogeographic importance of local endemic species. Botanical Journal of the Linnean Society. 146:107–121.
- Rahemi A, Fatahi R, Ebadi A, Taghavi T, Hassani D, Gradziel TM, et al. 2012. Genetic diversity of some wild almonds and related Prunus species revealed by SSR and EST-SSR molecular markers. Plant Systematics and Evolution. 298(1):173–192.
- 35. Rechinger KH. 1963–1992. ed., Flora Iranica: Flora des iranischen Hochlandes und der umrahmenden Gebirge, Graz, Austria.
- 36. Mobayen S. 1980–1996. Flora of Iran: Vascular Plants, 4 vols. Tehran.
- Thuiller W, Brotons L, Araújo M, Lavorel S. 2004. Effects of restricting environmental range of data to project current and future species distributions. Ecography. 27:165–172.
- Fick SE, Hijmans RJ. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology. 37(12): 4302–4315.
- Hengl T, De Jesus JM, MacMillan RA, Batjes NH, Heuvelink GBM, Ribeiro E, et al. 2014. SoilGrids1km —Global Soil Information Based on Automated Mapping. Plos one. 9(8): e105992. https://doi.org/10. 1371/journal.pone.0105992 PMID: 25171179
- 40. Hijmans R.J. 2017. Raster. Introduction to the 'raster' package. version 2.6–7 R package. Available: http://CRAN.R-project.org/package=Raster.
- 41. Mazangi A, Ejtehadi H, Mirshamsi O, Ghassemzadeh F, Hosseinianyousefkhani SS. 2016. Effects of climate change on the distribution of endemic *Ferula xylorhachis* Rech.f. (Apiaceae: Scandiceae) in Iran: Predictions from ecological niche models. Russian Journal of Ecology. 47(4): 349–354.
- Titeux N, Henle K, Mihoub JB, Regos A, Geijzendorffer IR, Cramer W, et al. 2017. Global scenarios for biodiversity need to better integrate climate and land use change. Diversity and distributions. 23 (11):1231–1234. https://doi.org/10.1111/ddi.12624
- Gogtay NJ, Thatte UM. 2017. Principles of Correlation Analysis. Journal of The Association of Physicians of India. 65:78–81. PMID: 28462548
- Stuart N. 2015. ArcGeomorphometry: A toolbox for geomorphometric characterization of DEMs in the ArcGIS environment'. Computers and Geosciences. https://doi.org/10.1016/j.cageo.2015.09.020
- 45. ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, CA.
- 46. Azevedo MCC, Araújo FG, Cruz-Filho AG, Pessanha ALM, Araújo Silva M, Guedes APP. 2007. Demersal fishes in a tropical bay in southeastern Brazil: Partitioning the spatial, temporal and environmental components of ecological variation. Estuarine, Coastal and Shelf Science. 75: 468–480.
- Heikkinen RK, Luoto M, Kuussaari M, Poyry J. 2005. New insights into butterfly–environment relationships using partitioning methods. Proceedings of the royal science. 272:2203–2210. <u>https://doi.org/10.1098/rspb.2005.3212</u> PMID: 16191631
- Borcard D, Legendre P, Drapeau P. 1992. Partialling out the spatial component of ecological variation. the Ecological Society of America. Ecology. 73(3):1045–1055.
- McGarigal K, Cushman SA, Stafford S. 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer Verlag, New York, New York, USA.
- Stacklies W, Redestig H, Wright K. 2018. pcaMethods. A collection of PCA methods. R package. Available: http://CRAN.R-project.org/package=pcaMethods
- R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <u>https://www.R-project.org</u>

- Cushman S, McGarigal K. 2002. Hierarchical, Multi-scale decomposition of species-environment relationships. Landscape Ecology. 17:637–646.
- 53. Walsh C, Nally RM. 2015. Package 'hier.part'. Variance partition of a multivariate data set. Version 1.0– 4. Available from: https://cran.r-project.org. Package = hier.part.
- 54. Warnes GR, Bolker B, Lumley T. 2018. gtools. Various R Programming Tools. Version 3.8.1. R package. Available: http://CRAN.R-project.org/package=gtools.
- 55. Smith TW, Lundholm JT. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography. 33:648–655.
- 56. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. 2018. Package 'vegan'. Available from: https://cran.r-project.org. Package = vegan.
- 57. Chen Y. 2013. A Multiscale variation partitioning procedure for assessing the influence of dispersal limitation on species rarity and distribution aggregation in the 50-ha tree plots of barro Colorado Island, Panama. Journal of Ecosystem and Ecography. 3(4):1–4. https://doi.org/10.4172/2157-7625.1000134
- **58.** Friedman J, Hastie T, Tibshirani R. 2000. Additive logistic regression: a statistical view of boosting. Annals of Statistics, 28, 337–374
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions, 14, 763–773.
- Heikkinen RK, Marmion M, Luoto M. 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography, 35, 276–288.
- Breiner FT, Guisan A, Bergamini A, Nobis MP. 2015. Overcoming limitations of modelling rare species by using ensembles of small models. Methods in Ecology and Evolution. 6:1210–1218. <u>https://doi.org/ 10.1111/2041-210X.12403</u>
- 62. Franklin J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, USA.
- Thuiller W, Georges D, Engler R, Georges MD, Thuiller CW. 2014. biomod2: Ensemble Platform for Species Distribution Modeling.
- Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation. 24, 38–49.
- Liu C, White M, Newell G. 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. Ecography, 34, 232–243.
- Elith J, Graham CH, Anderson RP, Dudi 'k M, Ferrier S, Guisan A, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography. 29: 129_/151.
- Hijmans R. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology, 93(3), 2012, pp. 679–688. https://doi.org/10.1890/11-0826.1 PMID: 22624221
- **68.** Grenouillet G, Buisson L, Casajus N, Lek S. 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography. 34:9–17.
- Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Howell MA. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. PNAS. 106-suppl. 2–19729–19736.
- Ghahreman N, Tabatabaei M, Babaeian I. 2015. Investigation of uncertainty in the IPCC AR5 precipitation and temperature projections over Iran under RCP scenarios. Un climate change conference. Paris.
- Liu C, Berry P, Dawson T, Pearson R. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.
- Hof AR, Jansson R, Nilsson C. 2012. The usefulness of elevation as a predictor variable in species distribution modelling. Ecological Modelling 246, 86–90.
- 73. Austin MP, Van Niel KP. 2010. Improving species distribution models for climate change studies: variable selection and scale. Journal of Biogeography. 38:1–8. https://doi.org/10.1111/j.1365-2699.2010.02416.x
- Beaumont LJ, Hughes L, Poulsen M. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecological Modelling. 186:250–269.
- 75. Porfirio LL, Harris RMB, Lefroy EC, Hugh S, Gould SF, et al. 2014. Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change. PLoS ONE 9(11): e113749. https://doi.org/10.1371/journal.pone.0113749 PMID: 25420020
- 76. Woodward Fl. 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge.

- Jump A, Matyas C, Peñuelas J. 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends in Ecology and Evolution. 24(12):694–701. https://doi.org/10.1016/j.tree.2009. 06.007 PMID: 19695735
- 78. Hogg EH, Brandt JP, Kochtubajda B. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian journal of forest research. 32:823–832. http://dx.doi.org/10.1098/rspb.2014.1779
- Peñuelas J, Ogaya R, Boada M, Jump SA. 2007. Migration, invasion and decline: changes in recruitment and forest structure in awarming-linked shift of European beech forest in Catalonia (NE Spain). Ecography. 30:830–838.
- Gitlin AR, Sthultz CM, Bowker MA, Stumpf S, Paxton KL, Kennedy K, et al. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology. 20:1477–1486 <u>https://doi.org/10.1111/j.1523-1739.2006.00424.x</u> PMID: 17002765
- Roots F. 1989. Environmental issues related to climate change in northern high latitudes. McCulloch J. A.W. (ed), Arctic Global Change, Climate Institute, Washington DC. 4–31.
- Hay RKM. 1990. The influence of photoperiod on the dry matter production of grasses and cereals. New Phytologist. 116: 233–254.
- Pakeman RJ, Leps J, Kleyer M, Lavorel S, Garnier E. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. Journal of Vegetation Science. 20:148–159.
- Singh G, Singh NT. 1998. Mesquite for Revegetation of Salt Lands, Central Soil Salinity Research Institute. Bulletin.
- Bornman TG, Adams JB, Bate GC. 2008. Environmental factors controlling the vegetation zonation patterns and distribution of vegetation types in the Olifants Estuary, South Africa. South African Journal of Botany. 74: 685–695.
- **86.** Rainer H. 1990. Community composition and soil properties in northern Bolivian savanna vegetation. Journal of vegetation science. 1:345–352.
- Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a reevaluation of processes and patterns. Advances in Ecological Research 30:1–67. https://doi.org/10.1016/S0065-2504(08)60016-1
- Martre P, North GB, Bobich EG, Nobel PS. 2002. Root deployment and shoot growth for two desert species in response to soil rockiness. American Journal of Botany 89:1933–1939. <u>https://doi.org/10.3732/ajb.89.12.1933</u> PMID: 21665622
- Raynaud X. 2004. Soil characteristics play a key role in modeling nutrient competition in plant communities. Ecology, 85, 2200–2214.
- Hageer Y, Esperón-Rodríguez M, Baumgartner JB, Beaumont LJ. 2017. Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species?. PeerJ, <u>https://doi.org/</u> 10.7717/peerj.3446 PMID: 28652933
- **91.** Midzi N, Kavhu B, Manangazira P, Phiri I, Mutambu SL, Tshuma C, et al. 2018. Parasites & Vectors. 11:47. https://doi.org/10.1186/s13071-017-2586-6 PMID: 29351762
- 92. Boulangeat I, Gravel D, Thuiller W 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecological Letters. 15:584–593. https://doi. org/10.1111/j.1461-0248.2012.01772.x PMID: 22462813