Heliyon e05220

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

Spatial distribution of *Poa scaberula* (poaceae) along the andes

Lidia R. Scrivanti *, Ana M. Anton

Sistemática y Filogeografía de Plantas. Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and F.C.E.F. y N. (UNC), Av. Vélez Sarsfield 1611, CP 5000 Córdoba, Argentina

ARTICLE INFO

Keywords:
Ecology
Environmental science
Plant biology
Biodiversity
Flora
Botany
Andean grass
Climatic variables
Grasslands
High elevation regions
South America
Global ecological change
Systems biology

ABSTRACT

Mountains support a great diversity of species and habitat types. Grasslands are the dominant landscape in the Andes and play an important ecological role. However, they are threatened by many factors, including climate change and human activities. The spatial distribution of species that compose, and the ecological and evolutionary factors that provide for the spatial biodiversity patterns, are little known. The largest *Poa* L. (Poaceae) genera are widely diversified and distributed in the Andes. In particular, *P. scaberula* Hook. f. shows great environmentally mediated phenotypic plasticity, and is distributed from North America to the tip of South America. However, the impact of environmental variables has on the spatial distribution of this species, remain largely unknown. Using high-resolution climatic data, herein we modeled the current suitable habitat for *P. scaberula* and identified the main climatic variables that best predict its potential distribution. In addition, we assess the species status in the predicted habitats through herbarium data and relate it with species distribution models. The models showed that *P. scaberula* has a suitable habitat of ca. 162.747 km^2 along the Andes and high elevation regions. The most influential variables with a 68.5% contribution to the distribution of the species, particularly high elevation areas, included mean cold hardiness, water vapor pressure and temperature seasonality. The areas of greatest suitability with the highest occurrence of the species were identified geographically by the models. The present study provides useful information that can assist in the identification of areas where the species is most sensitive to different variables, including climate change and human activities and contributes in assessing the conservation status of Andean grassland at a regional scale.

1. Introduction

Mountains comprise approximately 12% of the Earth's surface and high mountain areas almost 3%. About 10,000 alpine plant species are confined in high mountain areas, comprising approximately 4% of the global flowering plant species (Körner, 2004; Spehn et al., 2010). The Andes are the longest mountain range in South America with elevations exceeding 5000 m, which decrease along a North-South latitudinal gradient with increased rainfall and decreased temperature range as a result of a decrease in maximum temperatures towards the South.

Grasslands play an important ecological role in carbon (C) cycling, climate regulation and the maintenance of biological diversity (Han et al., 2018), and are the dominant landscape in the whole extent of the Andes. However, Andean grasslands are threatened by climate change and human practices including, among other factors, the erosion associated with overgrazing (Morrone, 2001; Bradley et al., 2006; Thibeault et al., 2010; Minvielle and Garreaud, 2011; Neukom et al., 2015). To better understand and address these issues, it is essential to identify the spatial distribution of species and learn about the ecological and evolutionary factors that contribute to their biodiversity patterns (Graham, 2001; Zhang and Ma, 2008; Moscoso et al., 2013). The geographical distributions of most Andean species remain poorly characterized and, on a regional scale, data are only available for a few species (Calderón Torres et al., 2015; Timaná de la Flor and Cuentas Romero, 2015; Báez et al., 2016; Cuyckens et al., 2016). The main components of the Andean grasslands are the grasses, *Poa* L. being the dominant genus, among others (Veblen et al., 2007). With over 500 species in the world, *Poa* is the largest genus of grasses that is widely distributed and diversified in the Andes. Widely distributed from North America to South America, *Poa scaberula* Hook. f. is found in moist and fertile soils and shady places, and high-elevation pastures and slopes, especially in high altitude and latitude regions of South America that occupy different geographical and climatic gradients (Scrivanti et al., 2014). This grass species is characterized by its phenotypic plasticity that allows it to adapt to diverse climatic and geographic conditions in the Andes and high elevation regions (Scrivanti et al., 2014). Although the observed morphological variation

* Corresponding author.
E-mail address: rscrivanti@imbiv.unc.edu.ar (L.R. Scrivanti).

https://doi.org/10.1016/j.heliyon.2020.e05220
Received 27 December 2017; Received in revised form 24 January 2018; Accepted 8 October 2020

of this species is mediated by environmental factors such as geography, elevation, temperature and precipitation (Scrivanti et al., 2014), the impact that environmental variables have on its spatial distribution remains unknown.

In the present study, we attempted to consolidate distributional information of the species in order to examine the role that climate might play in controlling biogeographic patterns of *P. scaberula*, and thus contribute to understanding the impact of climatic variables on the distribution of the Andean grasslands. To do this, we used species distribution models (SDMs) to correlate occurrence or abundance data of individual species at known locations to the information on the climatic characteristics of those locations (Gomez and Cassini, 2015). SDMs have contributed significantly to the prediction of areas that describe the most suitable climatic and geographic conditions for the survival of the species (Anderson et al., 2003; Guisan and Thuiller, 2005). In turn, this information was applied to investigate a variety of scientific and applied issues (Gomez and Cassini, 2015). To predict the spatial distribution range of *P. scaberula* along the Andes and high elevation regions of South America, we included 22 climatic variables. The spatial distribution of *P. scaberula* was analyzed with Maxent modeling methods under current climate conditions in order to model the current potential distribution range of *P. scaberula*, to identify the main climatic variables that best predict its potential distribution and to assess the species status in the predicted habitats through herbarium data and relate it with the SDMs.

2. Materials and methods

2.1. Study area and occurrence points

The study area covers 3,368,970 km^2 of the Andes from northwestern South America to the Patagonian regions of southern Argentina and Chile. Elevation ranges from 0 to 4600 m a.l.s. (Figure 1), average annual precipitation from 43 to 2600 mm and average temperature from 3.43 to 24.76 °C (Fick and Hijmans, 2017). The total distribution of *P. scaberula* ranges from 13°15′N to 58°25′S, and 91°27′ to 29°19′W (Figure 1), based on geographical coordinates corresponding to collection sites.

Occurrence records of *P. scaberula* were obtained through an exhaustive review of different herbarium data sources (BA, BAA, CORD, K, LIL, LP, LPB, MO, NY, P, SI, US, USM, W, WU) and from online database Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). The correct identification of each specimens was checked. Conversely, data were excluded either when the identity could not be verified or the collection site was not incorporated. Records before 1950 were not used in model fit since the current climate layers cover from 1950 to 2000 (Fick and Hijmans, 2017). When occurrence records lacked exact geo-coordinates, Google Earth was used to examine and determine the geographic locations of the specimens. The location of each specimen was transformed into geographic coordinates using a WGS84 datum that was visualized with DIVA-GIS 7.5 (Hijmans et al., 2012). A total of 185 *P. scaberula* presence records were collected (Supplementary Material), from which records that were less than 1 km apart were removed, thus 130 remaining points were used to build the SDM of the species.

2.2. Obtaining, cutting and selecting environmental variables

Climate data was obtained from the Worldclim database version 2.0 (Fick and Hijmans, 2017, http://www.worldclim.org). We used 22 bioclimatic variables at a resolution of 5 arc-minutes, including variations in temperature, precipitation, solar radiation, wind speed and water vapour pressure. The layers of WorldClim images were downloaded in geotif format and converted to ASCII raster grids in QGis 2.14.0. The QGIS program was used to cut the geographic region into 22 layers that included the entire known range of the species and potential areas of distribution in South America (13 °N to 29 °S, 58 °W to 91 °W). To account for multicolinearity, climatic variables were reduced after examining for cross-correlations (Graham, 2003). We used r $\leq$ 0.80 (Pearson correlation coefficient) as a cut-off threshold to determine the exclusion of highly correlated variables. The reduced number of predictor variables was eleven (Table 1).

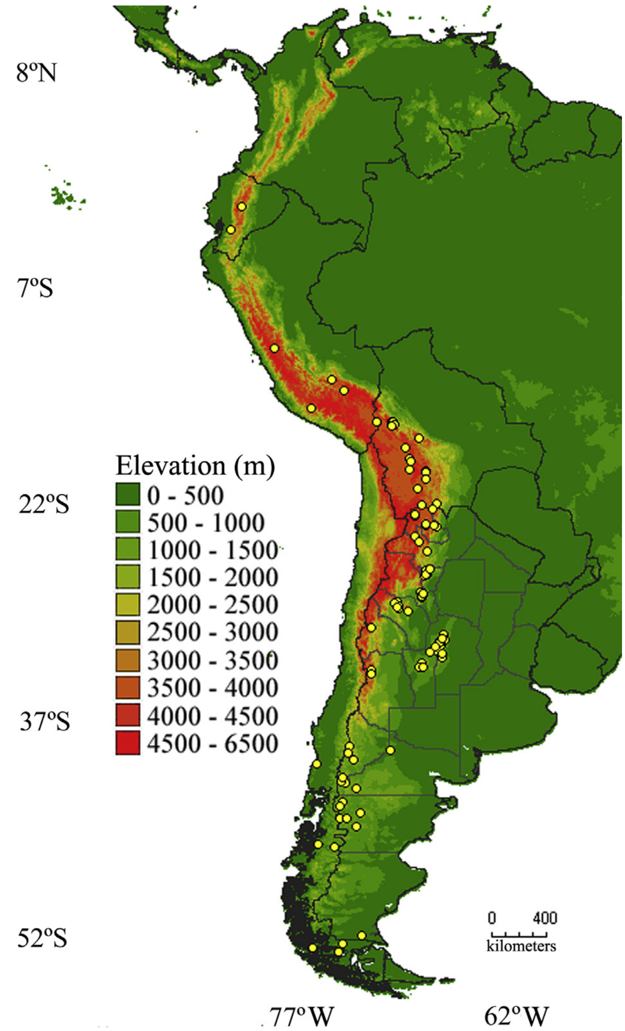

Figure 1. Map of geographical distribution of *P. scaberula* in South America with elevation data.

2.3. Model building and evaluation of SDM performance

To develop the current SDMs of *P. scaberula*, we used the maximum entropy algorithm implemented by MaxEnt v3.3.3k software, allowing for transformations of the covariates with the default thresholds for conversion, removing duplicate presence records, maximum number of background points = 10000; maximum number of iterations = 500; convergence threshold = 0.00001; fit regularization parameter = 1; default prevalence = 0.5; replicated run type = subsample. Of the 130 records, 70% were used for model training and 30% for testing. To validate the robustness of the model, we executed 100 replicated model runs for *P. scaberula* with a threshold rule of 10 percentile training presence. In each of the 100 interactions used in the modeling, the jackknife tests of the importance of the environmental variables was performed with the set of occurrence points used for training within the Maxent interface (Phillips et al., 2006). Validation is one of the most important steps of the modeling process to avoid incorrect interpretation. To evaluate model performance, model robustness was evaluated with the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Fielding and Bell, 1997; Phillips et al., 2006; Phillips and Dudik, 2008). The AUC values of the ROC plot for test points were

Table 1. Contribution of the climatic variables used to predict the potential geographic distribution of *P. scaberula*. The values were obtained by the average of 100 replicas. The variables without any value and the correlated were eliminated. Values in bold indicate higher loadings.

Code	Environmental Variables	Contribution (%)	Permutation importance (%)
BIO01	Annual mean temperature (°C)	5.0	4.5
BIO04	Temperature seasonality (standard deviation)	**10.9**	**9.2**
BIO06	Minimum temperature of coldest month (°C)	**46.5**	**27.1**
BIO07	Temperature annual range (BIO5-BIO6) (°C)	1.1	0.4
BIO09	Mean temperature of driest quarter (°C)	4.3	0.6
BIO12	Annual precipitation (mm)	3.0	4.0
BIO18	Precipitation of warmest quarter (mm)	5.7	2.7
BIO19	Precipitation of coldest quarter (mm)	6.6	6.5
WVP	Water vapour pressure (kPa)	**11.1**	**38.9**
SR	Solar radiation	1.7	2.1
WS	Wind speed	4.1	4.0

Values in bold indicate higher loadings according to Maxent models.

examined. AUC values below 0.8 indicates poor model performance, 0.8–0.9 moderate model performance, 0.90–0.95 good model performance and above 0.95 excellent model performance (Thuiller et al., 2005). To convert the models with probability values into binary (absence/presence), we used the 10th percentile training presence logistic threshold, where the threshold assumes a 10% error in the presence records, thus excluding the 10% lowest probability value. The 10th percentile is commonly used in conservation studies (Abba et al., 2012). We geographically projected the presence of the *P. scaberula* model, dividing the probability of occurrence into the following five categories: values below the threshold value were considered as absent, "low" threshold–0.25, "medium" 0.25–0.5, "high" 0.5–0.75, and "very high" ˃0.75. The final models were obtained with logistic output, and the minimum training presence and maximizing the sum of sensitivity and specificity thresholds were used to define the presence and absence of binary data. For each threshold, mean values of 100 iterations were used. From the values of the histogram graphs, the area occupied in South America was counted by the total number of squares of the environmental layers.

The occurrence dataset and predicted potential areas were mapped and overlayed on satellite images available on Google Earth (http://www.earth.google.com) to check habitat quality assessment. The application of Google Earth superimposition along with limited field observations is a powerful tool for habitat assessment of the species and could be a substitute of extensive field survey (Adhikari et al., 2012).

3. Results

The model calibration test for *P. scaberula* yielded satisfactory results with AUC $_{Train} = 0.972 \pm 0.003$ and $AUC_{Test} = 0.959 \pm 0.010$. The most influential variables, with 68.5% contribution to the MaxEnt model included mean cold hardiness (BIO06), water vapor pressure (WVP) and temperature seasonality (BIO04), whereas the rest input environmental variables contributed 31.5% to the habitat model of the species (Table 1). Considering the permutation importance, water vapor pressure (WVP), mean cold hardiness (BIO06) and temperature seasonality (BIO04) together had the maximum influence on the habitat model and contributed to 75.2% (Table 1). Other climatic variables that contribute to define habitat suitability general SDM were BIO19, BIO18, BIO01, BIO09, WS and BIO12. In fact, the variables BIO19 and BIO18 with very low values of precipitation in the hottest and coolest range, respectively, also influenced the model (Supplementary Table).

SDMs show that the *P. scaberula* species has a potentially wider distribution along the Andes and high mountainous areas from approximately 13°N to 58°S, comprising Ecuador, Peru, Bolivia, Chile, Argentina and small patches in Venezuela and Colombia (Figure 2). Spatial distributions with high suitability thresholds were located in the higher elevations above 1100 m–4620 m a.s.l. in northwestern

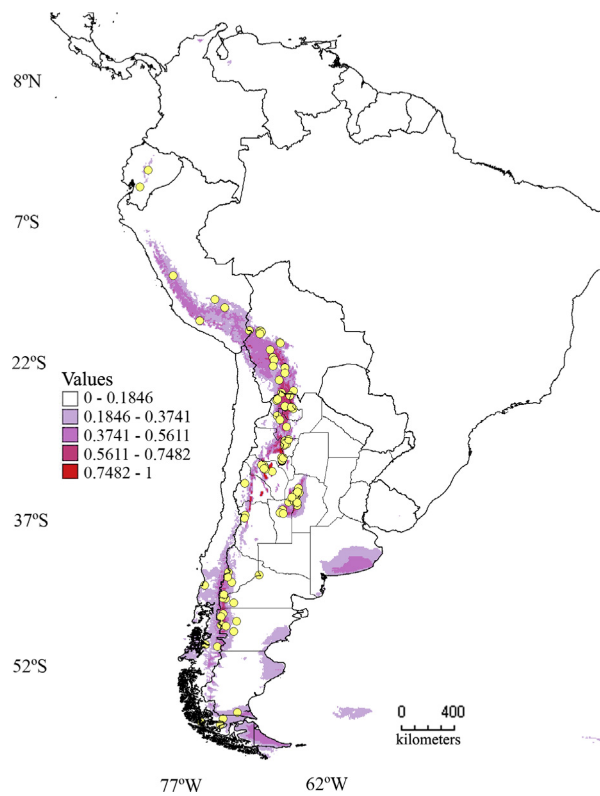

Figure 2. Spatial distribution modeled by Maxent for *P. scaberula* in South America under the current climate. Darker areas represent regions with higher relative probabilities of occurrence. 0 indicates completely unsuitable and 1 indicates optimal.

Argentina, Sierras Pampeanas of Central Argentina, and in some patches in the south of Peru and on the border between Peru and Bolivia (Figure 2), with mean cold hardiness between -11.80 °C and 6.40 °C, low water vapor pressure and low amplitude of temperature (Figure 3, Supplementary Table).

The current model is concordant with our knowledge about current distribution of species, except for Colombia, Venezuela and the Sierras de la Ventana and Tandil in southern Buenos Aires province (Argentina) which has not been registered thus far. In addition, according to the SDMs the probability of occurrence of the species in Ecuador is very low.

A total potential area of 162.747 km^2 along the Andes and high elevation areas of South America was predicted to be suitable for the species (Table 2). Most of the areas fell into the medium suitability class, covering an area of 48.744 km^2, followed by the low suitability class with

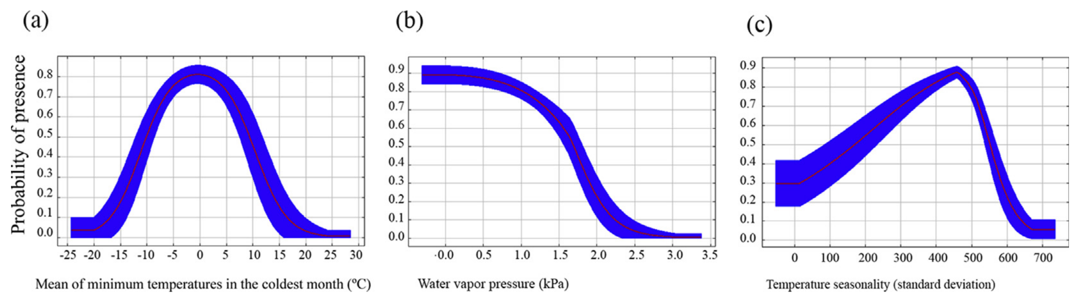

Figure 3. Response curves of the most important environmental variables in modeling habitat distribution for *P. scaberula*. (a) mean minimum temperature of the coldest month, °C (b) water vapor pressure, kpa (c) temperature seasonality, standard deviation.

Table 2. Average size of the area suitable according to Maxent models.

Habitat suitability	Area (km^2)
Total potential area	162.747
Low	98.919
Medium	48.744
High	12.348
Very high	2736

98.919 km^2. The high suitability area covers 12.348 km^2, and the very adequate area 23736 km^2.

According to Google Earth satellite imagery, the areas with high to very high habitat suitability for the species corresponded to highland grassland. The areas with medium to low habitat suitability corresponded in the South to forest and paramo areas, toward the North corresponded to scrublands areas. The areas with very low habitat suitability were grasslands, scrublands and open degraded forests.

4. Discussion

A set of climatic variables including rainfall, temperature, water vapor pressure and wind speed contribute to the spatial distribution of *P. scaberula* that covers approximately 162.747 km^2 in South America. The variables mean cold hardiness (BIO06), water vapor pressure (WVP) and temperature seasonality (BIO04) contributed strongly in determining the distribution of suitable habitats for the species. *Poa scaberula* occupies areas with lower amplitude of temperature conditions and dry habitats. Low temperatures appeared to be a relevant factor in preventing the expansion of the distribution range of *P. scaberula* to low lands along a latitudinal gradient from North to South. The results are consistent with those observed for various plant species that occur in high regions of South America, North America, Africa and Asia (Saatchi et al., 2008; Giannini et al., 2011; Chao-yun et al., 2012; Levsen et al., 2012; Vedel-Sørensen et al., 2013; De Cauwer et al., 2014; Salariato et al., 2015).

The highest probability of occurrence of the species were located in Northwestern Argentina, Sierras Pampeanas of Central Argentina and in some patches in the south of Peru and on the border between Peru and Bolivia, all consistent with inventory data. Therefore, these areas are ideally suitable habitat conditions for persistence of the species and correspond to highland grasslands with elevations above to 1600 m asl along the Andes and Sierras Pampeanas with very low temperatures and low rainfall.

Towards the south of the continent, the areas of occurrence include border areas of Neuquen, Rio Negro, Chubut, Santa Cruz and Tierra del Fuego provinces and Chile. According to SDMs the climate is cold temperate and rainfall is low (<200 mm), except in the southern and western borders, which are influenced by the effect of the cordilleran rainfall where the climate is more humid and colder (Cabrera, 1971; Morrone, 2001). In the southern tip of the continent (Argentina-Chile) from 47°S to Cape Horn and South of Argentina, the species adapts to cold and dry climates where xerophytic forests prevail (Cabrera, 1971; Morrone, 2001). According to SDMs, these sites have low to very low climatic suitability conditions for the species, which coincide with the low record of occurrence, prevailing degraded grassland, scrubland and open forest affected by anthropogenic activity (Cabrera, 1971; Morrone, 2001).

Poa scaberula has high phenotypic plasticity allowing the species to survive a wide variety of climatic and geographical conditions in the Andean and high elevation areas of South America. The capacity of organisms to fit their phenotype to changing conditions as an important mechanism to avoid migration or extinction under environmental change is well recognized (Valladares et al., 2014). Nevertheless, phenotypic plasticity is not generally included in models of species distribution responses to climate change or to the use of land, among other impacts on biodiversity (Reed et al., 2011; Schwartz, 2012; Valladares et al., 2014). Thus, its role should be discussed since populations are exposed to different environmental pressures (Valladares et al., 2014). Altitudinal and geographical distance are apparently important factors in the variation of the reproductive and vegetative phenotypes, as it has been shown by the significant association between vegetative and reproductive phenotypes and altitudinal distance, and also between vegetative and reproductive phenotypes and latitudinal gradient (Scrivanti et al., 2014). Vegetative characters and panicle size decrease at higher elevations; however, spikelet characters increase with elevation. Decreasing plant size as an adaptation to increasing elevation by slowing its groth rate is the most efficiently used resource in severe climatic environments (Grime, 1979; Bennington and McGraw, 1995; Hautier et al., 2009). However, the increase in spikelet size along both, altitudinal and latitudinal gradients, has also been documented for other alpine plants (Hautier et al., 2009; Maad et al., 2013), and could be an adaptation to extreme climatic conditions. Abiotic factors such as temperature and precipitation have also had an important role in adaptive characters variation in *Poa scaberula* since it has displayed patterns across the species range (Scrivanti et al., 2014). Furthermore, it has been demonstrated that low temperatures in the coldest period, humidity and seasonality of temperatures influence its distribution at high elevation areas. Vegetative characters increase in size with increasing temperatures and rainfall but reproductive characters decrease in size. Therefore, the phenotypic plasticity induced by environmental conditions allow to *P. scaberula* a broad adaptability under the current climate along altitudinal and latitudinal gradients in the Andes and at high elevation regions in South America. In addition to geographical and climatic factors, biotic factors such as the competition among plant species must be considered, especially in the low lands or environmental disturbances, which could negatively influence the distribution limits of the species, which leads to a reduction of its current distribution area.

Certainly, much of the suitable area of Andean grasslands might disappear due to climate change, anthropogenic practices, overgrazing and the associated erosion in their range (Morrone, 2001; Bradley et al., 2006; Minvielle and Garreaud, 2011; Thibeault et al., 2010; Neukom et al., 2015). Due to the alteration of temperatures and rainfall, high elevation regions are strongly susceptible to global warming, which would have a negative impact on the suitability of the species habitats (Spehn et al., 2010; Báez et al., 2016; Cuyckens et al., 2016). Mountain systems are the most susceptible to global warming; on account of that, rapid changes in temperature drive migrations of species to higher elevations (Spehn et al., 2010). Since plant species richness declines with increasing elevation because geographic area decreases as elevation increases (Körner, 2007; Jump et al., 2011), the number and size of the populations could decrease as the availability of suitable habitat decreases. Therefore, the species would be more susceptible to stochastic extinction (Jump et al., 2011). In addition, the reduction of the area and increase of competitors from lower altitudes -or other forms of habitat modification-could threat the populations that survive in high elevation and latitude gradients (Jump et al., 2011).

The minimum temperatures, rainfall, water vapor pressure and wind speed as well as decreasing land areas along altitudinal and latitudinal gradients, play an important role in controlling biogeographic patterns of *P. scaberula* in South America. Thus, the species distribution modelling can be of great help in predicting the potential habitats to identify the suitable areas where the *P. scaberula* is most sensitive to climate change as well as to human activities. This might contribute also in assessing the conservation status of Andean grassland on a regional scale.

Declarations

Author contribution statement

LIDIA R. SCRIVANTI: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

ANA M. ANTON: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

This work was supported by grants from the Agencia Nacional de Promoción Científica y Tecnológica (PICT, 2014-1095) and Universidad Nacional de Córdoba (SECyT-UNCRes 266/18).

Competing interest statement

The authors declare no conflict of interest.

Additional information

Supplementary content related to this article has been published online at https://doi.org/10.1016/j.heliyon.2020.e05220.

Acknowledgements

We are grateful to the curators of the following herbaria for their generosity in arranging specimen loans: BAA, CORD, LIL, LP, LPB, SI, USM and US. We thank both reviewers for their contribution to the improvement of the manuscript.

References

Abba, A.M., Tognelli, M.F., Seitz, V.P., Bender, J.B., Vizcaíno, S.F., 2012. Distribution of extant xenarthrans (Mammalia: Xenarthra) in Argentina using species distribution models. Mammalia 76, 123–136.
Adhikari, D., Barik, S., Upadhaya, K., 2012. Habitat distribution modelling for reintroduction of *Ilex khasiana* Purk., a critically endangered tree species of northeastern India. Ecol. Eng. 40, 37–43.
Anderson, R.P., Lew, D., Peterson, A.T., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol. Model. 162, 211–232.
Báez, S., Jaramillo, L., Cuesta, F., Donoso, D.A., 2016. Effects of climate change on Andean biodiversity: a synthesis of studies published until 2015. Neotrop. Biodivers. 2, 181–194.
Bennington, C.C., McGraw, J.B., 1995. Natural-selection and ecotypic differentiation in impatiens-pallida. Ecol. Monogr. 65, 303–323.
Bradley, R.S., Vuille, M., Diaz, H.F., Vergara, W., 2006. Threats to water supplies in the tropical Andes. Science 312, 1755–1756.
Cabrera, A.L., 1971. Fitogeografía de la República Argentina. Bol. Soc. Argent. Bot. 14, 1–42.
Calderón Torres, S., Sossa Arango, C., Khoury, C., 2015. Impacto del cambio climático para el 2020 en la distribución potencial de Achira (*Canna indica* L.) en Colombia usando tres modelos de circulación global de la familia de escenarios de emisión A2. Revista Ingeniería y Región 13, 91–102.
Chao-yun, H., Rui, F., Ribeiro, M.C., Le-he, T., Hua-song, W., Jian-feng, Y., Wei-quan, Z., Huan, Y., 2012. Modeling the potential geographic distribution of Black Pepper (*Piper nigrum*) in Asia using GIS tools. J. Integr. Agric. 11, 593–599.
Cuyckens, G.A.E., Christie, D.A., Domic, A.I., Malizia, L.R., Renison, D., 2016. Climate change and the distribution and conservation of the world's highest elevation woodlands in the South American Altiplano. Global Planet. Change 137, 79–87.
De Cauwer, V., Muys, B., Revermann, R., Trabucco, A., 2014. Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis* DC in southern Africa. For. Ecol. Manag. 315, 211–226.
Fick, S.E., Hijmans, R.J., 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol.
Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Giannini, T.C., Takahasi, A., Medeiros, M.C.M.P., Saraiva, A.M., Alves-dos-Santos, I., 2011. Ecological niche modeling and principal component analysis of *Krameria* Loefl. (Krameriaceae). J. Arid Environ. 75, 870–872.
Gomez, J.J., Cassini, M.H., 2015. Environmental predictors of habitat suitability and biogeographical range of Franciscana dolphins (*Pontoporia blainvillei*). Glob. Ecol. Conserv. 3, 90–99.
Graham, B., 2001. Neutral macroecology. Science 293, 2413–2418.
Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815.
Grime, J.P., 1979. Plant Strategies and Vegetation Processes. John Wiley & Sons, New York, p. 222.
Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.
Han, Z., Song, W., Deng, X., Xu, X., 2018. Grassland ecosystem responses to climate change and human activities within the three-river headwaters region of China. Sci. Rep. 8, 9079.
Hautier, Y., Randin, C.F., Stöcklin, J., Guisan, A., 2009. Changes in reproductive investment with altitude in an alpine plant. J. Plant Ecol. 2, 125–134.
Hijmans, R.J., Guarino, L., Mathur, P., 2012. DIVA-GIS. In: A geographic information system for the analysis of species distribution data, Version 7.5.
Jump, A.S., Huang, T.J., Chou, C.H., 2011. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. Ecography 35, 204–210.
Körner, C., 2004. Mountain biodiversity, its causes and function. Ambio 13, 11–17.
Körner, C., 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22 (11), 569–574.
Levsen, N.D., Tiffin, P., Olson, M.S., 2012. Pleistocene speciation in the genus *Populus* (Salicaceae). Syst. Biol. 61, 401–412.
Maad, J., Armbruster, W.S., Fenster, C.B., 2013. Floral size variation in *Campanula rotundifolia* (Campanulaceae) along altitudinal gradients: patterns and possible selective mechanisms. Nord. J. Bot. 31, 361–371.
Minvielle, M., Garreaud, R.D., 2011. Projecting rainfall changes over the south American Altiplano. J. Clim. 24, 4577–4583.
Morrone, J.J., 2001. Biogeografía de América Latina y el Caribe. Manuales & Tesis SEA, nro. 3. Sociedad Entomológica Aragonesa, Zaragoza (España).
Moscoso, V., Albernaz, A.L., de Salomão, R.P., 2013. Niche modelling for twelve plant species (six timber species and six palm trees) in the Amazon region, using collection and field survey data. For. Ecol. Manag. 310, 652–662.
Neukom, R., Rohrer, M., Calanca, P., Salzmann, N., Huggel, C., Acuña, D., Christie, D.A., Morales, M.S., 2015. Facing unprecedented drying of the Central Andes? Precipitation variability over the period AD 1000–2100. Environ. Res. Lett. 10, 084017.
Phillips, S.J., Dudik, M., 2008. Modeling of species distributions with MaxEnt new Extensions and a comprehensive evaluation. Ecography 31, 161–175.
Phillips, S.J., Anderson, R.P., Shapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. Ecol. Model. 190, 231–259.
Reed, T.E., Schindler, D.E., Waples, R.S., 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conserv. Biol. 25, 56–63.
Saatchi, S., Buermann, W., Steege, H., Mori, S., Smith, T.B., 2008. Modeling distribution of Amazonian tree species and diversity using remote sensing measurements. Remote Sens. Environ. 112, 2000–2017.
Salariato, D.L., Zuloaga, F.O., Cano, A., Al-Shehbaz, I.A., 2015. Molecular phylogenetics of tribe Eudemeae (Brassicaceae) and implications for its morphology and distribution. Mol. Phylogenet. Evol. 82, 43–59.
Schwartz, M.W., 2012. Using niche models with climate projections to inform conservation management decisions. Biol. Conserv. 155, 149–156.
Scrivanti, L.R., Mestre, L., Anton, A.M., 2014. Phenotypical variation and taxonomic correlates of five closely related Andean species of Poa (Poaceae) along geographic and climatic gradients. Phytotaxa 183, 121–144.
Spehn, E.M., Rudmann-Maurer, K., Körner, C., 2010. Global Mountain Biodiversity Assessment. GMBA-Diversitas, Basel, Switzerland.
Thibeault, J.M., Seth, A., Garcia, M., 2010. Changing climate in the Bolivian Altiplano: CMIP3 projections for temperature and precipitation extremes. J. Geophys. Res.

Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., Rouget, M., 2005. Niche-based modelling as tool for predicting the risk of alien plant invasions at a global scale. Global Change Biol. 11, 2234–2250.

Timaná de la Flor, M., Cuentas Romero, M.A., 2015. Biogeografía predictiva: técnicas de modelamiento de distribución de especies y su aplicación en el impacto del cambio climático. Espacio y Desarrollo 7, 159–179.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. 17, 1351–1364.

Veblen, T.T., Young, K.R., Orme, A.R., 2007. The Physical Geography of South America. Oxford University Press, New York, USA.

Vedel-Sørensen, M., Tovaranonte, J., Bøcher, P.K., Balslev, H., Barfod, A.S., 2013. Spatial distribution and environmental preferences of 10 economically important forest palms in western South America. For. Ecol. Manag. 307, 284–292.

Zhang, Y.B., Ma, K.P., 2008. Geographic distribution patterns and status assessment of threatened plants in China. Biodivers. Conserv. 17, 1783–1798.