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

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**A B S T R A C T**

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 km² 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 hardness, 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...
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 km² 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 vapour pressure. The layers of WorldClim images were downloaded in geotiff 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 multicollinearity, 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).

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
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 overlaid 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 ± 0.003 and AUC train = 0.959 ± 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 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 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 km² 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 km², followed by the low suitability class with

### 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.
In the southern tip of the continent (Argentina-Chile) rainfall where the climate is more humid and colder (Cabrera, 1971; Minvielle and Garreaud, 2011; Thibeault et al., 2010; Neukom et al., 2006; Minvielle and Garreaud, 2011). 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 panicule size decrease at higher elevations; however, spikelet characters increase with elevation. Decreasing plant size as an adaptation to increasing elevation by slowing its growth 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; Maal 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 Poa 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 Garreau, 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 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).

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 (km²) |
|---------------------|------------|
| Total potential area| 162.747    |
| Low                 | 98.919     |
| Medium              | 48.744     |
| High                | 12.348     |
| Very high           | 2736       |

98.919 km². The high suitability area covers 12.348 km², and the very adequate area 23736 km².

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 km² 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; Levens et al., 2012; Vedel-Sørensen et al., 2013; De Cauwer et al., 2014; Salaraito 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 Neuquén, 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

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would have a negative impact on the suitability of the species habitats (Sphn 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 (Sphn 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.

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