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GEOGRAPHICAL DISTRIBUTION AND ESTIMATION OF THE CLIMATIC TOLERANCE RANGES OF *POA SCABERULA* (POACEAE) IN SOUTH AMERICA

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Abstract

This paper analyzes the potential distribution of *Poa scaberula* (Poaceae) in South America. The study area includes the Andes and the Sierras Pampeanas of Central Argentina. Based on records of occurrence and environmental data, we modeled the potential distribution and identified the areas of high probability of presence, evaluating the contribution of climatic variables to the model, and estimating the ranges of climate tolerance. The species distribution models showed that *P. scaberula* has a suitable habitat of ca. 289,062 km^2 in the study region. We identified annual minimum temperature as the critical factor shaping *P. scaberula*. Moreover, the species shows a broad ecological tolerance, being able to withstand extreme conditions of low temperature (–11.8ºC) and rainfall (<664.5 mm annual) related to elevational and latitudinal gradients; these gradients strongly contribute to the delimitation of the species distribution in South America.

Key words: Andes, Climatic tolerance, Climatic variables, Potential distribution, Species distribution model.

Introduction

The geographical range of a species is limited by abiotic and biotic factors (Lewis *et al*., 2017). Moreover, the distribution area of a species is restricted to its environmental tolerance, as a consequence of different evolutionary processes that determine its presence in certain spaces (Wiens & Graham, 2005). The study of climatic variables can shed some light on the climatic tolerance of a species and therefore help to understand the limits of its spatial distribution (Wiens, 2004). Distribution data provide a good approximation of climatic tolerance of widespread species (Curtis & Bradley, 2016). Species distribution modeling (SDM) has become a useful tool to identify the environmental conditions that characterize the bioclimatic envelope of a species (Gomez & Cassini, 2015; Curtis & Bradley, 2016).

The genus *Poa* L. includes ca. 575 species distributed in temperate and cold regions of both hemispheres. Molecular phylogenetic studies indicate the monophyletic origin of the genus and recognize five subgenera; one of the -subgenus Poa- is the largest and contains two supersections: Poa and Homalopoa (Dumort.) Soreng & L. J. Gillespie. Most of the endemic species of South America belong to supersection Homalopoa, which includes eight sections: Acutifoliae Pilg. ex Potztal, Anthochloa Soreng & Gillespie, Dasypoa (Pilg.) Soreng, Dioicopoa Desvaux, Dissanthelium (Trin.) Refulio, Homalopoa Dumort., Madropoa Soreng, Monandropoa Parodi and the informal "Punapoa" group.

Poa scaberula Hooker f. is a member of section Dasypoa (Gillespie & Soreng, 2005; Gillespie *et al*., 2007, 2008). It has a disjunct distribution between Mesoamerica and South America, inhabits in moist soils and shady places, and is common in pastures and fertile soils in high mountain meadows. In South America, it is widely distributed from the northern Andes to the southern tip of the continent, occupying regions of high altitudes and latitudes along different geographical and climatic gradients. *Poa scaberula* is characterized by a woolly callus, lemmas with cilia in the middle or basal portion of the keel, perfect/hermaphroditic flowers (monoclines), small oval anthers and caryopsis strongly adhered to the palea (Fig. 1). In South America, several specimens of *P. scaberula*, *Poa anfamensis* Negrito & Anton, *P. dactyliformis* Steud., *P. maullinica* Phil., *P. micranthera* Hack. and *P. parviceps* Hack., exhibit high morphological variability; therefore, they were described as cryptic taxa, which led to delimitation problems due to phenotypic and spatial overlap. Systematic studies of closely related species to *P. scaberula* revealed that the observed polymorphism responded to environmental gradients (Scrivanti *et al*., 2014). Nevertheless, the distribution limits of *P. scaberula* are still unclear, and several controversies appear in the literature about its presence, especially in northern countries of South America. Soreng *et al*., (2003), Soreng & Peterson (2012) and Scrivanti *et al*., (2014) reconsidered about the presence of *P. scaberula* in Colombia; however, there is no material that confirms its presence there.

The aim of this study was to investigate the effects of temperature and precipitation ranges on the species distribution and estimate the ranges of climate tolerance of the species. We used species distribution modelling (SDM) to construct the bioclimatic envelope, based on an exhaustive review of presence data. We expect that our results will shed light on the geographical and climatic distribution of *P. scaberula* in South America.

Material and Methods

Study area and occurrence points: The study area covers the Andes from Ecuador to the Patagonian Andes of Argentina and Chile. Elevation ranges from 0 to 4600 m above sea level, average annual precipitation from 43 to 2600 mm and average temperature from 3.43 to 24.76°C (Fick & Hijmans, 2017). The total distribution of *P. scaberula* based on geographical coordinates corresponding to collection site ranges from 1°14' to 52°51' S, and 79°15' to 64°25' W (Fig. 2).

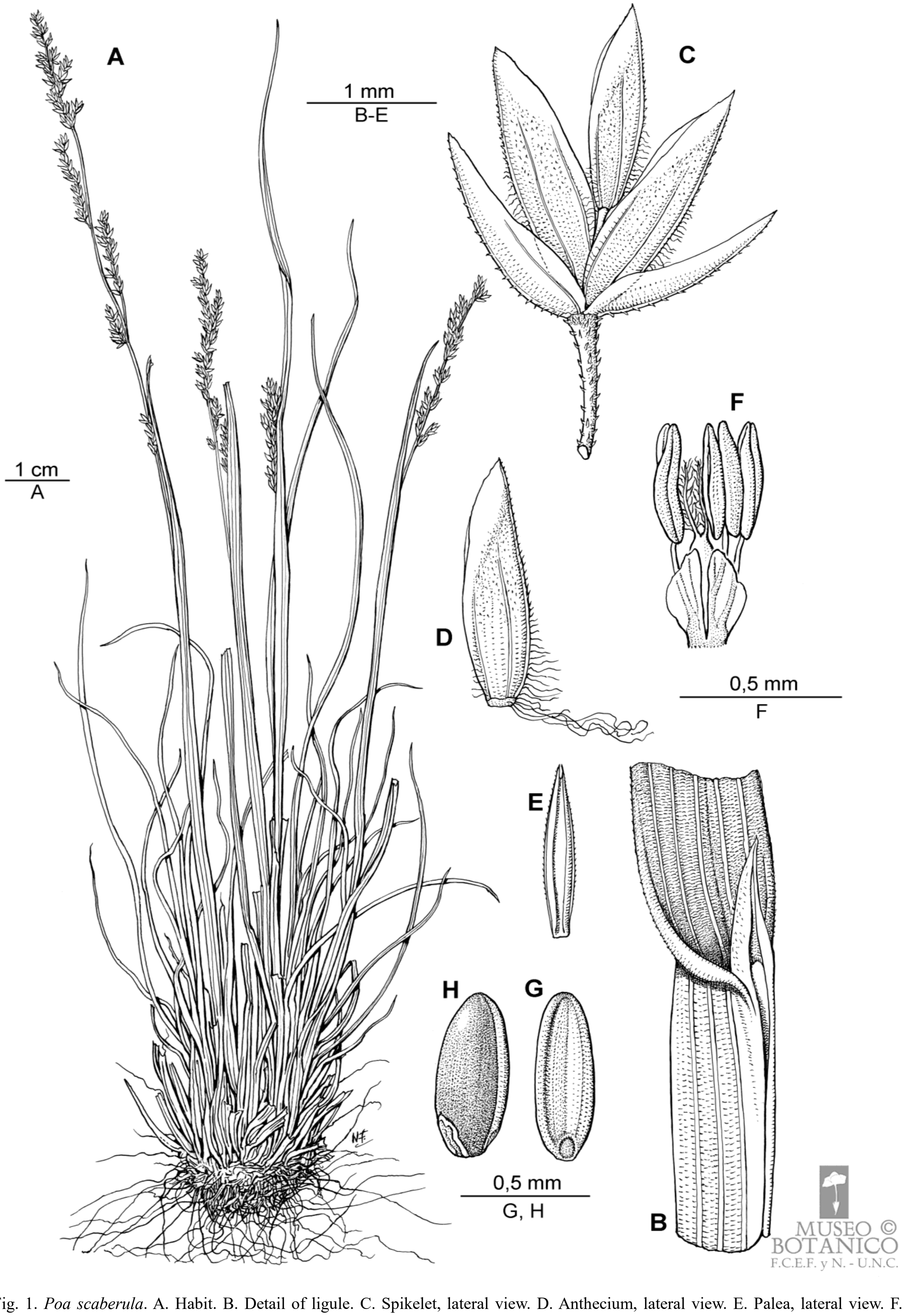

Fig. 1. *Poa scaberula*. A. Habit. B. Detail of ligule. C. Spikelet, lateral view. D. Anthecium, lateral view. E. Palea, lateral view. F. Hermaphrodite flower with lodicules. G-H. Carypsis, dorsal and lateral views. Illustrator: Nidia de Flury.

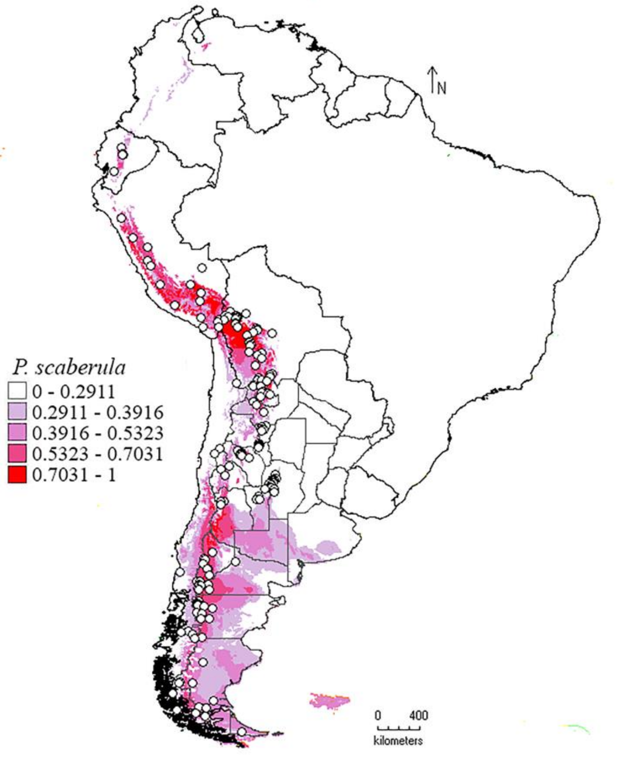

Fig. 2. Potential distribution map for *P. scaberula* in South America. Darker areas represent regions with higher relative probabilities of occurrence. 0 indicates completely unsuitable and 1 indicates optimal.

Occurrence records of *P. scaberula* were obtained through an exhaustive review of herbarium material (BA, BAA, CORD, F, HUSA, K, LIL, LP, LPB, MO, NY, P, S, SI, U, UCONN, US, USM, W, WU) and from Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). We verified the identification of the specimens and unreliable material were not incorporated. Records before 1950 were informative but were not incorporated in model fit because the current climate layers cover from 1950 to 2000 (Fick & Hijmans, 2017). When the geographic locations of the specimens were not available they were determined manually using Google Earth. The locality of each specimen was transformed into geographic coordinates using WGS84 datum. The locations of each specimen were visualized in DIVA-GIS 7.5 (Hijmans *et al*., 2012). A total of 297 *P. scaberula* presence records were collected (see Material Examined), after removing records that were less than 1 km apart, we retained 178 points that were used to build for species distribution models.

Obtaining, cutting and selecting environmental variables: Climate data was obtained from the Worldclim database version 2 contained data from 1950 to 2000 (http://www.worldclim.org). We used annual mean temperature (AMT) (ºC), annual maximum temperature (AMAXT) (ºC), annual minimum temperature (AMINT) (ºC) and annual mean precipitation (AMP) (mm) variables at a resolution of 5 arc-minutes, the selection of these variables is based on previous studies about the phenotypic variability of *P. scaberula* in relation to environmental gradients (Scrivanti *et al*., 2014). The layers of World Clim images were downloaded in geotif format and converted to ASCII raster grids in QGis 2.14.0. In the QGIS program, the layers were cut in a geographic region that included South America (long –91.45 to –29.30, lat 13.21 to –58.42), so including the entire known range of the species and potential areas of distribution.

Model building and evaluation of SDM performance: To develop the current species distribution models, 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 regulization parameter =1; default prevalence= 0.5; replicated run type = subsample. Of the 297 records, 70% were used for model training and 30% for testing. To validate the model robustness, 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, because avoid incorrect interpretation of models. Model robustness has been evaluated with the area under the curve (AUC) of the receiver operating characteristic (ROC) plot was employed to evaluate model performance (Fielging & Bell, 1997; Phillips *et al*., 2006; Phillips & Dudík, 2008). The values of the Area Under the Curve (AUC) of the Receiver Operating Characteristic (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. This threshold assumes an error in 10% of the presence records and therefore excludes the 10% with the lowest probability value. The 10th percentile is commonly used in conservation studies (Abba *et al*., 2012). We geographically projected the *P. scaberula* presence model and divided probabilities 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, the 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.

Material Examined

ARGENTINA. **Catamarca.** Depto. Ambato, 27º58'3.4"S 66º3'51.8"W, *Hunziker 19830* (CORD); 28º1'0.1"S 65º54'50"W, 18-I-1968, *Hunziker 19815* (CORD); 28-I-1968, *Hunziker 19702, 19830, 19993* (CORD); 20-II-1971, *Hunziker 20799* (CORD); 28-III-1968, *Hunziker 20067* (CORD); 14-I-1973, *Hunziker 22245* (CORD); 28º10'48"S 65º59'24"W, 15-I-2000, *Negritto 122*

(CORD); 28º10'48.4"S 65º59'26.2"W, 26-XII-1971, *Hunziker 21687* (CORD); 28º10'49.1"S 66º0'54.7"W, 14-I-1973, *Hunziker 22246* (CORD); 28º10'59.9"S 65º57'1.8"W, *Hunziker 20799* (CORD); 28º11'18.6"S 65º59'25.4"W, 22-II-1971, *Hunziker 20978, 20972, 20912, 20967* (CORD); 28º13'14.2"S 66º1'5.5"W, 21-II-1971, *Hunziker 20901* (CORD); 28º14'21.8"S 66º1'2.3"W, 21-II-1971, *Hunziker 20843* (CORD); 28º14'27.2"S 66º1'5.5"W, 21-II-1971, *Hunziker 20835* (CORD); 28º15'3.2"S 66º1'59.9"W, 21-II-1971, *Hunziker 20867* (CORD); 28º16'1.6"S 65º59'57.1"W, 28-I-1968, *Hunziker 19702a* (CORD); 28º16'23.9"S 66º2'34.8"W, 28-III-1968, *Hunziker 20040* (CORD); 28º16'26.4"S 66º1'24.2"W, *Hunziker 19815* (CORD); 28º17'14.3"S 66º1'42.2"W, *Hunziker 20067* (CORD); 28º19'26.8"S 66º1'18.8"W, *Hunziker 19993* (CORD).

Chubut. Depto. Carranleufú, 43º34'36.5"S 71º41'29.4"W, *Spegazzini 905* (LP). Depto. Cushamen, 42º31'34.7"S 71º31'17.8"W, *Illín 259* (US). Depto. Futaleufú, 23º28'8"S 65º0'36"W, 01-III-1940, *Burkart 11893* (SI); 42º45'56"S 71º41'45.3"W, 08-III-1952, *Beetle 242* (MO); 42º48'16.4"S 71º38'36.7"W, 03-II-1955, *Burkart 19772* (SI); 42º48'41.8"S 71º38'58.9"W, 31-III-1952, *Beetle 427* (MO); 42º48'52.6"S 71º42'46.8"W, 09-I-1948, *Soriano 2998* (SI); 42º49'1.9"S 71º42'56.5"W, *Burkart 19835* (US); 42º49'23.6"S 71º30'45"W, 30-III-1952, *Beetle 389* (MO); 42º51'33.3"S 71º37'59.3"W, 06-II-1955, *Burkart 19835* (MO, US); 42º53'12"S 71º36'20.1"W, 06-II-1955, *Burkart 19848* (SI); 43ºS 71ºW, 15-II-1901, *Illin 42* (US). Depto. Languiñeo, 43º12'38.2"S 70º14'25.1"W, 07-II-1988, *Nicora 9391* (SI); 43º40'0.1"S 71º15'0"W, 01-II-1947, *Soriano 2548* (SI). Depto. Río Senguer, 45º54'53.1"S 71º13'23.9"W, 29-IV-1925, *Bettfreund 2636* (MO). Depto. Tehuelches, 40º10'55.9"S 70º32'26.2"W, 01-II-1988, *Nicora 9307* (SI); 09-II-1989, *Nicora 9553* (SI); 03-II-1989, *Nicora 9491* (SI); 04-II-1995, *Nicora 10100* (SI); 44º10'48"S 70º32'24"W, 30-I-1992, *Nicora 9682* (SI); 44º11'6.4"S 71º20'37.7"W, 10-I-1998, *Nicora 10292* (MO). **Córdoba**. Depto. Calamuchita, 31º59'19"S 64º55'54.5"W, 15-I-1952, *Hunziker 9627* (CORD); 32º3'56.2"S 64º55'21"W, *Hunziker 9558* (CORD); 32º11'3.8"S 64º37'0.8"W, 13-I-1952, *Hunziker 9558* (CORD). Depto. Cruz del Eje, 31º17'45.6"S 64º43'41.2"W, 22-XII-1909, *Stuckert 20630, 20707, 20848, 20879, 20893, 21091*(CORD); 31º19'59.9"S 64º46'0.1"W, 21-XII-1909, *Stuckert 20848* (MO); 31º20'12.1"S 64º37'53.4"W, 19-XII-1909, *Stuckert 20739, 20801, 20803, 20806* (CORD); 31º20'31.6"S 64º44'26.9"W, 19-XII-1909, *Stuckert 21017* (CORD). Depto. Punilla, 30º50'39.8"S 64º29'57.5"W, 17-III-1917, *Hosseus s.n.* (CORD 729); 31º15'52.2"S 64º25'48.4"W, 12-XII-1885, *Kurtz 2929* (CORD); 31º11'55"S 64º35'1"W, 14-I-1940, *Burakrt 10204* (CORD); 01-II-1963, *Hunziker 16304* (CORD); 15-I-1965, *Hunziker 18025* (CORD); 31º19'58.1"S 64º36'14.8"W, *Hunziker 20997* (CORD); 20-XII-1909, *Stuckert 20999*, *21000, 21004* (CORD); 31º23'25.4"S 64º43'6.2"W, 25-III-1886, *Kurtz 3856b* (CORD); *Doering 15577* (CORD); 31º24'14.4"S 64º46'49.4"W, *Hieronymus s.n.* (CORD); 31º25'27.1"S 64º48'34.6"W, *Doering s.n.* (CORD 15616); 31º25'48.4"S 64º48'51.8"W, *Doering 26* (CORD); 31º25'50.5"S 64º48'49.7"W, 01-XII-1960, *Hunziker 15616* (CORD); 31º26'12.5"S 64º48'41"W, 01-I-1908, *Kurtz 15661* (CORD); 31º36'33.8"S 64º45'27"W, *Meyer 15536a* (LIL); 31º36'41.2"S 64º50'32.9"W, 29-XII-1935, *Burkart 7225* (SI); 31º37'21.7"S 64º40'41.2"W, *Hunziker 16304* (CORD); 31º40'54.6"S 64º50'12.9"W, *Burkart s.n.* (SI 265345). Depto. San Alberto, 31º31'49.1"S 64º51'51.8"W, 01-IV-1971, *Luti 5214* (CORD); 31º38'40.6"S 64º43'32.2"W, *Hieronymus s.n.* (CORD 471); 31º41'29"S 65º6'5"W, 19-III-1971, *Luti 5075* (CORD); 02-VII-1997, *Cabido 397* (CORD); 31º50'24"S 64º51'36"W, *Parodi 7493* (BAA); 32º2'43.1"S 64º56'16.1"W, *Cabido s.n.* (CORD 397); 32º26'48.1"S 64º37'26"W, 26-XI-2009, *Cantero 5363* (CORD). **Jujuy**. Depto. Cochinoca, 22º43'60"S 65º49'60"W, 09-II-1960, *Meyer 21221* (UCONN). Depto. Humahuaca, 23º12'36"S 65º41'24"W, 01-IV-1965, *Fernández 50* (BAA); 06-III-1965, *Fernández 1007* (BAA); *Buthsatz s.n.* (BAA 14572). Depto. Rinconada, 22º35'28"S 66º26'48.8"W, 01-II-1964, *Schwabe 908* (CORD); 23º17'20.4"S 65º44'1.7"W, *s.n.* (BAA 7148). Depto. Santa Catalina, 21º56'24.7"S 66º3'1.8"W, 21-I-1901, *Kurtz 11483* (CORD). Depto. Susques, 24º5'55"S 66º28'53"W, *Werner 211* (LP). Depto. Tumbaya, 23º39'1.4"S 65º49'4.4"W, 18-II-1991, *Peterson 10349* (US). Depto. Valle Grande, 23º19'0.1"S 65º7'59.9"W, 01-III-1940, *Burkart 11912* (MO). Depto. Yaví, 22º6'30.8"S 65º46'25.5"W, 10-II-1995, *Deginani 583* (SI); s.d., *Cabrera 7838* (BAA). **La Rioja**. Depto. Aguas Negras, 29º5'54.6"S 67º35'37.7"W, *Calderón 1011* (BAA). Depto. Chilecito, 29º17'35.5"S 66º56'35.2"W, *Morello 5230* (LP). Depto. Famatina, 26º44'28"S 65º35'55"W, *Calderón 1171* (BAA); 28º39'36"S 67º43'59.9"W, *Kurtz 14972a*, *15028* (CORD); 28º40'16"S 67º54'58"W, *Krapovickas 6265* (CORD); 28º52'1.9"S 67º34'12.4"W, 21-III-1906, *Kurtz 13993* (CORD); 28º53'24.4"S 67º39'47.9"W, *Kurtz 13993* (CORD); 28º57'16.2"S 67º38'38.4"W, 15/20-I-1879, *Hieronymus s.n.* (CORD 670); 28º54'58.6"S 67º40'42.7"W, 05-II-1927, *Parodi 8052* (BAA); 28º55'27.5"S 67º31'12.7"W, 03-IV-1949, *Krapovickas 6265* (CORD); 28º58'47.1"S 67º42'57.3"W, 13-I-1976, *Cabrera 27194* (MO); 28º58'48"S 67º43'12"W, *Cabrera 27191* (MO).

Mendoza. Depto. Tunuyán, 33º36'36''S 69º31'12''W, 20-III-1935, *Ruiz Leal 3207* (SI); 33º36'46.1''S 69º31'27.8''W, 07-XII-1947, *Ruiz Leal 11414* (BAA). Depto. Tupungato, 33º19'48''S 69º14'24''W, 17-I-1955, *Covas 3194* (SI); 33º22'20.6''S 69º28'19.6''W, *Melis 79* (US). **Neuquén**. Depto. Catan Lil, 39º32'22.2''S 70º37'15.6''W, 28-I-1965, *Rúgolo de Agrasar 356* (MO). Depto. Loncopue, 38º1'12''S 70º13'12''W, *Rúgolo de Agrasar 125* (BAA); 39º35'20.8''S 70º42'25.6''W, *Dawson 1174* (LP). Depto. Los Lagos, 38º55'33.2''S 68º8'57.8''W, 19-XII-1939, *Diem 218* (US); 40º43'55''S 71º40'30.5''W, 11-XII-1942, *Diem 440* (CORD); 40º45'19.1''S 71º26'29''W, 15-XII-1942; *Diem 455* (SI). Depto. Picunches, 38º39'9.4''S 71º0'21.2''W, 01-II-1920, *Parodi 3164* (US); 38º40'0''S 70º54'0''W, *Burkart s.n.* (SI 265200). **Río Negro**. Depto. Bariloche, 41º3'2.2''S 71º32'11.4''W, 16-II-1941, *Maldonado 600b* (US); 41º3'27.4''S 71º31'51.6''W, 16-II-1941, *Maldonado 600* (US); 41º7'46.6''S 71º16'7.3''W, *Cabrera 113* (LP); 41º25'48''S 71º32'60''W, *Parodi 11435* (BAA); 41º30'45''S 70º31'50.2''W, *Petersen 17331* (LP); 41º30'45.4''S 71º30'50.8''W, *Peterson 17331* (US). Depto. Pilcaniyeu, 40º58'12''S 70º36'36''W, 09-I-1964, *Vallerini 431* (SI). **Salta**. Depto. Chicoana, 25º6'38.9''S 65º35'25.1''W, 10-II-1996, *Sulekic s.n.* (SI 112867). Depto. Los Andes, 24º27'52.9''S 66º12'47.9''W, 24-III-2006, *Peterson 19538* (US). **San Juan**. Depto. Calingasta, 30º5'6.7''S 68º41'21.8''W, 16-I-1995, *Ruthsatz -1* (SI). Depto. Iglesias, 28º26'2''S 69º33'39.2''W, 23-XI-1981, *Nicora 8309* (SI); 30º23'48.5''S 69º30'33.8''W, *Carrizo 3* (BAA). Depto. Ullum, 30º57'0''S 69º4'48''W, 10-II-2000, *Kiesling 9446* (SI). **San Luis**. Depto. Coronel Pringles, 32º51'45''S 66º0'14''W, *Anderson 2007* (CORD). Depto. Junín, 32º8'33'S 65º24'38.2''W, 09-II-1956, *Hunziker 11807* (CORD); 33º8'51.7''S 66º12'54.7''W, *Hunziker 11807* (CORD). Depto. Santa Cruz: Guer Aike, 50º7'12''S 73º18'36'', 16-II-2009, *Giussani 403* (SI); 51º44'19.3''S 70º9'34.2''W, 17-I- 2003, *Peterson 17091* (US); 51º44'31.9''S 70º9'56.9''W, *Peterson 17091* (US). Depto. Lago Argentino, 49º58'34.9''S 73º13'54.1'', 19-I-1967, *Boelcke 12581* (MO, SI); 50º8'56.8''S 72º3'47.5''W, 22-II-1970, *Nicora 7552* (MO). Depto. Río Chico, 48º13'12''S 71º7'12''W, *Boelcke 12901* (BAA). **Tucumán**. Depto. Tafí del Valle, 26º35'47.1''S 65º46'13.3''W, 05-X-1904, *Lillo 3514* (LIL); 05-II-1907, *Dinelli 526* (BAA); 27-I-1933, *Parodi 10776* (BAA);

26º36'36''S 65º52'12''W, 13-I-1963, *De la Sota 2736* (BAA); 19-I-1964, *Giusti 3845* (BAA); 26º44'27.2''S 65º46'28.6''W, 21-III- 2006, *Peterson 19464* (US); 26º45'7.1''S 65º32'20.4''W, 24-I-1907, *Lillo 5468* (LIL, US); 26º50'3.1''S 65º47'15''W, *Lillo 3514* (LIL); 29º0'22.7''S 67º42'1.4''W, *Lillo 5468b* (LIL). Depto. Trancas, 26º19'9.8''S 65º24'15.1''W, 17-II-1912, *Lillo 11474* (W, SI, BAA); 26º24'38.5''S 65º42'2.6''W, 17-II-1912, *Rodríguez 575* (SI); 26º40'59.9''S 65º43'36.1''W, 17-II-1912, *Stuckert 22531* (US). **Tierra del Fuego**. Depto. Ushuaia, 54º36'9.4''S 67º35'9.3''W, *Guiñazú 256* (BAA).

BOLIVIA. **Cochabamba**. Depto. Ayopaya, 17º17'8.9"S 66º12'42.8"W, *Candia 3* (LPB). Depto.Carrasco, 17º48'41"S 64º46'5"W, 16-IV-2005, *Altamirano 473* (MO). Depto.Cercado, 17º19'8"S 66º13'47.6"W, 06-I-1924, *Hitchcock 22865* (US); 17º27'18.9"S 66º8'10.4"W, 06-I-1924, *Hitchcock 22859* (US); 17º29'15.6"S 66º5'27.2"W, 06-I-1924, *Hitchcock 22860* (US). Depto.Tequina, 17º20'6.4"S 66º11'36.6"W, *Hitchcock 22859, 22865* (US); 17º20'12.5"S 66º11'12.1"W, *Hitchcock 22860* (US). Depto. La Paz, Aroma, 16º55'17.9"S 68º6'27.9"W, 04-III-1993, *Peterson 12616b* (US); 16º55'42.6"S 68º6'34.6"W, 04-III-1993, *Peterson 12627* (US); 17º13'59.5"S 67º58'20.3"W, 09-III-1973, *Lara 20i* (MO). La Paz, 16º9'42.5"S 69º5'30.5"W, *Buchtien 8831* (US); 16º9'45.4"S 69º5'31.9"W, *Buchtien 370* (US); 16º13'18.9"S 68º51'12.4"W, *Steubel 60F* (US); 16º29'14.6"S 68º5'57.5"W, *Buchtien 8844* (US); 17º42'37.8"S 66º33'2.2"W, 17-II-1926, *Tate 130* (US). Depto. Larecaja, 15º46'9.55"S 68º38'48.5"W, 18-II-1859, *Mandon 1336* (US). Depto. Loayza, 16º50'42.4"S 68º9'11.2"W, 04-III-1993, *Peterson 12646* (US). Depto. Murillo, 15º59'7.3"S 67º11'41.8"W, 20-XII-1923, *Hitchcock 22598* (US); 16º8'60"S 68º7'0"W, 17-XI-1987, *Solomon 17448* (MO); 16º9'32.1"S 69º5'18.3"W, 24-II-1931, *Buchtien 8831* (US); 16º12'0"S 68º6'60"W, 08-III-1987, *Solomon 16247* (MO, LPB); 16º14'10"S 68º50'43.9"W, 01-I-1958, *Bettfreund s.n.* (MO 239390); 16º18'7.9"S 67º54'27"W, 0-II-1921, *Asplund 6466* (US); 16º19'20.6"S 67º55'1"W, 23-I-1931, *Buchtien 8539* (SI, US); 16º19'58.7"S 68º2'28.8"W, 23-IV-1988, *Fournet 795* (U); 16º27'46.6"S 68º6'6.3"W, 09-II-1931, *Buchtien 8844* (US); 16º28'54.4"S 68º7'1.4"W, 19-I-1921, *Asplund 2037* (S). Depto. Nor Yungas, 16º18'60"S 67º57'0"W, 01-I-1958, *Hitchcock 22761* (MO). Depto. Pongo, 16º19'47.3"S 67º56'9.6"W, *s.n.* (US 1388927). **Oruro**. Depto. Abaroa, 18º53'60"S 66º45'60"W, 31-III-1921, *Asplund 6478* (MO). Depto. Challapata, 18º54'2.5"S 66º45'0.7"W, *s.n.* (US 1099682); 18º54'20.4"S 66º45'18.6"W, 31-I-1921, *Asplund 3298* (S). Depto. Pagador, 17º58'34"S 67º7'28.2"W, 08-III-1993, *Peterson 12772b* (LPB), 16º12'24.5"S 68º0'59"W, *s.n.* (US 1099683); 18º34'46.2"S 66º51'54"W, 08-III-1993, *Peterson 12761, 12772* (US); 18º40'18.5"S 66º52'39.4"W, *Peterson 12772b* (LPB). **Potosí**. Depto. Frías, 19º35'21.1"S 65º45'12.6"W, *Wood 10753* (LPB); 19º37'44.8"S 65º46'14.2"W, 30-III-1993, *Peterson 13148* (US). Depto. Quijarro, 19º29'5.6"S 66º52'39.4"W, 10-III-1993, *Peterson 12816* (US). Depto. San Felipe, 20º46'3.7"S 66º17'24"W, *Hitchcock 22598a, b* (US); *Buchtien 8539* (SI). **Tarija**. Depto. José María Aviléz, 21º46'59.9"S 64º57'0"W, *Beck 27410* (LPB). Depto. Tarija, 21º32'28.5"S 64º46'11"W, 01-I-1958, *Bettfreund s.n.* (MO 3026490); 21º36'47.2"S 64º56'51.6"W, 12-III-1905, *Fiebrig 2936* (US).

CHILE. **Región Antofagasta**. Prov. Antofagasta, 22º22'34"S 68º1'7"W, 19-III- 2001, *Peterson 15575* (US). **Región Atacama.** Prov. Huasco, Vallenar, 28º53'8.5"S 70º2'39.8"W, 08-I-1926, *Johnston 6024* (US). **Región Aysén.** Prov. Aysén, 45º21'7.9"S 72º24'39.9"W, 23-II-1897, *Dusén 28* (US); 45º23'27.2"S 73º9'29.5"W, *Dusén s.n.* (US 1161179); 45º33'47.1"S 72º3'37.5"W, 18-I-1946, *Barros 5639* (US); 45º35'48.5"S 72º2'28.7"W, *Barros 5638, 5639, 5640, 5644* (US); 45º29'35.2"S 71º52'53"W, 06-II-2002, *Soreng 7304* (US). **Región Magallanes.** Prov. Magallanes, 51º6'0"S 73º50'60"W, 21-II-2002, *Soreng 7350* (US), *Peterson 7350* (US); 52º17'56"S 71º30'46.4"W, *s.n.* (LP 7908), *Spegazzini 863* (LP); 52º25'16.5"S 70º48'33.4"W, 01-III-1917, *Bonarelli 149* (SI); 52º37'26.8"S 73º32'20"W, *Anderson s.n.* (US1717778), *Philippi 415* (US); 52º51'40"S 71º47'52.8"W, *s.n.* (US 1761387); 53º8'29.4"S 70º57'38.2"W, 08-III-1867, *Cunningham s.n.* (K 000308322). Punta Arenas, 53º8'41.3"S 70º54'32.4"W, 08-III-1867, *King s.n.* (K 000433921); 53º8'60"S 70º54'60"W, 01-I-1853, *Lechler 1151* (MO). **Región de Los Ríos.** Prov. Valdivia, Los Ríos, 39º49'37.8"S 73º11'56.5"W, 01-I-1901, *Buchtien s.n.* (US 1099673).

ECUADOR. **Azuay**, 2º48'58"S 79º15'29.2"W, *Peterson 8856* (US). **Cotopaxi.** León, 0º37'9.4"S 78º34'32.1"W, 26-V-1939, *Asplund 6477* (MO). **Tungurahua**. Patate, 1º15'0"S 78º30'0"W, *Asplund 7968* (US); 1º17'22.4"S 78º23'43.1"W, 14-XII-1944, *Acosta Solís 9324* (US); 1º19'26.6"S 78º29'3.9"W, 01-VIII- 1939, *Asplund 7968* (US).

PERÚ. **Ancash**. Prov. Yungay, 8º58'60"S 77º33'60"W, 12-I-1985, *Smith 9096* (MO). **Arequipa**. Prov. Chiguata, 16º24'10"S 71º16'28.4"W, *Rodríguez 5470* (HUSA). **Ayacucho**. Prov. Parinacochas, 15º14'47"S 73º41'35.2"W, 01-III-2002, *Peterson 16350a* (US). **Cajamarca**. Prov. Cajamarca, 7º10'52"S 78º34'47.6"W, 24-III-1985, *Sánchez Vega 3730* (F). **Cuzco**. Prov. Cuzco, 14º47'30.8"S 71º24'36.7"W, 24-III-1956, *Vargas 11190* (US). Urubamba, 13º15'4.8"S 72º14'28.7"W, 05-XII-1923, *Hitchcock 22540* (US). Ollaantaytambo, 13º16'26.4"S 72º16'7.3"W, *Hitchcock 22540* (US). Espinar, 14º2'2.8"S 71º20'48.8"W, *Vargas 11202* (US). **Huancavelica**. Prov. Huaytara, 13º19'24.2"S 75º0'56.5"W, 13-III-2007, *Peterson 20431a* (US). **Junín**. Prov. Junín, 11º3'46.8"S 76º9'46.1"W, *Peterson 35* (USM); 11º31'43.7"S 75º53'40.9"W, 25-X-1923, *Hitchcock 22186* (US). **Madre de Dios**. Prov. Manu, 11º45'0"S 71º9'60"W, 10-VIII-1986, *Núñez Vargas 6706* (MO). **Moquegua**. Prov. Mariscal, 17º16'1.9"S 71º7'56.3"W, 28-II-1999, *Peterson 14550* (US). **Pachitea**. Prov. Huanuco, 9º52'49.3"S 76º9'14.9"W, 08-IX-1940, *Asplund 13521* (S). **Puno**. Prov. El Collao, 16º34'26.4"S 69º40'40.4"W, 03-III-1999, *Peterson 14612* (US); 16º45'17.6"S 69º45'39.2"W, 02-III-1999, *Peterson 14599* (US). Chucuito, 16º34'58.8"S 69º13'44"W, 05-III-1999, *Peterson 14639* (US). **Tacna**. Prov. Tarata, 17º11'58.7"S 69º39'34.8"W, 10-III-1999, *Peterson 14719* (US).

Results

Species distribution models show that *Poa scaberula* is widely distributed in South America along the Andes and mountainous areas from sea level to 4620 m above sea level, from approximately 1º N to 52º S, being present in Ecuador, Peru, Bolivia, Chile and Argentina (Fig. 2). The model calibration test for *P. scaberula* yielded satisfactory results with AUC $_{Train}$ = 0.938 ± 0.002 and AUC$_{Test}$= 0.925 ± 0.011. Annual minimum temperature (AMINT) was the most influential variable, with 82 % contribution to the MaxEnt model, whereas the remaining input variables contributed 18 % to the habitat model of the species. Considering the permutation importance, annual minimum temperature (AMINT) and annual mean precipitation (AMP) together had the maximum influence on the habitat model, with 96.2 % contribution (Table 1).

Spatial distributions with high suitability thresholds were located between 1000 and 4620 m above sea level in Peru, Bolivia and northwest of Argentina, and at lower elevations in mountains in the center and south of Argentina and Chile (Fig. 2), with annual minimum temperatures between –11.8 ºC and 2.5 ºC, and annual precipitation between 43 mm and 993.8 mm (Fig. 3).

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.

Code	Environmental variables	Contribution (%)	Permutation importance (%)
AMT	Annual mean temperature (ºC)	4.8	0.7
AMAXT	Annual maximum temperature (ºC)	4.1	3.1
AMINT	Annual minimum temperature (ºC)	82	91.8
AMP	Annual precipitation (mm)	9.1	4.4

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

Habitat suitability	Area (km^2)
Total potential area	289,062
Low	94,500
Medium	112,482
High	58,842
Very high	23,238

A total potential area of 289,062 km^2 along Andes and mountainous zones of South America was predicted to be suitable for *P. scaberula* (Table 2). Most of the areas fall into the medium suitability class, covering 112,482 km^2, followed by the low suitability class, with 94,500 km^2. The areas of high and very adequate suitability cover 58,842 km^2, and 23,238 km^2, respectively. The current model is consistent with our knowledge about the species' current distribution, except for Colombia, Venezuela, and Sierras de la Ventana and Tandil in southern Buenos Aires province (Argentina), where the species has not been recorded so far.

Along the elevational gradient, 74.41% of the specimens are distributed above 1000 m above sea level, with 1% above 4500 m above sea level, 17.17% between 500 and 1000 m, and 7.41 % below 500 m (Fig. 4). Areas above 1000 m above sea level include the Northern Andes in Ecuador, the Central Andes from Peru up to the parallel 28ºS and Sierras Pampeanas of Central Argentina whilst the areas below 500 m above sea level include mainly the Southern Andes, from parallel 28º S to Tierra del Fuego (Fig. 4).

According to the temperature variables, 71.90% of the specimens occurred in areas with annual minimum temperatures (AMINT) below –2.5ºC, 19.66% between –1.1 and 2.5ºC, 6.18% between 2.5–6.1ºC and a small proportion (2.24%) above 6.1ºC (Fig. 5). With respect to the annual maximum temperature values (AMAXT), 83.15% of the specimens were present in areas with annual maximum temperatures (AMAXT) between 12.9 and 27ºC and 14.61% tolerate maximum annual temperatures (AMAXT) above 27ºC (Fig. 6). In addition, 78.09% of the specimens were distributed in areas with average annual temperatures (AMT) between 3 and 12.3ºC and 11.24% between 12.3 and 15.4ºC (Fig. 7). The areas with average annual temperature (AMT) ranges of 15.4–18ºC were occupied by 15.4% of the specimens, whereas the areas with average temperatures below 3ºC held 1.18% of the specimens (Fig. 7).

Furthermore, 67.98% of the specimens were present in areas with annual precipitation below 664.5 mm and 20.79% in areas with ranges between 664.5 and 993.8 mm, whereas 5.62% were distributed in areas with annual precipitation of 993.8–1323 mm (Fig. 8). Humid areas with annual rainfall above 1323 mm had 5.63% of the specimens (Fig. 8).

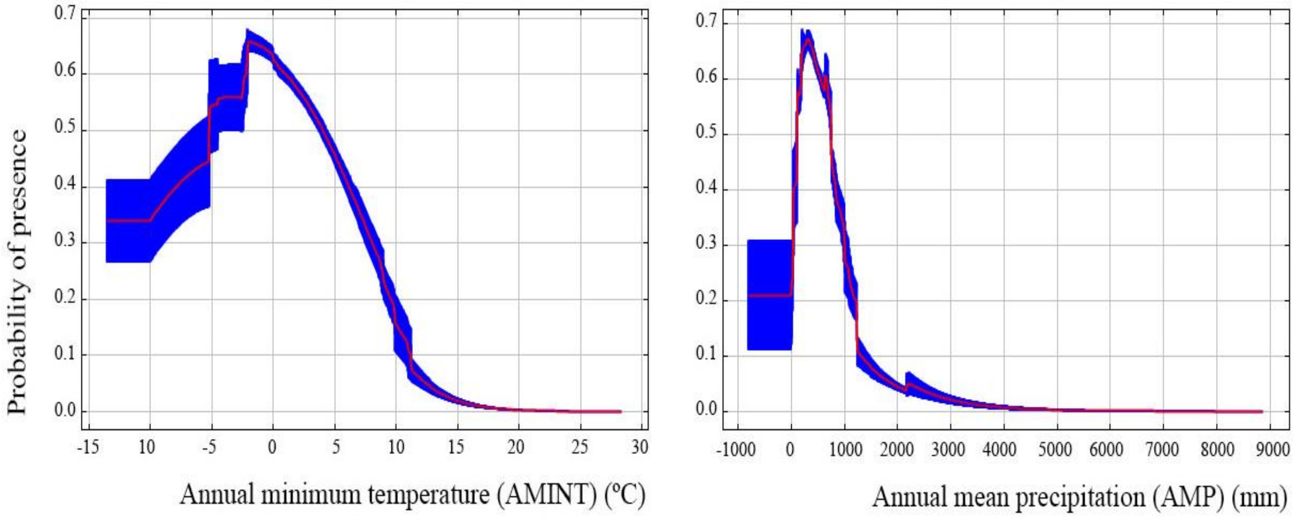

Fig. 3. Response curves of the two most important climatic variables in modeling habitat distribution for *P. scaberula*. A. Annual minimum temperature (ºC). B. Annual mean precipitation (mm).

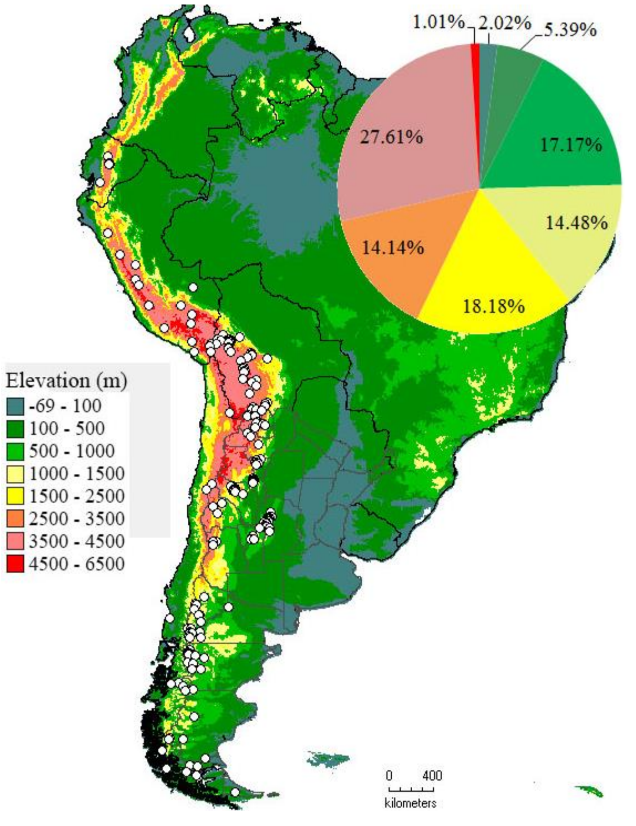

Fig. 4. Distribution map of *P. scaberula* according to the elevation gradient in South America. A pie chart showing the percentage of specimens along the elevation gradient.

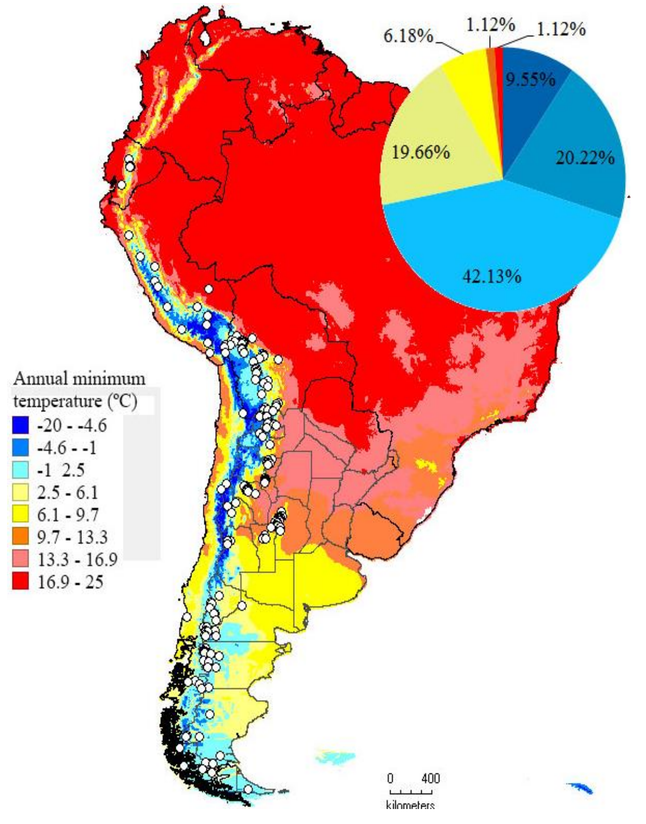

Fig. 5. Distribution map of *P. scaberula* according to annual minimum temperature gradient in South America. A pie chart showing the percentage of specimens along annual minimum temperature gradient.

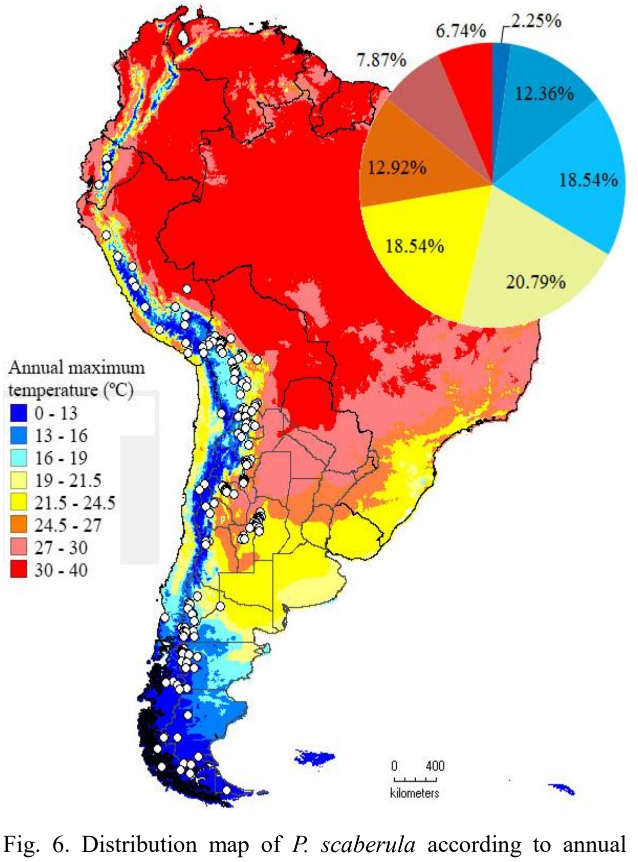

Fig. 6. Distribution map of *P. scaberula* according to annual maximum temperature gradient in South America. A pie chart showing the percentage of specimens along annual maximum temperature gradient.

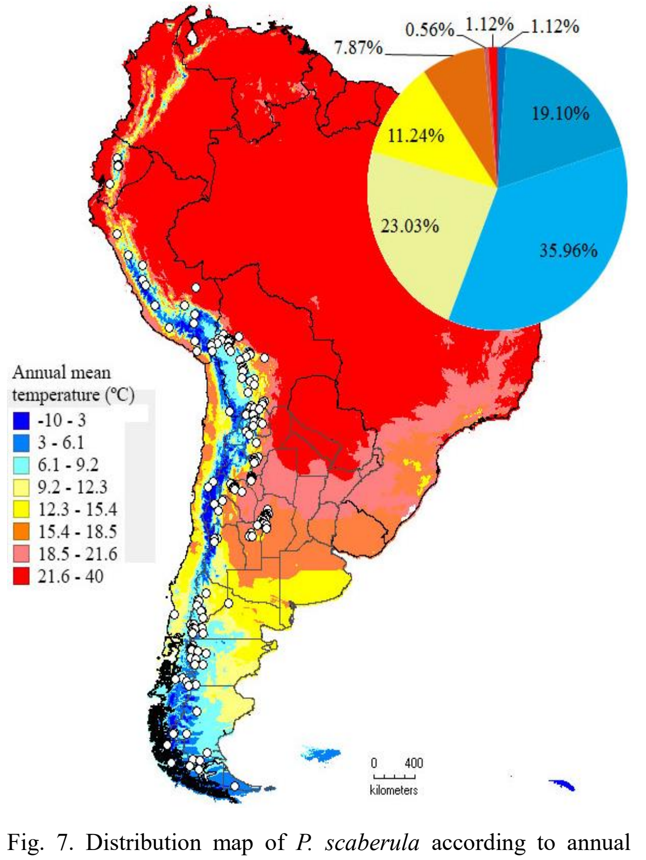

Fig. 7. Distribution map of *P. scaberula* according to annual mean temperature gradient in South America. A pie chart showing the percentage of specimens along annual mean temperature gradient.

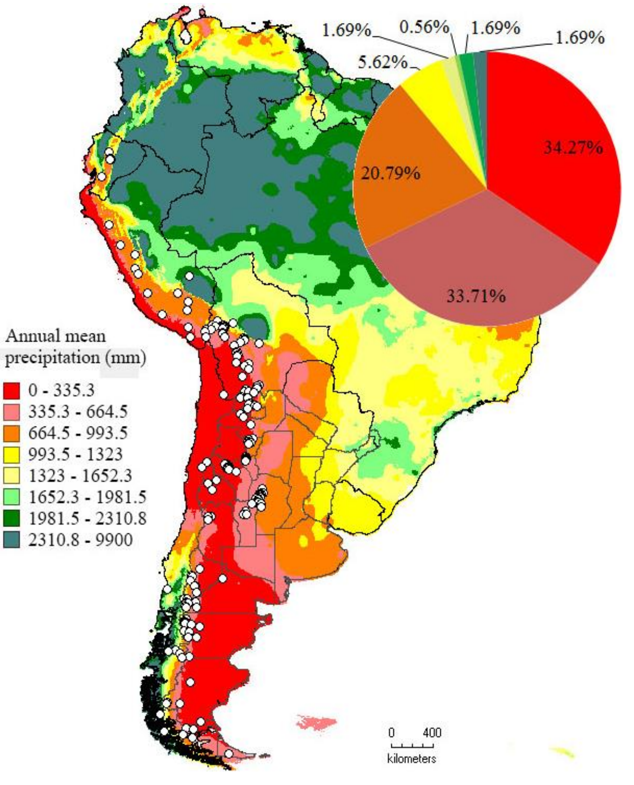

Fig. 8. Distribution map of *P. scaberula* according to a precipitation gradient in South America. A pie chart showing the percentage of specimens along the precipitation gradient.

Discussion

The variables annual minimum temperature and annual precipitation made a strong contribution in the determination of potential habitats for *P. scaberula*. This is in agreement with distribution studies of alpine species (Fang & Lechowicz, 2006; De Cauwer *et al*., 2014; Salariato *et al*., 2015; Lin *et al*., 2019). Minimum temperatures appeared to be an important factor preventing the expansion of the distribution range of *P. scaberula* to low lands along a north-south latitudinal gradient in South America. However, it is important to consider that the minimum temperature can indirectly favor *P. scaberula* by eliminating other plants that outcompete it in more benign environmental conditions.

According to the analyzed species distribution models, the distribution range of *P. scaberula* is extensive (approximately 289,062 km^2), covering high areas from the Northern Andes (from parallel 0º25' S) to the southern tip of the continent (parallel 54º35' S), corresponding to the Andean areas of Ecuador, Peru, Bolivia, Chile and Argentina. The areas of highest probability of occurrence of *P. scaberula* are located in Peru, Bolivia, northwest and Sierras Pampeanas of Central in Argentina, southwest of Chile and Argentina, and some patches in Ecuador; these areas exhibit the ideal suitable habitat conditions for persistence of the species. Model output showed that highly suitable habitats concurred with the distribution of highland grasslands above 1600 m above sea level along the Andes range, and Sierras Pampeanas of Central of Argentina with very low temperatures and low rainfall. Although the distribution models predict the potential presence of *P. scaberula* in Colombia, Venezuela and in the center of Argentina, particularly in La Pampa and Buenos Aires provinces, to date there are no records of its presence. The absence of *P. scaberula* in these potential areas may respond to several abiotic and biotic factors, such as geographical and dispersal barriers, microclimate conditions, evolutionary history, and biotic interactions.

Estimating the ranges of climatic tolerance of a species is useful to understand its distribution and evolutionary history. Herbarium records contribute to the estimation of the climatic tolerance and the understanding of the role of local adaptations and provenance variations of the species (Chown & Gaston, 2016). In addition, the climatic tolerance estimated for species with large ranges is more robust (Curtis & Bradley, 2016). Therefore, from the species distribution models we can infer optimal development of *P. scaberula* within an average temperature range from 3ºC to 15.4ºC, tolerating extreme cold temperatures of –11.8ºC and warm temperatures lower than 32ºC. In addition, most of these areas are above 1000 m above sea level (<4620 m), with extreme drought conditions (<664.5 mm annually). The areas of medium to low elevation occur along the latitudinal gradient, mainly below parallel 28º,S, with temperatures close to the annual averages and with frequent rainfall, reaching 2640 mm. The climatic tolerance interval becomes very wide as the latitudinal gradient increases and consequently the range of climatic regimes increases. The large distribution areas of *P. scaberula* at high latitudes are a consequence of a selective advantage of those specimens with a high climatic tolerance necessary for survival in these areas (Stevens, 1989). Similarly, specimens of *P. scaberula* located at high elevations are exposed to wide climatic regimes in a smaller geographical space; they successfully survive these conditions, showing greater climatic tolerance, especially minimal thermal tolerance.

In summary, *Poa scaberula* has a wide distribution in South America, particularly along the Andes and in mountain areas of central Argentina, being exposed to a wide climatic variability related to elevational and latitudinal gradients. As other mountain taxa in southern South America (Moore, 1975), *P. scaberula* shows a wide ecological tolerance, being able to withstand extreme conditions of low temperatures and rainfalls, which has a great impact on the limits of its potential distribution. Moreover, it is important to consider these results in the context of studies on the impact of climate change on Andean flora, because temperatures are expected to continue to rise in the coming years (Anon., 2018). The world's mountain ecosystems are the most vulnerable to climate change (Kohler *et al*., 2010; 2014). Particularly in the Northern Andes, an increase in extreme rainfall events along with temperature increase is expected, whereas in the Southern Andes a significant decrease in rainfall is predicted (Kohler *et al*., 2014). As a consequence of this variability in the temperature and rainfall regimes, in the last 30 years the Andean vegetation has moved to higher areas in search of new habitats or refuges (García, 2011; Kohler *et al*., 2014). In this context, some species may survive but others may not, depending on their capacity to adapt to the new habitat conditions. *Poa scaberula* has a wide climatic tolerance and a great phenotypic plasticity (Scrivanti *et al*., 2014), which allow it to adapt successfully to a variety of mountain environments in South America. Therefore, given a change in environmental conditions it is possible that it can acclimatize and eventually extend its distribution to higher latitudes and elevations, which could lead to changes in the Andean communities.

Acknowledgements

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