

Species distribution modeling and conservation assessment of the northwestern Argentinian highland papayas under global change scenarios

M. MANUELA URTASUN^{1,✉}, EUGENIA M. GIAMMINOLA¹; CAROLA Y. LAMAS¹; CAROL CAUDLE BASKIN^{2,3}; JOHANNA CROCE⁴; RAMIRO N. CURTI⁵ & MARTA L. DE VIANA⁶

¹ Banco de Germoplasma de Especies Nativas, Instituto de Ecología y Ambiente Humano, Facultad de Ciencias Naturales, Universidad Nacional de Salta-CONICET. Salta, Argentina. ² Department of Biology, University of Kentucky. Lexington, USA. ³ Department of Plant and Soil Sciences, University of Kentucky. Lexington, USA. ⁴ Instituto de Bio y Geociencias del NOA (IBIGEO), Universidad Nacional de Salta-CONICET. Salta, Argentina. ⁵ Laboratorio de Investigaciones Botánicas (LABIBO), Facultad de Ciencias Naturales, Sede Regional Sur, Universidad Nacional de Salta-CONICET. Salta, Argentina. ⁶ Banco de Germoplasma de Especies Nativas, Instituto de Ecología y Ambiente Humano, Facultad de Ciencias Naturales, Universidad Nacional de Salta. Salta, Argentina.

ABSTRACT. Wild species related to crops are a source of genes for improving crop tolerance of biotic and abiotic stresses. *Vasconcellea quercifolia* and *V. glandulosa* are wild relatives of papaya (*Carica papaya*). They are the southernmost-distributed members of the genus and have traits related to tolerance of temperature and precipitation seasonality. Climate and land-use changes, however, are threatening their persistence. Our objectives were to identify priority *ex situ* conservation areas based on the potential distribution of both species in northwestern Argentina under global change scenarios. The potential distribution of *Vasconcellea* spp. was modeled using occurrence data and five bioclimatic non-correlated variables. Distribution range shifts were assessed in two climate change scenarios for the year 2050, considering land-use changes. Gap analysis methodology was applied, and conservation priorities were identified by an integrated approach of conservation strategies. *Vasconcellea quercifolia* has a wider habitat suitability area than *V. glandulosa*, and the effect of land-use change on distribution was higher for the former than latter species. Conversely, climate change would be more negative on *V. glandulosa* than *V. quercifolia*, and the synergic effect of both climate and land-use changes would be higher for *V. quercifolia* than *V. glandulosa*. According to gap analysis, both *Vasconcellea* spp. are high priority species for further germplasm collection. We identified priority areas for *ex situ* conservation.

[Keywords: *Vasconcellea quercifolia*, *V. glandulosa*, crop wild relatives, climate change, land-use change, Maxent, *ex situ* conservation]

RESUMEN. Distribución y conservación de las papayas de altura del noroeste argentino bajo escenarios de cambio global. Las especies silvestres parientes de los cultivos son una fuente de genes para mejorar la tolerancia de éstos a estreses bióticos y abióticos. *Vasconcellea quercifolia* y *V. glandulosa*, parientes silvestres de la papaya (*Carica papaya*), se encuentran en el límite más austral de la distribución del género y presentan características relacionadas con la tolerancia a la estacionalidad de la temperatura y precipitación. La persistencia de las dos especies está en riesgo debido al cambio climático y al cambio en los usos del suelo. El objetivo de este trabajo fue identificar áreas prioritarias para la conservación *ex situ*, evaluando el efecto del cambio global sobre la distribución potencial de ambas especies en el noroeste de la Argentina. La distribución potencial se modeló a partir de datos de ocurrencia y de cinco variables bioclimáticas no correlacionadas. El efecto del cambio global sobre los rangos de distribución se evaluó en dos escenarios de cambio climático para el año 2050 y considerando el cambio en los usos del suelo. Las prioridades de conservación fueron identificadas mediante un enfoque integrado de estrategias de conservación *in situ* y *ex situ*. La distribución de *V. quercifolia* fue más amplia que la de *V. glandulosa*. La pérdida de hábitat disponible para *V. quercifolia* ocurrió principalmente por el cambio en los usos del suelo, mientras que para *V. glandulosa* ocurriría por el efecto del cambio climático. Además, el efecto sinérgico entre ambos factores sería mayor en *V. quercifolia*. Ambas *Vasconcelleas* son especies prioritarias para colecta de germoplasma. Se logró identificar áreas prioritarias de conservación para ambas especies.

[Palabras clave: *Vasconcellea quercifolia*, *V. glandulosa*, parientes silvestres, cambio climático, cambios en los usos del suelo, Maxent, conservación *ex situ*]

INTRODUCTION

Forests provide many direct (e.g., food, medicines and drugs, raw materials for industry) and indirect benefits (e.g., clean water and air, carbon sequestration, ecosystem stability, crop pollination) for human health and socio-economic development (FAO 2020a). South America is an important center for plant biodiversity with ~82052 species, many of which are threatened by habitat conversion and climate change (Ulloa Ulloa et al. 2017). In fact, South America has the second highest rate of deforestation in the world (2.6 million ha/year) (FAO 2020b), and it is included among the three continents with a forecast for the highest intensification of drought and floods in the near future (Mora et al. 2018).

Vasconcellea species (*Caricaceae*), often known as 'highland papayas' or 'mountain papayas', are widely distributed in tropical America, from Mexico to Argentina, and from sea level to 4300 m a. s. l. (Scheldeman et al. 2007). They show much potential and scope for domestication in different regions. Their edible fruits have appealing organoleptic properties (e.g., taste, aroma, color), and are consumed fresh in juices or other beverages, salads, or cooked in stews, jellies, syrups and jams. However, only two of the 21 species of the genus have been developed as a crop, and they are currently being commercialized in Andean countries (Colombia and Ecuador) and international markets (New Zealand, Australia, South Africa, Italy, Spain, Switzerland, the Netherlands and Canada) (Carrasco et al. 2009; Coppens d'Eeckenbrugge et al. 2014). The remaining species are commercially and socially important in their local setting; hence, they could supply specific niches in the national and international market. Mountain papayas secrete latex with high levels of proteases useful in pharmacological and industrial applications.

Additionally, *Vasconcellea* species are wild relatives of the common papaya (Vincent et al. 2013); therefore, they are a source of genes for papaya improvement, such as tolerance to Ringspot Papaya Virus (RSPV-P), low temperatures, as well as some traits related to sugar content (Coppens d'Eeckenbrugge et al. 2014). The current and future development of highland papayas as commercial fruits, as well as their use for the production of latex or in common papaya improvement programs, depends on knowledge of their biology

(phenotypic and genetic characterization, environment of growing) and germplasm collection and documentation. *Vasconcellea quercifolia* and *V. glandulosa* are the southernmost species of the genus; thus, they are expected to have atypical adaptations compared with the remaining *Vasconcellea* spp. In addition, *V. quercifolia* is one of the few *Vasconcellea* species that inhabits high altitudes, as well as lowlands (Scheldeman et al. 2007); thus, it could be cultivated in a wide range of environments. The species has high dietary potential, since its edible structures (fruits and medullar parenchyma) have high ash, protein, carbohydrate, fiber and carotenoid content (Folharini et al. 2019). Moreover, the fruits secrete latex with a higher specific activity than that of *C. papaya*, with the ability to coagulate milk and produce cheese (Torres et al. 2010). Finally, *V. quercifolia* has been widely used in papaya breeding programs with encouraging results (Drew et al. 2007; Siar et al. 2011).

These two species are the only members of the genus present in Argentina. *Vasconcellea quercifolia* is distributed in the northwest, northeast and one province in the center of the country, while *V. glandulosa* is only located in the humid forests of northwestern Argentina. In northwestern Argentina, both species inhabit the lower slopes of the Andes, and their wild populations are threatened mainly by habitat conversion (Malizia et al. 2012; Leake et al. 2016). In addition to land-use changes, temperature and precipitation changes have been observed in this region during the last 70 years, with further climate changes predicted for the next two or three decades (Barros et al. 2015).

Land-use and climate change are affecting biodiversity, and, therefore, most biological and ecological processes on Earth. Nevertheless, the effects of climate change are species-specific. For example, effects of climate change are expected to be less severe for widely- than narrowly-distributed species, since the former experience environmental heterogeneity and have a higher ability to cope with changing habitats than the latter (Valladares et al. 2014; Scheepens et al. 2018). In the last decades, species distribution models (SDMs) have been used to generate hypotheses about the potential consequences of global climate change on species distribution (Giamminola et al. 2020), to define priority areas for conservation (Parra-Quijano et al. 2012; Curti et al. 2017) and to assess the

representativeness of *ex situ* germplasm collections (Marinoni et al. 2015). Species Distribution Models have proven to be a successful tool for biodiversity analysis and the design of conservation strategies in the current context of global change.

Our overall purpose was to identify priority *ex situ* conservation areas based on the potential distribution of both species in northwestern Argentina under global change scenarios. The specific objectives of our study were to 1) develop models of the potential area of distribution of *V. glandulosa* and *V. quercifolia*, 2) assess the impact of climate change and land-use change on distributional range, and 3) identify priority conservation areas for germplasm collection. In this work, we expect that A) the retraction in potential distribution range due to effects of climate change will be higher for *V. glandulosa* than *V. quercifolia*, since the former has a narrower geographic range than the latter, B) the retraction in distribution range due to land-use changes will be higher for *V. quercifolia* than *V. glandulosa*, since the former inhabits both low and high-elevation habitats, and C) the relative magnitude of the negative effects will be higher for land-use than climate changes.

MATERIALS AND METHODS

Model inputs

A total of 167 *V. glandulosa* and 370 *V. quercifolia* occurrence records was acquired from the Global Biodiversity Information Facility (gbif.org). Data quality was checked with the Geoqual tool of the CAPFITOGEN program (capfitogen.net), which evaluates locations for inconsistencies between coordinates and province data. Incomplete, duplicate and incorrect coordinates were eliminated (Parra-Quijano et al. 2016). Then, to maximize the number of spatially independent localities and reduce overprediction, the occurrence dataset was spatially rarefied taking into account the combination of topographic with climatic variables, using SDMToolbox v2.4 software (Brown 2014). We removed the localities that were within 2.5 km of each other in heterogeneous habitats (steep slope environments where temperature and precipitation vary with elevation) and within 10 km of each other in homogeneous habitats (flat environments where climate variables are more constant). Twenty-four *V. glandulosa* and 46 *V. quercifolia* occurrence records were

used to model the potential distribution (Supplementary Material-Figure S1). From the 19 bioclimatic layers (worldclim.org) and one topographic (elevation) layer (geoportal.idesa.gob.ar), five were selected by the 'explore climate data' tool from SDMToolbox v2.4 software (Table 1) (Yang et al. 2013; Qin et al. 2017). This tool evaluates the correlations among all input environment data and then removes layers that are correlated at the user-specified level by a Pearson analysis (we used a correlation coefficient of 0.8). From the correlated variables, we selected those that best represent the original input climate data (as they directly reflect the actual measurements) and are not derived from several layers or a subset of the data (such as annual mean temperature, annual precipitation) (Brown 2014).

Model settings

The potential distribution of the two species was modeled in northwest Argentina (provinces of Jujuy, Salta, Tucumán, Santiago del Estero and Catamarca) using Maximum Entropy Algorithm (Maxent 3.4.0), which performs well compared to other methods (Elith et al. 2006a; Phillips et al. 2006; Aguirre-Gutiérrez et al. 2013). Modeling was performed at a spatial resolution of 30 arc-sec (~1x1 km cell size at the equator). To limit over-prediction, we defined species-specific geographical backgrounds using the 'buffered local adaptive convex-hull' tool of SDMToolbox, a buffer distance of 100 km and an alpha parameter value of 5 (Brown 2014). To optimize model performance, we calibrated the model with the 'Run Maxent: Spatial Jackknifing' tool of SDMToolbox, testing different combinations of the four model

Table 1. Environmental variables used in the potential distribution modeling of *Vasconcellea* spp.

Tabla 1. Variables ambientales utilizadas en la modelización de la distribución potencial de *Vasconcellea* spp.

Environmental variables	Units
BIO1: annual mean temperature	°C
BIO2: mean diurnal range (mean of monthly (max temp-min temp))	°C
BIO4: temperature seasonality (standard deviation×100)	%
BIO12: annual precipitation	mm
BIO14: precipitation of driest month	mm

feature class types (linear, quadratic, hinge, and product) and regularization multiplier (1 to 5) (Brown 2014; Radosavljevic and Anderson 2014). The best combination was the model with the lowest omission error rate (OER), and of those models, if multiple, the model with the highest area under the receiver operator curve (AUC). Lastly, if the model had an identically low OER and high AUC values, the feature class complexity was accounted for by selecting the model with the lowest complexity (further details in Supplementary Material). The best combination for *V. glandulosa* modeling was a regularization multiplier=2 with the four features classes. The best combination for *V. quercifolia* modeling was a regularization multiplier=5 with linear feature class. For the final model, we run 10 replicates, and we used an average of the probability maps for habitat suitability applying the 10 percentile training presence as threshold (more details in Supplementary Material). For display and further analysis, we imported the results of the models into QGIS 3.8. The Jackknife method was used to assess the contribution to the model of each variable. For each species, the response curves of the five variables were made to determine the environmental conditions of a probability higher than 0.8.

Impact of climate change (CC) and land-use change (LUC)

To model *Vasconcellea* spp. distributions under future global warming scenarios, two representative concentration pathways (RPCs) defined by the Intergovernmental Panel on Climate Change in the Fifth Assessment Report (IPCC AR5) were used. The RPC2.6 assumes that mitigation policies and actions will limit the generation of greenhouse gases (minimum emission hypothesis); conversely, RPC8.5 foresees an increase in greenhouse gases emissions (maximum emission hypothesis). One global climate model CCSM4 was downloaded from the Worldclim database under both scenarios for the year 2050. The bioclimatic variables and the model settings were the same as those in the current model (see Model settings subtitle). To assess possible changes in the potential distribution of *Vasconcellea* spp., the current and future models were combined, and range shifts were calculated to determine stable, retraction and expansion areas. Stable areas are low impact areas where climatic conditions are currently suitable for the species, and they also would

be suitable in the future. Retraction areas are high impact areas, where current climatic conditions are suitable for the species, but they will support other vegetation types in the future. Expansion areas are new suitable areas where current climatic conditions are not adequate for the species, but they would be in the future. Then, a land-use change layer until 2018 (geoportal.idesa.gob.ar) was combined with the current and future potential distribution of the species to assess the synergic effect. The area already lost due to land-use change was calculated, and for the future models, stable areas (stable areas in CC scenarios - lost areas for LUC) and retraction areas (retraction for CC + retraction for LUC) were calculated.

Conservation assessment

To determine the urgency of collecting seeds of highland papayas for *ex situ* conservation (e.g., gene banks), the gap analysis methodology proposed by Ramírez-Villegas et al. (2010) was used. The methodology consists of three scores: 1) sampling representativeness score (SRS) (compares the number of germplasm accessions to the total number of samples [germplasm plus species presence records]), 2) geographic representativeness score (GRS) (compares the species potential distribution area with that represented by samples in genebanks, estimated by creating a circular buffer of 50 km around each site where the accession was collected), and 3) ecosystem representativeness score (ERS) (assesses the number of ecosystems currently represented in *ex situ* collections, compared to the total number of ecosystems distributed within the potential distribution of the species).

The three scores were given equal weight and an average was calculated to obtain a Final Priority Score (FPS), which is classified in four categories: 1) high priority species (FPS=0-3), 2) medium priority species (FPS=3.01-5), 3) low priority species (FPS=5.01-7.5), and 4) well conserved species (FPS=7.51-10). See details about data acquirement in Supplementary Material.

Then, the *in situ* conservation status of each species was determined by evaluating the percentage of its geographic distribution currently protected in the Protected Areas System of Argentina (PASA). As no checklist of species is available for provincial and private reserves, the layer of *in situ* areas (ign.gob.ar) was overlapped with the potential distribution

map. The intersection area between the two layers was calculated. Finally, to determine the high priority areas for conservation, the current geographic coverage of germplasm collections and the *in situ* conservation areas were overlapped with the potential distribution of each species under the maximum emission hypothesis scenario of climate change. The non-conserved retraction zones for each species were identified and selected as high priority areas for *ex situ* conservation.

RESULTS

The potential distribution of *V. glandulosa* is restricted to three of the five provinces of the study area (OER: 0.09, AUC: 0.92±0.05) and occupies a surface of 21525 km² (28% of which is a low probability area [<0.60], 33% is a medium probability area [$0.60-0.80$] and 39% is a high probability area [$>0.80\%$]). Conversely, the potential distribution of *V. quercifolia* encompasses the five provinces of northwestern Argentina (OER: 0.07, AUC: 0.73±0.02) and occupies an area of 137499 km² (61%, 29% and 10% is a low, medium and high occurrence probability area, respectively) (Figure 1).

The Jackknife test showed that annual precipitation was a key variable in the model for both species. In addition, temperature seasonality and mean annual temperature also were important factors in the distribution of *V. glandulosa* (Supplementary Material-Figure S2), while mean diurnal range and precipitation of the driest month were

important for *V. quercifolia* (Supplementary Material-Figure S3). According to the response curves, both species require habitats with mean annual temperatures below 18 °C and annual precipitation higher than 650 mm. However, *V. glandulosa* requires environments with lower temperature seasonality and a higher mean diurnal range than *V. quercifolia*. Finally, *V. glandulosa* tolerates a wider range of precipitation of the driest month than *V. quercifolia* (Supplementary Material-Table S1, Figure S4 and S5).

The projected climate map resulted in a reduction in extent of suitable habitat for both species, as compared with the potential current distribution (Figure 2). By 2050, the retraction for *V. glandulosa* would represent 26% of its current distribution in the RCP2.6 scenario and a 36% in the RCP8.5 scenario. For *V. quercifolia*, the retraction in the RCP2.6 and RCP8.5 scenarios would be 12% and 24%, respectively. In both species and both scenarios, the stable area would be reduced and the expansion would be lower than 6%. The area of range contraction would be in the eastern region of the distribution of *V. glandulosa* and along the edge of the distribution of *V. quercifolia*. Expansion would be on the west of the distribution of *V. glandulosa* and in small patches towards the northwest and south of the distribution of *V. quercifolia*.

Land-use change as of 2018 already has caused a 4.9% (1047 km²) and 26% (34184 km²) decrease in the potential distribution area of *V. glandulosa* and *V. quercifolia*, respectively

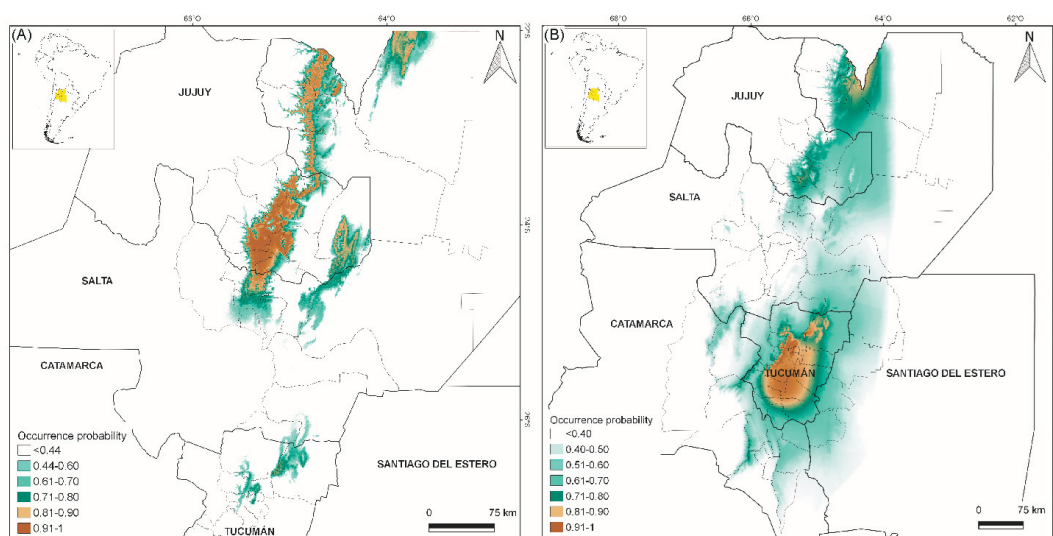


Figure 1. Current potential distribution area of *V. glandulosa* (A) and *V. quercifolia* (B).

Figura 1. Área de distribución potencial actual de *V. glandulosa* (A) y *V. quercifolia* (B).

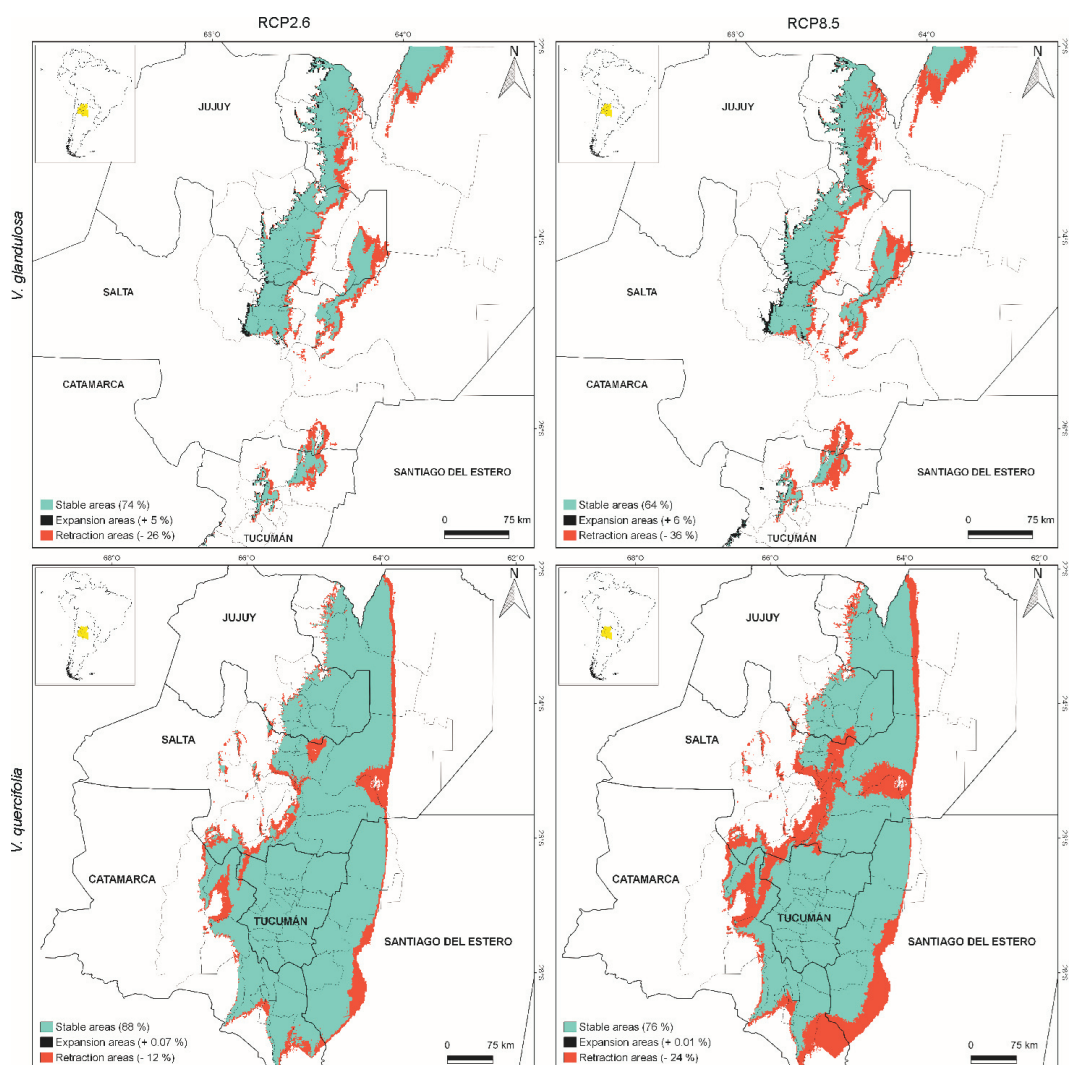


Figure 2. Potential future distribution of *V. glandulosa* (above) and *V. quercifolia* (below) under two climate change scenarios: RCP 2.6 (left) and RCP 8.5 (right).

Figura 2. Distribución potencial futura de *V. glandulosa* (arriba) y *V. quercifolia* (abajo) en dos escenarios de cambio climático: RCP 2.6 (izquierda) y RCP 8.5 (derecha).

Table 2. Variables for score calculation and priority categorization of each *Vasconcellea* species.

Tabla 2. Variables para calcular el puntaje y la categoría prioritaria de cada especie de *Vasconcellea*.

Variab/es/scores	<i>V. glandulosa</i>	<i>V. quercifolia</i>
Nº reference samples	121	325
Nº germplasm accessions	46	45
Potential area (km ²)	21525	137499
Buffer area (km ²)	8631	31101
SRS	0.27	0.12
GRS	4	2.26
ERS	3.55	4.5
FPS	2.61	2.3
Priority category	HPS	HPS

SRS: sampling representativeness score; GRS: geographic representativeness score; ERS: ecosystem representativeness score; FPS: final priority score

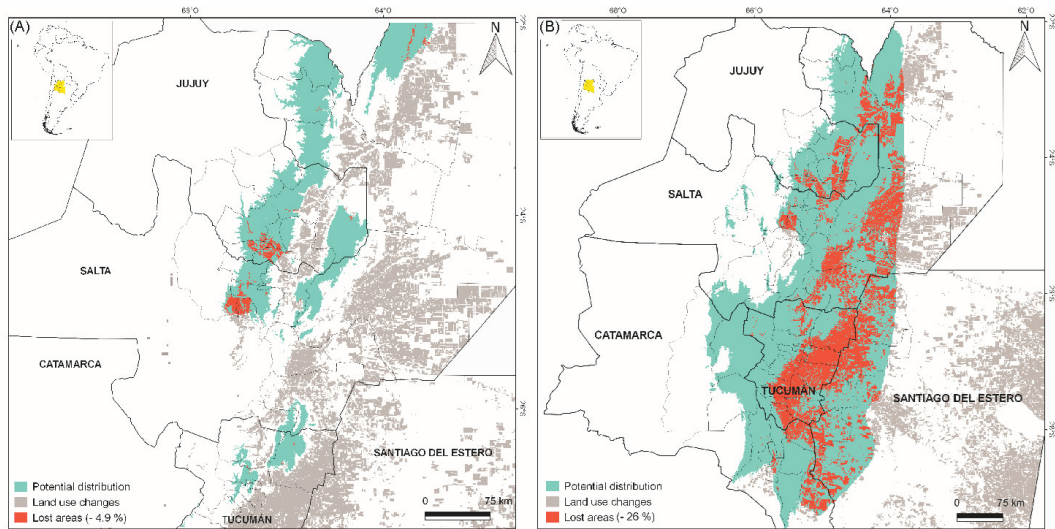


Figure 3. Effect of land-use changes on *V. glandulosa* (A) and *V. quercifolia* (B) current potential distribution.

Figura 3. Efecto de los cambios en los usos del suelo sobre la distribución potencial actual de *V. glandulosa* (A) y *V. quercifolia* (B).

(Figure 3). In both species, the retraction was mainly in low and high probability areas.

The synergic effect of changes in climate and land-use would cause an increased retraction of 4% and 22 - 24% in the potential distribution area of *V. glandulosa* and *V. quercifolia*, respectively. Consequently, the total unsuitable areas would represent 30-40% (RCP2.6 - 8.5) of its current potential distribution for *V. glandulosa* and 36-46% (RCP2.6 - 8.5) for *V. quercifolia* (Figure 4).

According to gap analysis, both *Vasconcellea* spp. are high priority species for further germplasm collection (Table 2). The ERS was slightly lower for *V. glandulosa* than for *V. quercifolia*, while the SRS and GRS were almost twice as high for *V. quercifolia* than for *V. glandulosa*. In both species, germplasm accessions are conserved in the Germplasm Bank of Native Species of the National University of Salta province (FAO-WIEWS ARG1132), and no accessions from Argentina are conserved in international genebanks.

In relation to the *in situ* conservation state of *Vasconcellea* spp., national, provincial and private reserves currently conserve 11.5% (2474 km²) of the potential distribution area for *V. glandulosa* and 3.4% for *V. quercifolia* (4661 km²). Finally, considering *ex situ* and *in situ* strategies, *V. glandulosa* priority areas for conservation encompass an area of 6200 km², which represents 29% of its current distribution. The areas are located in the

northern and central parts of Salta, eastern part of Jujuy and northern part of Tucumán provinces. *V. quercifolia* priority areas for conservation encompass an area of 16320 km², which represents 12% of its current distribution. The areas are mainly located in the northern, eastern, central and western parts of Salta, northwestern part of Tucumán, central part of the Catamarca and western part of Santiago del Estero (Figure 5).

DISCUSSION

We modeled for the first time the potential distribution of *Vasconcellea* spp. in northwestern Argentina to assess the conservation status of both species and identify priority areas for further *ex situ* conservation in genebanks. We looked for and selected the most suitable methodology to avoid over prediction and increase the prediction capacity of each model. However, a remarkable difference in the performance (AUC) of the *V. quercifolia* and *V. glandulosa* models was observed, although the modeling methods were similar. The lower value of AUC (<0.75) in the *V. quercifolia* model is probably related to the size of the buffer area. As shown in the current potential distribution map (Figure 1B), most of the study area has a medium or high occurrence probability, with only a few unsuitable surfaces. Therefore, the capacity of the model to discriminate was decreased, since the environmental conditions between presence and pseudo-absence sites were similar. Nevertheless, both models have

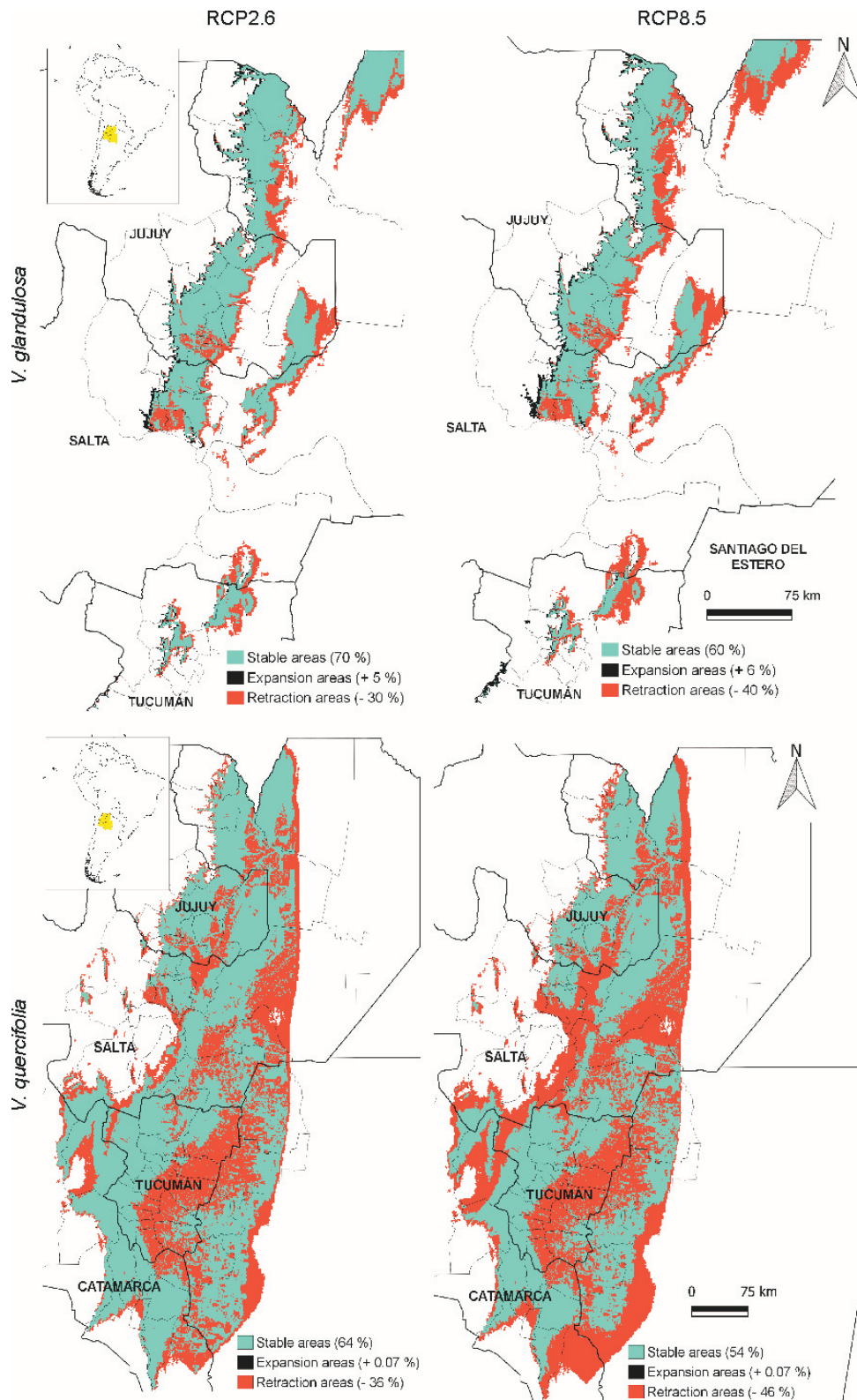


Figure 4. Synergic effect of climate and land use changes on potential distribution of *V. glandulosa* and *V. quercifolia*.
Figura 4. Efecto sinérgico del cambio climático y los cambios en los usos del suelo sobre la distribución potencial de *V. glandulosa* and *V. quercifolia*.

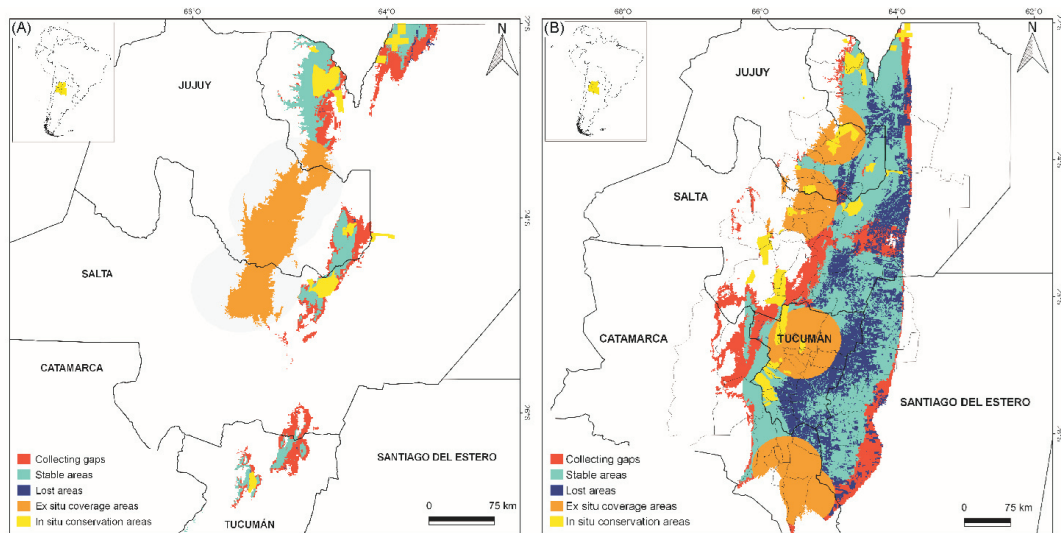


Figure 5. Collection gaps of *V. glandulosa* (A) and *V. quercifolia* (B) for *ex situ* conservation.

Figura 5. Áreas prioritarias para la conservación *ex situ* de *V. glandulosa* (A) and *V. quercifolia* (B).

enough discrimination capacity to be used in the planning of *ex situ* and *in situ* conservation strategies (Elith 2006b; Phillips et al. 2006). According to the Jackknife test, annual precipitation (bio12) is one of the variables that contributed the most to the potential distribution models. This result coincides with the reported by Scheldeman et al. (2007) that both species have a limited adaptability to variations in annual precipitation, which is expected to be a variable that restricts their distribution. In addition, we found that precipitation of the driest month (bio14) and temperature seasonality (bio4) also are important variables for *V. quercifolia* and *V. glandulosa*, respectively. The Argentinian Yungas vegetation (lower slope of the eastern side of the Andes Mountains) is distributed through an elevation gradient of 400 to 2300 m a. s. l. and it is characterized by two main and contrasting seasons that differ in temperature and precipitation (with summer being the warmest and wettest and winter the coldest and driest) (Bianchi and Cravero 2010; Malizia et al. 2012). The elevation gradient has a direct influence on climatic conditions since temperature decreases and precipitation increases with altitude. *Vasconcellea quercifolia* has a wider distribution than *V. glandulosa* and inhabits highland as well as lowland areas. Therefore, it is expected that precipitation during winter plays a key role in the survival of the species, since this is the season with the lowest amount of precipitation. On the contrary, *V. glandulosa* is distributed at higher elevations than *V. quercifolia*, where

precipitation is not a limiting factor, and there are minor differences within summer and winter temperatures compared to the lowlands (Bianchi and Cravero 2010).

Based on the current potential distribution maps, *V. quercifolia* has a wider latitudinal, longitudinal and altitudinal distribution than *V. glandulosa*, which coincides with the reported by Scheldeman et al. (2007). However, only 10% of the *V. quercifolia* distribution is a high probability area, and at least half of it has already been transformed by changes in land-use. However, the narrow distribution range of *V. glandulosa* has been less affected by changes in land-use than that of *V. quercifolia*, as we hypothesized. Considering the tendency for deforestation to occur on plains, we can expect a minimal loss in *V. glandulosa* potential distribution in the next few years but a continued decrease in the lower and flattest surfaces of *V. quercifolia* potential distribution.

On the other hand, climate change poses a greater threat to *V. glandulosa* than to *V. quercifolia* since the projected retraction of the former reaches almost 40% in the maximum emission scenario. This result supports our first hypothesis that the retraction due to climate change would be higher for *V. glandulosa* than for *V. quercifolia*, and it could be related to the narrower distribution of the former compared to the latter species. The possible range shifts in response to climate change would mainly depend on the physiological tolerance of each species. Thus, widely-distributed species are

expected to adapt, while narrowly-distributed ones are expected to migrate to new suitable areas, a tendency shown in our results. However, when the colonization of new places is limited by natural (e.g., mountains, rivers) or artificial barriers (e.g., urban centers, cleared areas, crop fields), a decrease in distributional range and an increase in the risk of extinction is observed (Broennimann et al. 2006; Maciel-Mata et al. 2015). Our projected distribution maps show that the expansion area of both species would be almost insignificant, and in the case of *V. glandulosa* they would be limited by the mountain range. Further work is needed to assess the phenotypic plasticity of the studied species to forecast their response to climate variability. Additionally, it would be interesting to compare our results with future projections using climatic variables from other global circulation models calibrated for the Southern Hemisphere.

A low percentage of the two studied *Vasconcellea* species is currently conserved in the Argentina germplasm bank network. Moreover, information collected from international genebanks revealed no accessions of *Vasconcellea* species from Argentinian populations. Our results showed that both species are of high priority for future collecting efforts due to severe gaps in *ex situ* collections. Moreover, since *V. quercifolia* has potential to be used in cultivation (Folharini et al. 2019) and breeding programs (Drew et al. 2007; Siar et al. 2011), a high demand of genetic material is expected in the future. Therefore, it is essential to ensure that the genetic diversity of both species is preserved in genebanks and that a complete morphological and physiological characterization of each collection is obtained. Future studies should focus on the most efficient strategy to collect and conserve *ex situ* the widest genetic variability possible from the gap areas (Parra-Quijano et al. 2012; Marinoni et al. 2015).

On another hand, through the *in situ* conservation analysis we could observe that the PASA is currently protecting a higher percentage of the potential distribution area of *V. glandulosa* than of *V. quercifolia*.

Nevertheless, as we used distribution maps to determine if the species were protected, further work in the field is needed to verify the presence-absence of these species and whether the populations are under any form of active *in situ* conservation management.

CONCLUSION

This study provides a region-wide distribution and conservation assessment of the two *Vasconcellea* species in Argentina. It shows that land-use changes pose a greater threat to *V. quercifolia* distribution than climate change, while the opposite response occurs for *V. glandulosa*. Thus, the relative magnitude of the negative effect of each global change process depends on the species. Argentinian populations of both species are underrepresented in national genebank collections and are not represented in international genebanks. The percentage of the potential distribution area conserved in national and provincial parks and reserves is low, but it is higher for *V. glandulosa* than for *V. quercifolia*. Both species are of high conservation priority. Future work should focus on collection strategies to conserve the widest genetic variability possible for the identified collection gaps. To ensure that *Vasconcellea* germplasm is available for conservation and breeding programs, urgent efforts are needed to fill the collection gaps in northwestern Argentina.

ACKNOWLEDGEMENTS. We thank Dr. Jesus Sajama and Dr. Pablo Gorostiague for modeling assistance and, Santiago Martínez, Mayra Tapia, Isabel Cornejo, Anabel Barbosa, Macarena Rojas and Gabriela Zárate for helping with field work. This paper was written in the context of the research project "Eco-ethnology: conservation and recovery of cultural and natural biodiversity" and it is part of the biological science PhD research of MMU at the Consejo Nacional de Investigaciones Científicas y Técnicas-CONICET. This work was supported by the CONICET (N° 4831/2014) and the Consejo de Investigación de la Universidad Nacional de Salta-CIUNSa (N° 2482/0).

REFERENCES

- Aguirre-Gutiérrez, J., L. G. Carvalheiro, C. Polce, E.E. van Loon, N. Raes, M. Reemer, and J. C. Biesmeijer. 2013. Fit-for-purpose: Species distribution model performance depends on evaluation criteria-Dutch hoverflies as a case study. *Plos ONE* 8:e63708. <https://doi.org/10.1371/journal.pone.0063708>.
- Barros, V. R., J. A. Boninsegna, I. A. Camilloni, M. Chidiak, G. O. Magrín, and M. Rusticucci. 2015. Climate change in Argentina: trends, projections, impacts and adaptation. *Climate Change* 6:151-169. <https://doi.org/10.1002/wcc.316>.

- Bianchi, A. R., and S. A. C. Cravero. 2010. Atlas climático digital de la República Argentina. First edit. Instituto Nacional de Tecnología Agropecuaria, Salta, Argentina.
- Broennimann, O., W. Thuiller, G. Hughes, G. F. Midgley, J. M. R. Alkemade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12: 1079-1093. <https://doi.org/10.1111/j.1365-2486.2006.01157.x>.
- Brown, J. L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution* 5:694-700. <https://doi.org/10.1111/2041-210X.12200>.
- Carrasco, B., P. Ávila, J. Pérez-Díaz, P. Muñoz, R. García, B. Lavandero, A. Zurita-Silva, J. B. Retamales, and P. Caligari. 2009. Genetic structure of highland papayas (*Vasconcellea pubescens* (Lenné et C. Koch) Badillo) cultivated along a geographic gradient in Chile as revealed by Inter Simple Sequence Repeats (ISSR). *Genetic Resources and Crop Evolution* 56:331-337. <https://doi.org/10.1007/s10722-008-9367-1>.
- Coppens d'Eeckenbrugge, G., R. Drew, T. Kyndt, and X. Scheldeman. 2014. *Vasconcellea* for papaya improvement. Pp. 433 in R. Ming and P. H. Moore (eds.). *Genetics and Genomics of Papaya*. First. Springer, New York, USA. https://doi.org/10.1007/978-1-4614-8087-7_4.
- Curti, R. N., J. Sajama, and P. Ortega-Baes. 2017. Setting conservation priorities for Argentina's pseudocereal crop wild relatives. *Biological Conservation* 209:349-355. <https://doi.org/10.1016/j.biocon.2017.03.008>.
- Drew, R., S. Ashmore, S. Somsri, N. Noor, T. Thi Hoa, O. Damasco, and R. Rao. 2007. Advanced technologies for germplasm conservation of tropical fruit species. *Acta Horticulturae* 760:91-98. <https://doi.org/10.17660/ActaHortic.2007.760.10>.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006a. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>.
- Elith, J. 2006b. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. Pp. 39-58 in S. Ferson and M. Burgman (eds.). *Quantitative methods for conservation biology*. Springer Science and Business Media, New York, USA. https://doi.org/10.1007/0-387-22648-6_4.
- FAO. 2020a. The state of food security and nutrition in the world. Rome, Italy.
- FAO. 2020b. Global forest resources assessment 2020 - key findings. Rome, Italy.
- Folharini, Z. F., C. R. Orlandi, M. C. Martini, F. Bruxel, T. Altmayer, D. T. Brietzke, T. E. Gonçalves, J. Finatto, E. M. Ethur, N. F. de Moura, L. Hoehne, and E. M. de Freitas. 2019. Nutritional characterization of *Vasconcellea quercifolia* a.St-hil.: Potential for the development of functional food. *Food Science and Technology* 39:432-438. <https://doi.org/10.1590/fst.18018>.
- GBIF.org (5 May 2020) GBIF *V. quercifolia* Occurrence Download. <http://doi.org/10.15468/dl.qz6uyt>.
- GBIF.org (5 May 2020) GBIF *V. glandulosa* Occurrence Download. <https://doi.org/10.15468/dl.pk5xs4>.
- Giamminola, E. M., M. M. Urtasun, C. Y. Lamas, and M. L. de Viana. 2020. Will global change modify the distribution of the *Anadenanthera colubrina* (Fabales: Fabaceae) plant, a key species in dry tropical forest? *Revista de Biología Tropical* 68:517-527. <https://doi.org/10.15517/rbt.v68i2.38610>.
- Leake, A., E. O. López, and M. C. Leake. 2016. La deforestación del Chaco Salteño. First. Fundación Refugio, Salta, Argentina.
- Maciel-Mata, C. A., N. Manríquez-Morán, P. Octavio-Aguilar, and G. Sánchez-Rojas. 2015. El área de distribución de las especies: revisión del concepto. *Acta Universitaria* 25:3-19. <https://doi.org/10.15174/au.2015.690>.
- Malizia, L., S. Pacheco, C. Blundo, and A. D. Brown. 2012. Caracterización altitudinal, uso y conservación de las Yungas Subtropicales de Argentina. *Ecosistemas* 21:53-73.
- Marinoni, L., M. Parra-Quijano, M. Zabala, and F. Pensiero. 2015. Evaluation and improvement of the ecogeographical representativeness of a collection of the genus *Trichloris* in Argentina. *Genetic Resources and Crop Evolution* 62:593-604. <https://doi.org/10.1007/s10722-014-0184-4>.
- Mora, C., D. Spirandelli, E. C. Franklin, J. Lynham, M. B. Kantar, W. Miles, C. Z. Smith, K. Freel, J. Moy, L. V. Louis, E. W. Barba, K. Bettinger, A. G. Frazier, J. F. Colburn IX, N. Hanasaki, E. Hawkins, Y. Hirabayashi, W. Knorr, C. M. Little, K. Emanuel, J. Sheffield, J. A. Patz, and C. L. Hunter. 2018. Broad threat to humanity from cumulative climate hazards intensified by greenhouse gas emissions. *Nature Climate Change* 8(12):1062-1071. <https://doi.org/10.1038/s41558-018-0315-6>.
- Parra-Quijano, M., J. M. Iriondo, and E. Torres. 2012. Ecogeographical land characterization maps as a tool for assessing plant adaptation and their implications in agrobiodiversity studies. *Genetic Resources and Crop Evolution* 59:205-217. <https://doi.org/10.1007/s10722-011-9676-7>.
- Parra-Quijano, M., E. Torres Lamas, J. M. Iriondo Alegría, and F. López. 2016. CAPFITOGEN - Programa para el fortalecimiento de las capacidades en programas nacionales de recursos fitogenéticos de América Latina. FAO.
- Phillips, S. J., R. P. Anderson, and R. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231-259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Qin, A., B. Liu, Q. Guo, R. W. Bussmann, F. Ma, Z. Jian, G. Xu, and S. Pei. 2017. Maxent modeling for predicting impacts of climate change on the potential distribution of *Thuja sutchuenensis* Franch, an extremely endangered conifer from southwestern China. *Global Ecology and Conservation* 10:139-146. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Radosavljevic, A., and R. P. Anderson. 2014. Making better Maxent models of species distributions: complexity,

- overfitting and evaluation. *Journal of Biogeography* 41:629-643. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Ramírez-Villegas, J., C. Houry, A. Jarvis, D. G. Debouck, and L. Guarino. 2010. A gap analysis methodology for collecting crop gene pools: a case study with *Phaseolus* beans. *PloS ONE* 5(10):e13497. <https://doi.org/10.1371/journal.pone.0013497>.
- Scheepens, J. F., Y. Deng, and O. Bossdorf. 2018. Phenotypic plasticity in response to temperature fluctuations is genetically variable, and relates to climatic variability of origin, in *Arabidopsis thaliana*. *AoB PLANTS* 10(4):1-12. <https://doi.org/10.1093/aobpla/ply043>.
- Scheldeman, X., L. Willems, G. Coppens D'Eeckenbrugge, E. Romeijn-Peters, M. T. Restrepo, J. Romero Motoche, D. Jiménez, M. Lobo, C. I. Medina, C. Reyes, D. Rodríguez, J. A. Ocampo, P. Van Damme, and P. Goetgebeur. 2007. Distribution, diversity and environmental adaptation of highland papayas (*Vasconcellea* spp.) in tropical and subtropical America. *Biodiversity and Conservation* 16:1867-1884. <https://doi.org/10.1007/s10531-006-9086-x>.
- Siar, S. V., G. A. Beligan, A. J. C. Sajise, V. N. Villegas, and R. A. Drew. 2011. Papaya ringspot virus resistance in *Carica papaya* via introgression from *Vasconcellea quercifolia*. *Euphytica* 181:159-168. <https://doi.org/10.1007/s10681-011-0388-z>.
- Torres, M. J., S. A. Trejo, M. I. Martín, C. L. Natalucci, F. Avilés, and L. M. López. 2010. Purification and characterization of a cysteine endopeptidase from *Vasconcellea quercifolia* A. St.-Hil. latex displaying high substrate specificity. *Journal of agricultural and food chemistry* 58:11027-11035. <https://doi.org/10.1021/jf904295x>.
- Ulloa Ulloa, C., P. Acevedo-Rodríguez, S. Beck, M. J. Belgrano, R. Bernal, P. E. Berry, L. Brako, M. Celis, G. Davidse, R. C. Forzza, S. R. Gradstein, O. Hokche, B. León, S. León-Yáñez, R. E. Magill, D. A. Neill, M. Nee, P. H. Raven, H. Stimmel, M. T. Strong, J. L. Villaseñor, J. L. Zarucchi, F. O. Zuloaga, and P. M. Jørgensen. An integrated assessment of the vascular plant species of the Americas. *Science* 358(6370):1614-1617. <https://doi.org/10.1126/science.aao0398>.
- Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, E. Gianoli, M. van Kleunen, D. E. Naya, A. B. Nicotra, H. Poorter, and M. A. Zavala. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* 17:1351-1364. <https://doi.org/10.1111/ele.12348>.
- Vincent, H., J. Wiersema, S. Kell, H. Fielder, S. Dobbie, N. P. Castañeda-Álvarez, L. Guarino, R. Eastwood, B. León, and N. Maxted. 2013. A prioritized crop wild relative inventory to help underpin global food security. *Biological Conservation* 167:265-275. <https://doi.org/10.1016/j.biocon.2013.08.011>.
- Yang, X., S. P. S. Kushwaha, S. Saran, J. Xu, and P. S. Roy. 2013. Maxent modeling for predicting the potential distribution of medicinal plant, *Justicia adhatoda* L. in Lesser Himalayan foothills. *Ecological Engineering* 51:83-87. <https://doi.org/10.1016/j.ecoleng.2012.12.004>.