Niche conservatism in a plant with long invasion history: the case of the Peruvian peppertree (*Schinus molle*, Anacardiaceae) in Mexico

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Background and aim – Invasive plants should only colonize habitats meeting the environmental conditions included in their native niches. However, if they invade habitats with novel environmental conditions, this can induce shifts in their niches. This may occur in plants with long invasion histories because they interacted with the environmental conditions of invaded regions over long periods of time. We focused on this issue and evaluated whether the niche of the oldest plant invader reported in Mexico, the Peruvian peppertree, is still conserved after almost 500 years of invasion history.

Methods – We compared climatic niches of the species between the native and invaded region. We later used species distribution models (SDM) to visualize the geographical expression of both niches in Mexico.

Results – The invasive niche of the Peruvian peppertree is fully nested within the native niche. Although this suggests that the niche is conserved, this also indicates that a large fraction of the native niche is empty in the invaded region. The SDM from the native region indicated that Mexico contains habitats meeting the conditions included in this empty fraction of the native niche and, thus, this invasion should continue expanding. Nevertheless, the SDM calibrated with data from the invaded region indicated that peppertrees have colonized all suitable habitats indicated by its invasive niche and, thus, their populations should no longer expand.

Conclusion – Our results suggests that the niche of the Peruvian peppertree is partially conserved in Mexico. This may have occurred because individuals introduced into Mexico constituted a small, nonrepresentative sample of the full niche of the species.

Keywords – Biogeographic equilibrium; biological invasion; climatic niche; distribution range; niche shift; niche conservatism; species distribution models.

INTRODUCTION

Climate is a primary barrier that constrains the establishment of alien plants after they arrive to new regions (Richardson et al. 2000; Alexander & Edwards 2010). Overall, biological invasions occur if alien species propagate beyond the site they arrived without human intervention (Richardson et al. 2000). If there are no dispersal limitations, these species will advance on the geographical space colonizing habitats that meet the climatic conditions required for their survival, and this process will continue until they reach the biogeographic equilibrium in the invaded area – i.e., when all climatically suitable habitats have been colonized (Václavík & Meentemeyer 2011; Peña-Gómez et al. 2014). Thus, estimating the distribution range of alien plants at the biogeographic equilibrium is critical for monitoring their spread (Céréghino et al. 2005).

Predicting the distribution ranges of alien plants at the biogeographic equilibrium usually assumes that the niche properties of species are conserved upon their arrival to new regions and, thus, climate matching approaches can be used (Wiens & Graham 2005; Sexton et al. 2009). This implies modelling the climatic conditions that define the distribution of species in their native regions and later projecting them on regions susceptible to be invaded (Wiens et al. 2010). However, if alien plants colonize habitats with novel climatic conditions, the ecological niches should differ between invaded and native regions (Gallagher et al. 2010; Broennimann et al. 2012). In this latter scenario, the niche conservatism principle is no longer useful to predict the biogeographic equilibrium of plants in invaded regions. This can occur in plants with long invasion histories, as they interacted with the climate of invaded regions over extensive periods of time and might have been subjected to new selective pressures that ultimately modified their original niches.

In this study, we focused on the biological invasion of the Peruvian peppertree (*Schinus molle* L., Anacardiaceae) in Mexico and assessed whether the niche of this alien tree is conserved. As far as we are aware, this is the oldest plant invasion documented in the American Continent, which resulted from the commercial exchange between the former Spanish viceroyalties of Peru (currently Peru, Bolivia, Ecuador and Colombia) and New Spain (currently Mexico, southern USA and Central America). This tree was introduced in the Valley of Mexico (central Mexico) by the middle of the 16th century, when the Peruvian viceroy sent seeds to New Spain arguing that the fast growth of peppertrees in semiarid environments could help people to quickly obtain raw materials (Alzate-Ramírez 1831; Jimenez 1875). For this reason, humans propagated peppertrees across Mexico during the last five centuries (Ramírez-Albores et al. 2016). Today, however, this tree is naturally recruiting in abandoned fields and disturbed areas (Ramírez-Albores & Badano 2013).

With almost five centuries of invasion history, the Peruvian peppertree offers a unique opportunity for assessing the long-term processes that regulate the spread of plant biological invasions. For this, we compared the climatic niches of the Peruvian peppertree between its native and invaded region. If the climatic niche properties of the species are conserved, its maximum distribution range in Mexico (at

the biogeographic equilibrium) should be defined by the climatic conditions that determine its distribution in the native region. Otherwise, if native and invasive niches partially or fully differ, the niche conservatism principle no longer applies, and it could be proposed that peppertrees are spreading under novel climatic conditions.

MATERIALS AND METHODS

Occurrence data of peppertrees

To compare the climatic niches of the Peruvian peppertree between its native region and the invaded region on which this study focuses (Mexico), we looked for occurrence points of this species in different databases available on the internet (table 1). We visualized these data in Google Earth Pro 7.3 (Google LLC 2018) and realized that this species occurs in different countries of Africa, America, Asia, Europe and Oceania. For this study, we only retained occurrence points located in the target invaded region (Mexico) and the region from which this species is native (Peru and Bolivia, according to Jaksic & Castro-Morales 2013). Because peppertrees are widely used as ornamental plants in both regions (Rodríguez-Laredo 2011; Ramírez-Albores & Badano 2013), we removed all points located in human settlements to prevent including occurrences subsidized by man (i.e., planted trees to which humans provide care to ensure their survival and growth), which can induce the presence of the species in sites where climate is not suitable for its development (Sax et al. 2013). We also looked for occurrence points located less than 1 km from each other and, in these cases, we only retained one of them to prevent biases due to overfitting of climatic niches (Elith et al. 2006).

This resulted in a database with 81 occurrence records for the native region (supplementary file 1). In Mexico, however, most occurrence points gathered from databases were located within human settlements, indicating that the occurrence of the species is strongly subsidized by man. For this reason, between August 2012 and July 2016, we conducted a series of field sampling trips across Mexico looking for naturally established peppertrees. The area that we sampled with this procedure ranged from 32.1°N to 15.2°N of latitude and from 92.1°W to 116.5°W of longitude, covering more than 88% of the continental surface of Mexico. During these field trips, we sampled plants at a minimum distance of 20 linear kilometres from each other and we always avoided sampling near human settlements to prevent including man-subsidized presences. At each sampling point, two well-trained observers (J.E. Ramírez-Albores and E.I. Badano) looked for naturally established peppertrees in a radius of 100 m, but sites where the species was absent were also recorded. Naturally established peppertrees are easy to recognize in the field because they grow isolated from conspecific individuals, while man-planted trees are usually located on the side of rural roads and cattle wirings. This resulted in 127 occurrence records of naturally established peppertrees and 209 points in which the species was absent.

Table 1 – Databases consulted to gather occurrence points of Peruvian peppertrees.
The table indicates that name of the name of the database provider, its webpage and the consulting date.

Database	Internet address	Date
Botanic Gardens Conservation International	https://www.bgci.org	2 Oct. 2016
New York Botanical Garden	http://sweetgum.nybg.org/science/vh	7 Nov. 2016
Center for Invasive Species and Ecosystem Health	https://www.bugwood.org	11 Oct. 2016
Consortium of Midwest Herbaria	http://midwestherbaria.org/portal	3 Dec. 2016
Global Biodiversity Information Facility	https://www.gbif.org	8 Oct. 2016
Global Invasive Species Information Network	http://www.gisin.org	17 Nov. 2016
Instituto de Botanica Darwinion	http://www.darwin.edu.ar	26 Oct. 2016
Intermountain Regional Herbarium Network	http://intermountainbiota.org	19 Sept. 2016
Natural History Museum	http://www.nhm.ac.uk	3 Nov. 2016
Southwest Environmental Information Network	http://swbiodiversity.org/seinet	14 Dec. 2016
Missouri Botanical Garden	http://www.tropicos.org	28 Sep. 2016
CONABIO-Biodiversidad Mexicana	https://www.biodiversidad.gob.mx	15 Jul. 2019

Climatic variables

Comparing climatic niches relies on the environmental variables associated to occurrence points of the target species. We gathered 19 bioclimatic variables from the layers of WorldClim 2.0 (Fick & Hijmans 2017). These layers are provided at a spatial resolution of 30 arc seconds (about 1 km^2 per pixel) and they were processed with ArcGis v.9 (ESRI 2011). In all analyses described below, the continental surface of Peru and Bolivia was used as background area of the native region, while the continental surface of Mexico was used as background area of the invaded region. Bioclimatic variables were complemented with elevation, which was obtained from the digital elevation models of the National Institute of Statistics and Geography of Mexico (available at www.inegi.org.mx).

As several environmental variables are usually spatially auto-correlated (Beaumont et al. 2005), we run Spearman correlations between all pairwise combinations of variables to minimize their redundancy (Elith et al. 2011). These analyses were run in R v.3.4 (The R Foundation 2018) looking for relationships with rank correlation coefficients above 0.70 (Warren et al. 2008). When several variables were related among them, we retained that one with higher correlation coefficients with most others (Elith et al. 2011). This resulted in a set of nine environmental variables for both, the native and invaded regions (table 2).

Niche conservatism

We compared climatic niches of the Peruvian peppertree between its native and invaded region by running a principal component analyses (PCA). For this analysis, environmental data associated to occurrence points were converted into occurrence densities using a kernel function, as this is required to smooth their distribution in the multidimensional ordination space (Broennimann et al. 2012). After that, we calculated the Schoener's similarity index (*D*) to estimate the degree of overlap between climatic niches. This index was computed as: , where and are occurrence densities at each ith point of the ordination space for the native and invaded regions, respectively (Warren et al. 2008). Values of *D* vary between 0 (zero) and 1 (one), where values close to 0 indicate low conserved niches and values close to 1 indicate highly conserved niches (Schoener 1970). To assess the statistical significance of this value, we generated 100 random niches for each region using Monte Carlo resampling procedures and computed the respective *D*-value at each run. Our null hypothesis stated that climatic niches are similar between regions if the empirical *D*-value does not differ from random values in 95% of the cases. Otherwise, the species is assumed to have different climatic niches between regions (i.e., the empirical *D*-value is higher or lower than those expected by chance). These analyses were conducted with the R-scripts of Broennimann et al. (2012).

Differences between climatic niches were also evaluated using the criteria of Petitpierre et al. (2012). This approach proposed that niche models derived from the PCA can show three distinctive zones. The first one is the *stable zone*, which comprises the fraction of the niche shared between native and invaded regions and indicates how much the niche of the species is conserved; this value is computed as the proportion of occurrence densities of the invaded region dropping within the native niche of the species. These authors also propose an *unfilled zone*, which is the fraction of the native niche that the species has not yet occupied in the invaded region; this value is computed as the proportion of occurrence densities of the native region dropping outside the invasive niche of the species. Finally, there is an *expansion zone* (*E*) that indicates the new environments that the species has occupied in the invaded region; this value is computed as the

Table 2 – Environmental variables used to model the climatic niches of the Peruvian peppertree in its invasive range (Mexico) and native range (Peru and Bolivia) using PCA.
The table also indicates the percent contribution of each variable to explain variance in the species distribution models (SDM) calibrated for the invasive and native range of the species.

Environmental variables	Invasive range	Native range
Elevation	8.7%	8.50%
Mean annual temperature	17.1%	18.00%
Mean diurnal range	11.5%	11.50%
Isothermality	35.6%	35.40%
Annual precipitation	18.6%	18.40%
Precipitation seasonality	3.5%	3.50%
Precipitation of driest month of the year	1.8%	1.70%
Precipitation of wettest month of the year	1.6%	1.50%
Precipitation of warmest quarter of the year	1.6%	1.50%

proportion of occurrence densities of the invaded region that are not shared with the native region. The values of these niche zones were estimated with the R-scripts of Petitpierre et al. (2012) using the smoothed portions of niches at 75% of similarity between the native and invaded regions, regarding 100% of background similarity between these areas.

Biogeographic equilibrium

We used a PCA ordination similar to that described in the former section to assess whether the Peruvian peppertree has reached its biogeographic equilibrium in Mexico. In this analysis, we compared the environmental conditions of sites where peppertrees were recorded in this country (i.e., the climatic niche shaped by presence data) against those of sites where the species was not detected (i.e., the climatic space shaped by absence data). After that, we also computed the Schoener's similarity index (*D*) between these two ordination spaces and used the same resampling protocol described above to assess the significance of this value. Peppertrees were assumed to have reached the biogeographic equilibrium in Mexico if these climatic spaces do not overlap (i.e., the empirical *D*-value differs from those expected by chance), as this would indicate that there are no additional suitable habitats to colonize.

Species distribution models

To visualize climatic niches of the Peruvian peppertrees in the geographical space, we calibrated species distribution models (SDM) with data from the native and invaded regions using MaxEnt v.3.4 (Phillips et al. 2006). Although other methods have been developed to model the distribution of species, we choose MaxEnt because (1) it generates more robust SDM than alternative methods when presence-only data are available (as occurred for the native region of peppertrees considered in this study), (2) these SDM can be transferred across different geographical regions with elevated efficiency, and (3) the SDM generated with MaxEnt procedures usually predict the distribution of the target species

with lower biases than SDM generated with other methods (details about the performance of MaxEnt can be consulted in Wisz et al. 2008; Elith et al. 2011; Manzoor et al. 2018; Draper et al. 2019; Wan et al. 2019).

The native and invasive SDM of the Peruvian peppertree were built with the bootstrap algorithm of MaxEnt, which randomly resampled 100 times 75% of the occurrence data from each region (training points). The remaining 25% of the data was used to assess the accuracy of models (test points) by building traditional ROC curves (receiver operating characteristic curves) and computing AUC (the area under the ROC curve). Values of AUC range between 0 (zero) and 1 (one), where values close to one indicate that the distribution of the target species is strongly correlated with the environmental variables used to calibrate the model, while values around 0.5 indicate that the model cannot differentiate between true and false occurrences of the species (Fielding & Bell 1997; Elith et al. 2006). The accuracy of SDM was also assessed with the AUC ratio, which summarizes the results of a series of partial ROC curves built over the fraction of the traditional ROC curve in which omission errors (false negatives) are low enough to meet some specific requirement of predictive ability (Peterson et al. 2008; Mas et al. 2013). The AUC ratio ranges between 0 (zero) and 2 (two), where values close to two indicate that the SDM accurately predicts the distribution of the species and values around one indicates that the model have random performance (Peterson et al. 2008). These analyses were conducted with NicheToolBox (Osorio-Olvera et al. 2018) setting an omission error of 0.5 and running 1000 bootstrap interactions for each SDM (native and invasive). After that, a *z*-test was performed to determine whether AUC ratios statistically differed from those expected in random models (i.e., AUC = 1.0).

The geographical expression of SDM are maps of occurrence probabilities for the species across the target region, which are provided at the same spatial resolution than the environmental variables used to calibrate them (approx. 1 km² per pixel, in our case). The SDM calibrated with occurrence

data from the native and invaded regions, respectively, were projected to Mexico in order to assess whether the distribution ranges of peppertrees they predict at the biogeographic equilibrium concurred. If the climatic niche of the Peruvian peppertree is conserved in Mexico, both SDM should predict similar distribution ranges. After that, both SDM were reciprocally projected on the native region of the Peruvian peppertree to corroborate these results.

RESULTS

Niche conservatism

The first two axes of the PCA used to compare the climatic niches of peppertrees between the native and invaded region explained 83.7% of variance across environmental data. The first PCA axis explained 65.4% of variance and the second axis explained 18.3% of variance (fig. 1). This analysis indicated that the climatic niche of invasive peppertrees is nested within the climatic niche estimated for the native region of the species. However, similarity between climatic niches was significantly lower than expected by chance (Schoener's similarity index $D = 0.364$, $p < 0.001$), indicating that the climatic niche of peppertrees in Mexico is not conserved.

The analyses performed with the criteria of Petitpierre et al. (2012) estimated a *stable zone* close to 100% (value = 0.999), which indicates that the climatic niche of invasive peppertrees is fully contained within the native climatic niche (fig. 1). These analyses also estimated an *unfilled zone* (fig 1) indicating that more than the half of the native niche

is empty in the invaded region (value = 0.641). Finally, these analyses estimated that the *expansion zone* (fig. 1) is almost negligible in the invaded region ($E < 0.001$).

Biogeographic equilibrium

The first two axes of the PCA addressed to compare environmental conditions associated with presences and absences of peppertrees in Mexico explained 66.3% of the total variance in the ordination space. The first axis explained 42.8% of variance, while the second axis explained 23.5% of variance (fig. 2). Similarity between these climatic envelopes was lower than expected by chance (Schoener's similarity index $D = 0.074$, $p = 0.027$), indicating that climate in sites where peppertrees are absent is not appropriate for the survival of the species.

Species distribution models

Among the environmental variables used to calibrate the SDM of the Peruvian peppertree, isothermality explained more than 30% of variance in the distribution of the species in both, the native and invaded region (table 2). It was followed by annual precipitation and mean annual temperature, which explained 17–18% of variance (table 2). The other environmental variables explained less than 12% of variance in the distribution of the species (table 2). AUC values computed from traditional ROC curves were close to one in the native and invaded regions (0.973 and 0.926, respectively). On the other hand, AUC ratios from both regions were significantly higher than one (1.845 for the native region and
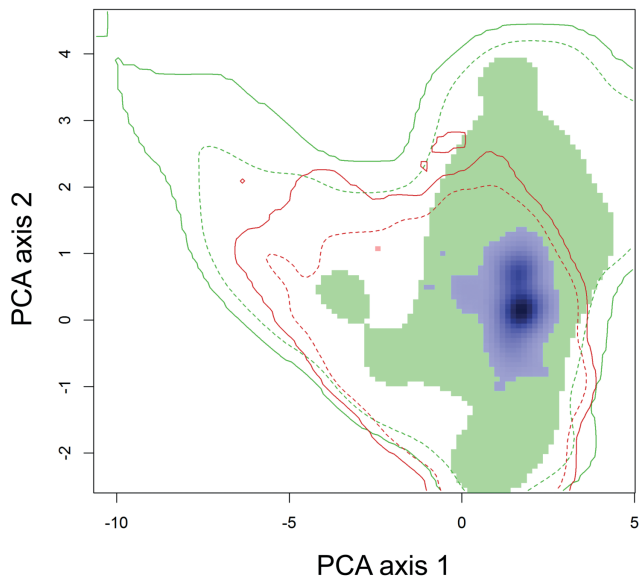
Figure 1 – Principal component analysis (PCA) comparing the climatic niches of the Peruvian peppertree between the native and invaded region. Contour lines indicate 100% (solid lines) and 75% (dashed lines) of the climatic environment that is available in the native region (green lines) and the invaded region (red lines). Coloured areas are the *stable zone* (blue area), the *unfilled zone* (green area) and *expansion zone* (red area) proposed by Petitpierre et al. (2012).
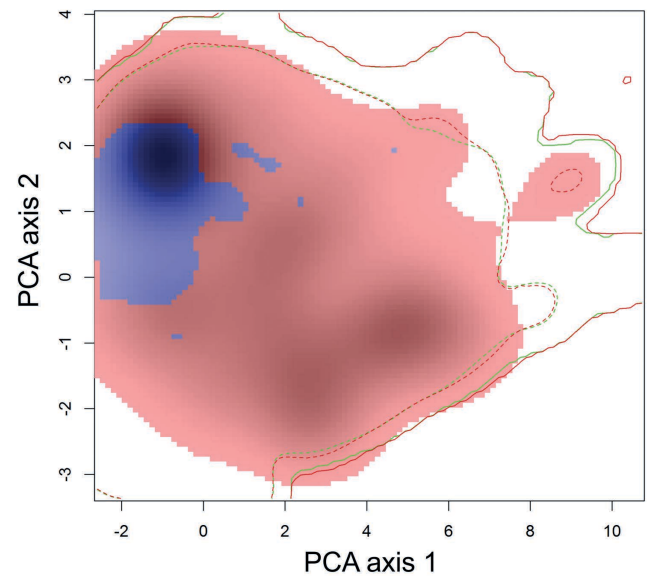
Figure 2 – Principal component analysis (PCA) comparing climatic envelopes associated with data of presence (blue area) and absence (red area) of Peruvian peppertrees in Mexico. Contour lines indicate 100% (solid lines) and 75% (dashed lines) of the climatic environment covered by sites where the species is present (green lines) or absent (red lines).

1.878 for the invaded region). These results indicate that the SDM calibrated for the native and invaded regions predict the distribution of the species with elevated accuracy.

For the interpretation of these SDM, we used the lower 10% percentile of models obtained with training data to define the threshold that discriminates between suitable and unsuitable habitats for the species. In other words, geographic areas with probability values below 0.1 were assumed as unsuitable climatic zones for peppertrees (fig. 3). Considering this minimum probability threshold, the SDM calibrated with data of the native and the invaded regions were projected to Mexico to assess whether predicted distributions of peppertrees concurred or differed. The SDM calibrated with data from the native region predicted that the distribution of peppertrees at the biogeographic equilibrium should cover about 57% of continental surface of Mexico, displaying increasing occurrence probabilities in north-south direction (fig. 3A). On the other hand, the SDM calibrated with data of the invaded region predicted that the distribution range of peppertrees should cover less than 25% of the surface area of

this country, with higher occurrence probabilities in the valleys of central Mexico (fig. 3B). When predictions of these models were overlapped, the distribution range of peppertrees estimated with data from Mexico was almost completely nested (99% of overlapping) within that predicted by the SDM calibrated with data form the native region.

These SDM models were later projected to the native region of the Peruvian peppertree (Peru and Bolivia) and the same criteria described above were used to predict the potential distribution the species. The SDM model calibrated with occurrence data from Peru and Bolivia indicated that the native range of the Peruvian peppertree should cover about 38% of the surface area of these countries (fig. 3C). On the other hand, the SDM calibrated with data from Mexico predicted a narrower distribution range which covered less than 10% of that region (fig. 3D). Predictions of these SDM were highly overlapped in the native region (91% of overlapping), indicating that the distribution range of peppertrees predicted with data from Mexico was almost completely nested within
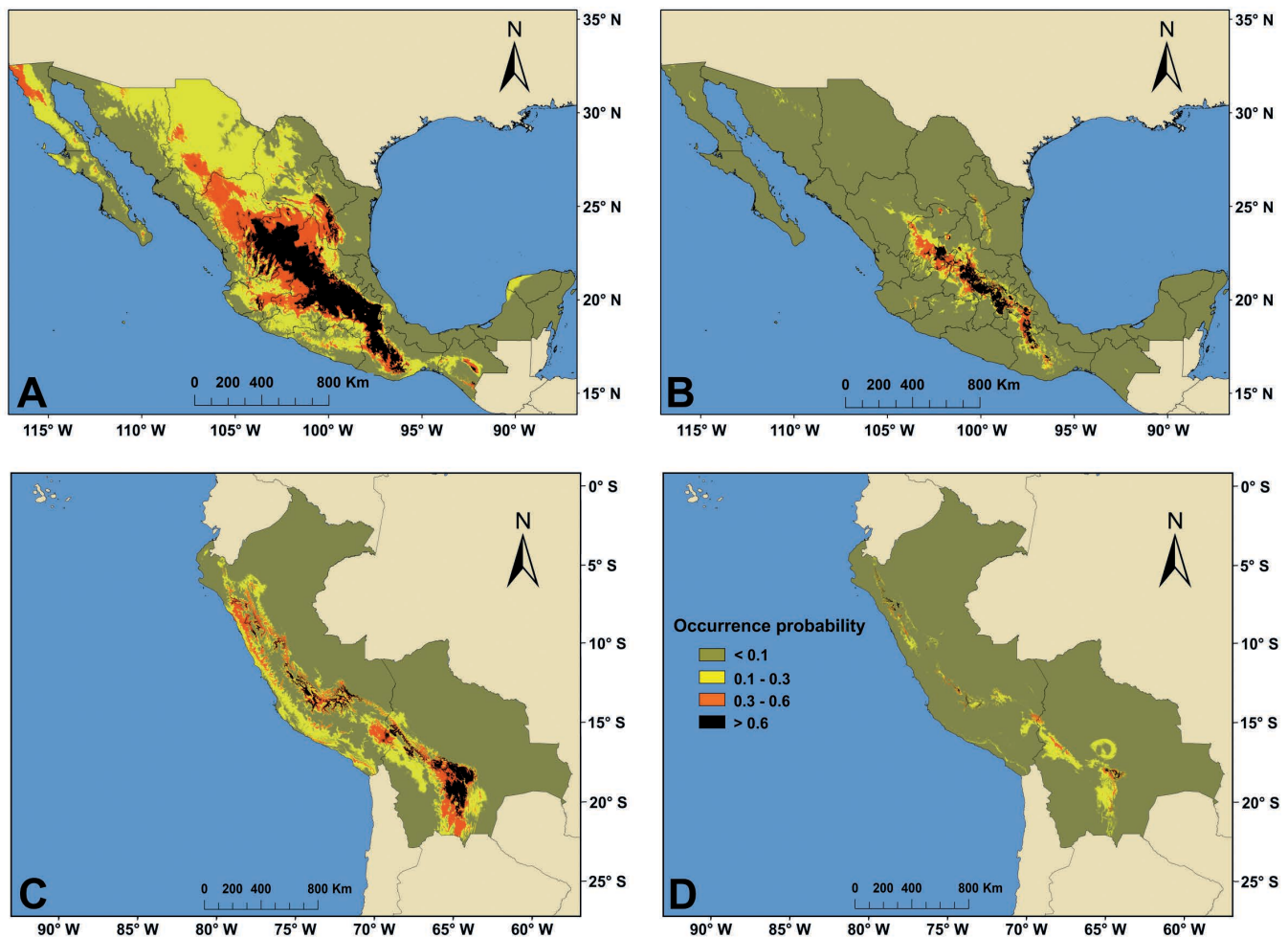
Figure 3 – Species distribution models (SDM) of the Peruvian peppertree projected to the geographic areas in which the species is invasive (Mexico) and native (Peru and Bolivia). **A**. SDM calibrated with data from the native region projected to the invaded area. **B**. SDM calibrated with data from the invaded region projected to the invaded area. **C**. SDM calibrated with data from the native region projected to the native area. **D**. SDM calibrated with data from the invaded region projected to the native area.

the distribution range predicted with data from Peru and Bolivia.

DISCUSSION

Our results suggest that the climatic niche of the Peruvian peppertree is conserved in Mexico, which is expected to occur when invasive plants colonize habitats that are environmentally similar to those they occupy in their native regions (Gallagher et al. 2010). Nevertheless, our analyses also indicated that the climatic niche of peppertrees in Mexico is fully nested within its native niche (i.e., *stable zone* ≈ 100%), while a large portion of the native niche is not occupied in the invaded region (i.e., *unfilled zone* > 60%). This partial filling of the native niche in the invaded region has been reported for other invasive plants (Petitpierre et al. 2012; Goncalves et al. 2014; Kolanowska & Konowalik 2014; Peña-Gómez et al. 2014), and there are several reason reasons by which this may occur with the Peruvian peppertree in Mexico.

The nesting of the invasive niche within the native niche indicates that peppertrees in Mexico have only colonized a fraction of the environments that are climatically suitable for their development and, thus, it could be suggested that this species will continue expanding its distribution range in this country. The projection of the SDM calibrated with data from the native region to Mexico reinforces this suggestion, as this procedure indicated that invasive peppertrees occupy the half of the surface area that meets the climatic conditions required for their establishment, according with the native climatic niche of the species. However, in opposition with these results, the comparison of climatic envelopes associated with presences and absences of the Peruvian peppertree in Mexico indicated that the species has colonized all climatically suitable habitats in this country (i.e., it has reached the biogeographic equilibrium) and, thus, no further expansion of this biological invasion should be expected to occur. This apparent contradiction between the results of our analyses could be explained by the manner in which humans intervened in the introduction of this species into Mexico.

When human activities translocate species across biogeographic areas, the provenance of introduced individuals often constitutes a biased sample of the genetic variability contained in original populations (Ward 2006; Chun et al. 2009). Therefore, invasive plants may fail in occupying the whole variability of climatic conditions included in their native niches, even when these conditions are available in the invaded regions (Early & Sax 2014; Alexander 2016). This may be the case of the Peruvian peppertree in Mexico, as the projection of the SDM calibrated with data from the invaded region to the native region suggests that the seeds introduced to Mexico came from populations that cover less than 10% of the full range of climatic conditions over which this species spread in its native region. Indeed, as far as we are aware, the Peruvian peppertree was introduced in this country only once, by the middle of the 16th century (Alzate-Ramírez 1831; Jimenez 1875; Kramer 1957; Ramírez-Albores et al. 2016), and no further introductions were reported since that date. Thus, as no genetic rescues occurred along the invasion history of the species (i.e., increased genetic variability due to reintroductions), invasive peppertrees per-

haps experienced a genetic bottleneck because a small, random and nonrepresentative fraction of the full niche of the species was captured when seeds were harvested in the native region. Although testing this proposal would also require comparing genetic profiles between the native and invasive peppertrees, our results are consistent with those of authors that reported severe genetic bottlenecks when invasive plants are introduced into new regions (Dlugosch & Parker 2008; Prentis et al. 2009).

The results of our study contradict those of authors that have analysed the invasion processes of the Peruvian peppertree in other countries. In South Africa, for example, the invasive potential of this species is elevated because individuals produce large seed sets that are successfully dispersed by birds, while amelioration of harsh environmental conditions beneath the canopy of native and alien trees facilitates the establishment and growth of peppertree seedlings (Iponga et al. 2009a, 2009b, 2010). However, in opposition with our results, this biological invasion is predicted to continue expanding in South Africa, as niche modelling approaches performed with occurrence data gathered in the field (as our case) indicate that the species has not yet reached the biogeographic equilibrium in this country (Richardson et al. 2010). This discrepancy between Mexico and South Africa may be due to differences in invasion histories, as the Peruvian peppertree has almost five centuries invading Mexico (Ramírez-Albores et al. 2016), while it was introduced about 150 years ago in South Africa (Richardson et al. 2010).

Invasive niches nested within native ones may also have important implications for the control and eradication of invasive plants. For instance, determining the potential distribution ranges of invaders at the biogeographic equilibrium is useful for optimizing the use of resources in programmes addressed to minimize their expansion (Céréghino et al. 2005). Under the assumption of niche conservatism, this can be performed by projecting SDM calibrated with occurrence data of the native region to the invaded region (Gallagher et al. 2010; Broennimann et al. 2012) and resources of control programmes should be mainly allocated to sites where SDM predict higher occurrence probabilities of the species. Although this approach may be used when no occurrence data of the species are available in the invaded region (Peterson & Vieglais 2001, Peterson et al. 2003), our study indicates that the distribution ranges of invasive plants may be oversized if species just preserve a fraction of their native climatic niches. This occurred with the Peruvian peppertree in Mexico, which reached its biogeographic equilibrium without invading all suitable habitats indicated by its native niche. This, in turn, led to a smaller distribution range of invasive peppertrees (less than 25% of the surface of Mexico) than that predicted by the set of environmental conditions that the species uses in its native region (about 57% of the surface of Mexico).

SUPPLEMENTARY FILE

One supplementary file is associated to this paper (Excel file with 3 spreadsheets). It includes longitude and latitude of occurrence points of the Peruvian peppertrees in its native range (Peru and Bolivia), occurrence points of the Peruvi-

an peppertrees in the invasive range (Mexico), and absence points of the Peruvian peppertrees in the invasive range (Mexico):

ACKNOWLEDGMENTS

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Communicating Editor: Alexandra Ley.