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CLIMATIC NICHE CONSERVATISM AND NON-
EQUILIBRIUM IN THE INVASION OF *ESCHSCHOLZIA*
CALIFORNICA (PAPAVERACEAE) IN CENTRAL CHILE

TESIS

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Francisco Tomás R. Peña Gómez

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Director de Tesis: Dr. Ramiro O. Bustamante Araya
Co Director de Tesis: Dr. Pablo C. Guerrero Martin

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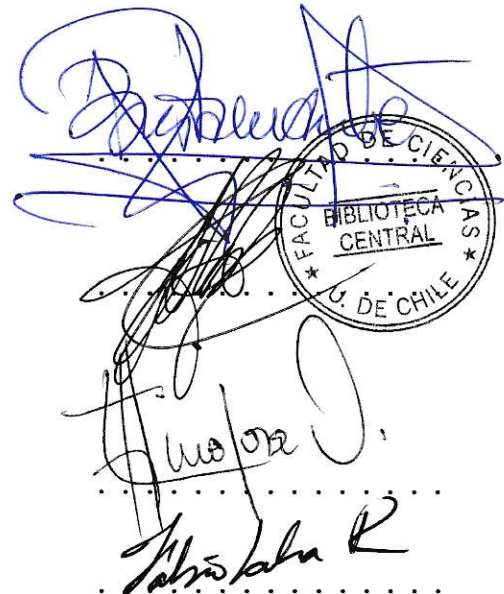
Director de Tesis:
Dr. Ramiro O. Bustamante A.

Co-Director de Tesis
Dr. Pablo C. Guerrero M.

Comisión de Evaluación de la Tesis

Dr. Luis Felipe Hinojosa O.

Dr. Fabio A. Labra R.



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A mi familia...

No busques ser exitoso, ser famoso..... prefiere ser valioso

A. Einstein

INDEX

FIGURES INDEX	<i>vii</i>
ABSTRACT	<i>viii</i>
RESUMEN	<i>ix</i>
INTRODUCTION	2
MATERIALS AND METHODS	6
Study system	6
Species Occurrence Data	7
Climate layers	8
Niche Comparisons	9
Species Distribution Models (SDMs)	10
Reciprocal comparisons between distribution models	11
RESULTS	13
Niche comparison	13
Reciprocal comparisons	14
DISCUSSION	18
BIBLIOGRAPHY	23

FIGURES INDEX

PCA climatic niche of <i>E. californica</i>	15
Mahalanobis distances climatic niche of <i>E. californica</i>	16
Species Distribution Models (SDMs) of <i>E. californica</i>	17



APPENDIX INDEX

Appendix 1	36
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ABSTRACT

Aim: Understanding to what extent the climatic niche is conserved in invasive plants is key to assessing invasion risk. This assumption has recently been challenged by empirical evidence, since niche shifts have been documented in some species, and niche conservatism in others. Here, we test whether climatic niche of *Eschscholzia californica* differs between California (native range) and central Chile (introduced range). Given that these regions exhibit a remarkable similarity in both their geography and climatic configurations, we expected niche conservatism in this plant species which ought to be expressed in similar geographical projections either from the native or the invaded niche.

Location: California and central Chile.

Methods: We used PCA and Mahalanobis distances to compare the climatic niche between Central Chile and California. We used species distribution models (SDMs) and reciprocal comparisons to compare potential distributions projected from the climatic niche in the native range vs the climatic niche projected in the introduced range.

Results: The climatic niche of *E. californica* in Chile is nested within the climatic niche expressed in California. In fact, the climatic niche in the invaded region represents a subset of the whole range of climatic conditions detected for this species in the native region. The SDMs projected in California from the native and invaded range were quite similar, while the SDMs projected in Chile although similar, the areal extent of the distribution projected from the native niche (California) was notably higher than that projected from the invaded niche (Chile).

Main conclusions: The climatic niche of *E. californica* is conserved in the invaded range. The populations of the invaded range are a subsample of the native populations of *E. californica*. In spite that potential distributions projected from the native and invaded range niche are similar as a whole, the extensive area projected from the native range niche, strongly suggests that this species is not in equilibrium in the invaded range, therefore we consider this exotic species to be expanding its range in Chile, in an active invasion process, with the potential to spread to more areas along southern South America.

RESUMEN

Objetivo: Comprender en qué medida los nichos climáticos de las especies exóticas se conservan, es fundamental para evaluar su riesgo de invasión. El conservatismo de nicho ha sido recientemente cuestionado por la evidencia empírica, puesto que, en algunos estudios se han detectado cambios de nicho. En el presente estudio, evaluamos si los nichos climáticos de *Eschscholzia californica*, difieren entre California (rango nativo) y el centro de Chile (rango introducido). Dado que estas regiones presentan una notable similitud, tanto en su geografía y configuraciones climáticas, esperamos conservatismo nicho en esta especie vegetal, lo cual debería expresarse también en una proyección geográfica similar.

Localización: California y centro de Chile

Métodos: Se utilizaron análisis de componentes principales (PCA) y distancias de Mahalanobis para comparar el nicho climático entre el centro de Chile y California. Utilizamos modelos de distribución de especies (SDMs) y comparaciones recíprocas para evaluar las diferencias entre las distribuciones potenciales proyectadas desde el nicho climático nativo versus las proyecciones desde el nicho climático introducido.

Resultados: El nicho climático de *E. californica* es un subconjunto del nicho climático que esta planta expresa en su rango nativo. Así, en el rango invadido, *E. californica* no ocupa todos los requerimientos expresados en su rango nativo. Los SDMs proyectados en California desde el rango nativo e introducido fueron muy similares; los SDMs proyectados en Chile (desde el rango nativo e introducido del nicho) también son similares, pero el área proyectada desde California fue notablemente superior, lo que informa de una mayor cantidad de espacio geográfico potencialmente invasible.

Conclusiones principales: El nicho climático de *E. californica* se conserva en el rango invadido. Las poblaciones del rango introducido son una submuestra de las poblaciones nativas de *E. californica*. A pesar de que la distribución del potencial proyectada desde los nichos del rango nativo e invadido son similares en su conjunto, la mayor extensión areal proyectada desde el nicho nativo en el rango invadido, sugiere que esta especie no está en equilibrio y está en un activo proceso de invasión en Chile Central, con el potencial de dispersarse a otras zonas del sur de Sudamérica.

INTRODUCTION

Human activities (e. g. as international trade, travel, and transport) are the main drivers of biological invasions (Pyšek et al., 2010). This process has led to the progressive mixing of biotas from different parts of the world (Hulme, 2009) and has significantly impacted ecological processes (Sala et al., 2000; Thuiller et al., 2007) and human society (Sharma et al., 2005; Burgiel & Muir, 2010). However, alien species provide unprecedented opportunities to explore the factors that limit the distribution of species (Kozak et al., 2008; Sax et al., 2007; Sexton et al., 2009).

The geographic spread of invasive species is essentially the result of the interaction among their niche requirements with dispersal abilities and biotic interactions (Sexton et al., 2009, Alexander & Edwards, 2010). The ecological niche is the set of abiotic and biotic conditions in which a species is able to persist and reproduce (Hutchinson, 1957). In fact, substantial evidences indicate that environmental variables control species distribution (Gaston, 2003; Pearson & Dawson, 2003; Thuiller et al., 2005).

The reciprocal correspondence between niche and species distribution constitutes a duality (Hutchinson, 1978, Colwell & Rangel, 2009), which offers

an interesting framework for analyzing geographical distribution of invasive species, and constitutes the foundation of species distribution models (SDMs, sensu Elith & Leathwick, 2009). SDMs relate occurrence (and sometimes absence) data with environmental variables, and estimate potential areas of distribution, identifying suitable habitats amenable to colonization (Elith & Leathwick, 2009; Soberón & Nakamura, 2009).

The set of abiotic variables (also called '*scenopoetic*' variables) constitutes the 'Grinnellian' niche (Soberón, 2007) and is important for the understanding of the geographic distribution of species on large spatial scales (Pearson & Dawson, 2003; Soberón, 2007; Peterson et al., 2011). By focusing on the Grinnellian niche, the duality immediately becomes operational, because *scenopoetic* variables can easily be made to correspond to cells in geographic grids (Soberón & Nakamura, 2009). On a broad spatial scale, climatic requirements are the principal determinant of species distributions (Gaston, 2003; Pearson & Dawson, 2003; Thuiller et al., 2005). The climatic correspondence between native and introduced ranges is important for correctly assessing the potential spread of invasive plants (Panetta & Mitchell, 1991; Curnutt, 2000; Pearson & Dawson, 2003; Thuiller et al., 2005).

For an accurate prediction of the extent of invasions relying exclusively using the climate data of the native range, two assumptions must be met: (i) the climatic niche is conserved during invasion, meaning that species tend to retain ecological traits over time (Wiens & Graham, 2005; Wiens, 2010), and (ii) the

invasive species rapidly reaches an equilibrium, this means that are present in all suitable areas and absent in unsuitable areas (Guisan & Thuiller, 2005; Miller, 2010). If the climatic niche is conserved, then it is possible to predict potential invaded areas from native niche requirements (Welk et al., 2002; Peterson et al., 2003; Peterson, 2003; Welk, 2004; Martinez-Meyer & Peterson, 2006).

Contemporary genetic studies demonstrate that adaptation to novel environments in plants can occur within 20 generations or less (Hendry et al., 2007; Rando & Verstrepen, 2007). In this sense, there are several examples of rapid evolutionary change in invasive plants (Leger & Rice, 2003; Maron et al., 2004; Blair & Wolfe 2004; DeWalt et al., 2004; Brown & Eckert 2005; Leger & Rice, 2007; Weinig et al., 2007; Barrett et al., 2008; Dlugosch & Parker; 2008). Similarly, the occurrence of climatic niche shift in the introduced ranges have been documented in plants (Broennimann et al., 2007; Beaumont et al., 2009; Treier et al., 2009; Barbosa et al., 2012). However recent findings revealed that climatic niche shifts are rare in terrestrial plant (Petitpierre et al., 2012). Therefore, it is not trivial assume conservatism or shift, in invasive plant spread. Thus, to elucidate whether invasive species conserved their niche in the invaded range, is becoming an interesting field of research in the biology of invasions.

Eschscholzia californica Cham. (Papaveraceae) is a native herb from the west coast in North America, is particularly interesting to study climatic niche dynamics in the invaded range because the plant size, fecundity, and resistance

to herbivores are significantly higher in the invaded range (central Chile), compared to the native range (California) (Leger & Rice, 2003; Leger & Forister, 2005; Leger & Rice, 2007). Additionally, there are experimental evidences, that suggest adaptive responses in the introduced range (Leger & Rice, 2003; Leger & Rice, 2007). On the other hand, California and central Chile shares very similar climates, topographies and vegetation types (Mooney, 1977; di Castri, 1991; Arroyo et al 2000. Sax, 2002), which might be consistent with an invasion mediated by climatic niche conservatism.

In this study, we assessed the climatic niche and geographic distribution of the invasive species *E. californica* in its native (California) and invaded (central Chile) ranges. Specifically, we will evaluate if the invasion process was promoted by climatic niche conservatism of *E. californica* in the invaded range. Given that central Chile and California exhibit a remarkable similarity of geography and climatic configurations (Mooney, 1977), we expected that the climatic niche of *E. californica* was conserved. If so, we expected that the geographic distribution projected in the invaded range from the native and invaded niche should be similar.



MATERIALS AND METHODS

Study system

The studied regions (California, 32° – 40° N; and central Chile 30° – 38° S) have Mediterranean-type climates, characterized by cold, rainy winters and hot, dry summers (Mooney et al., 1970; di Castri, 1991; Arroyo et al., 1995). Also the topography of the two regions is similar, with a longitudinal valley between two mountain ranges (Jimenez et al., 2007). The regions show a parallel latitudinal-climate gradient with higher precipitation and lower temperatures at higher latitudes, which has shaped convergent vegetation types (Mooney et al., 1970; Arroyo et al., 1995).

Eschscholzia californica is native to western North America. It grows across a wide range of environmental conditions in its native range, occupying open, naturally disturbed and human disturbed environments (Cook, 1962; Leger & Rice, 2003). Also, *E. californica* is a successful invasive species, spreading along Mediterranean climate regions worldwide (Stebbins, 1965). It was intentionally introduced to central Chile during the mid-1800s and early 1900s into botanical gardens, and it spread across vast areas near railroad tracks and

private gardens (Frias et al., 1975; Arroyo et al., 2000; Leger & Rice, 2003). The introduction was also promoted by the trade of alfalfa seeds from California to Chile during the mid-nineteenth century (Gillis, 1885; Hillman & Henry, 1928; Leger & Rice, 2003). In Chile, the first herbarium record (Quintero, central Chile, coast) dates back to 1890 (SGO), and in the present days this species is distributed between 30° and 38° S, and between 0 and 2200 m.a.s.l.

Species Occurrence Data

All recorded occurrences (georeferenced localities) in the native range of *E. californica* were compiled from the 'Consortium of California Herbaria' and 'Calflora' online databases (<http://ucjeps.berkeley.edu/consortium/> and <http://www.calflora.org/> respectively). The data was carefully filtered, in order to satisfied three conditions: (i) each occurrence point should contain accurate georeferenced associated information (i.e. Datum), (ii) the georeferenced point should be recorded after 1950 and (iii) and all points must have an associated voucher or should be identified by a botanist. After pooling and filtering the data from both databases, we obtained a total of 649 occurrence points from California. In the case of Chile, we obtained 50 occurrence points from the Herbarium of the Universidad of Concepción (CONC) and 10 occurrence points from Museo Nacional de Historia Natural (SGO). To increase the number of observations, in Chile, we conducted field recording campaigns during 2009 and 2010 (spring–summer), obtaining 1,500 additional occurrence points.

Climate layers

Climate variables were obtained from WORLDCLIM (<http://www.worldclim.org/>) with a spatial resolution of 30 arc-seconds (Hijmans et al., 2005), including a total of 19 variables, which summarize temperature and precipitation dimensions of the niche. Since collinearity of variables may lead to model overfitting (Beaumont et al., 2005), we selected a sub-sample of variables obtained after a correlation analysis using the SAM package (version 4, Rangel et al., 2010). This analysis, besides measuring the correlation between variables, corrects spatial autocorrelation of data (Rangel et al., 2010). For the selection of variables we used as a criterion that when correlation between pairs of variables was higher than 0.9 (Elith et al., 2006; Flory et al., 2012). Using this criterion, we selected eight variables: mean annual temperature (Bio1); maximum T° warmest month (Bio5); mean T° warmest quarter (Bio10); mean T° coldest quarter (Bio11); annual precipitation (Bio12); P seasonality (Bio15); P warmest quarter (Bio18); P coldest quarter (Bio19) (see Appendix 1a).

Niche Comparisons

A Principal Component Analysis (PCA) was performed to describe the climatic niche of *E. californica* in the native and invaded range (Broennimann et al., 2007). The PCA was conducted on the eight climatic variables, associated with the occurrence data of the species. To evaluate the differences between the climatic niches in Chile and California, we calculated the Mahalanobis distances to discriminate between the niches (Hua & Wiens, 2009). The Mahalanobis distance is the distance of a case to the centroid (a point representing the "means" for all independent variables) in the multidimensional space (Mahalanobis, 1936). We compared the mean value of the Mahalanobis distance (to the native centroid) in invasive occurrences with a histogram of Mahalanobis distances of the native occurrences to the native centroid (California). A significant (one-tailed) test indicates whether similarity (overlap) between native niche range and invaded niche range is more significant than a random distribution. We evaluated the differences between the climatic niches of Chile and California (as described above) from the empirical occurrence data: 1560 for Chile and 649 for California.

Species Distribution Models (SDMs)

SDMs were constructed using Maxent version 3.3.3e (Phillips et al., 2004; 2006). This software predicts species distributions, correlating environmental data with species occurrence. Maxent is a machine-learning method that assesses the probability of distribution of a species by estimating the probability distribution function of maximal entropy (Phillips et al., 2006). The method generally performs better than other software commonly used for SDMs and uses randomly selected pseudo-absences within an *a priori*-defined background area (Elith et al., 2006; Phillips et al., 2006; Ortega-Huerta & Peterson, 2008). Maxent is also more robust to spatial errors in occurrence data and uses only presence datasets to predict species distributions (Phillips et al., 2006; Graham et al., 2008). We divided the occurrence data into two parts for training and testing the model (75% and 25%, respectively). The performance of the model was evaluated using the AUC (area under the curve ROC, Phillips et al., 2006). AUC is a composite measure of model performance, and provides a global comparison of model fit to that of a random prediction. AUC values range from 0 to 1, where 1 is a perfect fit. Useful models produce AUC values of 0.7–0.9, and excellent models produce AUC values above 0.9 (Swets, 1988).

Reciprocal comparisons between distribution models

In order to test niche conservatism, we compared the distribution models using the reciprocal modeling approach (Fitzpatrick et al., 2007; Medley, 2010). Specifically, we did this analysis in two steps: (i) in the invaded area (Chile), we compared the distribution model projected from the native range data (California) with the model projected from invaded range data; (ii) in the native area (California), we compared the distribution model projected from the invaded range data (Chile) with the distribution model obtained from the native range data (Fitzpatrick et al., 2007; Medley, 2010). Thus we obtained four models, two for the native range (constructed with the occurrences from California and the projection from Chilean occurrences) and two models for invaded range (constructed with the occurrences from Chilean and the projection from Californian occurrences). If the climatic niche is conserved, then the potential distribution models projected in Chile and California should not differ from each other (Medley, 2010). All models were replicated 200 times, and then the averages (Flory et al, 2012) of each model were utilized for comparisons.

We evaluated the overlap between two pairs of SDMs (those projected in Chile and those projected in California) using the similarity index J (Corrected Hellinger distance, Warren et al., 2008) which measures the degree of overlap between the predicted distributions. This index ranges from 0 (no similarity) to 1 (total similarity) (Warren et al., 2008, Medley, 2010).

We also evaluated niche conservatism, correlating the occurrence probabilities obtained from SDMs. Specifically, we correlated (i) $P(O)$ projected from the native niche range in the invaded range with $P(O)$ projected from the invaded niche range in the invaded range and (ii) $P(O)$ projected from the invaded niche range in the invaded range with $P(O)$ projected from the native niche range in the invaded range. High correlation values indicate that the pairs of distribution models are similar. We conducted this correlation test using the ENMtools software (Warren et al., 2008).

RESULTS

Niche comparison

The climatic niche of *E. californica* may be described by the first three principal components (PCs). The first PC captures 47.42% of total variability and is correlated primarily with precipitation and temperature variables (Bio 1, Bio 11, Bio 12, Bio 15, Bio 18, Bio 19; see Appendix 1b); the second PC captures 30.06% of total variability and is associated with Bio 5 and Bio 10 (see Climate layers); the third PCA captures 12.91% of total variability and is not strongly associated with any variable. (Fig.1).

The climatic niche of Chile is included in the climatic niche of California; PC 1 is very similar in amplitude in both niches. However, extensive areas of the native climatic niche are not occupied by the invaded niche space (mainly PC 2, Fig. 1). Overall, the Mahalanobis analysis indicates significant similitude between native and invaded niches (Mahalanobis distances obs = 4.107; $P > 0.05$; Fig. 2).

Reciprocal comparisons

Maxent yielded a highly predictive model with an average test AUC value of 0.922 (\pm 0.002) for projected distributions from native niche range and an average test AUC value of 0.976 (\pm 0.002) for projected distributions from invaded niche range. We detected a significant and positive correlation in the invaded range between the P(O) of SDM predicted from the native niche range (California) and the P(O) of SDM predicted from the invasive niche range (Chile) ($r = 0.818$). In the native range, we also detected a positive correlation between the P(O) of SDM predicted from the native niche range and P(O) of SDM predicted from the invasive niche range ($r = 0.930$).

In Chile, the two predicted distributions (from native and invaded niche range) share 74.1% common area, while in California, this values is 94.2% (Fig. 3). The index (I) of overlap (between SDMs predicted from native and invaded niche ranges) in the invaded range was 0.8 (Chile) and in the native range was 0.93 (California).

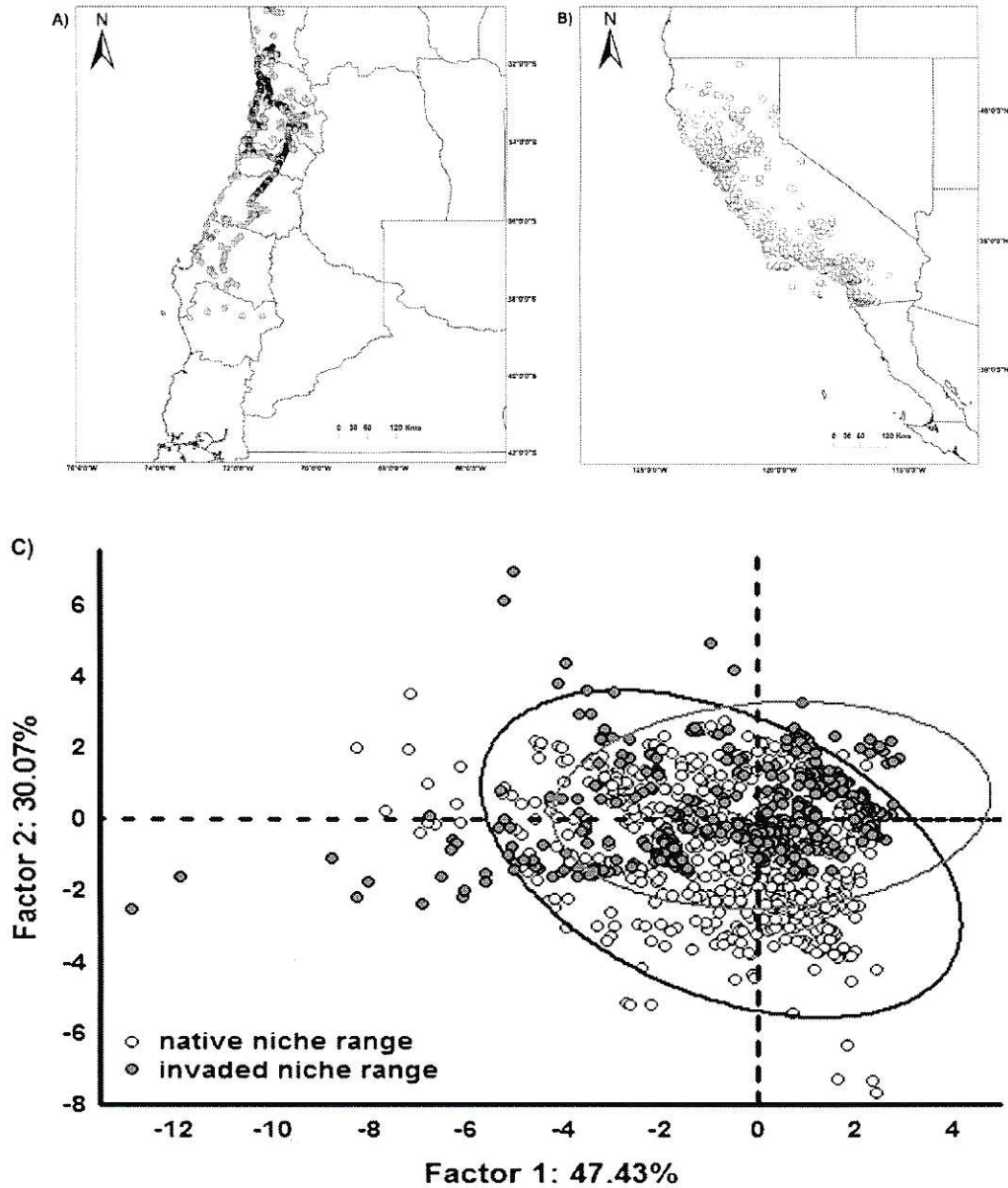


Fig.1. PCA climatic niche of *E.californica*. a) Central Chile and occurrence data from Chile; b) California state and occurrence data from California; c) Climatic niches of invaded and native range are plotted across the first two PCA axes. Ellipses contain 95% of the respective distribution data.

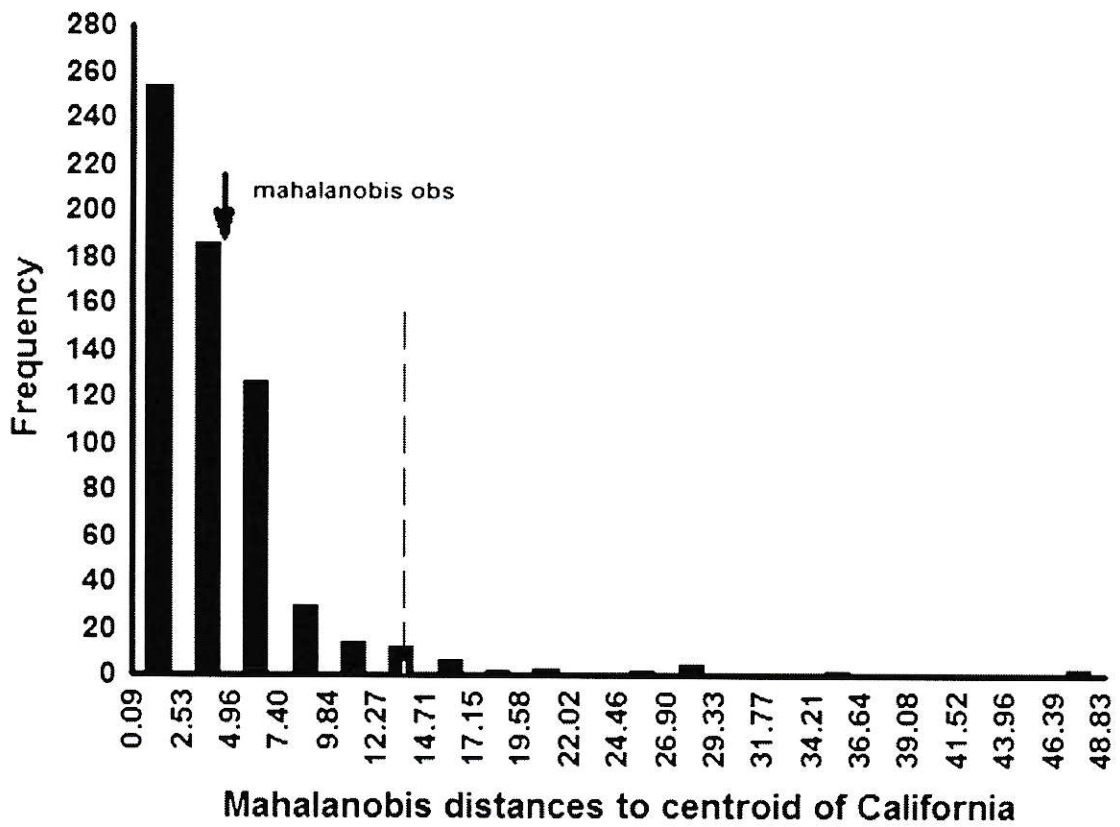


Fig 2. Comparison between Mahalanobis distances calculated from invasive niche range (mean of the observations, Mahalanobis observed) and a histogram of Mahalanobis distances obtained from the native niche range.

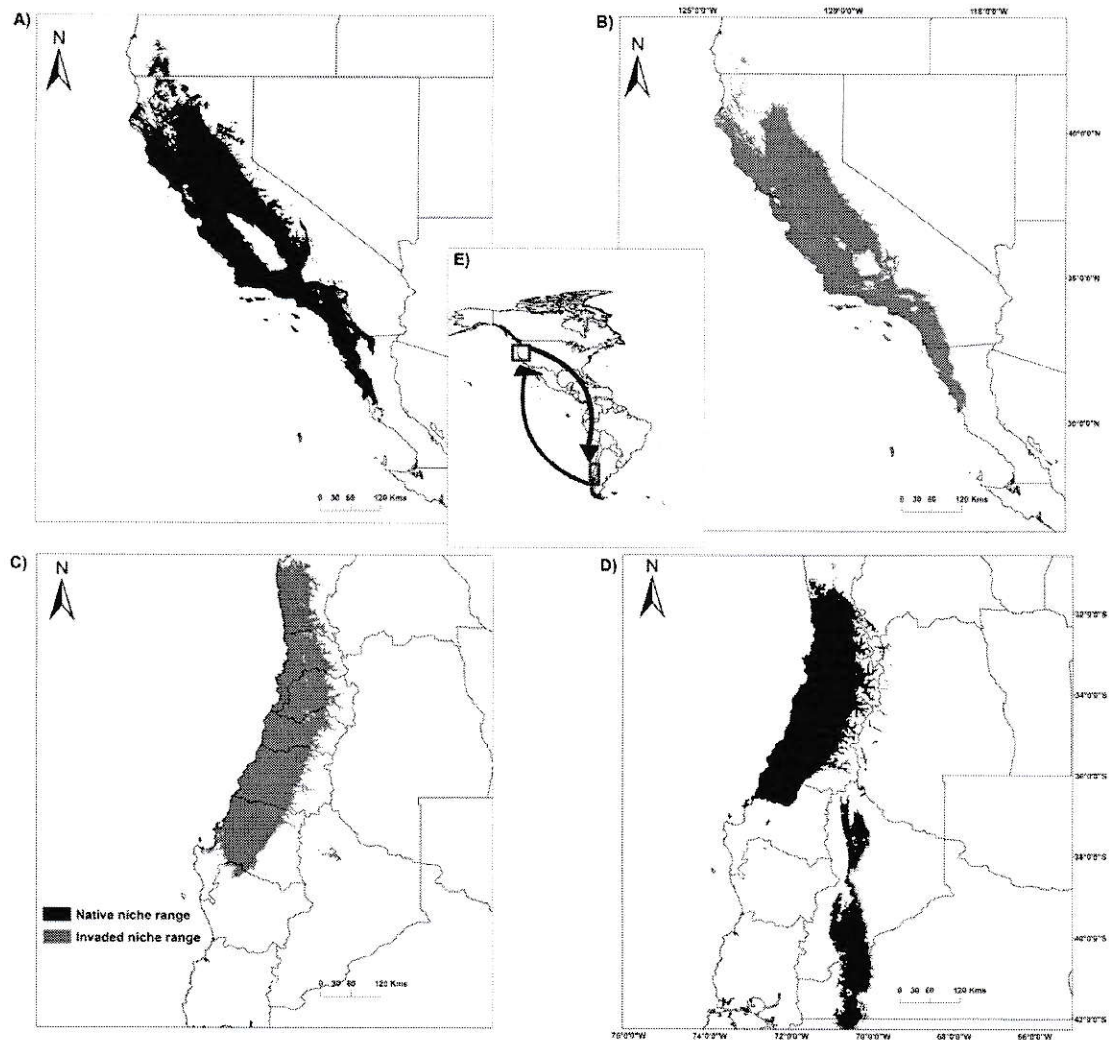


Fig 3. SDMs based upon maximum entropy niche models using environmental data and point occurrences for *E. californica*. Black represents high probability of occurrence (50–100%) projected by the native niche range toward Chile and California. Gray represents high probability of occurrence (50–100%) projected by the invaded niche range toward Chile and California. (A) Native model generated with occurrences in the native range. (B) Invaded niche range (Chile) projected onto California. (C) Native niche range (California) projected onto Chile. (D) Invaded model (Chile) generated with occurrences in the invaded range (Chile). (E) Reciprocal comparisons between distribution models.

DISCUSSION

Our results indicated that the climatic niches of *E. californica* in the native and invaded ranges are statistically similar (Figs. 2); therefore the occupied climatic conditions in the invaded area are equivalent to the native range. The Chilean climatic niche is a sub-set of the native original niche, suggesting that is conserved in the invaded range as populations in Chile and California occurs in homologous climatic areas, also Chilean populations represent a subsample of the Californian populations.

Petitpierre et al. (2012) has observed that climatic niche shifts are rare among terrestrial plant invaders. Using terrestrial plant invaders, these authors found that 85% of the analyzed species conserved their climatic niche after the invasion process. Although previous studies have documented niche shifts in invasive species (Broennimann et al., 2007; Fitzpatrick et al., 2007; Beaumont et al., 2009; Gallagher et al, 2010; Medley, 2010), these changes might be spurious because the studied species might have not reached the equilibrium in the invaded areas as they do not occupy all the available environments predicted by their native niches (Petitpierre et al., 2012). These disequilibria may reflect the ongoing spread of invasive species, dispersal limitation and / or

negative biological interactions (Welk, 2004; Thuiller et al., 2005; Alexander & Edwards, 2010). A similar scenario may be the case in the invasion process of *E. californica* in southwestern South America, where there is a large area of the native niche space not occupied by the populations inhabiting the invaded range (Fig. 1).

Comparisons of SDMs (Fig. 3) showed that the geographic distributions predicted by the niches of the native and invaded ranges are similar between the two ranges (percentage of overlap greater than 70% for both regions, and index I > 0.8 for both regions). Also, correlation analysis indicates that the probabilities of occurrence of SDMs predicted from native and invaded niches, are good predictors of occurrence probabilities of SDMs predicted to the invaded (Chile) and native ranges (California) ($r > 0.8$ for both regions). Both set of analyses support the idea that the climatic niche is conserved in the invasion process of *E. californica*.

SDMs predicted from the native and invasive climatic niches to the invaded range (central Chile), firstly, showed a high overlap in the predicted geographic distributions, suggesting (as we discussed early) climatic niche conservatism. Secondly, this same comparison showed that there are extended areas predicted by the native niche range not yet occupied by *E. californica* in the invaded area. This suggests strongly that *E. californica* is not in equilibrium in the invaded area as SDMs predict larger distributions along southern Chile and Argentinian Patagonia. In fact, we have field observations that some individuals

of *E. californica* are well established in San Carlos de Bariloche (Argentinian Patagonia). However, more quantitative observations are needed to assess this geographic expansion.

Also, comparisons of SDMs projected from the native and invasive climatic niches to the invaded range (central Chile), showed high geographic overlap. These geographic distributions are almost fully nested, which strengthens the argument that populations of *E. californica* in central Chile are a subsample of the California population. Besides, comparisons of SDMs in the native range can inform about the possible zones where the first propagules came out and colonized Chile. In our case the geographical distribution projected to California from the invaded niche, suggests that the colonization of plants to Chile come from diverse localities. This hypothesis can be tested comparing genetic diversity and similarity between populations of Chile and California and to our knowledge has not been tested before.

Another study has found that this plant has finite growth rates > 1 , either in the center of the distribution or in the invasion front in central Chile (Peña-Gomez & Bustamante, 2012). Given these evidences we can conclude that *E. californica* is in active expansion and has not reached the equilibrium along its new environment after more than 120 years of invasion in central Chile (Peña-Gomez & Bustamante, 2012).

One important aspect that deserves more attention is the idea of non-equilibrium of invasive species. The ecological and evolutionary processes underlying the non-equilibrium in the distribution of species has been widely discussed, but its biogeographic consequences have received little attention in the SDMs literature (Svenning & Skov, 2004; Araujo & Pearson, 2005; Pearson et al., 2006; Roura-Pascual et al., 2009). There are few empirical studies in which equilibrium or non-equilibrium support theoretical expectations (Welk, 2004; Roura-Pascual et al., 2009, Václavík & Meentemeyer 2011), as the full environmental niche of invasive species cannot be easily captured with data from actual distribution of species. Therefore, SDMs calibrated under non-equilibrium are less accurate to predict the potential habitat prone to invasion. SDMs of species in early stages of invasion are more likely to under predict potential distribution, than models for species in later stages of invasion (Václavík & Meentemeyer, 2011).

The study of plant invasion considering the analysis of either the climatic niche and the SDMs is a promising way of analysis since it allows us to examine the possibility of niche conservatism (or not) and the equilibrium condition (or not), on two levels: in an abstract space (climatic niche space) and in the geographic space (physical space), with appropriate methodologies in each level.

In this sense, if we want to predict the geographic distribution of an invasive plant, from the climate niche native, we must consider whether the plant conserves its climatic niche and if is in equilibrium. If the niche is conserved and the spread has reached the equilibrium, the potential distribution of invasive

species can be estimated properly. Special care should be made when we try to predict the geographic distribution of an invasive species that is not in equilibrium, given that can lead to underestimating the true potential distribution of the specie. On the other hand, if the niche is not conserved in invaded ranges, SDMs predictions will not adjust to reality. Thus, niche conservatism and equilibrium are very important factors to be taken into account in the predictions of the SDMs, and in this way in the control and management of invasive species. In summary, the climatic niche as well as the potential geographic distribution of species provides different but complementary information. We therefore encourage considering both niche dimension and biogeographic studies of invasive species.

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APPENDIX 1

<http://www.worldclim.org/bioclimate>

Bioclimatic variables are derived from the monthly temperature and rainfall values in order to generate more biologically meaningful variables. These are often used in ecological niche modeling (e.g., BIOCLIM, GARP). The bioclimatic variables represent annual trends (e.g., mean annual temperature, annual precipitation) seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). A quarter is a period of three months (1/4 of the year).

a) Bioclimatic variables selected:

BIO1 = Annual Mean Temperature

BIO5 = Max Temperature of Warmest Month

BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter

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b) PCA Info:

Eigenvalues of correlation matrix				
	Eigenvalue	% Total	Cumulative Eigenvalue	Cumulative
1	3.794009	47.42511	3.794009	47.4251
2	2.405414	30.06767	6.199422	77.4928
3	1.033150	12.91437	7.232572	90.4071
4	0.535712	6.69640	7.768284	97.1035
5	0.200820	2.51026	7.969104	99.6138
6	0.022112	0.27640	7.991216	99.8902
7	0.005219	0.06523	7.996435	99.9554
8	0.003565	0.04456	8.000000	100.0000

Factor loadings of the variables				
	PC 1	PC 2	PC 3	PC 4
BIO1	0.750346	-0.546556	-0.359692	-0.078191
BIO5	0.077590	-0.906001	0.277449	0.284006
BIO10	0.401842	-0.905632	0.047335	0.077638
BIO11	0.763380	-0.077270	-0.587739	-0.246191
BIO12	-0.869752	-0.221256	-0.404000	0.140613
BIO15	0.618941	0.537308	-0.276728	0.430072
BIO18	-0.812462	-0.317457	-0.135303	-0.328716
BIO19	-0.825284	-0.145875	-0.470121	0.263652