*Plant Ecology and Evolution* 148 (3): 318–328, 2015
http://dx.doi.org/10.5091/plecevo.2015.1147

REGULAR PAPER

# Ecological niche similarity between congeneric Mexican plant species

**Mario Ernesto Suárez-Mota[1,*], José Luis Villaseñor[2] & Lauro López-Mata[1]**

[1]Colegio de Postgraduados, Montecillo 56230, Estado de México, México
[2]Instituto de Biología, U.N.A.M. Departamento de Botánica, Apartado Postal 70-367
04510 México, D.F., México
*Author for correspondence: suarezmota.mario@gmail.com

**Background and aims** – Ecological niche conservatism describes the tendency of phylogenetically related species to maintain the characteristics of their ancestral fundamental niches. Our aim was to assess niche conservatism of species belonging to two plant genera of the Family Asteraceae endemic to Mexico: *Dyscritothamnus* includes two woody species restricted to the dry scrublands of central Mexico and *Loxothysanus* includes two herbaceous species distributed mostly in temperate environments from central Mexico southward.
**Methods** – Using geographical distribution data of species obtained from critically reviewed herbarium specimens (45 of *Dyscritothamnus* and 94 of *Loxothysanus*), niche models were obtained using the Maxent program. The climatic variables evaluated were chosen using principal component analysis. Subsequently, with the program ENMTools we quantified the degree of overlap and similarity between the niches of congeneric species using the equivalence ($D$) and similarity ($I$) parameters.
**Key results** – The two species of *Dyscritothamnus* are sympatric, influenced by common environmental features; accordingly, their niches show high equivalence values ($D = 0.563$), suggesting niche conservatism. On the other hand, the genus *Loxothysanus* shows a wider geographical distribution; their species niches are not equivalent ($D = 0.145$) and have a relatively low value of environmental similarity.
**Conclusion** – The distributions of the species of *Dyscritothamnus* support the hypothesis of niche conservatism because of their sisterhood and quite similar distribution patterns that result in high niche conservatism values. In contrast, species of *Loxothysanus* do not support clearly such a hypothesis, suggesting their niches have suffered adaptive changes to contrasting environments.

**Key words** – Niche conservatism and ecological niche modelling, ENMtools, *Dyscritothamnus*, *Loxothysanus*, Asteraceae, Mexico.

## INTRODUCTION

Current environmental conditions determine if species can thrive or not in a particular place. Environmental factors limit species distribution; temperature and rainfall are particularly important (Despland & Houle 1997, Hobbie & Chapin III 1998), and factors such as substrate composition or elevation (among many others) may influence distribution. Elevation, slope, and orientation may be equally strong determinants of the microclimatic conditions required by species to flourish (Archer 1984, McAuliffe 1994, Hsieh et al. 1998, Guerrero-Campo et al. 1999, Burke 2003). Although nearly all habitats in the biosphere are occupied by some plant life, a single species occupies only the geographic space defined as its Grinellian ecological niche (Hutchinson 1957, Brown & Lomolino 1998). Hutchinson (1957) formalized the concept of ecological niche to refer to the set of abiotic and biotic conditions where a species can persist indefinitely; he distinguished a fundamental niche, defined by the set of abiotic conditions interacting with the species and a realized niche, the space of the fundamental niche where the species actually occur (Chase & Leibold 2003).

Niche conservatism is the tendency of closely related species to maintain the characteristics of the fundamental niche occupied by its ancestral taxon; recent studies have highlighted its importance for understanding patterns and processes of speciation and distribution (Peterson et al. 1999, Webb et al. 2002, Wiens 2004, Wiens & Graham 2005, Wiens et al. 2010, Peterson 2011, Prinzing et al. 2001). Authors such as Peterson et al. (1999) conclude that speciation occurs first in a geographical context, with ecological differences appearing later. Differences among congeneric and co-occurring species in a community result from modifications of a shared common ancestor (Webb et al. 2002). Phylogenetically related species that distribute in ecologically similar areas show niche phylogenetic conservatism (Losos 2008). Therefore, niche conservatism is the tendency of lineages to maintain their ancestral ecological niche, failing to adapt to new environments.In recent years, there has been an increasing debate about whether phylogenetically related species occupy similar ecological niches, which would suggest niche conservatism (Harvey & Pagel 1991, Peterson et al. 1999, Pyron et al. 2014). Related species showing niche conservatism, when confronted with climate change scenarios, will adapt slower to environmental changes, facing an increased risk of extinction (Petitpierre et al. 2012). In contrast, with more divergent niches species can cope more easily with changing climate, colonize or invade new areas (Petitpierre et al. 2012), and decrease their risk of extinction. The niche conservatism concept can help to predict the impact of climatic change on species adaptation to new environments in space and/or time (Sinervo et al. 2010).

Several authors have proposed explanations for the existence of niche conservatism. For example, Harvey & Pagel (1991) proposed a scenario in which an empty ecological space is filled during dispersion (mobilism) of one or more species groups with similar ecological affinities; once the species groups become established in the new space, diversification then generates speciation. Stabilizing selection would then reinforce this situation; since all available spaces are already allocated, the sympatric species best adapted to the ecosystem ecological factors would prevent them from departing from their niche. Other authors (Wiens & Graham 2005) added genetic factors to these two scenarios. Gene flow limitations and low genetic variability are also proposed as stabilizing elements that impede flexibility that could shift a population's niche.

Peterson et al. (1999) propose that speciation occurs first in a geographic context and that ecological differences evolve later. Testing niche similarity to determine whether environmental niche models between closely related species predict their occurrences, they conclude that niches are conserved (Peterson et al. 1999, Kambhampati & Peterson 2007, Peterson & Nyári 2007). They also developed methods to measure niche similarity between species and attempt to test hypotheses about niche conservatism (Peterson et al. 1999).

Recently, Warren et al. (2008) developed tests/procedures for estimating ecological niche model (ENMs) similarity and equivalence and their degree of conservatism along the phylogeny. Niche similarity refers to how well the ENM of one species predicts the geographical presence of another, compared to the performance of a null model. Niche equivalence refers to how interchangeably two species can occupy each other's ENM-predicted geographical space (i.e. if their ecological niche models are indistinguishable from one another; Warren et al. 2008).

To assess similarity and equivalence, Warren et al. (2008) devised two measures of niche overlap (*D* and *I* parameters), which were submitted to different statistical tests to quantify both similarity and equivalence of niches. The first parameter (hereafter, *D*) is derived from Schoener's Index (Schoener 1970), used in ecology to quantifying the degree of niche overlap among species. The second parameter (hereafter, *I*), is derived from Hellinger's Distance (H), which compares probability distributions for both species in the environmental space (Warren et al. 2008, Peterson 2011). Both parameters can assume values between 0, indicating no overlap (or complete difference), to 1, indicating that the models overlap completely (are identical).

The use of species ecological niche models (ENMs) has increased in recent years (Guisan & Zimmermann 2000, Soberón & Peterson 2004, Graham et al. 2004, Araújo et al. 2005, Elith et al. 2006, Thuiller et al. 2009), to the point that ecological niche modelling is considered an emerging approach of ecology, biogeography, and conservation biology. ENMs are also used in analyses of niche conservatism among phylogenetically related species (Wiens 2004), or in cases of invasive species that have established in areas with different environmental conditions to their native area, suggesting they have increased the breadth of their fundamental niches (Medley 2010). The use of an algorithm such as Maxent to model potential ecological niches, also allows the estimation of potential species distribution in regions where they are not reported yet, but having the right conditions for their establishment (Elith et al. 2006, Peterson et al. 2007, Phillips 2008, Phillips & Dudik 2008).

This paper evaluates potential niche conservatism in two genera of flowering plants of the family Asteraceae endemic to Mexico. Each genus contains only two taxonomically accepted species. This warrants taxonomic sisterhood, since no known fossil record suggests intermediate forms. The genera and species are *Dyscritothamnus filifolius* B.L.Rob., *D. mirandae* Paray, *Loxothysanus pedunculatus* Rydb., and *L. sinuatus* (Less.) B.L.Rob. The aim of this study was to assess, using ecological niche models estimated using a set of environmental variables, how similar and equivalent are their niches and hence infer whether exists niche conservatism between species pairs.

To evaluate potential niche conservatism, we collated geographical distribution data (georeferences) for all four species from specimens deposited in several Mexican herbaria. With the data obtained, we generated ecological niche models for each species using the maximum entropy algorithm implemented in the Maxent package (Phillips 2008, Phillips & Dudik 2008). Subsequently, with the package ENMTools we evaluated overlapping between sites covered by the models using the parameters of equivalence and similarity (Schoener 1968, Warren et al. 2008).

## METHODS

We selected two genera of Asteraceae endemic to Mexico, *Dyscritothamnus* and *Loxothysanus*, each one with only two species (*Dyscritothamnus filifolius* and *D. mirandae*, and *Loxothysanus pedunculatus* and *L. sinuatus*). We obtained geographical information from specimens housed mainly at the National Herbarium of Mexico (MEXU) of the Instituto de Biología, National Autonomous University of México; we used the information to estimate, through ecological niche modelling, environmentally suitable places where these species could be found.

The two species of *Dyscritothamnus* (fig. 1) grow sympatrically on rocky outcrop slopes in xerophytic environments of central Mexico, in the states of Hidalgo and Querétaro (Robinson 1992, Paray 1954). They are rupicolous evergreen shrubs with simple, alternate leaves, radiate or discoid heads, yellow florets, densely pubescent cypselae and pappus of feathery bristles; the two species can be distinguished by leaf form (filiform in *D. filifolius*, lanceolate in *D. mirandae*) and presence or absence of radiate florets (present in *D. mirandae*, absent in *D. filifolius*). Although living together in many places, there is no evidence of hybridization. On the other hand, the *Loxothysanus* species (fig. 1) grow mostly on calcareous soils in eastern Mexico, from southern Tamaulipas to Chiapas (Turner 1974). They are small annual or perennial herbs with simple, opposite leaves, discoid heads, white florets, pilose cypselae and pappus of scales. *L. pedunculatus* distinguishes from *L. sinuatus* by their longer peduncles (shorter in *L. sinuatus*) and their puberulent leaves (densely tomentose in *L. sinuatus*).

We used Maxent to generate the ecological niche models for each species. According to Phillips et al. (2006), Maxent is a method of artificial intelligence applied to calculate the most probable geographical distribution of a species, subject to the condition that the expected value of each environmental variable coincides with the arithmetic mean. It has proven effective for generating predictions based on presence only data (Elith et al. 2006, Peterson et al. 2007, Phillips & Dudik 2008, Phillips 2008); it provides optimal probability distributions (maximum entropy, Phillips et al. 2006) and thus predicts well the habitat suitability for the species (Giovanelli et al. 2008).

In the analysis we used 23 variables, 19 climatic obtained from the WorldClim database (Hijmans et al. 2005) and four landscape-related (elevation, slope, aspect and topog-

*Dyscritothamnus filifolius*B.L.Rob. *Dyscritothamnus mirandae*Paray

*Loxothysanus pedunculatus* Rydb. *Loxothysanus sinuatus* (Less.) B.L. Rob.

**Figure 1** – Species of *Dyscritothamnus* and *Loxothysanus* analysed.

raphy) downloaded from GTOPO30 (https://lta.cr.usgs.gov/GTOPO30). All variables had a resolution of 1 km$^2$. The resulting models express the values of habitat suitability for the species as a function of the environmental variables. A high value for the distribution function in a given cell indicates highly favourable conditions for the presence of the species.

The most important variables for ecological niche models are determined by bioclimatic profiles obtained using the method implemented in the BIOCLIM ANUCLIM 6.1 package (Xu & Hutchinson 2011, 2013). BIOCLIM determines the likely environmental limits of species distribution, that is, it defines places with similar climatic conditions and generates a bioclimatic profile (maximum, minimum, average and standard deviation). This profile summarizes the climatic conditions of each locality where the species has been recorded to compare it with climatic attributes of the study area (Lindenmayer et al. 1991, Villaseñor & Téllez-Valdés 2004). This comparison permits the identification of sites climatically suitable for the species under study to be found. While each parameter contributes partially to the distribution of the species, it is important to determine the relative contribution of each parameter. Therefore, in this study a principal component analysis (PCA) was carried out to determine which variables have the strongest influence on the species distribution. PCA is frequently used to reduce autocorrelation among variables and identify those that best explain the observed variance in the set of variables. The PCA was performed with the SPSS version 6 package (SPSS Inc. 2004).

In ecological niche modelling it is important to consider the biogeographic limits of the species (the M of the BAM diagram of Soberón & Peterson 2005) when delineating the study area. In this analysis, the M study area was determined based on the localities where the species were recorded using a Geographical Information System (ArcMap 10.0). We superimposed the records of the species under study onto a map of Mexican physiographic provinces (Cervantes-Zamora et al. 1990) to determine the provinces where the species have been recorded (fig. 2). We considered these provinces as the

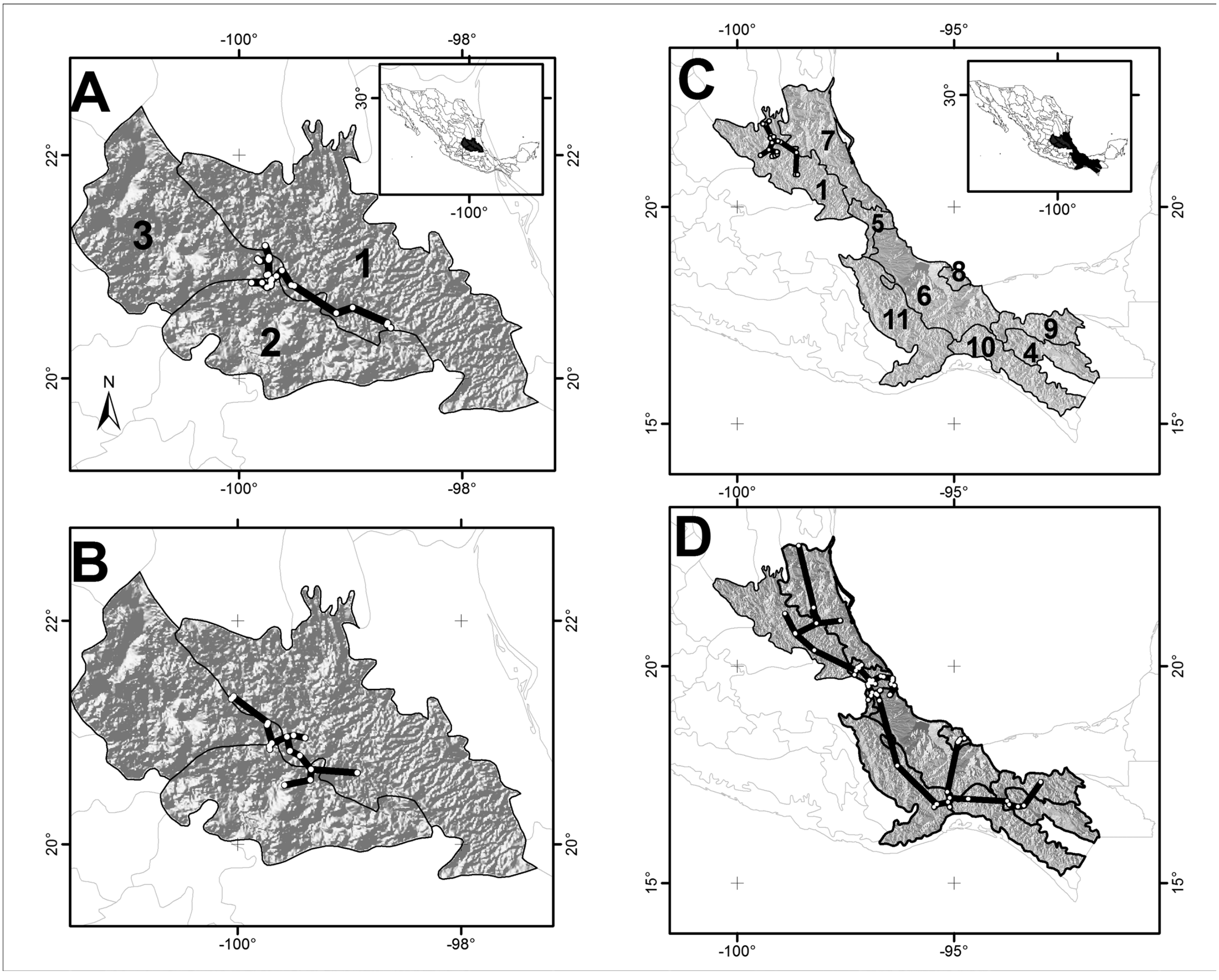

**Figure 2** – Collecting locations of: A, *Dyscritothamnus filifolius*; B, *D. mirandae*; C, *Loxothysanus pedunculatus*; and D, *L. sinuatus* in the physiographic provinces of Mexico. A minimum spanning network links the points to illustrate the species' biogeographic tracks. The names of the provinces are indicated in table 1.

biogeographic limits of the species (M), and we therefore restricted the selected environmental variables to the physiographic provinces where each species occurs to obtain their ecological niche models (fig. 3). We used 75% of data for training and the remaining 25% for testing. The models were generated using the logistic output format because it allows an easier biological interpretation of the estimated probability of occurrence for a species given the restrictions imposed by environmental variables (Phillips & Dudik 2008).

With the ecological niche models, the overlap between sites for each pair of sister species was assessed using the *D* and *I* parameters. Their values were obtained using the ENMTools v. 1.4 package (Warren et al. 2008, 2010). Both indices are important for the tests implemented in such package. One test (Niche equivalence) is used to estimate species' geographical overlapping and helps to evaluate whether ENMs generated from two or more species are more different than expected if they are drawn from the same underlying distribution (as the case of *Dyscritothamnus*). The other test (Niche similarity) is used to ask whether ENMs drawn from populations with partially or non-overlapping distributions are any more different from one another than expected by random (as the case of *Loxothysanus*).

Both indices (*D* and *I*) can take on values between 0 (no overlap) and 1 (total overlap, indicating identical models). The estimation of *D* and *I* values requires two key elements: the potential distribution area modelled for each species, and the optimal climatic conditions for each pair of species. As Maxent models are expressed as probabilities of finding satisfactory conditions for plants at any given pixel, we can compare such probabilities of finding a particular species in a determined pixel based on its own ENM versus the probability of finding it there based on the ENM of the other species. As implemented in ENMTools, the occurrence of two species, A and B in a locality *i* among the total set of localities indicates niche overlap. It is calculated as a proportion of the total number of localities occupied by both species A and B. Differences between A and B in a determined pixel indicate how similar the climate in such a pixel is with respect to known records for each species. Using ecological niche models, we can thus estimate the environmental properties of the compared spots.

To carry out the equivalence tests, the ecological niche models of each pair of sister species were generated, producing two set of data of the same size. For each set ENMTools uses Maxent to project one model and later estimate the *D* and *I* parameters by means of the predicted localities in each pixel. One hundred random replicates are carried out to produce a null distribution model and thus be able to compare the *D* and *I* values obtained both with the null model as with the initial model. The hypothesis of niche equivalence is rejected when *D* observed values are significantly lower than the expected values obtained with the null model ($P < 0.01$), and accepted when observed values are equal or higher. The

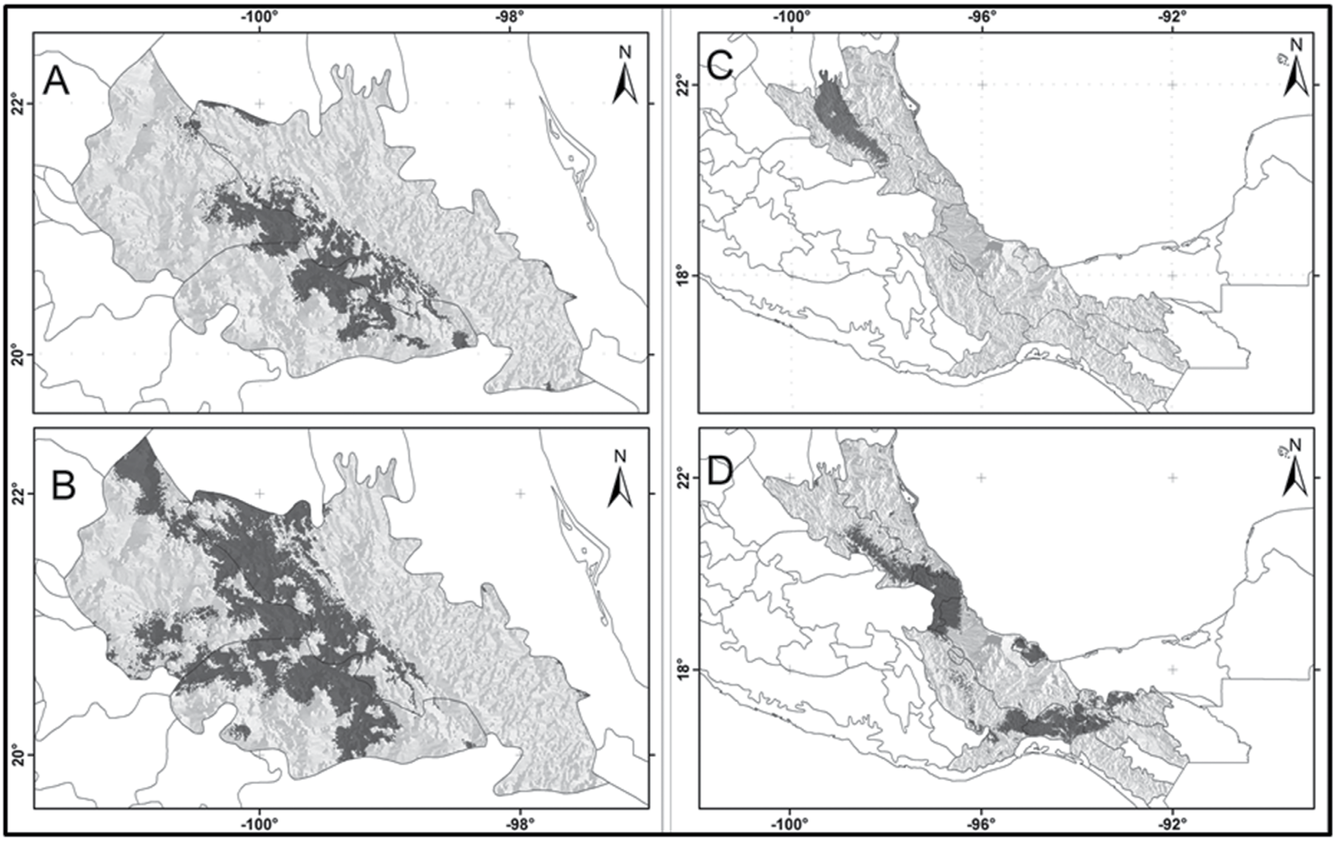

**Figure 3** – Potential distribution (dark gray) of: A, *Dyscritothamnus filifolius*; B, *D. mirandae*; C, *Loxothysanus pedunculatus*; and D, *L. sinuatus* along the physiographic provinces of Mexico (light gray).

**Table 1 – Distribution of species of genera *Dyscritothamnus* and *Loxothysanus* (Asteraceae) in the Mexico province's physiographic (Cervantes-Zamora et al. 1990) considered by Soberón & Peterson (2005) as their mobility areas (M).**
The code number relates the name of the province with its geographical position in figure 1.

| Species | Physiographic province | Code number | Ocurrences |
|---|---|---|---|
| *Dyscritothamnus filifolius*<br>*Dyscritothamnus mirandae* | Karst Huasteco | 1 | 28<br>20 |
| | Llanuras y Sierras de Querétaro e Hidalgo | 2 | |
| | Sierras y Llanuras del Norte de Guanajuato | 3 | |
| *Loxothysanus pedunculatus* | Karst Huasteco | 1 | 27 |
| *Loxothysanus sinuatus* | Altos de Chiapas | 4 | 73 |
| | Chiconquiaco | 5 | |
| | Karst Huasteco | 1 | |
| | Llanura Costera Veracruzana | 6 | |
| | Llanuras y Lomeríos | 7 | |
| | Sierra de los Tuxtlas | 8 | |
| | Sierras del Norte De Chiapas | 9 | |
| | Sierras del Sur de Chiapas | 10 | |
| | Sierras Orientales | 11 | |

test niche equivalence allows us to compare data sets; however, unless the exact points where specimens are found are climatically similar, the test tends to reject the idea that such points are identical, which suggest that niche conservatism is absent. The niche similarity test estimates how similar (or identical) niches under comparison are, considering the values of species bioclimatic profiles; in this case each pair of sister species.

## RESULTS

Collecting effort in the four species analysed revealed the occurrence of the two genera in eleven Mexican physiographical provinces (table 1). *Loxothysanus sinuatus* was the most widely distributed (nine provinces) whereas *L. pedunculatus* was the most restricted, registered in a single province (fig. 1, table 1).

The principal component analysis performed with the set of species climatic profiles (table 2) allowed the selection of 19 out of 23 environmental variables (table 3). Those variables with a loading factor above 0.7 in the first three components were considered important. In total, they explained more than 80% of variance (table 2). Ecological niche models obtained with these selected variables were supported by high AUC values and low omission rates (table 4).

## DISCUSSION

Ecological niche modelling estimates environmental requirements of a species; accordingly, models can be used to predict potential areas where species can occur if able to disperse (Di Febbraro et al. 2013). The predicted models for these four species can be considered robust based on their high AUC values. In addition the biogeographic tracks, that is, the lines connecting all the known collecting points allow to determine the geographical limits of distribution of a species (the M of the BAM model). Their use to select the area (number of physiographic provinces where the species occur) for obtaining the background points is relevant to generate more robust predictive models.

The two species of *Dyscritothamnus* are sympatric in three Mexican physiographic provinces (table 2); their occurrence in similar areas suggested they share similar habitats. On the other hand, the species of *Loxothysanus* are mostly allopatric and only coincide in a single province (Karst Huasteco province) of the nine where the genus occurs (table 5, fig. 2). They apparently occupy different habitats, suggesting niche divergence. The results of the more detailed comparisons using the *D* and *I* parameters support these predictions.

Results of niche equivalence and similarity showed low overlap between distributions of *Loxothysanus* species (table 5); therefore, we can reject the hypothesis of niche equivalence for this pair of species. In contrast, the species of *Dyscritothamnus* show values (table 5) that allow to suggest the existence of ecological niche equivalence. In summary, species of *Dyscritothamnus* show high similarities between their distribution patterns, whereas species of *Loxothysanus* share low ecological and geographic similarities (table 5).

Although niche conservatism has been repeatedly proposed (Harvey & Pagel 1991, Peterson et al. 1999) and is theoretically accepted, methodological complications for its empirical evaluation continue to raise doubt of its occurrence in nature (Peterson 2011), especially when niche models are obtained from limited occurrence data and at coarse scales. One approach to minimize such doubts is to better define the mobility and accessibility areas of species studied (Soberón & Peterson 2005). Choosing adequate variables to estimate the species potential distribution is also critical. We applied both of these measures in this study by using with biogeographic techniques (track biogeographic drawings) to determine the mobility area (geographic distribution) and using principal component analysis to reduce autocorrelation among the environmental variables that were included.

The ENMs here obtained interpolated a set of variables with reduced autocorrelation using principal component analysis. Among covariables used are elevation and slope orientation, which Archer (1984), McAuliffe (1994), Hsieh et al. (1998), or Guerrero-Campo et al. (1999) found as important factors influencing conditions required for species

**Table 2 – Contribution of the variables used in the principal component analysis.**
The variables in bold are those with the largest loadings and used to generate the ecological niche models.

| Variable | Description | ***Loxothysanus*** | | | ***Dyscritothamnus*** | | |
|---|---|---|---|---|---|---|---|
| | | Component | | | Component | | |
| | | 1 | 2 | 3 | 1 | 2 | 3 |
| **bio01** | Annual mean temperature | **0.989** | 0.110 | | **0.962** | 0.245 | |
| bio02 | Mean diurnal range | -0.155 | -0.386 | -0.534 | 0.486 | -0.620 | 0.415 |
| **bio03** | Isothermality | | 0.269 | **0.909** | -0.490 | **-0.746** | 0.116 |
| **bio04** | Temperature seasonality | **0.876** | 0.182 | 0.370 | **0.855** | 0.310 | 0.170 |
| **bio05** | Max temperature of warmest month | **0.844** | | -0.506 | **0.979** | 0.144 | |
| bio06 | Min temperature of coldest month | | 0.131 | **0.902** | **0.872** | 0.420 | -0.134 |
| **bio07** | Temperature annual range | **0.958** | 0.145 | 0.204 | **0.785** | -0.284 | 0.357 |
| **bio08** | Mean temperature of wettest quarter | **0.921** | 0.110 | -0.322 | **0.976** | 0.150 | |
| **bio09** | Mean temperature of driest quarter | **0.956** | 0.171 | 0.204 | **0.900** | 0.230 | |
| **bio10** | Mean temperature of warmest quarter | **0.946** | | -0.306 | **0.962** | 0.260 | |
| **bio11** | Mean temperature of coldest quarter | | **0.939** | -0.185 | **0.956** | 0.232 | |
| **bio12** | Annual precipitation | | **0.861** | 0.201 | -0.422 | **0.856** | 0.172 |
| **bio13** | Precipitation of wettest month | -0.315 | **0.822** | -0.203 | -0.247 | **0.947** | |
| bio14 | Precipitation of driest month | 0.406 | -0.595 | 0.320 | -0.637 | 0.689 | 0.162 |
| **bio15** | Precipitation seasonality | | **0.823** | | **0.707** | 0.655 | |
| **bio16** | Precipitation of wettest quarter | -0.290 | **0.854** | -0.238 | -0.267 | **0.897** | 0.220 |
| **bio17** | Precipitation of driest quarter | | **0.779** | 0.382 | **-0.821** | 0.498 | 0.153 |
| **bio18** | Precipitation of warmest quarter | | **0.841** | -0.454 | -0.548 | 0.619 | 0.239 |
| **bio19** | Precipitation of coldest quarter | -0.943 | -0.160 | | **-0.774** | 0.582 | |
| **Orien** | Orientation | -0.139 | 0.237 | 0.325 | **-0.750** | -0.445 | |
| **Alt** | Altitude (m above sea level) | 0.370 | -0.242 | | | 0.165 | **-0.829** |
| Slop | Slope | | | | | -0.196 | 0.453 |
| Topo | Topography | | | | | | 0.318 |
| | Eigenvalue | 7.49% | 5.86% | 3.35% | 11.43% | 6.14% | 1.56% |
| | Variance | 34.04% | 26.64% | 15.24% | 49.69% | 26.71% | 6.78% |
| | Accumulated variance | 34.04% | 60.68% | 75.912% | 49.69% | 76.40% | 83.18% |

establishment. However, in our results these variables were either non-significant, and thus excluded from our ENMs (table 3), or their importance was limited.

Several studies have evaluated either niche conservatism or divergence (Peterson 2011), especially with invasive species, since they are apparently more able to undergo niche change processes associated with invasion (Broennimann et al. 2007, Medley 2010). Peterson (2011) considers those studies involved large spatial scales, generating biases when interpreting results because they may be different if area size varies. Therefore, it is important to delimit properly the geographic distribution areas of species under study when the aim is to evaluate niche conservatism. This study defined the distribution of species on biogeographic grounds, limiting their distribution to the physiographic provinces where known occurrences have been recorded.

It is also important to consider in the evaluation of niche conservatism the degree of relatedness of the species under study (Ackerly 2003, Wiens & Graham 2005, Losos 2008, Pearman et al. 2008, Warren et al. 2008, Wiens 2008). This study approached the point by using two genera with only two species each; in this way, their close taxonomic relationship is warranted, without other extant members obscuring such relatedness. However, lack of fossil or molecular data prohibit the determination of the age of sisterhood or eliminate the possibility of intermediate relatives among these pairs of species. Undoubtedly, age of speciation processes is related to species' ability to disperse and occupy their entire

**Table 3 – Bioclimatic profiles of the four analysed species (standard deviation between parentheses).**
Variables abbreviations are indicated in table 2.

| Variable | *Loxothysanus pedunculatus* | | | *Loxothysanus. sinuatus* | | | *Dyscritothamnus filifolius* | | | *Dyscritothamnus mirandae* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Minimum | Average | Maximum | Minimum | Average | Maximum | Minimum | Average | Maximum | Minimum | Average | Maximum |
| bio1 | 17.1 | 20.8 (±2.2) | 25 | 14.9 | 21.3 (±2.7) | 25 | 15.4 | 18.1 (±1.4) | 20.4 | 16.3 | 18.7 (±1.5) | 20.5 |
| bio2 | 12.5 | 13.4 (±0.6) | 15.5 | 8.2 | 10.7 (±1.2) | 13.8 | 14.1 | 15.9 (±0.7) | 16.9 | 15.2 | 16 (±0.3) | 16.6 |
| bio3 | 5.4 | 5.84 (±0.2) | 6.1 | 5.1 | 6.1 (±0.4) | 7 | 6.3 | 6.5 (±0.1) | 6.6 | 6.3 | 6.4(±0.1) | 6.8 |
| bio4 | 27.36 | 33.2 (±2.9) | 38.97 | 14.97 | 22.9 (±4.9) | 38.19 | 23.68 | 27.1 (±1.7) | 29.28 | 23.88 | 27.9 (±2.1) | 30.81 |
| bio5 | 27.8 | 32.1 (±2.5) | 36.5 | 23.9 | 30.1 (±2.8) | 34.7 | 27.1 | 30.3 (±1.8) | 33.1 | 28.1 | 30.9 (±1.7) | 33.3 |
| bio6 | 6.3 | 9.2 (±1.9) | 13 | 6 | 12.6 (±2.9) | 16.9 | 3.2 | 5.8 (±1.1) | 7.6 | 4.3 | 6.2 (±1.4) | 8.3 |
| bio7 | 21.5 | 22.8 (±0.8) | 25.1 | 13.9 | 17.6 (±1.9) | 23.5 | 21.9 | 24.5 (±1.1) | 25.6 | 23.8 | 24.7 (±0.56) | 25.5 |
| bio8 | 19.2 | 23.6 (±2.5) | 28.3 | 16.7 | 23.1 (±2.8) | 28.4 | 17.7 | 20.3 (±1.5) | 22.6 | 18.3 | 20.9 (±1.5) | 22.9 |
| bio9 | 15 | 17.9 (±1.9) | 21.9 | 13 | 19.8 (±3.1) | 24.6 | 12.5 | 14.9 (±1.2) | 17 | 13.1 | 15.6 (±1.4) | 18.4 |
| bio10 | 20.2 | 24.4 (±2.5) | 29.1 | 17.5 | 23.8 (±2.8) | 28.4 | 18.3 | 21.2 (±1.5) | 23.7 | 19.3 | 21.8 (±1.7) | 24 |
| bio11 | 13.8 | 16.7 (±1.9) | 20.5 | 12.1 | 18.5 (±2.6) | 22.3 | 12.5 | 14.8 (±1.2) | 16.8 | 13.1 | 15.3 (±1.3) | 17 |
| bio12 | 924 | 1756 (±343) | 2154 | 813 | 1624 (±540) | 3221 | 457 | 607 (±71) | 772 | 453 | 596 (±74) | 743 |
| bio13 | 227 | 400 (±78) | 481 | 152 | 302 (±83) | 620 | 87 | 120(±23) | 176 | 84 | 119 (±20) | 167 |
| bio14 | 9 | 35 (±11) | 51 | 9 | 36 (±17) | 91 | 5 | 7 (±1.3) | 10 | 4 | 6 (±1) | 10 |
| bio15 | 65 | 78 (±4) | 90 | 43 | 71 (±13) | 99 | 73 | 80 (±3) | 84 | 76 | 81 (±4) | 87 |
| bio16 | 504 | 886 (±161) | 1062 | 421 | 779 (±227) | 1632 | 208 | 307 (±39) | 386 | 218 | 304 (±41) | 387 |
| bio17 | 34 | 116 (±33) | 157 | 29 | 120 (±60) | 327 | 23 | 28 (±4) | 38 | 22 | 28 (±4) | 39 |
| bio18 | 295 | 608 (±126) | 757 | 277 | 428 (±129) | 791 | 159 | 184 (±24) | 288 | 156 | 182 (±28) | 293 |
| bio19 | 50 | 119 (±32) | 164 | 43 | 155 (±101) | 497 | 28 | 36 (±6) | 53 | 27 | 35 (±6) | 49 |
| Alt | 126 | 1007 (±434) | 1548 | 4 | 800 (±522 | 1900 | 1445 | 1741 (±204) | 2167 | 1300 | 1657 (±236) | 2013 |
| Slop | 0 | 661 (±364) | 1307 | 37 | 454 (±309) | 1314 | 92 | 591 (±400) | 1586 | 140 | 621 (±293) | 1050 |
| Topo | 156 | 361 (±224) | 947 | 131 | 390 (±224) | 1229 | 126 | 329 (±153) | 810 | 146 | 410 (±295) | 1332 |
| Orien | -1 | 17114 (±10756) | 34952 | 586 | 12828 (±8335) | 33230 | 1318 | 17706 (±11276) | 34302 | 1155 | 20015 (±13125) | 32528 |

**Table 4 – Results of model accuracy using the area under the curve (AUC) and binomial tests omission.**
With a binomial test was evaluated the omission rate for every model. A binomial test indicated significant omission rate minor than a prediction random. The *P*-values for all omission test were or 0.001.

| **Species** | **Number of records** | **AUC** | **Omission rate** |
|---|---|---|---|
| *Dyscritothamnus filifolius* | 28 | 0.972 | 0.07 |
| *Dyscritothamnus mirandae* | 20 | 0.925 | 0.05 |
| *Loxothysanus pedunculatus* | 27 | 0.986 | 0.15 |
| *Loxothysanus sinuatus* | 73 | 0.915 | 0.06 |

**Table 5 – Values of equivalence (*D*) and similarity (*I*) obtained from the comparison of potential distribution models at a significance value of *P* < 0.01.**

| Values with observed data | *D* | *I* |
|---|---|---|
| *Dyscritothamnus filifolius* and *D. mirandae* | 0.563 | 0.823 |
| *Loxothysanus pedunculatus* and *L. sinuatus* | 0.145 | 0.351 |
| Values with expected data | *D* | *I* |
| *Dyscritothamnus filifolius* and *D. mirandae* | 0.599 | 0.472 |
| *Loxothysanus pedunculatus* and *L. sinuatus* | 0.675 | 0.878 |

fundamental niche. It is surprising to find that the shrubby species showed a more restricted distribution than the herbaceous ones. Generally, woody species are thought to be older than herbaceous ones, although the latter can show more efficient dispersal strategies, reaching their equilibrium faster than other life forms. Ecological niche models have demonstrated their usefulness for understanding the geographical distribution of species that have low vagility, are endemic, and are ecologically poorly known (Raxworthy et al. 2007), as occurs with the genera *Dyscritothamnus* and *Loxothysanus*.

Tests of niche equivalence and similarity (Warren et al. 2008, 2010) provide evidence of whether a species shifts niche or finds an equivalent one outside its native area, as in invasive species (Broennimann et al. 2007, Fitzpatrick et al. 2007, 2013, Medley 2010). Results show that niche conservatism is apparently verified in *Dyscritothamnus*, with both its species occupying comparable environments. Similarity between their niches is high, as demonstrated by their presence in the same geographical area. However, their low equivalence (overlapping) values suggest they are initiating processes of niche diversification.

The geographical distribution of *Loxothysanus pedunculatus* is restricted to a single physiographic province where it overlaps with its sister species (*L. sinuatus*), which has a wider distribution. Results indicate low niche conservatism in the genus, and niche divergence suggest the species already occupy different climatic spaces. Either the tests of niche equivalence or similarity show significant differences between species niches, as evidenced by the fact they occupy different habitats. Undoubtedly, these differences are reinforced by the differential habitat availability within the regions they inhabit.

Observed differences between the pairs of species studied consider only the realized niche because there is no data available of their biological interactions (Soberón & Peterson 2011). In addition to not considering biological interactions, differences between observed niches may result from the number of environmental variables employed or the lack of sufficient distribution records (Peterson 2011). Our results indicate species of *Dyscritothamnus* have a sympatric distribution and similar and conserved fundamental and potential niches; the same tests in *Loxothysanus* show contrasting results, indicating that its species have shifting niches without evident conservatism.

The similar distribution and high niche conservatism values of the two *Dyscritothamnus* species support hypothesis of niche conservatism. On the contrary, *Loxothysanus* species showed divergent niches, and are therefore more likely able to confront changing climate by colonizing or invading new areas (Petitpierre et al. 2012). Our contrasting results highlight the importance of evaluating additional taxonomic groups in order to determine more precisely how niche conservatism varies among plants and infer with higher confidence the possible impact climatic change will have on plant species distributions.

## ACKNOWLEDGMENTS

The first author is grateful to CONACyT for funding a postdoctoral fellowship (163037) associated with the Colegio de Postgraduados. We acknowledge Francisco J. Espinosa and Claudio Delgadillo for their comments and suggestions on the manuscript. Enrique Ortiz provided technical advice in handling the database. Lynna Kiere revised the English version of the manuscript.

## REFERENCES

Ackerly D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Sciences 164: S165–S184. http://dx.doi.org/10.1086/368401

Araújo M.B., Pearson R.G., Thuillery W., Erhard M. (2005) Validation of species-climate impact models under climate change. Global Change Biology 11: 1504–1513. http://dx.doi.org/10.1111/j.1365-2486.2005.01000.x

Archer S. (1984) The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. The American Midland Naturalist 111: 138–142. http://dx.doi.org/10.2307/2425551

Broennimann O., Treier U.A., Müller-Schärer H., Thuiller W., Peterson A.T., Guisan A. (2007) Evidence of climatic niche shift during biological invasion. Ecology Letters 10: 701–709. http://dx.doi.org/10.1111/j.1461-0248.2007.01060.x

Brown J.H., Lomolino M.V. (1998) Biogeography. 2nd Ed. Sunderland, Sinauer Associate.

Burke A. (2003) How special are Etendeka mesas? Flora and elevation gradients in an arid landscape in north-west Namibia. Journal of Arid Environment 55: 747–764. http://dx.doi.org/10.1016/S0140-1963(02)00293-8

Cervantes-Zamora Y., Cornejo-Olguín S.L., Lucero-Márquez R., Espinosa-Rodríguez J. M., Miranda-Víquez E., Pineda Velásquez A. (1990) Clasificación de Regiones Naturales de México, IV. Atlas Nacional de México. Vol. II. Escala 1: 4, 000, 000.

Chase J.M., Leibold M.A. (2003) Ecological niches: interspecific interactions. Chicago, The University of Chicago Press.

Despland E., Houle G. (1997) Climate influence on growth and reproduction of Pinus banksiana (Pinaceae) at the limit of the species distribution in eastern North America. American Journal of Botany 84: 928–937. http://dx.doi.org/10.2307/2446283

Di Febbraro M., Lurz P.W.W., Genovesi P., Maiorano L., Girardello M. (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: A case with the American Eastern Grey Squirrel. PLoS ONE 8: e66559. http://dx.doi.org/10.1371/journal.pone.0066559

Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A., Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J.M.M., Peterson A.T., Phillips S.J., Richardson K., Scachetti-Pereira R., Schapire R.E., Soberón J., Williams S., Wisz M.S., Zimmermann N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151. http://dx.doi.org/10.1111/j.2006.0906-7590.04596.x

Fitzpatrick M.C., Weltzin J.F., Sanders N.J., Dunn R.R. (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography 16: 24–33. http://dx.doi.org/10.1111/j.1466-8238.2006.00258.x

Fitzpatrick M.C., Gotelli N.J., Ellison A.M. (2013) MaxEnt versus MaxLike: empirical comparisons with ant species distributions. Ecosphere 4: 1–15. http://dx.doi.org/10.1890/ES13-00066.1

Giovanelli J., Haddad C., Alexandrino J. (2008) Predicting the potential distribution of the alien invasive american bullfrog (Lithobates catesbeianus) in Brazil. Biological Invasions 10: 585–590. http://dx.doi.org/10.1007/s10530-007-9154-5

Graham C.H., Ron S.R., Santos J.C., Schneider C.J., Moritz C. (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in Dendrobatid frogs. Evolution 58: 1781–1793. http://dx.doi.org/10.1554/03-274

Guerrero-Campo J., Alberto F., Hodgson J., García-Ruiz J.M., Montserrat-Martí G. (1999) Plant community patterns in a gypsum area of NE Spain. I. Interactions with topographic factors and soil erosion. Journal of Arid Environments 41: 401–410. http://dx.doi.org/10.1006/jare.1999.0492

Guisan A., Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186. http://dx.doi.org/10.1016/S0304-3800(00)00354-9

Harvey P.H., Pagel M.D. (1991) The comparative method in evolutionary biology. Oxford, Oxford University Press.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. http://dx.doi.org/10.1002/joc.1276

Hobbie S.E., Chapin III F.S. (1998) An experimental test of limits to tree establishment in Arctic tundra. Journal of Ecology 86: 449–461. http://dx.doi.org/10.1046/j.1365-2745.1998.00278.x

Hsieh C., Chen Z.-S., Hsu Y.-M., Yang K.-C., Hsieh T.-H. (1998) Altitudinal zonation of evergreen broad-leaved forest on Mount Lopei, Taiwan. Journal of Vegetation Science 9: 201–212. http://dx.doi.org/10.2307/3237119

Hutchinson G.E. (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427. http://dx.doi.org/10.1101/SQB.1957.022.01.039

Kambhampati S., Peterson A.T. (2007) Ecological niche conservation and differentiation in the wood-feeding cockroaches, Cryptocercus, in the United States. Biological Journal of the Linnean Society 90: 457–466. http://dx.doi.org/10.1111/j.1095-8312.2006.00734.x

Lindenmayer D.B., Nix H.A., McMahon J.P., Hutchinson M.F., Tanton M.T. (1991) The conservation of Leadbeater's possum, Gymnobelideus leadbeateri (McCoy): a case study of the use of bioclimatic modeling. Journal of Biogeography 18: 371–383. http://dx.doi.org/10.2307/2845479

Losos J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11: 995–1003. http://dx.doi.org/10.1111/j.1461-0248.2008.01229.x

McAuliffe J.R. (1994) Lanscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert Bajadas. Ecological Monographs 64: 111–148. http://dx.doi.org/10.2307/2937038

Medley K.A. (2010) Niche shifts during the global invasion of the Asian tiger mosquito, Aedes albopictus Skuse (Culicidae), revealed by reciprocal distribution models. Global Ecology and Biogeography 19: 122–133. http://dx.doi.org/10.1111/j.1466-8238.2009.00497.x

Paray L. (1954) Nuevas Fanerógamas de México. Boletín de la Sociedad Botánica de México 16: 20–22.

Pearman P.B., Guisan A., Broennimann O., Randin C.F. (2008) Niche dynamics in space and time. Trends in Ecology & Evolution 23: 149–158. http://dx.doi.org/10.1016/j.tree.2007.11.005

Peterson A.T., Soberón J. Sánchez-Cordero V. (1999) Conservatism of ecological niches in evolutionary time. Science 285: 1265–1267. http://dx.doi.org/10.1126/science.285.5431.1265

Peterson A.T., Nyári A. (2007) Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, Schiffornis sp., in the Neotropics. Evolution 62: 173–183. http://dx.doi.org/10.1111/j.1558-5646.2007.00258.x

Peterson A.T., Papes M., Eaton M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30: 550–560. http://dx.doi.org/10.1111/j.0906-7590.2007.05102.x

Peterson A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography 38: 817–827. http://dx.doi.org/10.1111/j.1365-2699.2010.02456.x

Petitpierre B., Kueffer C., Broennimann O., Randin C., Daehler C., Guisan A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335: 1344–1348. http://dx.doi.org/10.1126/science.1215933

Phillips S.J., Anderson R.P., Shapire R.E. (2006) Maximum entropy modeling of species distributions. Ecological Modelling 190: 231–259. http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips S.J. (2008) Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 31: 272–278. http://dx.doi.org/10.1111/j.0906-7590.2008.5378.x

Phillips S.J., Dudík M. (2008) Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. Ecography 31: 161–175. http://dx.doi.org/10.1111/j.0906-7590.2008.5203.x

Prinzing A., Durkan W., Klots S., Brandl R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society of London 268: 2383–2389. http://dx.doi.org/10.1098/rspb.2001.1801

Pyron R.A., Costa G.C., Patten M.A., Burbrink F.T. (2014) [Early View online] Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. Biological Reviews http://dx.doi.org/10.1111/brv.12154

Raxworthy C.J., Ingram C.M., Rabibisoa N., Pearson R.G. (2007) Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (Phelsuma) from Madagascar. Systematic Biology 56: 907–923. http://dx.doi.org/10.1080/10635150701775111

Robinson B.L. (1922) Dyscritothamnus, a new genus of composite. Contributions from the Gray Herbarium of Harvard University 65: 24–28.

Schoener T.W. (1968) The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704–726. http://dx.doi.org/10.2307/1935534

Schoener T.W. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408–418. http://dx.doi.org/10.2307/1935376

Sinervo B., Méndez-de-la-Cruz F., Miles D.B., Heulin B., Bastiaans E., Villagrán-Santa Cruz M., Lara-Resendiz R., Martínez-Méndez N., Lucía Calderón-Espinosa M., Meza-Lázaro R.N., Gadsden H., Avila L.J., Morando M., De la Riva I.J., Sepulveda P.V., Duarte Rocha C.F., Ibargüengoytía N., Puntriano C.A., Massot M., Lepetz V., Oksanen T.A., Chapple D.G., Bauer A.M., Branch W.R., Clobert J., Sites Jr. J.W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899. http://dx.doi.org/10.1126/science.1184695

Soberón J., Peterson A.T. (2004) Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London B 359: 689–698. http://dx.doi.org/10.1098/rstb.2003.1439

Soberón J., Peterson A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10. http://dx.doi.org/10.17161/bi.v2i0.4

Soberón J., Peterson A. T. (2011) Ecological niche shifts and environmental space anisotropy: a cautionary note. Revista Mexicana de Biodiversidad 82: 1348–1355.

SPSS (Statistical Package for Social Science) Inc. Released (2004) SPSS for Windows, Version 6.0. Chicago, SPSS Inc.

Thuiller W., Lafourcade B., Engler R., Araújo M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32: 369–373. http://dx.doi.org/10.1111/j.1600-0587.2008.05742.x

Turner B.L. (1974) Taxonomy of Loxothysanus (Compositae, Helenieae). Wrightia 5: 45–50.

Villaseñor J.L., Téllez-Valdés O. (2004) Distribución potencial de las especies del género Jefea (Asteraceae) en México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica 75: 205–220.

Warren D.L., Glor R.E., Turelli M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883. http://dx.doi.org/10.1111/j.1558-5646.2008.00482.x

Warren D.L., Glor R.E., Turelli M. (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33: 607–611. http://dx.doi.org/10.1111/j.1600-0587.2009.06142.x

Webb C.O., Ackerly D.D., McPeek M.A., Donoghue M.J. (2002) Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475–505. http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wiens J.J. (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58: 193–197. http://dx.doi.org/10.1111/j.0014-3820.2004.tb01586.x

Wiens J.J., Graham C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution and Systematics 36: 519–539. http://dx.doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wiens J.J. (2008) Commentary on Losos (2008): niche conservatism déjà vu. Ecology Letters 11: 1004–1005. http://dx.doi.org/10.1111/j.1461-0248.2008.01238.x

Wiens J.J., Ackerly D.D., Allen A.P., Anacker B.L., Buckley L.B., Cornell H.V., Damschen E.I., Davies T.J., Grytnes J.A., Harrison S.P., Hawkins B.A., Holt R.D., McCain C.M., Stephens P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310–1324. http://dx.doi.org/10.1111/j.1461-0248.2010.01515.x

Xu T., Hutchinson M.F. (2011) ANUCLIM Version 6.1. Australia, Fenner School of Environment and Society, Australian National University. Available at http://fennerschool.anu.edu.au/research/products/anuclim-vrsn-61 [accessed 1 Jun. 2015].

Xu T., Hutchinson M.F. (2013) New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. Environmental Modelling & Software 40: 267–279. http://dx.doi.org/10.1016/j.envsoft.2012.10.003

Manuscript received 8 Apr. 2015; accepted in revised version 7 Jul. 2015.

Communicating Editor: Pierre Meerts.