Ecological niche overlap among species of the genus *Zaluzania* (Asteraceae) from the dry regions of Mexico

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

[1]División de Estudios de Postgrado, Universidad de la Sierra Juárez, Avenida Universidad S/N, Ixtlán de Juárez, Oaxaca, México C.P. 68725, Mexico
[2]Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado postal 70-367, 04510 México, D.F., Mexico
*Corresponding author: mesuarez@unsij.edu.mx

Background and aims – The hypothesis of ecological niche conservatism postulates that closely related species share ecologically similar environments; that is, they tend to maintain the characteristics of their fundamental niche over time. The objective of this study is to evaluate the similarity and equivalence of the ecological niches among species of the genus *Zaluzania* (Asteraceae), characteristic of the Mexican arid and semi-arid regions, to infer their potential niche conservatism.

Methods – Based on critically reviewed herbarium occurrence data, potential distribution models for eight species of *Zaluzania* were generated using the MaxEnt algorithm. The overlap between potential distribution areas was then evaluated using equivalence and ecological niche parameters implemented in the ENMTools software; for this we quantified the degree of overlap and similarity between the niches using the equivalence (*D*) and similarity (*I*) parameters.

Key results – The resulting models show that species display areas of high suitability along the Mexican dry regions, as well as overlapping heterogeneous values. All models showed high AUC (Area Under the Curve) values (> 0.8). The *D* and *I* values between each pair of species showed low values of overlap.

Conclusions – Each species of the genus shows a fundamental niche distinct from their sister species. The genus thus offers an example of niche divergence among species, with each one adapting to different environmental pressures. Our results do not support the hypothesis of niche conservatism in the genus, suggesting that the species evolved in divergent environments.

Keywords – Centroid; ecological niche; MaxEnt; niche conservatism; niche overlap; *Zaluzania*.

INTRODUCTION

Species inhabit the geographical space in which they find their ecological niche (Hutchinson 1957; Brown & Lomolino 1998). The ecological niche is a concept that describes how organisms at different levels of organization interact with their environment at different spatio-temporal scales (Maguire 1973; Chase & Leibold 2003; Leibold & Geddes 2005). It is one of the most useful concepts to explore how

and where organisms live and how they relate to their environment. Since its introduction (Grinnell 1917), the concept has changed considerably with new knowledge about how organisms function within their habitats.

The niche concept can be conceived and evaluated under different approaches (e.g., Grinnell 1917; Hutchinson 1957). During the last 15 years, ecological niche modelling has been widely used to estimate the geographic distribu-

tion of species at different scales for conservation purposes (Peterson 2011). Another use for niche models is focused on predicting abundance of species, for which the results have not been very convincing (VanDerWal et al. 2009; Tôrres et al. 2012; Yañez-Arenas et al. 2012). Ecological niche models are based on the concept of Grinnell (1917), in the sense that what is actually modelled is the Grinnellian niche and the result of the analysis indicates, with a certain probability, the geographic space that is favourable for a species (Soberón 2007; Ricklefs 2008; Soberón & Nakamura 2009).

The application of niche modelling for a species provides a better understanding of its distribution (Kearney & Porter 2009; Bellier et al. 2010). It is important to understand that the ecological niche of a species deals with different characteristics of the fundamental niche as well as different ecological and evolutionary properties (Soberón & Nakamura 2009). For example, speciation occurs in the geographical dimension and it is rarely accompanied by ecological innovation when populations move to a new environment (Peterson et al. 1999; Pyron & Burbrink 2009; Peterson 2011). However, if the species can adapt to a new environment, natural selection could promote adaptation and facilitate speciation leading to divergence in ecological niches of the species (Graham et al. 2004; Wiens & Graham 2005; Sánchez-Fernández et al. 2011).

The species' ecological niche models used to estimate their potential distribution can predict the areas that are likely to be occupied based on environmental conditions suitable for the species' establishment. Accordingly, these models are geographic representations of the suitable ecological places for the presence of a species as a function of the variables used to generate the representation (Guisan & Zimmermann 2000). The use of potential distribution modelling of species 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; Pyron et al. 2015), representing one of the new emerging approaches in ecology, biogeography, and conservation biology. In addition, they are employed in the analysis of niche conservatism when phylogenetic data on sister species is available (Wiens 2004; Pyron et al. 2015). The use of an algorithm, such as MaxEnt, for modelling the species' potential distribution allows the estimation of the species' distribution in regions where it has not yet been reported, but that have suitable conditions for its establishment (Elith et al. 2006; Peterson et al. 2007; Phillips 2008; Phillips & Dudík 2008).

Ecological niche conservatism supports the hypothesis that the environments of closely related species are more ecologically similar than expected by chance, while divergence predicts that they occupy distinct niches. In other words, closely related species tend to maintain the characteristics of their fundamental niche over time (Peterson et al. 1999; Webb et al. 2002; Wiens 2004; Wiens & Graham 2005; Wiens et al. 2010; Peterson 2011). Niche conservatism can even explain species richness patterns at different scales and could reveal the role of ecology in speciation processes (Wiens et al. 2010).

Peterson et al. (1999) argue that speciation occurs in a geographic context first, with ecological differences evolving later. The conclusion that niches are conserved results from evidence of niche similarity, where it is assessed whether potential environmental niche models among sister species predict the presence of one or the other (Peterson et al. 1999; Kambhampati & Peterson 2007; Peterson & Nyári 2007). In this way, methods have been developed to estimate how similar niches are between species, providing support for hypotheses about niche conservatism (Peterson et al. 1999; Warren et al. 2008).

Warren et al. (2008) developed a series of tests to quantify ecological niche similarity and compared the equivalence versus the conservatism of the niche. Such tests are based on two main concepts, similarity and niche equivalence. Niche similarity evaluates whether the ecological niche model of one species predicts the presence of another species better than would be expected under a random model. Niche equivalence refers to whether two niche models of different species are indistinguishable from one another, i.e., whether each species can inhabit either niche interchangeably (Warren et al. 2008).

This work evaluates the potential existence of niche conservatism in the genus *Zaluzania* (family Asteraceae, tribe Heliantheae), which includes 11 species (Olsen 1979; Turner 2012): *Zaluzania augusta* (Lag.) Sch.Bip., *Z. delgadoana* B.L.Turner, *Z. discoidea* A.Gray, *Z. durangensis* B.L.Turner, *Z. megacephala* Sch.Bip., *Z. mollissima* A.Gray, *Z. montagnifolia* (Sch.Bip.) Sch.Bip., *Z. pringlei* Greenm., *Z. parthenioides* (DC.) Rzed., *Z. subcordata* W.M.Sharp, and *Z. triloba* (Ortega) Pers. The genus is endemic to Mexico, half of the species are perennial herbs (*Z. discoidea*, *Z. durangensis*, *Z. megacephala*, *Z. parthenioides*, and *Z. triloba*) and the other half are shrubs (*Z. augusta*, *Z. delgadoana*, *Z. mollissima*, *Z. montagnifolia*, *Z. pringlei*, and *Z. subcordata*). Its distinctive features are its alternate leaves, heterogamous heads with paleaceous receptacles, ray florets with a pappus of short scales, and disc flowers devoid of a pappus. The genus mainly inhabits dry environments, where the dominant vegetation consists of xerophytic scrubs, seasonally dry tropical forests, or dry temperate pine, oak, or juniper forests. Based on the arguments of Wiens & Graham (2005) and Wiens et al. (2010) that niches between species are mostly conserved in some way but rarely identical (Wiens & Graham 2005), the present study aims to test if the ecological niches of these species of a single genus are ecologically more similar to each other or if there is some degree of divergence, depending on the localities they occupy. The aim of this study is then to evaluate, based on potential distribution models estimated with a set of environmental variables, the equivalence of the ecological niches of the species in the *Zaluzania* genus and test the existence of niche conservatism.

MATERIAL AND METHODS

Eight of the 11 species of *Zaluzania* had a number of records (at least 5) adequate to estimate their potential distribution models; species with fewer records were not included in the analysis. Under this criterion, the selected species were *Zaluzania augusta*, *Z. megacephala*, *Z. mollissima*, *Z. montagnifolia*, *Z. parthenioides*, *Z. pringlei*, *Z. subcordata*, and *Z. triloba* (table 1, supplementary file 1). Data obtained from

Table 1 – **Mexican physiographic provinces where the genus *Zaluzania* occurs and the number of records for each species.**
Zaug = *Z. augusta*, Zmeg = *Z. megacephala*, Zmol = *Z. mollissima*, Zmon = *Z. montagnifolia*, Zpar = *Z. parthenioides*, Zpri = *Z. pringlei*, Zsub = *Z. subcordata*, Ztri = *Z. triloba*.

Physiographic province	Zaug	Zmeg	Zmol	Zmon	Zpar	Zpri	Zsub	Ztri
Altos de Jalisco	3							
Bajío Guanajuatense	2				1			
Chiconquiaco								1
Cordillera Costera del Sur				2		8		
Depresión del Balsas				1				
Gran Sierra Plegada		12	1		7			5
Karst Huasteco	19	12			6			3
Lagos y Volcanes del Anáhuac	50			9		4	5	17
Lanuras de Ojuelos-Aguascalientes	4							12
Llanuras y Sierras de Querétaro e Hidalgo	36	14			13			19
Llanuras y Sierras Potosino-Zacatecanas	2				6			9
Mesetas y Cañadas del Sur	4	2						
Mil Cumbres	2							
Mixteca Alta				5			5	
Pliegues Saltillo-Parras		4			6			
Sierra de Guanajuato	1							
Sierras Centrales de Oaxaca				18		2	9	
Sierras Orientales				20		3	4	
Sierras Transversales		2	12		11			3
Sierras y Bajíos Michoacanos	2							
Sierras y Llanuras Coahuilenses								1
Sierras y Llanuras de Durango	3							
Sierras y Llanuras del Norte								1
Sierras y Llanuras del Norte de Guanajuato	37	4	2		12			16
Sierras y Llanuras Occidentales		5			28			16
Sierras y Lomeríos de Aldama y Río Grande			1		7			2
Sierras y Valles de Oaxaca				9				
Sierras y Valles Guerrerenses				9		13		
Sierras y Valles Zacatecanos	3				1			2
Sur de Puebla				7		5		

the geographic coordinates of the sites where the species were collected (herbarium specimens at MEXU) were used to estimate, through a potential distribution model, the sites environmentally suitable for their establishment (table 2). To evaluate spatial autocorrelation between the collecting sites, a Moran's I test was carried out, using the analysing patterns tool implemented in ArcMap 9.3, based on the distances between localities. This index determines whether they are grouped, scattered, or randomly distributed, allowing a subset of them to be selected within this latter pattern.

MaxEnt is a machine-learning method to estimate the most probable geographical distribution of a species, subjected to the condition that the expected value of each environmental variable coincides with its arithmetic mean (Phillips et al. 2006). In this analysis, a total of 58 environmental variables were used at a spatial resolution of 1 km^2 (Cruz-Cárdenas et al. 2014; table 3). A list of the names and acronyms of these variables is provided in supplementary file 2. The model output expresses the habitat suitability value for the species as a function of the environmental variables. A high value of the distribution function in a given cell in-

Table 2 – Species of *Zaluzania* analysed and number of records used to generate their potential distribution models. The area under the curve (AUC) values obtained both for training and for testing of the models are indicated.

Species	Number of records	AUC for training	AUC for testing
Zaluzania augusta	168	0.985	0.892
Zaluzania megacephala	55	0.971	0.926
Zaluzania mollissima	16	0.908	0.815
Zaluzania montagnifolia	80	0.962	0.962
Zaluzania parthenioides	98	0.950	0.852
Zaluzania pringlei	35	0.972	0.976
Zaluzania subcordata	23	0.994	0.974
Zaluzania triloba	107	0.953	0.851

dicates favorable conditions for the presence of the species (Guisan & Zimmermann 2000; Soberón & Peterson 2004; Araújo et al. 2005; Elith et al. 2006; Thuiller et al. 2009; Pyron et al. 2015).

An important point to consider when making potential distribution models is to delimit the areas of analysis carefully (Soberón & Peterson 2005). To this end, this work considers the proposal of Soberón & Peterson (2005), explained with a diagram (BAM: biotic, abiotic, and mobility factors) that defines the delimitation of the geographical distributions of the species. This framework allows the area of analysis to be defined based on the localities where the species has been recorded. The study area (M of the BAM diagram) for the species of the genus *Zaluzania* was first defined using a known distribution map of the genus, obtained with the records of the analysed species and using a Geographic Information System (ArcMap 9.3). The map obtained was superimposed on a map of the physiographic provinces of Mexico (Cervantes-Zamora et al. 1990), one of several regionalisations of the country based on topographic characteristics. In this way, the study area (M) was adjusted, selecting only those physiographic provinces where records were located (fig. 1). Then, the potential distribution models were constructed using the delimitation of the known distribution areas of each species and the selected environmental variables.

The 58 environmental variables proposed by Cruz-Cárdenas et al. (2014) were selected (see supplementary file 2). Considering that each variable contributes partially to the distribution of the species, it is important to determine the relative contribution of each variable. To discard the redundant (auto-correlated) variables, a principal component analysis (PCA) was carried out with the values of the 58 bioclimatic layers. PCA helps to reduce the collinearity of the data (variables) and identify those that best explain the variance observed in a set of variables. The PCA was performed using the vegan package, implemented in R (Oksanen et al. 2008; R Development Core Team 2008). The variables with the largest contribution values in the components (table 3) were selected to compute the niche models.

To estimate the species' potential distributions, the MaxEnt algorithm was used (Phillips et al. 2006). It has proven

its efficacy when predictions are based on information of presence-only data (Elith et al. 2006; Peterson et al. 2007; Phillips 2008; Phillips & Dudík 2008). MaxEnt guarantees distributions with optimal probabilities (maximum entropy, Phillips et al. 2006), in addition to predicting the availability of habitat for the species (Giovanelli et al. 2008). The models were obtained using 75% of the data for training and the remaining 25% for testing. The Raw output format was used following the recommendations of Warren et al. (2008) in the interpretation of data analysed with niche conservatism methods. Automatic features (linear or quadratic) were used because they are determined by MaxEnt depending on the number of records used in the model. We used the cross-validation type because it is recommended when there are 25 or more occurrence data points, and it selects sample points randomly from the background (Peterson 2011; Elith et al. 2011; Liu et al. 2011). The regularization value was the default to obtain homogeneous projections from models obtained with all subsets. The threshold setting used was maximum sensitivity training plus specificity, as recommended by Liu et al. (2011). We used the AUC (Area Under the Curve) of the Receiver Operating Characteristic (ROC) graphic to evaluate the efficacy of the models using AUC values larger than 0.7 as indicators of good model performance (Elith et al. 2011).

Once the models were obtained, the overlap between the sites for each pair of species was evaluated, using the indices of equivalence (*D*) and similarity (*I*) of the tests proposed by Warren et al. (2008, 2010). The first index (*D*) is derived from Schoener's index (1968), used in ecology to evaluate food niche and microhabitat overlap. The second index (*I*), is derived from Hellinger's distance, based on the comparison of probability distributions. Both indices can take values ranging from 0, which indicates no overlap, up to 1, which indicates that the models are identical. The ENMTools v.1.4 package was used to carry out the two tests (Warren et al. 2008, 2010, 2019). Determination of the *D* and *I* parameters requires two key information elements: the distribution of the potential area modelled for each species, and information on the preferred environmental conditions of each pair of species of the genus under study. The results are expressed as the probability of finding the right conditions for the plants

Table 3 – Contributing values of the environmental variables selected using the principal component analysis to carry out the potential distribution models of the *Zaluzania* species.

The list, names, and acronyms of the selected variables, as well as the full list of variables (including those not selected) are described in supplementary file 2.

Variables		First Component	Second Component
Acronym	**Definition**		
bio03	Isothermality (bio1/bio7) × 100	0.80	0.80
bio04	Temperature seasonality (standard deviation × 100)	0.96	0.96
bio05	Maximum temperature of warmest month	0.55	0.55
bio07	Annual temperature range (bio5-bio6)	0.71	0.71
bio08	Mean temperature of wettest quarter	0.62	0.62
bio10	Mean temperature of warmest quarter	0.58	0.58
bio12	Annual precipitation	0.51	0.51
IVNH	Humid months of year normalized index	0.52	0.04
Slope	Slope	1.00	0.31
IVNABR	April vegetation normalized index	0.50	0.00
IVNDIC	December vegetation normalized index	0.62	0.26
IVNENE	January vegetation normalized index	0.59	0.10
IVNFEB	February vegetation normalized index	0.58	0.04
IVNJUL	July vegetation normalized index	0.51	0.01
IVNMAR	March vegetation normalized index	0.53	0.04
IVNNOV	November vegetation normalized index	0.60	0.22
IVNOCT	October vegetation normalized index	0.51	0.02
PPH	Precipitation of the humid months	0.54	0.54
IVNS	Dry months of vegetation normalized index	0.60	0.15
TH	Mean temperature of the humid months	0.58	0.58
TRI	Terrain rugosity index	0.89	0.31
THI	Topographic humidity index	0.69	0.29
Component's Importance			
Standard deviation		6.45	7.27
Proportion of Variance		0.98	0.01

in any pixel, within the area under consideration, allowing for the adequacy of the climate in each determined pixel. We can therefore compare the probability of finding a species within each pixel using the species' own potential distribution model with the probability of finding the species in the same pixels, but using the sites recorded by the model of the other species (Warren et al. 2010). As implemented in ENM-Tools, niche overlap is calculated as a proportion of shared pixels between two species: the number of localities in which both species A and B are found is divided by the sum of the number of localities in which species A is found plus those

where species B is found. The differences between A and B for a given pixel indicate how similar the climate is in that pixel, with respect to the requirements of each species. By means of potential distribution models of the analysed species, an environmental similarity between the compared sites is obtained.

For the equivalence test, the potential distribution models of the *Zaluzania* species were also used. This process generates two sets of data of the same size. For each data set, ENMTools uses MaxEnt to project a distribution model and then calculates the parameter *D* based on the estimated oc-

currences for each pixel. Unless the exact points where the organisms at the two sites were found to be climatically similar, the test tends to reject the idea that the sites are identical, suggesting there is no niche conservatism (Warren et al. 2008, 2010).

It has been postulated that abundance declines with geographical distance to the range centre of a species (Martínez-Meyer et al. 2013). Although there is no abundance data for this investigation, the geographical centroid of each species' distribution was estimated to compare their geographic concordance with respect to a genus' centroid that includes all the environmental variability evaluated. First, using GIS, we combined the maps showing the maximum consensus values of the environmental layers used to construct the species potential distribution maps. This generated a matrix in which the columns contain the values of each environmental variable and the rows the geographic points where the species was predicted to be present. Second, the environmental variables were standardized to a standard normal distribution (Z), so the mean value of each variable is equal to zero; this multidimensional point corresponds to the environmental centroid. Third, the Euclidean distances to the environmental centroid

of the genus were calculated for each species. Finally, the geographical centroid of each species' distribution was estimated to compare the geographic concordance among the species. These estimates were carried out by using the central feature tool as implemented in ArcMap 9.3.

RESULTS

Figure 1 shows the collection sites of the *Zaluzania* species, which were used to determine in which physiographic provinces the genus occurs and to define the area M (of the BAM model). This M includes 32 provinces (out of 185 Mexican provinces) that were used to generate the species ecological niche models (table 1, fig. 2). Inside this area, MaxEnt selected the collection and background points needed to compile the ecological niche models for each of the eight species analysed. Based on the PCA, 22 variables (from a total of 58) were selected from the first two principal components, which explained 99% of the accumulated variance. Using these variables and the defined area M, the ecological niche models of the selected species were carried out (fig. 2, table 3).
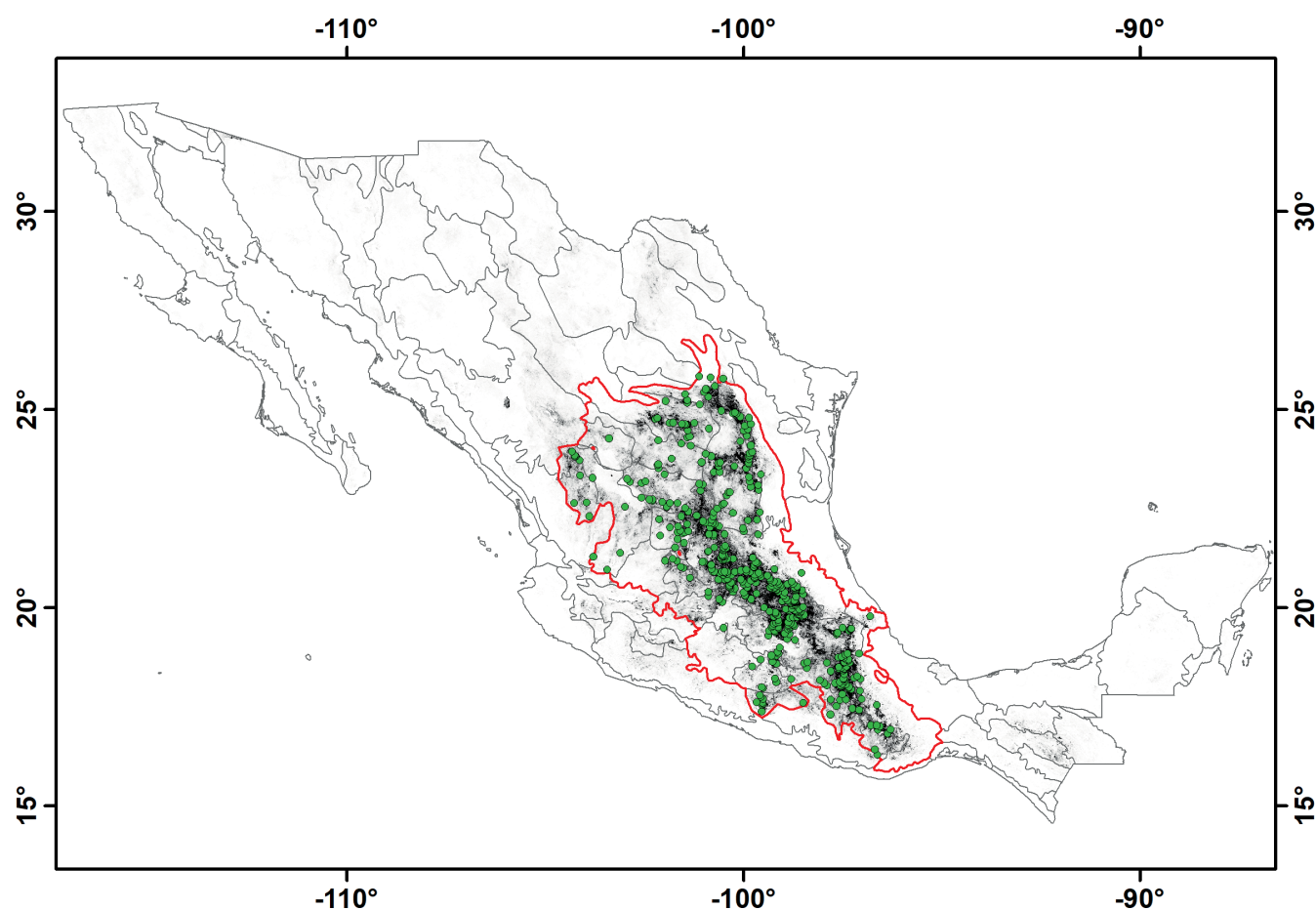

Figure 1 – Map of the physiographic provinces of Mexico on which the study area (area M, Soberón & Peterson 2005) is delineated with a red line. The ecological niche models were constructed using this area. The occurrences of all records of the eight *Zaluzania* species studied are indicated with green circles. Map created using ArcMap 9.3 (https://www.arcgis.com). © Esri and its licensors, all rights reserved. This image is not distributed under the terms of the Creative Commons license of this publication. For permission to reuse, please contact the rights holder.
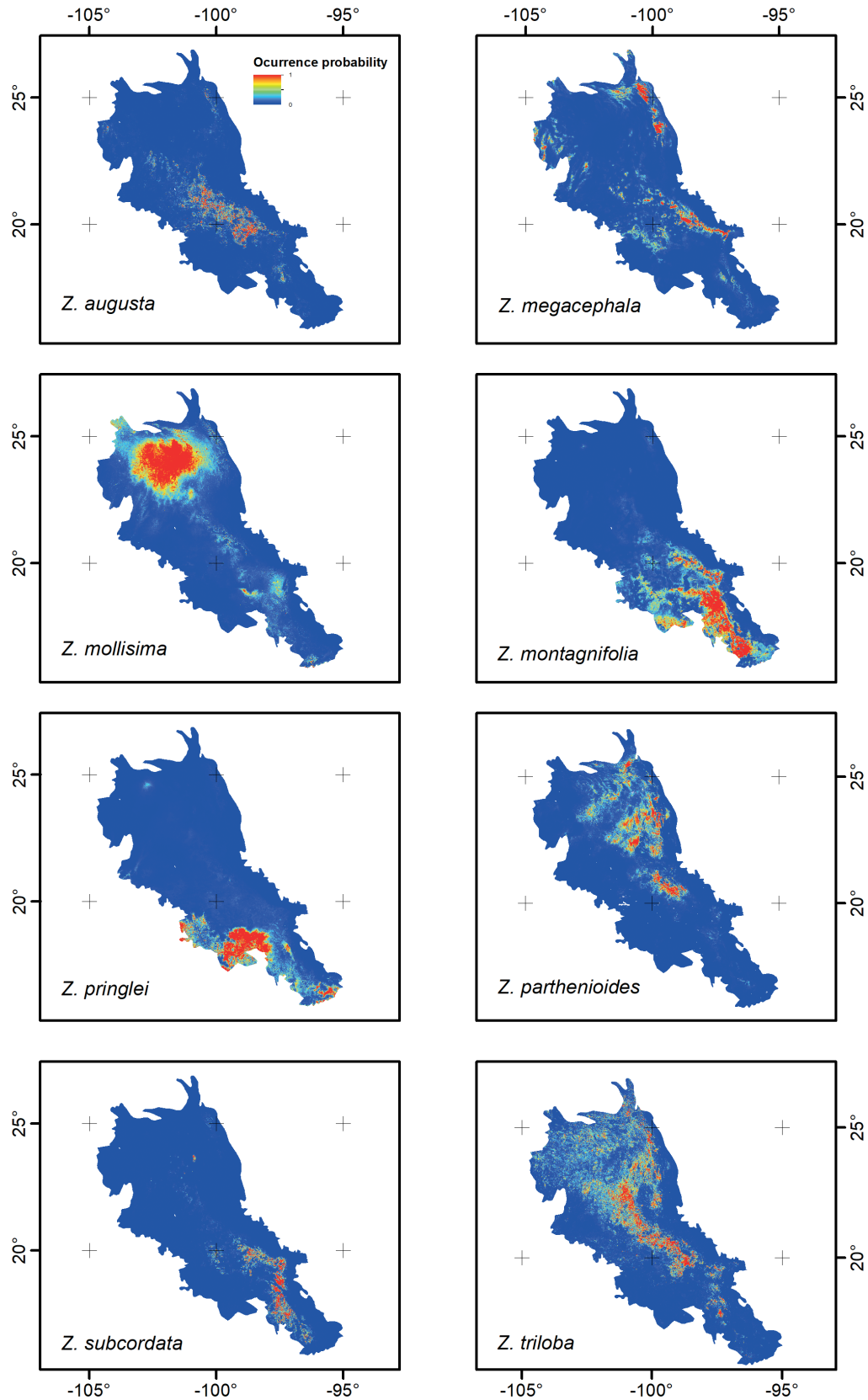
Figure 2 – Potential distribution models obtained for the eight *Zaluzania* species studied. Maps created using ArcMap 9.3 (https://www.arcgis.com). © Esri and its licensors, all rights reserved. This image is not distributed under the terms of the Creative Commons license of this publication. For permission to reuse, please contact the rights holder.

Table 4 – **Overlap values of the analysed species obtained using the *D* = Schoener's and *I* = Hellinger's indices.**
The observed data values are shown below the diagonal, while the expected data are at the top. Zaug = *Z. augusta*, Zmeg = *Z. megacephala*, Zmol = *Z. mollissima*, Zmon = *Z. montagnifolia*, Zpar = *Z. parthenioides*, Zpri = *Z. pringlei*, Zsub = *Z. subcordata*, Ztri = *Z. triloba*.

				Expected values (*D*)				
Species	Zaug	Zmeg	Zmol	Zmon	Zpar	Zpri	Zsub	Ztri
Zaug	1	0.59	0.41	0.64	0.88	0.56	0.55	0.68
Zmeg	0.16	1	0.46	0.64	0.53	0.59	0.55	0.67
Zmol	0.11	0.15	1	0.46	0.50	0.48	0.44	0.56
Zmon	0.16	0.13	0.12	1	0.59	0.59	0.64	0.67
Zpar	0.16	0.08	0.32	0.33	1	0.55	0.54	0.71
Zpri	0.08	0.13	0.13	0.33	0.06	1	0.48	0.58
Zsub	0.14	0.10	0.08	0.07	0.05	0.11	1	0.58
Ztri	0.31	0.16	0.34	0.13	0.39	0.09	0.09	1

Observed values (D)

				Expected values (*I*)				
Species	Zaug	Zmeg	Zmol	Zmon	Zpar	Zpri	Zsub	Ztri
Zaug	1	0.85	0.71	0.89	0.63	0.83	0.82	0.91
Zmeg	0.39	1	0.76	0.88	0.81	0.86	0.84	0.89
Zmol	0.30	0.15	1	0.74	0.78	0.78	0.75	0.84
Zmon	0.40	0.13	0.12	1	0.89	0.86	0.85	0.91
Zpar	0.38	0.08	0.32	0.33	1	0.82	0.81	0.92
Zpri	0.26	0.13	0.13	0.33	0.06	1	0.78	0.85
Zsub	0.34	0.10	0.08	0.07	0.05	0.11	1	0.85
Ztri	0.58	0.40	0.65	0.32	0.68	0.27	0.24	1

Observed values (I)

The models were evaluated using the area under the curve (AUC) described by Phillips et al. (2006). The AUC values for both the training and testing of the models are indicated in table 2. All of the models recorded high AUC values (table 2).

Following the methodology proposed by Warren et al. (2008) and Suárez-Mota et al. (2015), we determined levels of niche conservatism between species using the Niche Equivalence Test (Identity) using 100 replicates of the potential distribution models of each species. For both *D* and *I*, the expected values were higher than the observed values, suggesting a low level of niche conservatism between pairs of species (table 4).

The environmental centroids of two species (*Z. augusta* and *Z. triloba*) are closest to the genus centroid. The centroids of the other six species varied in their distances from the genus centroid, with *Z. megacephala* closest and *Z. subcordata* furthest (fig. 3).

DISCUSSION

The genus *Zaluzania* comprises 11 species distributed mostly in the arid and semi-arid regions of Mexico (fig. 1). The genus has been taxonomically reviewed by Olsen (1979)

and Turner (2012) and the species' circumscriptions are not in doubt. The species of this genus are distributed in heterogeneous areas, including 32 physiographic provinces. *Zaluzania augusta* and *Z. triloba* are found in the most provinces (14 both), while *Z. mollissima* and *Z. subcordata* are restricted to four and three provinces, respectively (table 1). Accordingly, the genus was a good candidate to evaluate the existence of niche conservatism among its species.

Niche conservatism, understood as the tendency of congeneric species to maintain ancestral ecological characteristics, implies a certain degree of incapacity to adapt to conditions different from those of its ancestral niche, determining to a large extent its area of distribution (Peterson et al. 1999; Webb et al. 2002; Wiens 2004; Wiens & Graham 2005; Wiens et al. 2010; Peterson 2011). Niche comparison among the *Zaluzania* species suggest low or no identity (table 2), as a consequence of their occurrence in different geographic areas (fig. 2). The low identity values (table 4) may be explained in part by the fact that certain climatic parameters change over time, while others may be conserved in the different physiographic provinces in which the species are distributed.

Pliscoff & Fuentes-Castillo (2011) mention a relationship between niche conservatism and phylogeny; the closer

the species' phylogenetic proximity, the more similar their climatic space, suggesting a greater value of niche overlap (conservatism). Although a phylogeny is lacking for *Zaluzania*, the paired comparison among all of the species showed low values of conservatism (table 4). This suggests that the species underwent a process of fragmentation of their ancestral area of distribution, adapting to environmental conditions different from those of their ancestors (niche divergence), as suggested by several authors (e.g., Peterson et al. 1999; Webb et al. 2002; Wiens 2004; Wiens & Graham 2005; Wiens et al. 2010; Peterson 2011; Suárez-Mota et al. 2015).

Olsen (1979) discussed a closer taxonomic relationship between *Z. montagnifolia* and *Z. pringlei*, however, conservatism values are likewise low and the distance between their geographical centroids suggest their niches have diverged rather than remained conserved (fig. 2, table 4). If a close relationship exists between these species, then allopatric speciation better explains such niche divergence.

The higher number of points close to the environmental centroids of the two species with the higher number of records (*Z. augusta* and *Z. triloba*), could indicate greater abundance, as suggested by Martínez-Meyer et al. (2013). No abundance data is available and therefore field observations are needed to confirm if a larger number of points near the centroid implies a greater abundance. The geographical centroids help to understand the distribution patterns of the species of *Zaluzania*, and to explain the heterogeneity of its areas according to its position in the different physiographic provinces. Centroids placed in the same province suggest some degree of sympatry (for example *Z. montagnifolia* and *Z. subcordata*), with centroids almost overlapping although their *D* and *I* value support a low conservatism between their niches (fig. 2, table 4). These species seem not to be closely related (sister species). Turner (2012) proposes a closer re-

lationship of *Z. montagnifolia* with *Z. pringlei*, and consequently their sympatry is probably derived from secondary contact between their ancestors.

As suggested by Martínez-Meyer et al. (2013), the environmental centroid reflects values closer to the environmental suitability of a species. In the environmental centroid, the average of the different variables or factors that determine the presence of a species converge (Maguire 1973; Maciel-Mata et al. 2015). Environmental centroids of *Z. augusta* and *Z. triloba* overlap with the centroid of the genus in general, but their identity and similarity values are low, indicating a lack of niche conservatism (table 4). Each species of the genus apparently has a fundamental niche defined by environmental heterogeneity distinct from their sister species. The genus *Zaluzania* therefore offers an example of niche divergence among congeneric species, in a relatively small territory.

Our results illustrate the need for robust methods to assess niche differences (Broennimann et al. 2012). Data such as those shown here, and others such as those presented by Broennimann et al. (2012) with different methods, can help measure the degree to which the environmental niche of a group of taxonomically related species has changed over time. More study cases on niche conservatism of plant species are needed, in order to find which species support the hypothesis and which do not (e.g., Suárez-Mota et al. 2015; Manzanilla-Quiñones et al. 2019), especially when their geographical distributions are quite similar.

SUPPLEMENTARY FILES

Two supplementary files are associated with this paper:

Supplementary file 1: Geographical data of the collection sites of the analysed species.
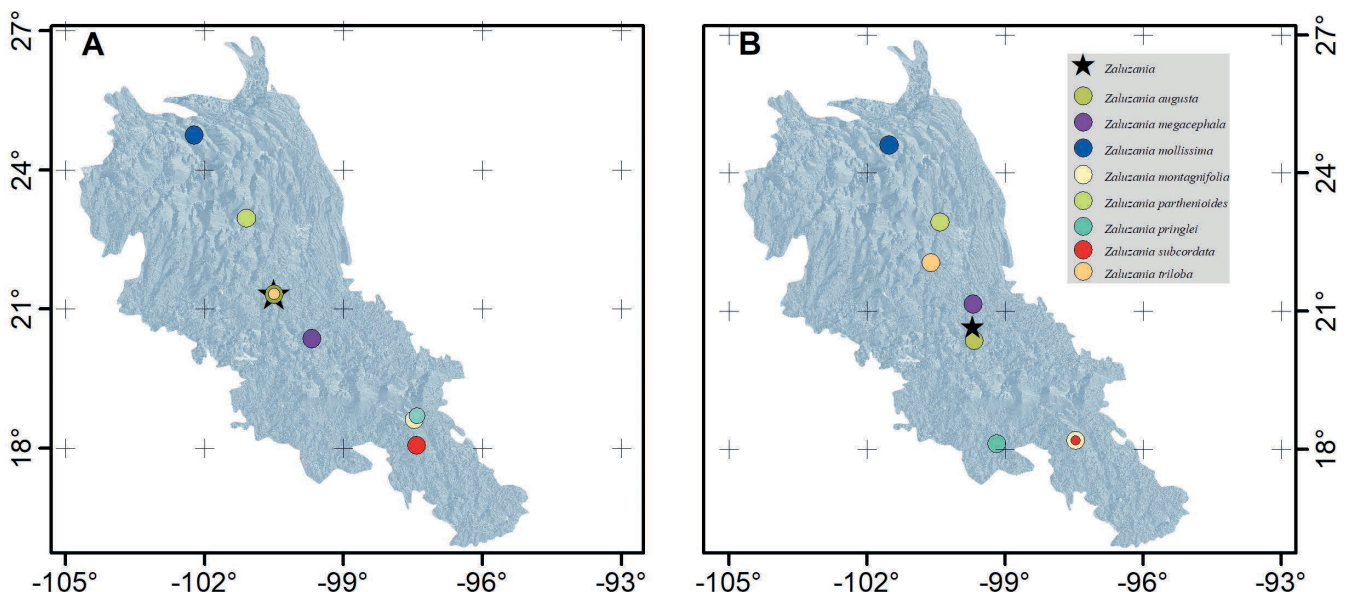
https://doi.org/10.5091/plecevo.2020.1633.2211

Figure 3 – Environmental and geographic centroids of the genus *Zaluzania* as a whole (star) and the eight *Zaluzania* species analysed (circles). **A**. Environmental centroids. **B**. Geographic centroids. Maps created using ArcMap 9.3 (https://www.arcgis.com). © Esri and its licensors, all rights reserved. This image is not distributed under the terms of the Creative Commons license of this publication. For permission to reuse, please contact the rights holder.

Supplementary file 2: List of variables used in the niche models of the analysed species.

https://doi.org/10.5091/plecevo.2020.1633.2213

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