

Analysis and Comparison of the Ecological Niche of Two Endemic Species of the Genus *Diploglossus* (Sauria: Diploglossidae)

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Abstract

Of all the Cuban reptile species, lizards have the greatest richness and diversity. Among them, little is known about the natural history of the species of the genus *Diploglossus*, so that studies on their ecological niche would provide relevant and novel information about their ecology. Because of that, we proposed to characterize the climatically suitable areas of *D. delasagra* and *D. nigropunctatus* and to evaluate the niche overlap between them. We compiled information from 123 georeferenced presence records. Bioclimatic variables of WorldClim were used as predictive variables for the generation of ecological niche models in Maxent program. The final averaged models were binarized to generate presence-absence maps with the ArcGis program. The models obtained were evaluated as useful and excellent according to the difference between the training and testing AUC values, reflecting their high predictive capacity. The contribution of the variables to the resulting models varied between the two species, and in both cases the variables derived from temperature were those with the greatest contribution. The climatically suitable areas completely included the areas of known presence and included other areas. The potential distribution areas of the climate niche for both species showed very different distribution patterns, being higher for *D. delasagra* (221 123.84 km²) and smaller for *D. nigropunctatus* (6 173.82 km²). The Principal Components Analysis showed a very low niche overlap between the species, being D. delasagra the one with the greatest ecological plasticity and D. nigropunctatus the one with the least, the latter with preference of environments with lower values of seasonality in temperatures and a regime of abundant rainfall all year. The ecological niche breadth was also described using the B1 index in the ENMTools program, and the position and amplitude of the niche along the climatic axes. The Discriminant Analysis showed 95.24% of correct classifications, so there is no overlap between the ecological niches of both species. In conclusion, D. delasagra presents a wide distribution with respect to D. nigropunctatus, restricted to the main mountainous massifs of the east of Cuba, and both niches differ in environmental requirements and amplitude, defined by different variables.

Keywords: Diploglossus; Ecological Niche Modeling; Climatically Suitable Areas; Niche Breadth; Niche Overlap; Cuba

Introduction

Reptiles are an important element in ecosystems acting as predators controlling the populations of rodents and invertebrates. At the same time, they are prey to other predators, which is why they are so important in the trophic chains of the places where they live, where they play a vital role as secondary consumers and indicators of habitat quality [1,2]. In Cuba three of the four living orders of reptiles (Testudines, Crocodylia and Squamata) are present, for a total of 161 species grouped in 21 families and 32 genera, with an endemism of the 88%, only overcome by amphibians among Cuban vertebrates [3,4].

However, the disappearance of reptiles in the world is unquestionable [2]. The direct and indirect effects of climate change, the fragmentation and loss of habitat, the introduction of exotic species, the very restricted distribution of many of the species and environmental contamination are potential factors in the decline of the natural populations of this zoological group in our country and worldwide [5].

Of all the species of Cuban reptiles, the lizards (Suborder Lacertilia) present the greatest diversity, represented by 108 species and 84.02% of endemism, been the most diverse group in terms of species shapes and richness [4]. Among them, three belong to the genus *Diploglossus*, which is included within the Family Diploglossidae: *D. delasagra*, *D. garridoi* and *D. nigropunctatus* (Figure 1). These species are commonly known as "four-legged snakes" because of their morphology, and all three are endemic, but data on their natural history are barely available [6]. In addition, two of them, *D. nigropunctatus* and *D. garridoi* are threatened with extinction, so studies of this nature would provide relevant and novel information about the ecology of this group [7,8].



Figure 1: The three species of *Diploglossus* endemic to Cuba: (A): *D. delasagra*, (B): *D. garridoi* and (C): *D. nigropunctatus* respectively. © T. M. Rodríguez-Cabrera, © A. Fong and © G. Begué, respectively.

For all this, it is necessary to know the current status of their populations, habitat requirements and distribution limits, in order to provide the most appropriate management and establish conservation priorities within the National System of Protected Areas. However, knowledge about the distribution of Cuban reptiles is insufficient [9,10], although recent works have offered lists and geographic representations of the localities where these species live [4,11]. In the case of rare species, obtaining this information can be a great challenge, because its detection is positively associated with its abundance, which complicates the efforts to obtain accurate geographic distribution data [12,13]. One of the techniques most used in recent years to generate this type of information are the ecological niche models (ENMs), which allow identifying areas with the appropriate environmental conditions for the presence of a species [13]. The results of studies employing optimal niche theory [14] have shown that some regions are more suitable for a species than other areas, based on factors such as climatic conditions, resource availability and abundance of predators. In Cuba, these tools have been used for lizards of the genus *Sphaerodactylus* by Velazco, et al. [15].

In the particular case of the three Cuban species of the genus *Diploglossus*, there are practically no studies that

address their ecology. In this way, this paper describes for the first time the potential distribution patterns of the ecological niche of two of these species, the adequate environmental requirements for their presence and infers some of their ecological differences. Therefore, this research has as main objectives: 1. the characterization of the climatically suitable areas of *Diploglossus delasagra* and *D. nigropunctatus*; and 2. the evaluation of the niche overlap between these two species.

Materials and Methods

Description of the Study Area

The island of Cuba is located in the northwest end of the Caribbean basin, specifically between 74°08'03" (Punta de Quemado, Maisí) and 85°57'07" (Cape of San Antonio) of west longitude, and the 19°43'38" (Punta del Inglés) and 23°17'09" (Cayo Cruz del Padre) north latitude [16]. The main island presents around 107 466 km² of extension and its maximum width is of 191 km between the north coast of Camagüey and the southeast portion of Granma.

The proximity of Cuba to the North American continent, its relatively little rugged relief, its condition as an island, and the amount of solar radiation that affects its surface, determine its moderate tropical climate [16,17]. In addition, hurricanes and cold fronts are frequent. The most notable thermal variations are found in altitudinal gradients, with up to 6°C of difference between coasts and mountainous systems [17]. Rainfall is the climatic factor that undergoes the greatest change: only in the rainy

season, from May to October 80% of the total annual rainfall (1 375 mm) is recorded, while in the dry season the other 20% is registered (344 mm).

The vegetation of Cuba is characterized by an extraordinary richness of species and considerable endemism, mainly in the mountainous regions, where the areas with the greatest forest coverage are located [18]. It is divided into five large groups: forests, shrubs, herbaceous vegetation, vegetation complexes and secondary vegetation. Capote, et al. [19] defined 29 vegetation formations.

Obtaining the Presence Data

For the modeling, was compiled information from 123 localities with records of the presence of *D. delasagra* and *D. nigropunctatus* from 34 different sources, among which were included publications, management plans, data from Cuban (BIOECO, CZACC, MNHNCU) and foreign (AMNH, MCZ, USNM) zoological collections, personal communications and field data. The compendium of Rodríguez Schettino, et al. [10] was the main source of consultation. Each of these presence records was georeferenced in decimal coordinates according to the description of the sampling sites (Figure 2), for which cartographic sheets were used in the WGS84 projection, with a scale of 1:50 000. To reduce the effect of the spatial autocorrelation in the presence data, all duplicate data were eliminated for each 1 km² cell per species, as recommended by Phillips, et al. [20]. The entire process was performed in the ArcMap 10.2 GIS program [21].



Figure 2: Spatial distribution of the presence points used in the modeling of the ecological niche of *Diploglossus delasagra* and *D. nigropunctatus* (Sauria: Diploglossidae) in Cuba.

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Selection of the Area for the Calibration of the Models

During the modeling process, the presence points are compared with random points within calibration areas (background), to detect the conditions under which a species can potentially live. Taking this into account, random points equidistant 0.5 km were generated in the entire area occupied by the Cuban territory. In the case of *D. delasagra*, this whole area was used for the modeling of its ecological niche, whereas with *D. nigropunctatus* only the Western region was used, to avoid increases in the rate of commission errors (i.e. false positives), [22,23].

Obtaining Environmental Data

The bioclimatic variables used in the processing were extracted from the WorldClim database with a spatial resolution of 0.8960 km² and with the WGS84 datum [24]. In addition, the variables vegetable coverage (based on satellite images and a supervised classification analysis) and digital elevation model (DEM) were included. Between five and six variables were selected to model the ecological niche of both species (Table 1), according to the combination of two different criteria: their contribution to the model and the degree of correlation with the others [24]. The contribution of each of the variables to the calibration process of the model was evaluated using the Jackknife method, which calculates the gain in models

produced with all the variables except one and then in models that include a single variable [20]. This was calculated with the Maxent 3.3.3 k program, with 10 replicas. In addition, to avoid the use of variables that provide the same information [25] a Pearson correlation was performed in the Statistica 8 program, and then those that were not correlated with the others were selected (i.e., with $|\mathbf{r}| < 0.8$), giving priority to the variables defined above as the most important as a result of the Jackknife test [25].

Obtaining Models of Environmental Suitability

For the preparation of the models of the two species we used their presence data (Figure 2) and the environmental variables that were selected based on the previous analysis (Table 1). As background, the same random points were used within the calibration areas generated in the previous process of evaluating the variables. These models were generated with the program Maxent 3.3.3 k [20], which is based on the principle of maximum entropy, which states that the best approximation to an unknown distribution is one that is more expanded but subject to known restrictions. From this assumption, the algorithm estimates, by means of a set of predictor variables, the distribution that adjusts to those values of the predictive variables in the locations where the presence of the species is known.

Variable	D. delasagra	D. nigropunctatus
Mean Diurnal Range (BIO2)	Х	
Isothermality (BIO3)	Х	
Max Temperature of Warmest Month (BIO5)	Х	Х
Temperature Annual Range (BIO7)		Х
Mean Temperature of Wettest Quarter (BIO8)		Х
Precipitation of Driest Month (BI014)	Х	Х
Precipitation Seasonality (BIO15)		Х
Precipitation of Coldest Quarter (BIO19)	Х	Х

Table 1: Variables used in the analysis of the ecological niche of *Diploglossus delasagra* and *D. nigropunctatus* (Sauria: Diploglossidae) in Cuba. Marked with an X appear those variables that were chosen for the generation of the models of each species.

For each of the analyzed species, the final models were the average of 50 replications. We used 75% of the presence data as a training sample to generate the models and the remaining 25% to validate it. We ran 500 iterations to obtain each model and the resampling method used was Bootstrap, which is very useful when there are not very large sample sizes [26]. The contribution of each of the variables was evaluated again, this time with those that were selected for the definitive

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models. The rest of the parameters were maintained with their characteristics and recommended values by default [20].

The outputs of these models produce continuous maps where the value of each pixel equals the probability of presence of a suitable environment for the species, given in continuous values between 0 and 1. For the creation of the presence-absence results (binary), the minimum training presence threshold was used as the cut-off threshold, since it is the least restrictive. Peterson, et al. [27] suggests that Maxent generates better models at low threshold values, while when raising them there is an overfitting of the training data. The reclassification in binary maps was done with the program ArcGis ver. 10.1 [21].

Validation of Ecological Niche Models

The effectiveness of the models was analyzed using the ROC curve (Receiver Operating Characteristic) that represents the relationship between sensitivity and the complement of specificity (1-specificity). Sensitivity is a measure of the rate of true positives and indicates errors of omission, while specificity measures the fraction of negatives classified as presences and represents commission errors [28]. From the ROC curve, the value of the AUC index (area under the curve) was calculated, which measures the ability of the model to discriminate between localities where the species is present or absent. To evaluate the predictive value of the models, the AUC of the training and test data was used and the two were compared to evaluate their differences [29]. For the classification of the models, we followed the criterion of Broennimann, et al. [30], who argue that models with AUC < 0.7 are considered poor, useful between $0.7 \le AUC < 0.9$, and excellent those with AUC \geq 0.9.

Description of the Environmental Suitability Patterns and Characterization of the Known Distribution Areas

The areas with suitable climatic conditions for the presence of the two Diploglossus species studied were described, based on binary presence-absence maps and trend maps. To estimate the area of potential climatic suitability in each model, the area of each one of the pixels of presence of the species in the final models of potential distribution was added. The species were classified using the PPD (percentage of potential distribution), defined as (number of pixels of presence of the species * 100)/total number of pixels of Cuba, in: species with restricted species distribution (0-30%), with intermediate distribution (31-59%) and species with wide distribution (60-100%).

To characterize ecologically the areas of known presence of each species, the values of all the variables were extracted (Table 1) in the presence points with the ArcGis ver. 10.1 [21]. To achieve a better visualization of the results, reduce the redundancy of bioclimatic

variables and decrease the number of parameters, a Principal Components Analysis (PCA) was carried out. The ecological niche breadth was calculated using the B1 index or inverse concentration of Levins in the ENMTools program [31]. From the results of the PCA, the position and amplitude of the niche were also extracted along the climatic axes, similar to the procedure described by Thuiller, et al. [32]. The result of this analysis is the description of the average position of the niche (pCP1, pCP2) in any of the gradients or principal components selected for each species, which represents a measure of the distance between the average conditions used by the species and the average conditions of the study area for the same gradient. For each selected gradient, the variability of the habitat conditions used by each species was estimated, through the calculation of the variance of the coordinates of its presence points in that axis (varCP1, varCP2...varCPn), and this was also considered as a measure of the breadth of the niche. Then, through the descriptive statistics provided by Past 2.17 [33], the environmental ranges that tolerate the species in these areas were calculated [33]. With this same program, a Discriminant Analysis [34] and a Hotelling Test [35] were conducted to evaluate the degree of overlap of the ecological niche of the two species.

Results

Ecological Niche Models

The highest value of AUC for training data obtained for the models corresponded to *D. nigropunctatus* (0.9555), while the lowest was that of *D. delasagra* (0.782), for a general average of 0.8687. According to these values, *D. nigropunctatus* had excellent performance, and *D. delasagra* had an AUC considered useful for modeling [36]. The test AUC values behaved in the same way as the training values. The differences between the training and test AUC values were between 0.0586 and 0.0726, which shows that the models were not over-adjusted to the data [37].

According to Jackknife's test the contribution of the variables to the resulting models varied between the two species, and in both cases the variables derived from temperature were those with the greatest contribution. The precipitation of the coldest quarter (BI019) reached the highest percentage of contribution in the construction of *D. nigropunctatus* model (Table 2). It is followed by the max temperature of the warmest month (BIO5) and the mean temperature of the wettest quarter (BI08). With regard to the species *D. delasagra*, the variable of greatest

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contribution was the isothermally (BIO3), followed by the max temperature of the warmest month (BIO5) and the precipitation of the coldest quarter (BIO19). In general, in the species *D. nigropunctatus* a greater dependence of the

variables related to the precipitations was observed than in the species *D. delasagra*, which is more widely distributed, and whose contributions of the temperatures variables were significantly higher.

Variable	D. delasagra	D. nigropunctatus
Mean Diurnal Range (BIO2)	5.9	-
Isothermality (BIO3)	43.0	-
Max Temperature of Warmest Month (BIO5)	22.9	26.6
Temperature Annual Range (BIO7)	-	5.0
Mean Temperature of Wettest Quarter (BIO8)	-	16.6
Precipitation of Driest Month (BIO14)	9.5	6.9
Precipitation Seasonality (BI015)	-	4.0
Precipitation of Coldest Quarter (BIO19)	18.7	40.90

Table 2: Contribution of environmental variables to the ecological niche models of two Cuban species of the genus *Diploglossus* (Sauria: Diploglossidae). The contribution values are shown in percentages.

Potential Distribution of the Climatic Niche of the Species of the Genus *Diploglossus*.

Because of the process of selection of variables, neither the DEM, nor the vegetation coverage was included for the construction of the ecological niche models, only the bioclimatic variables. Therefore, in the future it will be treated as a *climate niche*, and the resulting areas as *climatically suitable areas* (CSA).

The current potential distributions of the climate niche of the studied species coincide spatially with the presence records and include other areas climatically similar to the training ones. The largest CSA corresponded to that of *D. delasagra* (221 123.84 km²) and the lowest was that of *D. nigropunctatus* (6 173.82 km²) (Figures 3B and 3D). From the percentage values of the potential distribution (PPD), which is no more than a relative measure of the climatic niche dimensions of the species, *D. nigropunctatus* was classified as a species of restricted distribution (DR), and *D delasagra* showed a wide distribution (DA). It should be taken into account that ENM techniques predict areas that, on average, are climatically adequate for the species, but not the presence of these in those areas [30].



Figure 3: Climatic suitability models for (A) *Diploglossus delasagra* and (C) *D. nigropunctatus*, and their climatically suitable areas (B and D, respectively).

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When obtaining the potential distribution maps of the climatic niche for both species of the genus *Diploglossus*, it was observed that these had very different distribution patterns (Figure 3). The CSA of *D. delasagra* are continuously distributed throughout the country, except for the southern plain of Camagüey -Manaibón, the plains of Cauto-Guacanayabo, the northern base of the Sierra Maestra and the plains of Moa - Baracoa (Figure 3B). The higher probability of presence coincides with the points of known presence of the species (Figure 2 and 3A). For D. *nigropunctatus* there are small discontinuous CSAs of over prediction towards the center and west of the country (Figure 3D). The highest climatic suitability values were obtained towards the easternmost tip of Cuba and in the main mountain ranges, mainly in Sierra de los Órganos, Sierra del Rosario, Sierra de Trinidad, Sierra de Sancti Spíritus, Sierra Maestra, Sierra de la Gran Piedra and in Nipe-Sagua-Baracoa massif (Figure 3C).

Ecological Niche Breadth

As for this analysis the 21 original variables were used, in the future it will be referred to as *ecological niche*. In Tables 3 & 4 appears the data obtained from the descriptive statistics of the values of the variables in known points of presence. These values allowed characterizing from the environmental point of view the areas of real distribution of the species, as well as the ranges of tolerance of each one, variable to variable. In general, the variables that contributed the most to climate niche models did not varied much in terms of minimums and maximums for each species, except variable BI019 (precipitation of the coldest quarter). In the case of D. delasagra this variable ranges from 60.85 mm to 217.97 mm, while in *D. nigropunctatus* ranges between 9.20 mm and 46.60 mm. However, the variables with the lowest contribution to climate niche modeling were more plastic with respect to their limits. For both cases, the variable with the least standard deviation was BIO3 (isothermality) (Tables 3 & 4).

Variable	Mean	Minimum	Maximum	Standard deviation
BIO1 (°C)	24.78	19.62	24.63	1.03
BIO2 (°C)	9.78	8.00	11.64	0.85
BIO3	6.26	5.71	6.89	0.28
BIO4 (°C)	19.63	14.48	21.78	2.01
BIO5 (°C)	32.19	25.94	33.82	1.19
BIO6 (°C)	16.67	13.15	19.33	1.02
BI07 (°C)	1.55	1.28	1.73	0.97
BIO8 (°C)	26.59	21.03	27.67	1.05
BIO9 (°C)	22.25	17.59	24.93	1.14
BIO10 (°C)	27.02	21.41	28.47	1.08
BIO11 (°C)	220.07	175.88	241.30	9.97
BIO12 (mm)	136.40	94.55	173.92	15.89
BIO13 (mm)	21.49	15.62	27.44	2.80
BIO14 (mm)	3.31	1.30	6.95	1.14
BIO15 (mm)	57.92	37.52	71.94	6.70
BIO16 (mm)	553.81	397.18	712.77	74.97
BIO17 (mm)	122.33	60.85	213.47	33.92
BIO18 (mm)	503.24	227.15	664.04	96.13
BIO19 (mm)	126.47	60.85	217.97	36.57
Vegetal coverage (%)	7.31	0	27.00	6.57
DEM (meters asl)	118.08	0	1034.00	177.24

Table 3: Descriptive statistics of the values of the predictor variables in the areas of known presence of *D. delasagra* (Sauria: Diploglossidae).

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Variable	Mean	Minimum	Maximum	Standard deviation
BIO1 (°C)	22.69	20.65	26.20	1.73
BIO2 (°C)	9.16	7.44	9.99	0.53
BIO3	6.56	6.24	6.71	0.11
BIO4 (°C)	15.94	14.71	17.03	0.61
BIO5 (°C)	29.47	27.44	32.55	1.65
BIO6 (°C)	15.63	13.65	20.23	1.85
BIO7 (°C)	1.38	1.19	1.50	0.64
BIO8 (°C)	23.74	22.17	26.64	1.21
BIO9 (°C)	20.69	18.50	24.80	1.95
BIO10 (°C)	24.54	22.54	27.91	1.70
BI011 (°C)	20.53	18.51	24.14	1.76
BI012 (mm)	150.01	83.57	219.74	23.53
BI013 (mm)	22.99	17.25	30.72	2.64
BI014 (mm)	6.18	2.36	11.22	2.01
BI015 (mm)	43.39	30.94	60.24	7.38
BI016 (mm)	53.87	38.56	77.37	6.85
BI017 (mm)	21.30	9.20	36.05	6.01
BI018 (mm)	38.56	12.85	49.38	7.70
BI019 (mm)	23.15	9.20	46.60	7.81
Vegetal coverage (%)	17.33	3.00	30.00	8.79
DEM (meters asl)	517.76	13.00	825.00	268.32

Table 4: Descriptive statistics of the values of the predictor variables in the areas of known presence of *D. nigropunctatus* (Sauria: Diploglossidae).

PC	Eigen value	% variance	% cummulative variance
1	63589.00	53.02	53.02
2	46741.70	38.97	91.98
3	7170.15	5.98	97.96
4	1075.66	0.90	98.86
5	749.62	0.62	99.48
6	417.64	0.35	99.83
7	87.09	0.07	99.90
8	61.02	0.05	99.96
9	32.41	0.03	99.98
10	11.53	0.01	99.99
11	3.62	0	99.99
12	3.13	0	100.00
13	2.28	0	100.00
14	1.00	0	100.00
Z	0.33	0	100.00
16	0.14	0	100.00
17	0.05	0	100.00
18	0.02	0	100.00
19	0	0	100.00

Table 5: Own values, percentage of variability explained and accumulated according to the PCA performed with the bioclimatic variables for *Diploglossus delasagra* and *D. nigropunctatus* (Sauria: Diploglossidae).

Table 5 shows the Eigenvalues or magnitude of each vector of the Principal Components Analysis (PCA), together with the percentage of variability explained and accumulated by each of them. In this table, it can be observed that it is possible to adequately represent the variability of the data with the first two components or eigenvectors, with ca. 91.98% of the total variability represented.

The first principal component, which reflects 53.02% of the total variation in the distribution of the species, represents a temperature seasonality gradient since the variable with the highest participation was BIO4, in a positive direction. The second gradient, which explains the 38.97% of the variation, includes the annual precipitation since it received a greater positive contribution from the variable BIO12 (Figure 4).



fundamental niche of *Diploglossus delasagra* and *D. nigropunctatus* (Sauria: Diploglossidae).

From the dispersion ellipses for 95% of the data (Figure 5), the mean position of the niche of each species was determined in the both gradients obtained (pCP1 and pCP2), which represents a measure of the distance between the average conditions used by the species and the average conditions of the study area (Cuba) for each gradient. In addition, the variance of the coordinates of each point of presence in the given component was calculated to estimate the variability of the habitat conditions used by each species, that is, the niche breath in each climatic gradient (varCP1 and varCP2). In the graphical representation of the distribution of both species with respect to the first two principal climatic components (Figure 5), at first sight it is observed that *D*. delasagra is more eurioic than D. nigropunctatus, since its climatic niche has a central tendency (pCP1 = 104.0; pCP2 = -30.9) and at the same time greater amplitude (varCP1 = 39 517.32, varCP2 = 36 579.42). The data of D. nigropunctatus show a smaller dispersion in the X axis (varCP1 = 5 203.21), being located towards its negative region (pCP1 = -311.90, pCP1 = 92.69), so it can be considered a marginal or specialist species with preference for environments with lower values of

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seasonality in temperatures and a regime of abundant rainfall throughout the year (varCP2 = 68 552.7288).



Figure 5: Graphic representation of the climatic fundamental niche of *Diploglossus delasagra* and *D. nigropunctatus* (Sauria: Diploglossidae) given by the two most important principal components.

At the same time, based on Maxent's predictions about the climatic suitability of the habitats of each species, we calculated the inverse concentration B1 with the ENMTools program [38], which is a traditional estimate of niche breadth. For the *D. delasagra* species a high amplitude value was obtained (B1=0.7554), while for the species *D. nigropunctatus* the value was much lower (B1=0.0786). These results correspond to the previous ones, and to those obtained from the PPD.

Analysis of Ecological Niches Overlap

As a result of the Discriminant Analysis, 95.24% of correct classifications were obtained, that is, only 4.76% of the presence points of both species could not be discriminated, since they represent localities with similar environmental conditions (Figure 6). In the same way, highly significant differences were obtained with Hotelling T2 (T2 = 363.42, F = 13.085, p < 0.01), which confirms that there is no overlap between the ecological niches of these two species.



Discussion

The climatic suitability models obtained for the two species showed a predictive capacity that can be considered useful to excellent, since the AUC values for training data were above 0.75, according to the classification of Broennimann, et al. [36]. These predictive capacity values, according to this author, provide high reliability to the obtained models as has been demonstrated by others in similar studies [39-41]. The models generated for the specialist species tended to have a greater predictive power with respect to those of the generalists, as has been observed in other investigations, in which the precision of the model improves when the focal species has a small geographic range [12,41]. Even though the WorldClim database provides 19 bioclimatic variables for modeling, in this research two other topographic and vegetation variables were chosen, which could influence some ecological parameters of both *Diploglossus* species, and which have been widely used in similar studies [42-45]. According to Jiménez-Valverde, et al. [28], using only bioclimatic variables is an error since, often, the distribution of the species is strongly conditioned by geographical aspects.

The contribution of the variables to the resulting models varied between the two species (Table 2), and in all cases the variables derived from temperature were those with the greatest contribution. The precipitation of the coldest quarter (BIO19) was the variable that reached the highest contribution percentage in the construction of the *D. nigropunctatus* model, as did max temperature of

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the warmest month (BIO5) and the mean temperature of the wettest guarter (BIO8). Meanwhile, with the species D. *delasagra* the variable with the highest contribution was the isothermality (BIO3), followed by the mean temperature of the wettest quarter (BIO8) and the precipitation of the coldest quarter (BIO19). This coincides with that was found by Clusella-Trullas, et al. [46], which state that two of the components of the fitness of the squamate ectotherms (mainly lizards and snakes), the maximum critical temperature and the optimum temperature, are more related to the variation in temperature and rainfall, than to the average temperature conditions. Due to this, the variation in temperature, either the diurnal or interannual range between the extreme values, is the major determining factor in their performance and, therefore, the distribution of this zoological group, mainly under the conditions of the tropics.

According to other investigations in lizards of the genus *Sphaerodactylus* [15] and the results obtained from this work, there seems to be a trend towards the annual temperature range (BIO7) being one of the variables with the greatest influence on the distribution of the species of the Eastern region, as it is the case of *D. nigropunctatus*. In the same way, the middle diurnal range (BIO2) seems to be one of the variables of greater contribution in species of wide distribution and great ecological plasticity as *D. delasagra*.

The distributions of the climatic niches of the two species of the Diploglossus genus studied coincided in a large extent with the distributions offered in lists and geographic representations of the localities where these species live [10,47]. As for the extension of the CSA, we obtained values similar to those of Fong, et al. [48,49], which reports an extension of occurrence of 214 902 km² for *D. delasagra* and 6 314 km² for *D. nigropunctatus*. The classification by the PPD resembles the classification of the Cuban herpetofauna according to different geographic distribution patterns (PDG, in Spanish) of Rodríguez Schettino, et al. [41] for the case of *D. nigropunctatus*, which they consider Regional. However, it does not coincide with D. delasagra, which they also classify as Regional, but which in the present contribution was classified as a wide distribution species.

Regarding the niche breadth (index B1), *D. delasagra* obtained a value almost 100 times greater than that of *D. nigropunctatus*. These results reaffirm that *D. delasagra* has a wider niche, that is, it has a greater ecological plasticity; while *D. nigropunctatus* lives in narrower

environmental conditions, that is to say that it is less tolerant or stenoic. These results correspond to their distribution patterns. According to Martínez Reyes, et al. [50], *D. nigropunctatus* is a species with subterranean habits, so it requires very specific environmental conditions to live, more stable from the climatic point of view.

D. delasagra, according to Schwartz, et al. [51] is a mesophilic species, that is, it lives close to the ground, under leaf litter looking for humidity and low temperatures, so it was expected that variables such as BI012 (annual precipitation), and BI016 (precipitation of the rainiest quarter) had high mean values that directly influenced the habitat of this species. It is possible that this behavior allows it to tolerate a greater range of temperatures throughout the year, as evidenced by the results of amplitude and position of the niche obtained here. In the case of *D. nigropunctatus*, even little is known about its ecology and habitat preferences [6]. Its underground habits reported by Martínez Reyes, et al. [50], corresponds to the tendency described here to inhabit places with an abundant annual water regime, which could favor the adequate conditions of soil moisture that this species needs for its penetration. In the case of the results of the descriptive statistics (mean, minimum, maximum and standard deviation), the variables that contributed the most to the ecological niche models did not vary much with respect to their minimum and maximum values, with the exception of BIO19 (precipitation of the coldest quarter), which presented a large oscillation between 60.85 mm and 217.97 mm in D. delasagra, and between 9.20 mm and 46.60 mm in D. nigropunctatus. Other interesting results that were obtained were with the variable DEM, which in the case of *D. delasagra* oscillated from 0 to 1 034 m above sea level (with the mean at 118,08 m above sea level), in correspondence with its generalist character, because it does not seem to have a marked preference for a certain height. However, D. nigropunctatus models located it almost exclusively at elevations, in correspondence with the mean values of DEM (517.76 m). These values are similar to those reported by Fong, et al. [52], which locates the latter species between 150 and 800 m above sea level. The highest vegetal coverage values for this species with respect to those of D. delasagra, coincide with the consistent forest habitats where Fong. et al. [7.8] have collected *D. nigropunctatus*: montane, submontane and low altitude rainforest, although it can also appear in secondary vegetation. Meanwhile, it is possible that D. delasagra exploits more open habitats, such as forest

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edges, gardens and orchards [6], as confirmed by our results.

The Discriminant Analysis confirmed the great difference that exists between the ecological niches of these two species, since they only presented a 4.76% of overlap. Incorrectly classified points of presence may correspond to sympatric localities between these two species, which has never before been described in the literature. The results of the Hotelling Test corroborated that there is practically no overlap between the fundamental niches of *D. delasagra* and *D. nigropunctatus*. These results support the conclusions of Losos, et al. [53] who states that phylogenetically related species do not necessarily have ecological similarities [54].

Conclusion

The distribution of the climatically suitable areas of *D. delasagra* is wide in relation to that of *D. nigropunctatus*, which are restricted to the main mountainous massifs of the east of the country. The ecological niches of both species differ in their environmental requirements and their breadth, and they are defined by different bioclimatic variables, so there is little overlap between them.

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