PHYLOGENETIC ANALYSIS OF THE EVOLUTION OF THE NICHE IN LIZARDS OF THE *ANOLIS SAGREI* GROUP

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Abstract. Recent advances in ecological niche modeling (ENM) algorithms, in conjunction with increasing availability of geographic information system (GIS) data, allow species' niches to be predicted over broad geographic areas using environmental characteristics associated with point localities for a given species. Consequently, the examination of how niches evolve is now possible using a regionally inclusive multivariate approach to characterize the environmental requirements of a species. Initial work that uses this approach has suggested that niche evolution is characterized by conservatism: the more closely related species are, the more similar are their niches. We applied a phylogenetic approach to examine niche evolution during the radiation of Cuban trunk-ground anoles (*Anolis sagrei* group), which has produced 15 species in Cuba. We modeled the niche of 11 species within this group using the WhyWhere ENM algorithm and examined the evolution of the niche using a phylogeny based on ~1500 base pairs of mitochondrial DNA.

No general relationship exists between phylogenetic similarity and niche similarity. Examination of species pairs indicates some examples in which closely related species display niche conservatism and some in which they exhibit highly divergent niches. In addition, some distantly related species exhibit significant niche similarity. Comparisons also revealed a specialist–generalist sister species pair in which the niche of one species is nested within, and much narrower than, the niche of another closely related species.

Key words: anole; Anolis; *Cuba; ecological niche modeling; fundamental niche; niche conservatism; niche evolution; phylogenetics.*

INTRODUCTION

The fundamental niche, which encompasses the theoretical range of conditions a species can occupy (Hutchinson 1957), provides a conceptual framework to predict the potential geographic distribution of a species (MacArthur 1972, Soberón and Peterson 2005). Species traits, whether morphological, physiological, or behavioral, are often obviously linked to the niche and generally susceptible to the processes of evolution. Consequently, the shaping of niche characteristics can be viewed as an evolutionary phenomenon. Because the fundamental niche provides details about the potential distribution of species, and the niche is determined by the processes of evolution, understanding evolutionary patterns of niche diversification can reveal valuable insights into factors related to the diversity and distribution of species.

Studies of the niche have historically involved detailed analyses of local habitat requirements of an organism (Chase and Leibold 2003). Recently, the availability of

global climate and land cover Geographic Information System (GIS) and remote-sensing data has provided environmental information at a regional scale. These data, when integrated into ecological niche modeling (ENM) algorithms, have provided a powerful opportunity to characterize the habitat requirements of a variety of species and assess patterns of niche differentiation in a comparative framework. The majority of recent niche modeling efforts have focused on predicting species' distributions, species' response to climate change, and potential distributions of invasive species (Guisan and Zimmerman 2000, Peterson 2001, 2003, Peterson and Vieglais 2001, Oberhauser and Peterson 2003, Peterson and Robins 2003, Illoldi-Rangel et al. 2004, Peterson et al. 2004). While these studies have provided novel insights into aspects of broad-scale ecological niche characteristics, recent research has begun to realize the potential to examine the results of niche modeling efforts in an evolutionary context (Peterson et al. 1999, Rice et al. 2003, Graham et al. 2004).

Two approaches have been taken to integrating information on evolutionary relationships into niche modeling studies. On one hand, some studies have focused on recent evolutionary events by comparing pairs of closely related taxa (either subspecies or sister
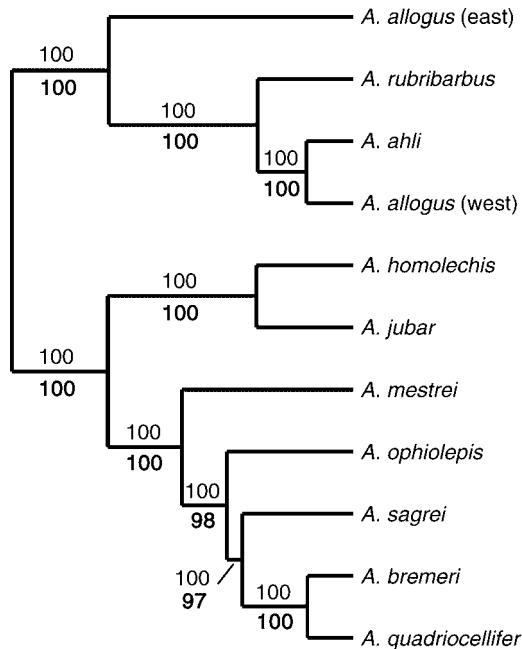
FIG. 1. Ultrametric phylogeny for the *Anolis sagrei* group derived from Bayesian phylogenetic analysis of ~1500 base pairs of mtDNA. The support values and simplified tree presented here were generated by culling taxa from a larger tree that included 306 unique sequences obtained from 315 individuals representing 11 of 15 *A. sagrei* group species. Numbers above nodes represent posterior probabilities obtained from Bayesian analysis. Boldface numbers below nodes represent bootstrap values obtained from 200 bootstrapped data sets analyzed via maximum parsimony.

species [Peterson et al. 1999, Peterson and Holt 2003]). Results from these studies suggest that conservatism, where taxa that are more closely related possess characteristics that are more similar (Harvey and Pagel 1991, Lord et al. 1995, Webb et al. 2002), is a frequent occurrence and characterizes evolutionary patterns of niche diversification. Alternatively, other studies have included deeper evolutionary divergence by using phylogenetic methods to reconstruct the niche of ancestral taxa (Rice et al. 2003, Graham et al. 2004). Results from these studies suggest that niche conservatism might not be a consistent characteristic during diversification. Both of these approaches have limitations: the former approach has limited scope and only applies to evolutionary events in the recent past, whereas the accuracy of the latter approach is questionable because a number of studies have demonstrated that phylogenetically derived estimates of ancestral states will in many cases have low accuracy and extremely high uncertainty (Schluter et al. 1997, Losos 1999, Martins 1999, Oakley and Cunningham 2000, Webster and Purvis 2002).

We propose an alternative approach, similar to one applied by Rice et al. (2003), that makes full use of phylogenetic information and thus permits inferences beyond comparison of closely related taxa, while avoiding the pitfalls of ancestor reconstruction. Specifically, following the logic of Harvey and Pagel's (1991) "non-directional approach," we examine the extent to which niche similarity among extant species is a function of phylogenetic similarity. Like the widely used independent-contrasts method (Felsenstein 1985), this approach allows the integration of phylogenetic information into comparative analyses without requiring inference concerning the characteristics of hypothetical ancestral taxa.

Caribbean lizards of the genus *Anolis* are a particularly good group for such studies (see Plate 1). Anoles are abundant and diverse on Caribbean islands, with as many as 57 species on a single island (Cuba) and up to 11 species occurring sympatrically, and their ecology has been extensively studied (reviewed in Losos [1994] and Roughgarden [1995]). Moreover, recent research has established a firm phylogenetic framework for the Caribbean anole radiation (Poe 2004, Nicholson et al. 2005). Our focus in this study is on the *A. sagrei* species group on Cuba. This clade contains 15 species, all but one of which use similar microhabitats, occurring on tree trunks and other broad surfaces low to the ground, and using the ground extensively for foraging and intraspecific interactions (the "trunk ground ecomorph" niche of Williams [1983]). Several species occur widely throughout Cuba, whereas others have restricted distributions; as many as four occur sympatrically (Losos et al. 2003). Recent phylogenetic work (Glor 2004) has provided the phylogenetic framework for the investigation of the evolution of the niche and community composition.

In this study, we examine the evolution of niche characteristics in species within the *A. sagrei* group on Cuba. We characterize the broad-scale environmental components of the niche using ENM algorithms and GIS data. We then incorporate the results of these analyses with information on the phylogenetic relationships within the *A. sagrei* group to examine patterns of niche diversification within this island group.

METHODS

Phylogenetic relationships among members of the Anolis sagrei group

We obtained an mtDNA phylogeny for the *A. sagrei* species group from Glor (2004). This tree was reconstructed from 306 unique sequences obtained from 315 individuals representing 11 of 16 *A. sagrei* group species and including extensive intraspecific sampling within most widespread species (Glor 2004). We treat *A. allogus* as two separate species, *A. allogus* (east) and *A. allogus* (west), because they are highly divergent genetically and do not form a clade (Glor 2004) (Fig. 1); thus the discrepancy between the 15 recognized species and the 16 species referred to in our analyses. Maximum-parsimony analysis implemented by PAUP* 4.0b10 (Swofford 2002) and Bayesian analysis implemented in MrBayes 3.0 (Huelsenbeck and Ronquist 2001) yielded

TABLE 1. Results of niche modeling predictions for species in the *Anolis sagrei* group.

Species	N†	GARP external accuracy mean (range)	WhyWhere External accuracy	WhyWhere Z statistic
A. ahli	16	0.748 (0.500–0.999)	0.490	31.15***
A. allogus (east)	65	0.542 (0.466–0.972)	0.758	23.19***
A. allogus (west)	23	0.500 (0.500–0.500)	0.945	29.26***
A. bremeri	25	0.545 (0.500–0.952)	0.845	30.40***
A. homolechis	146	0.962 (0.951–0.972)	0.595	18.50***
A. jubar	63	0.594 (0.500–0.984)	0.736	22.00***
A. mestrei	35	0.597 (0.500–0.993)	0.958	30.13***
A. ophiolepis	43	0.814 (0.500–0.973)	0.756	19.16***
A. quadriocellifer	24	0.735 (0.500–0.992)	0.981	30.73***
A. rubribarbus	21	0.547 (0.500–0.971)	0.971	30.23***
A. sagrei	124	0.953 (0.937–0.968)	0.627	17.80***

*** $P < 0.001$ for all of the WhyWhere predictions.
† Number of localities for each species.

congruent and well-supported topologies (Fig. 1). Phylogenetic analysis of a nuclear DNA fragment (the third intron of the rhodopsin-encoding gene) for a subset of the taxa included in the mtDNA phylogeny also yields a topology that is concordant with all of the nodes presented in Fig. 1 (Glor 2004).

We then converted the Bayesian mtDNA tree into an ultrametric form using Sanderson's (2002) penalized-likelihood approach, as implemented by the program r8s (Sanderson 2003). A smoothing value for the penalized-likelihood analysis was determined via cross-validation. Following conversion of the tree into an ultrametric format, taxa within monophyletic groups were pruned until a single representative of each species remained (Fig. 1). In the case of *A. allogus*, we retained two individuals representing the genetically distinct eastern and western populations. This pruned tree was then used to derive patristic distances among all pairwise taxonomic comparisons.

Niche characteristics of members of the Anolis sagrei group

Ecological niche modeling provides the ability to estimate the niche of a species based on known species localities and environmental parameters characterized in GIS data sets. This estimation is then used to predict the potential geographic distribution of a species based on the same GIS data (Peterson 2001). These predictions are based on broad-scale environmental data and do not account for microhabitat characteristics. Consequently, microhabitat partitioning among sympatric anoles, which has been an important component in the community structure and evolutionary diversification of anoles (e.g., Williams 1983, Losos et al. 2003), is not considered in the ENM algorithms. Similar broad-scale ENM analyses have suggested a high predictive ability for geographic distribution with the ENM algorithms (Peterson 2001, 2003, Peterson and Vieglais 2001, Oberhauser and Peterson 2003, Peterson and Robins 2003, Illoldi-Rangel et al. 2004, Peterson et al. 2004). In other words, the broad-scale ENM approach is useful

for predicting whether a species will occur in a particular region, but is not insightful regarding microhabitat differences among co-occurring species.

We compiled locality information for 11 species in the *A. sagrei* group from natural history museum collection records (American Museum of Natural History; California Academy of Sciences; Field Museum; Museum of Comparative Zoology, Harvard University; Museum of Vertebrate Zoology, University of California-Berkeley; Smithsonian National Museum of Natural History; University of Kansas Natural History Museum) and published data (Schwartz and Henderson 1991, Rodríguez-Schettino 1999) (Table 1). The five species for which phylogenetic data are not available are known from an extremely limited number of individuals or localities (Rodríguez-Schettino 1999).

We predicted the niche of each species in the *A. sagrei* group using the WhyWhere niche modeling program (Stockwell 2006; software *available online*).[5] The Why-Where algorithm (newly available in June 2004) affords greater predictive ability and decreased computational time compared to the commonly used GIS-based Genetic Algorithm for Rule-Set Prediction (GARP) ENM application (Stockwell and Peters 1999). To achieve results, WhyWhere converts environmental data layers into multicolor images and applies a data-mining approach to image processing methods to sort through large amounts of data to determine the variables that best predict species occurrences. Testing of the predictive ability of each model is performed by calculating the accuracy of the model based on species presence data and randomly generated pseudo-absence points within a specified geographic region (similar to GARP) (Stockwell and Peters 1999), in this case Cuba.

We used the WhyWhere ENM algorithm, 184 terrestrial environmental data layers (see Stockwell [2006] for information on data layers), and georeferenced species occurrence data to predict the niche of each species in the *A. sagrei* group. These ENM

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[5] ⟨http://biodi.sdsc.edu/ww_home.html⟩

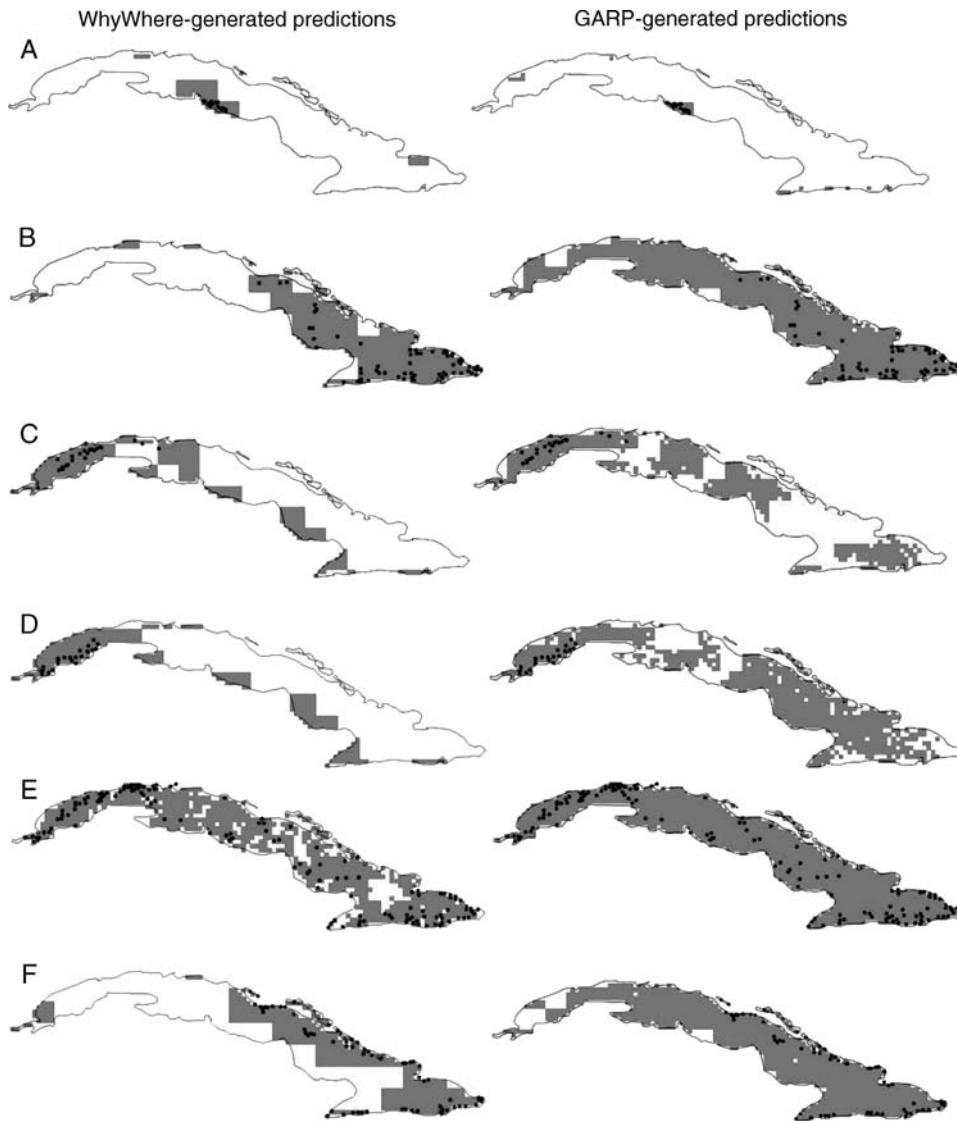WhyWhere-generated predictions   GARP-generated predictions

Fig. 2. Potential distributions of species in the *Anolis sagrei* group based on WhyWhere and Genetic Algorithm for Rule-Set Prediction (GARP) ecological niche modeling predictions. Points represent locality data used in model development and testing for each species. Species designations are as follows: A, *A. ahli*; B, *A. allogus* (east); C, *A. allogus* (west); D, *A. bremeri*; E, *A. homolechis*; F, *A. jubar*; G, *A. mestrei*; H, *A. ophiolepis*; I, *A. quadriocellifer*; J, *A. rubribarbus*; K, *A. sagrei.*

predictions reflect the potential geographic distribution of each species on Cuba based on the ENM algorithms and the GIS data used to construct each prediction. Each prediction was calculated based on a 0.1° resolution per grid cell, a 0.5 occurrence cut for each prediction, and a 1.28 Z score termination condition. For each species, 50% of the locality data were used for model training (internal accuracy), while 50% were held back for testing of model accuracy (external accuracy). We determined accuracy of each prediction using the same protocol as GARP (Stockwell and Peters 1999).

Although WhyWhere has been demonstrated to generate predictions with higher accuracy than the frequently used GARP ENM (Stockwell 2006), we also modeled the niche of each species using GARP for

qualitative assessment of the WhyWhere application. Both GARP and WhyWhere were developed by the same person/research group, and both applications calculate model accuracy in a similar manner (Stockwell and Peters 1999, Stockwell 2006). Thus, the accuracy of predictions generated by the two ENM algorithms are qualitatively comparable.

Using the *Anolis* locality data and the GARP ENM application, we again predicted the niche of each species in the *A. sagrei* group. GIS data sets were at a 0.1° resolution and included layers describing topography (elevation, slope, aspect, flow accumulation, and flow direction) and climate (annual means of total, minimum, and maximum temperature, precipitation, solar radiation, vapor pressure, and wet days). We developed 100

WhyWhere-generated predictions　　　　　　GARP-generated predictions
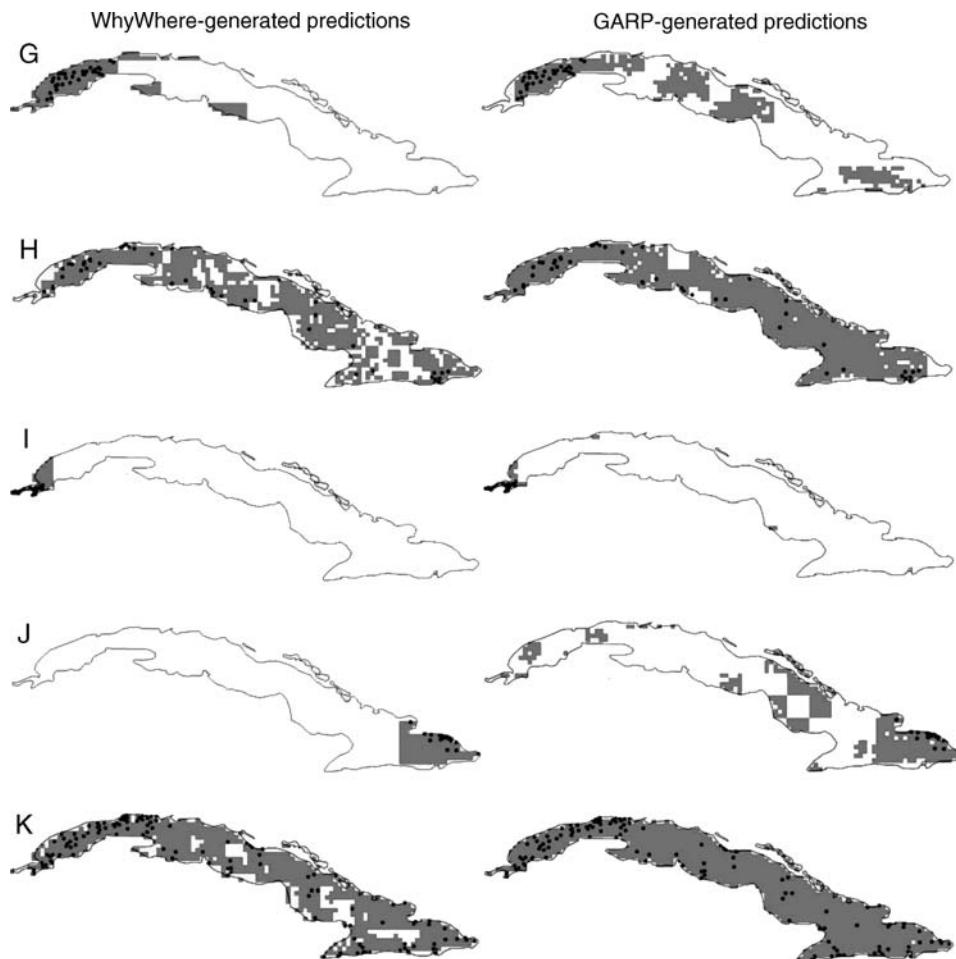

Fig. 2. Continued.

niche models for each species based on locality data. The GARP algorithm was run for 1000 iterations or until a convergence limit of 0.1 was achieved for each species. During model development, 50% of the localities were used for model training, while 50% of the localities were held back to test model accuracy. Using the best-subset selection criteria (Anderson et al. 2003), we chose 20 models that had an omission error of <5% based on the localities used to test each model. From these 20 "best" models, we then selected the 10 models that exhibited an intrinsic commission index closest to the mean intrinsic commission index for the 20 models (Anderson et al. 2003; similar to Oberhauser and Peterson [2003]). We then imported these models into GIS software (DIVA-GIS [Hijmans et al. 2001]), identified the areas of predicted occurrence that were present in all 10 models, and used this area as our prediction for each species. The use of areas that only occur in the predictions of all 10 models is a conservative approach; however, this methodological choice still resulted in predictions that encompassed all of the locality data for each species.

We investigated the relationship between niche similarity and phylogenetic relatedness in a geographic context by examining the frequency that known localities from a particular species fall within the ENM predicted geographic distribution of another species (similar to Peterson et al. [1999]). Using a binomial probability distribution, we determined if the number of times that the occurrence data points of one species overlapped the predicted distribution of another species was nonrandom. For the binomial probability calculation, the null expectation was that the percentage of actual occurrence data points that fell within the predicted range of the other species would correspond to the proportion of Cuba lying within the predicted distribution range. For each species pair, we conducted reciprocal tests for each species. In sister species pairs, greater than expected overlap by both species indicates niche conservatism, and less than expected overlap in both species indicates niche divergence. Also, in sister species pairs, greater than expected overlap by one species and less than expected overlap by the other could suggest a case of niche specialization. In more distantly

TABLE 2. Pairwise comparisons of percentage of locality points of one *Anolis* species that fall within the predicted range of a second *Anolis* species.

Species 1	Species 2					
	A. ahli	*A. allogus* (east)	*A. allogus* (west)	*A. bremeri*	*A. homolechis*	*A. jubar*
A. ahli						
A. allogus (east)	**4.6, 0.0**					
A. allogus (west)	4.3, 93.8	**8.7, 6.2**				
A. bremeri	0.0, 93.8	**4.5, 10.8**	*100, 91.3*			
A. homolechis	6.5, 68.8	*59.4, 95.4*	*47.8, 95.7*	39.9, 91.3		
A. jubar	**0.0, 0.0**	60.3, 69.2	**6.3, 0.0**	**14.3, 12.0**	50.8, 39.1	
A. mestrei	0.0, 93.8	**0.0, 0.0**	*97.1, 95.7*	*97.1, 100*	94.3, 35.5	**8.6, 0.0**
A. ophiolepis	11.6, 93.8	41.9, 73.8	58.1, 82.6	*44.2, 100*	90.7, 62.3	**30.2, 42.9**
A. quadriocellifer	0.0, 0.0	54.2, 0.0	91.7, 4.3	*91.7,* **26.1**	66.7, 5.8	37.5, 0.0
A. rubribarbus	25.0, 0.0	40.0, 56.9	0.0, 0.0	0.0, 0.0	35.0, 18.1	40.0, 12.7
A. sagrei	10.2, 25.0	39.8, 86.2	51.7, 95.7	*44.9, 100*	**70.3, 76.1**	30.5, 57.1

Notes, Percentages in boldface represent cases in which a smaller than expected number of locality points of one species fall within the predicted range of the second species. Percentages in italics represent cases in which a greater than expected number of locality points of one species fall within the predicted range of the second species. In each cell, the value on the left represents the percentage of locality points from Species 1 that fall in the predicted range of Species 2. The value on the right represents the percentage of locality points from Species 2 that fall in the predicted range of Species 1.

related species pairs, greater than expected overlap could suggest either niche convergence or suggest that the species have both retained the ancestral condition (i.e., stasis).

In addition to the geographic approach to niche overlap using species locality data and the predictions generated by the ENM algorithms, we also examined overlap of the "environmental envelopes" of species pairs using GIS-derived environmental data extracted from localities for each species. We generated the environmental envelope for each species based on data extracted from WorldClim Global Climate GIS data sets (30-second resolution; WorldClim interpolated global terrestrial climate surfaces, version 1.3; data and software *available online*)[6] (Hijmans et al. 2004). The WorldClim data sets consisted of 19 bioclimatic variables including annual mean temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter, with all temperatures reported in degrees Celsius and all precipitation amounts reported in millimeters. Environmental data for each species was compiled by importing species locality points into DIVA-GIS (Hijmans et al. 2001) to generate longitude–latitude layers for each species. Environmental data at each locality were then extracted from each GIS data set to provide 19 climatic measures at each species locality. All climatic data were $\log_{10}$-transformed to standardize data for statistical analyses.

A principal-components analysis (PCA) was performed on the correlation matrix of transformed environmental data to generate an environmental envelope for each species. To generate the environmental envelope, the first two axes of the PCA for each species were plotted in *x–y* space using ArcGIS (version 9.0). A minimum convex polygon (MCP) was then calculated around the points for each species using the Hawth's Tools extension in ArcGIS (*available online*).[7] The area for each species MCP was then calculated in ArcGIS. The percentage niche overlap for each species pair was calculated as the ratio of the sum of the overlap areas in each species' MCP to the total area of each species' MCP, with the resulting quotient multiplied by 100 to yield a percentage.

While the geographic approach applied to the ENM predictions and species locality data is useful for assessing similarities between individual species pairs, the environmental-envelope method allows for the examination of the relationship between niche similarity and phylogenetic similarity among all members of the clade. The environmental envelope could not be used to assess differences between individual species pairs, because we do not know the breadth of the environmental envelope for all of Cuba. Consequently, we could not apply a binomial probability calculation to the overlap between species pairs. We calculated the correlation between niche similarity (i.e., percentage envelope overlap) and phylogenetic similarity (patristic distance between taxa) among all species pairs using a Mantel test. A significant negative correlation indicates niche conservatism between closely related species and niche divergence between distantly related species.

[6] ⟨http://biogeo.berkeley.edu⟩

[7] ⟨http://www.spatialecology.com/htools⟩

TABLE 2. Extended.

A. mestrei	*A. ophiolepis*	*A. quadriocellifer*	*A. rubribarbus*
48.8, 82.9			
91.7, 11.4	*41.7, 7.0*		
0.0, 0.0	*25.0, 14.0*	*0.0, 0.0*	
42.4, 97.1	*66.9, 88.4*	*7.6, 75.0*	*11.8, 50.0*

RESULTS

Niche characteristics of members of the Anolis sagrei group

The modeled niche of each species served as an accurate predictor of the species' distribution in all cases (Table 1, Fig. 2). The GARP application provided 10 "best" models. We used the average accuracy of these models for comparisons with WhyWhere model accuracy. Prediction accuracy was higher with the Why-Where algorithm than with GARP for 7 of 11 species (Table 1), thus we used the WhyWhere predictions to assess individual species pair overlap.

When locality data from one species were compared to the predicted distribution of a sister species using the WhyWhere predictions, significant cases of niche conservatism are recovered (Table 2). Additionally, several cases occurred in which distantly related species had niches that are more similar than would be expected by chance, whether resulting either from convergence or stasis (Table 2). There are also cases in which species pairs exhibit less overlap than expected by chance; however, whether this limited overlap is due to selection-driven divergence or random diversification is unclear. In all of these previous scenarios, both members of the sister species pair exhibited the same reciprocal relationship. In addition, in one case, *A. quadriocellifer* and *A. bremeri*, the relationship was not reciprocal: although a significant percentage of locality data from *A. bremeri* does not fall within the *A. quadriocellifer* prediction, a significant percentage of locality data from *A. quadriocellifer* does fall with in the *A. bremeri* prediction. We regard this as indicating that *A. quadriocellifer* resides in a specialized component of the *A. bremeri* niche (Fig. 3).

The first and second principal components explained 42.4% and 25.7% of the overall variance in the PCA, respectively (Table 3). The Mantel test examination of the relationship between percentage of environmental envelope overlap and phylogenetic similarity indicates no consistent pattern in the evolution of the species niche among species in the *A. sagrei* group ($r = 0.10$, $P = 0.26$) (Fig. 4). Indeed, the most closely related taxa show

little overlap, and most of the cases of the greatest overlap are among distantly related species pairs.

DISCUSSION

A common finding related to trait evolution is that conservatism is the expected pattern during species diversification (Webb et al. 2002). In terms of niche evolution, this conservatism has been hypothesized to result from active, stabilizing selection (Lord et al. 1995), or from fixation of ancestral traits that limit the potential range of outcomes during niche evolution (Westoby et al. 1995; see review in Webb et al. [2002]). Initial ENM work examining niche overlap in species pairs separated by a geographic barrier supported the prediction that niche conservatism characterizes evolutionary diversification (Peterson 2001). However, more recent ENM work has suggested that patterns of niche evolution beyond sister taxa can be inconsistent and not conserved (Rice et al. 2003). Our results from the environmental-envelope overlap analysis are congruent with these more recent findings. No evidence of generalized niche conservatism exists for the *A. sagrei* group in Cuba. Overall, no relationship was found between phylogenetic and niche similarity. This results because some closely related species have greatly divergent niches, whereas some distantly related species are quite similar in their niches.

A closer look at patterns of niche similarity using the ENM predictions and species locality data allows a more detailed level of inference. All combinations of phylogenetic relatedness and degree of niche overlap are seen in the data (Table 2). Examples of closely related taxa with significantly high niche overlap (e.g., *A. bremeri–A. ophiolepis, A. bremeri–A. sagrei, A. mestrei–A. ophiolepis*) indicate niche conservatism. Additionally, high levels of niche differentiation are seen in close relatives that exhibit significantly little niche overlap (e.g., *A. allogus* (east)–*A. allogus* (west), *A. homolechis–A. jubar*).
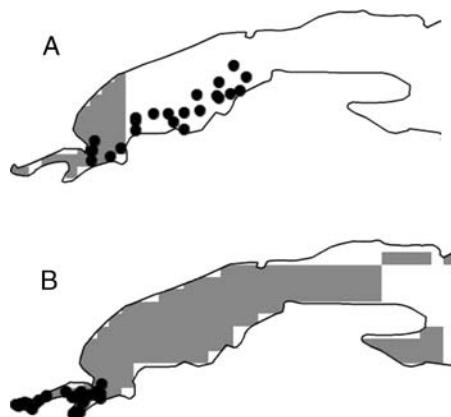

FIG. 3. (A) Predicted distribution of *A. quadriocellifer* with actual localities (points) of *A. bremeri*. (B) Predicted distribution of *A. bremeri* with actual localities (points) of *A. quadriocellifer*.

TABLE 3. PC1 and PC2 loadings from principal-components analysis of environmental variables for species in the *Anolis sagrei* group.

Environmental variable	PC1 loadings	PC2 loadings
Elevation	−0.738	−0.061
Mean annual temperature	0.921	−0.145
Mean diurnal temperature	−0.006	0.731
Isothermality	0.023	−0.061
Temperature seasonality	−0.099	0.562
Maximum temperature, warmest month	0.867	0.148
Minimum temperature, coldest month	0.801	−0.537
Temperature annual range	−0.020	0.864
Mean temperature, wettest quarter	0.803	0.337
Mean temperature, driest quarter	0.837	−0.427
Mean temperature, warmest quarter	0.891	−0.038
Mean temperature, coldest quarter	0.892	−0.330
Annual precipitation	−0.794	−0.027
Precipitation, wettest month	−0.709	0.045
Precipitation, driest month	−0.501	−0.718
Precipitation seasonality	0.301	0.835
Precipitation wettest quarter	−0.684	0.216
Precipitation, driest quarter	−0.565	−0.705
Precipitation, warmest quarter	−0.520	0.644
Precipitation, coldest quarter	−0.461	−0.796

Many cases of low niche overlap among distantly related taxa are also apparent (e.g., *A. allogus* (east)–*A. bremeri*, *A. mestrei*–*A. rubribarbus*). In these cases, examination of species' niches in a phylogenetic context makes evolutionary interpretation, either conservatism or divergence, obvious. By contrast, the evolutionary explanation for similar niches among distantly related taxa is not so clear-cut: long-term conservatism or convergence are both possibilities.

Although the natural history of many members of the *A. sagrei* group is poorly studied, there appear to be at least four axes along which the members of this group partition habitat: heliothermy (sun vs. shade-loving), forest type (xeric vs. mesic), habitat openness (woodland vs. open habitat), and substrate type (trunks vs. rocks) (Ruibal 1961, Ruibal and Williams 1961, Schwartz and Henderson 1991, Rodríguez-Schettino 1999, Losos et al. 2003). Only one of these axes (i.e., forest type) involves a geographic scale of niche partitioning that is appropriate for the methods discussed here. A previous study (Glor 2004) suggested that divergence along this axis, and with respect to substrate type, has occurred repeatedly, perhaps accounting for the observed lack of conservatism. The two other axes (heliothermy and habitat openness) meanwhile, appear more conserved in the sense that they characterize large deeply divergent clades (Glor 2004). Consequently, further study may reveal a greater degree of niche conservatism, particularly along these axes, than we discuss.

Our approach differs from previous niche modeling exercises (Rice et al. 2003, Graham et al. 2004) in which phylogenetic methods have been used to infer the niche of hypothetical ancestral taxa. Because in many cases ancestral reconstructions probably have low accuracy (Schluter et al. 1997, Losos 1999, Martins 1999, Oakley

and Cunningham 2000, Webster and Purvis 2002), we have avoided this approach by focusing only on the niches of extant species in the context of their phylogenetic similarity. The trade-off of this "nondirectional" (sensu Harvey and Pagel 1991) approach, however, is that we are less able to make statements about the direction in which evolution has occurred. In particular, we have a number of cases in which nonsister taxa, and indeed sometimes taxa that are only distantly related, have significantly similar niches. Two processes could account for such cases. On the one hand, two species might have retained the ancestral niche through the course of time; in other words, their conserved niche similarity would be an example of evolutionary stasis. Alternatively, the two species might have independently derived the same niche through convergent evolution. Without inferring ancestral niches, these two possibilities are difficult to distinguish.

One other interesting situation occurred between the sister taxa *A. quadriocellifer* and *A. bremeri*, in which a significant proportion of *A. quadriocellifer* localities fall within the *A. bremeri* prediction, whereas the reciprocal pattern is not exhibited. We interpret this to indicate that the *A. quadriocellifer* niche is more specialized than, and nested within, the *A. bremeri* niche. Again, however, the direction in which this evolutionary change occurred, whether from generalist to specialist or vice versa, is difficult to discern. Nevertheless, the sister taxon to the *A. quadriocellifer*–*A. bremeri* species pair (Fig. 1) is *A. sagrei*, a species that has a broad niche similar to that of *A. bremeri* (Table 2). Consequently, the parsimonious conclusion is that a broader niche is ancestral and the narrower niche of *A. quadriocellifer* is derived in this species.

Despite methodological differences, our results are broadly congruent with previous studies on dendrobatid frogs (Graham et al. 2004) and *Aphelocoma* jays (Rice et
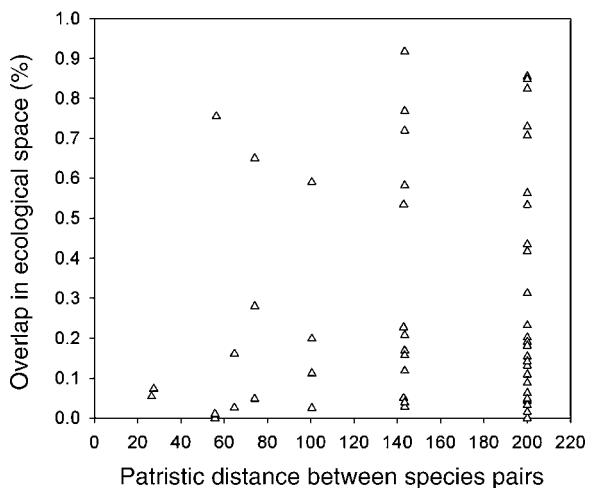

FIG. 4. Relationship between patristic distance and ecological-envelope overlap in species pairs of the *Anolis sagrei* group.

PLATE 1. Example of a Cuban trunk-ground anole lizard species (*Anolis rubribarbus*) from Guantanamo Province at Sendero Natural et Recreo de Nibujon, Cuba. Photo credit: R. E. Glor.

al. 2003): in all three cases, many instances of closely related taxa that diverge greatly in niche have been discovered. Thus, the balance of evidence to date provides little consistent evidence that environmental niches are phylogenetically conservative. The main counterexample to date is a study of Mexican bird species that showed that allopatric populations on either side of the Isthmus of Tehuantepec tend to exhibit niche conservatism (Peterson et al. 1999, Peterson and Holt 2003). Although it is tempting to suggest that the focus on allopatric populations explains these discrepant findings, this conclusion is unwarranted, as closely related allopatric sister taxa show divergence in dendrobatid frogs and anoles.

The broad-scale environmental data used in ENM algorithms successfully predict anole occurrence on a regional scale. Investigating the role that adaptation to different climatic niches has played in anole evolution will contribute importantly to understanding the genesis of the incredible diversity of this species-rich clade. Nonetheless, this approach has limitations. First, the resolution of the GIS data limits analysis to regions, rather than specific localities. Thus, this approach can only investigate environmental determinants of regional co-occurrence, rather than true sympatry. Second, current species distributions may be a result of recent allopatric speciation and not a consequence of species distributions actually tracking climatic conditions. This can present an interpretive dilemma for sister species that appear to diverge in niche characteristics. This scenario is displayed by only one species pair in our data set (*A. jubar*–*A. homolechis*). Finally, an important component of anole community ecology and evolution is partitioning of habitats (e.g., cool/hot; high/low) within a site (Schoener 1968, Williams 1983, Losos et al. 2003), a scale of habitat far too small to be detected by these sorts of data. Clearly, a next step in niche modeling will be the integration, of broad- and fine-scale niche characteristics to elucidate the determinants of local and regional distributions and habitat use.

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