DIVERSITY PATTERNS, NICHES, AND CONSERVATION: HERPETOLOGICAL CASE STUDIES

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Understanding patterns of global diversity and their underlying causes has important implications for conservation. However, analyses at broad geographical scales with local natural history information are rarely undertaken, even when most conservation decisions are made at state or municipal levels. Here I cover three geographical scales and processes toward that end.

Although latitudinal gradients of species richness have been explained in terms of water and energy, different groups respond differently to those variables. I describe patterns of species richness for 112 species of pitvipers throughout the Western Hemisphere and test five hypotheses that might explain those patterns, using geographical information systems and spatial statistics: area, water-energy, habitat heterogeneity, prey availability, and an index of phylogenetic diversity. The main explanatory factor was phylogenetic diversity, followed by prey diversity, then temperature, with other variables contributing only marginally.

Next, I look at the factors that regulate patterns of species occurence at the Neotropic-Nearctic realms border as a way to understand distributional limits. I investigated potential limiting variables for two species of neotropical snakes as they reach the Nearctic realm by using ecological niche modeling. I identify limiting factors for the distribution of those species, the differential way they adapt to local conditions, and suggest marked niche separation for one species, but only moderate differences for the other. These results illustrate the need for intimate knowledge of the organisms to take full advantage of ecological niche modeling.

Finally, I evaluate how humans impact the persistence of vertebrates at local and regional scales in central Mexico. By combining re-surveys with 50-year-old museum collections, field notes, and landscape photographs, I document an increase of species known for Aguascalientes and identify at least one species that might be eradicated. I also provide evidence for extensive habitat modification, and discuss the threat of local extinction at species' distributional limits has broader implications for regional biotas. My findings illustrate the conservation value of intensive small-scale studies, focused on the natural history of particular species and localities, as complements to large-scale biodiversity assessments.

BIOGRAPHICAL SKETCH

Jose Jesus Sigala Rodriguez was born in México City in 1972. At the age of seven he moved North with his family to Aguascalientes in the southern tip of the Mexican Plateu, where we received a *Licenciatura en Biología* degree from the Universidad Autónoma de Aguascalientes in 1995. Between 1993 and 2000 he taught High School biology, coordinated the environmental area in a student-run consulting office, worked in a management position in the private sector, as a law enforcement officer in natural resources for the Mexican Federal government, as an assistant advisor in natural resources for the Governor in the state of Aguascalientes, in teaching/research activities for the Universidad Autónoma de Aguascalientes, and briefly for Arizona State University. In 2000 he moved with his family to Ithaca, NY, US to start graduate studies at Cornell University. Jesus is married to Ernestina Meza Rangel and they have the best children they could have wished for, Sofia and Eric Sigala Meza.

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CHAPTER 1

THE IMPORTANCE OF HISTORY AND RESOURCE AVAILABILITY IN GEOGRAPHICAL PATTERNS OF DIVERSITY

ABSTRACT

Understanding geographical diversity patterns and their underlying causes has important implications for conservation. The widely observed pattern that species richness increases toward the Equator has generally been explained in terms of water and energy, but obviously different groups respond differently to those variables in different regions. Here I examine a case in detail with the goal of testing hypotheses as to the causes for patterns of diversity in the New World and to demonstrate the value of studies of these patterns focusing on particular groups. I focus on pitvipers as a group well suited for analysis of species richness, and start by describing their patterns of species richness, then use geographical information systems and spatial statistics to test five hypotheses that might explain those patterns: area, water-energy, habitat heterogeneity, prey availability, and an index of phylogenetic diversity. The main explanatory factor for patterns of species richness of pitvipers was phylogenetic diversity, followed by prey diversity, then temperature, but there were no significant relationship between species richness and area, habitat heterogeneity, and some environmental variables entailed by the energy hypothesis. My results have specific and broader implications, in a specific context I found that this group of snakes offers many possibilities for more mechanistic ecological and physiological studies of species richness patterns, while in a more general way, they underscore the need for more work documenting patterns of diversity in different regions, with different taxa and at different scales.

INTRODUCTION

Understanding patterns of biological diversity is of paramount importance in conservation efforts at global scales. The increase in number of species as one travels from the poles towards the Equator is among the oldest and most famous ecological patterns in the world (von Humboldt 1808; Wallace 1878; Gaston 2000). This latitudinal gradient in species richness has received attention from generations of ecologists and biogeographers and has been documented in myriad biologic groups in many regions of the world (Pianka 1966; Rosenzweig 1992; Koleff and Gaston 2001; Hillebrand 2004). Species richness or number of species in a given area is among the simplest ecological measurements that can be made in natural areas, and thus together with endemism is especially useful in prioritizing the conservation of biological diversity (Lamoreux et al. 2006).

Studies of the latitudinal gradient have historically focused on descriptions of patterns for different taxonomical groups, with much less effort devoted to mechanisms that explain these patterns (Cardillo et al. 2005). Given the broad geographical scale of patterns of species richness, large areas must be considered to identify factors responsible for those patterns, and this results in the majority of studies being of correlative nature. Unfortunately, this approach often cannot differentiate between direct and indirect effects of the correlated variables under investigation (Hawkins et al. 2003).

Latitude per se doesn't explain the distributional patterns of any group of organisms (Hawkins and Diniz-Filho 2004) but describing latitudinal patterns is a good starting point for understanding global variation in biodiversity (Flores Villela et al. 2005; García et al. 2007). Moreover, so called latitudinal gradients in species diversity are not always as cleanly represented as would be expected, and I frequently see that longitude, area and elevation are also strongly correlated with variations in species richness. Accordingly, it may be more appropriate to think of geographical patterns rather than just latitudinal gradients in species diversity (Hawkins and Diniz-Filho 2004).

More than thirty hypotheses have been proposed to explain this ubiquitous pattern (Chown and Gaston 2000; Colwell and Lees 2000; Hawkins et al. 2003; Currie et al. 2004), ranging from the evolutionary history of the tropics and the temperate regions, to contemporaneous ecological interactions, to a correlation with patterns of climate and energy distribution. For practical purposes, these hypotheses can be categorized as follows: i) Random factors, like age and extent of the tropics; ii) resources availability factors, as in the water-energy hypothesis (temperature, humidity, evapotransporation, amount of sun, etc.), biotic interactions (predation, competition, host-parasite relationships), habitat heterogeneity; and iii) historical factors (Pianka 1966; Currie 1991; Hawkins et al. 2003; Vázquez and Stevens 2004).

It has been claimed that latitudinal gradients can be explained by one or two general mechanisms (Rosenzweig 1992), and there is substantial evidence that climatic factors, mainly in the form of available energy and water availability, are the predominant explanations of global patterns in species richness (Hawkins et al. 2003; Rodríguez et al. 2005; Whittaker et al. 2007). However, there is also evidence for factors that are intrinsic to particular groups or peculiar to certain regions (Diniz Filho et al. 2002; Torras et al. 2007). In tropical Yucatan, Mexico, for example, species densities for amphibians are mostly governed by amount and seasonality of rainfall, whereas snakes and lizards are associated with plant height and plant cover (Lee 1980); in China the most important variables are water for amphibians and temperature for reptiles (Qian et al. 2007); while in the Western Hemisphere coral snakes show peaks of species richness at different latitudes than pitvipers (Reed 2003). Although interactions among species are generally not considered, they also might be important (Arnold 1972; Greene 1988).

Most of the cases in which geographical patterns in species richness have been attributed to environmental factors actually refer to contemporary climatic situations, but clearly historical climate change may affect contemporary diversity patterns. Quaternary climate changes, for example, better predict species richness variation in European amphibians and reptiles than contemporary climate (Araújo et al. 2008).

There is evidence for higher diversification rates in clades present in tropical areas (Mittelbach et al 2007), and although many analyses focus on geographical causes to explain the gradient of species richness, more studies are needed that take phylogeny (Cardillo et al. 2005) and niche dynamics (Rangel et al. 2007) into consideration. History is generally not considered as an explanation for geographical patterns of species richness, but several recent efforts underscore its importance in shaping patterns of biodiversity both in the long (Bini et al. 2000; Araújo et al. 2008) and the short term (La Sorte and Boecklen 2005; Wilson et al. 2008). Furthermore, historical habitat stability and the past spatial variation in forested areas are useful in predicting biodiversity patterns, as well as ultimately usable in the targeting of areas or groups for conservation purposes (Graham et al. 2006; Carnaval and Moritz 2008).

The evolutionary time hypothesis views the tropics as a “diversity pump” and holds that more species live there because young species have not had time to disperse to temperate regions; however this hypothesis cannot be used as a generalized explanation for all taxa (Leighton 2005). In selected groups of birds and mammals, elevated speciation and extinction rates would also increase turnover rates at temperate latitudes (Weir and Schluter 2007; but see Tobias et al. 2008). Recently, analyses have become increasingly complex and take into account not only correlations among contemporary environmental variables, but also modeling evolutionary processes like niche evolution, range shifts, extinction and speciation (Wiens and Donoghue 2004;

Wiens and Graham 2005; Rangel et al. 2007; Arita and Vazquez-Dominguez 2008).

Ultimately, understanding geographical patterns in species richness will serve conservation in a myriad of ways. Not only it will be possible for example, to target species-rich localities for conservation measures, but also to predict the impacts of future climate changes on different groups (Araújo et al. 2008), and to understand the ways human population density relates to and affects species diversity (Luck 2007; Moreno-Rueda and Pizarro 2007), among many other applications that can only be inferred from the understanding of the factors behind the pattern. It is therefore important to document patterns of species richness in diverse taxa and understand their causes, especially in less intensively studied tropical regions. Here I examine the distributional patterns of New World pitvipers, a monophyletic snake clade that arrived from Asia via the Bering Bridge (Gutberlet and Harvey 2004); compare those patterns in terms of twelve environmental, phylogenetic and biological variables; and use spatially explicit modeling methods to support or reject causal hypotheses for geographical patterns of species richness.

The Western Hemisphere, or New World, with its 42,165,000 sq. km., covers a third of the land in the planet and is composed of two land masses, referred to as continents or subcontinents. North America has an area of 24,346,000 sq. km. and by convention extends from the Isthmus of Panama at 8°N to northern Canada, where the mainland reaches 79°N. South America has an area of 17,819,000 sq. km., extends 7,640 km from northern Colombia at 12°North to southern Chile at about 55°South and at its broadest area extends about 5,300 km from East to West (Cohen 2005, Table 1.1).

Crotalinae (pitvipers) is one of three subclades in the Viperidae (vipers). Pitvipers occur in the Old and New World, and often exhibit great diversity in temperate and tropical regions (Campbell and Lamar 2004). Pitvipers provide an ideal group to address questions about species diversity patterns because: i) they are monophyletic and we understand their geographical deployment as subclades (Parkinson et al. 2002), ii) they are ecologically diverse in the New World, iii) the constraints associated with the simplified body form of a snake minimizes diversification when compared to other vertebrates, iv) they have a relatively low mobility when compared with groups like birds and mammals, and v) a great deal of baseline information for the group is available (Campbell and Lamar 1989; Campbell and Lamar 2004).

In this work I describe geographical patterns of species richness for New World pitvipers, and search for factors that can explain those patterns by looking for correlations with other variables. I describe these patterns based on latitude and longitude, and then look at how they relate to continental area available, several factors that are part of the resources availability hypothesis: climate, topography, environmental heterogeneity, and prey availability; to end with a historical factor, the phylogenetic diversity index. I thereby test the following five hypotheses regarding causes of geographical variation in species richness:

Area hypothesis: I start by testing the area hypothesis which holds that the tropics have more species because of the larger area in those latitudes. If this is true, we would predict there is a positive correlation between the number of pitviper species and area.

Water-Energy hypothesis: This hypothesis holds that contemporary climate is the main factor explaining patterns of biodiversity, and predicts an increase in the number of species of vipers as variables that are related to the balance of water and energy increases. The variables that I consider here are humidity, precipitation, and net primary productivity, which results from the interaction between water and energy variables.

Habitat heterogeneity hypothesis: This hypothesis predicts that two indirect measurements of habitat heterogeneity, elevational range and diversity of ecological regions, are positively correlated with pitviper species richness.

Prey availability hypothesis: Given the importance of prey in the evolution of pitvipers (Arnold 1972; Greene 1992), I would expect a positive correlation between pitviper species diversity and prey availability.

Phylogenetic diversity hypothesis: This hypothesis implies that presence of distinct lineages within a clade enhances species richness, and therefore I predict a positive correlation between maximum patristic distance and number of species present in a cell.

MATERIALS AND METHODS

There are 118 species of pitvipers in the Western Hemisphere, with North America containing 69 species and South America 55. Only six species are present on both continents (*Bothriechis schlegelii*, *Bothrops asper*, *B. punctatus*, *Lachesis acrochorda*, *Porthidium lansbergii* and *P. nasutum*), while all others are restricted to either of the two landmasses. Maps with the distribution of the 118 species of mainland pitvipers in the Americas were created by Jonathan Campbell using Macromedia FreeHand software (Campbell and Lamar 2004). I converted them to windows metafiles (.wmf format) in order to import them as images in the geographical information system (GIS). The georeferenciation process was done in Manifold GIS adding a variable number of control points for each map, and using the Affine (Triangulation) method, as this was consistently better than the more computationally intensive Numerical Method. Once the images were correctly georegistered and projected, each distribution area was digitized in order to clean the maps and analyze them. Because I did not consider islands, the following species of pitvipers were excluded: *Bothrops alcatraz, B. caribbaeus, B. insularis, B. lanceolatus, Crotalus catalinensis,* and *C. tortugensis*. I thus had 112 maps for my analyses.

Table 1.1 Area and species numbers for pitvipers in the Western hemisphere. Counts are for the Crotalinae and its two primary subclades.

	North America	**South America**	**Total**
Area (millions of sq. km.)	24.3	17.8	42.1
Total pitviper species	69	55	118
Nearctic pitvipers	36	1	37
Neotropical pitvipers	18	53	81

The area hypothesis for the latitudinal gradient of species richness holds that the larger extent of the tropical areas explains higher species richness in those regions (Rosenzweig 1992). I tested this hypothesis by importing in Manifold GIS all the distribution maps for pitvipers and dividing the continents in latitudinal bands of 1° of extension. Then a spatial query was written to count the number of species present and identify the species in each latitudinal band. This allowed us to evaluate the relationship between pitviper species richness and area in each latitudinal band in the Western Hemisphere.

After evaluating the species richness patterns in latitudinal bands, I created a grid that divided the Western Hemisphere in cells of 1° by 1°, and created a spatial query that permitted us to obtain the number of species of pitvipers that were present in each individual cell. Then I produced a map of species richness and a matrix that identified each individual cell in the Americas with the number of species of pitvipers present in them.

I obtained or created 12 different variables for the Western hemisphere that could be important drivers of geographical patterns of species richness: elevational range, actual evapotranspiration, potential evapotranspiration, humidity, annual total precipitation, net primary productivity, mean temperature, minimum temperature, seasonality, number of ecoregions, mammal prey diversity and an index of phylogenetic diversity. Those 12 variables are listed and described below:

Elevational range and number of ecoregions in a cell were included as a measure of habitat heterogeneity. The inclusion of a measurement of habitat heterogeneity follows the consideration that a cell with more habitat heterogeneity would have a higher number of species given the fact that this heterogeneity would allow for a finer niche partition. Elevational range was the difference between the minimum and maximum values in each cell, extracted from the GTOPO30 surfaces (U. S. Geological Survey, http://www.usgs.gov), and ranged from 1 to 6581 meters above sea level, with the biggest ranges in the Andes of South America. The number of ecological regions present in each cell was obtained from the World Wildlife Fund compilation (Olson et al. 2001), and ranged from 1 to 8 per cell, with the maximum occurring once each in Colombia and another in Ecuador.

Five variables were included as measures of water-energy balance (Hawkins et al. 2003), with the expectation that a region with higher energy values would be indirectly impacting species richness of pitvipers through food availability for pitviper prey. Net primary productivity (NPP) was included as a measure of energy in each grid cell; these data were downloaded from the Atlas of the Biosphere at http://atlas.sage.wisc.edu/ (Foley et al. 1996; Kucharik et al. 2000), and ranged from 0 to 1.32 kg-Carbon per square meter per year, with the highest measurements are in eastern Colombia. Actual evapotransporation (AET) is the amount of water removed from each grid cell through evaporation and transpiration and potential evapotransporation (PET) is the amount of water that would be removed if the amount of water present in each grid cell were not a limiting factor. AET was generated in the Climate Research Unit, Univ. of East Anglia (New et al. 1999) and PET in the Center for Climatic Research, University of Delaware (Willmott and Kenji 2001), measured in mm per unit area and ranging from 0 to 152.7 and from 0 to 172, respectively; both were obtained from the Atlas of the Biosphere. The amount of water vapor in the air or humidity and the annual total precipitation on an average year were included to represent the water component. Both datasets were generated by the Center for Climatic Research, University of Delaware (New et al. 1999) and obtained from the Atlas of the Biosphere. Humidity ranged from 11 to 91 percent, while precipitation varied from 0 to 18,000 mm per year, with the highest measurements occurring in northern Canada and in eastern Colombia, respectively.

Three additional environmental variables were included. Seasonality has been proved to be important in the distribution of reptiles (Lee 1980) and I included temperature seasonality, which is the standard deviation of the weekly mean temperatures expressed as a percentage of the mean of those temperatures; the mean in degrees Kelvin is used to avoid the possibility of having to divide by zero. Mean temperature and minimum temperature were retrieved and scaled down from the Atlas of the Biosphere (http://atlas.sage.wisc.edu/). The measurements were in centigrade degrees, and mean temperatures ranged from -17 in northern Canada to 27 in northern Venezuela, while minimum temperatures ranged from -35 degrees in northern Canada to almost 27 degrees in areas of Venezuela and Colombia.

The main diet of adult pitvipers is rodents, and taxonomic variation in prey is probably mainly a reflection of prey availability (Greene 1992), which might be indirectly related to energy availability. Significant correlations have been found in the species richness of snakes and their prey (Arnold 1972), but that study used a small number of point localities instead of grid cells, so I more systematically measured prey diversity by counting selected mammalian species in each of the grid cells. Although there are reports of bats in the diet of a few pitvipers (Davis et al. 1962; Esberard and Vrcibradic 2007; Forks and Hughes 2007), they were not included because i) those events seem rare in the literature, ii) the large number of species would swamp the results, and iii) flying mammals are not likely available for most pitvipers. Shrews (Soricidae), like bats, are relatively speciose and rarely eaten by pitvipers, so they were omitted from the analysis, as were moles (Talpidae). Solenodontidae (solenodons) and a few species of rodents were excluded because they are present only on islands. Castoridae (beavers), Hydrochaeridae (cabybara) and Myocastoridae (nutria) were excluded on basis of large size, probably beyond the limits of what any pitviper can eat. Among the remaining rodents I included Dasyproctidae (agouties) and Erethizontidae (porcupines), and marsupials in the Caluromyidae, Didelphidae, Glironiidae and Marmosidae because they are recorded in the diets of a few species of pitvipers (Greene 1992; Greene pers. obs.). I thus included 1087 species of mammals as potential pitviper prey, and individual cell values ranged from 1 species in the coast of central Chile to 88 in southeastern Peru.

Pitvipers evolved in Asia and arrived in the Western Hemisphere with a single invasion via North America, perhaps as early as 70 million years ago (Parkinson 1999; Parkinson et al. 2002). Phylogenetic relationships within this group have received attention in the last decades, and although there is no consensus on the relationships of some genera, the majority of the nodes are resolved and I can identify two major clades (Parkinson et al. 2002; Gutberlet and Harvey 2004; Castoe and Parkinson 2006): a Nearctic clade including 37 species in *Crotalus, Sistrurus* and *Agkistrodon*, and a Neotropical clade including 81 species in *Atropoides, Cerrophidion, Bothriechis, Bothriopsis, Bothrocophias, Bothrops, Lachesis, Ophryacus* and *Porthidium* (Figure 1.1).

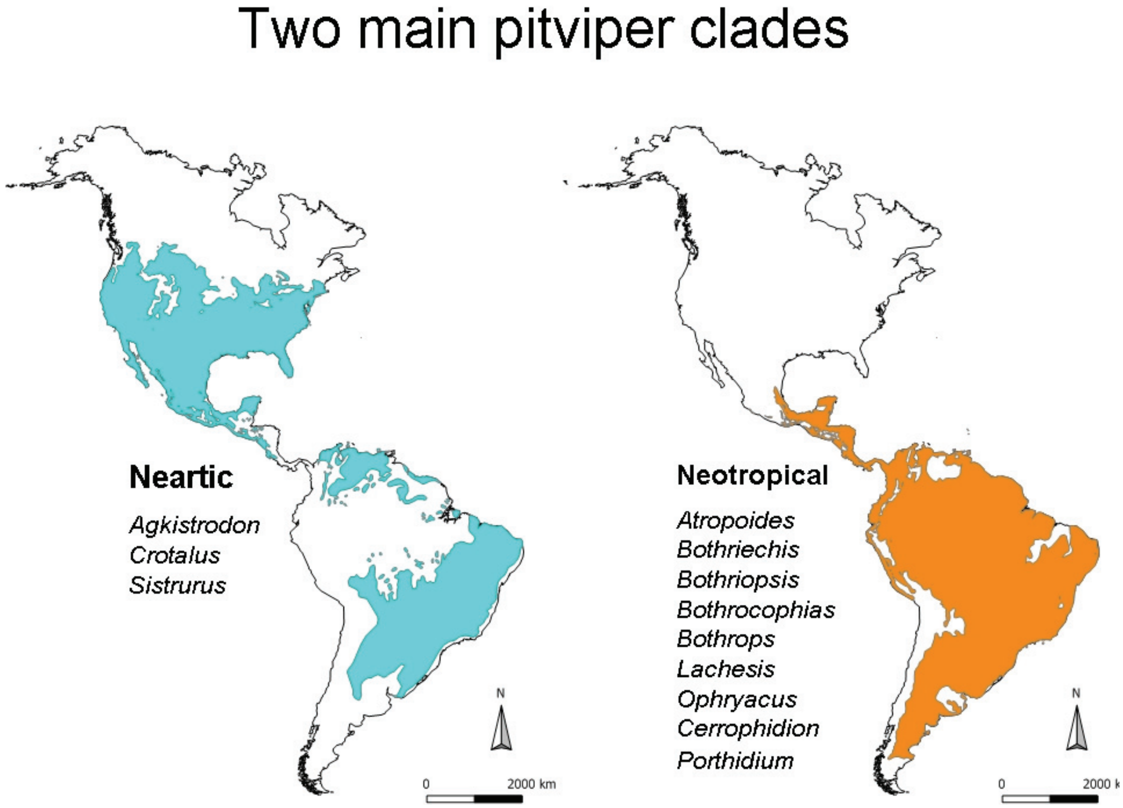


Figure 1.1 Distribution and containing genera of the two main clades of pitviper species in the Western Hemisphere.

Because I am interested in accounting for historical effects on assembly structure, I used the most up to date and complete phylogeny for Crotalinae (Castoe and Parkinson 2006), from which I obtained a full pairwise matrix of patristic distances for all taxa (from tip to tip) in the phylogeny. I obtained the patristic matrix using TreeEdit (Rambaut and Charleston 2002) by adding the branch lengths separating every pair of species. From the resulting matrix I eliminated species not included in my study, and used an average of the genus for species that were present but not in the tree. Using scripts written in the Python programming language I extracted the patristic distances between all the species present, and obtained four values for each cell by querying the matrix: minimum, maximum, mean and median patristic distance.

From the different values of patristic distances I used the maximum value as an index of phylogenetic diversity in each cell for several reasons: i) this value avoids the problem of underestimating phylogenetic diversity by using minimum values, ii)prevents erroneously estimating phylogenetic diversity by using mean values, iii)provides an index that closely represents phylogenetic diversity, and iv)estimates overlap of taxa in each cell. My index ranged from 0.3976 in many cells with two closely related species in several parts of the continents, particularly in the extreme northern, southern and coastal areas, to cells with a value of 1.3506 in eastern Brazil.

Traditional parametric statistics are not fully reliable in the analyses of cells in maps because they rely on the assumption that the observations in the data are independent (Fortin and Dale 2005). There is always spatial structure in geographical and macroecological data, and the tendency for nearby locations to have similar measurements is called spatial autocorrelation (Fortin et al. 2002, Segurado et al. 2006), sometimes also called Tobler's first law of geography: "Everything is related to everything else, but near things are more closely related than distant things" (Miller 2004). I used the freeware package SAM version 3.0 (Spatial Analysis in Macroecology) to do exploratory spatial analysis (Rangel et al. 2006) of the digitized distribution maps and all the variables that I included in the dataset. To take into account spatial autocorrelation I checked the data by producing correlograms that contained an automatically defined number of distance classes. I then ran Ordinary Linear Regression analysis to obtain the coefficient of determination (r^2) of the set of 12 variables for the pattern of species richness. Next, I used the Model Selection feature in SAM to identify the model that best explained the richness pattern based on the coefficient of determination (r^2), the number of conditions and the Akaike Information Criterion (AICc). Once the best model was identified, I ran a spatial autoregressive (SAR) model using a variable alpha value to keep the error below 0.1 in the correlogram. Finally, the results from the autoregressive model identified and ranked the predictor variables that best explained patterns of distribution of species richness of pitvipers in the Western Hemisphere.

RESULTS

Pitvipers are distributed from 51° N in southern Canada to 48° S in southern Argentina. The shapes of the North and South American Continents are similar in having extensive northern areas and drastically reduced southern ends. However, this results in North America having large extensions of temperate areas and reduced tropical areas, while South America follows the opposite pattern, having large tropical areas but reduced temperate ones. This has obvious implications for latitudinal patterns in species richness.

I first mapped the pattern in latitudinal bands to simply illustrate the species richness pattern (Figure 1.2). Of the 180 latitudinal bands that exist between the poles, 141 of them contain land, and only 106 contain at least one species of pitviper. The number of species per band was distributed as follows: 10 bands with 1 species, 29 with 2 to 8 species, 32 with 9 to 15, 32 with 16 to 22, and 3 bands with 23 species. The three bands with 23 species are in Central South America at latitudes -14, -15 and -17.

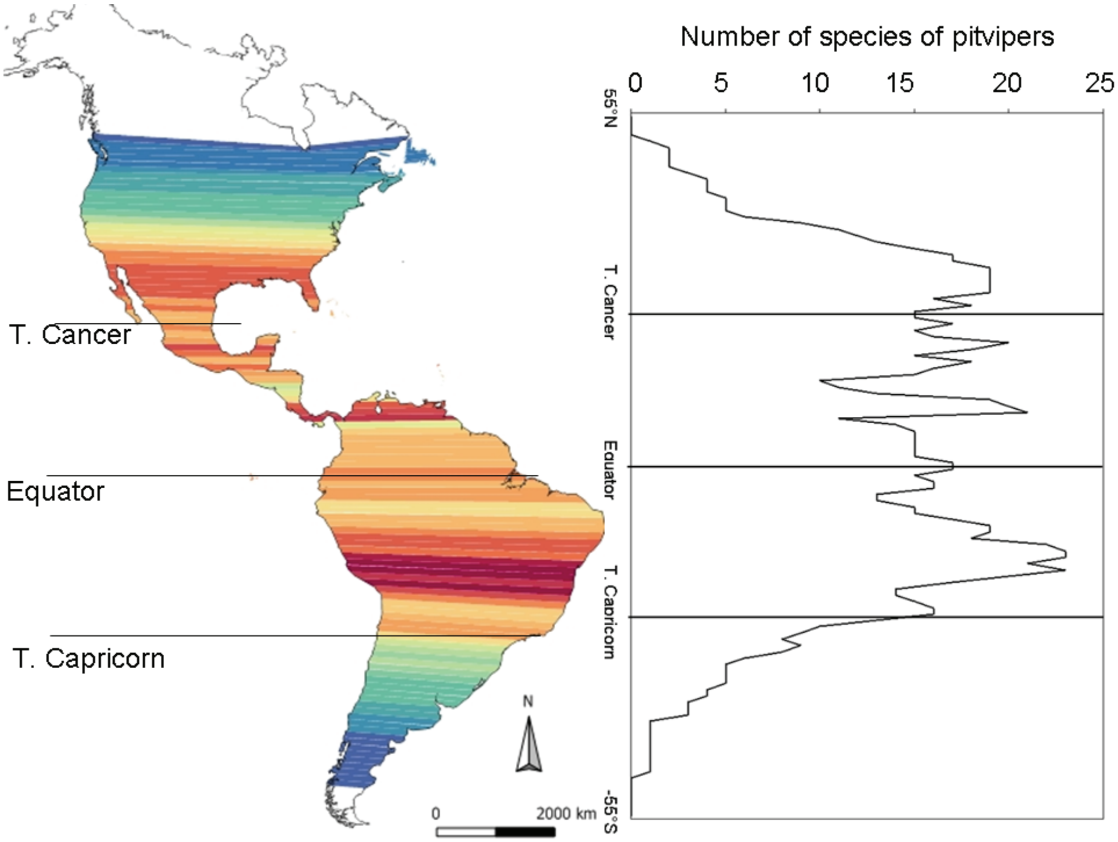


Figure 1.2 Latitudinal gradient in species richness of pitvipers in the Western Hemisphere. The latitudinal degree bands go from zero species in the poles in colder blue colors, to 23 species in three dark red colored bands in Central South America. The graph in the right side shows the non-linear increase in species richness in tropical areas.

Clearly there was an increase in species numbers as one travels from the poles into the tropical zones, but the increase was not linear and certainly not positively correlated with area, as Central America and Mexico had high species richness without having large areas. Area and species richness had a different relationship with each other in North America than in South America, and while figure 1.3 shows an inverse relationship among area and species richness, figure 1.4 shows the opposite pattern, with area and species richness positively correlated. A multiple regression analysis for North America identified the relationship between species richness and area as non significant (D.F.=2, r^2=43.8%, p=0.554) and between species richness and latitude as significant (p=0.024). For the case of South America (D.F.=2, r^2=79%), the relationship between species richness and area is significant (p=0.020), but the one with latitude is not (0.343).

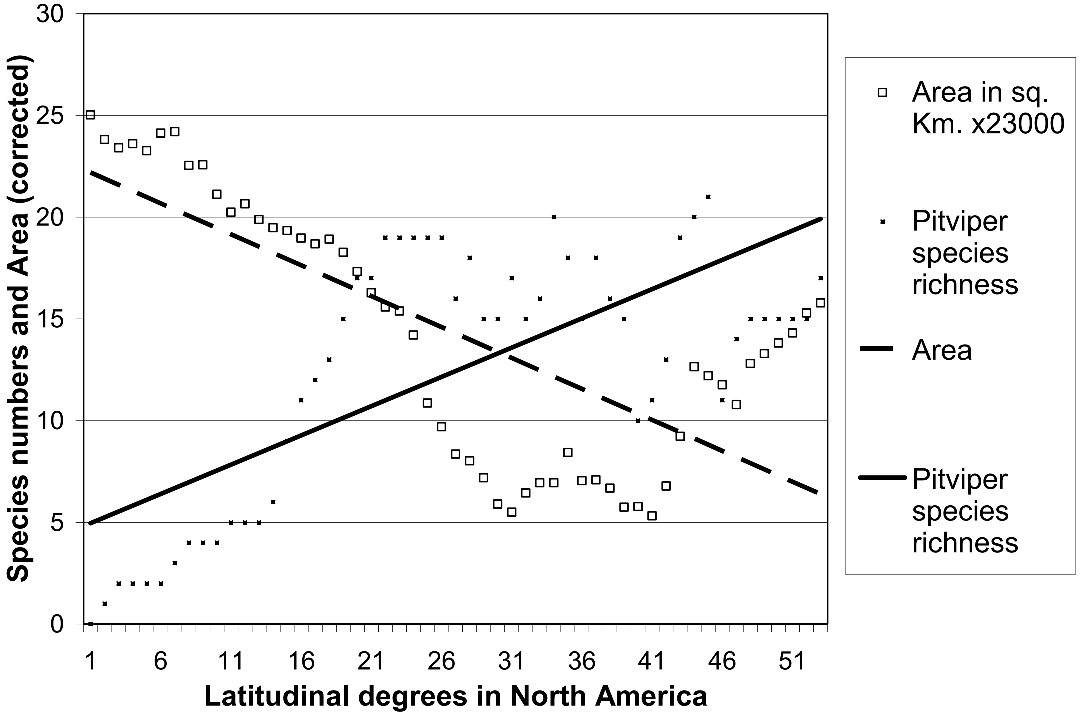


Figure 1.3 Negative relationship between species richness of pitvipers, area and latitude in North America.

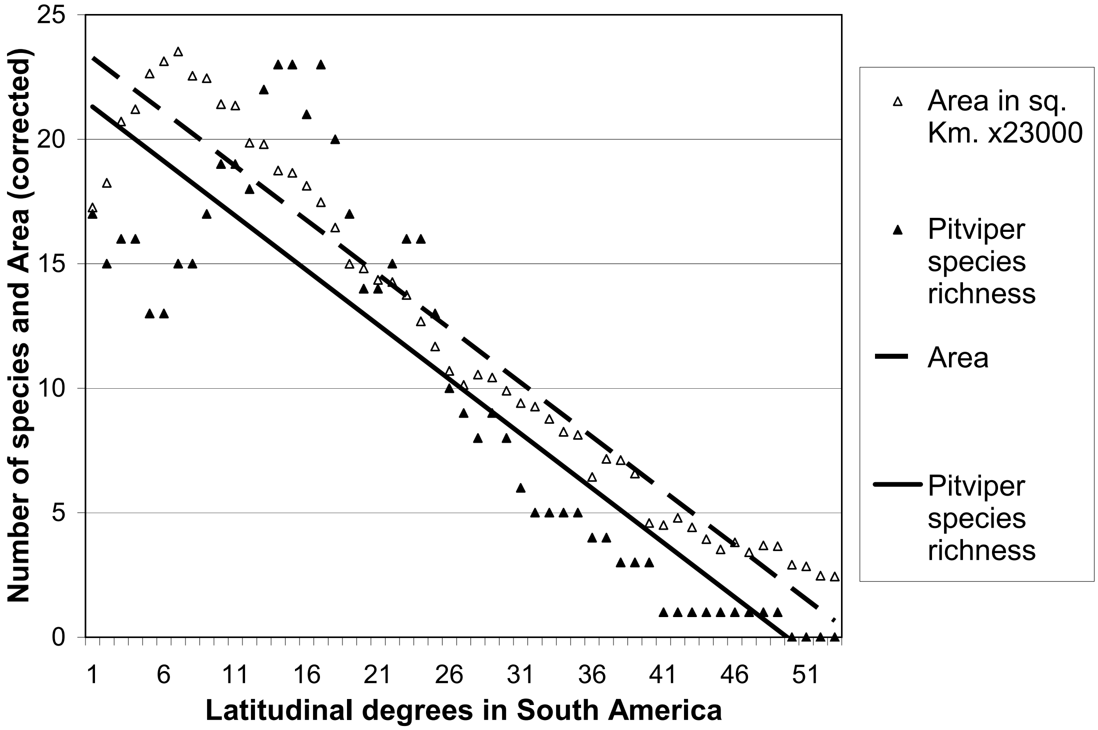


Figure 1.4 Positive relationship between species richness of pitvipers, area and latitude in South America.

After having the pattern mapped in latitudinal bands, I divided further the Western Hemisphere continental area in cells of 1 by 1 latitudinal degrees and obtained a grid of ~4220 individual cells, for each of which I identified the number of pitviper species present by using Manifold GIS. The pattern of species richness of pitvipers roughly corresponds with the expected gradient in latitudinal diversity. In the map in Figure 1.5 is possible to identify the areas with high species richness, corresponding to darker colored cells, and areas with low species richness cells, represented by lighter colored cells. The lightest cells contain a single species of pitviper, and the darker cells contain up to 13 species as it is the case in southern Costa Rica.

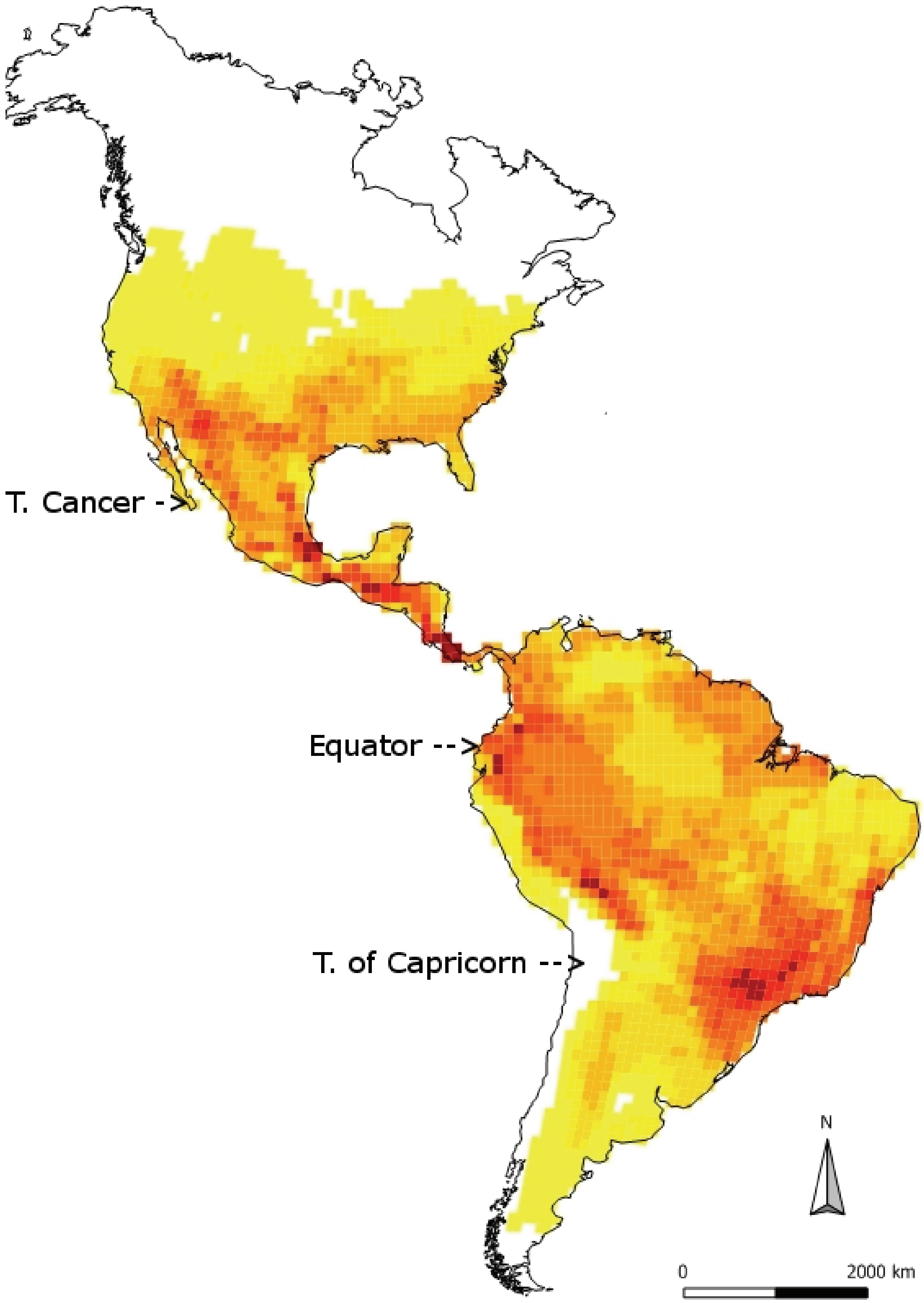


Figure 1.5 Geographical pattern of pitviper species richness in the Western Hemisphere. The values vary from one species in light cells to 13 species in the darkest cells in southeastern Costa Rica.

Visual inspection of the map shows that although there is an increase in the number of species as one travels from high latitudes (North or South) toward the Equator, the pattern of species richness when longitudinal effects are taken into consideration is even farther from linear than when latitude alone is considered. We can see species-rich areas in southern Mexico, several countries in Middle America, central Ecuador, the eastern versant of the Andes around the border of Peru and Bolivia, and southern Brazil. The two cells that contain the highest number of species are both in Costa Rica (n=13 and n=12), while there are five cells with eleven species distributed in four countries: two in Ecuador, one in eastern Panama, one in central Guatemala and one in central eastern Mexico.

I started the analysis by doing exploratory statistics in the SAM package to detect outliers, skewness, kurtosis, and potential mistakes in the data for each of the 12 variables included in the analysis as potential drivers of the geographical pattern in species richness for pitvipers. I used Moran's I in SAM to describe the spatial autocorrelation in species richness of pitvipers in the Western Hemisphere and found that is positively autocorrelated at short distances, with a Moran's I value of 0.625 in the first distance class which was defined automatically by SAM as 377.957 kms. (Figure 1.6)

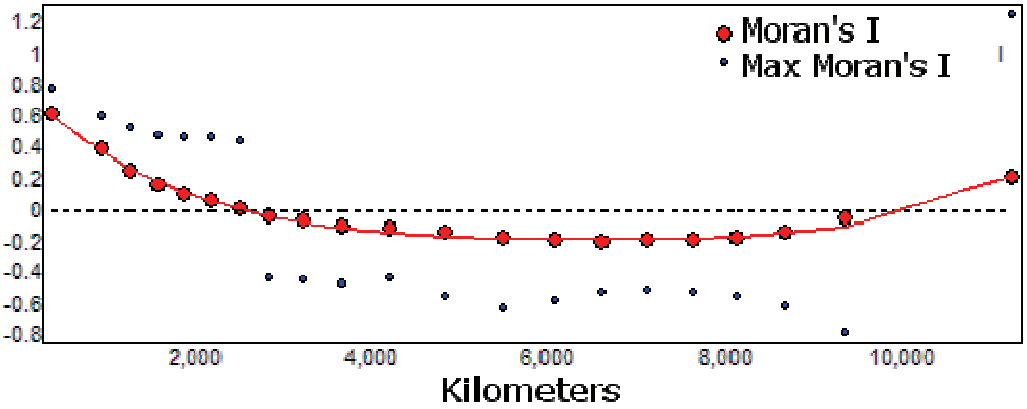


Figure 1.6 Correlogram for Moran's I value for pitviper species richness in the Western Hemisphere. Values that deviate from 0 show autocorrelation, and for the case of pitviper species richness, the Moran's I value for the first distance class at 377.957kms is of 0.625, with the autocorrelation values decreasing as distance increase.

I ran a linear regression model with the 12 variables that potentially would predict the pattern of pitviper richness in the Western Hemisphere and found they had an $r^2 = 0.728$. Although this linear regression did not take space into account, its coefficient is valid for the whole set of included variables. Next, I used the Model Selection feature in SAM to identify variables for a spatial autoregressive model that would take into account the autocorrelated nature of the data.

The selection of variables to include in the autoregressive model was done using the model selection and multi-model inference in SAM, by including the 12 variables as predictor variables for the pitviper species richness. This would evaluate the 4095 possible models and give a list of those models ranked according to r^2, the number of conditions and the Akaike Information Criterion (AICc); a list of the variables included in each model was also given. From the models that included the minimum number of variables that I was interested in testing, I chose the best model, based on the smallest AICc, to run the spatial autoregressive model.

The best model (r^2=0.728, Cond. Num.= 68.891 and AICc=9190.571) resulting from the Model Selection procedure suggested the exclusion of three variables: AET, NPP and elevational range. I used the variables suggested by the best model to carry out spatial autoregressive analysis for pitviper richness and the 11 potential predictor variables. I ran several models and looked at the autocorrelation values in the correlogram, and if the autocorrelation values were still higher than 0.1, it meant that a spatial component could be added and, thereby obtain a better model. This spatial component is represented by alpha, and I experimented with increasing values of alpha and looking at the correlogram to bring the correlation error below 0.1. Changing the values of alpha was done with care, because high values might cause coefficient shifts and overfitting of the variables to unacceptable levels. I found that alpha=2.5 would bring the correlation error to 0.059, and the model would bring the r^2 value from 0.728, obtained from the ordinary linear regression, up to 0.809. I was thus able to identify variables with the highest importance for the model based on their t-value (Table 1.2). The two most important variables explaining the pattern of pitviper species richness ones were phylogenetic diversity and prey diversity. The other variables were not statistically significant in addition to having lower values of importance.

Table 1.2 Variables of importance for the model, ranked by order of importance. Provided are the t-value, representing the strength of the relationship, as well as the p-value.

Order of importance	Variable	t-value	p-value
1	Phylogenetic diversity	t=26.405	p=<0.001
2	Prey diversity	t=15.3	p=<0.001
3	Precipitation	t=7.253	p=<0.001
4	Mean temperature	t=4.846	p=<0.001
5	Number of ecoregions	t=2.893	p= 0.004

To further explore the issue, I took advantage of the existence of two monophyletic clades inside of the pitviper radiation in the Western Hemisphere: the Nearctic pitvipers clade that is mostly restricted to North America, and the Neotropical pitvipers clade, mostly in South America although with good representation in Central America (figure 1.1). Considering these two monophyletic groups, I repeated the spatial analysis procedure described above to see if variables that predict species richness for the whole group are the same when only the Nearctic or the Neotropical clades are considered separately. In addition, as mentioned above, both of those clades have most of their species restricted to their corresponding continent, and given their predominantly temperate versus tropical nature, there is the possibility that the controlling variables could be different in the two land masses. Therefore, I also ran the spatial analysis for the Nearctic clade only in North America and for the Neotropical clade only in South America. The maps in Figure 1.7 show the pattern of species richness for each of those four cases, with darker cells showing high species richness values and light cells with low species richness.

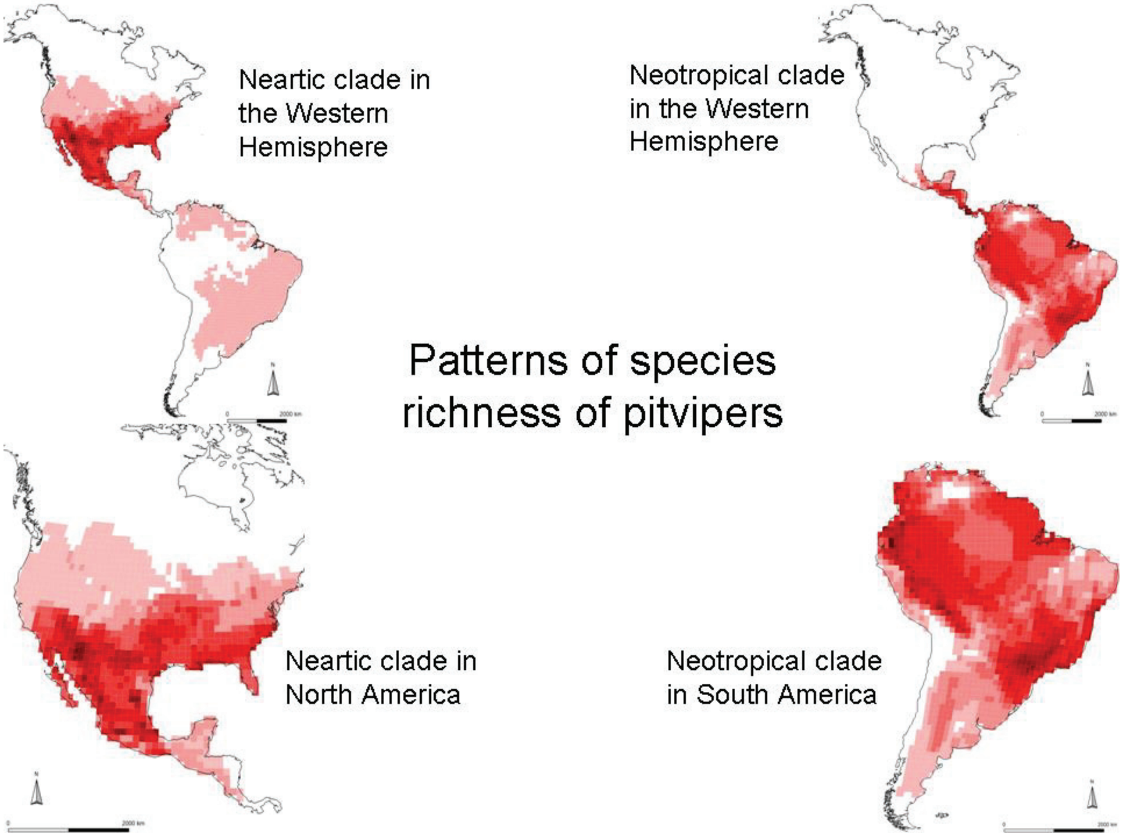


Figure 1.7 Maps of patterns of species richness for the two pitviper clades in the two subcontinents. Clockwise from right top corner: Neotropical clade in the Western Hemisphere, Neotropical clade in South America, Nearctic clade in North America, and Nearctic clade in the Western Hemisphere.

Once I obtained the species richness pattern for those other four scenarios, I also modified the 12 variables layers to correspond to the area/taxonomical composition, in order to run spatial analysis models with them. I followed the same spatial analysis modeling approach described above for the case where the two clades and the two landmasses are considered together. The analyses resulted in the ranked variables of importance for each case based on its importance in the model (t-value). For the Nearctic clade in both continents the variables in order of importance were phylogenetic diversity, mean temperature, prey diversity, and seasonality. For the Nearctic clade only in North America the important variables were phylogenetic diversity, prey diversity, elevational range, and mean temperature. For the Neotropical clade in both continents the most important variables were phylogenetic diversity, prey diversity, precipitation, and mean temperature. And finally, for the Neotropical clade only in South America I identified phylogenetic diversity, prey diversity, precipitation, and mean temperature as the important variables. All of those relationships were statistically significant and are summarized in Table 1.3 and 1.4.

Table 1.3 Comparative of statistical results per model for the cases where the clades and regions were considered individually. The original analysis (both clades and both continents) is included for reference. Nearctic=NArc and Neotropical=NTro. The columns have the following information: "r^2 ols" refers to the coefficient of determination from the ordinary linear regression procedure; "r^2 sar" is the coefficient of determination after space was taken into account in the spatial autoregressive model, and the alpha value needed to bring the error line below 0.1 in the correlogram.

	r^2 ols	**r^2 sar**	**alpha value**
Both-clades&cont.	0.728	0.81	2.5
NArc-clade&both	0.802	0.801	2
NArc-clade&NAm	0.8	0.819	2.5
NTro-clade&both	0.668	0.832	3
NTro-clade&SAm	0.694	0.845	3

Table 1.4 Comparative results for the cases where the clades and regions were considered individually. The original analysis (both clades and both continents) is included for reference. A list of the variables, with their t-values underneath, that were identified in the SAR model as the most important variables explaining the distribution of pitviper species richness in the Western Hemisphere. NArc=Nearctic clade, NTro=Neotropical clade, NAm=North America, SAm=South America.

Clades & Continent	**Variables of importance with their corresponding t-values**			
Both-clades&cont.	PhylDiv	PreyDiv	Precip	MeanTemp
	26.358	14.28	6.857	4.724
NArc-clade&both	PhylDiv	MeanTemp	PreyDiv	Season
	33.1	12.281	6.259	3.292
NArc-clade&NAm	PhylDiv	PreyDiv	Elevation	MeanTemp
	20.407	5.231	3.207	3.041
NTro-clade&both	PhylDiv	PreyDiv	Precip	MeanTemp
	25.363	9.646	3.758	3.045
NTro-clade&SAm	PhylDiv	PreyDiv	Precip	MeanTemp
	22.511	9.02	3.554	2.895

DISCUSSION

Geographical patterns in species richness of pitvipers are clearly obvious in my analysis when latitude is considered by itself. The tropics are richer than temperate areas in general, although the highest peaks in species richness are not around the equator, as would be expected for a simple latitudinal gradient, and are instead in the latitudinal bands -14, -15 and -17 in central South America. The latitudinal gradient is even weaker when longitude is taken into consideration, and the highest peaks of species richness identified in the latitudinal bands in the Western Hemisphere don’t correspond with the peaks that are evident when longitude is also included. The highest peaks in species richness in the degree by degree grid are cells in Costa Rica, Ecuador, eastern Panama, central Guatemala and central eastern Mexico, in that order. This result is understandable given the fragmentation of the distribution areas of pitvipers in large areas of the continent (Reed 2003). For example, species composition in latitudes -14 and -15 is different on either side of the continental divide in South America. Those two bands combined have 15 species on both Atlantic and Pacific sides, but they only share 5 of those 15 species. Considering only latitude in patterns of species richness would mask the more detailed pattern that is unraveled when variation in longitude is included.

In addition to the importance of considering latitude and longitude together in correlative studies, variables that are significant at one spatial scale may not be at others (Willis and Whittaker 2002). Also, when more localized studies are carried out, it is possible to take into account other factors that could be more important for certain groups, e.g., physiological constraints at the northern distributional limits of painted turtles and vine snakes (St Clair and Gregory 1990; Van Devender et al. 1994; see also Chapter two).

Phylogenetic diversity within cells was the most important explanatory variable in all the scenarios for which I ran analyses, implying that high species richness results from the co-occurrence of distantly related species. Because I used maximum phylogenetic diversity values, my approach is independent of the number of species present in each cell. The results confirm that, at least for pitvipers, environmental factors are less important than phylogeny in explaining patterns of species richness, and reinforce the importance of historical factors in macroecological and community ecology studies (Greene 2005).

Prey diversity had a major explanatory role for the geographical patterns in species richness for pitvipers, second to phylogenetic diversity. Even though mammalian prey diversity is strongly correlated with pitviper species richness, this correlation might result from the selected mammalian species responding to the environmental variables in the same way as pitviper species. Nonetheless, that coexistence of multiple species of pitvipers is associated with lineage diversity implies that competitive interactions might be important in structuring these assemblages.

Temperature also plays an important role in explaining the distribution patterns in my analyses, but it was generally less important than phylogenetic diversity, prey diversity and precipitation. The Nearctic clade was exceptional when considered in both the North and South American continents, in that mean temperature was the second most important variable only after phylogenetic diversity. This result also supports Hawkins et al.'s (2007) assertion that temperature might be an unreliable estimator of species richness in broader considerations of the methabolic theory.

Area has been used as an explanatory factor for the latitudinal gradient of species richness, with the rationale that tropical regions have more species because they are more extensive than temperate zones (Rosenzweig 2003). By using terrestrial birds of North America, the northern Palearctic, Australia and the Afrotropics, Hawkins and Porter (2001) concluded that although the tropical biomes are indeed larger, "there is no significant species-area relationship for birds at the biome scale of resolution". My results with pitvipers in the Western Hemisphere reject the area hypothesis: in South America area and species richness are significantly and positively correlated, whereas in North America they are negatively correlated: high species richness is still high in drastically reduced tropical areas. However, it is also important to keep in mind that I have only considered the contemporary distribution of tropical vegetation, which in evolutionary time has fluctuated greatly and sometimes included more extensive areas than the past (Mittelbach 2006); I also did not include an age component, that according to Fine & Ree (2006), should be included in any test of the area hypothesis.

The two measures of habitat heterogeneity played only a marginal role in my analyses. Number of ecoregions was the least important of the variables that had a significant relationship with species richness for the analysis for the two clades in the Western Hemisphere, while elevational range was the third factor of importance when the Nearctic clade was considered only in North America.

The variables that were included to test for the potential role of energy explaining the pattern of diversity for pitvipers did not appear as significant in any of my scenarios. Although potential evapotransporation, a measure of energy in the environment, had been identified previously for North American vertebrates as supporting the energy hypothesis (Currie 1991), it is not a significant factor for pitvipers. Water variables on the other hand might be more important than energy, in that precipitation significantly affects pitviper richness and more so for the Neotropical clade than for the Nearctic one. In the same vein, seasonality was important only in the scenario in which I considered the Nearctic clade in the Western Hemisphere.

The map of residuals (Figure 1.8) is one of the most important results provided by the spatial autoregressive model that I ran in SAM; it gives a graphical representation of variation unaccounted for by the explanatory variables and points to areas in the map that should be studied for variations from those patterns. Now I will discuss some of the most striking deviations from the expected patterns.

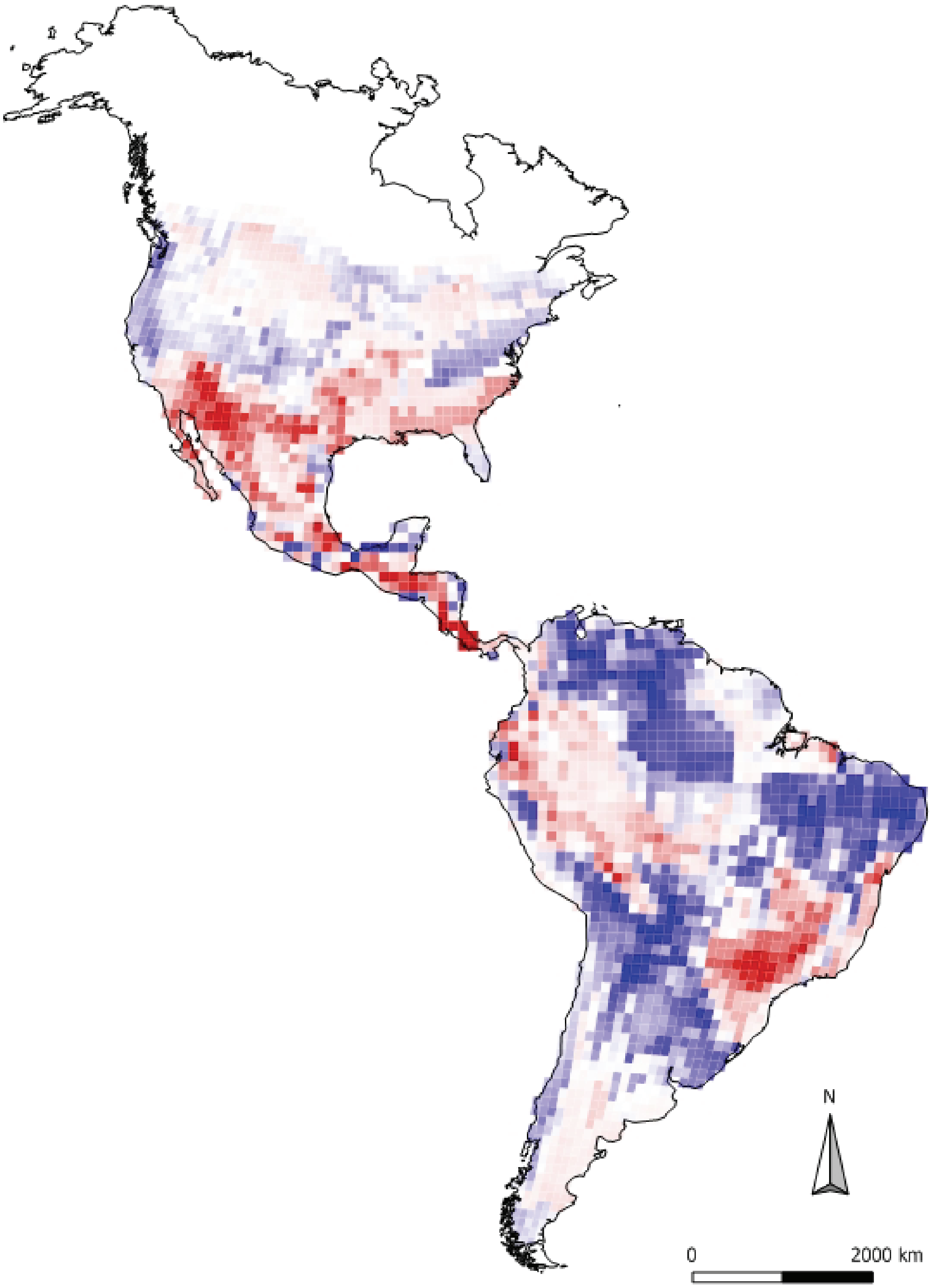


Figure 1.8 Map displaying the geographical distribution of the residuals from the spatial autoregressive model that identified the most important variables for the distribution of pitviper species richness in the Western Hemisphere. The dark red cells represent cells with higher than expected richness, the dark blue cells represent cells with lower than expected richness, while the white cells are middle values.

Cells that have higher than expected richness are scattered around the continent, but three large concentrations of them are discussed. There is high species richness of rattlesnakes (*Crotalus* and *Sistrurus*) from the North American clade of pitvipers in northwestern Mexico-southwestern US. Another important area is composed of southern Mexico, Guatemala, Nicaragua and particularly Costa Rica, where a few widely distributed species occur with others with more restricted distributions, both from the Nearctic and Neotropical pitviper clades, and where almost all genera of pitvipers co-occur (the only exceptions being *Bothriopsis*, *Bothrocophias* and *Sistrurus*). The third large concentration of cells with higher than expected species richness is in southeastern Brazil, an area that corresponds roughly to the junction of the Atlantic forest vegetation and the Araucaria Plateau, where the composition of species is dominated by *Bothrops* along with *Crotalus durissus* and *Lachesis muta*. These strikingly rich areas clearly warrant additional study.

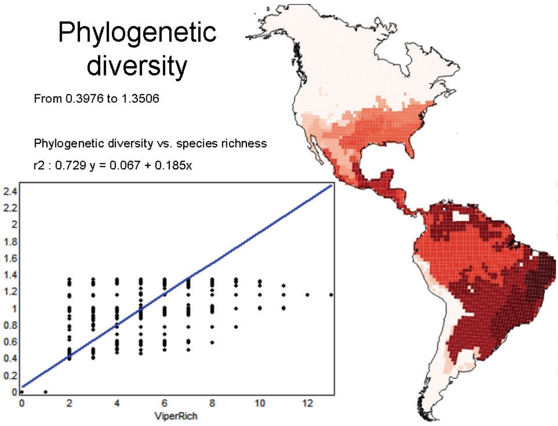
Areas with less species than expected are widely dispersed but more prevalent in South America. Isolated species-poor cells often occur near cells with more species than expected, suggesting that local factors are responsible for those discrepancies at such small scales. There are however, three large areas in South America characterized by substantially fewer species than predicted by my spatial autoregressive model. One such area covers most of Venezuela and the north-central portion of the Amazon basin. Because it covers a large area, it has a good representation of many species of the Neotropical clade of pitvipers, with the addition of the only species of pitviper of the Nearctic clade that reaches South America, the rattlesnake *Crotalus durissus*. Another depauperate area covers the northeastern portion of cerrado and caatinga vegetation types in eastern Brazil, where less than a dozen species of *Bothrops* co-occur with *Lachesis* and *Crotalus*. The third large area of reduced species richness is centered on the shared borders of Argentina, Bolivia and

Paraguay. This area encompasses lower montane wet forest and the western portion of chaco vegetation, which is dryer than the eastern portion, where less than a dozen species of pitviper occur. Parts of the mentioned areas are topographically simple, with vast extensions of flat monotonous ecosystems, but as with areas of exceptionally high richness, these species poor areas deserve further study.

This study is unusual among attempts to understand geographical variation in species richness, in that it focuses on a well-understood evolutionary deployment of a single clade of prominent vertebrates across two temperate-tropical patterns. Three major conclusions are that i) although generally consistent with increased tropical diversity, the patterns of variation are complex; ii) history has played a prominent role in determining those patterns, followed in importance by prey species richness and certain climatic factors; iii) even within a monophyletic group, unique attributes of particular lineages and landscapes are important determinants of patterns. This last point is underscored by the fact that models for the Neartic pitviper clade account for 80% of the variation in the Western Hemisphere and 80.2% in North America, while models for the Neotropical clade explain only 66.8% of that variation in the Western Hemisphere and 69.4% in South America. Of course only experimental manipulations of independent variables can conclusively demonstrate causality, e.g., with comparative studies of physiological ecology, but my findings underscore this overarching conclusion: given the idiosyncratic nature of distributional patterns and their implications for conservation, documenting geographic variation in biodiversity and its underlying causes is more urgent than ever.

APPENDIX

Maps, scatter plots, coefficient of determination (r^2) and regression equations for the 12 explanatory variables for species richness of pitvipers.

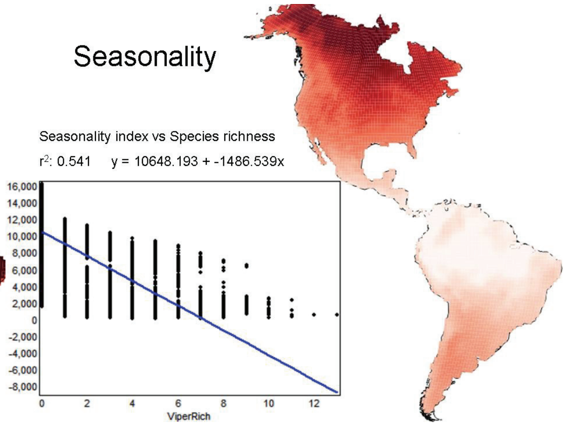


Phylogenetic diversity

From 0.3976 to 1.3506

Phylogenetic diversity vs. species richness

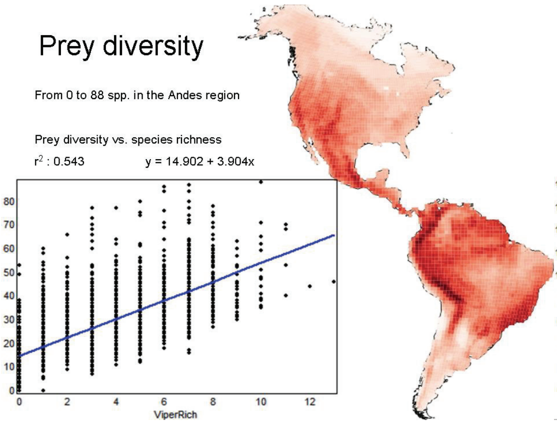
r2 : 0.729 y = 0.067 + 0.185x



Seasonality

Seasonality index vs Species richness

r^2: 0.541 y = 10648.193 + -1486.539x

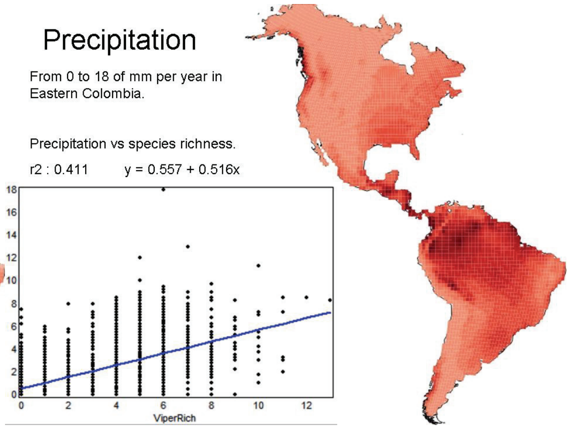


Prey diversity

From 0 to 88 spp. in the Andes region

Prey diversity vs. species richness

r^2 : 0.543 y = 14.902 + 3.904x

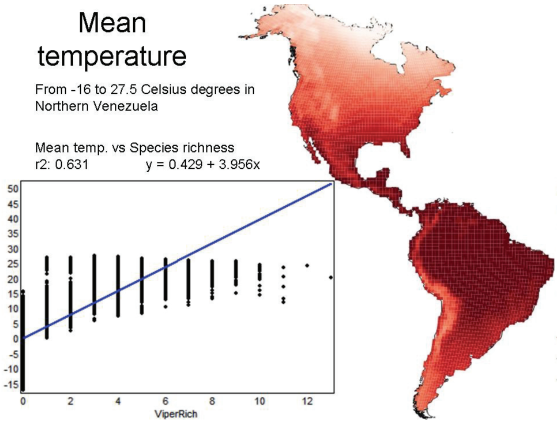


Precipitation

From 0 to 18 of mm per year in Eastern Colombia.

Precipitation vs species richness.

r2 : 0.411 y = 0.557 + 0.516x

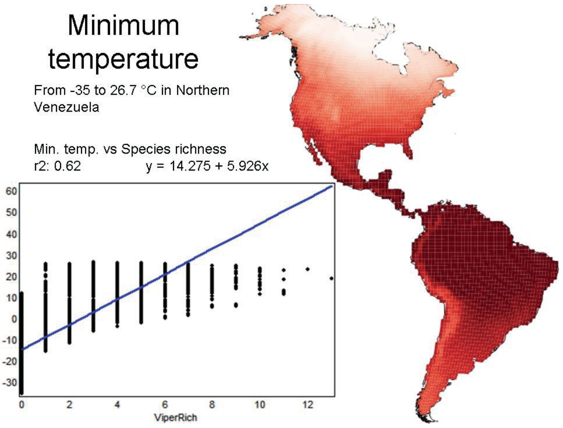


Mean temperature

From -16 to 27.5 Celsius degrees in Northern Venezuela

Mean temp. vs Species richness

r2: 0.631 y = 0.429 + 3.956x



Minimum temperature

From -35 to 26.7 °C in Northern Venezuela

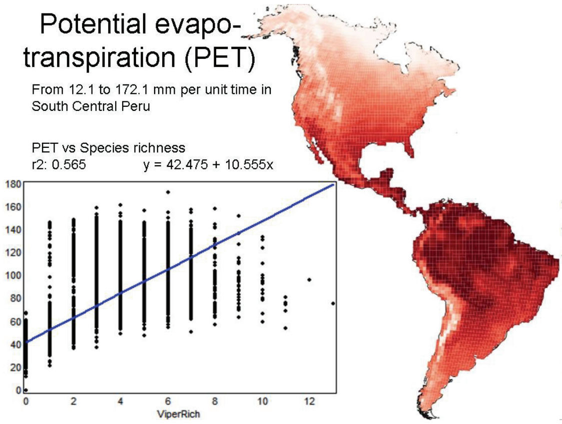
Min. temp. vs Species richness

r2: 0.62 y = 14.275 + 5.926x

Potential evapo-transpiration (PET)

From 12.1 to 172.1 mm per unit time in South Central Peru

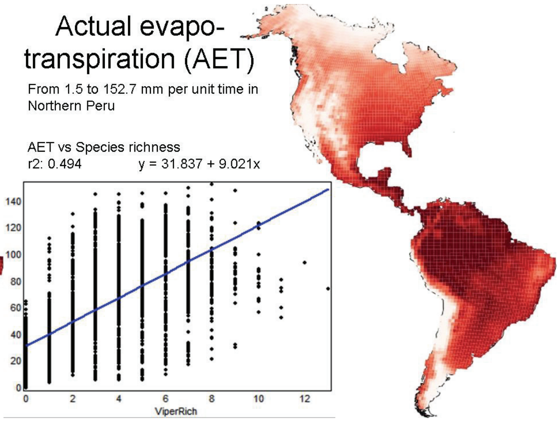
PET vs Species richness
r2: 0.565 y = 42.475 + 10.555x



Actual evapo-transpiration (AET)

From 1.5 to 152.7 mm per unit time in Northern Peru

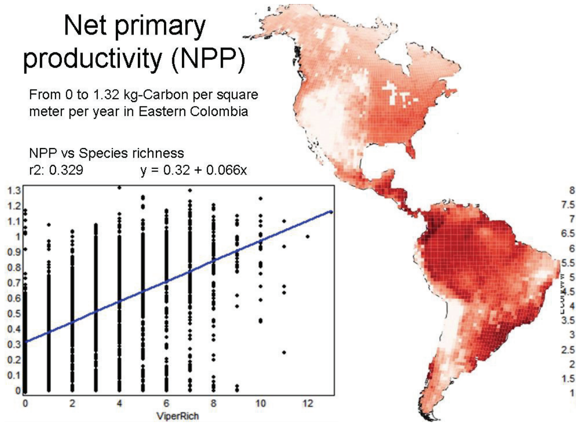
AET vs Species richness
r2: 0.494 y = 31.837 + 9.021x



Net primary productivity (NPP)

From 0 to 1.32 kg-Carbon per square meter per year in Eastern Colombia

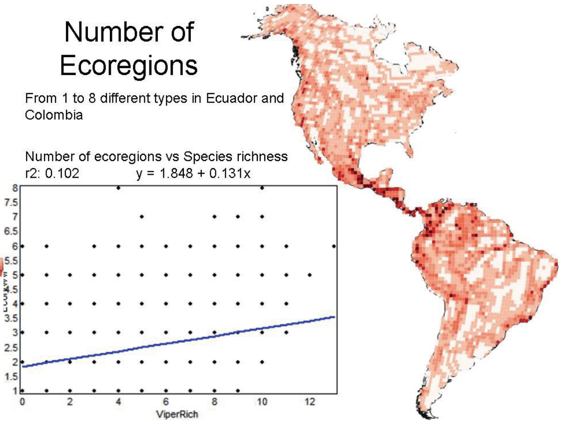
NPP vs Species richness
r2: 0.329 y = 0.32 + 0.066x



Number of Ecoregions

From 1 to 8 different types in Ecuador and Colombia

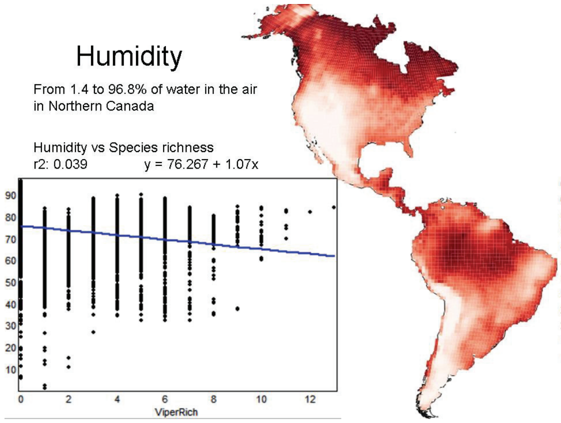
Number of ecoregions vs Species richness
r2: 0.102 y = 1.848 + 0.131x



Humidity

From 1.4 to 96.8% of water in the air in Northern Canada

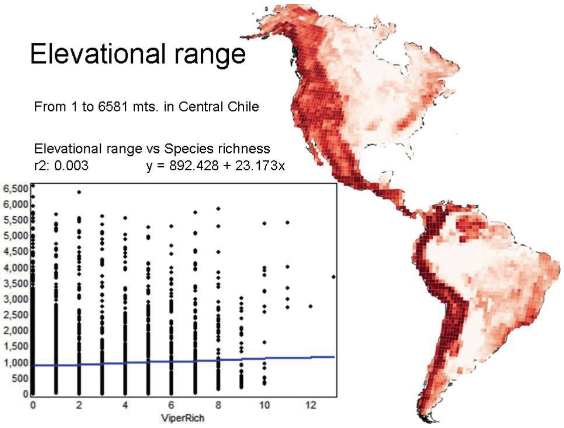
Humidity vs Species richness
r2: 0.039 y = 76.267 + 1.07x



Elevational range

From 1 to 6581 mts. in Central Chile

Elevational range vs Species richness
r2: 0.003 y = 892.428 + 23.173x



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CHAPTER 2

DISTRIBUTIONAL LIMITS OF WIDESPREAD TROPICAL SPECIES: A NICHE MODELING APPROACH WITH SNAKES

ABSTRACT

Although biogeographical realms have been accepted for decades and there are many groups whose distributions coincide with their borders, the factors that regulate these patterns for particular taxa remain poorly known. The study of those factors at local scales can help clarify factors that affect the distribution of biodiversity at broader scales. I defined the northern distributional limits of two widely distributed species of neotropical snakes as they reach the Nearctic realm, then investigated potential limiting variables by using ecological niche modeling. *Drymarchon melanurus* is limited mainly by annual mean temperature, temperature seasonality and minimum temperature of the coldest month, whereas *Oxybelis aeneus* is more limited by precipitation seasonality, as well as mean and minimum temperatures. Comparison between the versants for *D. melanurus* revealed that the western distribution is mostly determined by temperature and precipitation seasonality, followed by amount of rain while for the eastern distribution mean temperature, temperature range and winter precipitation are the important factors. In the case of *O. aeneus* the differences were not as marked, as annual mean temperature and precipitation seasonality were important in both versants, and only mean temperature of the warmest month was significantly different, being of moderate importance in the western versant but not at all in the eastern side. These findings suggest a marked niche separation between versants for *D. melanurus* but only moderate differences for *O. aeneus*, consistent with adaptive divergence in the former and morphological uniformity in the later. The results show that limiting factors for closely related organisms, can vary in different ways, even in realms where there should be a set of similar factors maintaining the

boundary, and thus illustrate the need for intimate knowledge of the organisms to validate results obtained with techniques like the one used here.

INTRODUCTION

Patterns in distributions of individual species are central to explaining more general geographical variation of biodiversity, and although many works deal with the analysis of such patterns at large scales (Pianka 1966; Hawkins et al. 2003), less attention has been focused on local interactions and particular species. This paper tackles those related issues by focusing on the boundary between biogeographical realms in the Americas and the ways in which two neotropical snakes respond to their ecogeographic borders.

Biogeographical realms were proposed about 150 years ago, based on the distribution patterns of passerine birds (Sclater 1858), and they remain useful today because the distributions of many other groups conform at least broadly to these realms. In the Americas we have the Neotropical and the Nearctic realms, and the blending of faunas and floras in the region of northern México presents a fascinating biotic mosaic rarely equaled elsewhere (Campbell 1999). This boundary reflects many distributional limits (Lomolino et al. 1998), and the study of such regions where biogeographic assemblages intersect are a priority for conservation efforts (Spector 2002).

The border between the Neotropics and Nearctic regions is itself a topic of debate, although it can be arbitrarily defined as the Tropic of Cancer at ~23.4° latitude. Alternatively, it has been placed in the Isthmus of Tehuantepec, at about 19° latitude, coinciding with the approximate northernmost distribution limit of the tropical rainforest and a major lowland gap in the mountain cordilleras running the length of western North America (Marshall and Liebherr 2000). A third view places the border further north in Tamaulipas, at 23.6°latitude, arguing that the tropical deciduous forest is more important than the tropical rainforest in facilitating the neotropical elements to be in northern México (Martin 1958). Regardless of where the border line for these two realms is drawn, it coincides with the distribution limits for many neotropical and neartic taxa. As a result of the particular requirements of each taxon, there will always be species that cross the boundary, and focusing on those exceptions, we can learn about factors limiting their distributions.

My objective here is to analyze the distributional patterns of two related species of neotropical snakes that cross the boundary, thereby revealing factors that limit their distribution and contribute to geographic variation in biodiversity. Because many species distribution areas coincide with the boundary realms, it is possibe that a set of factors could be maintaining this boundary. Investigating the distribution limits of two related species and how they end in relation with the Neotropics-Nearctic realms boundary will allow us to differentiate among factors maintaining the distribution for the two species and the response each species has to those factors.

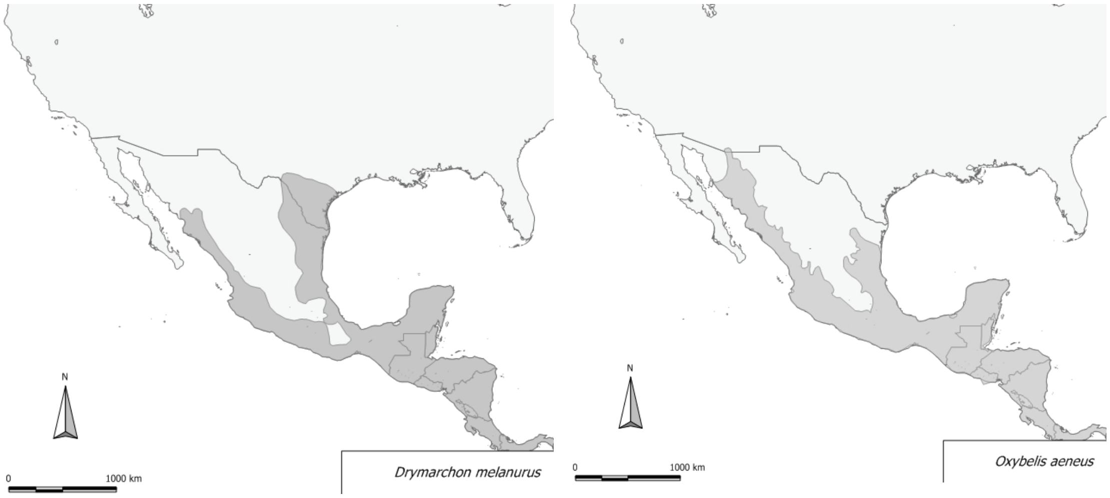

Figure 2.1 Distribution of *D. melanurus* in North America (left, modified from McCranie 1980). Distribution of *O. aeneus* in North America (right, modified from Keiser 1982).

Snakes are an ideal group for studying distributional patterns given their restricted mobility when compared to birds and mammals, and I therefore examined environmental factors associated with the northern range limits of two netropical colubrines, *Drymarchon melanurus* and *Oxybelis aeneus*. The two species have significantly different body shapes and habitat preferences, but both are of netropical origin, where they are widely distributed, and reach the southern US via the western and eastern versants of northern Mexico avoiding the dryer central Mexican Plateau (McCranie 1980; Keiser 1982). The northernmost record on the western side for *D. melanurus* is in southern Sonora, while in the eastern side is ca. 300 km. north in southern Texas. Conversely, *O. aeneus* is present in southern Arizona in the western versant, and about 300 km. south in central Nuevo Leon and Tamaulipas in the eastern side (Figure 2.1).

Range maps are central to studying geographical patterns of distribution, and the more frequently used dot maps and shaded outline maps have shortcomings: outline maps attempt to depict the distribution of the species in question by including areas surrounding collecting localities, and even when this process takes into account many environmental factors, it is still subjective and tends to overestimate the distribution. Dot maps on the other hand, while more accurately estimating known localities, tend to greatly underestimate real distributions in poorly sampled regions (Anderson et al. 2002). Ecological niche modeling is an increasingly used technique to predict distributions based in environmental conditions, species occurrence locality information, and algorithms that estimate climatic niche envelopes using the environmental and locality data (Guisan and Zimmermann 2000; Graham et al. 2004). Despite some uncertainties intrinsic to this technique (Pearson et al. 2006), it has a great range of applications from niche conservatism theory and speciation (Peterson et al. 1999; Wiens 2004), climate change (Peterson et al. 2002; Ballesteros-Barrera et al.

2007), invasive species biology (Peterson 2003), biological sampling for rare species (Guisan et al. 2006; Pearson et al. 2007), agriculture (Sanchez-Cordero and Martinez-Meyer 2000), human and animal health (Peterson et al. 2003; Peterson et al. 2005), and competitive exclusion and release (Anderson et al. 2002), among many other issues (Kozak et al. 2008). Advantages of ecological niche modeling techniques over direct sampling, include the time efficiency and accuracy, both of which improve on techniques frequently used for conservation purposes, like GAP analysis (Peterson and Kluza 2003). Additionally, ecological niche modeling can create acceptable distribution predictions with a small number of collecting points (Pearson et al. 2007).

I therefore used ecological niche modeling to answer the following questions: What are the factors that limit the distribution areas for *D. melanurus* and *O. aeneus*? Are those factors the same for the two species? And if so, Do the two species respond in the same ways to the factors limiting their distribution areas?

MATERIALS AND METHODS

Even the best distribution maps represent a highly simplified picture of the geographic distribution of a species (Lomolino et al. 2005), and because my approach would require a representation of the distribution area as close to reality as possible, I decided to remake the northern part of the distribution maps by ecological niche modeling techniques. I started by contacting every museum and scientific collection that contained specimens of *D. melanurus* and *O. aeneus*, and requested all the collecting data associated with each specimen. I also considered collecting localities from published references, reliable personal observations and used Herpnet (http://herpnet.org/index.html) to guide the search for specimens in museums.

I assigned latitude and longitude coordinates to the collection localities using a wide variety of sources and software to achieve the highest accuracy. For this I considered several factors based on the date of the collection, collector, historical change on towns and cities borders, and any additional notes that came with the record of the specimen (See Appendix for a list of the sources and software). Additionally, I only considered localities for which I had the highest confidence in the accuracy of the locality.

I used Maxent, a program that uses locality records and environmental variables to predict the distribution of a species in a geographical area by using maximum entropy theory (Phillips et al. 2004; Phillips et al. 2006; Phillips and Dudík 2008), and that has performed well in comparisons with other software (Elith et al. 2006). The modeling procedure in Maxent closely followed the methodologies that have resulted in the most reliable predictions in previous references (Phillips et al. 2006).

Ecological niche modeling is an increasingly used technique, but one must acknowledge the real possibility of significant niche variation across broad distributions (Hernandez et al. 2006; Murphy and Lovett-Doust 2007). To avoid this difficulty for the widely distributed *D. melanurus* and *O. aeneus*, I only considered collecting localities that were above the Isthmus of Tehuantepec in southern Mexico, just before the distribution areas bifurcate into eastern and western versants.

The choice of variables can affect the results of niche modeling (Peterson & Nakazawa 2008), and to reduce the number of the 19 climatic variables from the Worldclim dataset (freely available at http://www.worldclim.org/), I extracted the values for each variable associated with each collecting locality for *D. melanurus* and *O. aeneus* using Manifold System 8.0 Ultimate Edition GIS, and performed a Pearson-product correlation matrix with the variables. From this correlation matrix I chose the ones that had a coefficient of determination above 0.75 ($p \leq 0.001$) (Kozak and Wiens 2006), and eliminated the ones that were highly correlated, targeting the ones that were redundant and favoring the inclusion of the variables that represented extreme values rather than mean values.

For producing updated distribution maps for both species, I created preliminary models in Maxent with and without testing localities. For the models with testing localities I used 75% of the collecting points to build or train the model and set aside the other part for testing. The last part of the ecological niche modeling procedure is to define a threshold that would allow for the estimation of the species range by converting the logistic output from Maxent in a binary map of presence/absence. There are several methodologies to define the threshold, and they can result in great variability in the predicted distribution. I used the sensitivity-specificity sum maximization (or Maximum training sensitivity plus specificity) approach because it overpredicts less than others that I tried, has a threshold that is similar in both the models with and without testing localities, has been shown to be one of the most robust approaches for threshold definition (Liu et al. 2005), and is not an artificial threshold with a lack of a biological basis like the frequently used values of 0.5 or 0.05.

Maxent can also estimate the relative contributions of the variables used in the model built, and I used this feature for both species. Additionally, I performed a jackknife analysis with Maxent in order to identify the variables with the most useful information that was not present in the other variables (Phillips et al. 2006). Maxent implements this is by creating several models: with all variables, deselecting one variable in turn, and with a single variable. The results from the jackknife analysis, together with the estimation of the relative contributions of each variable to the model, are a good way to identify variables that are important for the studied species.

To determine if limiting environmental variables on the western side of the continent were the same on the eastern side for these two species, I created ecological niche models that considered separately not only the two species, but also the western and eastern versants of their distribution in northern Mexico and southern US. This permitted us to obtain accurate predictions for each versant independently, because they reflect two independent invasions of the nearctic realm by each species. I built these models using the same area as the models that considered the two versants together; and because I didn't trim the background layers to adjust to only each of the versants of each species, I cannot claim the models that were built for the eastern versant of *O. aeneus* for example, can predict the distribution of that species in the western versant or vice versa, a method called transferability, used in studies of invasive species and that focuses on the distribution areas prediction (Peterson et al. 2007). Instead, I performed a selection of localities ("sample selection bias" Phillips 2008), that although would not accurately predict distribution areas, is useful to identify and differentiate the environmental variables that would be important for each versant for the two species of snakes.

The distributional data can be analyzed in terms of four groups of localities: the *D. melanurus*-western group considered all localities in central Mexico below the 22° latitude plus localities in the western versant, that together consisted of 63 records; *D. melanurus*-eastern contained 114 records of the same localities below 22° latitude plus all localities in the eastern versant; *O. aeneus*-western contained 98 records including the ones below the 20° latitude and localities from the western versant; and finally, *O. aeneus*-eastern contained 35 records that included localities in central Mexico below the 22° latitude, plus the ones from the eastern versant.

I also associated the locality records with vegetation and soil type. However, the classification methodologies and/or detail of the GIS layers in US and Mexico were so different, that using data for both countries would have biased the results. Instead, I conducted this analysis separately and only included data from Mexico for two reasons: most of the distribution range that I analyzed of these two species is in Mexico, and the two environmental layers were produced with the same methodologies, detail and scale by the Comision Nacional para el conocimiento de la biodiversidad (CONABIO). The consideration of only Mexican localities excluded 36 out of 144 *D. melanurus* records and 16 out of 110 *O. aeneus* records. I extracted the information from the 12 environmental layers, altitude, vegetation and soil type for the mentioned localities in Mexico, and used the samples with data (SWD) approach in Maxent. For the SWD I included a file with absences taken randomly in areas without collecting records in order to test is the values identified with the full models were as important as with this reduced subset.

RESULTS

After eliminating the variables with highest values of correlation, I identified 12 environmental variables along with elevation to be included in my final Maxent models for *D. melanurus* and *O. aeneus* (Table 2.1).

Table 2.1 Variables included in the Maxent models, short name used in some figures of this work, and the name they receive in the WorldClim dataset.

Variable	Short name	WorldClim name
annual mean temperature	AnnMeanTemp	bio_1
mean monthly temperature range	MeanMonthTemp	bio_2
isothermality	Isothermality	bio_3
temperature seasonality	TempSeason	bio_4
max temperature of warmest month	MaxTempWarmMonth	bio_5
min temperature of coldest month	MinTempColdMonth	bio_6
temperature annual range	TempAnnRange	bio_7
mean temperature of warmest quarter	MeanTempWarmQuart	bio_10
precipitation seasonality	PrecipSeason	bio_15
precipitation of wettest quarter	PrecipWettestQuart	bio_16
precipitation of driest quarter	PrecipDriestQuart	bio_17
precipitation of coldest quarter	PrecipColdQuart	bio_19
elevation	Elevation	alt

Maxent produces a visual representation of the model in the form of an image file and an ascii file that can be included in a GIS. This image identifies the probability of habitat suitability, where warmer colors represent habitat with high probability of being suitable for the species, and cooler colors represent areas non suitable for the species (Figure 2.2).

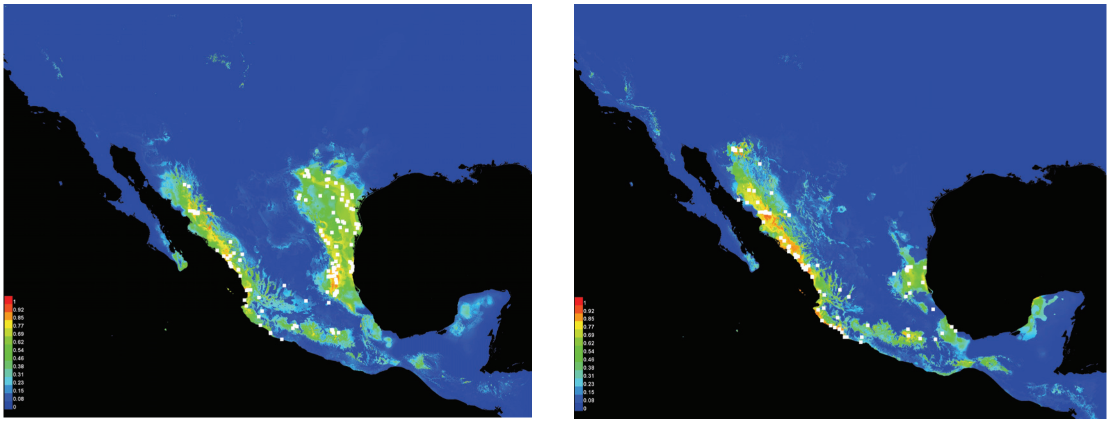

Figure 2.2 Graphical representation of the model for *D. melanurus* (left) and *O. aeneus* (right). The result is given in a logistic format and identifies areas with high probabilities of containing suitable habitat for the species in warmer colors, to areas containing unsuitable habitat for the species for which the model was built.

To convert the continuous output from Maxent in distribution maps, I used the "Maximum training sensitivity plus specificity" approach. This approach identifies threshold values that enable us to convert the cited output into a binary map, and the threshold used for *D. melanurus* was 0.330, while for *O. aeneus* it was of 0.159. The application of the threshold to the logistic output produced the distribution maps for the northern distribution areas for the two species Figure 2.3.

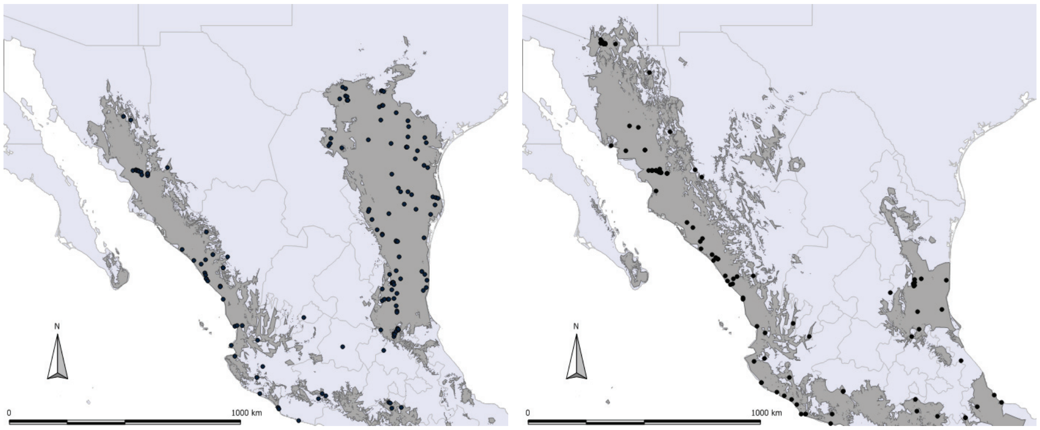

Figure 2.3 Distribution area maps for the northern distribution of *D. melanurus* (left) and *O. aeneus* (right) produced by Maxent and processed in manifold GIS in order to show a binary result. The dots in the maps are the collecting localities used in the construction of the model.

Variables of importance for *D. melanurus*.

The model for *D. melanurus* identified five variables that accounted for 82.6 percent of the environmental variability to the construction of the model with Maxent (Table 2.2), with annual mean temperature taking the biggest share of the variation.

Table 2.2 Relative contribution of the five most important environmental variables to the Maxent model for *D. melanurus*.

Variable	Percent contribution
annual mean temperature	42.2
temperature seasonality	11.3
precipitation of wettest quarter	10.7
precipitation of coldest quarter	10.4
temperature annual range	8

The jackknife analysis in Maxent also identified annual mean temperature as the most important variable for *D. melanurus*. When used in isolation, this variable was the one with the highest gain, followed closely by minimum temperature of coldest month. On the other hand, the variables that decreased the gain of the model the most when they were excluded were temperature seasonality, followed by precipitation of coldest quarter and precipitation of wettest quarter, meaning that those variables contained the most information that was not present in any of the other environmental variables (Figure 2.4).

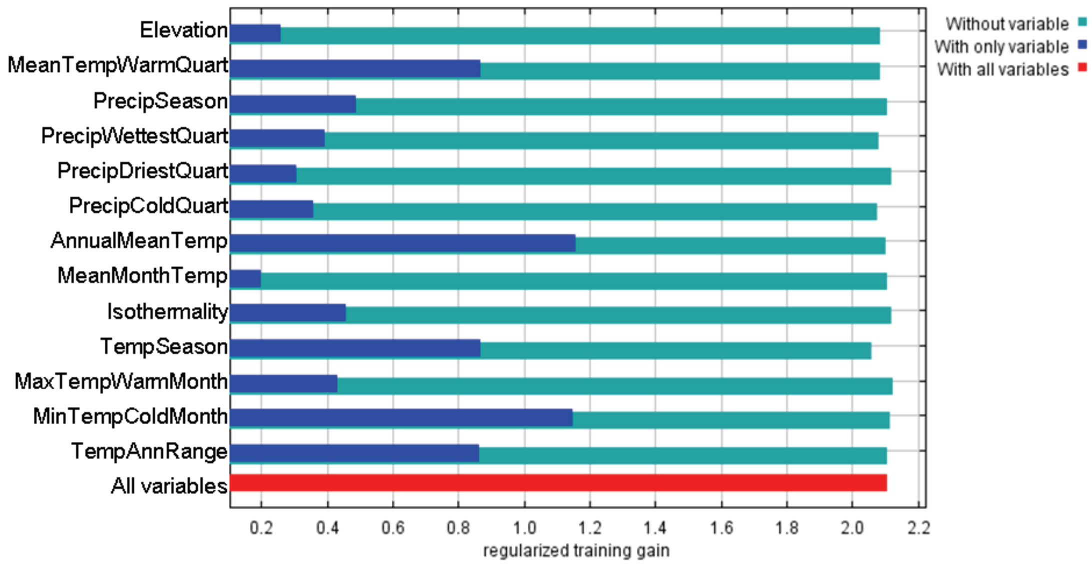

Figure 2.4 Results of the jackknife analysis to identify variables of importance for *D. melanurus*. Shown here are the gains for the models created in this part: In addition to the model that used all variables (represented by the red bar), several models were created by using all but one of the variables (turquoise colored bars), and then by building models with a variable in isolation (blue bars).

Variables of importance for *O. aeneus*.

The model for *O. aeneus* identified five variables that accounted for 80.5 percent of the environmental variability (Table 2.3), with precipitation seasonality being the most important and explaining almost half of the variation for that species.

Table 2.3 Relative contribution of the five most important environmental variables to the Maxent model for *O. aeneus*

Variable	Percent contribution
precipitation seasonality	43.2
annual mean temperature	15.3
precipitation of wettest quarter	8.5
isothermality	7.2
temperature seasonality	6.3

The jackknife analysis in Maxent also identified precipitation seasonality as the most important variable for *O. aeneus*. When used in isolation, this variable was the one with the highest gain, followed closely by minimum temperature of coldest month. On the other hand, the variables that decreased the gain of the model the most when they were excluded were precipitation of coldest quarter, followed by temperature seasonality and precipitation of wettest quarter, meaning that those variables contained the most information that was not present in any of the other environmental variables (Figure 2.5).

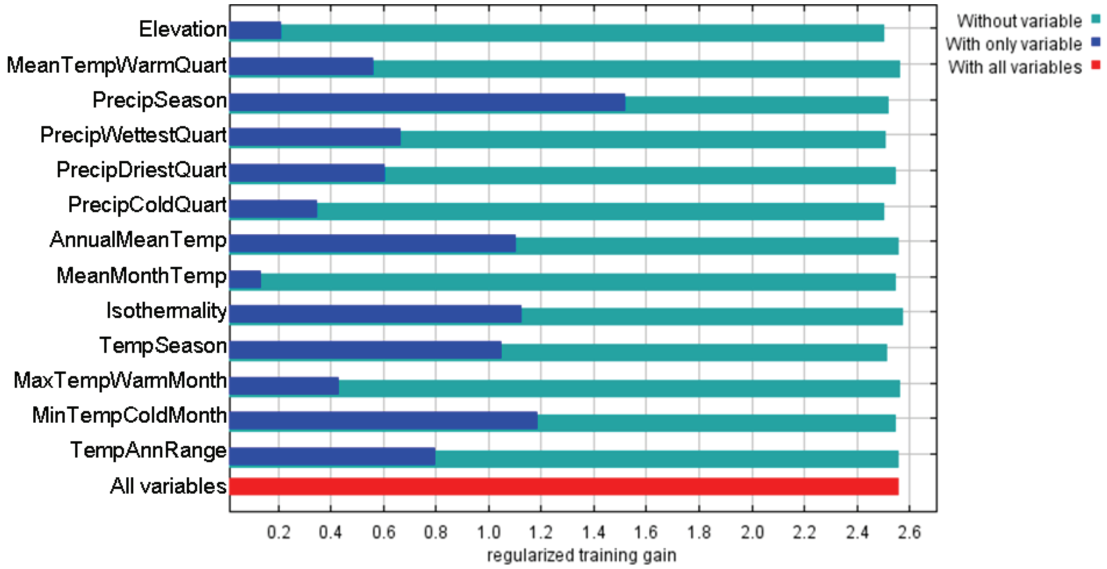

Figure 2.5 Results of the jackknife analysis to identify variables of importance for *O. aeneus*. Shown here are the gains for the models created in this part: In addition to the model that used all variables (represented by the red bar), several models were created by using all but one of the variables (turquoise bars), and then by building models with a variable in isolation (blue bars).

The variables identified as most important based on their relative contribution to the model (Tables 2.2 and 2.3) depend on the particular path that Maxent takes to produce the prediction (Phillips 2006), so comparing that information with the results from the jackknife analysis can be helpful in determining the variables of importance.

From that comparison, I conclude that the most important variables, and probably the ones limiting the northern distribution of *D. melanurus* are annual mean temperature (the minimum value in my sample is 11.9°C), temperature seasonality (this is a temperature variation coefficient and the values in my sample ranged from 1334 to 7528) and minimum temperature of the coldest month (the lowest value in my sample is 0.6°C). Conversely the limiting factors for *O. aeneus* are precipitation seasonality (the values in my sample for this coefficient of precipitation variation ranged from 54 to 128), annual mean temperature (the minimum value in my sample es 12.7°C) and minimum temperature of the coldest month (which in my sample it was -2.2°C).

Variables of importance for each versant of the two species

The models created with only the western or eastern versants have the advantage of identifying more precisely the variables that are important for *D. melanurus* and *O. aeneus* in each of those versants. I used the same 12 environmental variables plus altitude, and in the resulting models the order of importance of each of those changed among the two versants. For *D. melanurus*, precipitation seasonality, precipitation of wettest quarter and temperature seasonality were most important, accounting for 81.7% of the variability in the western side, but in the eastern side of the distribution annual mean temperature, temperature annual range and precipitation of coldest quarter where most important, contributing 70.8% to the model. Temperature annual range was in second place of importance in the eastern side with 16.2%, but was the last in the western side with a 0% contribution to the model, while bio_19 was in third order of importance in the eastern side (15.1%) but on the tenth on the western versant with a contribution of 0.3% (Table 2.4).

The three most important variables for the model built for *O. aeneus* in the western versant were precipitation seasonality, annual mean temperature and precipitation of wettest quarter, with a contribution of 70.3% to the model, while in the eastern side, the variables of importance for *O. aeneus* were temperature seasonality, annual mean temperature and precipitation seasonality, with a contribution of 75.3% (Table 2.5). Although there are differences in the order of importance of the variables considered for *O. aeneus*, the differences among the two versants were not as marked as with *D. melanurus*.

Table 2.4 Order of importance and percent contribution for the 12 variables considered for the eastern or Pacific versants and western or Gulf versants of *D. melanurus*.

Order of importance	***D. melanurus* western**	***D. melanurus* eastern**
1	PrecipSeason - 48.9	AnnMeanTemp - 39.5
2	PrecipWettestQuart - 23.9	TempAnnRange - 16.2
3	TempSeason - 8.9	PrecipColdQuart - 15.1
4	AnnMeanTemp - 5.2	MeanMonthTemp - 6.9
5	Isothermalithy - 5.2	PrecipWettestQuart - 6.5
6	Elevation - 3.4	TempSeason - 3.5
7	MinTempColdMonth - 2	MeanTempWarmQuart - 3.1
8	PrecipDriestQuart - 0.9	PrecipDriestQuart - 3
9	MaxTempWarmMonth - 0.8	MinTempColdMonth - 1.9
10	PrecipColdQuart - 0.3	PrecipSeason - 1.4
11	MeanTempWarmQuart - 0.3	MaxTempWarmMonth - 1.2
12	MeanMonthTemp - 0	Isothermalithy - 0.9
13	TempAnnRange - 0	Elevation - 0.7

Table 2.5 Order of importance and percent contribution for the 12 variables considered for the eastern or Pacific versants and western or Gulf versants of *O. aeneus*.

Order of importance	***O. aeneus* western**	***O. aeneus* eastern**
1	PrecipSeason - 51.5	TempSeason - 34.3
2	AnnMeanTemp - 10.3	AnnMeanTemp - 31.7
3	PrecipWettestQuart - 8.5	PrecipSeason - 9.3
4	MeanTempWarmQuart - 6.6	PrecipColdQuart - 8.4
5	TempSeason - 4.5	TempAnnRange - 4.8
6	PrecipColdQuart - 4.4	MinTempColdMonth - 4.1
7	Isothermalithy - 3	PrecipDriestQuart – 2
8	Elevation - 2.8	PrecipWettestQuart – 2
9	PrecipDriestQuart - 2.6	Elevation - 1.8
10	TempAnnRange - 2.3	Isothermalithy - 1.3
11	MinTempColdMonth - 2.1	MaxTempWarmMonth - 0.3
12	MeanMonthTemp - 1.3	MeanMonthTemp - 0.1
13	MaxTempWarmMonth - 0	MeanTempWarmQuart - 0

Seasonality, both in terms of temperature and precipitation, along with the amount of rain are more important for *D. melanurus* in the western versant than for *D. melanurus* in the eastern versant, where temperature plays a bigger role in the form of mean temperature and temperature range (both monthly and yearly), along with the amount of rain in winter.

In the case of *O. aeneus*, annual mean temperature and precipitation seasonality play an important role in both versants, temperature seasonality a moderate role in the western versants but an important one in the eastern versant, and winter precipitation a moderate role in both versants. The biggest difference among the two versants is that mean summer temperature plays as moderate role on the western side but none on the eastern.

Vegetation and soil types seemed to play unimportant roles for both species in the model built with the SWD for Mexican localities. For *D. melanurus*, soil accounted for 4.5% of the variation explained by the model, and vegetation for 0.6%; while in the case of *O. aeneus*, vegetation contributed a little more than 2%, and soil about 0.5%. In both cases, they were far from the variables identified as important in this and the previous models built without considering soil or vegetation (Tables 2.2 and 2.3).

DISCUSSION

An observed difference between the maps that predict the distribution of the two species is that it is apparently more difficult to model *D. melanurus* than *O. aeneus* in central Mexico, evidenced by the number of collecting points that were missed by the model built close to the Isthmus of Tehuantepec. There are several potential non-exclusive explanations for this: It might be an artifact of my sampling bias, where the exclusion of collecting points to the south is fooling the model into considering that the *D. melanurus* distribution area ends there. Another possibility may be that the model fails to accurately predict the distribution of *D. melanurus* in the isthmus of Tehuantepec because the ecological niche for the specimens in that area is truly different from specimens further north, thus mirroring the subspecifical differences recognized taxonomically.

The inclusion of soil and vegetation data for a restricted portion of a study area gives an idea of the limited role those factors play in the maintenance of distribution limits for *D. melanurus* and *O. aeneus*. Because soil properties have been found important for *Drymarchon couperi*, the Eastern Indigo Snake (Dieme and Speake

1983), my results assigning little importance to soil should be taken cautiously and future studies might fruitfully examine distributional limits in *D. melanurus* throughout its enormous New World distribution.

Diet was not among my predictor variables, and likely plays no role in limiting the northern distribution of these two species. *Drymarchon melanurus* eats a wide variety of prey, including snakes, lizards, rodents, anurans and fish (Keegan 1944; Bogert and Oliver 1945; Hardy and McDiarmid 1969), but it prefers mainly snakes and frogs (Greene unpublished data). *Oxybelis aeneus* feeds mainly on locally common lizards (Bogert and Oliver 1945; Alvarez del Toro 1982).

Local adaptation may be underlying the differential patterns of distribution in the two versants, and my results support such a scenario by identifying environmental variables of importance for both species in each versant. Furthermore, the differences in the modeled ecological niches are coincident with a simple measure of morphological diversity in those species. *Drymarchon melanurus* is sufficiently differentiated that eastern and western versant populations are recognized as subspecies, based on differences in color pattern and scalation (McCranie 1981). *Oxybelis aeneus* is so morphologically uniform that no subspecies are described for this extremely widely distributed snake (Keiser 1982).

There are cases where the software producing the distribution maps include areas where the species is not likely to be present (overprediction). Rather than considering those areas as a failure of the program, they can be instructive when the biology of the organism is taken into consideration. There are two such cases of overprediction in the distributional limits implied by Maxent for the two species of snakes in this work (Figure 2.6). The first is for *D. melanurus* in central Texas, where the predicted suitable habitat includes a finger like projection north and east of the documented range. Because no *D. melanurus* has ever been taken in this heavily populated and well studied area we are confident the species does not occur there; however, there is a strong association with this species and habitats along major streams (Diemer and Speake 1983). The northernmost records for *D. melanurus* are from immediately to the west, in river drainages that pass southward through the known distribution of the species. The overpredicted range segment is drained by the San Marcos river, which flows southeastward and never enters the distribution of *D. melanurus* ¬ Indigo snakes could live there but they have never been able to reach that area.

A similar situation happens with the prediction of habitat suitability for *O. aeneus* well within the Mexican Plateau in eastern Chihuahua (Figure 2.6). The penetration of *O. aeneus* at several parts of the western edge of the Mexican Plateau is facilitated by humid drainages that allow tropical deciduous forest to reach those areas. Although the habitat in isolated, more interior basins is evidently suitable for *O. aeneus,* high elevations and arid conditions make it impossible for vine snakes to penetrate them.

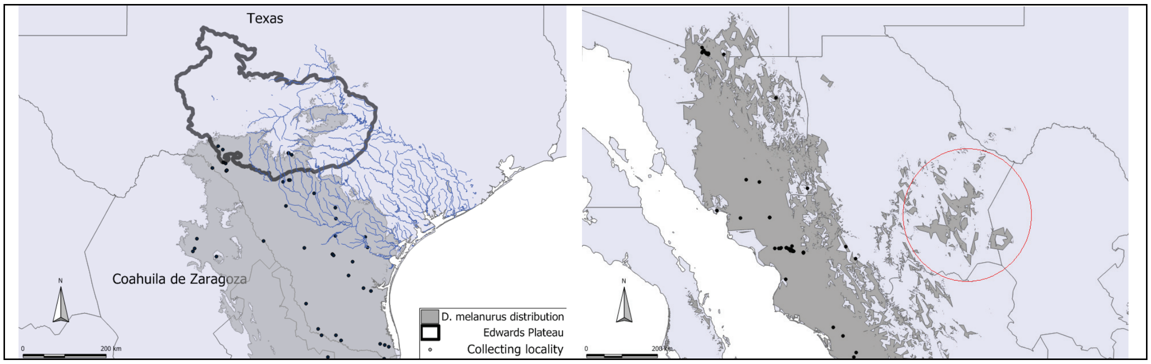

Figure 2.6. Overpredicted areas discussed in the text for *D. melanurus* in central Texas, US (left) and *O. aeneus* in eastern Chihuahua, Mexico (right)

The use of species distribution modeling software is a relatively new technique, and as such, it is still an area of active research with corresponding caveats.

Several pitfalls must be avoided to obtain reliable predictions: there should be no bias or correlation in the collecting efforts; no errors in the occurrence localities or identification of specimens; and temporal correspondence between collection of environmental data and specimens (Phillips et al. 2006). I have largely circumvented these problems in that these two species of snakes are conspicuously different and easy to identify; I took pains to precisely georeference collecting localities; the inclusion of records from many individuals make sampling bias unlikely; and finally, the vast majority of my records are from within the past century, and thus correspond reasonably closely to the availability of environmental data.

By extending the geographical scope and including a larger suit of specific environmental variables as potential explanatory factors this study confirms and elaborates on earlier qualitative assertions about distributional limits for the two species. Diemer and Speake (1983) pointed to soil properties and habitat characteristics important for *D. corais*, and my results coincide by stressing the importance of drainages, associated habitats, and temperature and seasonality. Van Devender et al. (1994), identified winter freezing and aridity as important factors limiting the distribution of *O. aeneus*, and my results enhance their claims by also identifying the environmental variables of importance: precipitation seasonality, as well and mean and minimum temperature values.

Comparing the way these two neotropical species reach their northern limits of distribution demonstrates similar factors regulating the distribution of two species that are relatively closely related but extremely divergent ecological and morphologically, which could be used as evidence of ecological niche conservatism. Being able to compare the two versants for each species further illustrates the differential response that a single species can have to the same set of environmental factors, and thus reflecting the ability to adapt to local conditions.

More generally, considering the study of range limits roughly coincident with the realms boundary, I contributed to the clarification of alternative responses to the northern limits of tropicality, and set the stage for experimental studies linking physiological ecology with distributions (Diemer and Speake 1983; St Clair and Gregory 1990; Van Devender et al. 1994; Wiens and Graham 2005).

APPENDIX

Georegistration of specimen’s localities.

I assigned latitude longitude coordinates (georeferenciacion or georegistration) by using a wide variety of sources in order to be as accurate as possible in the georegistration process, choosing the more detailed sources whenever it was possible and cross-checking with two or more sources. For Mexican collecting localities I used mainly the software packages SIIGE (Sistema Integrado de Información Geográfica y Estadística) and IRIS versions 2.0, 3.0 and 4.0, both from the INEGI (Instituto Nacional de Estadística, Geografía e Informática), as well as cartographical and historical data from INEGI, the Atlas Nacional de México from the Instituto de Geografía of the Universidad Nacional Autónoma de México, and the Secretaría de Comunicaciones y Transportes (SCT). For US localities I used MapCard, TopoZone, GoogleEarth, the RandMcNally atlas and a series of maps from the Perry Castañeda online library for Texas and Arizona. For some localities I also used GEOlocate and the gazeeters provided by the Museum of Vertebrate Zoology from the University of California. The Mexican collecting points were obtained in ITRF92 datum from the program IRIS (INEGI), and all of them were converted to NAD27 datum using the TRANINV conversion tool provided by INEGI. Finally all points in NAD27 datum were converted to WGS84 using the Coordinate Converter (available online at http://www.bivouac.com/MultiConvert.asp).

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CHAPTER 3

LANDSCAPE CHANGE AND CONSERVATION PRIORITIES: MEXICAN HERPETOFAUNAL PERSPECTIVES AT LOCAL AND REGIONAL SCALES

ABSTRACT

Few studies have demonstrated historical human impact on biodiversity at local and regional scales, largely due to lack of baseline information and long term monitoring for most taxa. In 1958 and 1959 researchers from the Museum of Vertebrate Zoology (MVZ) visited the Mexican state of Aguascalientes and increased its documented amphibian and reptile fauna from 21 to 30 species. Using MVZ collections, field notes, and landscape photographs taken during that expedition, I resurveyed those same localities in 2004 to document herpetofaunal changes coincident with greatly increased human activities. Despite its small area, Aguascalientes encompasses several biogeographic regions and the threat of local extinction at species' distributional limits has broader implications for regional biotas. New discoveries raise to 71 the number of species known for that state, but the comparisons suggest a gloomy future for amphibians and reptiles in Aguascalientes. Paradoxically, human impact is managed primarily at state and municipal levels, often devoid of locally relevant context. My findings illustrate the conservation value of intensive small-scale studies, focused on the natural history of particular species and localities, as complements to large-scale biodiversity assessments on country wide and continental scales.

INTRODUCTION

Biological conservation is fundamentally concerned with human impacts on species and their environments; however, few studies have shown in detail how I have historically affected the persistence of vertebrates in natural habitats, due in large part to lack of long term monitoring. Most temporal comparisons of diversity span less than one generation of the organisms under study (Willis et al. 2005) and we generally lack baselines with which to evaluate biotic changes. Repetitions of historical surveys thus provide excellent opportunities to assess long-term changes due to anthropomorphic effects, especially if collecting efforts and techniques can be replicated. Re-censusing can supply information on presence and absence of species, as well as document changes in population size and distribution, promote the discovery of new species, and guide management of natural areas (Knight 2003).

Projects that evaluate landscape change with historical information are scarce and their results contradictory: some have increased the number of species known for a surveyed region, others reported persistence of species, and still others documented species extinctions and colonizations (Lannoo et al. 1994; Robinson 1999; Mendoza-Quijano et al. 2001; Gibbs et al. 2005; Hossack et al. 2005). Although frequently qualitative rather than quantitative, and only rarely repeatable in a consistent and statistically comparable fashion, historical databases have nonetheless been important because they are the only standard we have with which to estimate diversity, population trends, and suggest factors responsible for species declines and colonizations (Lannoo et al. 1994; Robinson 1999; Brodman et al. 2002; Gibbs et al. 2005). Historical studies of landscape changes have been used to document the effects of human activities (Mendoza-Quijano et al. 2001), assess extinction risks for songbirds (Schrott et al. 2005), and evaluate changes in species richness and population sizes (Robinson 1999).

Most studies of historical ecological change have focused on temperate regions and conservation assessments have increasingly emphasized large spatial scales. The recent publication of a country-wide analysis of distributional patterns in México’s herpetofauna (Ochoa Ochoa and Flores Villela 2006) is an invaluable contribution to tropical conservation planning and underscores the need for complementary, fine scale studies. I chose the central Mexican state of Aguascalientes for analysis of landscape change and conservation of amphibians and reptiles for several reasons: 1) historical information from expeditions by personnel from the University of California Museum of Vertebrate Zoology (MVZ) almost 50 years ago is available as a baseline; 2) Aguascalientes has an area of 5,589 km^2 (INEGI 1995), making it the fifth smallest state in México and suitable for rapid, yet thorough assessment; 3) Aguascalientes is positioned at the intersection of several biogeographically interesting faunal components: Sierra Madrean and Trans-Volcanic Belt forests, arid Mexican Plateau deserts, and subtropical vegetation dividing the two main forested areas, Sierra Fría and Sierra del Laurel (INEGI 2005).

Using the MVZ records and documented collection localities, we resurveyed amphibians and reptiles across Aguascalientes, with the goal of assessing faunal changes concomitant with almost a half century of continuing human impact. My results show that the herpetofauna remains substantially intact but is widely threatened by extensive land conversion; I also pinpoint specific taxa and ecosystems for emphasis in management planning, and highlight the importance of natural history research in local and regional conservation activities (Greene 2005).

MATERIALS AND METHODS

The amphibians and reptiles of Aguascalientes began to receive attention early in the past century, and intensive collecting efforts commenced more recently when W. Z. Lidicker and colleagues at the MVZ surveyed the state in 1958 and 1959 (Anderson and Lidicker 1963). This expedition was the most important zoological collecting effort up to that time, in both number of species newly reported for the state and geographic coverage. The MVZ expedition sampled almost every major physiographic region and increased from 21 to 30 the known number of species of amphibians and reptiles in the state. Several publications since then dealt exclusively with the state's reptiles and amphibians, and thus the herpetofauna is becoming well known. As of 2008, 71 species of amphibians and reptiles were recorded for Aguascalientes, representing the 6% of the species reported for the country and making it one of the states with the lowest number of species of amphibians and reptiles (Flores Villela & Gerez 1994; Flores-Villela & Canseco 2004). The rate of species discovery has been constant since 1945 and shows no sign of an asymptote (Figure 3.1), with all species being native but *Hemidactylus turcicus* (Mediterranean Gecko) and *Ramphotyphlops braminus* (Braminy Blind Snake).

I used the baseline information from the MVZ (Anderson and Lidicker 1963) to compare the status of several collection localities for amphibians and reptiles over a period of ca. 45 years. I examined all relevant field notes and specimens, and interviewed W. Z. Lidicker Jr. regarding details of the expedition. For brevity, I sometimes refer to the 1958-1959 expeditions as "original" or "MVZ" and to our 2004 surveys as "recent."

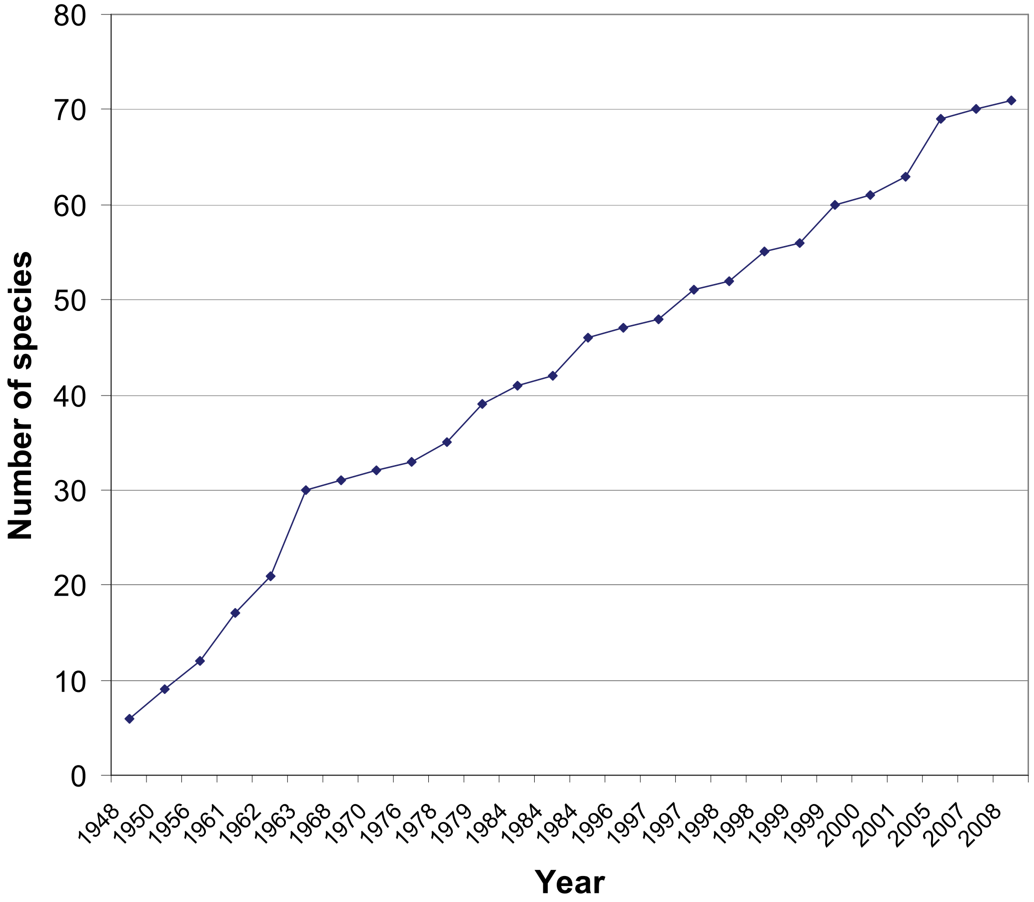

Figure 3.1 Increase in the number of species of amphibians and reptiles reported from Aguascalientes, México. Years on the X axis correspond to dates of publications that added species (based on Burt 1931; Smith and Taylor 1945; Smith and Taylor 1948; Smith and Taylor 1950; Chrapliwy 1956; Chrapliwy et al. 1961; Banta 1962; Anderson and Lidicker 1963; Zweifel 1968; McDiarmid and Scott 1970; Thomas and Dixon 1976; Harris and Simmons 1978; Smith and Smith 1979; Wilson and McCranie 1979; McCranie and Wilson 1984; Camper 1996; Sigala Rodríguez and Vázquez-Díaz 1996; Vázquez-Díaz and Quintero-Díaz 1997; Ramírez-Bautista et al. 1998; Vázquez-Díaz et al. 1998a; Vázquez-Díaz et al. 1998b; Vázquez-Díaz et al. 1998c; Quintero-Díaz et al. 1999b; Quintero-Díaz et al. 1999a; Vázquez-Díaz and Quintero-Díaz 1999; Vázquez-Díaz et al. 1999a; Vázquez-Díaz et al. 1999b; Quintero-Díaz et al. 2001; Vázquez-Díaz and Quintero-Díaz 2005; Quintero-Díaz et al. 2007; Sigala Rodríguez et al. 2008).

The original expeditions included an exploratory/non-collecting trip in 1956 and periods of intensive fieldwork in July of 1958 and 1959. Eighteen collecting localities were mentioned by Anderson and Lidicker (1963) and six localities were photographed with recognizable landscape features. After checking field notes and visiting the actual collecting localities we determined that two were the same site visited on two separate occasions, five were geographically too close to recognize individually (making them effectively two localities), and two did not yield herpetological material. The final number of collecting localities in 2004 was thus reduced to twelve (Figure 3.2), and field work was planned such that roughly the same amount of time was spent at each locality. The MVZ expeditions spent a total of 36 days in the field between July 8-28 in 1958 and 1959, whereas we worked for 26 field days between July 6 and August 20 in 2004.

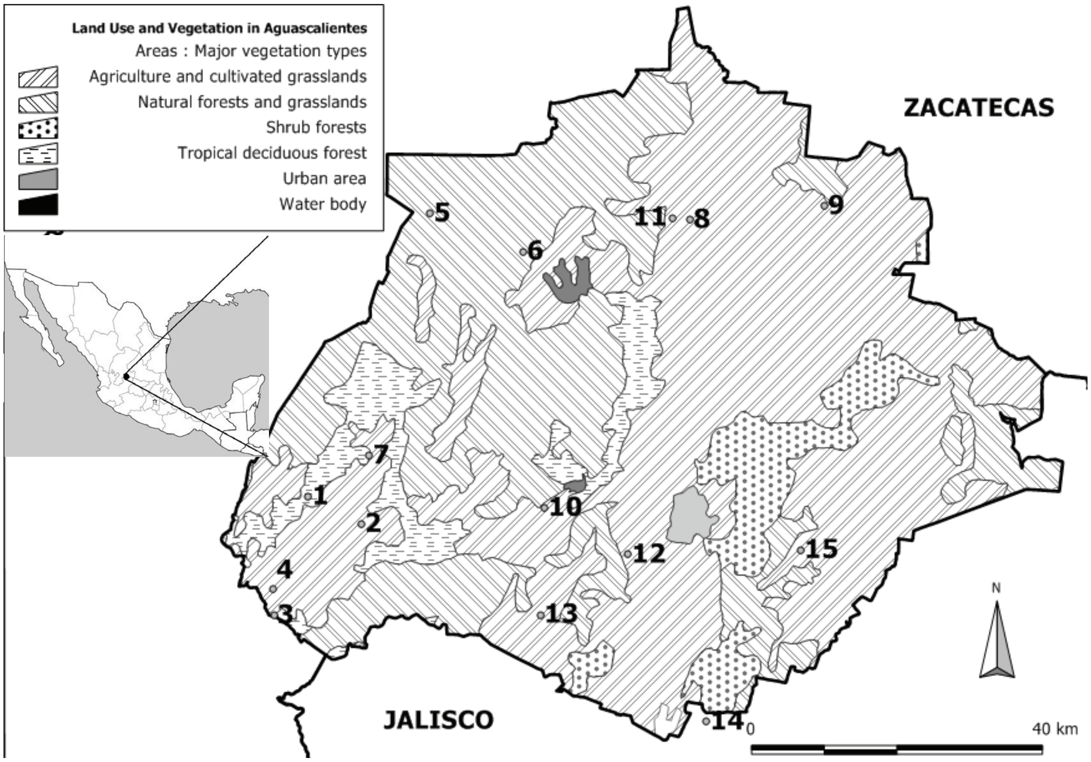

Figure 3.2 Major vegetation types and current land use patterns in Aguascalientes, México (Modified from CONABIO 1998). Numbers correspond to localities that were surveyed and/or photographed, locality details can be seen in Table 3.1.

The number of people participating in fieldwork was the same in both surveys. We sampled opportunistically, walking in the areas surrounding the localities and paying attention to suitable microhabitats (Casas Andreu et al. 1991; Simmons 2002), such that 579 person-hours were spent searching, looking for original locations, and questioning local residents about photographs when it was difficult to find the original photographed locality. We also re-photographed six sites that had recognizable features in the 1956 to 1959 images, insofar as possible from the same vantage points, to evaluate historical changes at the landscape level. Finally, shared ecological characteristics of species have proved important for identifying causes of populations declines and extinctions (Kotiaho et al. 2005), and I therefore used natural history data for the Aguascalientes herpetofauna to identify species especially prone to conservation threats.

Table 3.1 Details for the surveyed localities. For each site the following information is given: Site ID refers to the numbers in map in Figure 3.2, locality, general locality as originally stated in Anderson and Lidicker (1963), latitude and longitude in decimal degrees, and whether the site was collecting locality, photographed locality, or both.

Table 3.1

Site 1: El Tigre, Calvillo, Ags., “4½ miles northwest of Calvillo”, 21.901167, -102.76737 , Collecting locality, landscape photographs available.

Site 2: El Chiquihuitero, Calvillo, Ags., “2 miles north of Calvillo”, 21.8697, -102.70212, Collecting locality.

Site 3: Road Calvillo-Jalpa, east of state boundary with Jalisco, Ags., “¼ mile east of the state boundary”, “8 miles southwest of Calvillo” and “7½ miles west-southwest of Calvillo”, 21.764883, -102.81018, Collecting locality.

Site 4: Presa Media Luna, Calvillo, Ags., “5½ miles west of Calvillo”, 21.79595, -102.81152, Collecting locality.

Site 5: north of Presa de la Araña, Sierra Fría, Ags., “3 miles north of Cerro del Jaguey”, 22.224033, -102.61683, Collecting locality, landscape photographs available.

Site 6: Barranca Ventanillas, San José de Gracia, Ags., two visits to “8 miles west-northwest of Col. Pres. Calles”, 22.180533, -102.50197, Collecting locality, landscape photographs available.

Site 7: La Labor, Calvillo, Ags., “1 km. south of La Labor” and “½ mi. south of La Labor”, 21.947533, -102.69243, Collecting locality.

Site 8: east of Rincón de Romos, Ags., “1¼ miles east of town” Rincón de Romos, 22.219454, -102.31677, Collecting locality.

Site 9: east of Tepezalá, Ags., “2 mi. east of Tepezalá” 22.232833, -102.12987, Collecting locality.

Site 10: Venaderos, west of the city of Aguascalientes, Ags. “Venadero (sic)… 13 miles west of Aguascalientes”, 21.887967, -102.47555, Collecting locality.

Table 3.1 (Continued)

Site 11: south of Rincón de Romos, Ags., “1/3 mile south” of Rincón de Romos, 22.216917, -102.29598, Collecting locality. Surveyed in 1958 but just briefly in 2004 because it is composed of small inhabited properties.

Site 12: Ciudad de los Niños, Ags., “Ciudad de los Niños (1/3 mile west)”, 21.834591, -102.37258, Collecting locality, this place was being used as an extended cattle enclosure when we visited in 2004.

Site 13: Los Caños, Aguascalientes, not mentioned in the article, 21.765883, -102.48033, non-collecting locality, landscape photographs available.

Site 14: Road 45, junction to Teocaltiche, not mentioned in the article, 21.643407, -102.27553, non-collecting locality, landscape photographs available.

Site 15, Road 70 to San Luis Potosí, not mentioned in the article, 21.839749, -102.15906, non-collecting locality, landscape photographs available

RESULTS

The total number of specimens encountered in the surveys was 99 in 1958-1959 and 114 in 2004. I documented 37 species in 2004, compared to 18 in the original surveys. We found 16 out of the 18 species found in 1958-1959 and 21 additional species (Table 3.2). Among those found in 2004, the colubrid snakes *Coluber taeniatus* (Striped Whipsnake) and *Tantilla wilcoxi* (Chihuahuan Black-headed Snake), both from the poorly studied northeastern portion, were new records for Aguascalientes (see references in Figure 3.1). In addition, reports in progress on *Pseudoeurycea bellii* (Bell's Salamander), the gecko *Hemydactylus turcicus*, and the snakes *Pituophis catenifer* (Gopher Snake) and *Storeria storerioides* (Mexican Brown Snake) will bring the total number of species of amphibians and reptiles to 71 (Vázquez-Díaz and Quintero-Díaz 2005). We did not find two species that were recorded in 1958-1959, *Craugastor augusti* (Barking Frog) and *Holbrookia maculata* (Lesser Earless Lizard).

The six localities photographed in the original surveys represent a diverse array of environments and regions in Aguascalientes, encompassing the more xeric eastern portion of the state, high elevation oak forest in the west, and mid-elevation thorn shrub in central and southern parts of the state (see Figure 3.3 for a selection of photographs). Comparison between the original and the new photographs reveal several patterns: all of them show signs of human disturbance in one way or another; five of the six photographs show agricultural crops replacing almost completely the natural vegetation; three have drastic changes in vegetation composition that are not due to agricultural crops, but only one displays favorable changes in the sense of an increase in oaks, while in the other two oaks and grasses were replaced by *Dodonaea viscosa*, a plant indicative of habitat degradation. Four photographs have bigger or new roads in them and one shows the increase in size of Calvillo, the most populous human settlement in western Aguascalientes.

Table 3.2 Species found in the original (1958-1959) and the recent surveys, common names following Crother ed. (2008), Liner (1997), and relative abundances as considered by Vázquez-Díaz and Quintero-Díaz (2005): AB=Abundant, CO=common, RA=rare.

Table 3.2

Species	English common name	Found 1958/ 1959	Found in 2004	Relative Abundance
Anaxyrus compactilis	Plateau Toad		X	CO
A. punctatus	Red-spotted Toad	X	X	AB
Craugastor augusti	Barking Frog	X		CO
Hyla arenicolor	Canyon Treefrog	X	X	AB
H. eximia	Mountain Treefrog		X	AB
Hypopachus variolosus	Sheep Frog		X	CO
Lithobates montezumae	Montezuma Leopard Frog		X	AB
L. pipiens	Northern Leopar Frog	X	X	RA
Spea multiplicata	Mexican Spadefoot	X	X	CO
Kinosternon integrum	Mexican Mud Turtle	X	X	AB
Anolis nebulosus	Clouded Anole	X	X	CO
Aspidoscelis gularis	Common Spotted Whiptail	X	X	CO
Barisia ciliaris	Imbricate Alligator Lizard	X	X	CO
Holbrookia maculata	Lesser Earless Lizard	X		?
Plestiodon lynxe	Oak Forest Skink		X	CO
Phrynosoma orbiculare	Mountain Horned Lizard	X	X	CO
Sceloporus grammicus	Mesquite Lizard	X	X	AB
S. horridus	Horrible Spiny Lizard	X	X	AB
S. jarrovii	Yarrow's Spiny Lizard		X	AB
S. scalaris	Bunch Grass Lizard		X	CO
S. spinosus	Spiny Lizard	X	X	CO

Table 3.2 (Continued)

Species	English common name	Found 1958/ 1959	Found in 2004	Relative Abundance
Sceloporus torquatus	Crevice Swift	X	X	AB
Urosaurus bicarinatus	Tropical Tree Lizard		X	CO
Coluber bilineatus	Sonoran Whipsnake		X	RA
C. mentovarius	Neotropical Whipsnake		X	RA
C. taeniatus	Striped Whipsnake		X	RA
Conopsis nasus	Large Nose Earthsnake		X	AB
Crotalus lepidus	Rock Rattlesnake	X	X	AB
C. molossus	Black-tailed Rattlesnake	X	X	CO
Hypsiglena torquata	Night Snake		X	RA
Oxybelis aeneus	Brown Vinesnake		X	RA
Pituophis deppei	Mexican Bullsnake		X	RA
Salvadora bairdi	Baird's patchnose snake		X	RA
Senticolis triaspis	Green Ratsnake		X	CO
Tantilla bocourti	Boucort's Blackhead Snake		X	RA
T. wilcoxi	Chihuahuan black-headed Snake		X	RA
Thamnophis cyrtopsis	Black-necked Gartersnake			CO
T. eques	Mexican Gartersnake	X		CO
T. melanogaster	Mexican Blackbelly Watersnake		X	RA

DISCUSSION

My study evaluated changes in the herpetofauna of Aguascalientes over a period of almost 50 years, by using historical data and landscape photographs in the context of intensive re-sampling. Of the only two species missing in our recent surveys, *Craugastor augusti* is a frog with cryptic behavior and ecology (Goldberg and Schwalbe 2004), and I have found it in previous years in the Sierra Fría, so it is still present in the state. The first specimen of *Holbrookia maculata* in Aguascalientes was collected in 1959, several individuals were observed and one collected in 1971 (Anderson and Lidicker 1963; McCranie and Wilson 2001), and its absence in our recent surveys is puzzling, especially because this is a conspicuous species in other localities where it does occur (Stebbins 2003). The *H. maculata* locality is in the middle of the first irrigation district in México, and its establishment, with the subsequent increase in agricultural activities and change in land use, might explain the absence of *H. maculata*. Perhaps this species is more vulnerable than previously thought, as elsewhere it has disappeared even where it was abundant as recently as 1982 (Taggart 2006). Although I can not confidently assert that the species is eradicated from Aguascalientes, I encourage studies focused on this species to determine with certainty its status in the state.

The taxonomic status of the several species of *Lithobates* (Frost et al. 2006) in the southern part of the Mexican Plateau has been historically in flux, and older references to *L. pipiens* may have pertained to several species in the *L. pipiens* complex (Hillis 1988). The specimens found in Aguascalientes in 1958 and 1959 seem to be part of what is now known as the *Stertirana* complex (Hillis and Wilcox 2005) and most similar to *L. montezumae*, a species common throughout the state and that we found in 2004.

Several new records of amphibians and reptiles for Aguascalientes resulted from our 2004 and other recent surveys, and clearly, the rate of species discovery has not yet reached a plateau. That we encountered more species in 2004 than were found in 1958-1959 cannot be attributed to the improvement of habitat conditions in subsequent decades, and invasions seem unlikely. Instead, I think the differences reflect the MVZ expeditions' preoccupation with mammals and birds, whereas we focused exclusively on amphibians and reptiles; they recorded 40 species of birds and 39 species of mammals, and contemporary studies might well document changes in those groups relative to the MVZ baseline collections.

A common criticism of comparative studies of survey data is that they could easily be biased by high environmental variability among years. This problem is especially relevant for amphibians and reptiles because their daily and seasonal activities are heavily influenced by environmental conditions. In Aguascalientes, as in many other regions, the number of species found in dry years is typically small compared to those with high precipitation. Fortunately for my comparisons, both 1959 and 2004 were years with high levels of precipitation following a period of drier years in Aguascalientes (Sosa Ramírez 1998).

Figure 3.3 Selected original and recent landscape photographs. They correspond to Site 1 El Tigre (top), Site 5 Sierra Fría (middle), and Site 13 Los Caños (bottom). Recurrent issues in these and other photographs are evident: growth of populated places, replacement of natural vegetation by agricultural fields, appearance of roads and urban vegetation (top and bottom), and the recovery of the oak forests in Sierra Fría (middle).

The original and new landscape photographs provide a glimpse of historical changes at a geographically and ecologically diverse set of localities, and have important implications for conservation planning. My findings reveal extensive corn plantations replacing thorn shrub vegetation, guava fruit plantations displacing large areas in the southwestern portion of the state that were formerly tropical deciduous forest, and widespread urbanization. These habitat modifications undoubtedly diminish the likelihood that many species of vertebrates can persist in the long term. Photographs from Sierra Fría, the largest remaining forests in Aguascalientes, show an increase in oak (*Quercus sp.*) coverage, with much of the change visible as young trees. This corroborates previous research comparing aerial photographs that revealed a replacement of pines and pine-oak forests by *Juniperus deppeana* and other arbustive species after the intensive logging extraction in Sierra Fría between 1920 and 1950 (Minnich et al. 1994). The consequences of these changes for faunal communities remain to be explored.

Tropical deciduous forest hosts high levels of biological endemicity, is globally endangered (Flores-Villela and Gerez 1994), and its persistence in Aguascalientes might be threatened. This vegetation type covers a small area in the southwestern part of the state, harbors elements of the humid Pacific Coast biota, and unfortunately, as shown in the photographs, has recently been extensively displaced by fruit plantations. Otherwise widely distributed species that reach Aguascalientes only in tropical deciduous forest, like the colubrid snakes *Drymarchon melanurus* (Central American Indigo Snake), *Oxybelis aeneus* (Brown Vinesnake), and *Senticolis triaspis* (Green Ratsnake) will likely become locally extinct when this habitat type disappears.

Ecological and natural history data suggest that certain species are particularly vulnerable to extinction in Aguascalientes. Among amphibians, *Smilisca dentata* (Upland Burrowing Treefrog) has a highly restricted distribution and is present only in the southern tip of the state and nearby areas in northern Jalisco; the Aguascalientes locality is heavily used by cattle and there are plans to subdivide and sell the land (Quintero Díaz, pers. comm.). The plethodontid salamander *Pseudoeurycea bellii*, was only discovered in Aguascalientes in 2003 in the Sierra Fría after being missed in previous years of work; its presence was predicted (McCranie and Wilson 2001), and perhaps this species is particularly secretive or unusually rare there. Most Mexican ambystomatids are declining due to pollution, habitat modification, loss of preferred habitats, and widespread introduction of exotic fishes for human consumption (Huacuz Elías 2001). While pollution and intense farming don't seem to threaten *Ambystoma tigrinum* (Tiger Salamander) in New México, USA (Degenhardt et al. 1996), the effects of those impacts and non-native predators have not been evaluated in Aguascalientes.

Among reptiles in Aguascalientes, *Phrynosoma modestum* (Round-tailed Horned Lizard) is at the southernmost limit of its distribution (Sherbrooke 2003) and known from a single specimen (McCranie and Wilson 2001) in the northeastern part of the state; several attempts to locate additional specimens have been unsuccessful. *Drymarchon melanurus* is large, active and in Aguascalientes associated with humid environments in tropical deciduous forest; the first specimen dates to 1980 (McCranie 1980) and a second one was captured in 2005 (Quintero-Díaz, pers. comm.). *Crotalus pricei* (Twin Spotted Rattlesnake) is known for the state from only three specimens, reaches the southern tip of its distribution there, and although it occurs widely in the Sierra Madre Occidental and Sierra Madre Oriental, the population in Aguascalientes is isolated and has proven elusive despite intensive efforts in the last decade. Similarly, the distribution of *C. aquilus* (Queretaran Dusky Rattlesnake) barely reaches Aguascalientes through the Sierra del Laurel in the southwestern part of the state; this species is primarily associated with the Trans-volcanic belt in central México.

Those species of amphibians and reptiles recorded by at most a few specimens emphasize that Aguascalientes, despite its small size, encompasses the distributional limits of several species due to the junction of several diverse physiographical regions. The study of peripheral populations and comparison with those in the core of the distribution ranges are critical in the conservation efforts of endangered species (Channell and Lomolino 2000), and emphasizes the importance of the state for the biogeography and conservation of Mexican herpetofauna.

Aguascalientes has between 60% and 80% of its surface altered by human activity (Flores-Villela and Gerez 1994), and unfortunately this mirrors the global environmental crisis. My results call attention to high rates of change as natural environments are displaced by anthropogenic activities, as well as a key way that scientific collections, given their intrinsically historical nature, can aid in conservation. More than a century ago, Joseph Grinnell at the MVZ envisioned this role for natural history museums (Shaffer et al. 1998), and I urge increased support for field research in the service of protecting nature (Greene 2005).

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