

Toward a Periodic Table of Niches, or Exploring the Lizard Niche Hypervolume

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ABSTRACT: Widespread niche convergence suggests that species can be organized according to functional trait combinations to create a framework analogous to a periodic table. We compiled ecological data for lizards to examine patterns of global and regional niche diversification, and we used multivariate statistical approaches to develop the beginnings for a periodic table of niches. Data (50+ variables) for five major niche dimensions (habitat, diet, life history, metabolism, defense) were compiled for 134 species of lizards representing 24 of the 38 extant families. Principal coordinates analyses were performed on niche dimensional data sets, and species scores for the first three axes were used as input for a principal components analysis to ordinate species in continuous niche space and for a regression tree analysis to separate species into discrete niche categories. Three-dimensional models facilitate exploration of species positions in relation to major gradients within the niche hypervolume. The first gradient loads on body size, foraging mode, and clutch size. The second was influenced by metabolism and terrestrial versus arboreal microhabitat. The third was influenced by activity time, life history, and diet. Natural dichotomies are activity time, foraging mode, parity mode, and habitat. Regression tree analysis identified 103 cases of extreme niche conservatism within clades and 100 convergences between clades. Extending this approach to other taxa should lead to a wider understanding of niche evolution.

Keywords: evolutionary convergence, lizard ecology, niche diversification, niche dimensionality, niche hypervolume, clade niche breadth and overlap.

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Dedication

I predict there will be erected a two or three way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form for organisms of type A, in environments of structure B, such and such relationships will hold. (MacArthur 1972)

Introduction

The niche, a central concept in ecology, describes not only the environmental conditions required for survival and positive fitness but also the organism's potential impact on its environment. The niche concept has had a long and sometimes controversial history in ecology (Chase and Leibold 2003; Colwell and Rangel 2009). Some ecologists even have argued against use of the term because the word has been used in so many different ways (Margalef 1968; Williamson 1972). The first ecologist to use the word was Grinnell (1917), for whom the niche included everything that affected the existence of a species at a given location, including abiotic factors (temperature, rainfall, geomorphology, nest sites, and shelter) as well as biotic factors (food, competitors, mutualists, parasites, predators, and potential mates). Later, Grinnell (1928) linked the niche to the concept of ecological equivalents, convergent species with similar ecologies found in different geographic regions.

Elton (1927, p. 64) defined the niche as “the animal's place in its community, its relations to food and enemies.” Elton imagined a behavioral niche, comparing a species' niche to its profession: “When an ecologist says ‘there goes a badger’ he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if

he had said ‘there goes the vicar.’” Elton’s functional niche is essentially a measure of a population’s phenotype.

Perhaps the most influential treatment of the niche concept was that of Hutchinson (1957), who proposed a hypervolume definition encompassing all environmental conditions under which a given target species has positive population growth. Hutchinson distinguished a fundamental niche—representing the potential space occupied in the absence of negative effects from other species—from a narrower realized niche when such effects are present. In accordance with this Hutchinsonian concept, niches have often been modeled as series of bell-shaped resource utilization curves, each corresponding to a particular resource or niche dimension (MacArthur and Levins 1967; MacArthur 1970; Pianka 1976; Schoener 1977).

Regardless of which concept is adopted, niches are multi-dimensional and dynamic, responding to temporal and spatial variation in abiotic conditions, resources, and competitor and predator populations, among other things (Hutchinson 1957; Pianka 1976; Schoener 1977; Chase and Leibold 2003; Colwell and Rangel 2009; Holt 2009; Goodyear and Pianka 2011). This complexity poses a great challenge to empirical efforts to describe and compare ecological niches. Nevertheless, the multitude of known or suspected convergences in many taxa across the globe suggests that construction of a niche scheme—a framework analogous to chemistry’s periodic table of elements—might be possible (Pianka 1974). Countering criticism of the idea of periodic tables in ecology (Steffen 1996), Winemiller et al. (2015) argued that ecologists, natural resource managers, and conservationists already use a variety of methods that rely on functional traits and niche classification criteria, and therefore, standardized methods for creating niche frameworks need to be explored. They proposed an approach that uses functional trait data organized according to five fundamental niche dimensions to produce two types of niche classification schemes: one that facilitates analysis of species relationships within the multivariate niche space (continuous periodic tables) and one that classifies species into niche categories (discrete periodic tables). Given the multidimensional nature of niches, the framework proposed by Winemiller et al. (2015) is not structurally equivalent to the periodic table of elements; rather, it is conceptually analogous.

As a first step toward this complex challenge of creating a niche ordination and classification framework for a major taxonomic group, we analyze lizard niches using extensive ecological data gathered by E. R. Pianka and L. J. Vitt during the course of lizard community ecology research conducted in diverse habitats on four continents over the past half-century. Our analysis treats species’ niches as static entities, an obviously false assumption but one that allows for broad comparisons to facilitate development of a general theory of niches. We employ the approaches recently

proposed by Winemiller et al. (2015) that use multivariate statistics for species ordination within niche space and species classification based on components of niche dimensional sets.

Of the 10,272 extant reptile species (birds excluded), 9,905 (96.4%) are squamates. Snakes are represented by 3,576 species (34.7% of reptiles) and amphisbaenians by 193 species (1.9% of reptiles). Although some lizards (such as the pygopodid *Lialis*) are ecological analogs of snakes, we could not include snakes or amphisbaenians because complete data for all variables and niche dimensions required for this study are lacking. The remaining squamates are referred to as lizards, even though both snakes (Serpentes) and amphisbaenians (Amphisbaenia) are nested among the currently recognized 38 lizard families (Uetz 2016b). Lizards are currently estimated to comprise 63.4% of all reptiles and clearly are among the most taxonomically and ecologically diverse groups of tetrapod vertebrates. Except in very cold regions, lizards occur virtually anywhere that still contains relatively undisturbed natural habitats, and a few species even persist in degraded areas. Similar to other ectotherms, lizards obtain their body heat solely from the external environment, as opposed to endotherms (such as birds and mammals) that produce their own heat internally by means of oxidative metabolism. Moreover, along with other ectotherms such as insects, lizards are low-energy animals (Pough 1980). Bennett and Nagy (1977, p. 700) underscore the great “economy of the saurian mode of life” by pointing out that “one day’s food supply for a small bird will last a lizard of the same body size more than a month.” Ectothermy has distinct advantages over endothermy under harsh and unpredictable conditions (Schall and Pianka 1978); by means of this thermal tactic, lizards can conserve water and energy by becoming inactive during the heat of midday, during resource shortages, or whenever difficult physical conditions occur (such as during heat waves or droughts). Endotherms must endure these inhospitable periods at a substantially higher metabolic cost or migrate to more hospitable regions. Ectothermy thus confers lizards with an ability to capitalize on scant and unpredictable food supplies, presumably giving them a competitive advantage over endotherms in resource-scarce and unpredictable environments (Dunham 1978).

Most lizards are insectivorous and hence attain relatively high positions in the trophic structure of their communities: as a result of this and the fact that lizards are often locally abundant, competition for limited resources is probably common and a significant driver of niche diversification (Pianka 1986, 1993). Lizards usually ingest prey items intact, greatly facilitating stomach contents analysis for estimation of diet. Indeed, lizards have proven to be exceedingly tractable subjects for ecological research (Huey et al. 1983; Pianka 1986; Vitt and Pianka 1994; Vitt et al. 2003;

Losos 2009). According to Schoener (1977, p. 121), “Lizards have not only proven ecologically exciting in their own right, but they may well become paradigmatic for ecology as a whole.”

In a review of the lizard ecological niche, Pianka (1993) emphasized five major dimensions: space, time, food, reproduction, and escape. Following the approach proposed by Winemiller et al. (2015) for constructing what they termed “periodic tables of niches,” analogous to the periodic table of elements as envisioned by Pianka (1974), we compiled a data set from the life’s work of E. R. Pianka and L. J. Vitt on the ecology of desert and Neotropical lizards. The data set includes variables associated with functional morphology, habitat and microhabitat, anatomy, foraging mode, diet, life history, diel activity, thermoregulation, and defensive tactics. Overall, 134 lizard species representing 24 of the 38 extant families (Uetz 2016a) were analyzed using multivariate methods for ordination and classification.

Lizard niche dimensions appear to evolve in concert; for example, recent evidence indicates synchronous transitions in life history and trophic traits. Some lizard clades reveal great dietary or life-history diversification, whereas others do not. The families in which Mesquita et al. (2016a) found phylogenetic structure for life-history traits were nearly the same as those identified by Vitt and Pianka (2005) as having phylogenetic structure with respect to diet, with a few exceptions, such as Anguillidae. In addition, the families for which Mesquita et al. (2016) did not detect phylogenetic structure also were similar, mainly families within the Gekota (Vitt et al. 2003; Vitt and Pianka 2005), even though a different phylogenetic hypothesis was used. These similarities further suggest that many important functional traits are correlated and coevolved (Vitt and Congdon 1978; Huey and Pianka 1981; Shine and Schwarzkopf 1992; Pianka 1993; Vitt et al. 2003; Vitt and Pianka 2005; Cooper 2007; Reilly et al. 2007; Goodman et al. 2009; Pyron and Burbrink 2009; Kearney et al. 2010). These observations hint as to how to construct a periodic table of niches. If dietary and life-history dimensions covary, much of the variation in lizard ecology might be captured within a space of relatively low dimensionality. Combined with a thermoregulator-thermoconformer axis and the trade-offs between foraging mode and reproductive tactics (Vitt and Congdon 1978; Huey and Pianka 1981), we attempt to develop a general theory for the evolution of niche space occupied by lizards. Different ecological requirements may lead to different organismal designs through natural selection, generating specialized ecomorphs (Brown and Wilson 1956; Hutchinson 1959, 1978; Williams 1972, 1983; Losos 2009). However, some patterns among form-function relationships are repeated across divergent lineages representing evolutionary convergence (Winemiller et al. 2015). These can be viewed as species of different lineages clustering

around adaptive peaks within the selection landscape. Our challenge is to reduce dimensionality to identify lizard taxa that have converged in a multidimensional niche space, signaling convergent evolution.

We compare and evaluate two hypotheses (fig. 1). The null hypothesis (H_1) is that clades evolve to fill contiguous regions in niche space, which implies that niche conservatism is prevalent during evolution and niche diversification is more or less random and evenly distributed with regard to clades and zoogeographic regions (Holt 1996; Wiens et al. 2010). The alternative niche convergence hypothesis (H_2) states that some lineages depart from other members of their own clade and evolve characteristics of other clades, and this process is driven by similar adaptive responses to similar selective regimes in different places and/or time periods (Grinnell 1928; Luke 1986; Revell et al. 2007; Edwards 2014; Blom et al. 2016; Edwards et al. 2016).

Specific goals of this study are (1) to identify key components of lizard niches and to compile data for as many lizard species as possible to build a global data set based on standard criteria for as many variables as possible, representing the five major niche dimensions proposed by Pianka (1993) and Winemiller et al. (2015); (2) to analyze these data to reduce dimensionality for construction of a niche classification scheme (i.e., ecological analog of the periodic table of elements); (3) to examine relationships of niche dimensional gradients to one another; (4) to compare regional differences in lizard niche diversification; (5) to compare niche diversification of major phylogenetic lineages; and (6) to identify convergent species pairs.

Methods

Data

Most data used here were collected by E. R. Pianka (71 desert species) and L. J. Vitt (53 Neotropical species) over many decades. We searched the literature for comparable data for other species but were able to extract complete data for all five major niche dimensions from only 10 additional species. Although our sample is relatively small, it has taken two lifetimes of dedicated fieldwork to collect this amount of detailed information for so many species. Data were obtained on all lizards of both sexes (with the exception of certain life-history variables) and age categories. E. R. Pianka and L. J. Vitt used the same criteria to take lizard measurements in their studies. Some variables had to be excluded from analyses when discrepancies occurred. Although several sources of variation are associated with the data used (e.g., sex bias, age, seasonal differences), consistency in the methods used over the years and between E. R. Pianka and L. J. Vitt allowed us to construct a database of unique characteristics. Some variables are continuous, and others are

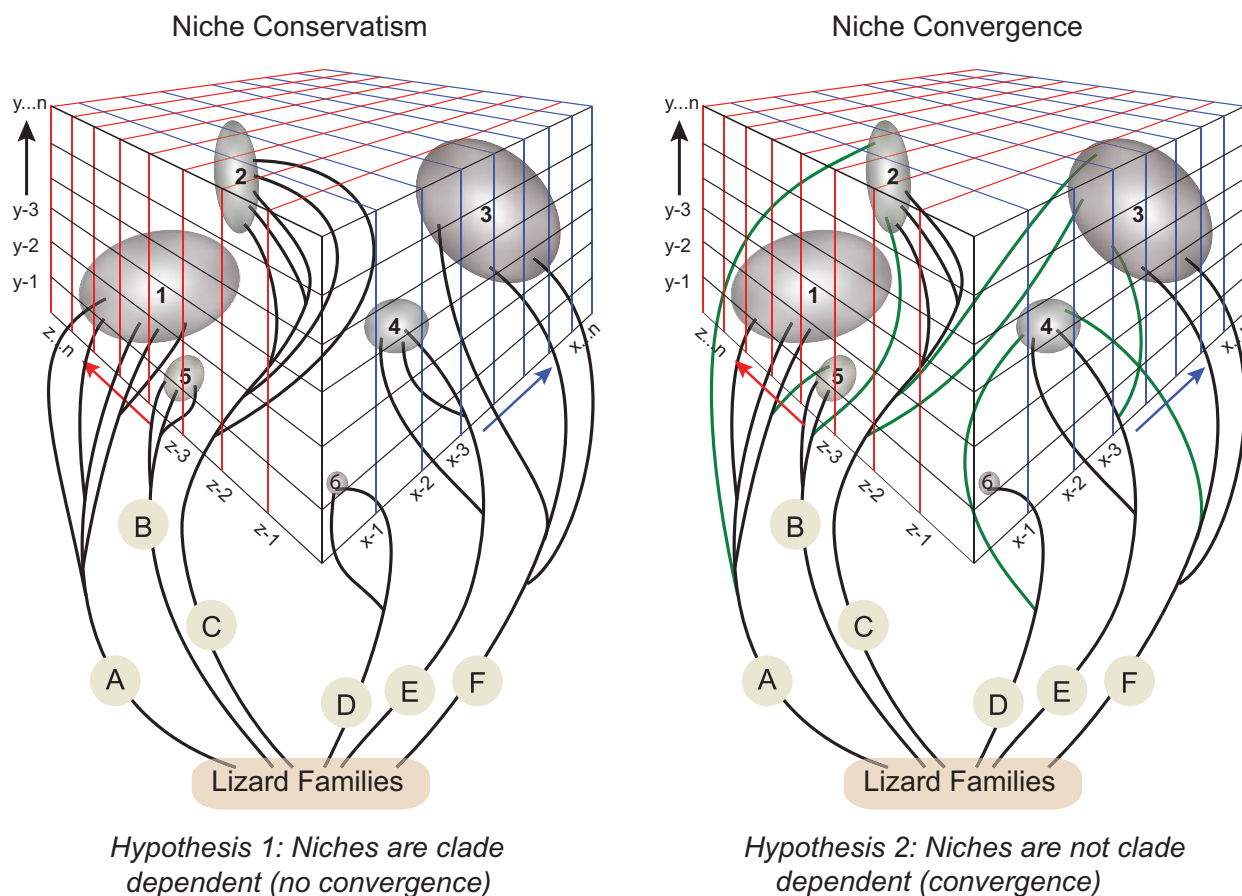


Figure 1: *Left, H₁:* niche conservatism. Clades map directly onto contiguous regions of niche space. *Right, H₂:* niche convergence. Some lineages (green lines) diverge from other members of their own clade and converge on members of other clades. Evidence for H₂ supports the idea of niche periodicity, whereby multiple species (including phylogenetically divergent taxa) occupy the same niche within the niche classification scheme.

discrete. The authors agreed on criteria to classify categorical variables, leading to standardized criteria for all included species. Among the 50+ total independent variables, variables with direct relationships to a given major niche dimension were selected and assembled into five data sets for analysis as follows.

*Habitat and Microhabitat: Anatomical
Correlates of Ecology*

Lizards inhabit a broad range of habitats, including deserts, grasslands, chaparral, rock outcrops, deciduous forest, and rain forest. Others are semiaquatic. Many lizards are diurnal, but most geckos are nocturnal. Some pygopodids are crepuscular. Certain species of lizards are climbers, others are subterranean or live in leaf litter, whereas others are surface dwellers (although most lizards exploit burrows as retreats). Among the latter, some tend to be found in open areas, whereas others frequent the edges of vegetation. Be-

cause such spatial and temporal differences limit the frequency of encounters between species as well as expose them to differing food resources, any potential effects of interspecific competition would tend to be ameliorated. Indeed, avoidance of competition is perhaps the most plausible basis for the evolution and maintenance of such microhabitat differences.

Traits allowing for more efficient use of resources may be shaped by natural selection to avoid competition among closely related sympatric species and may generate specialized ecomorphs (Brown and Wilson 1956; Hutchinson 1959, 1978; Williams 1972, 1983; Losos 2009). Several ecomorphotypes have been proposed for species adapted to various habitats (Vanhooydonck and Van Damme 1999). Ground-dwelling species tend to have laterally compressed bodies and long limbs that provide greater lateral flexion, enhance maneuverability, and allow them to reach higher speeds (Snyder 1954; Van Damme et al. 1997). On the other hand, with the exception of chameleons and other lizards with ad-

hesive structures in their feet, species that climb tend to be dorsoventrally compressed, which lowers the body's center of gravity and reduces the chances of toppling back while climbing (Jaksić et al. 1980; Pounds 1988; Sinervo and Losos 1991). Chameleons differ from other arboreal lizards in having highly prehensile tails and zygodactylus feet, allowing them to securely hold on to tree and shrub branches. This ability to grasp branches allows them to move about in arboreal habitats even though their center of gravity is high. In saxicolous species, a flat body could also allow them to find refuge in rock cracks and crevices (Vitt 1981; Miles 1994; Revell et al. 2007; Goodman et al. 2009). Lizards with longer hindlegs spend more time in the open away from cover and can run faster than lizards with shorter legs (Pianka 1969, 1986). Active foragers have longer tails and more slender builds than ambush species. Fossorial species are elongate with reduced limbs and short tails.

Even though generalizations about anatomy and performance may not apply to every lizard species (see, e.g., Jaksić et al. 1980; Zaaf et al. 2001), morphologies nonetheless reflect habitat use, diet, and other ecological traits. Ecomorphological patterns therefore facilitate ecological predictions because anatomical data can serve as surrogates for ecological measurements. Morphological measures can often be estimated more objectively than ecological parameters. Morphometrics may represent average long-term responses to natural selection and hence may reflect environmental conditions better than direct measurements of immediate ecological conditions (Ricklefs et al. 1981).

We use five major microhabitat categories, as follows: fossorial, terrestrial, arboreal, saxicolous (rock dwelling), and semiaquatic. Semifossorial and semiarboreal species were scored in two of the five categories. Eight continuous anatomical variables were analyzed: mean snout-vent length (SVL), average length of unbroken tail, cubic root of body weight in grams, head length, head width, head depth, foreleg length, and hindleg length. These eight variables are highly correlated (average $r = 0.79$). Because data on body thickness were incomplete, we used the cubic root of body weight as a proxy for body thickness.

Trophic Dimension: Foraging Mode and Diet

Lizards forage in two distinctly different ways (Pianka 1966; Huey and Pianka 1981; Perry 1999; Reilly et al. 2007), which strongly affect lizard diets (Vitt and Pianka 2005). In the sit-and-wait mode, a predator waits in one place until a moving prey comes by and then ambushes the prey; in the widely foraging mode, a lizard actively searches out its prey. The second strategy requires greater exposure and energy expenditure than the first. The success of the sit-and-wait tactic usually depends on one or more of three conditions: fairly high prey density, high prey mobility, and low predator energy re-

quirements. The widely foraging tactic also depends on prey density and mobility and on the predator's energy needs, but here the distribution of prey in space and the predator's searching abilities assume paramount importance. Whereas ambush foragers rely on crypsis to avoid predators, active foragers attract the attention of potential predators because they are constantly on the move and therefore must be alert and rely on speed and agility for escape. Vitt and Congdon (1978) and Huey and Pianka (1981) discussed several correlates of these foraging modes. We included foraging mode as a component of the trophic niche dimension, scoring iguanians as sit-and-wait ambush predators and most anguimorphs (with the exception of Kalahari lacertids [some species forage by ambush]) as widely foraging active predators. Geckos and herbivores plus a few other taxa were scored using both sit-and-wait and widely foraging as intermediate or mixed foragers.

Prey categories. Volumetric dietary data were obtained from Vitt et al. (2003). To standardize the global dietary data set, data were reduced to seven major functional categories based on prior studies, as follows: (1) ants; (2) termites; (3) arachnids; (4) large insects (beetles, bugs, roaches, and orthopterans); (5) insect larvae, pupae, and eggs; (6) vertebrates; and (7) plants. These seven categories represented more than 80% of the total volume consumed by each lizard species included in this study. Including three discrete foraging modes (ambush, active, intermediate), the trophic dimension thus consists of nine to 10 variables, of which the seven prey categories are continuous variables.

Life History

Lizard life histories are multifaceted and have received a great deal of attention (Tinkle et al. 1970; Dunham and Miles 1985; Dunham et al. 1988; Vitt 1992), most recently by Mesquita et al. (2015, 2016a) and references therein. Here we consider the following nine female life-history variables.

Variable 1. Clutch or litter size, a continuous variable. Clutch size is the average number of eggs deposited or young produced at one time. In all anoles, some geckos, and some gymnophthalmids, clutch size is fixed at 1; in other geckos and gymnophthalmids, clutch size is 2. Some anoles contain two eggs (one in each oviduct) but deposit them at different times.

Variable 2. Relative clutch mass, a continuous variable. Relative clutch mass is clutch or litter mass divided by total female mass, including eggs and/or babies (Andrews and Rand 1974; Vitt and Price 1982).

Variable 3. Clutch frequency, a categorical variable. Few data exist for most species, so we use reasonable categories

based on what we see in the lizards. For example, if a female anole has two oviductal eggs (different stages) and two enlarged ovarian follicles (different size but vitellogenic), then four clutches is a minimal estimate. Our discrete categories are therefore 1, 2, 3, and 4, with the proviso that these are minimal estimates.

Clutch frequency is difficult to estimate, and accurate data can be derived only from capture-recapture studies (Tinkle 1969). Because our data are based on necropsies of lizards collected for ecological studies, we base our estimates of clutch frequency on whether individuals contain evidence of one, two, three, or four or more clutches/litters. A few species are biennial and thus produce less than one clutch per year. Lizards in temperate zones have restricted breeding seasons (temperature and season length are major limiting factors) and produce one or two clutches/litters per year as a consequence. Lizards in tropical regions experience extended breeding seasons (thermally) but may be limited by wet-dry seasonality, although wet-dry seasonality may affect lizard species in the same habitat quite differently (James and Shine 1985; Vitt 1992). Within tropical lizard populations, necropsy estimates of clutch frequency can vary considerably. Tropical anoles provide a good example, with individuals showing evidence of as few as one clutch (single oviductal egg or enlarged follicle) to as many as four (allochronic ovulation limiting clutch size to one egg; an individual female can contain a vitellogenic follicle in each ovary of different sizes as well as an egg in each oviduct but in different stages of shell development, thus indicating at least four clutches). To minimize underestimation of clutch frequency, we use the maximum number of possible clutches on the basis of our necropsy data. Thus, in a population of anoles, for example, even though many females might show evidence of only two or three clutches, if several individuals showed evidence of four clutches, then we estimate the number of clutches to be four or more. Although this categorization likely underestimates the number of clutches for many tropical species (e.g., some *Anolis* can produce an egg as frequently as every 7 days; Andrews 1985), it provides a realistic conservative estimate of the number of clutches per season. Consequently, we assigned lizard species to one of the following five categories: 0.5, less than one clutch/litter per year (biennial); 1, one clutch/litter per year; 2, two clutches per year; 3, three clutches per year; 4, four or more clutches per year.

Variable 4. Offspring size, using SVL (investment per progeny), a continuous variable.

Variable 5. Female SVL at maturity, a continuous variable.

Variable 6. Parity mode (oviparous or viviparous), a discrete variable.

Variable 7. Mean SVL of adult females, a continuous variable.

Variable 8. Mean weight of adult females, a continuous variable.

Variable 9. Sexual versus asexual (parthenogenetic), a discrete variable.

Metabolism: Thermoregulation

Huey and Slatkin (1976) identified the slope of the regression of active body temperature on ambient temperature as a measure of the degree to which a given lizard species is a thermoconformer versus a thermoregulator. For any given species, a regression of body temperatures on ambient temperatures produces an equation for a least squares straight line that best fits the data. Pianka (1986, 1993) suggested that the slope and intercept of these regressions are measures of microhabitat and time of activity and, as such, represent useful surrogates that inform us about a lizard's ecology. The slope of such regressions can be used as a unidimensional indicator of time and place of activity. Most but not all diurnal lizards tend to be thermoregulators, and nocturnal species are thermoconformers; however, all degrees of intermediate thermoregulatory tactics also are observed, and some tropical forest-dwelling diurnal lizards are thermoconformers. We compiled additional data for mean ambient air or substrate temperature and active body temperature, making a total of four continuous variables. Three discrete variables based on diel time of activity (diurnal, crepuscular, or nocturnal) were also included in this niche dimension. Species with crepuscular times of activity were scored in both the diurnal and the nocturnal columns.

Defense Tactics

Many lizard species, especially ambush foragers, rely on crypsis to evade detection. Crypsis can take many forms, including background matching associated with coloration and/or pattern and lack of movement. Others, such as active foragers, attract attention because of constant motion and therefore must remain alert and wary, relying mostly on speed and agility to escape predator attacks (Huey and Pianka 1981). Many but not all lizard species can shed their tail in a process known as autotomy (Arnold 1984; Zani 1996). Some lizard species have osteoderms in their scales (Strahm and Schwartz 1977), whereas others protect themselves with spines (Wiens and Reeder 1997). Some unique defense strategies were also included: Australian *Strophurus* geckos squirt noxious sticky mucous from glands in their tails (Rosenberg and Russell 1980). *Liolaemus lutzae* feign death (thanatosis) when captured (Rocha 1993), and the pygopodid *Delma*

butleri leaps energetically when disturbed (saltation; Bauer 1986; Turner 2007). We recognize the following 14 discrete defensive variables: armor (including osteoderms), crypsis, color change, tail colors, mimicry, saltation, thanatosis, autotomy, spines, mucous, bite, flee, threat, and venom, all of which are discrete variables.

In summary, variables included in each of the five dimensional data sets are as follows. Numbers in parentheses are the total number of niche variables in a given dimension. Some are ranges because we used double scoring to represent semiarboreal, semifossorial, crepuscular, and mixed foraging categories. Raw data used in these analyses are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.db901> (Pianka et al. 2017).

Habitat (13–15). We recognize five discrete microhabitat categories: fossorial, terrestrial, arboreal, saxicolous (rock dwelling), and semiaquatic. Semifossorial and semiarboreal species were scored in two categories, making a total of seven discrete variables. Eight continuous anatomical variables included mean SVL, average length of unbroken tail, cubic root transform of body weight, head length, head width, head depth, foreleg length, and hindleg length.

Trophic (9–10). These variables represent foraging mode (three discrete variables) and proportional representation of seven prey categories by volume (seven continuous variables).

Life History (9). These variables are mixed and include both discrete and continuous variables, including adult female SVL and weight, clutch or litter size, relative clutch mass, clutch frequency, progeny size, parity mode (oviparous or viviparous), relative clutch mass, and parthenogenesis.

Metabolism (6–7). These variables include thermoregulation (mean air and body temperatures of active lizards and the slope and intercept of regressions of active body temperature on ambient temperature, all continuous variables). We also include diurnal versus nocturnal as well as crepuscular time of activity (discrete variables).

Defensive Tactics (14). These variables include armor, crypsis, tail autotomy, spiny body armor, color change, tail colors, mimicry, saltation, thanatosis, mucous, bite, flee, threat, and venom, all of which are discrete variables.

Statistical Analyses

Each of the five data sets was analyzed using principal coordinates analysis (PCoA) based on Gower distances to derive dominant niche gradients for each dimension. The 24 variables that scale as real numbers on a continuum (e.g., SVL) were log transformed and standardized by z-transformation.

Thirty other variables are discrete and scale as cardinal (e.g., clutch frequency) or ordinal (e.g., parity) numbers. With such a mixture of variables, Euclidean distances and standard principal components analysis (PCA) could not be used. Therefore, for each data set we calculated Gower (1966) distances using the R package cluster (Suzuki and Shimodaira 2006) and then performed a PCoA using the package vegan (Oksanen et al. 2016) for R (R Development Core Team 2016). Then a PCA was performed to ordinate species within continuous niche space using species scores on the first three components from each of the five PCoAs. Following the methodology of Winemiller et al. (2015), species scores on the first three components from each of the five PCoAs were used as response variables in a regression tree analysis to generate a discrete niche classification for each dimension. We used the package rpart to make regression trees (Therneau et al. 2015) and pruned trees conservatively using the 1 SE rule. Results for each dimension were then combined to create a discrete classification based on all dimensions.

When evaluating niche convergence based on regression tree results, one must bear in mind that convergence is always relative (i.e., relative to the original sets of independent variables compiled, relative to the precision and accuracy of measurements of those variables, relative to the criteria selected for doing the regression tree analysis, and relative to the criterion for claiming convergence vs. nonconvergence). Regression tree analysis assigns each species a category on each niche dimension and allows one to identify matches that correspond to species assigned the same category. This method organizes variation in gradient space defined by trait combinations into a discrete classification system and provides a means to identify similar species. Species can match in one, two, three, four, or five niche dimensions. For a conservative criterion to infer niche similarity, we identified those pairs of species that matched in four or five of the dimensions. Species belonging to the same clade and faunal continent that matched according to this criterion were considered cases of niche conservatism. Matches among species belonging to distantly related taxa and different geographical units were considered examples of convergent evolution. This definition will overestimate occurrence of conservatism (unless members of families or genera never evolve similar niches from different ancestral character states). Of course, the possibility exists that members of families or genera could evolve similar niches independently, especially if the family or genus is widespread.

To facilitate exploration of species relationships within the multidimensional niche hypervolume, we created a set of interactive, rotatable three-dimensional (3D) plots (<http://www.zo.utexas.edu/faculty/pianka/modelsMK/index.html>) using package rgl (Adler et al. 2017). Using these 3D plots, a viewer can (1) examine species ordination within the space defined by the first three axes from the PCA that was done

using the PCoA scores as input, (2) highlight some convergent species pairs of ecological equivalents, (3) view each of the five natural trait group dichotomies, and (4) examine species' positions in 3D niche space by geographic region of origin. PCoA ordination plots for each of the five dimensional data sets also can be explored separately using data in supplementary material C1 (available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.db901> [Pianka et al. 2017]) and table A1 (available online).

We tested whether the number of species pairs found using regression tree analysis was significantly different than expected by chance. A null model was developed, where species were randomly assigned to niche dimensions from a uniform distribution in 1,000 randomizations. Pairs of species matching in four or more niche dimensions were extracted for each run, and the resulting distribution of random pairs was then contrasted to the observed number of species pairs through a Wilcoxon test.

Results

The first PCoA axis for the habitat dimension accounted for 36.8% of the variation in that data set (axis 2 = 26.41%, axis 3 = 11.5%). Anatomical variables were highly intercorrelated (mean $r = 0.79$) and defined gradients along groups of species defined by habitat. For the trophic dimension, the first PCoA axis modeled 43.16% of the variation (first three axes captured 68.97% of total variation). Three groups of species formed along this axis according to foraging mode. The first two PCoAs of the life-history dimension captured 62.69% of variation, grouping species mainly by clutch frequency and clutch size. The third axis was associated with reproductive mode. The first axis from the PCoA of the metabolic dimension data set accounted for 74.79% of total variation (axis 2 = 9.91%, axis 3 = 4.77%). Species grouped mainly by diel activity. Diurnal species are arranged along a thermoregulator/thermoconformer gradient. For variables associated with defensive tactics, the first two axes from PCoA captured 55.58% of the variation in the data set (table 1). Species relying on passive defensive methods (such

as crypsis and color change) are opposed to those that actively escape by fleeing. Also, species with caudal autotomy were opposed to aggressive species that use threat and bite as main defensive tactics.

PCA was performed using species loadings on the first three axes from each of the five PCoAs (tables 1, A1). Species' scores on the first two PCA axes were plotted to ordinate species within a continuous two-dimensional ordination of lizard niches (fig. 2). The first axis is dominated by size and foraging mode, whereas the second corresponds to terrestrial versus arboreal microhabitat. The third axis (fig. 3) represents diurnal versus nocturnal time of activity and captures 15.49% more of the variance for a total of 61.71%.

A discrete ordination from regression tree analysis identified 100 convergent pairs in different families from different continents with matches on most dimensions (fig. 4) as well as 103 niche conservatisms (fig. 4). This is significantly more than the combined number of matched pairs expected when species are randomly assigned niche categories from a uniform distribution (Wilcoxon rank sum test; $W = 328$, $P = .04$).

Discussion

Lizard niches reveal a marked diurnal-nocturnal separation, which is largely associated with thermal strategies of the metabolic niche dimension. Considerable diversity in trophic, life history, defense, and habitat strategies was observed within both diurnal and nocturnal lizards. Niche conservatism is observed when closely related species have similar niches, whereas convergence has occurred when species from different clades have similar niches. Widespread niche conservatism is evidenced by numerous phylogenetic clusters within niche space; that is, many closely related species are clustered within a restricted region of lizard niche ordination space (derived from PCA) that represents continuous niche variation (figs. 2, 3). Niche conservatism also is evident when species from the same lineage match for categories in four or five of the niche dimensions according to the discrete niche representation derived from regression

Table 1: Summary of the percentage of total variation captured by the first three axes from principal coordinates analysis (PCoA) performed on each of the five data sets, and the total variance modeled by the first three axes from principal components analysis (PCA) performed using species scores on the first three axes from each dimensional PCoA

Niche dimension	No. variables	Axis 1	Axis 2	Axis 3	Cumulative (1 + 2 + 3)
Habitat + anatomy	13–15	36.80	26.41	11.50	73.91
Metabolic	6–7	74.79	9.91	4.77	89.47
Life history	9	43.48	19.21	9.36	72.05
Trophic	9–10	43.16	16.81	9.00	68.97
Defense	14	30.98	24.60	11.04	66.62
PCA of three PCoAs	15	28.08	18.14	15.49	61.71
Corrected values	15	20.76	13.40	11.26	45.42

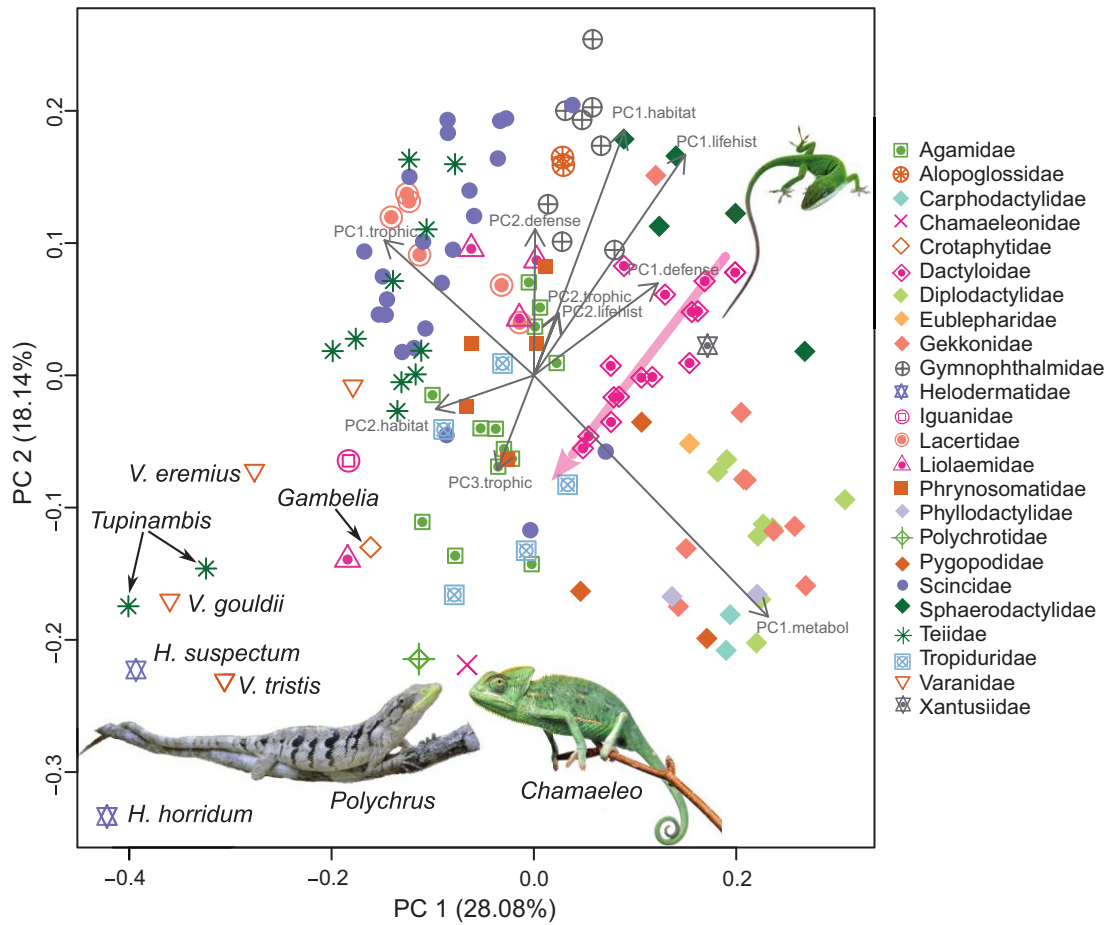


Figure 2: Plot of the first two axes from a principal components (PC) analysis based on species scores for three axes resulting from principal coordinates analysis performed on each of five niche dimensions, showing positions occupied by representatives of various families of lizards in the PC1 versus PC2 plane. The first two PCs captured 46.22% of the variance, and the third PC reduced residual variance by an additional 15.49% for a total of 61.71% (table 1). The first axis is dominated by size and foraging mode, whereas the second corresponds to terrestrial versus arboreal microhabitat. The third axis (not shown here; but see fig. 3) represents diurnal versus nocturnal time of activity and captures 15.49% more of the variance. The larger varanoids (*Heloderma* and *Varanus*) and their ecological counterparts from South America (*Tupinambis*, family Teiidae) occupy the lower left. The convergent species pair *Polychrus* + *Chamaeleo* is shown in the lower center and an *Anolis* in the upper right with a pink arrow fitted by eye to the Dactyloid clade. Another convergent species pair (not labeled) is the Australian agamid *Moloch* and the North American phrynosomatid *Phrynosoma*. Many other convergent pairs remain hidden inside the larger cluster of species and can be viewed in the second of the 13 three-dimensional plots.

tree analysis (fig. 4). On the basis of this admittedly subjective criterion for matching, 103 pairs represent niche conservatism out of the 8,911 possible species pairings.

We also found ample evidence of niche convergence. Pairs of distantly related species are tightly clustered within the continuous niche space defined by the three major gradients derived from PCA (figs. 2, 3; “3D Models,” available online; as one rotates the cloud of species in 3D space, they stay together). Some of these are obvious—such as *Chamaeleo* + *Polychrus*, *Moloch* + *Phrynosoma*, and *Varanus* + *Tupinambis*—but others are less apparent (e.g., Australian *Varanus eremius* and North American *Gambelia wislizeni*). Convergence was also detected in the discrete niche

representation derived from regression tree analysis. Of the 8,911 possible species pairs, regression tree analysis identified 100 convergences, when the criterion for convergence was matching of categories for at least four of the five niche dimensions (fig. 4). This is significantly greater than the combined number of matched pairs expected when species are randomly assigned niche categories from a uniform distribution (Wilcoxon rank sum test; $W = 328, P = .04$). Of course, convergence of phenotypes and niches is never all or none, and varying degrees of convergence exist (Wine-miller et al. 2015). Consequently, our criterion for recognizing species convergence according to the discrete niche scheme is necessarily subjective. First, the number of niche

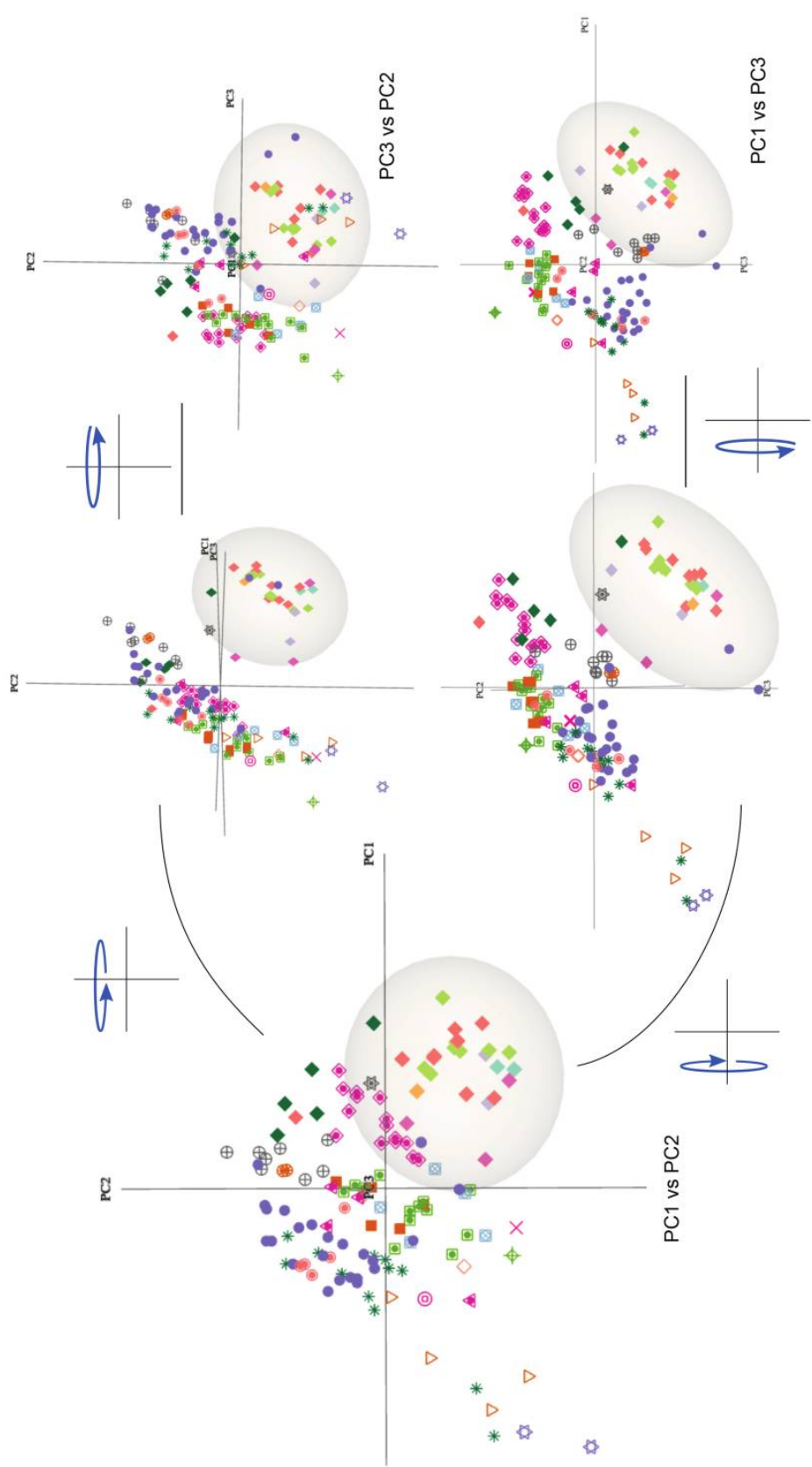


Figure 3: Scatterplots representing rotated versions of principal component (PC) 1 versus PC2 (fig. 2) showing distributions of data in PC2 versus PC3 and in PC1 versus PC3. Nocturnal members of the clade Gekkota are enclosed in gray ellipses. Two nocturnal Australian skinks are shown (purple circles). Plot rotation reveals the clear separation between diurnal and nocturnal lizards within the three-dimensional (3D) ellipsoid. Crepuscular lizards and species with extended activity occupy positions near the border of the ellipsoid. For interactive versions of these 3D plots, see “3D Models,” available online (<http://www.zo.utexas.edu/faculty/pianka/pianka/ModelsMK/index.html>). For explanation of symbols representing families, see figure 2.



Figure 4: Prevalence of conservatism and convergence in the studied lizards in a phylogenetic and geographic context. Lizard species are color coded by geographic regions (red, Australia; blue, North America; green, Neotropics; black, Africa). Niche conservatism within clades are connected by black lines on the left of species names, and niche convergences between clades are connected by green lines on the right.

dimensions for which species must have matching categories was chosen subjectively (i.e., we could have relaxed this criterion by requiring as few as three dimensions to match, which would have yielded more cases of convergence but also potential mismatches). The resolution chosen for criteria used in regression tree analysis is subjective (we could have chosen a finer resolution that would have yielded fewer matched species pairs). Applicability of the periodic table of niches concept and choice of continuous versus discrete methods of representation and data analysis will depend on the nature of the research problem being addressed or intended research application (for further discussion, see Winemiller et al. 2015).

The African *Chamaeleo* and South American *Polychrus* were strongly convergent. These distantly related species both move slowly and have prehensile tails and eyes that move independently, two traits not included in our data set. Although *Moloch* and *Phrynosoma* are distantly related and found on different continents, both are ant specialists that defend themselves with spines and cryptic coloration. The Australian pygmy monitor *V. eremius* and the North American crotaphytid *G. wislizeni* are ecological equivalents that prey on smaller lizards. The widely foraging Kalahari lacertid *Nucras tessellata* and the North American teiid *Aspidoscelis tigris* are convergent with the South American teiid *Teius oculatus*. The Kalahari terrestrial skink *Trachylepis occidentalis* has converged on the niche occupied by several widely foraging Australian *Ctenotus* skinks. The widely foraging Kalahari lacertid *Heliobolus lugubris* has also converged on the niche space occupied by Australian *Ctenotus* skinks. Many ambush foragers also exhibit convergence: in South America, *Gonatodes* geckos are convergent with South American dactyloid anoles. A diurnal arboreal South American gecko *Lygodactylus klugei* is convergent with the dactyloid *Anolis humilis*, although a key difference is that *L. klugei* occurs in open tropical habitats whereas *A. humilis* occurs in lowland tropical forest. The sit-and-wait terrestrial diurnal Kalahari lacertids *Meroles suborbitalis* and *Pedioplanis lineocellata* are convergent with the North American phrynosomatid *Uta stansburiana* and the Australian agamid *Ctenophorus isolepis*. The large Australian agamid *Pogona minor* is ecologically equivalent to the Kalahari agamid *Agama aculeata*. The herbivorous North American iguanid *Dipsosaurus dorsalis* is an ecological counterpart to the Australian agamid *Ctenophorus nuchalis* (Pianka 1971).

Lizard niches are evolutionarily constrained because of phylogenetic relatedness as well as by trade-offs between foraging mode and reproductive tactics. Position on a thermoregulatory-thermoconformer axis and anatomy are useful surrogates for habitat and microhabitat. Natural dichotomies, such as diel activity patterns and parity modes, also separate species. Evidence of niche convergence between distantly related species belonging to different clades living

on different continents (teiids vs. lacertids and/or agamids vs. phrynosomatids) support the idea that a niche scheme exhibits periodicity; in other words, certain functional trait combinations are repeated across divergent clades and regional faunas, presumably as legacies of similar selection regimes, past and present.

Tropical species are scattered throughout the niche hypervolume, which is not surprising, considering their ecological and taxonomic diversity, which is likely driven by a combination of a warm climate and high habitat structural diversity. Interestingly, a large number of species from at least four divergent clades line up along the metabolic and anatomical axes. This further illustrates the value of a periodic niche scheme, in this case, the ordination plot that allows species placement along continua; species from different clades and continents often cluster tightly together along certain gradients within niche space. If it were the case that patterns of functional trait variation arranged species strictly according to their phylogenetic relationships, then a niche scheme would be redundant with phylogeny and of little use. However, this is clearly not the case, at least for lizards. For example, anoles and geckos cluster along a gradient strongly influenced by life-history, metabolic, and defense dimensions, involving traits such as low clutch size, crypsis, and autotomy. However, these two groups are completely separated on the diel time-of-activity axis.

Temperature drives the diurnal-nocturnal separation. Although phylogenetic clustering in niche space (niche conservatism) is quite evident, within each cluster are species from other families, ecological analogs that arose via convergent evolution (Duellman and Pianka 1990). One interpretation for these patterns is that sets of ecological traits that promoted fitness under historical environmental conditions drove diversification within the clade, and extant species possess traits that reflect that legacy but with certain species having evolved into new regions of trait/niche space in new settings. Within each clade, some species diverged to take advantage of specific high-abundance resources (e.g., ants) producing ecological equivalents from deeply divergent clades (e.g., *Phrynosoma* and *Moloch*). These results support the notion that a set of potential niches exists, in effect a periodic table of lizard niches, but not all of these will be occupied within a given locality or region because of historical contingency.

A new giant chameleon-like anole *Anolis landestoyi* from Hispaniola was recently described (Mahler et al. 2016). We can speculate where it would fall in our 3D plot of lizard niche space. Dactyloids (anoles) are well represented in our data set (15 species), filling a cylindrical ellipsoid whose longer axis is oriented toward the position of *Polychrus* and *Chamaeleo*. This new anole species likely will lie at the end of the ellipsoid facing them near the head of the pink arrow in figure 2. Scores could be generated for its position in the 50+ hypervolume. The specificity of this prediction reveals

the utility of a periodic niche scheme. One could have postulated that such a lizard might exist even before the species was discovered. *Polychrus* is sister to a large iguanian group containing dactyloids and was once classified as a polychrotid along with anoles but later was assigned to its own subfamily Polychrotinae (Conrad et al. 2007). Whereas all dactyloids have small clutches of only 1 egg, *Polychrus* have large clutches (mean clutch size for *Polychrus acutirostris* is 11.5 in our sample).

Ecologists have argued for and against the concept of empty niches (Walker and Valentine 1984; Grime 2002). The periodic table scheme can be exploited to ask what ecological attributes and traits occupants of hypothetical niches would have to possess. For example, why do there seem to be no widely foraging nocturnal arboreal lizards? Many geckos are arboreal and nocturnal, indicating that insect foods are available, but they do not appear to forage widely. All skinks are active foragers, but most require high body temperature. Some Australian desert skinks (*Eremiascincus*, *Liopholis*) have evolved nocturnality, even including elliptical eye pupils, but all have remained terrestrial. Diurnal arboreal skinks occur in both Australia (*Cryptoblepharus*) and the Kalahari (*Trachylepis*), but none have become nocturnal. Perhaps in other parts of the world arboreal nocturnal skinks could exist.

Rotating 3D plots is an effective way to explore constraints and trade-offs in the evolution of lizard niches. Rotation in 3D space facilitates visualization of the manner in which species overlap or separate on the basis of habitat, size, foraging mode, diet, life history, metabolism, and/or time and place of activity. Given that it is not possible to view a five-way rendition of space (only a three-way graph is feasible), we believe that 3D rotatable plots are the most effective way of revealing species niche relationships within a continuous niche hypervolume. More than 60% of the overall variance in 50+ niche dimensions can be captured in just three dimensions, suggesting that lizard niches are tightly constrained.

Our 3D plots also suggest that empty niche space exists. However, this could be an artifact of incomplete taxon sampling, given that our data set includes only a fraction of global lizard diversity. Moreover, areas within the total lizard niche space perceived to be empty could be occupied by other terrestrial vertebrates. Other questions could be explored. The phenomenon of gaps or holes in niche hypervolumes could be examined (Blonder 2016). How evenly distributed are species in niche space? Do they fill it up with few gaps, or are there regions of clustering? How do species' positions in niche space vary in space and time? Gaps in niche space should be expected partly because of the temporal nature of species' existence. For example, apparent gaps may have been filled in the past or could be in the future. In theory, the only way all (or at least most) gaps could be filled (all

niches occupied) would be if all species coexisted concurrently.

To summarize, our study (1) proposed key components of lizard niches and compiled data for 134 species, (2) produced a niche ordination scheme, (3) revealed major niche dimensional gradients within total niche space and patterns of species ordination along these gradients and within the space defined by them, (4) demonstrated that niche diversification appears to have occurred differently among geographical areas, (5) revealed that some lineages exhibit high niche diversity whereas others do not, and (6) detected 100 convergences. These findings reinforce the utility of the periodic niche scheme proposed by Winemiller et al. (2015) and further developed herein. Niche conservatism was evident within most clades, even though cases of extreme niche convergence were identified and niche convergence was significantly greater than expected by chance. Considering our relatively low taxon sampling, many more convergences would be expected as additional data are collected. Combining our results for lizards with Winemiller et al.'s (2015) results for fishes, we suggest that construction of periodic niche schemes for other organisms could provide insights into when and how adaptive radiations of different groups of organisms occurred. Finally, our study reinforces MacArthur's (1972, p. 257) prediction that "there will be a two- or three-way classification of organisms and their geometrical and temporal environments."

Future Directions

In the real world, niches are dynamic entities, constantly changing over evolutionary time as well as on shorter ecological timescales in response to changing demographics and abiotic and biotic environmental conditions. Here we have treated niches in an oversimplified way as being static, that is, as mere points in a hypervolume fixed in time and space. Whereas lizards from 24 families and four continents are included in this analysis, only 2.2% of the known described species of lizards are represented. Our study includes almost all species with available data on morphology, habitat use, diet, life history, thermoregulation, and defense mechanisms, a reminder of how badly more field research is needed to provide empirical data to expand data matrices to produce niche schemes for testing ecological questions. Although our data set may seem small for this initial undertaking, it nonetheless included multiple species from eight major clades (agamids, dactyloids, gekkota, gymnophthalmids, lacertids, phrynosomatids, skinks, and teiids). Missing are species from the rich lizard fauna of Southeast Asia (Das 2010; Grismer 2011), which if included would undoubtedly yield many niche convergences with Neotropical lizards. As more ecological data with better geographic and taxonomic coverage are gathered

and published, this analysis should be expanded to construct a more complete niche scheme and assessment of periodicity.

With a more comprehensive data set, many interesting questions could be addressed. For example, the 3D niche spaces occupied by various clades could be quantified as ellipsoids and compared. Anoles fall within a compact cylindrical volume that reflects their niche conservatism, whereas other groups, such as phrynosomatids and skinks, are distributed within larger ellipsoids. Clades that dominate in different parts of the world reveal that extensive convergences—such as New World teiids versus Old World lacertids or Old World agamids versus New World phrynosomatids—should have broadly overlapping ellipsoids. Estimates of clade niche breadth and overlap will be informative. As more periodic tables are created, comparative analyses among more distantly related clades (fish-frogs-salamanders-lizards-snakes-birds-mammals) will become possible, ultimately leading to a wider understanding of niche evolution among vertebrates.

Acknowledgments

We dedicate this article to the memory of the late R. H. MacArthur, who proposed the concept of a periodic table of lizard niches to E.R.P. at Princeton University in 1965. Constructing such a niche scheme has been a long-term goal for half a century but has taken this long to come to fruition. E.R.P. has been supported by the National Geographic Society and the Denton A. Cooley Centennial Professorship in Zoology at the University of Texas at Austin. L.J.V. acknowledges support from the University of Oklahoma Research Council via a George Lynn Cross Research Professorship. N.P. was supported by a postdoctoral funded by the Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina. D.B.F. and K.O.W. acknowledge support from National Science Foundation (NSF) DEB 1257813 and NSF Integrative Graduate Education and Research Traineeship 065453377. We thank D. Beck for sharing his information on body temperatures of *Heloderma*, which allowed us to include this family of lizards in our analysis. We also thank F. B. Cruz for sharing unpublished information on diet for *Liolaemus chacoensis*, J. C. Acosta and G. M. Blanco for letting us use their unpublished data on *Liolaemus* lizards from Argentina, and M. R. Pinilla for sharing data on Gymnophthalmids from Colombia. V. Corbalán kindly helped us to gather information on *Phymaturus*. S. M. Leão collaborated in the conceptualization and aesthetics of figures. We thank J. L. Bronstein, E. D. Brodie III, and P. Morse as well as two anonymous reviewers for helping us greatly improve this effort.

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