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Notes and Comments

Niche Expansion and the Niche Variation Hypothesis: Does the Degree of Individual Variation Increase in Depauperate Assemblages?

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abstract: The niche expansion and niche variation hypotheses predict that release from interspecific competition will promote niche expansion in depauperate assemblages. Niche expansion can occur by different mechanisms, including an increase in within-individual, among-individual, or bimodal variation (sexual dimorphism). Here we explore whether populations with larger niche breadth have a higher degree of diet variation. We also test whether populations from depauperate lizard assemblages differ in dietary resource use with respect to variation within and/or among individuals and sexual dimorphism. We found support for the niche expansion and niche variation hypotheses. Populations in assemblages with low phylogenetic diversity had a higher degree of individual variation, suggesting a tendency for niche expansion. We also found evidence suggesting that the mechanism causing niche expansion is an increase in variation among individuals rather than an increase in within-individual variation or an increase in bimodal variation due to sexual dimorphism.

Keywords: Cerrado, individual specialization, islands, lizards, niche variation hypothesis, niche width.

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The niche variation hypothesis (NVH; Van Valen 1965) predicts that populations with wider niches are more variable than populations with narrower niches. The greater niche variation exhibited by generalist populations suggests that trade-offs might limit individual niche breadth, with the consequence that individual specialists may be more fit than individual generalists (Van Valen 1965; Soulé and Stewart 1970; Bolnick et al. 2007). Indeed, the degree to which populations represent collections of specialized individuals rather than ecological equivalents has been largely overlooked, and a recent review suggested that individual specialization might be a widespread phenomenon (Bolnick et al. 2003).

Several assessments of the NVH brought heavy criticism, and numerous studies using different organisms have failed to find any relationship between population niche breadth and variance among individuals (i.e., Dennison and Baker 1991; Diaz 1994; Simberloff et al. 2000; Meiri et al. 2005). Recently, Bolnick et al. (2007) suggested that the major problem with previous tests of the NVH was that they overemphasized morphological variation. Although the NVH was originally developed to test for morphological variability, Bolnick et al. (2007) argued that the increased variation in resource use does not necessarily need to be mirrored by an increase in morphological variation. If a phenotypic trait (morphological, behavioral, etc.) allows an individual to use a novel set of resources that minimize intraspecific competition, this trait might be favored by selection (Bolnick et al. 2003). In their analysis, Bolnick et al. (2007) used direct measures of dietary resource use instead of morphology as a surrogate and found that more generalized populations also exhibited higher among-individual variation, supporting general predictions extracted from the NVH (Bolnick et al. 2007).

Numerous studies argued that many island vertebrates expand niche dimensions when released from constraints of mainland competitors (reviewed in Grant 1998; Whittaker 1998). This phenomenon is often referred to as "niche expansion" (MacArthur et al. 1972; Pianka 1994; Ricklefs and Miller 1999). This increase in niche breadth

could be achieved either by all individuals shifting to use a larger spectrum of available resources or by each individual continuing to use a narrow range of resources but diverging from conspecifics to minimize intraspecific competition. Under the latter scenario, larger niche breadth would be achieved by an increase in among-individual variation (Van Valen 1965).

Together, the niche expansion and niche variation hypotheses generate two major predictions: (1) release from interspecific competition will promote niche expansion in depauperate assemblages, and (2) niche expansion will occur via increased variation among individuals. The results of Bolnick et al. (2007) supported the latter prediction, but they did not test whether release in interspecific competition was responsible for the niche expansion. In a recent study, Mesquita et al. (2007) found little evidence for niche expansion in populations from depauperate lizard assemblages. However, demonstrating niche expansion may be difficult because variation in resource availability from different localities may influence niche width. This has been observed with respect to habitat niche breadth: because some islands have much lower habitat diversity than comparable mainland areas, the island populations might actually offer narrower niches (i.e., Grant 1971). Nevertheless, populations with similar niche breadths can still exhibit different levels of individual variation independent of resource availability. It just depends on how individual resource use contrasts with the entire population resource use (Bolnick et al. 2002). Therefore, a better test for the predictions of niche expansion and niche variation hypotheses should compare the degree of individual variation among populations (see fig. 1 for a graphical model). For example, differences in the degree of individual variation between island and mainland populations would constitute evidence for a tendency for niche expansion and could identify the underlying mechanism for such expansion.

It has also been suggested that sexual dimorphism can decrease competition by increasing discontinuous variation in a bimodal manner (Rothstein 1973; Patterson 1983; Shine 1989). Therefore, depauperate assemblages should be more likely to show an increase in sexual dimorphism in which sexes would differ in resource use rather than higher individual specialization. Ebenman and Nilsson (1982) examined within- and between-sex variation in island and mainland populations of chaffinches (*Fringilla coelebs*) and found that partitioning of habitat use by sexes was more pronounced in island than in mainland environments.

Here, we use a large data set on lizard diets from a natural system that mimics an island/mainland system (Mesquita et al. 2007) to test whether populations from depauperate assemblages have a higher degree of diet variation among individuals and exhibit greater sexual dimorphism in dietary resource use and whether populations with larger niche breadth are associated with a higher degree of diet variation.
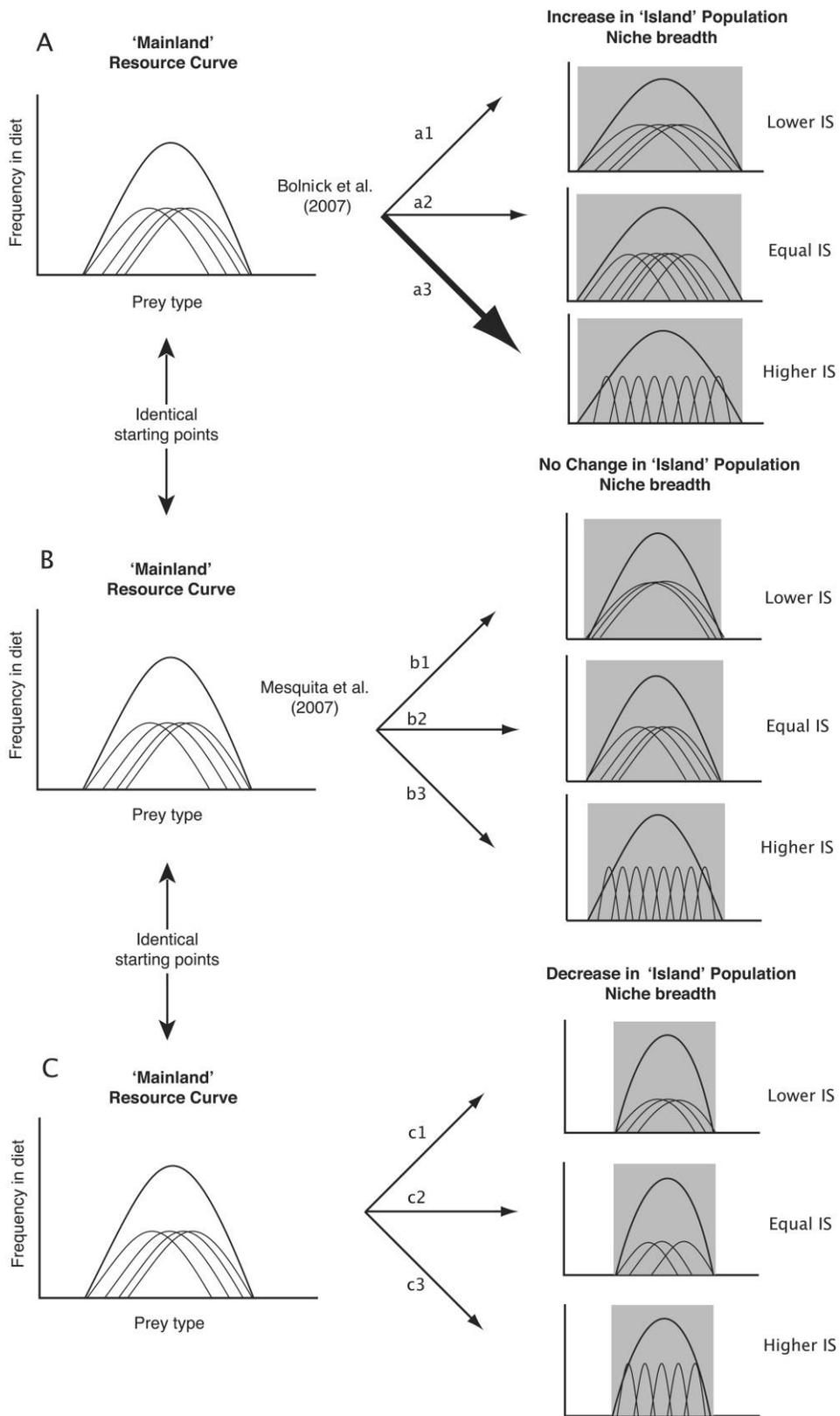
Methods

Study System

As our study system, we use lizard populations from the Brazilian Cerrado. The Cerrado is the second-largest biome in South America, originally occupying about 20% of Brazil's land surface (Ab'Saber 1977; Ratter et al. 1997; Silva and Bates 2002). It is located mainly in central Brazil and shares contact zones with almost all other Brazilian biomes. The core area of the Cerrado consists of savanna vegetation distributed in a gradient from open grassland to forested sites with closed canopy (Eiten 1972). A recent overview of the Cerrado fauna and flora was done by Oliveira and Marquis (2002).

Isolated patches of Cerrado in a forest matrix within Amazonia provide species-depauperate islands that contain a subset (lower diversity) of the Cerrado fauna and flora (Eiten 1978; Gainsbury and Colli 2003; Mesquita et al. 2007). The origin of these patches is attributed to global climatic fluctuations, which have promoted extreme changes in the vegetation cover of tropical regions. During glacial periods (dry climate), savannas expanded and replaced forest, whereas during interglacial periods (humid climate), savannas retreated as forest expanded (Haffer 1969; Van der Hammen and Absy 1994). Consequently, isolated areas are considered vestiges of a large savanna that extended from central Brazil to the Guianas (Prance 1996). We use the terms "island" to refer to the isolated depauperate assemblages and "mainland" to refer to the species-rich nonisolated assemblages in the Cerrado region.

During a 6-year period, from 1998 to 2004, we sampled 11 islands in Amazonia and six mainland sites within the core of Cerrado (fig. 2). With the exception of *Ameiva ameiva*, no other open-area lizard species occurs in the adjacent forest; likewise, forest species do not occupy open areas (Mesquita et al. 2007). Lizard faunas were highly similar between island and mainland, with several species and/or lineages occurring in both. Further, species richness in island areas was lower than in mainland areas (Gainsbury and Colli 2003; Mesquita et al. 2007). Tables A1 and A2 in the online edition of the *American Naturalist* respectively show lists of species from open areas and species from surrounding forest, and figure A1 in the online edition of the *American Naturalist* shows satellite images of some of the studied areas. These natural characteristics

A   'Mainland' Resource Curve

Frequency in diet

Prey type

Increase in 'Island' Population Niche breadth

Bolnick et al. (2007)

a1
a2
a3

Lower IS

Equal IS

Higher IS

Identical starting points

B   'Mainland' Resource Curve

Frequency in diet

Prey type

No Change in 'Island' Population Niche breadth

Mesquita et al. (2007)

b1
b2
b3

Lower IS

Equal IS

Higher IS

Identical starting points

C   'Mainland' Resource Curve

Frequency in diet

Prey type

Decrease in 'Island' Population Niche breadth

c1
c2
c3

Lower IS

Equal IS

Higher IS

provide an ideal situation to test the predictions of the niche expansion and niche variation hypotheses.

Diet Data

Details of lizard and diet collection methods are provided by Mesquita et al. (2007). Briefly, we analyzed stomach contents of each individual under a stereomicroscope, identifying prey items by order. Because most prey are arthropods, ordinal-level identifications separate prey morphotypes quite well. For all prey items, we recorded body length and width (to 0.01 mm) of intact prey items with digital calipers and estimated individual prey volume (Vol) as an ellipsoid:

$$\text{Vol} = \frac{4}{3}\pi\left(\frac{l}{2}\right)\left(\frac{w}{2}\right)^2,$$

where w = prey width and l = prey length. We then used the prey volume of each prey type in analyses.

Because we are examining variation among individuals within populations, we selected only species for which we had large sample sizes (>20 individuals). We also used a resampling procedure to determine whether our results were influenced by sample size (described below). With these considerations, we restricted our analysis to *Ameiva ameiva*, *Anolis* spp., *Cnemidophorus* spp., *Tropidurus* spp., *Gymnodactylus carvalhoi*, *Micrablepharus maximiliani*, and *Vanzosaura rubricauda*. Species of *Anolis*, *Cnemidophorus*, and *Tropidurus* varied among sites, but species within each genus are relatively similar in body size and ecology. In total we used 28 populations from isolated areas and 15 populations from nonisolated areas (table A3 in the online edition of the *American Naturalist*).

Niche Width and Individual Diet Variation

To calculate dietary niche breadth and the degree of individual diet variation, we followed the methods described by Bolnick et al. (2007). We calculated the total niche width (TNW) for each population by using the Shannon-Weaver diversity index, following Roughgarden (1979). To measure diet variation among individuals, we calculated the similarity between the diet proportions of each individual and the averaged population diet distribution. Proportional similarity is calculated as

$$\text{PS}_i = 1 - 0.5\sum_j \left| p_{ij} - q_j \right| = \sum_j \min\left(p_{ij}, q_i\right),$$

where p_{ij} is the proportion of prey type j in the diet of individual i and q_j is the proportion of prey type j in the overall population's diet. We calculated q_j by averaging proportions across individuals to control for uneven volume of prey across individuals (Bolnick et al. 2002). For each population, mean PS_i represents the average level of diet overlap between individuals and the population as a whole, that is, the degree of individual specialization (IS; Bolnick et al. 2002, 2007). We also used a more intuitive measure, the index V, defined as $V = 1 - \text{IS}$ (Bolnick et al. 2007). This index ranges from 0, when all individuals use the full range of resources used by the population, to higher decimal values, when each individual uses a unique portion of the population diet distribution.

To test whether larger niche breadth is achieved by increase in diet variation among individuals, we regressed the values of V on TNW for each population. To test whether populations released from interspecific competition will have a higher degree of diet variation, we used ANOVAs to compare the mean V values for island versus mainland populations. Also, to search for differences between island and mainland populations that could be hidden by among-species variation, we contrasted the average V for island versus mainland by using Wilcoxon signed-rank tests paired by species of the same genus.

Stomach size or resource competition may constrain the number of prey recorded per individual. Thus, gut contents (a short-term measure) may underestimate the long-term diversity of prey eaten by an individual. Therefore,

Figure 1: Three different scenarios and subsequent predictions from the niche expansion and niche variation hypotheses. *A*, Comparisons between "mainland" and "island" populations show that niche breadth increases in island populations. This niche expansion could be achieved by all individuals shifting to use a larger spectrum of available resources, resulting in a lower degree of individual specialization (IS; *a1*), an unchanged degree of IS but with decreased between-individual overlap (*a2*), or each individual continuing to use a narrow range of resources but diverging from conspecifics to minimize intraspecific competition (higher IS; *a3*). Bolnick et al. (2007) demonstrated that scenario *a3* occurs. However, they did not assess whether niche expansion was a result of competitive release. *B*, No difference in niche breadth is found between mainland and island populations, and individuals shift to use a larger spectrum of available resources (lower IS; *b1*), individuals in islands continue to use resources similarly to individuals in mainland populations (equal IS; *b2*), or individuals in island population diverge from conspecifics (higher IS; *b3*). *C*, Niche breadth decreases in island populations, and individuals present lower IS (*c1*), equal IS (*c2*), or higher IS (*c3*). Niche expansion might not occur because variation in resource availability from different localities may influence niche width. Therefore, no difference or narrower niche breadth in islands may be a result of lower resource availability (e.g., Grant 1971). Lower or higher IS regardless of niche breadth may be evidence that niche expansion would occur in case there were no differences in resource availability.
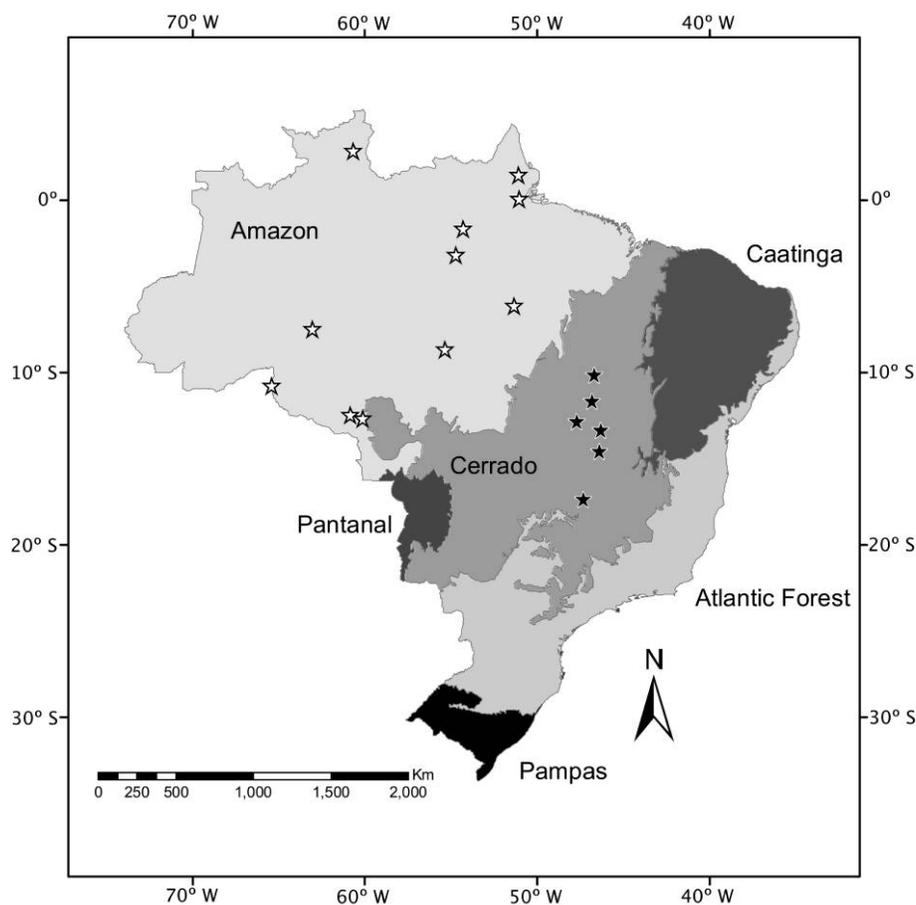
Figure 2: Map of Brazil showing the major ecosystems and localities that were sampled (*stars*). Solid stars represent localities within the Cerrado central area (nonisolated or "mainland" populations); open stars represents patches of savanna that are surrounded by a forest matrix (isolated or "island" populations).

diet studies tend to overestimate variation among individuals. This problem becomes more severe as the actual diet breadth increases, because samples of diets of individuals are proportionally smaller and hence more likely to underestimate individual niche breadth (Bolnick et al. 2007). In this case, a positive relationship between TNW and V should result from this sampling artifact. We used a Monte Carlo bootstrap procedure to re-create this artifact as a null expectation for the relationship between TNW and V for each population. The diet of each individual observed to have consumed any volume of prey was randomized based on the population diet frequencies. The null degree of diet variation was calculated based on randomized diets of individuals. For each population, we carried out 1,000 resampling estimates. Next, we regressed mean resampled V against observed TNW to test the null hypothesis that limited individual diet data also generate a positive relationship between these measures. For each

population, we also evaluated whether the observed values of V were greater than expected by chance by determining the number of Monte Carlo simulations with V values larger than the observed V value.

To avoid pseudoreplication arising from phylogenetic nonindependence, we performed regressions using phylogenetic independent contrasts for V, TNW, and null values of V. We constructed a supertree (fig. A2 in the online edition of the *American Naturalist*) for our species based on a combination of published phylogenies (Frost et al. 2001; Poe 2004; Lee 2005; Giugliano et al. 2006), and the relationships among conspecific populations were inferred by geographic proximity. Recent phylogenetic analyses of widespread Amazonian lizard clades (*Anolis* [Glor et al. 2001] and *Gonatodes* [Gamble et al. 2008]) show that geographic distance is generally correlated with phylogenetic distance. We calculated contrasts using the software CAIC, version 2.6.9 (Purvis and Rambaut 1995). Calculations of
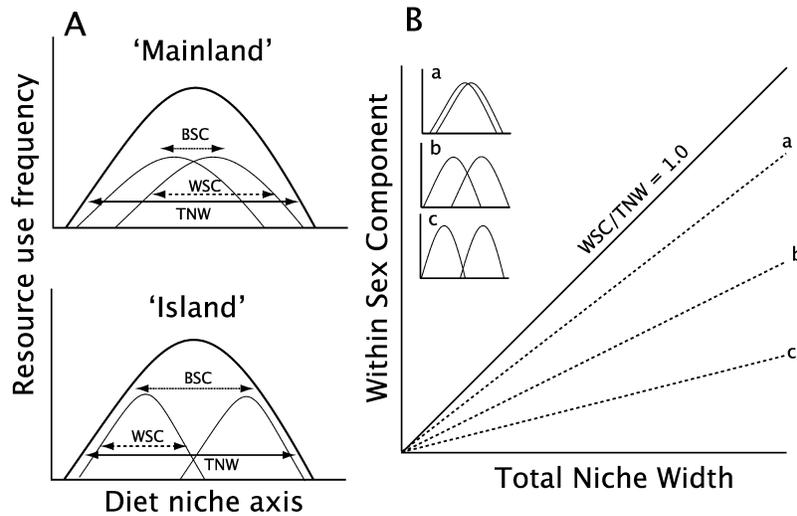
Figure 3: *A*, Schematic diagram of theoretical predictions on how resource use between sexes could differ in "island" and "mainland" populations. The total niche width (TNW) is the variance of total resource use of all sexes. TNW = WSC + BSC, where WSC is the average of sex niche widths, and BSC is the variance in mean resource use among sexes. In a population where sexual dimorphism is low, WSC is a large proportion of TNW, whereas in populations with prominent sexual dimorphism BSC will be higher than WSC. In island populations, theory predicts that sexes will differ more prominently (see text for details). Although the idealized Gaussian curves used here are a poor description of niche shapes for many real organisms, they usefully convey the concept of between-sex variation. *B*, Sexual dimorphism in resource use is part of a continuum from where the within-sex component equals the total niche width (on the solid diagonal, WSC = TNW, BSC = 0; WSC/TNW = 1) to where WSC is a small proportion of TNW (close to the *X*-axis). *a–c* represent the approximate positions on the diagram of hypothetical populations with high WSC/TNW (*a*), medium WSC/TNW (*b*), and low WSC/TNW (*c*). Based on theoretical and some empirical evidence, island populations should have a lower WSC/TNW. Figure adapted from Bolnick et al. (2003).

TNW, *V*, and the Monte Carlo procedures were performed in IndSpec 1.0 (Bolnick et al. 2002). Regressions, ANOVAs, and Wilcoxon signed-rank tests were performed in SAS for Windows, version 9.1. For more information and details on the methods used and indices calculated, see work by Bolnick et al. (2002, 2007). IndSpec 1.0 documentation is available at http://www.esapubs.org/archive/ecol/E083/056/default.htm.

In addition, to explore other factors that might influence the degree of individual variation, we built a multiple regression model where *V* was the dependent variable and TNW, species richness in the assemblage, phylogenetic diversity index (PD), and body size (measured as snout-vent length [SVL] in mm) were independent variables. After assembling a supertree representing phylogenetic relationships among species found in all localities (fig. A2), we calculated the PD for each locality using Faith's (1992) index, which is given by the sum of lengths of all branches connecting the species present in each locality:

$$PD = \sum_k b_k,$$

where b_k is the length of the *k* branches of the phylogeny. When branch length is unknown, such as in our case,

lengths can all be assigned unit length so that phylogenetic diversity then will depend only on the branching pattern of the phylogeny (Faith 1992). To calculate the PD, we used the software Phylocom, version 3.41 (Webb et al. 2007).

Sexual Dimorphism

To explore whether lizard populations in islands have a higher degree of sexual dimorphism in dietary resource use than mainland populations, we applied a method similar to that of Ebenman and Nilsson (1982). We used the software IndSpec 1.0 (details above) to calculate WSC (within-sex component) and BSC (between-sex component).

$$WSC = \sum_s p_s \left(-\sum_j p_{sj} \ln p_{sj} \right),$$

$$BSC = - \left[\sum_s p_s \ln (p_s) \right] - \left\{ \sum_j q_j \left[-\sum_s \gamma_{sj} \ln (\gamma_{sj}) \right] \right\},$$
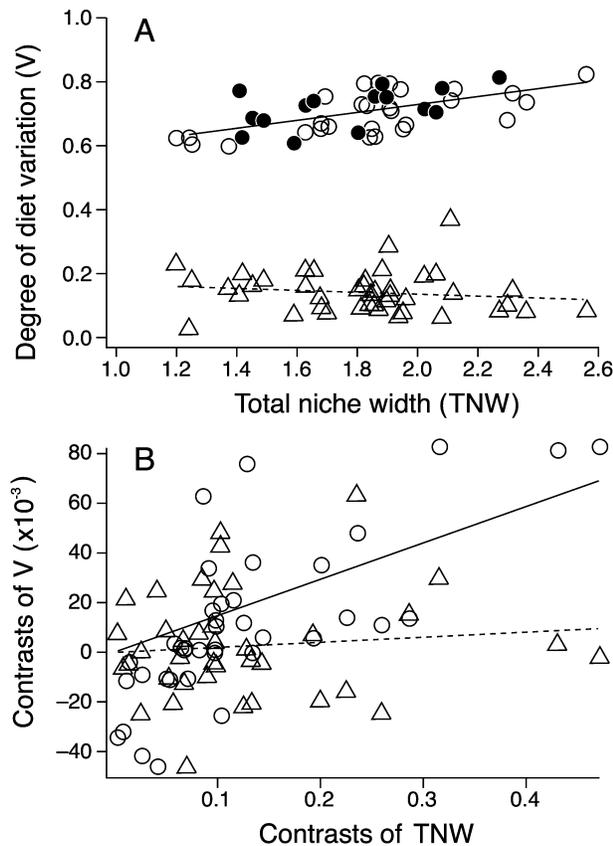
Figure 4: *A*, Correlation between diet variation among individuals (*V*) and total niche width (TNW) of the studied populations. Empirical results are shown with circles: solid circles represent nonisolated populations, and open circles represent isolated populations. Triangles (and dashed regression line) represent the expected trend under a null model in which diet variation arises only by individuals randomly sampling a limited set of prey from a shared prey distribution. *B*, Correlation between phylogenetic contrasts of *V* and TNW and null values of *V*. Note: independent contrasts have an expectation of zero and regressions must pass through the origin. Thus, the degrees of freedom remain equal to the number of contrasts (number of nodes minus 1). For details, see Eisenhauer (2003) and Garland et al. (1992).

where q_j is the proportion of the *j*th resource category for the pooled sexes, p_s is the proportion of all diet data contributed to the data set by sex *s*, and γ_{sj} is the proportion of the population's total use of resource *j* that was used by sex *s*. Next, we calculated the ratio WSC/TNW. Higher values of WSC/TNW indicate that sexes do not differ much in dietary resource use, and lower values indicate higher segregation in resource use between sexes (see fig. 3 for a graphical model). We then conducted a nonparametric ANOVA (Kruskal-Wallis test) comparing WSC/TNW of island versus mainland populations, both pooling all species and for each species. For this analysis, we used only

species for which we had large samples for both males and females.

Results and Discussion

Total niche width and degree of individual variation (*V*) were positively related ($R^2 = 0.35$, $P < .01$, $V = 0.12\text{TNW} + 0.48$, $N = 43$; fig. 4*A*). Applying phylogenetic independent contrasts actually improved the relationship ($R^2 = 0.5$, $P < .01$, $V = 0.15\text{TNW}$, $N = 39$; fig. 4*B*). This result indicates that populations with larger niche breadth exhibit higher levels of among-individual variation. We found no association between null values of *V* and TNW ($R^2 = 0.02$, $P = .41$, $N = 43$; fig. 4*A*), with similar results based on phylogenetic independent contrasts ($R^2 = 0.25$, $P = .33$, $N = 39$; fig. 4*B*). Therefore, the positive association we found is not an artifact resulting from limited diet information for each individual, and gut contents of individual lizards do not underestimate the diversity of prey actually eaten by the entire population. This could happen because stomachs are sufficiently large to hold a wide diversity of prey and/or because the diversity of prey eaten by the whole population is not excessively high. For all populations, the degree of diet variation was higher than expected by chance (all Monte Carlo simulations $P < .01$).

These results together with those of Bolnick et al. (2007) suggest as a general mechanism that larger population niche breadth is achieved by an increase in among-individual variation rather than an increase in within-individual variation. This generalization seems to hold whether analyzing different populations of the same species (Bolnick et al. 2007) or comparing across populations and different species (this study). However, the degree of among-individual diet variation did not differ between island and mainland populations, either using all species *V* ($F = 0.78$, df $= 1, 42$, $P = .38$) or comparing species pairs (Wilcoxon tests, all P values >.05; table 1). These results indicate that among-individual variation is not higher in depauperate assemblages. Nevertheless, the multiple regression model showed that when species richness, body size, and total niche breadth are taken into account,

Table 1: Results of comparisons of the degree of among-individual diet variation between "island" and "mainland" populations within species of the same genus

Lizard species	N	χ^2	P
Ameiva ameiva	15	2.88	.09
Anolis spp.	5	.33	.56
Cnemidophorus spp.	8	.55	.46
Tropidurus spp.	8	.53	.44

Note: N = number of populations used, and df = 1.

Table 2: Results of multiple regression model

Variable	β	SE	t	P
TNW	.12	.02	4.48	<.01
Richness	.01	<.01	3.12	<.01
PD	−.33	.15	−2.20	.03
SVL	<.01	<.01	.41	.69
Intercept	.46	.05	9.34	<.01

Note: The model explores the effects of total niche width (TNW), species richness in the assemblage, Faith's (1992) phylogenetic diversity index (PD), and body size (snout-vent length [SVL] in mm) on the degree of individual variation. Full model $F = 9.96$, $r^2 = 0.51$, df = 4, $P < 0.01$, $N = 43$, $\beta =$ regression coefficient, and $t = t$ statistic.

PD has a negative regression coefficient (table 2), indicating that higher *V* values are achieved in lower-PD assemblages. This is a very interesting result, which suggests that assemblages with less phylogenetic diversity may be released from interspecific competition and respond as predicted by the niche expansion and niche variation hypotheses. Although PD tends to be correlated with species richness (Tôrres and Diniz-Filho 2004), areas with similar species richness may have different values of PD depending on the lineages present and diversity within lineages. Reduction of phylogenetic diversity may provide the necessary competitive release, independent of species richness, if reduction of PD is caused by the loss of related species that are more likely to compete for resources.

Another important implication of this analysis is that it indicates that species richness per se may not be a good proxy of interspecific competition. This has been observed previously, for instance, in plankton and plant systems, where different explanations have been proposed for the lack of relationship between richness and interspecific competition. Because of allelopathy, the strength of competitive interactions in plankton systems is not related to the total number of species present but instead to which species are present (for details, see Granéli and Hansen 2006 and references therein). In addition, some species of phytoplankton can facilitate the coexistence of others by adding chemicals to the water. In some instances, the degree of competition will be related not to species richness

or composition but instead to the species composition at an earlier time (see Roelke and Buyukates 2001 and references therein). In plants, a new mechanism termed "lumpy coexistence" was recently proposed (Scheffer and van Nes 2006). In this case, competition between species within lumps along a resource gradient is very low, despite species richness. However, competition is very intense between lumps along the resource gradient, regardless of species richness within each lump (Scheffer and van Nes 2006). Among lizards, classical literature on Caribbean anoles highlights the importance of interspecific competition (e.g., Schoener 1983). However, a recent review using data for more than 50 lizard assemblages distributed worldwide pointed out that in general, lizard assemblages are not structured by interspecific competition when compared to assemblages in null models (Luiselli 2008). Furthermore, when structure is indeed found, it does not seem to be related to species richness (Luiselli 2008). Therefore, although the detailed mechanisms on how interspecific competition may affect lizard assemblages still must be determined, our study and recent evidence suggest that species richness may not play a major role.

Our multiple regression analysis also showed that there was no effect of body size on the degree of individual variation. Previous work has shown that larger predators tend to consume prey that are more variable in size (Vézina 1985; Costa et al. 2008). However, a recent study using a large data set on predaceous lizards showed that larger predators avoid very small prey and therefore tend to consume a narrower diversity of prey (Costa et al. 2008). Our results add to those studies by pointing out that although larger lizards tend to eat less diverse and more variable-sized prey, populations of larger lizards do not differ from populations of smaller lizards in the degree of variation among individuals.

Our sexual dimorphism analysis showed that overall there are no differences in resource use between sexes (table 3). Both island and mainland populations exhibit very high WSC/TNW ratios, indicating that males and females utilize resources in a similar way. The role of sexual

Table 3: Results of comparison of resource use between sexes in the "islands" and "mainland" populations

Species	Island mean WSC/TNW	Mainland mean WSC/TNW	N	χ^2	P
All species	.91	.94	17	.45	.50
Ameiva ameiva	.88	.90	4	.60	.44
Anolis spp.	.85	.94	4	2.4	.12
Cnemidophorus spp.	.98	.97	3	1.5	.22
Tropidurus spp.	.92	.96	6	.42	.51

Note: WSC = within-sex component, TNW = total niche width, and $N =$ sample size, or number of populations used.

dimorphism in the NVH is controversial, with some studies supporting the model (Ebenman and Nilsson 1982; Simberloff et al. 2000; Pearson et al. 2002) and others not supporting it (Dunham et al. 1978; Blondel et al. 2002; Meiri et al. 2005). Meiri et al. (2005) argued that the smaller variability and similar degree of sexual size dimorphism in insular populations of carnivores might result from differences in the number and perhaps the size distribution of potential prey, which may be smaller on islands. A later study comparing island and adjacent-mainland populations of mustelids also reached the same conclusions (Meiri et al. 2007). This might be the case in our system, where there is no difference in niche breadth between island and mainland (Mesquita et al. 2007), but we found evidence that areas with lower phylogenetic diversity have a higher degree of individual variation, suggesting that niche width properties might be constrained by resource availability.

In summary, we found support for predictions of the niche expansion and niche variation hypotheses. Populations in assemblages with low phylogenetic diversity differ in the degree of individual variation, suggesting a tendency for niche expansion, although a wider niche itself was not observed in the island assemblages of this system (Mesquita et al. 2007). However, niche breadth may be influenced by differences in resource availability in the different environments (Grant 1971; Meiri et al. 2005). Therefore, we suggest that comparisons of degree of individual variation may be a better indicator of the tendency of niche expansion than comparisons of niche width. We also found evidence for the mechanism underlying niche expansion. An increase in variation among individuals rather than an increase in within-individual variation or an increase in discontinuous variation, such as in sexual dimorphism, may cause niche expansion.

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