

Sean T. Giery¹ and James T. Stroud²

¹Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT USA

²Department of Biology, Washington University, St Louis, MO, USA

Geographic variation in trophic ecology of the Brown anole (*Anolis sagrei*): species-rich communities are composed of more diverse populations

ABSTRACT

Here we analyze a large dataset of the diet of the brown anole (*Anolis sagrei*). We asked how the trophic niche varies among populations with the specific goal of testing a long-standing model of adaptive diversification – ecological release. Our results do not support the predicted inverse relationship between community richness and niche breadth. Instead, we find that population niche breadth increases with increasing community richness. Using a subset of data for which we have individual-level data we also find that variation in niche structure along this community richness gradient is driven by increasing variation within and among individuals. Our results show that a widely cited dynamic underpinning ecological models of adaptive diversification – ecological release – does not appear to explain interpopulation niche variation in *A. sagrei*. While we do not have data sufficient to explain this incongruence between theory and observation, we briefly discuss some ideas worth exploring. Ultimately, we hope our findings stimulate new ideas and further evaluation of the relationship between community richness, competition, and the origins of intrapopulation diversity.

INTRODUCTION

Burgeoning interest in intrapopulation diversification (e.g., individual specialization) and ecological speciation has fueled a wave of research into the processes of ecological and phenotypic diversification (Dieckmann and Doebeli 1999, Schluter 2000, Bolnick et al. 2003, Ackermann and Doebeli 2004, Bolnick and Fitzpatrick 2007, Nosil 2012). Indeed, much of this work has focused on understanding the behavioral and ecological mechanisms that reduce geneflow within populations subject to divergent selection – that is, reinforcement. Besides some well investigated model systems (e.g. Galapagos finches: Grant and Grant 1989, three-spined stickleback: Hendry et al. 2009, Timema stick insect: Farkas et al. 2013), advances in divergence with-gene-flow models have tended to overlook earlier stages in the diversification process that generate phenotypically diverse populations. Consequently, a general model describing how

phenotypically (or ecologically) diversified populations arise is lacking. Instead, a rather limited set of eco-evolutionary predictions seems to dominate the way evolutionary ecologists currently think about the origin of ecological diversity within populations (Yoder et al. 2010, Wellborn and Langerhans 2015).

The prevailing model of adaptive ecological diversification generally includes some version of *ecological release*. While the ideas underlying ecological release existed prior (Mayr 1942, Simpson 1944, 1953, Lack 1947), it seems Wilson was the first to name it (Wilson 1961). In his 1961 paper on taxon cycling in ant communities of southeast Asia, Wilson used the term to describe what happens when species from species-rich habitats (e.g., mainlands) colonize species-poor ones (e.g., oceanic islands). Wilson's simple verbal model articulates a clear prediction, "...the ecological amplitude of both expanding and endemic species should be negatively correlated ... with the size of the local fauna to which they belong.". In contemporary language, the immediate, or non-evolutionary, consequences of ecological release consist of increased population size (density compensation) and increased population variance in resource use (expanded population niche width). Essentially, the model describes what happens when a species encounters and exploits what we would now recognize as ecological opportunity arising from altered heterospecific interactions such as competition and predation (Stroud and Losos 2016).

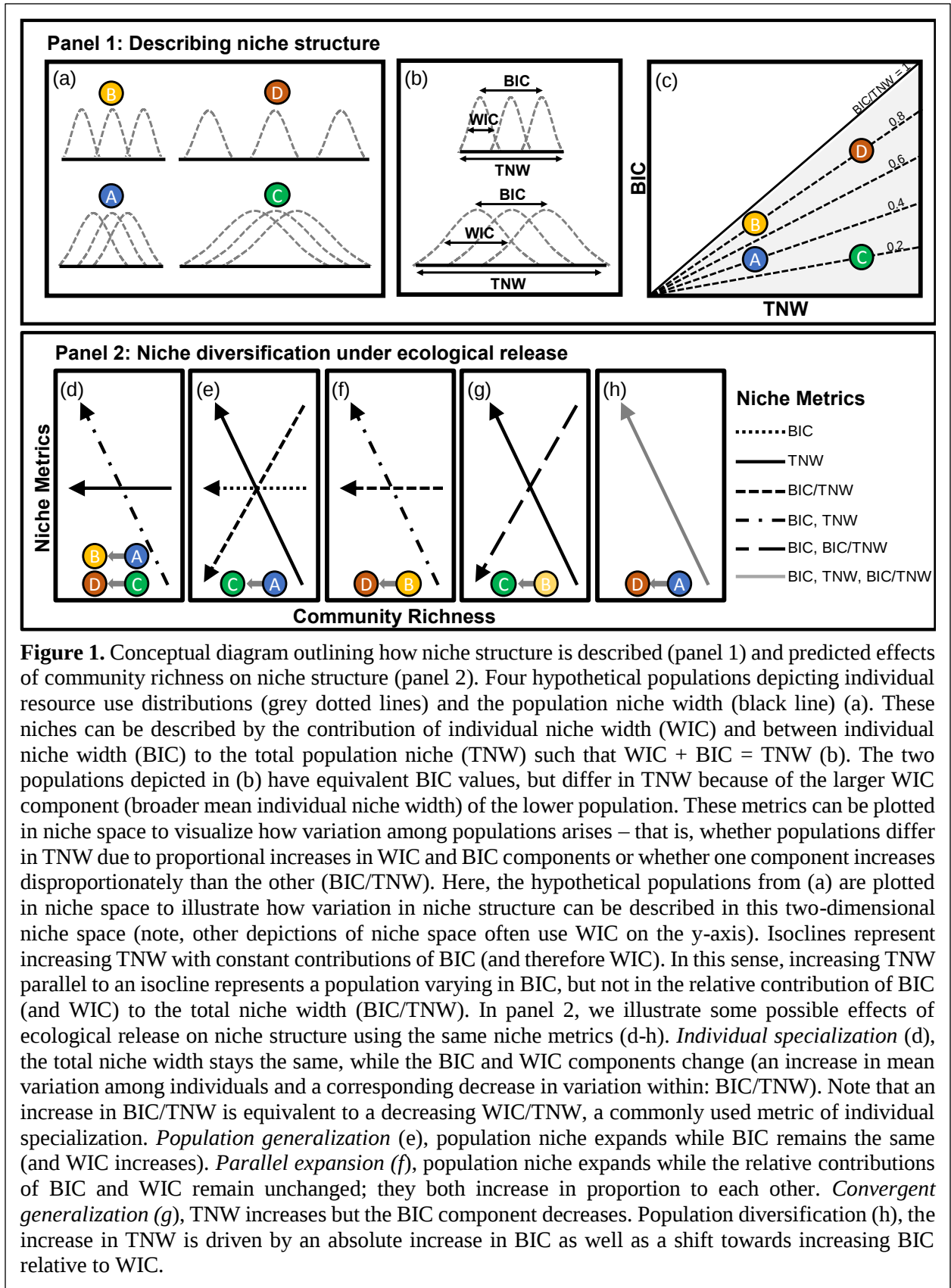
It's important to note that evolution was not integral to Wilson's ecological release model. Nevertheless, the evolutionary implications were clear – filling an important gap in developing theory about the ecological dynamics of adaptive evolutionary diversification (Losos and Queiroz 1997, Schluter 2000). Specifically, ecological release suggested that population niche expansion (increased phenotypic variance) emerged when and where relaxed heterospecific interactions prevailed. But niche expansion alone does not explain how species or populations diversify. Rather, it simply posits that a population's niche would expand, not diversify per se. This limitation, famously outlined in Van Valen (1965) is important because the next stage in the ecological model of adaptive diversification is disruptive selection – a discriminating ecological force hungry for intrapopulation variation (Roughgarden 1972). Without intrapopulation phenotypic variation, any form or strength of selection would simply depress population mean fitness rather than promote adaptive diversification (Ackermann and Doebeli 2004). While not part of Wilson's ecological release hypothesis, the niche variation hypothesis – broader niches are also more diverse – has become a core component of adaptive diversification theory (Roughgarden 1972, Lister 1976a, 1976b, Bolnick et al. 2010, Yoder et al. 2010).

Understanding how ecological release promotes ecological diversification requires an understanding of the ecological mechanisms that generate intrapopulation niche diversification (Bolnick et al. 2003, Rueffler et al. 2006, Araújo et al. 2011). The answer is somewhat counterintuitive; diversification does not arise directly from niche expansion (as might seem an appealing route). Instead, ecological diversification comes from the other symptom of ecological

release - density compensation (Crowell 1962, MacArthur et al. 1972, Case 1975, Wright 1981, Buckley and Roughgarden 2006, Buckley and Jetz 2007). Density compensation, the numerical response to ecological opportunity, is the critical ecological link between heterospecific interactions and evolutionary diversification that has fueled most recent work in this area. The model works as follows: 1) low interspecific competition drives density compensation, 2) increased population density increases intraspecific resource competition, 3) negative frequency dependent selection favors extreme (or specialist) phenotypes resulting in a diversified population (Roughgarden 1972, Bolnick 2001, 2004, Rueffler et al. 2006, Svanback and Bolnick 2007, Nosil 2012, Martin and Wainwright 2013). Reinforcement by phenotype or geographic isolation may subsequently drive the evolutionary side of the process towards reproductive isolation and speciation.

Together, ecological release and negative frequency dependent selection by intraspecific competition form the prevailing hypothesis for ecological diversification. We call this integrative model the ecological release paradigm. In whole or part, this model figures prominently in adaptive diversification theory and is a fixture of speciation with gene-flow dynamics. The crucial role of ecological release derives from a mechanistic ecological linkage between ecological opportunity and a diversified population – interspecific competition has a negative effect on intrapopulation variation. The history of this idea goes back quite far yet a review of the ecological release paradigm does not exist, as far as the authors know. However, in one of a series of papers questioning components of the paradigm, Abrams (2008b) traces its roots back to MacArthur and Levin's analysis of limiting similarity (MacArthur and Levin 1967). In his brief review Abrams (2008b) undermines the assumptions of niche theory propping up the ecological release paradigm. This thorough deconstruction raises new questions about the effects of interspecific competition and the ecological conditions favoring adaptive diversification.

As far as we can tell, few studies assessed the ecological release paradigm in *Anolis* lizards. All are observational, comparing phenotypic variation across a gradient of community richness – a proxy for interspecific competition. The evidence in support of the ecological release paradigm is mixed. Indeed, while quite a few studies clearly show evidence that congeneric competitors can drive niche shifts at macroevolutionary (Losos and Queiroz 1997), microevolutionary (Lister 1976a, 1976b, Losos et al. 1994), and ecological timescales (Jenssen et al. 1984, Stuart et al. 2014), evidence for the predicted effects of ecological release on resource use variation (niche expansion and specialization) is rather thin (Roughgarden 1974, Lister 1976a, 1976b, Mesquita et al. 2007, Costa et al. 2008). At the very least, a role for ecological release in the diversification of *Anolis* remains unclear. And while many important questions



remain regarding this textbook case of adaptive radiation, one that has remained for decades is: does ecological release facilitate the evolution of ecological diversity within *Anolis* populations?

We approach this question by examining intraspecific ecological variation within the brown anole, *Anolis sagrei*. In many ways, this study is an extension of earlier work that yielded mixed results as to the role of ecological release in niche diversification in this system (Lister 1976b, 1976a). However, here we include a more extensive diet dataset to more rigorously evaluate the predictions of ecological release (Table 1, Figure 1). Specifically, we test whether 1) *population niche width is inversely correlated with species richness*, and 2) *whether intrapopulation niche variation decreases with species richness*. Note that results reported here are part of an ongoing effort to address these questions. Consequently, these unpublished results are provisional in the sense that our inference may change once additional resource axes are added, morphology is included, and reviewer comments are heeded. For now, we report our results for dietary data, confident those encompass the geographic variation in the trophic niche of *A. sagrei* and the potential effect of interspecific competition on adaptive diversification.

METHODS

Focal organism - *Anolis sagrei* is a geographically widespread species native to the West Indies and introduced broadly (Bermuda, Taiwan, Singapore, Ascension Island, Ecuador, Hawaii, Brazil, Costa Rica, California, Texas, the southeastern US, and several countries in Central America) (Kolbe et al. 2007, Huang et al. 2008, Stroud et al. 2017, 2018). Throughout this geographic range *A. sagrei* succeeds in a variety of ecological contexts and coexists with a number of ecologically similar lizard species. A trunk-ground ecomorph, *A. sagrei* is known to use a variety of habitats, from sparsely vegetated rocky coastlines, to cities and dense forest. This breadth of habitat use, coupled with its huge geographic range, means that *A. sagrei* are components of many different communities. In some habitats, *A. sagrei* are the sole lizard species present, and in others, they are syntopic with several species of *Anolis* and a range of other diurnal insectivorous lizards (Table 1 & 2). *Anolis sagrei* has been subjected to several dietary studies. As with other small invertivore lizards, including *Anolis*, the diet generally consists of small arthropods such as ants, cockroaches, caterpillars, and spiders. As a whole, the diets of *A. sagrei* are unremarkable, and at coarse taxonomic levels (e.g., Order), the diets of *A. sagrei* are not much different from other semi- arboreal anoles such as *A. cristatellus* (Stroud 2018).

Table 1. Study locations and sources of data used in our analysis. 1 – same as diet data, 2 – Powell et al. 2012, 3 – Personal Observation, 4 – iNaturalist.

Region	Site	Latitude	Longitude	Diet	Richness
Bahamas	Abaco	26.403	-77.095	Lister 1976	1
	Abaco – Marsh Harbour	26.532	-77.058	Giery unpub.	3
	Abaco – Pine forest	26.217	-77.212	Giery unpub.	3
	Abaco – Robinson’s bight	26.332	-77.027	Giery unpub.	3
	Abaco – Wilson City	26.376	-77.003	Giery unpub.	3
	Exuma – Georgetown	23.503	-75.869	Lister 1976	1, 2
	Exuma – Moss Cay	23.505	-75.759	Wright 2009	1
	Exuma – North Gaulin Cay	24.198	-76.462	Wright 2009	1
	Exuma – Staniel Cay	24.167	-76.442	Wright 2009	1
Bermuda	South Bimini	25.708	-79.290	Schoener 1968	1, 2
	Paget Parish	32.292	-64.772	Stroud et al. 2017	3
	Pembroke Parish	32.300	-64.792	Stroud et al. 2017	3
Cayman Islands	Cayman Brac	19.724	-79.780	Lister 1976	1, 2
	Little Cayman	19.692	-80.035	Lister 1976	2
	Little Cayman – N	19.690	-80.066	Wright 2009	1
	Little Cayman – S	19.677	-80.062	Wright 2009	1
Florida	FL. Keys – Big Pine (hammock)	24.705	-81.391	Giery unpub.	3 4
	FL. Keys – Big Pine (pine)	24.701	-81.376	Giery unpub.	3, 4
	Gainesville – FNHM	29.644	-82.344	Wright 2009	4
	Gainesville – Neighborhood	29.634	-82.426	Wright 2009	4
	Gainesville – University garden	29.645	-82.357	Wright 2009	4
	Gainesville – McCarty Woods	29.646	-82.344	Wright 2009	4
	Miami – Banyan Drive	25.688	-80.284	Stroud 2018	3
	Miami – Doug Barnes Park	25.738	-80.310	Stroud 2018	3
	Miami – Fairchild Garden	25.677	-80.272	Stroud 2018	3
	Miami – Florida International University	25.758	-80.381	Stroud 2018	3
	Miami – Kendallwood Park	25.693	-80.345	Stroud 2018	3
	Miami – Matheson Hammock	25.682	-80.281	Stroud 2018	3, †
	Miami – Red Road Canal	25.682	-80.284	Stroud 2018	3
	FL. Keys – No Name Key	24.695	-81.328	Giery unpub.	3, †
	North Miami – Biscayne Bay	25.906	-80.137	Giery et al. 2013	3, †
	Tampa – Hillsborough Preserve	28.070	-82.391	Wright 2009	†
Jamaica	Savanna – La-Mar	18.221	-78.135	Lister 1976	1
Swan Islands	Great Swan Island	17.411	-83.900	Lister 1976	2

Community composition - To estimate the number of species coexisting and presumably interacting with *A. sagrei* we used a variety of data sources. In many cases the lizard community was described by authors. However, in many cases the community was determined from direct observation in collection localities by the authors, occasionally being supplemented by photographic observation records from iNaturalist (www.inaturalist.org) and museum records in VertNet (vertnet.org). Searches were performed in July 2018. These sources are detailed in Table 2. We considered a species as coexisting with *A. sagrei* if they can be found in the same habitat and potentially competing for space and/or food resources, that is, they are diurnal, invertivore lizards. For example, *Hemidactylus* spp. geckos were excluded from inclusion, as were large, herbivorous species such as *Iguana iguana* and *Cyclura* spp.. Note that we did not consider other species of vertebrates such as birds in our dataset. While birds likely interact with *A. sagrei* as predators and perhaps competitors (Wright 1979, 1981, Buckley and Roughgarden 2006, Buckley and Jetz 2007) we chose to restrict the analysis to the lizard community at this time.

Also note that although intraguild predation can strongly affect how *A. sagrei* use habitats and food resources we did not differentially treat species that might also eat *A. sagrei* (e.g., *Leiocephalus* spp.). Further partitioning of the effect of predation on resource use is an obvious next step.

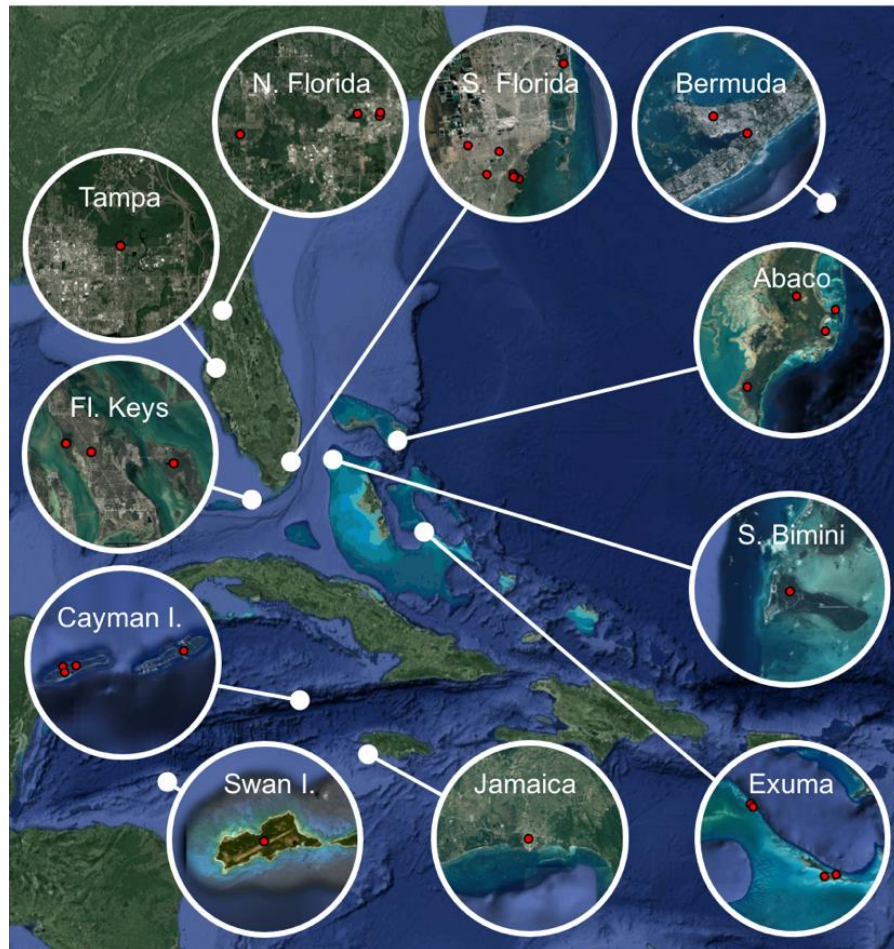


Figure 2. Map of study sites where *A. sagrei* used in this study were sampled. Each red dot indicates a collection location within the region of study. Names within inset study regions correspond to labels in Figures 2 and 3.

Diet data - Our primary dataset consists of the diet of *A. sagrei* as inferred from analysis of their stomach contents. We searched the literature for published data on *A. sagrei* diets – often presented in summary tables. We also included unpublished diet data collected by the authors. Given the diverse origin of data included in this analysis and the various schemes used to report and categorize them, we analyzed these data at a rather coarse level. While some studies identified diets to a finer taxonomic level, most examined diet at a taxonomic level corresponding with Order and a few more inclusive categories (e.g., miscellaneous arthropods). While it may obscure some detail, we chose to collapse finer resolved data (family, genus or

even species) into the coarsest, that is, lowest resolution categorization to allow comparison across a wider range of population. Because many earlier studies of *A. sagrei* only included adult males, here we restricted our analysis to adult males.

From these data we calculated several metrics summarizing population and individual-level diet variation. Population niche width (Total Niche Width - TNW) was estimated as the inverse Shannon-Weaver index following Bolnick et al. (2002). A subset of our data allowed measurement of within-population components of population niche width, BIC and WIC. BIC is the amount of niche variation explained by among individual variance. WIC is the variance explained by individual niche width (Roughgarden 1972, 1974, Bolnick et al. 2002). We used these intrapopulation metrics to describe variation in niche structure among populations and compare them to possible diversifying responses (Figure 1). Niche structure can diversify in various ways. Individuals may become more dissimilar from each other without an expanded population niche – *individual specialization* (Figure 1d). Population diversification also includes scenarios whereby the population niche expands from a combination of increased individual niche width and / or increased among individual variance: individuals may become more generalized – *population generalization* (Figure 1e), individuals may become more generalized and more dissimilar from one another - *parallel expansion* (Figure 1f), individual niches may expand and become more similar - *convergent generalization* (Figure 1g), and finally, individual niches may become more dissimilar - *population diversification* (Figure 1h). Population diversification is also known as the niche variation hypothesis (Bolnick et al. 2010). After examining how niche structure varies, we tested the effect of community richness on niche structure by examining the relationship between species richness and three measures of niche variation: BIC, WIC, and TNW.

Non-independence of samples - We collected diet data for populations spanning the natural and introduced geographic range of *A. sagrei* (Table 1, Figure 2). This dataset consists of fieldwork done by a variety of different authors for a diversity of ecological aims which complicates analysis and inference. First, data are unevenly distributed within the range of *A. sagrei* – meaning that samples are spatially non-independent in some cases (Figure 2). For example, we have several samples geographically clumped in South Florida while we have only one sample from the entire island of Jamaica. Second, we lack detailed quantitative data on ecological conditions for each sampling location – notably lizard community composition, *A. sagrei* population density, and prey community composition – all of which should influence the trophic ecology of *A. sagrei*. Last, the ecological and evolutionary history of each population differs drastically – some populations have long been isolated on small islands such as the Swan Islands, some have recently (decades – century) established on continental mainlands such as Florida (Giery et al. 2013), and yet others have very recently (~ 2014) invaded small islands such as Bermuda (Stroud et al. 2017). Further analysis of these divergent histories might yield interesting caveats to our analysis and interpretation. However, we do not address these aspects

here. Nevertheless, we attempt to account for a few of these issues analytically.

Table 2. Community composition of study sites used in this study. N = Native, I = Introduced.

Species	Abaco	Abaco – Marsh Harbour	Abaco – Pine forest	Abaco – Robinson's bight	Abaco – Wilson City	Exuma – Georgetown	Exuma – Moss Cay	Exuma – North Gaulin Cay	Exuma – Staniel Cay	South Bimini	Paget Parish	Pembroke Parish	Cayman Brac	Little Cayman	Little Cayman – north	Little Cayman – south	Big Pine Key (hammock)	Big Pine Key (pine)	Gainesville – FNHM	Gainesville – Neighborhood	Gainesville – University	Gainesville – McCarty Woods	Miami – Banyan Drive	Miami – Doug Barnes Park	Miami – Fairchild Garden	Miami – Florida International	Miami – Kendallwood Park	Miami – Matheson Hammock	Miami – Red Road Canal	No Name Key	North Miami – BBC	Tampa – Lower Hillsborough	Savanna-la-Mar	Great Swan Island	
<i>Anolis sagrei</i>	N	N	N	N	N	N	N	N	N	N	I	I	N	N	N	N	N	N	N	N	I	I	I	I	I	I	I	I	I	I	I	N	N	N	
<i>A. carolinensis</i>																																			
<i>A. distichus</i>		I				N			N	N							I	I					I		I	I	I		I	I	I				
<i>A. equestris</i> *																							I	I				I	I		I				
<i>A. cristatellus</i>																							I	I			I	I							
<i>A. grahami</i>											I																						N		
<i>A. smagdarinus</i>		I				N	N	N	N	N																									
<i>A. angusticeps</i>						N				N																									
<i>A. lineatopus</i>																																		N	
<i>A. valencienni</i>																																		N	
<i>A. opalinus</i>																																		N	
<i>A. leachi</i>											I																								
<i>A. maynardi</i>														N	N	N																			
<i>A. conspersus</i>													N																						
<i>Agama agama</i>																									I										
<i>Celestus maculatus</i>														N	N	N	N																		
<i>C. cruscus</i>																																		N	
<i>Ophiasaurus ventralis</i>																				N	N	N	N										N		
<i>Basiliscus vittatus</i>																								I	I	I			I						
<i>Leiocephalus varius</i>															I	I																		I	
<i>L. cairinatus</i>		N	N	N		N		N		N			N	N																					
<i>Pleistodon laticeps</i>																				N	N	N	N												
<i>P. inexpectatus</i>																	N	N	N	N	N	N		N				N		N	N	N			
<i>P. fasciatus</i>																			N	N	N	N													
<i>Scincella lateralis</i>																			N	N	N	N											N		
<i>Spondylurus fulgidus</i>																																		N	
<i>Aspidoscelis sexlineatus</i>																	N																N		
<i>Pholidoscelis auberi</i>						N		N	N	N																									
<i>P. dorsalis</i>																																		N	
<i>Anolis richness</i>	1	3	1	1	1	4	2	2	3	4	3	1	2	2	2	2	3	3	2	2	2	2	3	4	5	3	3	4	5	3	4	2	5	1	
Total Richness	2	4	2	2	1	6	2	4	4	6	3	1	4	4	4	4	4	5	7	7	7	7	3	5	8	4	3	5	6	4	5	6	8	2	

Three variables important to our study are likely to vary in a spatially autocorrelated fashion: lizard community richness, the composition of prey communities, and *A. sagrei* genetics. Spatial covariance among these variables could yield causally spurious relationships if, for example, lizard community richness and *A. sagrei* phenotypes respond similarly (or dissimilarly) to an underlying spatial gradient. Spatial autocorrelation between prey community composition (i.e., taxonomic richness of prey) and lizard community richness could also yield a

false impression of causality if, as we predict, lizard community richness is correlated with *A. sagrei* phenotypes.

Our approach to accounting for autocorrelation was to first assess the degree to which geographic distance underlies similarity in our focal variables. We used Mantel tests and Moran's I to check for spatial autocorrelation in our predictor (lizard community richness) and response variables (TNW). Second, we used spatial regression to analyze the relationship between community richness and TNW. Because spatial regression includes the geographic distance between sample points, it accounts for spatial autocorrelation between samples while testing our overall hypothesis.

We first used AIC to choose among several model structures. Our base model was a linear model including TNW as the response variable and community richness as the predictor. We then fit three spatial regression models with different distribution structures: Gaussian, spherical, and ratio. We repeated the model selection procedure with three additional base models including the number of individual lizards in each sample (n lizards) as a covariate. We also included a series of models in which community richness was log-transformed. Not part of our initial prediction, the log-transformation was included after examining the residuals of a linear fit to the data. Best fit models from each base model set were then compared by AIC. Note that because of our small sample of individual-level data used to explore niche variation components, BIC and WIC, we only applied this spatial regression analysis for our analysis of range-wide variation in TNW. Mantel tests, Moran's I, and spatial regression were performed in nlme and vegan packages in R. All geographic distances were calculated using rdist.earth in the Fields package.

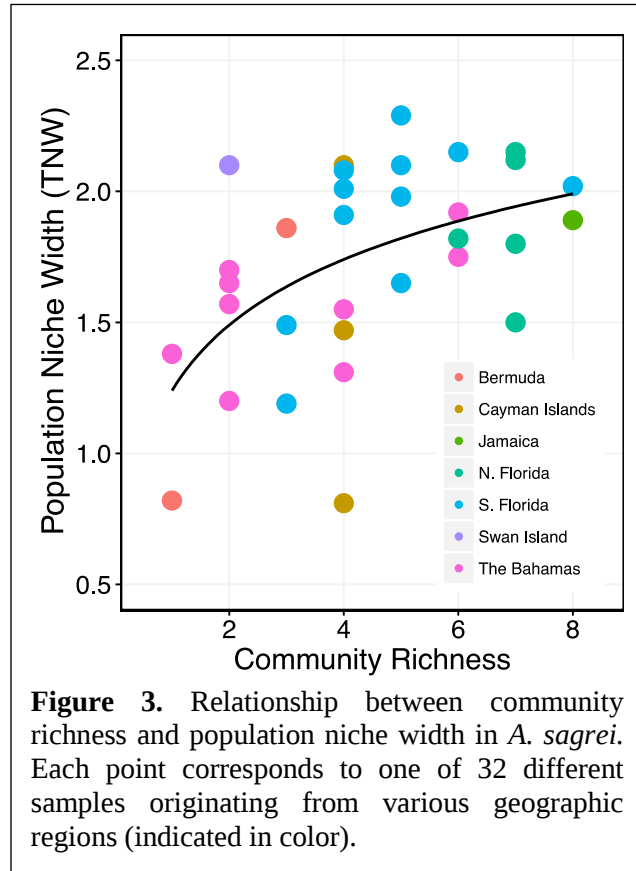
RESULTS

Our dataset included dietary data for 875 adult male *A. sagrei* and more than 8200 prey items from 32 populations (Table 1, Figure 2). For 13 populations we had individual-level diet data allowing us to examine intrapopulation niche variation. Among all study sites, *A. sagrei* cooccurred with at least 30 different species of lizard from eight families (Table 2). The number of lizard species in the community varied substantially among sampling locations. Several of the communities consisted of single species (i.e., only *A. sagrei*); the richest communities included up to eight (mean = 3.7, mode = 3).

Prediction 1: Population niche width is inversely correlated with species richness – Our test of this prediction yielded significant, but counterintuitive results. That is, the observed relationship between TNW and community richness was positive – opposite our prediction – even after accounting for spatial autocorrelation.

Indeed, while Mantel tests showed that spatial autocorrelation existed, it did not explain the positive relationship between community richness and TNW. Specifically, samples geographically near each other were more similar in TNW and lizard community richness as indicated by positive and significant spatial autocorrelation for TNW and community richness ($r = 0.25$ and $r = 0.3$, respectively). However, a partial Mantel test showed a positive correlation between TNW and community richness despite spatial autocorrelation, presumably arising from shared ecological and genetic backgrounds among near samples ($r = 0.18$, $p = 0.06$). Similarly, Moran's I showed spatial autocorrelation for lizard community richness ($p < 0.01$), but no spatial

autocorrelation for TNW ($p = 0.56$). Further, analysis of residual TNW derived from a linear model in which community richness was the independent variable also failed to reveal evidence of autocorrelation ($p = 0.63$)



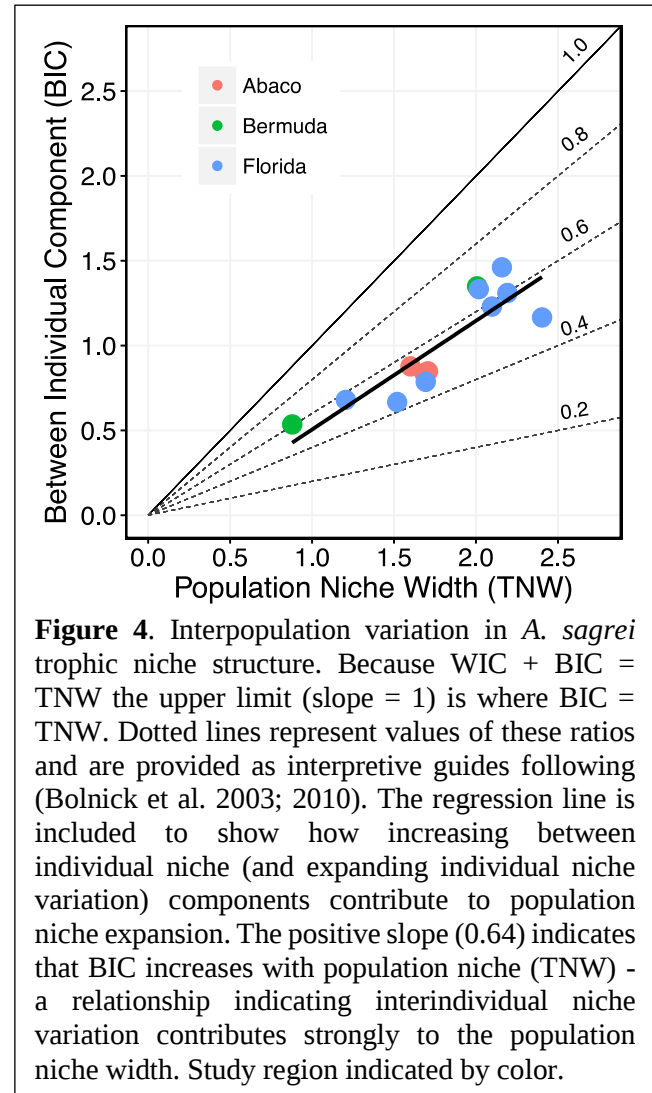
Ultimately, *A. sagrei* population niche width (TNW) increased with the natural log of community richness and spatial regression models showed that geographic distance was a poor predictor of TNW. Within each base model structure, spatial models performed worse than base models and tended to perform worse overall as judged by AIC (Table 3). In all models, community richness was a significant predictor of TNW regardless of model structure and whether space was included in the regression. The best overall model included a nonlinear, $\log(\text{community richness})$ predictor indicating a strong positive and saturating effect of

community richness on *A. sagrei* population niche width whether or not spatial variance – our proxy measure of underlying, and unaccounted for, ecological and genetic autocorrelation – is included in the model or not. (Table 3, Figure 3).

Prediction 2: Intrapopulation niche variation decreases with species richness –

We tested this prediction with several metrics of intrapopulation niche variation, the within individual component. Our analysis of the structure of *A. sagrei* trophic niche showed that WIC and BIC both contributed to TNW expansion. The significant relationship between TNW and WIC (slope = 0.35, $p = 0.010$) indicates a slight increase in individual niche breadth contributes to population expansion. Similarly, the significant positive relationship between TNW and BIC (slope = 0.63, $p < 0.001$) indicates a moderate - strong increase in interindividual niche variation (~ low individual overlap) contributes to population expansion. In combination with no significant increase in BIC/TNW across the TNW range, these data clearly suggest that *A. sagrei* niche structure follows a pattern of parallel niche expansion roughly parallel to the BIC/TNW = 0.6 isocline (Figures 1 & 4).

Our analysis of ecological release revealed a similar result; WIC, BIC, and TNW increased along the community richness gradient, although the WIC relationship was not significant (Figure 5). BIC/TNW (a measure analogous to individual specialization) was not correlated with community richness. These data show that total niche width expands with increasing species richness, primarily from greater niche difference among individuals (Figure 5). While the within individual component did not show a significant increase along the species richness gradient, a positive correlation between richness and WIC suggests a moderate contribution of individual niche expansion to the total niche width – parallel expansion (Figure 1f)



DISCUSSION

Trophic niche variation in *A. sagrei* does not match the predictions of the ecological release model. Our data clearly show that population niche width expands with increasing community richness (Figure 3). In effect, *A. sagrei* populations in species-poor areas (Bermuda, Abaco, Cayman Islands) tend to have narrow population niche widths while those from species-rich sites (Florida, Jamaica, Exuma Islands) have broad ones. Further, our data suggest that intrapopulation niche structure varies predictably with community richness (Figure 5). Specifically, individuals tend to be more generalized (higher WIC) and less similar (higher BIC) in species rich communities. This latter result matches a pattern of parallel expansion of niche components – wider population niches are composed of more dissimilar, and perhaps more generalized individuals – a result qualitatively similar to the niche variation hypothesis, but in the direction opposite that predicted by the ecological release paradigm (Van Valen 1965, Roughgarden 1972, Bolnick et al. 2007, Svanback and Bolnick 2007, Yoder et al. 2010). The pattern of geographic niche variation in *A. sagrei* emerging from our data is clear, the ecology underpinning it is not. Indeed, without additional analyses and experimental tests, we can only speculate as to the eco-evolutionary mechanism(s) underlying the observed pattern. Below, we examine and discuss potential drivers of geographic variation in *A. sagrei* resource use in hopes of stimulating new research directions in the evolutionary ecology of adaptive diversification.

Exploitative Competition

Anolis lizards are often food limited. A series of studies on *A. sagrei* in The Bahamas routinely show that subsidies can boost population size and individual growth rates (Spiller et al. 2010, Wright et al. 2013). They also demonstrate that *A. sagrei* can deplete prey abundances and alter prey community composition in favor of small, low-value prey (Schoener and Toft 1983, Schoener and Spiller 1987, 1999, Spiller et al. 2016). Food limitation and depletion by *Anolis* lizards strongly suggests the potential for exploitative competition to shape resource use. But outside of character displacement, evolutionary theory has little to say about a diversifying role for interspecific competition (for a review of the assumptions underpinning adaptive diversification theory see Abrams et al. 2008b). However, ecological theory does, and meta-analyses show that consumer richness tends to exacerbate resource depletion (Cardinale et al. 2006, Griffin et al. 2013). One might expect that resource partitioning, such as that characterizing *Anolis* ecomorphs, might alleviate some of this interspecific pressure on shared resources (Schoener 1968, Giery et al. 2013). However, empirical studies routinely show that resource depletion is stronger when competing species partition resources (Snyder et al. 2006, Finke and Snyder 2008, Northfield et al. 2010) – a finding in accord with theoretical analysis (Abrams and Rueffler 2009). To the authors' knowledge no study has investigated this in *Anolis* lizards. However, experimental removals of *Anolis* has

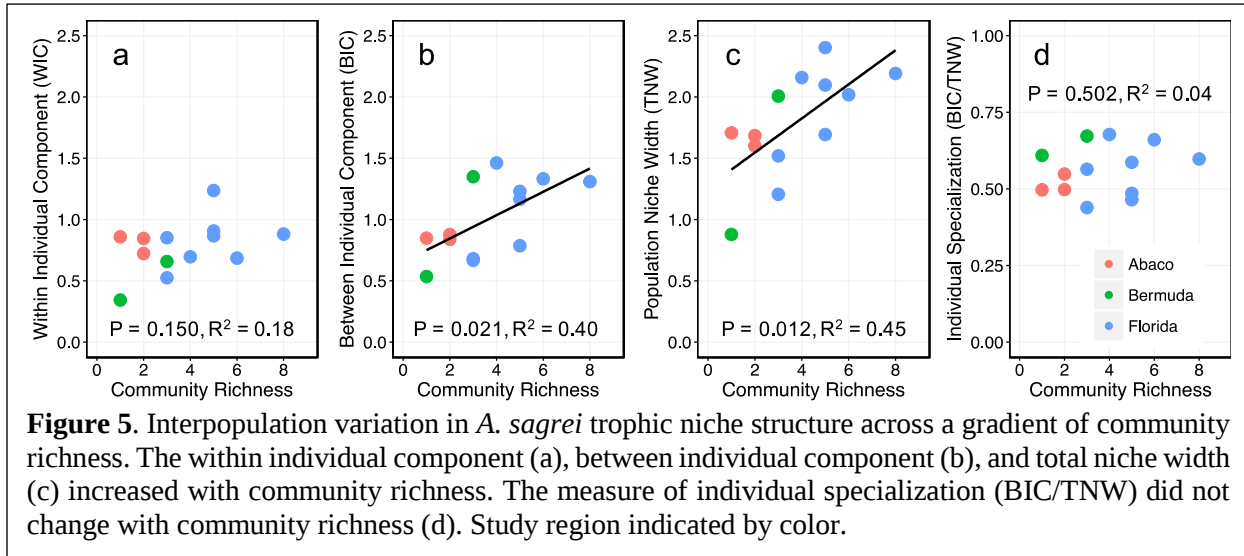
Table 3. Results of spatial regression including alternative models evaluated with AIC. Among all alternative models, model 3, which included the log of community richness proved the best fit overall. Comparisons among models including spatial information (Gaussian (G), Ratio (R), and Spherical (S) residual structures) and one without (Base (B)) showed that the base model performed best, as judged by AIC.

Model	AIC				Beta	St Err	df	F	P	R ²
	Base	G	R	S						
3 Intercept	31.1	36.1	36.1	36.1	1.24	0.16	1,30	882.7	0.000	0.33
log(community richness)					0.36	0.11		11.5	0.002	
1 intercept	35.1	39.9	39.9	40	1.32	0.15	1,30	841.6	0.000	0.34
community richness					0.09	0.03		9.5	0.004	
4 Intercept	43.5	49.1	49.1	49.1	1.20	0.17	1,29	868.7	0.000	0.33
log(community richness)					0.36	0.11		11.3	0.002	
n individuals					0.00	0.00		0.5	0.475	
2 intercept	47.4	52.8	52.8	52.9	1.28	0.16	1,29	828.5	0.000	0.34
community richness					0.09	0.03		9.4	0.005	
n individuals					0.00	0.00		0.5	0.471	

shown that prey depletion is at least as strong in multispecies communities as it is in single species ones (Pacala and Roughgarden 1984, Dial and Roughgarden 1995). In sum, all things equal, empirical data and theoretical analysis suggests resource depletion should be most severe in diverse lizard communities including species that partition resources.

How does resource depletion affect niche width? Efforts to understand the effects of competition on the evolution of population niche breadth have spanned decades, typically geared towards understanding how individuals exploit resources depleted by heterospecific and conspecific consumers (Case 1981, Connell 1983, Taper and Case 1985, Futuyma and Moreno 1988). Two of these models make predictions consistent with our results – niche compression (MacArthur and Wilson 1967), and intermediate competition diversification hypotheses (Jones and Post 2013, 2016). The niche compression hypothesis formulated in (MacArthur and Wilson 1967) extends the basic ecological release scenario by incorporating foraging theory developed in (MacArthur and Pianka 1966) to explore optimal resource use in populations experiencing varying degrees of interspecific competition, among other things. The critical difference between Wilson’s earlier ecological release hypothesis and niche compression is that the population-level niche response to competition depends on the attributes of the limiting resource and the behavior of the focal species. As discussed in (MacArthur and Wilson 1967) niche compression makes several predictions about how a generalist should respond to an increase in interspecific

exploitative competition. First, habitat use should narrow. Second, and more relevant to our study, the population trophic niche should expand as resource depletion forces active, generalist foragers to consume a larger fraction of less-preferred taxa and/or forage over a larger area – effects that would increase WIC and BIC, respectively. This is a clear parallel to the ecological model of adaptive diversification in that interspecific competition also drives negative frequency dependent selection on resource use when consumer niches overlap and resources can be depleted. Heretofore, the niche compression hypothesis has only occasionally interested theoreticians (Schoener 1974, Schoener et al. 1979), and has yet to receive more than a modicum of empirical support (Crowell 1962, Huey and Pianka 1977). Nevertheless, population niche expansion via amendment of resource subsets to the population niche in species-rich communities (increased BIC) suggests optimal foraging by generalist consumers for depleted resources might explain the geographic niche diversification in *A. sagrei* we observe here (Figures 3 & 5).



A newer model making similar predictions has been termed the intermediate competitive diversification hypothesis (Jones and Post 2016). In many ways this model echoes several aspects of niche compression. Specifically, population niche width expands as increasing exploitative competition depletes preferred resources subsequently driving consumers towards less-preferred taxa. However, the model differs in that it explores the extreme upper end of the competition gradient at which all preferred prey are depleted, leaving only non-preferred taxa. The result is a non-monotonic function with TNW increasing and then decreasing across the resource depletion gradient (Jones and Post 2013). Interestingly, the hump-shaped pattern described in the verbal model seems to reflect the highly contingent nature of ecological release effects seen in nature. Jones and Post originally developed their verbal model for intraspecific

competition, but the model is adaptable enough to encompass interspecific competition based on the assumption that species richness increases resource depletion and the overall intensity of competition when consumers are general and resources are fine-grained. Further testing of this model is needed, however the incorporation of nonlinearities in niche theory is clearly worth investigating (Abrams et al. 2008b, 2008a).

Behavioral Interference

Another route by which interspecific interactions shapes resource use is interference competition (Peiman and Robinson 2010). To date, ecological release models have focused on exploitative competition as the critical ecological link between competitors. But a surging interest in behavioral, non-consumptive effects of interspecific interactions has begun to quantify the role of interference competition in resource use. As defined in Grether (2017), interference competition is, “*any costly interaction between individuals over access to a resource, aside from resource depletion, regardless of whether the resource is shared or limiting; includes fighting, dominance, territoriality, and allelopathy (chemical inhibition)*”. Conceptual models of interspecific competition incorporating behavioral interference are beginning to emerge (Peiman and Robinson 2010, Grether et al. 2013, 2017). Behavioral interference is well known among *Anolis*, however, the consequences of interference for niche variation are still rather vague (Jenssen et al. 1984, Hess and Losos 1991, Edwards and Lailvaux 2013, Kamath and Stuart 2015). Fortunately, a series of detailed studies of *Anolis* lizards in South Florida has generated insights into the direct interactions among and within *Anolis* species and their effect on resource use. Briefly, the system consists of two ecologically and morphologically similar species introduced into South Florida, the brown anole *A. sagrei*, and the Puerto Rican Crested Anole (*Anolis cristatellus*). Short-term density reduction experiments conducted by (Losin 2012) in this system suggests weak exploitative competition between these species (as well as within). However, a recent comparative study by (Stroud 2018) that included detailed behavioral observations and dietary analysis shows that when sympatric, the behaviorally subordinate *A. sagrei* moves more frequently, perches lower, consumes more terrestrial prey, and has a wider population niche width. These data suggest that the community richness effect we observe here could arise, in part, from persistent behavioral interference between *A. sagrei* and other members of the community such as *A. cristatellus* (Stroud 2018). These data clearly show that the nature of interspecific interactions between *A. sagrei* and other community members includes direct, behaviorally mediated interactions that change how *A. sagrei* forage without invoking prey depletion (i.e., exploitative competition). This rare coupling of detailed interference behavior, habitat use, diet, and prey depletion provides good evidence that interspecific behavioral interference – an increasingly recognized interaction in *Anolis* and other animals – is likely to shape how resource use responds to interspecific competition. These data show that interference intensity probably increases with species richness and drives a corresponding expansion of the

population niche.

Covarying Diversity Gradients

Because our study is a pattern-based analysis we cannot exclude a host of confounding variables that might explain the observed result. These variables include geographic variation in prey and predators. First, we do not account directly for the composition of prey communities. It is quite possible that geographic variation in trophic niche we observe is ultimately determined by geographic variation in prey communities. If prey diversity is correlated with lizard diversity, then the observed pattern may simply reflect consumption of prey in proportion to their availability. While we cannot exclude this possibility, we find it unlikely that an underlying gradient in prey diversity could explain our results. Perhaps the biggest reason we doubt this effect is that our dietary analysis is done at a coarse taxonomic level – order. Geographic variation in the richness of higher taxonomic levels such as order should be rather low (Gaston et al. 1995). Second, predation can also affect how consumers interact with prey (Roughgarden and Feldman 1975, Chase et al. 2002). Several of the lizards we include in our community richness gradient are predators of *A. sagrei* as well as competitors. For example, the curly-tailed lizard (*Leiocephalus carinatus*) is a well-known predator of *A. sagrei* where they co-occur (e.g., Bahamas and Florida) (Giery *unpublished data*). In this analysis we did not differentiate between species based on the types of interaction with *A. sagrei*. Given the diverse effects of intraguild predators on prey we could not speculate as to how this gross categorization might affect our observed patterns. However, terrestrial predators such as *L. carinatus* are known to affect *A. sagrei* behavior and population density (Schoener and Spiller 1999, Chejanovski et al. 2017, Lapiedra et al. 2018). Indeed, altered behaviors and density should influence the trophic niche and deserve further consideration. In addition to these two interspecific interactions, climatological and productivity gradients might also influence niche breadth (Roughgarden 1974, Gainsbury and Meiri 2017). We did not assess them here.

Ecological Release: Shifting Ideas and New Opportunities

In sum, our results clearly do not fit the ecological model of adaptive diversification putting them at odds with initial data for *Anolis* (Roughgarden 1974, Lister 1976a, 1976b), as well as more recent research on stickleback (Svanback and Bolnick 2007, Bolnick et al. 2010), yellow perch (Svanbäck and Persson 2004), and Bahamian mosquitofish (Araujo et al. 2014). Instead, the data presented here indicate that interspecific interactions may generate patterns of niche variation that differ from the classic ecological release scenarios that dominate adaptive diversification models such as that depicted in Yoder et al. (2010) and Wellborn and Langerhans (2015). Clearly, there is still much to be explored and explained about why population niche breadth increases with community richness in *A. sagrei*. What is clear however, is that a foundational assumption of adaptive diversification does not hold for our data on the trophic

niche of *A. sagrei*. Further, previous studies of the ecological release paradigm in *Anolis* have yielded mixed results (Lister 1976b, 1976a). Clearly, additional work is needed to understand the processes generating the observed pattern. The contrast between theory and our data leads us to suppose that the ecological release paradigm insufficiently explains how populations respond to variation in interspecific interactions. We believe, this clear incongruity demands a closer examination of the mechanistic links between ecological opportunity and diversification.

Along those lines, emerging models, new data, and an increasing appreciation for behavioral interference provide exciting opportunities for understanding consumer competition and community dynamics (Fukami et al. 2007, Grether et al. 2013, Fukami 2015, McPeck 2017). In the case of adaptive diversification, evolutionary models have largely failed to integrate the contingent ecological and evolutionary dynamics that could provide alternatives to the ecological release paradigm (discussed in Abrams et al. 2009). Predicting how populations respond to ecological variation should not overlook these complexities. For example, as judged by our data, models of interpopulation niche variation that consider optimal foraging in heterogeneous environments (e.g., niche compression) and nonlinearities (e.g., intermediate competition diversification) better predict geographic niche variation in *A. sagrei*.

Building evidence for and general appeal of the ecological release paradigm has made it the favored eco-evolutionary bridge between ecological opportunity and adaptive diversification (Schluter 2000, Yoder et al. 2010, Nosil 2012). The crucial ecological mechanism linking ecological release to adaptive diversification is an eco-evolutionary response (negative frequency dependent selection) to intensified intrapopulation resource competition arising from a reduction of interspecific exploitative competition and density compensation (Bolnick 2001, 2004, Bolnick and Lau 2008). However, pattern-based evaluations of ecological release and niche variation hypotheses reveal diverse responses (Crowell 1962, Roughgarden 1974, Lister 1976b, Huey and Pianka 1977, Vassallo and Rice 1981, Losos et al. 1994, Losos and Queiroz 1997, Mesquita et al. 2007, Svanback and Bolnick 2007, Costa et al. 2008, Araújo et al. 2009, Thomas et al. 2009, Nimmo et al. 2011, Jones and Post 2013, 2016, Araujo et al. 2014). This diversity suggests that intensified intraspecific competition attending release from interspecific competition is not the only way to generate phenotypic diversity in populations. As discussed in Abrams et al. (2008b), the conditions underpinning the ecological model of adaptive diversification are rather narrow and unlikely to reflect how generalist consumers interact with resource arrays. Indeed, a wide range of conditions are likely to generate disruptive selection on consumer resource use and a comprehensive survey of existing data is sorely needed to better summarize the evidence. We specifically recommend that behavioral interference, interspecific competition, foraging behavior, and predation need more attention in the ecological release literature. Ultimately, a unified conceptual synthesis is needed for the field to advance.

How could such modifications alter the dynamics of the ecological theory of adaptive radiation? First, it would shift the model away from an ecological release paradigm. What we mean here is that the initial stages of adaptive diversification would not rely on an inverse

relationship between competitor richness and niche breadth to generate phenotypic diversity. Rather it would broaden the range of ecological components in the direction of species interactions in general – which are obviously much more diverse than the ecological release paradigm suggests. Doing so would uncover important new dynamics. For example, if the effect of community richness on *A. sagrei* diversification we illustrate here is reflective of initial ecological stages of adaptive diversification, it suggests that adaptive diversification processes are subject to a positive feedback (i.e., diversity begets diversity) driven by adaptive responses to increasing competition (i.e., not just intraspecific competition). Ultimately, it seems that niche diversification is not just a phenomenon attending low community richness (the classic model of ecological release), but a more general pattern emerging under a broad range of ecological circumstances. Stated succinctly, the pattern we uncover here suggests that more diverse communities are composed of more diverse populations.

In conclusion, the ecological release paradigm underpinning the ecological theory of adaptive radiation seems incongruent with our findings. Surprised by our results, we find ourselves without a satisfying explanation of their origin. Nevertheless, we find the overall pattern compelling. Our search for an explanation has identified new opportunities for exploration – in particular, the eco-evolutionary dynamics at the root of adaptive diversification. Much remains to be explored in the dataset we’ve assembled. For example, analysis of variation in prey size, prey habitat, and *A. sagrei* habitat use along the community richness gradient will help identify the mechanisms of niche evolution in *Anolis*. Nevertheless, we hope that our foray into the geographic variation in *A. sagrei* trophic niche stimulates new ideas about the adaptive diversification of *Anolis* lizards and a closer look at the ecological release paradigm.

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