



# Broad-scale gradients of resource utilization by phyllostomid bats in Atlantic Forest: patterns of dietary overlap, turnover and the efficacy of ecomorphological approaches

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## Abstract

Identifying mechanisms that promote coexistence at the local level is enigmatic for many organisms. Numerous studies have indirectly demonstrated that biotic interactions may not cause deterministic patterns reflective of the coexistence of interacting bat species. Nonetheless, demonstration of the partitioning of resources by phyllostomid bats by directly examining diet matrices may illuminate a mechanism of coexistence. I examined the dietary overlap of phyllostomid bats across 23 sites in the Atlantic Forest of South America. I also examined components of beta diversity (turnover and nestedness) of resources among species as well as the degree to which morphology can act as a surrogate for dietary similarity in each community. Bats exhibited high overlap. Nonetheless, dietary beta diversity was more related to turnover than nestedness of items suggesting substantive species-specific affinities. Niche breadth and dietary overlap were positively related to the number of species and the number of resources consumed in communities. Accordingly, changes in richness across Atlantic Forest may be facilitated by increases in resources available at the community level. There were positive, yet weak relationships between morphological and dietary distance. The relationship between morphology and diet was invariant relative to geography, species richness, number of dietary resources, average diet breadth and average dietary overlap indicating that in the Atlantic Forest morphology is a consistent surrogate of dietary relationships of species. Atlantic Forest is one of the most anthropogenically modified tropical forests in the world. This in combination with distinct climatic seasonality likely causes higher dietary overlap, weaker ecomorphological relationships and persistence of only the most general bat species.

**Keywords** Atlantic Forest · Bats beta diversity · Dietary overlap · Ecomorphology

## Introduction

Biological processes that allow the coexistence of potentially interacting species within ecological communities have peaked the interest of ecologists and evolutionary biologists for decades (Cody and Diamond 1975; Diamond and Case 1986; Strong et al. 1984). Indeed, partitioning of food (Schoener 1974), habitat (MacArthur 1958) or time (Craighead and Craighead 1956) are frequently cited means whereby interspecific competitors are able to coexist within

ecological communities. Such partitioning can result from either short-term behavioral modifications (Shkolnik 1971) or more long-term phenotypic evolution (Brown and Lieberman 1973) that enhances the relationship between form and function regarding the processing and ultimately partitioning of different resources.

Selection is the differential success of some species over others within particular communities that are often expressed as differences in distribution and abundance (Vellend 2017). To date, selection is the most frequently cited mechanism underlying the structure of ecological communities and interspecific competition has historically been the most frequent form of selection examined (Vellend 2017; O'Connell and Hallet 2019; Stevens and Estrada-Villegas 2020). A common assumption is that competition manifests as partitioning of resources at the community level (MacArthur and Levins 1967) and the diet matrix describing the frequency of items consumed by a group of coexisting

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species is often used to quantify interspecific interactions (Gotelli and Graves 1996). A number of approaches have been developed to examine the information in a dietary matrix to better understand the coexistence of species. A traditional approach is to examine patterns of dietary overlap (MacArthur and Levins 1967). A number of indices have been developed, most of which ultimately estimate average pairwise overlap among species within a community, and resource partitioning is indicated by overlap indices that are lower than those generated under a null model (Gotelli and Graves 1996).

Other nonrandom patterns of resource use can result even when processes do not manifest as nonrandom patterns of pairwise overlap. A dietary matrix is a resource-use analog to a number of other kinds of matrices used to characterize patterns of coexistence in community ecology. For example, a dietary matrix is composed of rows (consumers) and columns (resources) and this is analogous to the rows (sites) and columns (species) of a community composition matrix. Thus, the power of many of the quantitative approaches used to examine nonrandom patterns of species co-occurrence (Arita et al. 2012) can be harnessed to better understand the distribution of resource utilization among coexisting species and shed light on the mechanistic basis of community organization.

One recent development in the analysis of patterns of species co-occurrence that could illuminate mechanisms underlying resource utilization of coexisting species comes from quantification and partitioning of spatial beta-diversity of ecological communities (Baselga 2013, 2017). Beta-diversity can be partitioned into the two different components of turnover and nestedness that are the product of very different structuring mechanisms. Strong spatial turnover can result from species-specific habitat affinities in heterogeneous landscapes and reflects the role of selection (Vellend 2017) on community organization. In contrast, nestedness can occur when species differentially colonize habitat patches randomly but differences in abundance allow some species to colonize more patches than others (Coleman et al. 1982) or when extinction probabilities vary in a systematic fashion among species (Patterson 1987). Turnover and nestedness are very different determinants of beta diversity that result from fundamentally different biological processes (Baselga 2013) and partitioning beta diversity into these different components has provided a number of insights regarding the mechanistic basis to community organization along environmental gradients (Leprieur et al. 2011; Batista et al. 2020; Ribeiro et al. 2020).

From a similar perspective involving species co-occurrence, strong species-specific differences resulting from competitive interactions or phenotype-performance interactions can cause strong partitioning of the diet matrix that corresponds to the turnover component of beta diversity.

Accordingly, community-level resource partitioning of the dietary matrix can be detected by the demonstration of high degrees of turnover. Similarly, if species consume resources as they are encountered (i.e., randomly) and there are differences in the abundance of resources and consumers, this would give rise to dietary matrices that are nested, a pattern corresponding to the nestedness component of beta-diversity (Coleman et al. 1982; Almeida-Neto et al. 2008; Baselga 2017). Examining aspects of the entire matrix, as opposed to averages of pairwise overlaps, may allow these two processes to be disentangled.

Lastly, ecomorphological approaches are often used to estimate similarity in resource use to evaluate nonrandom patterns among coexisting species reflective of the partitioning of resources, an important form of deterministic community structure (Ricklefs and Travis 1980; Willig and Moulton 1989; Ricklefs and Miles 1994). Such an approach assumes a strong correspondence between form and function whereby phenotypic characteristics are significantly and strongly correlated with dietary constituents of species (Wainwright 1994). Despite substantial evidence of relationships between form and function (Hespenheide 1973; Werner 1974; Karr and James 1975; Dumont et al. 2012), few studies have verified the degree to which morphological similarity is related to dietary similarity at the community level and thus the efficacy of ecomorphological approaches for understanding resource-mediated coexistence of species. Such an assumption underlies much of ecometrics (Eronen et al. 2010; Polly et al. 2011) but allows inference of the determinants of community structure when direct data on resource utilization are unavailable, it is rarely ever tested. Here I perform such a test.

Phyllostomid bats (Phyllostomidae: Chiroptera) are ideal candidates for examination of patterns of dietary overlap, turnover and ultimately generality of ecomorphological relationships. They are exceedingly biodiverse (Fleming et al. 2020) and dominate most bat communities in the New World tropics and subtropics (Stevens 2004). One important facet of phyllostomid biology that contributes to their biodiversity is the vast forms of resources that are consumed across the family (Giannini and Kalko 2005). Indeed, phyllostomid bats are more ecologically diverse than any other family-level taxon in Mammalia (Baker et al. 2003) and consume invertebrates, vertebrates, fruit, nectar, and the blood of other vertebrates (Kalko 1998). Associated with this ecological diversity is an impressive amount of phenotypic diversity that is strongly related to performance underlying the association between form and function, in particular how the cranium (Dumont et al. 2012) or wings (Norberg and Rayner 1987) determine what kind of resources that are consumed and the different foraging strategies used to obtain them. Indeed, phyllostomid bats exhibit a variety of related morphological

and foraging characteristics (i.e. syndromes) that are tightly related to resource acquisition. Such syndromes characterize major divisions in the family related to insectivory, carnivory, frugivory, nectarivory and sanguinivory (Kalko 1998). Even within the most diverse ecological group, the frugivores, there are syndromes of understory *Piper spp.* specialization by species of the genus *Carollia*, understory *Solanum spp.* specialization by species of the genus *Sturnira* and widespread *Ficus spp.* and *Cecropia spp.* specialization by the subfamily Stenodermatinae (Fleming 1986; Giannini and Kalko 2005; Sanchez and Giannini 2018).

Herein, I describe a compilation of 23 different datasets describing resource utilization by phyllostomid bats across the Atlantic Forest of South America. I use these data to address five broad aims. The first is to describe the pattern of dietary overlap among phyllostomids and to characterize interspecific interactions across this expansive ecoregion. Second, I examine aspects of turnover and nestedness within dietary matrices to disentangle syndrome-related and passive sampling-related variation. Third, I characterize the relationship between proximity in dietary resource space and proximity in morphological space, estimate the strength of relationships across Atlantic Forest, and more specifically characterize the efficacy of ecomorphological approaches when used to understand resource utilization patterns at the local level. Fourth, I describe biogeographic patterns of resource utilization of phyllostomid bats across the Atlantic Forest with the aim to better understand how patterns of resource utilization ultimately facilitate the pattern of diversity in this ecoregion. Finally, I further explore relationships among beta diversity, overlap and ecomorphology associated with the dietary matrix to better understand resource partitioning within this system.

## Theoretical predictions

### Dietary structure

If phyllostomid bats partition resources at the community level in Atlantic Forest, I expect dietary overlap measured for each site to be frequently lower than expected based on a null model. To this end, across a number of communities the median standardized effect size of dietary overlap based on comparison with a null model should be significantly smaller than zero. Partitioning of resources should also cause variation in the dietary matrix to be more related to species-specific differences than passive sampling based on availability; I expect additive partitions of total beta diversity to be significantly greater for turnover than for nestedness. Moreover, if the morphology of

phyllostomid bats determines resource use then I expect that across a number of communities a strong, positive and significant association between the morphological distance of species and dietary distance will be reflected in the median correlation being significantly greater than zero.

### Relationships among variables

Given the large battery of variables describing bat diets and community structure quantified here, I evaluated a number of a-priori predictions. First, if the use of morphological distances to estimate dietary distances is a valid surrogate to estimate trophic relationships among species then the relationship should be invariant and not change systematically with geography, local bat species richness, number of resources used by bats in a community, average diet breadth or degree of dietary overlap among species.

If turnover and nestedness components of beta diversity of dietary matrices correspond to the partitioning of diets and passive sampling of the resource base, respectively, these beta diversity metrics should be related to the degree of dietary overlap and ecomorphological structure of communities but in different ways. Specifically, if the magnitude of the turnover partition reflects the degree of specialization and partitioning of diets then it should also be negatively related to dietary overlap and positively related to the strength of the ecomorphological structure. Given the same logic, passive sampling of dietary constituents should be related to higher measures of dietary overlap and lower ecomorphological structure. Accordingly, partitions of nestedness should be positively and negatively related to these characteristics, respectively.

### Relationship between resource utilization and diversity of communities

There is a considerable and long-standing theoretical basis for how variation in resources is related to variation in species richness of consumers. Coexistence of higher numbers of species can be facilitated by three distinct processes: (1) increases in the number of available resources, (2) decreases in the dietary breadth of species, or (3) increases in overlap among species regarding those resources (MacArthur 1972). Accordingly, gradients indicative of how variation in resources are related to the diversity of consumers should also exist: (1) average dietary breadth or average dietary overlap should be positively related to the number of available resources, (2) overlap should increase or niche breadth should decrease with greater numbers of consumers and (3) there should be a positive relationship between the number of consumers and the number of available resources.

## Materials and methods

### Atlantic Forest and its bat communities

Atlantic Forest is the second-largest tropical forest in the New World, originally covering approximately 150 million acres (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2009). Atlantic Forest is clearly distinct from Amazonian Forest, being both geographically separated by the extensive Cerrado biome as well as possessing a distinct flora (Oliveira-Filho and Fontes 2000). Atlantic Forest represents the longest latitudinal gradient of tropical forest in the world (Galindo-Leal and Camara 2003; Ribeiro et al. 2009) and as such exhibits substantial heterogeneity from floristic, edaphic and climatic perspectives (Fundacao Instituto Brasileiro de Geografia e Estatistica 1993; Oliveira-Filho and Fontes 2000). Perhaps the best-characterized bat fauna in the world exists in Atlantic Forest and much is known regarding spatial variation in distribution and abundance of this important mammalian taxon (Muylaert et al. 2017). Despite relatively low diversity in Atlantic Forest, bats exhibit strong spatial gradients of species richness (Stevens 2013) and turnover (Batista et al. 2020) as well as other important dimensions of biodiversity (Stevens and Gavilanez 2015).

### Data on dietary patterns of phyllostomid bats in Atlantic Forest

To construct a database on dietary patterns of bats across a number of communities in Atlantic Forest, I began with a Web of Science search using the terms “Atlantic Forest and Bat and Diet”. This search was conducted on 3 August 2020. Based on the studies identified, I examined the literature cited sections of each to obtain additional records. I also queried each library of each state and national university in the states of Brazil that overlapped the Atlantic Forest. I examined all theses and dissertations related to bats and perused the literature cited sections of these documents to obtain additional records. I also included literature discovered serendipitously during this search. In total, I encountered 56 different studies describing at least some aspect of the diets of Phyllostomidae in the Atlantic Forest. Publications dates of studies ranged from 1985 to 2021. I retained and analyzed data on phyllostomid bat diets from 23 different communities described by 22 studies distributed throughout Atlantic Forest (Appendix 1, Fig. 1). Most of the studies that were not included in analyses did not report diets of all phyllostomids at the study site (i.e. only reported on the frugivory component of bat consumption or only reported diets on a subset of



**Fig. 1** Distribution of 23 studies examining bat diets across the Atlantic Forest. Black dots represent the location of sites. White shading represents the extent of Atlantic Forest in South America

species or just those frugivores that consumed one or a few focal plant species) or did not quantify a number of interactions (i.e. presence/absence or proportional studies were excluded). For each community dietary data was represented by a species by dietary item (different species of fruit-plants, unidentified fruit pulp, arthropods, vertebrate blood, etc.) matrix.

### Quantitative analyses

I used the Pianka index (Pianka 1973) based on the number of observations for each dietary category for each species in each community to characterize dietary overlap between species at each site. I used the mean across all species pairs as the summary statistic for each community which is recommended by Gotelli et al. (2015). Magnitude of overlap indices is best interpreted relative to a random distribution generated from a null model (Gotelli and Graves 1996). Thus, when characterizing the degree of dietary overlap I considered the standardized effect size



of the Pianka index. I used EcosimR (Gotelli et al. 2015) to generate null distributions of mean overlap based on the RA3 randomization algorithm. The RA3 algorithm retains the niche breadth of each species by assigning the same number of resources used but randomizing the identity of resources; it reshuffles the rows of the dietary matrix. RA3 has been shown to perform well in detecting non-random overlap patterns (Winemiller and Pianka 1990) and is recommended by Gotelli and Graves (1996). I used a one-sample Wilcoxon signed-rank test (Sokal and Rohlf 1995) to examine whether the median SES-Pianka was different from zero.

Methods to decompose a species by site composition matrix to distinguish between species-specific habitat differences (i.e., turnover) and passive sampling of habitat patches (i.e., nestedness) have been well developed in the beta-diversity literature (Baselga 2013, 2017; Ribeiro et al. 2020). A species by diet matrix can be treated the same way to distinguish the relative effects of partitioning (i.e., turnover or balanced variation) and passive sampling (i.e. nestedness or abundance gradients). I applied the methods of Baselga (2013) to distinguish between turnover and nestedness and the methods of Baselga (2017) to distinguish between balanced variation and abundance gradient forms of variation, analogs of turnover and nestedness that consider information on frequencies. I used the *adespatial* package in R (Dray et al. 2018) to partition beta diversity. To distinguish significant differences between the sizes of turnover and nestedness partitions of beta diversity I used a paired *t*-test (Sokal and Rohlf 1995).

I used a Mantel test (Sokal and Rohlf 1995) to examine the relationship between distance in dietary space and distance in morphological space for bats in each community. For the number of each dietary item consumed by each bat species I calculated a Bray–Curtis distance (Bray and Curtis 1957) to estimate dietary distance. I calculated a Euclidean distance between species based on log-transformed morphological variables (below) to estimate morphological distance. Distances were calculated and mantel tests were conducted using package *Vegan* (Oksanen et al. 2017) in R. To examine an overall relationship between morphology and diets across all 23 communities, I tested whether the median of the correlations determined by Mantel tests was different from zero based on a one-sample Wilcoxon signed-rank test (Sokal and Rohlf 1995). To evaluate invariance of the relationship between diet and morphology, I used a Pearson product-moment correlation coefficient (Sokal and Rohlf 1995) to examine relationships between the magnitude of the mantel statistic for each community and its latitude, longitude, species richness of bats, number of dietary resources, average dietary breadth and dietary overlap of bats. All correlation analyses, *t*-tests and Wilcoxon's Signed-Rank tests were performed in SPSS version 25 (IBM Corp. 2017).

To characterize the morphology of species, I collected data from the literature on forearm length, the greatest length of skull, condylobasal length, width across the post orbital constriction, breadth of the braincase, length of the maxillary toothrow, breadth across the upper molars, breadth across the canines and mastoid breadth measured with digital calipers (Alvarez et al. 1991; Gannon et al. 1989; Garbino et al. 2020; Hurtado and D'Elia 2019; Lim et al. 2003, 2008; Lopez-Gonzalez 2005; Moratelli and Dias 2015; Norguero et al. 2003; Oprea et al. 2009; Ortega and Alarcon-D 2008; Simmons and Voss 1998; Solmsen and Schiliemann 2008; Stuhler et al. 2019; Swanepoel and Genoways 1979; Velazco and Lim 2014; Webster and Owen 1984; Williams et al. 1995; Willig 1983). These measures characterize body size as well as the size and shape of the cranium, two important trophic apparatus of bats (Norberg and Rayner 1987; Dumont et al. 2012). Of the 297 means across the 33 species used in analyses, I was unable to obtain 48 measurements (16%). I used a maximum likelihood estimator of missing values (Little and Rubin 1987) to estimate the 48 missing measurements.

## Relationships among variables

I used Pearson product-moment correlation coefficients (Sokal and Rohlf 1995) to examine relationships between the SES-Pianka index, number of dietary resources, bat species richness and niche breadth. Number of dietary resources was simply the number of different kinds of items consumed across all bats in a particular community. To determine niche breadth I counted the number of dietary resources consumed by each bat species in a community and averaged these counts across all species.

I used Pearson product-moment correlation coefficients (Sokal and Rohlf 1995) to characterize relationships between different partitions of beta diversity and the standardized effect size of dietary overlap. To examine how different beta diversity partitions were related to ecomorphological patterns I again used Pearson product-moment correlation coefficients. To estimate relationships for corresponding partitions of beta diversity I estimated the Bray–Curtis (abundance based) and Sorrensen's (presence/absence based) distances based on dietary items for each community. I then conducted a mantel test between the Euclidean distance based on morphology and distance, either Bray–Curtis or Sorrensen's distances for diets. I did the same for each partition of beta diversity (i.e. Turnover, Nestedness, Balanced Variation and Abundance Gradients). I then correlated the relationship between a partition of beta diversity and morphology with the relationship between the corresponding overall measure of beta diversity and morphology. All correlations were performed in SPSS version 25 (IBM Corp. 2017).

## Results

Communities in Atlantic Forest were variable in terms of resources, bat consumers and how bats consumed those resources. Across sites, there was an average of 18.09 resources utilized by an average of 8.52 phyllostomid bat species. Average bat dietary breadth was 5.05 resources suggesting substantive turnover among species in terms of what they consume. Dietary overlap, indicated by the Pianka index was low and averaged 0.32. Nonetheless, when compared to null models, overlaps were consistently higher than expected due to chance alone (Fig. 2). Of the 23 dietary matrices examined, 17 were significantly different from null matrices with 16 exhibiting significantly high dietary overlap. Median SES-Pianka was 3.22 and significantly different from zero (one-sample Wilcoxon signed-rank test,  $P < 0.001$ ,  $N = 23$ , Fig. 2).

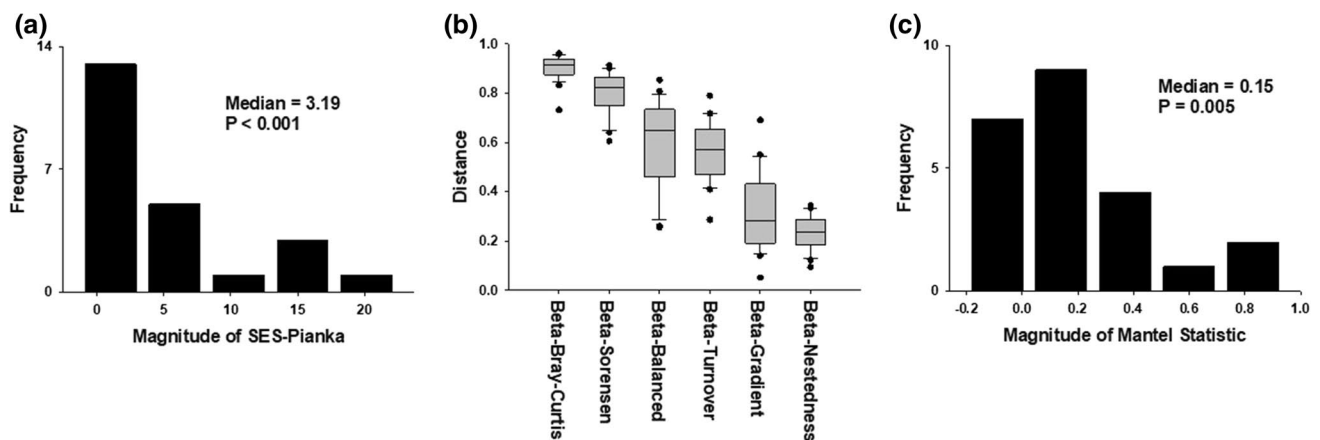
The relationship between dietary distance and morphological distance was variable and often weak across communities. Of the 23 sites, 18 exhibited positive Mantel statistics but only 4 were significant ( $P < 0.05$ ) on their own. The median mantel statistic was 0.14 but significantly greater than zero (one-sample Wilcoxon signed-rank test,  $P = 0.006$ ,  $N = 23$ , Fig. 2). The relationship between morphological and dietary distance was relatively invariant and did not systematically change with latitude or longitude (Latitude:  $r = 0.25$ ,  $P = 0.252$ ,  $df = 21$ ; Longitude:  $r = 0.27$ ,  $P = 0.217$ ,  $df = 21$ ), with bat species richness ( $r = -0.40$ ,  $P = 0.060$ ,  $df = 21$ ), number of dietary resources at sites ( $r = -0.14$ ,  $P = 0.537$ ,  $df = 21$ ), average dietary breadth of species at sites ( $r = 0.19$ ,

$P = 0.379$ ,  $df = 21$ ) or degree of dietary overlap ( $r = -0.28$ ,  $P = 0.184$ ,  $df = 21$ ).

Turnover and nestedness both contributed to variation in dietary matrices. Distances and variation partitions were greater when calculated based on abundance (i.e. frequency of dietary items) as opposed to incidence (Fig. 2) and in two of the three cases differences were significant ( $\text{Beta}_{\text{Sor}}$  vs  $\text{Beta}_{\text{Bray}} - t_{22} = -9.38$ ,  $P < 0.001$ ;  $\text{Beta}_{\text{Turn}}$  vs  $\text{Beta}_{\text{Bal}} - t_{22} = -0.88$ ,  $P = 0.391$ ;  $\text{Beta}_{\text{Nest}}$  vs  $\text{Beta}_{\text{Grad}} - t_{22} = -2.96$ ,  $P = 0.007$ ). For both incidence- and abundance-based analyses (Fig. 2), partitions reflecting species-specific differences (i.e., turnover and balanced variation) were larger than partitions reflecting passive sampling (i.e., nestedness and abundance gradients) and these two differences were significant ( $\text{Beta}_{\text{Turn}}$  vs  $\text{Beta}_{\text{Nest}} - t_{22} = 8.72$ ,  $P < 0.001$ ;  $\text{Beta}_{\text{Bal}}$  vs  $\text{Beta}_{\text{Grad}} - t_{22} = 3.94$ ,  $P < 0.001$ ). The biggest variation component in dietary matrices was related to species-specific differences among bats in terms of diets.

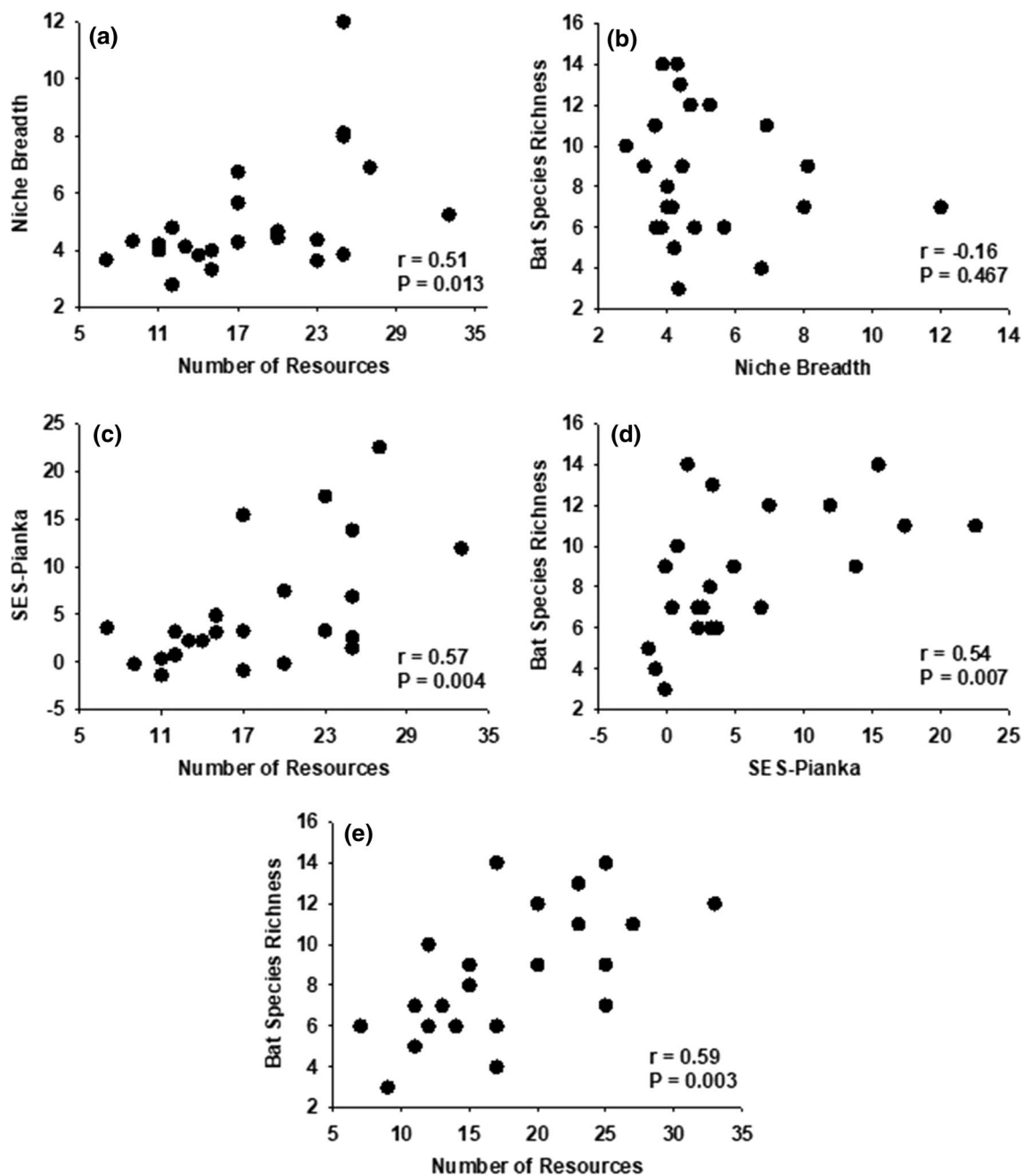
## Geographical ecology of bat resource use

Across sites, the number of resources was positively related to average niche breadth, degree of dietary overlap and phyllostomid species richness (Fig. 3). Degree of dietary overlap increased and average diet breadth was unrelated to bat species richness (Fig. 3). Increases in the number of phyllostomid species were related to increases in the number of resources and increases in dietary overlap in more diverse communities.



**Fig. 2** Patterns of dietary overlap (a), beta diversity within dietary matrices (b) and relationships between morphological distance and dietary distance for 23 phyllostomid bat communities in Atlantic Forest (c). Relative magnitude of dietary overlap was expressed as the standardized effect size of the Pianka index after comparison with a null model. Beta diversity was measured as the Bray–Curtis and Sorensen dissimilarity indices that characterized differences based on

the frequency of dietary items or their presence/absence, respectively. The Bray–Curtis index was partitioned into balanced variation (Balanced) and abundance gradients (Gradient) whereas the Sorensen index was partitioned into turnover and nestedness. For the examination of ecomorphological structure, mantel statistics were calculated to estimate the relationship between Euclidean morphological distance and Bray–Curtis dietary distance



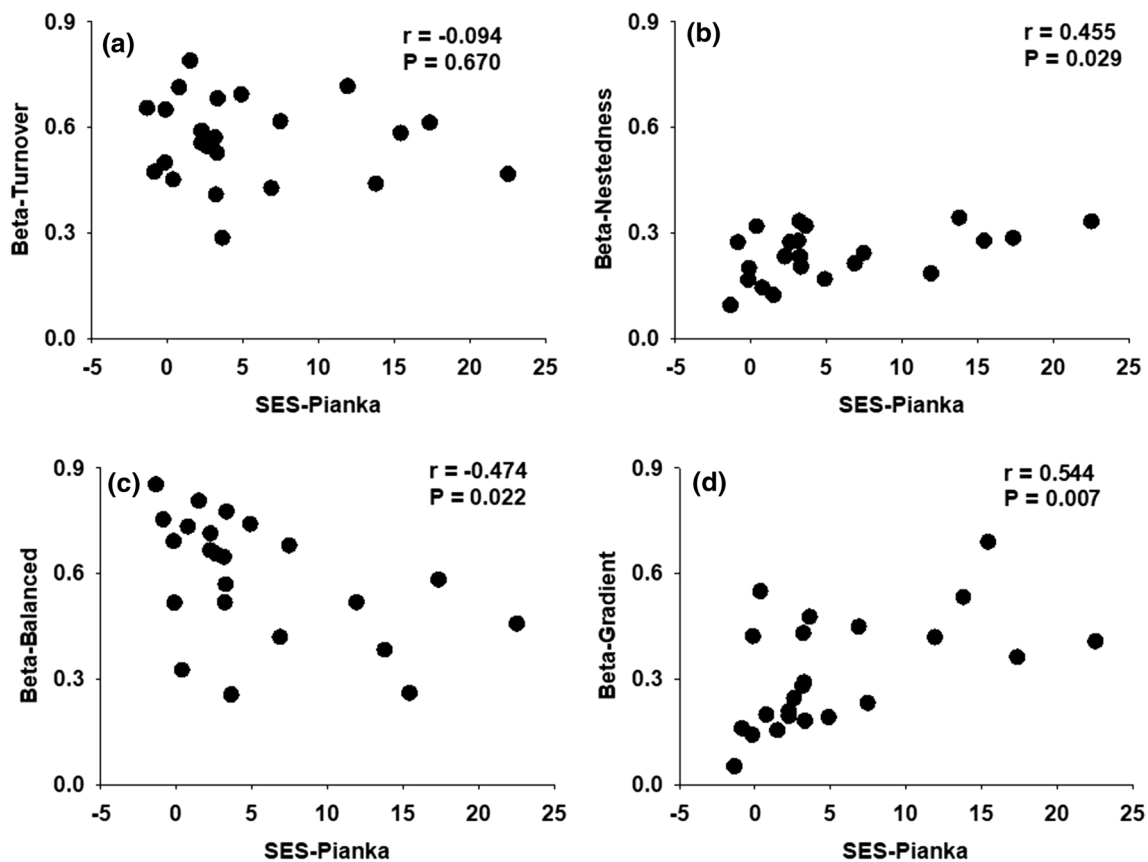
**Fig. 3** Gradients of resource utilization and diversity across 23 phyllostomid bat communities in Atlantic Forest. Relationships and their significance were determined by Pearson product-moment correlation

tests. SES-Pianka refers to the standardized effect size of the Pianka index of dietary overlap

### Correlates of beta diversity of dietary matrices

Turnover-balanced and nestedness-gradient partitions of dietary distance matrices reflected different ecological processes. Partitions of beta diversity were significantly related to dietary overlap but in different ways (Fig. 4). As predicted, measures of turnover-balanced variation were negatively related to dietary overlap but only significantly

so for balanced variation. The more specialized species were in a community the less overlap and greater the balanced variation components. Measures of nestedness-abundance gradients exhibited the opposite pattern. In situations of high overlap, there is little specialization and beta diversity of the dietary matrix is more related to differences in abundance that contribute to nestedness or abundance gradients.



**Fig. 4** Relationships between partitions of beta diversity and dietary overlap across 23 phyllostomid bat communities in Atlantic Forest. Relationships and their significance were determined by Pearson

product-moment correlation tests. SES-Pianka refers to the standardized effect size of the Pianka index of dietary overlap

Beta-diversity partitions of the dietary matrix were strongly related to the strength of ecomorphological patterns within communities providing further support that ecological insights can come from beta-diversity partitions (Fig. 5). Strength of the correlation between morphology and diet was positively related to the turnover-balanced variation partition and strongly negatively related to the nestedness-abundance gradient partition. When diets were more specialized and exhibited higher turnover-balanced variation there was greater ecomorphological structure as demonstrated by a higher Mantel statistic. Conversely, when diets were more stochastically related to morphology, the nestedness-abundance gradient partition was larger, reflecting greater niche breadth related to passive sampling of the resource base by more abundant consumers.

## Discussion

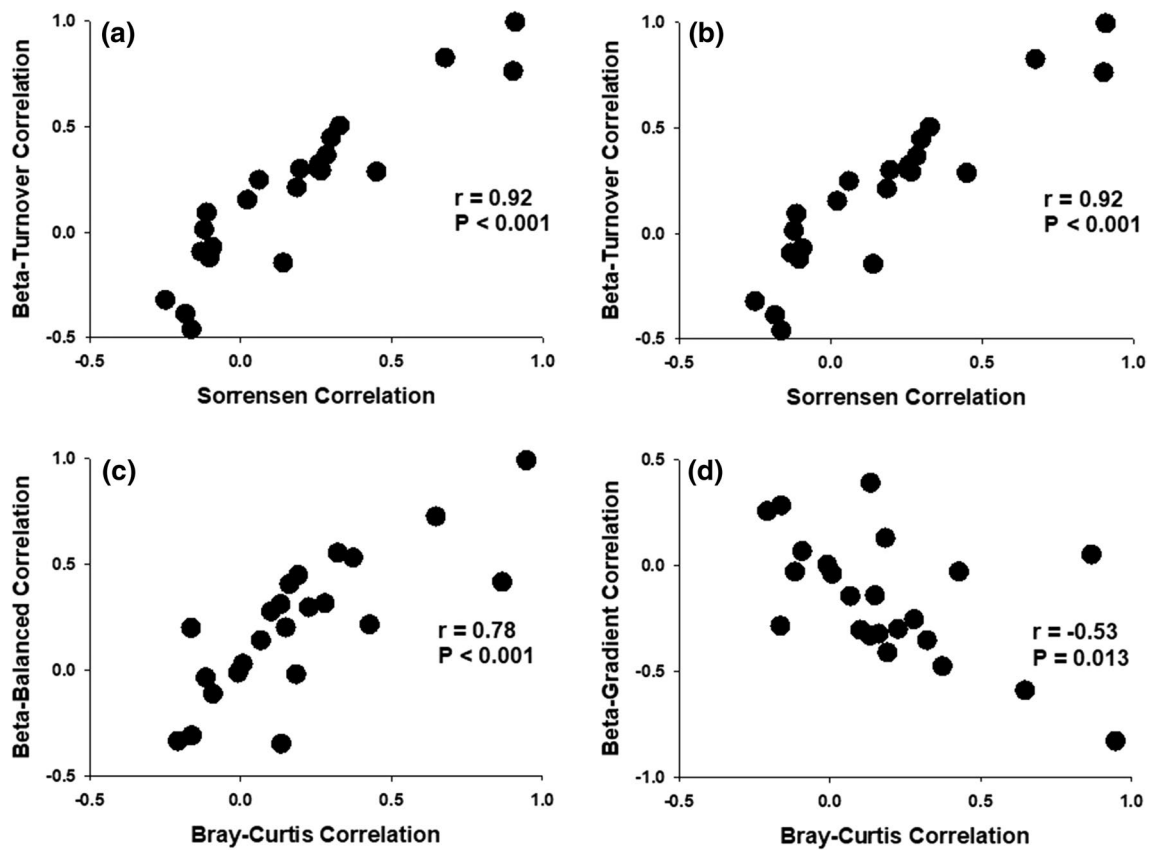
Consumption of resources by bats in the Atlantic Forest was variable and weakly yet significantly structured. Phyllostomid bats in the Atlantic Forest exhibit low dietary overlap.

Nonetheless, the overlap was relatively greater than expected based on the RA3 null model. Low overlap is related to species-specific differences in diets that are likely influenced by unique characteristics of the Atlantic Forest ecosystem (see below) that may mitigate resource partitioning. Related to this is a significant, yet weak, relationship between the morphology of species and what they consume and greater turnover-balanced variation across dietary matrices than nestedness-abundance gradients. Diversification of phyllostomid bat communities in Atlantic Forest appears to be related at least in part to resource availability and utilization. Phyllostomid species richness was significantly related to number of resources. Moreover, increases in bat species richness were related to increases in dietary overlap potentially facilitated by increases in number of resources.

## Beta-diversity of diet matrices

Decomposing beta diversity into components of turnover-balanced variation and nestedness-abundance gradients effectively provided insights into biological processes important to the structure of dietary matrices. First, the





**Fig. 5** Relationships between beta diversity partitions and the strength of ecomorphological relationships across 23 phyllostomid bat communities in Atlantic Forest. For each figure, the correlation between morphological distance and the overall beta diversity represents the X-axis. The Y-axis represents the correlation between

morphological distance and a particular partition (i.e. turnover, nestedness, balanced variation or abundance gradients) of beta diversity. Each figure represents the degree to which a particular partition of beta diversity is related to the overall ecomorphological pattern

degree of dietary overlap was directly related to the magnitude of both partitions of beta diversity. High overlap is related to high degrees of nestedness-abundance gradients that indicate that when the dietary overlap is high, species exhibit greater nestedness-abundance gradients that likely result from each species passively sampling the resource base to a greater extent. Moreover, lower degrees of overlap reflect more specialized diets and greater amounts of turnover-balanced variation across the dietary matrix.

Phyllostomid bat diets can exhibit a core structure (Fleming 1986; Giannini and Kalko 2005; Sanchez and Giannini 2018) that often times is characterized by plant genus to bat genus matching. For example, species of the bat genera *Carollia*, *Sturnira* and *Artibeus* often tend to specialize in fruits of the plant genera *Piper*, *Solanum* and *Ficus*, respectively (Fleming 1986). Such genus-specific differences in diets are weak but evident in Atlantic Forest phyllostomid bats (Sanchez et al. 2012a, b, Stevens 2022). Such differences directly translate into variation in the turnover-balanced variation partition of beta diversity of

the dietary matrix. Moreover, the turnover-balanced variation partition was consistently the largest form of beta diversity of dietary matrices indicating that while dietary specialization by bats in the Atlantic Forest may be weak, it is still the primary component of differentiation among species in terms of their diets. Degree of specialization and core structure of diets are likely spatially variable across the entire geographic distribution of Phyllostomidae as indicated by only weak specialization in Atlantic Forest (Stevens 2022). This is also supported by dietary overlap being consistently greater than expected by chance as indicated by these data. Amount of overlap was positively related to nestedness-abundance gradient partitions of beta diversity with such overlap likely related to passive sampling of dietary items by bats in these communities. Indeed, examining dietary matrices from the perspective of beta diversity and decomposing variation into components of turnover-balanced variation and nestedness-abundance gradient variation provides complementary views on the coexistence of species based on resource utilization.

## Weak ecomorphological relationships

The weak yet significant relationship between morphology and diets was surprising and admonished the indiscriminant use of characteristics such as traits as a surrogate for the ecological characteristics of species. Use of such surrogates necessitates a statistically significant relationship between traits and ecological characteristics, as seen here, but also assumes a strong direct relationship (Wainwright 1994; Ricklefs and Miles 1994) between these two suites of characteristics. Weak relationships between traits and ecology likely serve to cloud inference into important determinants of community organization when they are used to characterize more direct aspects of ecology such as a diet that are difficult to measure. There are a number of potential reasons for weak relationships between morphology and diets found here. First, coexistence could be mediated based on a small portion of the diets of bats that are only rarely encountered and morphological differences may account for disproportionately more of the variation in these rare constituents. If this were the case then very large samples would be needed to more comprehensively characterize the diets of species. Exhaustive samples on diets of bats are complicated by the fact that in some situations, a large proportion of individuals do not produce a dietary sample (Lou and Yurrita 2005) and of the ones that do, accumulating a very large sample may require prohibitively large amounts of time and energy. The largest samples used here that were the result of large amounts of effort yielded only 2602 and 1917 different dietary items (Stevens and Amarilla-Stevens 2021). In general, the data used here were based on samples that were relatively large. Of the 23 studies, the average number of dietary items characterizing the study was 398, a sizeable average sample. Moreover, there was no significant correlation between the magnitude of the mantel statistic calculated between morphological and dietary distances and a number of samples characterizing the study ( $r = -0.224$ ,  $P = 0.303$ ,  $df = 21$ ). It is unlikely that failure to robustly characterize diets contributes to the weakness of the ecomorphological pattern among phyllostomid bats in the Atlantic Forest.

Second, perhaps the traits measured here were not related to diet in phyllostomid bats or trait averages applied to species irrespective across all locations where they occur could have weakened relationships. This too likely is not the case. Greater among-species than within species morphological variation is typical in mammals thereby making species-level averages an effective and more convenient means of characterizing ecomorphological relationships. Moreover, cranial morphology of phyllostomid bats based on species-level averages has been related to dietary differences among species based on numerous independently collected datasets and perspectives, and in some cases using the very measurements used here. Indeed, across large samples of

phyllostomid bats there are strong and direct relationships between cranial morphology and diets (Freeman 1988, 2000; Stevens and Willig 1999; Aguirre et al. 2002; Giannini and Kalko 2005; Monteiro and Nogueira 2009; Santana et al. 2010, 2011; Dumont et al. 2012; Mello et al. 2019). Because the cranium is intimately related to what a bat can fit into its mouth and process thereafter, such an ecomorphological structure is an obvious place to begin examining the relationship between morphology and diet. Nonetheless, this does not necessarily imply that I completely characterized ecomorphological relationships. For example, bite strength (Aguirre et al. 2002; Norgueira et al. 2009; Santana et al. 2010) and tooth microstructure (Santana et al. 2011) are other aspects of cranial morphology that manifest as differences in diets among bats. Moreover, the cranium is only one of at least two important trophic apparatus that are central to the foraging activities of bats. Wing morphology is also important as it can determine the kinds of micro-environments (i.e., cluttered or open) that bats are able to forage in (Kalko 1998). Bat communities also exhibit variable degrees of the structure relative to wing morphology (Tavares 1999, 2013; Villalobos and Arita 2014). Moreover, a canonical ecomorphological effect on diets could result from the interaction between the wing and cranial aspects of morphology. Future research should better explore these effects, in particular how such relationships are mediated through phylogeny.

Methodological issues aside, another reason for a weak ecomorphological pattern among bats in Atlantic Forest may have to do with adaptive landscapes (Wright 1932). Consumption of resources within a particular bat community is an extremely local process. Moreover, entries into a typical dietary matrix involve consumption by local populations of species, each of which with a geographic distribution that spans numerous local communities at regional to continental scales. This is especially true in Atlantic Forest. The typical Atlantic forest bat community comprises species, many of which have very large geographic ranges, spanning much of the Neotropics (Stevens et al. 2004). Adaptive landscapes characterize peaks and valleys of fitness related to spatial or temporal variation in the degree to which particular adaptations maximize fitness (Wright 1932). Accordingly, adaptations may not be adaptive at all sites inhabited within the geographic range of a species. Moreover, since many bat species encountered in Atlantic Forest bat communities have large geographic ranges, adaptations may confer better performance in communities found elsewhere than those in Atlantic Forest. Nonetheless, these species are likely to be able to persist successfully because of generalized ecologies that is reflected in the dietary matrix. While allowing persistence, such ecological generality degrades the relationship between morphology and diet and this may explain the weak relationship in Atlantic Forest phyllostomid bats.

Strength of ecomorphological structure was directly related to the degree to which turnover-balanced variation characterized variation of the dietary matrix. When species were the most specialized and exhibited the greatest turnover-balanced variation in their diets they exhibited the strongest Mantel statistic between diet and morphology. When species exhibited greater nestedness-abundance gradients, the ecomorphological structure was weaker. Although the morphological structure was invariant to more extrinsic characteristics of the dietary matrix such as its location or the diversity of the system it characterized, it was dependent on interactions among species within the system. When species exhibit the greatest specialization they exhibited the greatest morphological structure. Historically, bat ecologists have looked to ecomorphological patterns expecting great promise for the understanding of coexistence of species and ultimately the structure of communities (Willig and Moulton 1989; Arita 1997; Stevens and Willig 1999; Villalobos and Arita 2014), but to no avail. These results suggest that ecomorphological models are good surrogates for resource partitioning. The reason for a lack of strong ecomorphological structure likely is that there is only weak resource partitioning among phyllostomid bats within communities in general.

### Greater overlap than expected

While dietary overlaps were typically low, they were often relatively greater than expected based on the random shuffling of the observed dietary matrix. Previously described dietary syndromes (Fleming 1986; Giannini and Kalko 2005; Sanchez and Giannini 2018) would result in strong partitioning of resources and low dietary overlap. Many of the sites examined here occur at high subtropical southerly latitudes. Twenty sites were farther than approximately 20 °S and eight were at or farther south than the Tropic of Capricorn. Latitudinal gradients in diversity are ubiquitous across all forms of life (Willig and Presley 2018). Implications are that plant diversity decreases rapidly outside of the tropics (Lomolino et al. 2010) and extratropical frugivorous bats must subsist on fewer resources (Sanchez and Giannini 2018). Indeed, in this Atlantic Forest system latitude and a number of different kinds of resources consumed by bats at sites are significantly related ( $r = -0.396$ ,  $P_{\text{one-tailed}} = 0.031$ ,  $df = 21$ ). Decreases in the number of different kinds of resources may force greater overlap among phyllostomid bats in Atlantic Forest despite dietary syndromes.

Any nonequilibrium ecological phenomenon could increase dietary overlap despite partitioning and give rise to a situation where the overlap is low, yet greater than expected due to chance alone. For example, an environmental factor potentially contributing to higher dietary overlap is the seasonal climate experienced throughout much of the Atlantic Forest that causes concomitant

seasonal changes in the diets of bats (Mello et al. 2004; Sanchez et al. 2012a, b; Laurindo et al. 2017; Stevens and Amarilla-Stevens 2021). Moreover, in the interior Atlantic Forest of Paraguay, the overlap was significantly greater in winter than in summer (Stevens and Amarilla-Stevens 2021). Seasonal changes in diet may force bat species to be more general in their resource utilization thereby causing them to exhibit greater overlap than in less seasonal environments.

Atlantic Forest is perhaps the most human-modified tropical forest in the world (Ribeiro et al. 2009). Bats often times exhibit idiosyncratic responses to deforestation and forest fragmentation with some groups such as frugivorous and nectarivorous bats actually increasing in species richness and abundance in some disturbed areas (Gorresen and Willig 2004; Klingbeil and Willig 2009). Even after disturbance, secondary forests in the Neotropics tend to be numerically dominated by frugivorous and nectarivorous phyllostomids (Meyer et al. 2016). Such changes are perhaps facilitated by increases in resource overlap of interacting species. For example, in the southern Atlantic forest, despite no significant difference in a number of bats species between fragmented and continuous forest, bat-fruit interaction networks were characterized by fewer fruit species in fragments (Laurindo et al. 2019), the logical conclusion being that frugivorous bats overlap more in their diets in fragmented than continuous landscapes. Habitat modification may cause increases in overlap via a number of other avenues too. First, disturbance or fragmentation may alter density-dependence that maintains strong resource partitioning (Krebs 1994; Willig and McGinley 1999). In some situations, anthropogenic disturbance causes species to overlap more in their resource use to avoid human contact or contact with disturbed areas (Seveque et al. 2020). Disturbance can also increase overlap by facilitating the presence of novel resources items that are shared among consumers (Silveira et al. 2011; Manlick and Pauli 2020). Tropical and subtropical semi-deciduous forest such as Atlantic Forest are the phytophysionomy with the second largest number of invasive species in Brazil (Zenni and Ziller 2011). Degraded or fragmented habitats may be easily invaded by novel fruiting plants and this may also degrade strong resource partitioning. As demonstrated by the ubiquitous human modification and resultant habitat fragmentation of the Atlantic Forest, we now reside in the Anthropocene, a time of unprecedented human modification of the biota. While it is often desirable to study unaltered systems, especially because equilibrium systems are often simpler and such simplicity can more rapidly expedite ecological understanding, equally valuable and perhaps more representative insights will come from a study of heavily modified systems such as the Atlantic Forest that are more representative of the Anthropocene.

## Gradients of diversity

There are a number of modes whereby variation in resources or variation in how those resources are consumed at the community level can facilitate increases in diversity. One means is when the number of resources utilized by a group of species increases along a gradient (MacArthur 1972). Accordingly, a number of resources used by bats at the community level in Atlantic Forest was positively related to a number of bat species. Indeed, in this and other systems (Janz et al. 2006; Stevens and Tello 2011; Maynard et al. 2017), diversity begets diversity.

Changes inherent to groups of consumers can also facilitate increases in diversity. For example, decreases in average resource breadth or increases in resource overlap can facilitate the coexistence of more species (Hutchinson and MacArthur 1959; MacArthur, MacArthur 1972). Bat diversity was unrelated to average diet breadth indicating that bats did not have narrower dietary niches in more species-rich communities despite theoretical expectations (Hutchinson and MacArthur 1959; MacArthur, MacArthur 1972; Klopfer and MacArthur 1960; Pianka 1966) and findings from other systems (Fox 1981; Eeley and Foley 1999; Granot and Belmaker 2019). Nonetheless, there was a positive relationship between dietary overlap and number of bat species. Thus, it appears that increases in diversity are facilitated by increases in the degree to which bat species share dietary resources. Number of resources was also related to dietary overlap whereby bats species shared more resources in systems where more were consumed. Thus, increases in the number of resources and greater overlap in their consumption characterize the gradient of increased bat species richness in the Atlantic Forest. Moreover, as has been suggested by other studies (Gainsbury and Meiri 2017; Granot and Belmaker 2019) gradients of dietary niche breadth are likely more of a consequence than a driver of increased diversity.

## Conclusions

Resource utilization by bats in Atlantic Forest is complex. Dietary overlap is low yet greater than random expectations. Much of the interspecific variation in diets at particular sites is related to turnover among species that would be expected from previously reported foraging syndromes (Fleming 1986; Giannini and Kalko 2005; Sanchez and Giannini 2018) and to a lesser degree to nestedness that would be indicative of consuming resources as they are randomly encountered. Ecomorphology is related to resource utilization but the relationship is weak and worthy of further study to better understand this interaction. Increases in diversity at the community level are related to increases in a

number of resources and increases in dietary overlap. Niche breadth has been frequently suggested to also contribute to the diversification of communities. Nonetheless, patterns described here suggest that variation in niche breadth may be more a consequence of the diversification process than a driver of increases in species richness at the local level. Much data has accumulated on resource utilization of bats at the community level in Atlantic Forest and other Neotropical systems over the last quarter of a century. Comparative analyses across these other systems could address the veracity and generality of comparative results obtained from the Atlantic Forest. This ecosystem is unique in that much of its experiences considerable seasonality of temperature and precipitation and has faced unprecedented amounts of anthropogenic modification. Future studies should better explore these effects on resource utilization, perhaps even attempting to better understand the interactive effects of these two important phenomena on community structure in general.

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**Author contribution statement** RDS conceived and designed the study. RDS collected the data. RDS analyzed the data. RDS wrote the manuscript.

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