Received: 11 February 2023 | Accepted: 23 February 2023

DOI: 10.1002/ecs2.4495

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Freshwater Ecology

Niche specialization and community niche space increase with species richness in filter-feeder assemblages

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Funding information
The National Science Foundation, Grant/Award Number: DEB-1831512

Handling Editor: Debra P. C. Peters

Abstract

Ecological theory posits that higher species richness should be associated with greater exploitation of resources and niche packing resulting from either increasing species niche overlap or specialization of species' niches. Research evaluating niche theory in animals tends to focus on organisms among functional feeding guilds, while resource partitioning might be more critical within functional groups. Freshwater mussels (Family: Unionidae) are a diverse and imperiled group of animals that are ideal models to test niche occupancy due to their functional similarity as filter-feeders and their occurrence in spatially and temporally stable multispecies aggregations. We evaluated the relationship between species richness and the trophic niche area for 25 mussel species occurring in 22 aggregations in the southeastern United States using stable isotope analysis (δ^{13}C and δ^{15}N) of soft tissue ($n = 1057$). Mean species standard ellipse area decreased with species richness, whereas ellipse overlap was not related to richness, indicating increased niche specialization may be the primary mechanism allowing coexistence in species-rich communities. Total community isotopic area increased with richness, suggesting species-rich communities also use a broader range of resources and may not be species-saturated. Overall, our data support the niche-packing hypothesis by illustrating the importance of niche partitioning within a species-rich guild of aquatic animals.

KEYWORDS
freshwater mussels, niche partitioning, species coexistence, stable isotopes

INTRODUCTION

Understanding the mechanisms underlying niche occupancy variation and species richness is a fundamental goal of ecological research (Hutchinson, 1957; Li et al., 2018). MacArthur (1965) proposed the niche-packing hypothesis, which states that species can coexist in diverse communities by modifying their niche breadth through two nonexclusive mechanisms: the narrowing of each coexisting species' niche (hereafter specialization) or multiple species using the same resources, resulting in greater niche overlap (hereafter overlap). At the community level, greater resource availability and heterogeneity can lead to greater richness and result in expansion of community niche space as species use unexploited resources (Finke & Snyder, 2008; MacArthur, 1965).

Coexistence of species has been studied across ecosystems with mixed results. Plant community research has shown different species can partition resources creating niche separation (Silvertown, 2004). However, niche packing has mostly been studied in animal communities with coexisting consumers representing different functional groups. In terrestrial animal communities ranging from birds to small mammals, specialization has proven to be a dominant mechanism explaining niche occupancy when using functional trait space (Pellissier et al., 2018; Pigot et al., 2020; Van de Perre et al., 2020). In aquatic ecosystems, studies assessing niche packing have focused on fishes and ecomorphological traits (e.g., body size, fin length), showing that packing occurs through greater species niche overlap (Werner, 1977; Winemiller, 1991). Studies on marine invertebrates, especially with invasive species, have also attempted to discern mechanisms of niche partitioning and in this case showed evidence of niche overlap in native species and niche specialization from invasives (Karlson et al., 2015).

The trophic niche can be a good indicator of overall niche partitioning (Bearhop et al., 2004) and a useful tool to test the underlying mechanisms of niche occupancy (Keppeler & Winemiller, 2020). Stable isotopes can be used to evaluate community-wide trophic niche structure and trophic resource partitioning at the species level (Peterson & Fry, 1987), and can also provide data on assimilation over longer time periods than classical diet studies that only provide a snapshot in time. Specifically, δ^{13}C values indicate carbon source diversity (e.g., algae, terrestrial detritus), whereas δ^{15}N indicates trophic position, as δ^{15}N increases with trophic level (Post, 2002). Stable isotope analysis allows for visualization and quantification of the isotopic niche area and overlap among species (Jackson et al., 2011), thus allowing the inference of use and assimilation of food resources by co-occurring consumers.

Freshwater mussels (Family: Unionidae) are a species-rich group (~360 North American species) of sedentary filter-feeding invertebrates that occur in dense, multispecies aggregations that are heterogeneously distributed and temporally stable in aquatic systems (Haag, 2012; Sansom et al., 2018). Although mussels are classified in the same feeding guild of filter-feeders and presumably occupy similar trophic niches, similar functional classification may not result in trophic redundancy (Vaughn, 2010). Mussel resource use spans a continuum ranging from algae, bacteria, zooplankton, and detritus that is highly dependent on habitat and species (Atkinson et al., 2011; Nichols & Garling, 2000; Vander Zanden & Rasmussen, 1999). Evidence of seston resource partitioning and selective assimilation of particles has been documented in previous studies (Atkinson et al., 2010; Tran & Ackerman, 2019) and differences in evolutionary history and related behavioral, physiological, and morphological traits might promote variation in foods consumed (Atkinson et al., 2020). Because dispersal occurs primarily at the larval stage via a host fish, mussel assemblages provide a unique scenario where animals have limited dispersal capabilities as adults and multiple species are restricted to an area where they must coexist. Thus, mussel assemblages represent a good model to evaluate the niche-packing hypothesis.

We assessed niche occupancy of freshwater mussels from assemblages spanning a taxonomic richness gradient across the southeastern United States to test whether specialization or overlap of the trophic niche underlie species coexistence and to what extent the trophic niche varies as a function of taxonomic richness, focusing on broadscale community patterns. We combined complementary mussel assemblage surveys with stable isotope data to test the following hypotheses. (1) Community and species trophic niche increase with greater food resource availability and heterogeneity (Figure 1a). (2) Niche packing occurs as taxonomic richness increases in mussel assemblages by: (2A) increasing species niche specialization (Figure 1b) or (2B) increasing species niche overlap (Figure 1c). (3) If resources are not limiting, community niche space increases as taxonomic richness increases (Figure 1b,c).

METHODS

Study region and field collection

We sampled mussels at 22 sites across seven rivers in the Tennessee and Mobile River basins (Figure 2), which harbor 60% of mussel diversity in North America (Parmalee & Bogan, 1998; Williams et al., 2008). We intentionally selected sites that provided a gradient of mussel species richness based on historical data. Before surveying each site, we delimited the extent of mussel aggregations using visual searches. Sites ranged from 40 to 100 m in river length. To assess species richness, we performed quantitative surveys and timed searches at each site as in Hopper, Chen, et al. (2021) as a combination of qualitative and quantitative methods in delineated mussel beds provides the most accurate representation of the mussel assemblage (Vaughn et al., 1997). Individuals were identified to species based on morphological characteristics following nomenclature in Williams et al. (2017). During surveys, we

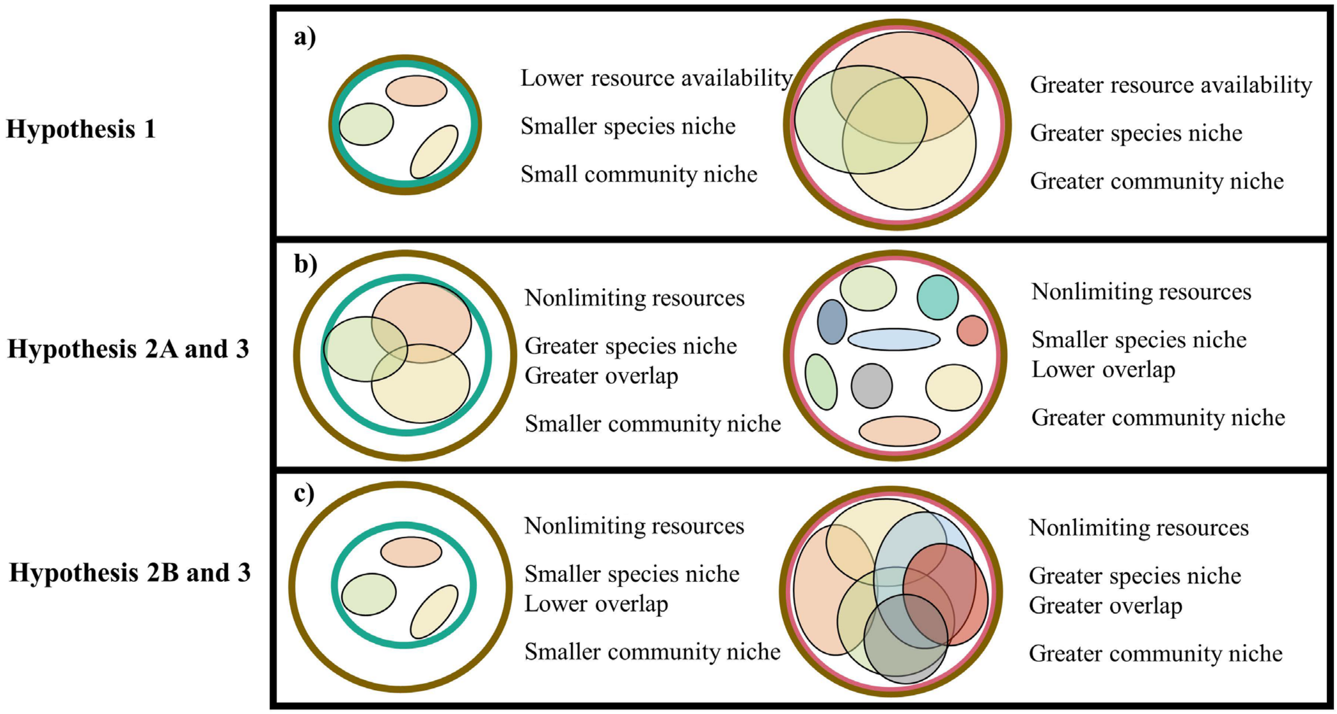

FIGURE 1 Conceptual diagram depicting the three study hypotheses: (a) Community and species trophic niche increase with greater food resource availability and heterogeneity; (b) species trophic niche decreases through specialization while community niche increases as taxonomic richness is greater; (c) both species and community niche increase with richness. Brown circles represent resource availability, green and red circles represent a gradient of community niche size, and ellipses represent species niches.

collected 3–10 individuals of US federally nonlisted species present at each site from July 2019 to September 2020 (Appendix S1: Table S1); due to the presence of threatened or endangered species, the number of species collected for isotope analysis did not always correspond to overall richness at the sites. To measure potential food resource availability and characteristics at each site, we collected water column seston during low flow conditions in 2019 and 2020 (Appendix S1: Table S2). We filtered 1 L of stream water ($n \geq 2$/site) on ashed, pre-weighed filters (GF/F; 0.7-μm pore size; Millipore) and calculated ash-free dry mass (AFDM, in milligrams per liter).

Stable isotope analysis

We transported mussels and seston collected for isotope analysis on ice to the University of Alabama. Seston samples were stored at −20°C until processing. Mussels were euthanized by flash-freezing in liquid nitrogen and stored at −80°C. We separated soft tissue from the shell and from the gastrointestinal tract and lyophilized and ground the tissue separately for individuals. Mussel and seston samples were sent to the Alabama Stable Isotope Laboratory (ASIL) where they were combusted in a Costech 4010 elemental analyzer (Costech Analytical Technologies) and δ^{13}C and δ^{15}N stable isotope signatures were determined using a Thermo Delta V Plus mass isotope-ratio spectrometer (ThermoFisher Scientific).

Statistics for hypothesis testing

We performed complementary analyses with isotope data at the species and community levels. We used ellipse-based metrics for our analyses of trophic niche space, which allow for comparison of community datasets with variable sample sizes (Jackson et al., 2011; Appendix S1: Figure S1).

To test hypothesis 1, we calculated Bayesian standard ellipse area ($\mathrm{SEA_B}$) for seston samples as an indicator of the range of food resources available at each assemblage using the R package "SIBER" (Jackson et al., 2011). To test hypothesis 2A, we averaged $\mathrm{SEA_B}$ of all species at each site as a measure of trophic niche breadth. We created standard ellipses with the function estEllipse in the R package "rkin" (Eckrich et al., 2020) and calculated the proportion of overlapping area with the function calcOverlap to estimate species trophic niche overlap and test hypothesis 2B. To test our hypothesis that community isotopic niche space increases with species richness under the assumption that resources are not limiting (hypothesis 3), we

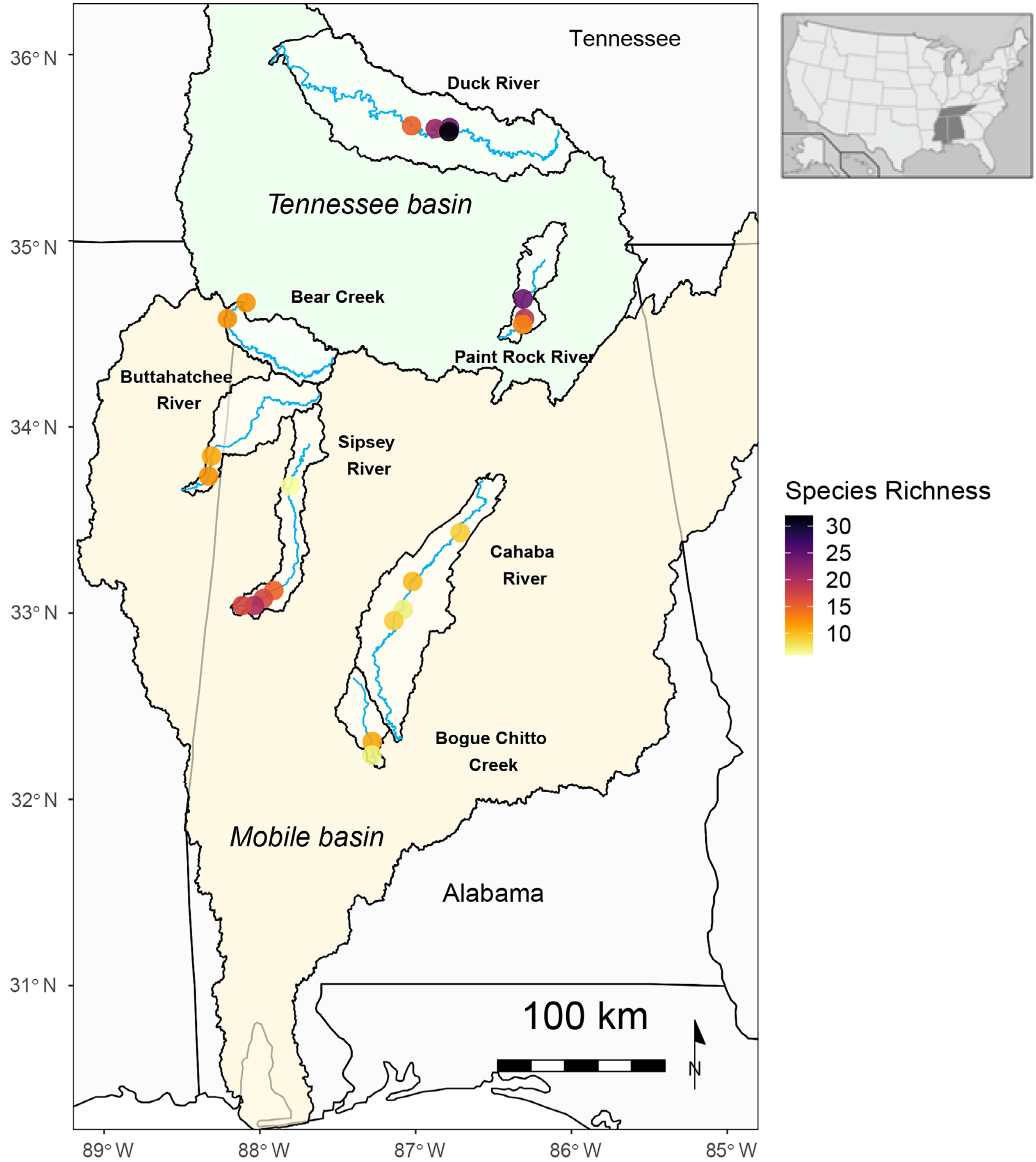

FIGURE 2 Map of the study area with focal rivers labeled within major basins. Points indicate survey and collection sites. The inset map provides the relative position of the study area in relation to the rest of the United States.

calculated Layman's total area (TA) using Bayesian methods with the R package "SIBER" (Jackson et al., 2011). Bayesian TA accounts for differences in community sample size and provides a robust description of community niche space (Jackson et al., 2011). Sites had to have more than two sampled species to calculate TA, hence we excluded one of the sites (Bogue 2) from the analysis. We further visualized $\mathrm{SEA_B}$ and TA across assemblages in a bubble plot with bubble sizes corresponding to species $\mathrm{SEA_B}$. Although isotope data are usually conveyed in biplots, this technique depicts the niche-packing patterns we identified more clearly (see *Results*).

To assess the relationships between species richness and isotopic niche metrics as well as food resource availability (i.e., seston concentration and range), we performed linear models using the function lm using species richness or resource range as the predictor, and niche metrics (SEA_B, overlap, and TA) or seston concentration as the dependent variable. We performed stepwise backward model selection with corrected Akaike information criterion (AIC_c, function AICc) to determine whether incorporating river basin as an additive or interaction term, and river as a random effect, in the analysis provided better support for the models. If the difference in AIC_c was <2 we retained the simpler model. All analyses were performed in R v 4.0.5 (R Core Development Team, 2021).

RESULTS

Our mussel taxonomic richness ranged from 4 to 32 species/site across the 22 surveyed sites. We encountered 4156 mussels in quadrats and collected a total of 1057 from 25 different species for isotope analysis (Appendix S1: Tables S1 and S3). Mean species SEA_B across sites ranged from 0.29 to 3.14, while overlap spanned from 0.14 to 0.45. At the community level, TA ranged from 0.21 to 3.59. Seston quantity varied from 1.53 to 13.73 mg AFDM/L while seston SEA spanned from 0.12 to 4.03 (Appendix S1: Table S2).

Resource availability and niche metrics

Despite the possibility that resource availability could result in an increase of species, seston quantity (AFDM) was not correlated with assemblage richness: [Seston (AFDM) ~ Richness] ($F_{1,19} = 0.09$, $R^2 = -0.04$, $p = 0.76$; Figure 3a; Appendix S1: Table S4). Additionally, there was no relationship between the range of resource available to the different mussel assemblages and their niche metrics (hypothesis 1): [Seston SEA_B ~ SEA_B] ($F_{1,19} = 1.20$, $R^2 = 0.01$, $p = 0.29$; Figure 3b), [Seston SEA_B ~ TA] ($F_{1,18} = 2.71$, $R^2 = 0.08$, $p = 0.12$; Figure 3c; Appendix S1: Table S4). Overall, food resource availability and heterogeneity were not related to mussel trophic niche use.

Richness and niche metrics

To test the relationship between species richness and species niche breadth (SEA_B), we selected the simplest model [Richness ~ SEA_B] ($\text{AIC}_\text{c} = 44.60$) for further analysis as it had a lower AIC_c value, fewer variables than the models including basin (Appendix S1: Table S5): [Richness ~ SEA_B + Basin] ($\text{AIC}_\text{c} = 50.39$), [Richness ~ SEA_B × Basin] ($\text{AIC}_\text{c} = 47.38$), and provided evidence for a significant negative relationship between assemblage taxonomic richness and mean SEA_B ($F_{1,19} = 6.73$, $R^2 = 0.22$, $p = 0.02$; Figure 3d; Appendix S1: Table S4). Analysis of this model supports niche packing through specialization (hypothesis 2A). The AIC_c selection process for the models with richness and overlap yielded similar results. The simplest model [Richness ~ Overlap] ($\text{AIC}_\text{c} = -42.70$) had a greater value than the model including basin [Richness ~ Overlap + Basin] ($\text{AIC}_\text{c} = -43.52$) but was selected for further analysis as it was within 2 AIC_c values. The model with basin as an interactive effect had the highest AIC_c value overall [Richness ~ Overlap × Basin] ($\text{AIC}_\text{c} = -41.58$). The model showed no significant relationship between species richness and niche overlap ($F_{1,20} = 1.93$, $R^2 = 0.04$, $p = 0.18$; Figure 3e; Appendix S1: Table S4), and thus does not support niche packing through overlap (hypothesis 2B).

To test the relationship between species richness and community niche space (TA), the simplest model [Richness ~ TA] ($\text{AIC}_\text{c} = 50.08$) was best supported in comparison to the models including basin [Richness ~ TA + Basin] ($\text{AIC}_\text{c} = 52.08$) [Richness ~ TA × Basin] ($\text{AIC}_\text{c} = 54.96$) (Appendix S1: Table S5). No significant relationship was observed between TA and richness ($F_{1,19} = 0.40$, $R^2 = -0.03$, $p = 0.54$). However, TA for one of the sites was notably larger than the rest and was a significant outlier (Dixon's Q test, $Q = 0.68$, $p < 0.01$). Running the models without the outlier yielded qualitatively similar AIC_c results [Richness ~ TA] ($\text{AIC}_\text{c} = 24.24$), [Richness ~ TA + Basin] ($\text{AIC}_\text{c} = 26.82$), and [Richness ~ TA × Basin] ($\text{AIC}_\text{c} = 30.28$), but revealed a significant positive relationship for community niche space and species richness ($F_{1,18} = 6.69$, $R^2 = 0.23$, $p = 0.02$; Figure 3f; Appendix S1: Table S4), supporting community niche expansion in species-rich communities through use of unexploited resources (hypothesis 3). Overall, all the models that had river as a random effect had substantially greater AIC_c values and were not considered for further analysis (Appendix S1: Table S5). Collectively, our results show that while individual species trophic niche decreases along the richness gradient, community niche increases (Figure 4).

DISCUSSION

Our study expands on previous research comparing among-guild niche variation (Pellissier et al., 2018; Winemiller, 1991), focusing on within-guild niche variation at the species and community levels. We found evidence supporting the niche-packing hypothesis in a group of organisms that are typically classified under

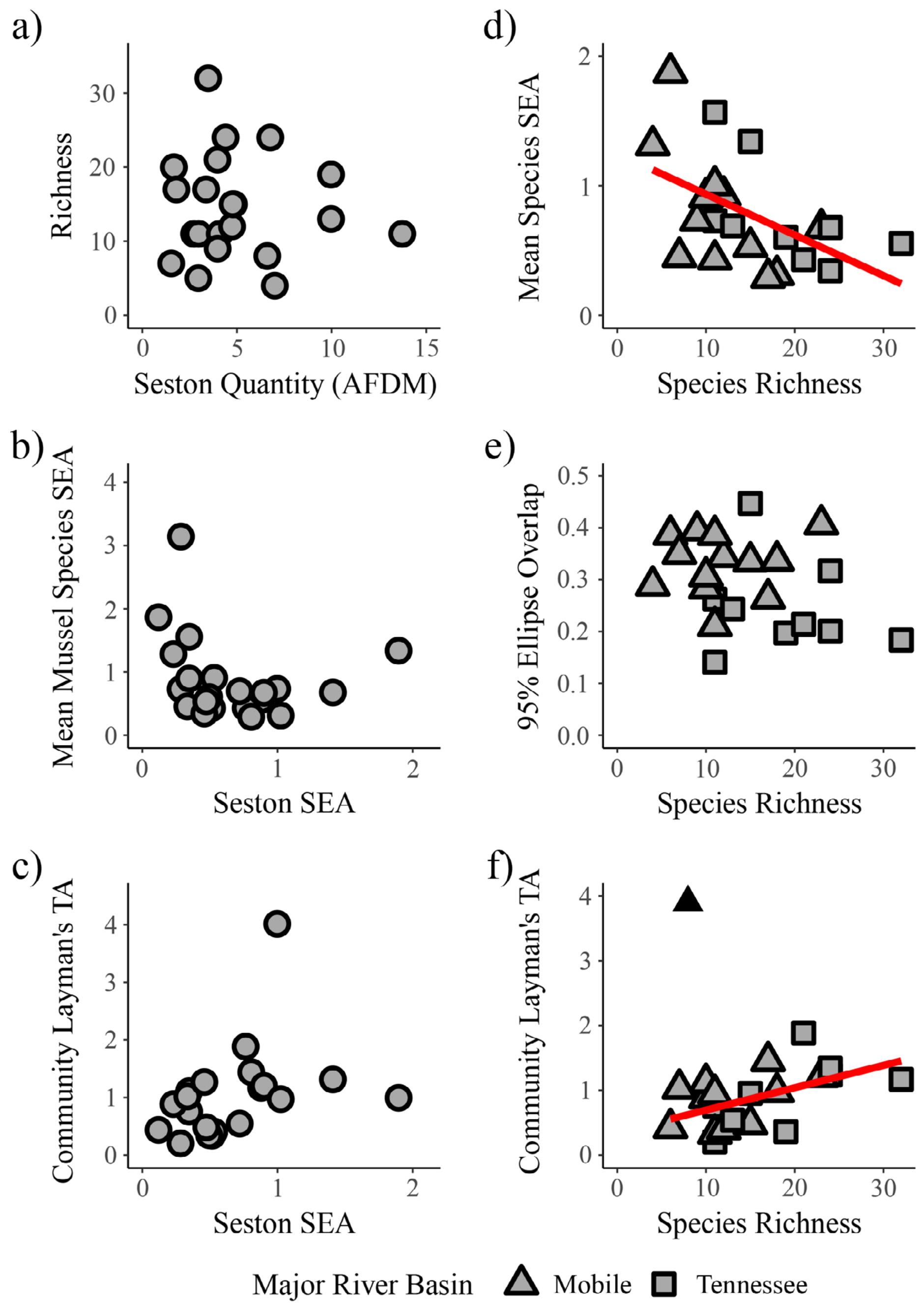

FIGURE 3 Regression describing relationships among niche metrics or overlap and richness across the 22 sampled sites: (a) relationship between seston quantity (ash-free dry mass, AFDM) and richness; (b) relationship between seston standard ellipse area (SEA_B) and mussel SEA_B; (c) relationship between seston SEA_B and community niche area (total area, TA); (d) relationship between richness and mean species SEA_B; (e) relationship between richness and species niche overlap; (f) relationship between richness and total community isotopic area; black data point represents an outlier not used in analysis.

the same functional feeding group (e.g., Haag, 2012). Our results suggest that greater resource partitioning through increased specialization of species trophic niches may be a primary mechanism underlying coexistence in the species-rich communities studied here (Figure 3). The alternative mechanism for niche packing (Klopfer & MacArthur, 1961) was not supported, as we found no relationship between species mean trophic niche overlap and richness. Overall, we provide support for niche packing and show a positive relationship between community niche space and assemblage richness, highlighting functional diversity within a diverse family of filter-feeders.

In our study, assemblages with larger community niches also showed greater species niche specialization. Although this relationship could seem contradictory, it

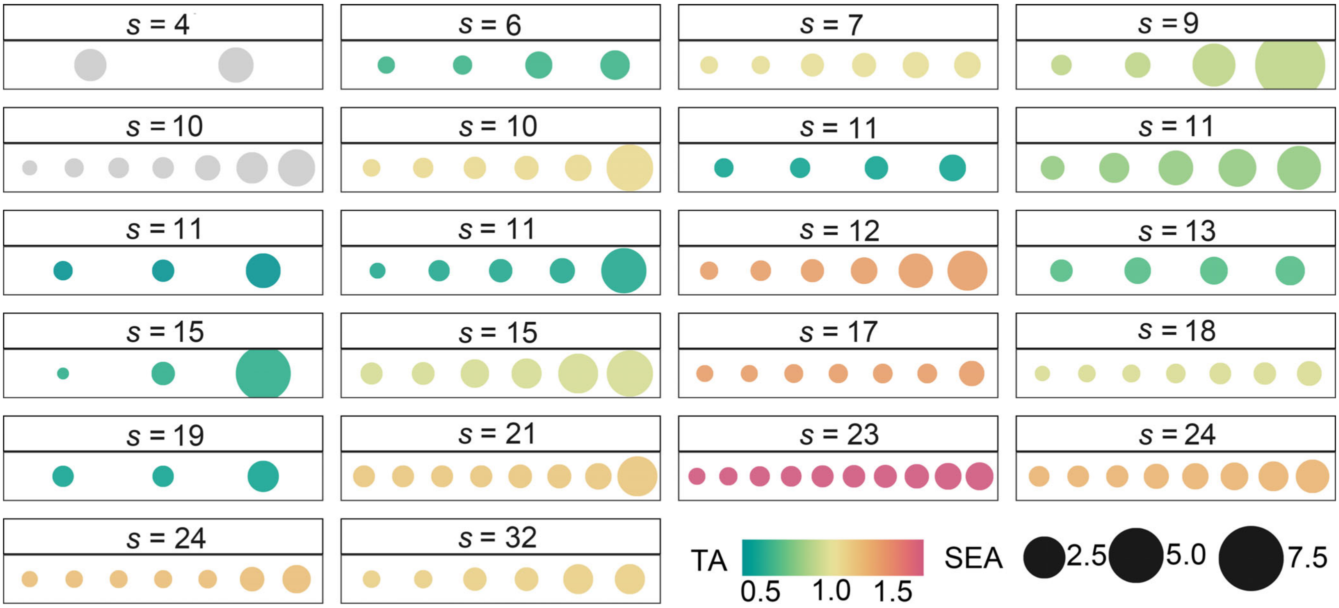

FIGURE 4 Species standard ellipse area (SEA_B) for each species at each site organized by richness. Each point represents a species in the assemblage and size is scaled to SEA_B. s indicates survey richness at the sampled site. Colors are a gradient based on Bayesian total area (TA) of the community. Gray color indicates that the site has been excluded from TA analysis due to not having enough species in the community ($s = 4$) or because the site was an outlier ($s = 10$).

could be explained by the presence of more specialist species in communities with greater species richness, which can lead to greater niche separation and broader community niche space (Finke & Snyder, 2008). Resource partitioning could be especially important when assessing community assembly and the roles of species in ecosystem function. Previous experimental studies have shown that ecosystem function increases as more species are added to the community through complementarity (Cardinale et al., 2012; Loreau & Hector, 2001). However, resource use and ecosystem function are not exclusively related to the number of species present in the community, but also to their identity, as specialists can use unoccupied regions of the trophic niche space leading to a more efficient use of resources, while the presence of generalists might not produce to the same result (Finke & Snyder, 2008; Worm et al., 2006). In contrast to our observed patterns, communities can also increase in niche space through niche overlap (Klopfer & MacArthur, 1961; Pool et al., 2017; Van Valen, 1965; Figure 1c). We note that one outlier assemblage showed larger community niche space with low species richness, which suggests that most of the species at this site are using a greater subset of the available resources, acting as generalists, and increasing community niche space. Overall, we did not find any relationship between species richness and overlap, which suggest this is a less common mechanism of species coexistence, but local variation leading to deviations from the general pattern can occur in observational studies of natural assemblages (Lawton, 1999; Underwood et al., 2000). However, determining species-specific effects and the effect of intraspecific variation is beyond the scope of our study. Our results indicate broadscale patterns showing species-rich assemblages have greater community trophic breadth and species with more specialized niches, which supports previous conclusions that resource partitioning through specialization leads to greater community niche space (Finke & Snyder, 2008; MacArthur, 1970; Figure 1b).

Resource availability was not related to species richness or assemblage niche metrics, even though more productive systems can host more species (Gillman et al., 2015; Waide et al., 1999). Sites with greater ranges of resources also did not show greater community niche space. Increased nutrient loading can lead to greater quality and quantity of food for mussels (Strayer, 2014), and overall, the potential resources across our sites clearly support large and species-rich mussel communities (Hopper, Chen, et al., 2021; Kelley et al., 2022). These patterns as well as the wider range of resources used by communities (TA) in species-rich mussel beds suggest that these communities are not species-saturated (Srivastava, 1999), which may be characteristic of low-trophic position animals in freshwaters (Gido & Franssen, 2007; Hugueny & Paugy, 1995).

Isotopic niche metrics provide ecologically meaningful information about the trophic axis of the n-dimensional niche, which might be influenced by a suite of other factors including resource availability (Hette-Tronquart, 2019). Food resources did not appear to be limiting to assemblages in our study, but species-rich assemblages had more specialized species niches that may be linked to factors constraining other axes of the niche that restrict access to the complete breadth of available resources. Species distribution is not only shaped by resource availability but also by environmental and habitat restrictions (González-Salazar et al., 2013; Hutchinson, 1959). Different types of habitats can also lead to different access to food resources. Although mussel assemblages usually occur in defined areas, variation in physical characteristics within a river (e.g., substrate, velocity) reach provide an array of potential microhabitats (Frissell et al., 1986) that may influence access to trophic resource pools that allow trophic separation among species. For instance, increased water velocity can be associated with greater δ^{13}C values, which suggest greater algal presence (Graba et al., 2013). Furthermore, mussels often primarily feed on benthic resources in small lotic systems and reservoirs, even when suspended organic matter is available to them (Fogelman et al., 2022). But, larger systems, such as the rivers our study took place, may provide adequate suspended food resources in addition to detrital sources. Both our seston and mussel tissue isotopic data suggest that mussels can use a range of resources spanning from bacterial- to detrital-based trophic resources (Newton et al., 2013; Weber et al., 2017). We hypothesize that food variability at the microhabitat level could further explain isotopic niche variation patterns within and among species that are not solely related to biotic interactions that we cannot explore with our current methods.

Temporal variability of abiotic factors controlling food availability as well as physiological changes within an organism could also be affecting the isotopic niche (Fogelman et al., 2022; Karlson et al., 2018). Isotope analysis assumes that species have similar turnover rates and that if different mussels within or among species consume the same food source their isotopic signature will be identical (Karlson et al., 2015). Despite being in the same functional group, mussel species have different stoichiometric requirements that are linked to their growth rates (Atkinson et al., 2020; Hopper, Dickinson, & Atkinson, 2021), which could lead to differences in isotopic fractioning and signatures among species. Mussel responses to changes in food availability and other environmental stressors are understudied (Aldridge et al., 2022). Although we tried to characterize food resources at our sites at low flows to control for temporal variability, events such as droughts and floods can also limit the access to and type of resources that species and populations can obtain (Atkinson et al., 2009) over longer periods of time. Changes in temperature and light can lead to seasonal differences in the pool of food resources (Christian et al., 2004; Fogelman et al., 2022), and unionid physiological stress can also lead to changes in uptake and isotopic assimilation and overall trophic niche (Fogelman et al., 2023). Further work is required to better understand unionid feeding ecology, but also disentangle the role of spatial and temporal variability in mussel trophic niche partitioning (Aldridge et al., 2022; Galbraith et al., 2009).

CONCLUSION

Our study of diverse aggregations of filter-feeding mussels supports species specialization as the main mechanism acting on the trophic axis of the niche in relatively stable species-rich animal communities. However, total community trophic niche space also increased with species richness, indicating there is no species saturation. Future efforts are needed to disentangle the influence of resource limitation from species interactions that allow coexistence among functionally similar organisms or drive variation in diversity. Collectively, our study provides strong evidence for the niche-packing hypothesis and illustrates controls on trophic variation within a single functional feeding group.

ACKNOWLEDGMENTS

We thank Austin Beets, Marlène Chiarello, Ansley Hamid, Taylor Kelley, Mark McCauley, Josh Millwood, Austin Omer, the Alabama Aquatic Biodiversity Center, and Tennessee Valley Authority for assistance in field work. Matt Lodato, Chelsea Smith, Shannon Speir, and dissertation committee members Jon Benstead, Paul Johnson, and Nate Jones provided useful suggestions on earlier versions of the manuscript. The National Science Foundation DEB-1831512 provided support for this project. Freshwater mussel collection was conducted under USFWS permit #TE68616B-1, TWRA permit #1807, ALCDNR permit #2019118497068680, and MS permit #0715191. This paper was completed as part of a dissertation at the University of Alabama and is a contribution to the Center for Freshwater Studies at the University of Alabama. This publication was made possible with the help from The University of Alabama – Alabama Water Institute.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code used to perform the analysis (Sánchez González, 2023) are available from Open Science Framework: https://doi.org/10.17605/OSF.IO/WH8KC.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sánchez González, Irene, Garrett W. Hopper, Jamie R. Bucholz, Megan E. Kubala, Jeffrey D. Lozier, and Carla L. Atkinson. 2023. “Niche Specialization and Community Niche Space Increase with Species Richness in Filter-Feeder Assemblages.” *Ecosphere* 14(5): e4495. https://doi.org/10.1002/ecs2.4495