Received: 20 November 2023 | Revised: 12 June 2024 | Accepted: 14 August 2024

DOI: 10.1002/ecy.4454

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Gastrointestinal morphology is an effective functional dietary proxy that predicts small mammal community structure

Olivia S. Chapman | **Bryan S. McLean**

Department of Biology, University of North Carolina at Greensboro, Greensboro, North Carolina, USA

Correspondence
Olivia S. Chapman
Email: oschapman@uncg.edu

Funding information
University of North Carolina at Greensboro (Faculty Startup Funds, W. John O' Brien Award for Field Research); American Society of Mammalogists (Annie M. Alexander Award); National Science Foundation, Grant/Award Number: 2233467

Handling Editor: Madan K. Oli

Abstract

The availability and quality of food resources can alter the intensity of competition and predation pressure within communities. Understanding species capacity to respond to global change-driven shifts in resource distribution is therefore crucial for biodiversity conservation. Small mammal communities are often structured by competition for food resources, but understanding and monitoring these processes are currently hindered by lack of functional dietary trait information in these hard-to-sample systems. In this study, we collected a comprehensive suite of gastrointestinal (GI) measurements from 26 small mammal species (including some never reported), compared them with more traditional craniodental traits in predicting dietary guild, and used them in a novel way to understand how diet structures 22 small mammal communities across the Appalachian Mountains of eastern North America. As predicted, we found GI traits to be effective dietary trait proxies; they were equally or more accurate than craniodental proportions in predicting the dietary guild of individual species. Furthermore, at the community level, we found that both the mean and functional dispersion of GI length were positively correlated with latitude and measures of temperature seasonality. Our results indicate that small mammal communities in more seasonal environments are filtered to include species with longer GI tracts (on average) as well as those that can partition food resources more finely, as expected based on the lower productivity of these regions. Conversely, communities in less seasonal environments display functional redundancy from the addition of species with short to intermediate GI lengths. Proportions of the GI tract represent novel dietary traits that can illuminate community assembly processes across regional environmental gradients and in the face of changing timing and availability of resources.

KEYWORDS
functional dispersion, functional trait, gastrointestinal tract, gut, habitat filtering, seasonality

INTRODUCTION

The quest for energy shapes many communities, and understanding how global changes are altering distribution of food resources is critical for biodiversity conservation. For example, the average temperature of the globe has increased by roughly 1.1°C over the past 125 years and is expected to continue to increase (IPCC, 2023). Coupled with an insect apocalypse (Goulson, 2019), accelerated drought and desertification in some regions (Han et al., 2021), defaunation (Dirzo et al., 2014; Galetti et al., 2015), and phenological shifts of plant or animal prey species (Damien & Tougeron, 2019), populations may be increasingly susceptible to altered food availability and increased competition, which can lead to local extirpation of species (Lancaster et al., 2016). Simultaneously, habitat loss and fragmentation (e.g., Malhi et al., 2008) constantly alter the spatial and ecological contexts within which individuals must acquire energy, grow, and reproduce (Crooks et al., 2017). Understanding how these changes impact community structure requires phenotypic proxies that are informative about the ways in which individual species maintain energy balance and maximize fitness within explicit environmental and community contexts.

Terrestrial small mammal communities are often structured by competition for food resources; accordingly, many species possess morphological, physiological, or behavioral traits that facilitate partitioning of these resources. Herbivorous small mammals existing in syntopy commonly partition niches by using different types of habitats and feeding on different plant species or on different parts of the same plant species (Bodmer, 1991). In North American deserts, where small mammal diversity and community composition is biased toward granivores (Brown, 1973; Brown et al., 1979; Kelt et al., 1996), species diversity is closely correlated with annual precipitation, which can be used to predict seed abundance (Brown, 1973). Even within these communities, however, coexistence is mediated by variation in morphological or behavioral traits that facilitate feeding on seeds of different sizes or foraging in separate areas (Jezkova et al., 2011).

Identifying traits that are not only informative about species and community ecology but also sensitive to global change drivers is a major goal in biodiversity science and conservation (Schmeller et al., 2017). Yet, despite the clear influence of dietary niche partitioning in structuring and maintaining small mammal communities, few functional phenotypic proxies exist for the important axis of dietary diversity. This is partly because small mammals can be secretive and difficult to monitor with respect to diet and foraging behavior. Another factor is that small mammal species often exhibit varying degrees of opportunism in their diets, which might change seasonally and across geographic scales (Samuels, 2009; Sassi et al., 2011). Thus, to date, many studies have relied acutely on qualitative assessments (e.g., diet guilds) or, less commonly, quantitative and continuous measurements of the feeding apparatus (e.g., cranial proportions, measurements of the dental battery) gathered from skeletons. These approaches are potentially problematic, for two reasons.

First, qualitative designations such as dietary guild (e.g., carnivore, omnivore, granivore) are coarse, effectively truncating our view of the continuous variation in diet that is often present among mammalian species. These designations are also typically compiled at the species level, making them non-representative of the substantial geographic, temporal, or functional diversity that might exist within species, especially those that are geographically widespread. Both shortcomings (coarseness among, as well as within, species) make it difficult to parse the influence of diet on community structure and global change response in local ecological contexts, where it is often needed most.

Second, although quantitative craniodental measurements are a common proxy for food procurement and processing ability in mammals (Ungar, 2015), and are straightforward to obtain from museum specimens, they rarely are perfectly representative of diet. Prior studies show that craniodental measurements applied to small mammals at large taxonomic scales correctly assign most species to dietary guild (Samuels, 2009; Verde Arregoitia & D'Elía, 2021), but that dietary misclassification may result when applied to local or regional faunas (Kohli & Rowe, 2019; this study). One cause is that mammals may process different food items with similar cranial and dental architecture, especially omnivores, which make a living by their ability to acquire and process resources opportunistically. For example, in small mammals of the Great Basin, USA, craniodental proportions were shown to predict diet with only 75% accuracy (32 species total; Kohli & Rowe, 2019). Alternatively, mammals using similar food items may display craniodental differences unreflective of diet. A study on African grazers found that although craniodental anatomy differed significantly among species, stable carbon isotope compositions within grazers were not significantly correlated with craniodental anatomy (Codron et al., 2008). This indicated that although obligate grazers and facultative browsers do have measurable craniodental differences, these were not functionally reflective of the large variation in their diets. Ultimately, craniodental anatomy reflects the long-term history of a lineage; it may or may not match with what individuals do throughout the course of their life (Davis & Pineda-Munoz, 2016), and it may be functionally constrained and thus unlikely to evolve on ecological timescales in response to changing food type availability.

Given its intimate relationship to diet, maintenance of energetic balance, and overall health, the gastrointestinal (hereafter, GI) tract has the potential to be used as a high-resolution, continuous dietary trait (Chivers & Langer, 2002; Naya et al., 2008). It is well known that mammalian carnivores possess relatively unspecialized GI tracts, a result of their high-quality diets, while GI tracts of herbivores are complex and often contain special structures or chambers that aid in processing high-fiber diets. These differences exist regardless of body size; even among small mammals, GI morphology varies among dietary guilds, with small herbivores (e.g., voles, lemmings, lagomorphs) having longer and more complex GI tracts than small omnivores and granivores (e.g., mice, rats, squirrels; Schieck & Millar, 1985), including relatively larger large intestines and ceca which aid in breaking down fibrous plant material (Schieck & Millar, 1985; Wang et al., 2003). Unfortunately, GI morphology is incompletely characterized across the mammal Tree of Life (Duque-Correa et al., 2021), and measurements are difficult to obtain from museum specimens since a majority are stored as skins and skeletons (Greiman et al., 2018; Quay, 1974) and because fixatives cause tissue shrinkage in fluid-preserved specimens (Kingston, 2018).

The purpose of this work was to understand how diet mediates community assembly processes in small mammal faunas of the Appalachian Mountains ecoregion of eastern North America and to test whether GI morphology is a useful proxy for this purpose. Specifically, we sought to (1) quantify gastrointestinal and craniodental morphology in the regional species pool, including some species lacking published GI measurements; (2) assess the extent to which these two trait types predict dietary guild; and (3) evaluate dietary functional structure of small mammal communities across a latitudinal and seasonality gradient that mediates annual food availability. We predicted that GI traits would contain greater dietary signal than traditional craniodental measurements. We also predicted that functional diversity of community-wide GI traits would vary in response to environment, with higher functional diversity found in more seasonal environments (i.e., those characterized by lower total productivity and shorter growing seasons). More broadly, we seek to reveal the importance of both trait types in maintaining small mammal communities and increase scientific capacity for tracking response to environmental change (including climate change and habitat fragmentation) in the future.

MATERIALS AND METHODS

Community and trait datasets

The Appalachian Mountains cordillera spans 13 US states (Table 1; Appendix S1: Figure S1) and is an area of elevated mammalian species diversity relative to surrounding lowlands (Antonelli et al., 2018; Badgley et al., 2017; Hall, 1981). Specifically, Appalachian faunas include a mixture of species characteristic of both higher (i.e., boreal) and lower (eastern temperate forest) latitudes, making it an ideal place to examine community assemblage. We compiled community datasets by conducting a literature search for small mammal census efforts from our study region, defined broadly. We also used small mammal trapping data generated by the National Ecological Observatory Network (NEON; 7 sites), which we formatted into community matrices. Our spatial thresholds were broad to ensure sampling across a large environmental and elevational gradient, including three sites in Indiana (our furthest from the main Appalachian cordillera). Our methodological thresholds were that sampling effort included (1) a minimum of 2000 trap nights, with a minimum of two separate types of traps used; or (2) a minimum of 10,000 trap nights if a single trap type was used. These thresholds were chosen to ensure that the entire small mammal community was reasonably sampled, as different mammal species are best sampled with different trap types (box traps, pitfall traps, etc.). For two sites (Coweeta and Powdermill Long Term Ecological Research sites), numbers of trap nights were not available, but Coweeta includes a species list dating back to 1758 and regular trapping at Powdermill ran for 20 years (1979–1999), allowing us to be confident that these particular communities were well-sampled.

For every community dataset, a comprehensive species list of every small mammal (defined as body mass less than 300 g) was compiled (Table 1; Appendix S1: Table S1). Abundances were also recorded if available. NEON data were obtained by downloading latest-release small mammal trapping data from the NEON data portal (https://www.neonscience.org/data) for all sites falling within our focal region. We used custom R scripts to parse NEON trapping records, harvest information on captures, identify unique individuals (from ear tag IDs), and write records to a community matrix based on either (1) total captures or (2) total individuals. Scripts for harvesting NEON small mammal community data are available on Zenodo: https://doi.org/10.5281/zenodo.13837769.

We compiled GI trait data for the entire species pool by measuring a substantial number of GI tracts, including some species never before measured or published. All

TABLE 1 Metadata for the 22 small mammal sampling sites included in our study, arranged by decreasing latitude.

Site code	State (all United States)	Latitude	NPP	Reference
HOLT	Maine	44.1540	1.14	Wood et al. (2016)
BART	New Hampshire	44.0639	0.72	NEON (2022)
LTER1	New York	44.0618	0.65	Demers (2018)
HARV	Massachusetts	42.5369	0.71	NEON (2022)
LTER3	Pennsylvania	40.1707	0.91	Merritt (2019)
PENN1	Pennsylvania	39.9965	0.64	Stewart et al. (2008)
IN1	Indiana	39.2558	0.84	Kellner et al. (2013)
IN2	Indiana	39.2558	0.84	Nelson et al. (2019)
BLAN	Virginia	39.0337	0.75	NEON (2022)
SCBI	Virginia	38.8929	0.81	NEON (2022)
IN3	Indiana	38.8667	0.62	Urban and Swihart (2011)
WV2	West Virginia	38.7016	1.03	Kaminski et al. (2007)
WV1	West Virginia	38.6406	0.92	Francl et al. (2004)
VIRG3	Virginia	38.25	0.96	McShea et al. (2003)
VIRG1	Virginia	37.8086	0.94	Mitchell et al. (1997)
MLBS	Virginia	37.3783	0.78	NEON (2022)
VIRG2	Virginia	37.3371	0.9	Francl and Small (2013)
ORNL	Tennessee	35.9641	1.02	NEON (2022)
GRSM	Tennessee	35.6890	0.76	NEON (2022)
NC1	North Carolina	35.1855	1.15	Ford et al. (1999)
NC2	North Carolina	35.1855	1.15	Ford (2000)
LTER2	North Carolina	35.0516	0.8	Coweeta LTER (2016)

Abbreviation: NPP, net primary productivity.

GI tracts were processed by OSC following the methods outlined in Chapman and McLean (2023). For species without a cecum (i.e., shrews and moles), we separated tracts into two sections for measurement; stomach and intestine (the latter not differentiating between small and large intestines). The GI tracts were from specimens captured during our own field work or donated by museums and other scientists at the State University of New York College of Environmental Science and Forestry, the Virginia Museum of Natural History, and Miami University (OH). We also obtained a large number of GI tracts from the NEON Biorepository (https://biorepo.neonscience.org/portal/, 2023; Thibault et al., 2023; Yule et al., 2020). Any mammals that we captured and processed for this work were trapped and handled following guidelines of the American Society of Mammalogists (Sikes et al., 2016) and an active Institutional Animal Care and Use Protocol at University of North Carolina Greensboro. Dried small intestines for each individual were archived post-processing with voucher specimens in the UNCG Mammal Collection (McLean, 2023).

For each species in our dataset, we calculated mean length, wet mass, and dry mass of each GI section, as well as totals across all sections (Appendix S2: Table S1). All measurements of individual sections, as well as the total GI tract, were scaled by the head–body length of each individual. For length measurements, raw values were divided by the head–body length of an individual (total length minus tail length). For mass measurements, the cubic root of the raw values was divided by the head–body length of an individual. Finally, we calculated the ratio of the large intestine (LI) to the small intestine (SI) (LI:SI) for each species (after removing species lacking a cecum) as a relative metric of degree of herbivory, since total GI length may be a poorer predictor of diet than some constituent sections, especially the small and large intestines (Schieck & Millar, 1985).

For species for which we could not obtain GI tracts, we imputed total GI tract length (our most-used metric) using PhyloPars (Bruggeman et al., 2009), considering both phylogeny and body size. We did this by first pruning a phylogeny of all mammals (Upham et al., 2019) to those in our species pool. We then created a feature matrix of all of species with available total GI tract lengths and their mean head–body lengths, allowing us to model the strong evolutionary allometry in GI length (e.g., Duque-Correa et al., 2021). Species average head–body lengths were those measured by us (specimens we had GI tracts from) or reported previously in the PanTHERIA database (Jones et al., 2009). PanTHERIA did not contain the head–body length for the Allegheny woodrat (*Neotoma magister*), so we averaged the female and male head–body lengths listed in Castleberry et al. (2006). Imputed total GI lengths were scaled by the head–body length from the feature matrix, as we did previously.

Last, we developed a comparable craniodental morphological dataset by measuring skulls of five adults for each species in our dataset (with the exception of *Glaucomys sabrinus*, for which we only had access to two adult specimens). We did not measure any skulls for *Oryzomys palustris* (rice rat) or *Peromyscus gossypinus* (cotton mouse), two species that were rare in our dataset and only found in two southern communities. For each skull, electronic calipers (Mitutoyo, Kanagawa, Japan) accurate to a hundredth of a millimeter were used to take eight individual measurements of the skull and dental battery under a dissecting scope. These were the same measurements shown by Kohli and Rowe (2019) to predict diet. Craniodental measurements were taken on specimens of the North Carolina Museum of Natural Sciences (NCMS) and the University of Michigan Museum of Zoology (UMMZ).

Comparing trait functional signals

Each species was assigned to dietary guild as in the MammalDIET dataset (Kissling et al., 2014), with one exception. That dataset classified *Sorex longirostris* as an omnivore, but we reclassified it here as a carnivore based on dietary analyses of French (1980). Diets of some species in our dataset were re-estimated in the MammalDIET2 dataset (Gainsbury et al., 2018), but were identical to those we used from Kissling et al. (2014). A priori dietary classifications of each species can be found in Appendix S2: Table S2. To test predictive accuracy of guild classification based on our traits, we used linear discriminant analysis (LDA) with jackknife cross validation in R v4.0.2. Inputs were the scaled GI measurements and the raw craniodental measurements. As an additional test of how well the dietary guilds were discriminated by GI traits, we ran a multivariate analysis of variance (MANOVA) for all 26 species we obtained GI tracts for; we did this only for the novel GI measurements and not for subsequent craniodental or combined LDAs.

For craniodental traits, we ran an LDA for all 32 species with available measurements. For GI traits, we performed a series of LDAs since not all species possess all traits (i.e., of ceca). First, we analyzed all 26 species with GI measurements based on nine GI traits (length, wet mass, and dry mass of the stomach, cecum, and intestine). For species lacking a cecum (e.g., shrews and moles), we did not differentiate between the small and large intestine. For rodents, we included the small intestine and large intestine into the intestine trait. For those species lacking a cecum, the length, empty mass, and dry mass of the cecum were set as zero. We also ran a separate LDA on the eight craniodental traits of these same 26 species, in order to directly compare the accuracy of the different trait types on the same species set.

Next, since not all GI traits exist for all species, we ran subsequent LDAs with fewer species but based on all GI traits. To do this, we dropped all of the carnivores (as well as a mole classified as an omnivore and which lacks a cecum) from the LDA and analyzed the remaining 18 species with a full matrix of 12 GI traits (length, wet mass, dry mass of stomach, cecum, small intestine, large intestine). Again, for direct comparison with craniodental traits, we also ran an LDA on the eight craniodental traits of these same 18 species.

Finally, in order to assess the predictive power of both trait types combined, we ran an LDA on all craniodental ($N = 8$) traits and GI ($N = 9$) traits of the 26 species we obtained GI data for. For all LDAs enumerated above, the prior probability of guild membership was based on group sizes.

Functional dietary diversity of Appalachian small mammals

From small mammal community datasets, we created presence–absence matrices as well as abundance-weighted matrices (if available), the latter reflecting proportional representation of species in each community. For two NEON sites (Bartlett Experimental Forest [BART] and Harvard Forest [HARV]), a small number of *Peromyscus* individuals were of unknown identity and listed as "*Peromyscus leucopus/maniculatus*." To best utilize these records, we assigned them to one of the two species according to proportions of positively identified *P. leucopus* and *P. maniculatus* at each site. This allowed us to retain abundance information without altering the proportional representation of species.

To obtain paired environmental data for each community, we obtained geocoordinates for all sites and downloaded standard bioclimatic variables in raster format from the WorldClim 2.1 database (Fick & Hijmans, 2017) at a five arc-minute spatial resolution. We loaded the rasters into QGIS 3.10 to extract the annual mean temperature

(MAT), temperature seasonality (SD × 100) (TS), annual precipitation (AP), and precipitation seasonality (CV) (PS) values for each community. We also used the web app "AppEEARS" (https://appeears.earthdatacloud.nasa.gov/) to download net primary productivity (NPP) at each of our sites during the year of 2021. Our full environmental dataset thus consisted of five environmental variables.

In order to visualize differences in small mammal community composition across sites, we performed non-metric multi-dimensional scaling (NMDS). Prior to analysis, we dropped species that made up less than 0.1% of the total number of individuals at each site (for sites where abundances were available) to avoid bias from species that are exceedingly rare within communities. To visualize potential latitudinal differences among communities, we colored sites in community space according to three approximately equally sized latitudinal bins; high (44.16–41.12°), medium (41.12–38.08°), or low (38.08–35.04°). We also visualized taxonomic turnover among the sites by classifying species in the NMDS to six taxonomic clades: shrews, moles, squirrels, voles, mice and rats, and lemmings.

Our community metrics for GI traits were mean GI tract length (again, scaled by body size) and functional diversity of GI length. We used the "weighted.mean" function in the "base" package of R to calculate community-weighted means and the "fd_fdis" function in the "fundiversity" package (Laliberté & Legendre, 2010) to calculate functional dispersion (FDis). Functional dispersion is an index of functional diversity defined as the mean distance of all species to the community centroid in trait space, and it can be calculated for presence–absence data as well as data including relative abundances (Laliberté & Legendre, 2010; Valdivia et al., 2017). This is preferable to the metric of functional divergence in our case, as the former can also accommodate datasets with more traits than species, the inclusion of quantitative and qualitative traits, and the inclusion of missing data (Laliberté & Legendre, 2010). As a test of whether more seasonal environments filter for species with longer GI tracts on average, we ran regressions of both community means and community-weighted means for scaled GI tract length against the environmental variables described above. Community means were based on the presence–absence data, so all 22 sites were included in regressions. The regressions with community-weighted means were based on only 15 sites with species abundance data. We ran multiple linear regressions in each case, with MAT, TS, AP, PS, and NPP as predictors and using the "stepAIC" function in the "MASS" package (Venables & Ripley, 2002) to determine the top-ranked model, after ensuring none of the environmental variables were correlated ($p < 0.70$ for all pairwise correlations).

As a test of whether these same environmental and seasonality gradients represent filters for functional diversity in small mammal communities, we calculated the functional dispersion of all 22 (based on presence absence data) or 15 (those with abundances) communities and ran multiple linear regressions of functional dispersion against the same five environmental variables (MAT, TS, AP, PS, and NPP), employing stepwise model selection identically as above. We also ran a separate regression of community mean and community-weighted mean GI functional dispersion against latitude for visualization purposes.

Similar to tests based on GI traits, our community metrics for craniodental morphology were community mean and functional dispersion of the suite of eight skull measurements, which we summarized and transformed using standard principal components analysis (PCA). Methods, results, and discussion of those analyses can be found in Appendix S3: Section S1. As with GI traits, we performed environmental regressions and AIC-based model selection using community means and functional dispersion of PCA-transformed craniodental morphology data.

Results from the community-weighted mean GI length and functional dispersion regressions are discussed in Appendix S2: Section S1. Model outputs for all regressions discussed above are available in Appendix S4.

RESULTS

Dietary classification using functional traits

We examined a total of 22 small mammal community datasets across eastern North America (Appendix S1: Figure S1, Table 1) spanning 10 different states which also met our spatial and methodological thresholds. There were a total of 34 small mammal species detected across all communities. Community richness ranged from six to 29 species per site, with a mean of 12.2 and a CV of 36.9%.

Considering GI traits, although we observed strong allometry in GI length, there was not strong discrimination among the three dietary guilds considered here in terms of the relative GI tract length (Appendix S2: Figures S1 and S2A). However, when examining the LI:SI ratio in only those species possessing a cecum, we found stronger guild-specific patterns that confirm that herbivores tend to have longer large intestines relative to small intestines than omnivores and carnivores (Appendix S2: Figure S2B).

Out of 34 small mammal species in the regional pool, we were able to obtain GI tracts and measurements for 26 (76.47%; Appendix S2: Table S1). The number of GI tracts we measured per species ranged from one (for two species; *Cryptotis parva* and *Scalopus aquaticus*) to 102 (*P. maniculatus*), with a median of five GI tracts per species. For species with a cecum, we obtained 12 individual GI traits (length, wet mass, dry mass of sections), while we obtained six GI traits for species lacking a cecum (length, wet mass, dry mass of two sections). For the remaining eight species for which no GI measurements are available, we imputed the total GI tract length.

Our craniodental LDA of all 32 species for which we obtained skull measurements was 68.75% accurate at predicting the dietary guild of a species (Table 2). The carnivores were most accurately classified (81.82%), followed by the herbivores (66.67%) and omnivores (58.33%). Our GI LDA of all of the species we obtained GI measurements from was slightly more accurate (73.08%) at predicting dietary guilds (Figure 1, Table 2). The carnivores were most accurately classified (85.71%), followed by omnivores (75%) and herbivores (57.14%; Table 2).

A MANOVA conducted on these GI LDA scores was also statistically significant (Wilks $\lambda = 0.050$, approximate $F = 38.331$, $p < 0.001$). However, when we limited our craniodental LDA to the same 26 species contained in the GI analysis, it was 69.23% accurate at predicting the dietary guilds (Figure 1); classification accuracies were 71.43% for carnivores, 42.86% for herbivores, and 83.33% for omnivores (Table 2).

Two further classification analyses allowed us to compare GI and craniodental trait efficacy separately as well as in combination. First, when we excluded the carnivores (and one omnivorous mole) due to the lack of a cecum, we were able to leverage all 12 GI traits (instead of nine). Our GI LDA of 18 remaining species was 72.22% accurate at predicting herbivorous or omnivorous diet (71.43% vs. 72.73%, respectively, for these guilds; Table 2). Our craniodental LDA of these same 18 species was more accurate (83.33%) at predicting dietary guild (71.43% for

TABLE 2 Accuracy of dietary guild classifications for each linear discriminant analysis (LDA) based on two different trait types.

LDA input	Carnivore	Herbivore	Omnivore
GI	85.71% (6/7)	57.14% (4/7)	75% (9/12)
CD	71.43% (5/7)	42.86% (3/7)	83.33% (10/12)
GI (no carnivores)	...	71.43% (5/7)	72.73% (8/11)
CD (no carnivores)	...	71.43% (5/7)	90.91% (10/11)
GI + CD (combined)	85.71% (6/7)	71.43% (5/7)	58.33% (7/12)

Abbreviations: CD, craniodental traits; GI, gastrointestinal traits.

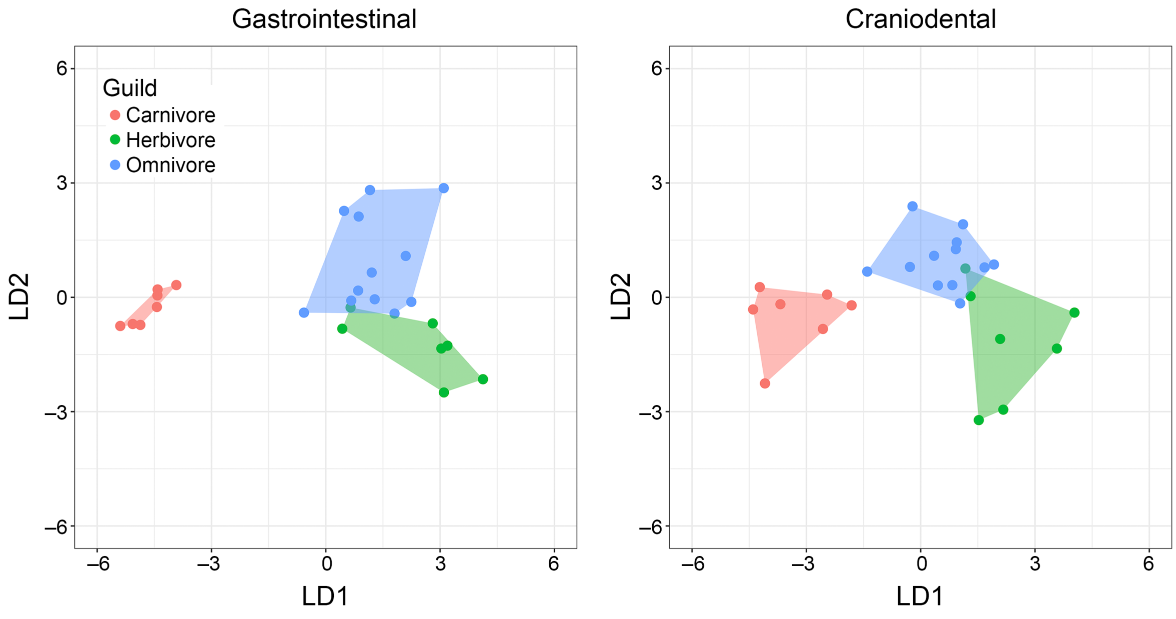

FIGURE 1 Linear discriminant (LD) analysis plots of 26 species for eight craniodental traits (right) and nine gastrointestinal traits (left). Species are plotted according to their scores on the first two discriminant axes for each analysis.

herbivores and 90.91% for omnivores; Table 2; Appendix S2: Figure S3). Second, our joint craniodental and GI LDA (containing 26 species and 17 traits) was 69.23% accurate at predicting dietary guild, similar to the traits analyzed separately, with carnivores most accurately classified at 85.71%, followed by herbivores at 71.43% and omnivores at 58.33% (Table 2).

Taxonomic and functional dietary diversity

The site-level small mammal studies we compiled for this study were highly dispersed spatially (latitudinal range of 9.09°) within our study region, but there were nevertheless some similarities in species composition. Northern short-tailed shrews (*Blarina bravicauda*) were present at every site, and eastern chipmunks (*Tamias striatus*) were present in every community but two. In addition, each community contained either the mice *P. maniculatus*, *P. leucopus*, or both, consistent with the abundance of these species across eastern North America. There was no separation of latitudinally binned communities in NMDS space (Figure 2); however, we did observe that northern sites contained less diversity than the mid-latitude or southern sites, indicating there is a core Appalachian Mountains mammal fauna endemic to the northern sites that is also constituent, along with additional low-latitude species, of southern sites. However, the identities of the low-latitude species present at southern sites varied by site. One low latitude site had cotton mice (*Peromyscus gossypinus*), which were not found at any other site, while another low latitude site had marsh rice rats (*Oryzomys palustris*) present, a species that was also not found at any other site.

We found a positive relationship between community mean scaled total GI tract length and latitude, showing generally that sites at higher latitudes are composed of species with longer GI tract lengths on average (Figure 3).

The top-ranked regression of community mean scaled GI tract length against climatic variables included two of these variables: temperature seasonality and precipitation seasonality. In this model, GI lengths were significantly and positively associated with TS, indicating more seasonal sites contain species with longer scaled GI tract lengths on average (Figure 4). GI length was also significantly and negatively associated with PS, indicating sites that were more seasonal in terms of precipitation had shorter mean scaled total GI tracts lengths (Figure 4).

As with mean GI lengths, our regression of GI functional dispersion against latitude showed a significant and positive relationship, with sites at higher latitudes containing species with more even distributions of GI tract length than those at lower latitudes (Figure 3; Appendix S2: Figure S4), the latter of which sometimes displayed an excess of species with intermediate-length GI tracts.

The top-ranked regression of community functional dispersion in GI tract length against climatic variables included TS and PS, similar to the community mean

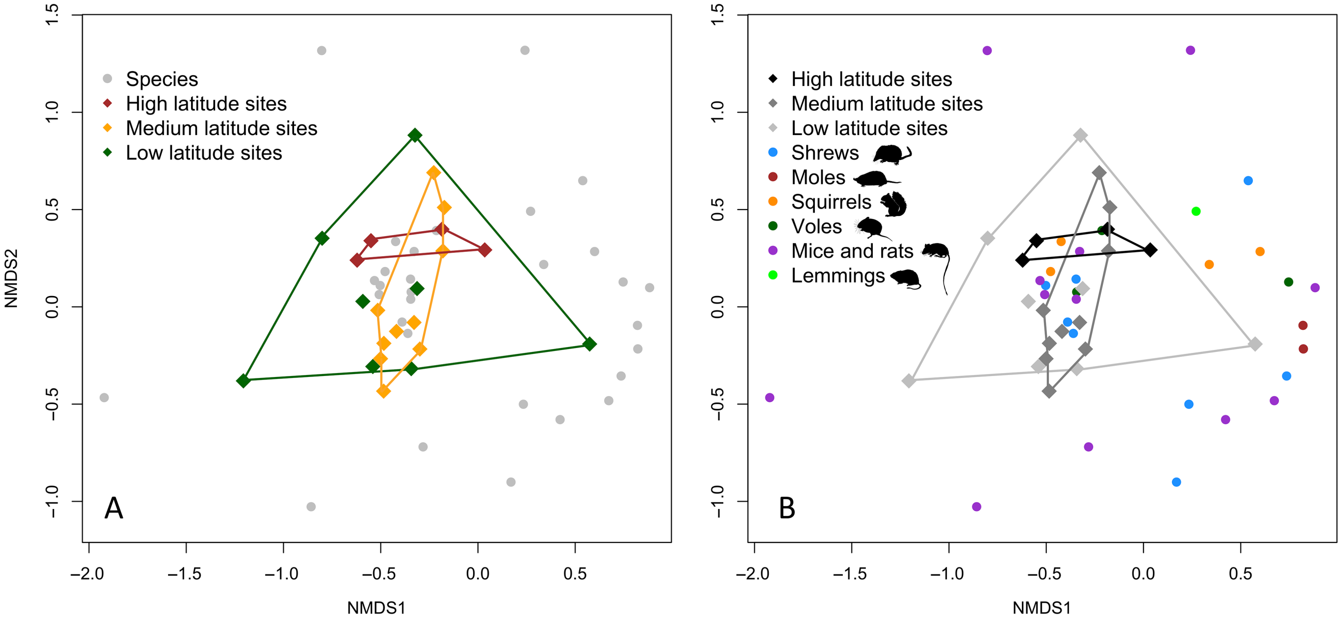

FIGURE 2 Nonmetric multidimensional scaling (NMDS) plots of 22 small mammal communities used in this study and their constituent species. The same ordination is plotted with (A) sites colored by broad latitudinal bin and species unlabeled; (B) species colored by clade.

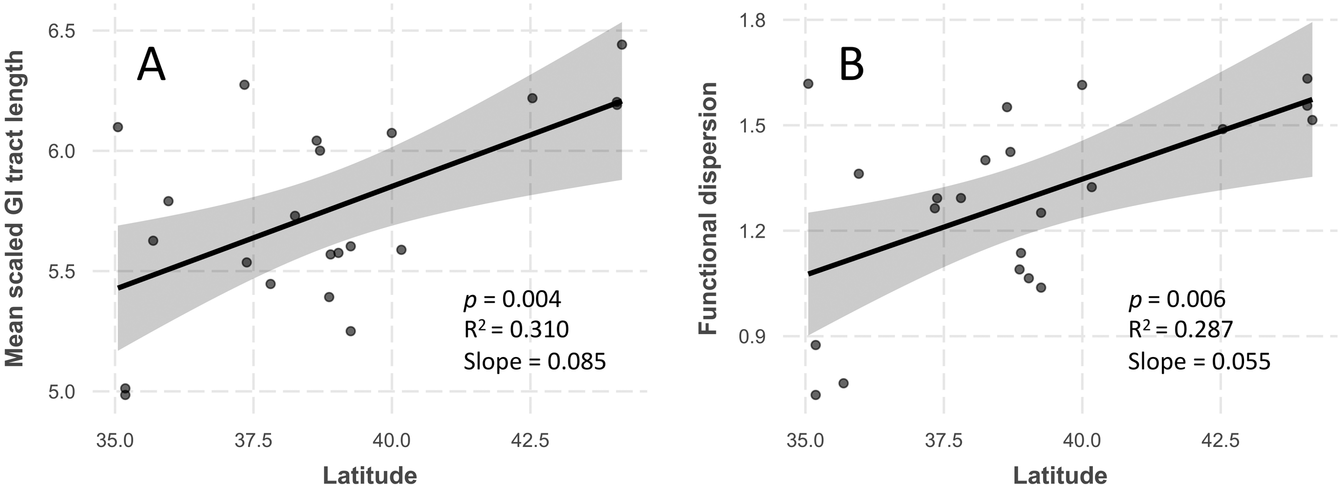

FIGURE 3 Separate general linear regressions of (A) community mean total gastrointestinal (GI) tract length and (B) functional dispersion of GI tract length versus latitude for 22 Appalachian small mammal communities.

regressions above. The relationship with TS was significant and positive (Figure 4), indicating that sites with higher temperature seasonality had not only longer average GI tract lengths but also greater functional dispersion. The relationship of GI functional dispersion with PS was significant and negative (Figure 4), indicating sites with higher precipitation seasonality had lower functional dispersion in GI length (in addition to their shorter average GI lengths).

Results of craniodental regressions did not correspond with the above patterns, and most environmental predictors were not statistically significant. We did not compare the slopes of the GI regressions against the craniodental PC1 regressions because of the strong correlation with PC1 and head–body length in this set of traits. None of the craniodental PC2 regressions against climatic variables were significant (Appendix S3: Figure S2), again suggesting that GI traits are more predictive of the structure of small mammal communities across this particular environmental gradient.

DISCUSSION

An improved understanding of the functional traits that ensure species persistence and coexistence is critical for global conservation efforts (Schmeller et al., 2017). Small mammal communities are an excellent study system for identifying how dietary niche partitioning shapes community structure and, further, how current changes in the abundance and timing of plant and insect biomass in ecosystems could alter faunal assemblages. The GI tract is an organ system tasked with maintaining energetic balance in support of growth and reproduction, and its morphology varies with the type and quality of diet consumed, so simple measurements of the GI tract have enormous but untapped potential as quantitative functional traits deployed at the species and community levels. The purpose of our study was to leverage GI morphology for the first time to understand functional dietary structure of small mammal communities and apply this approach to a biodiverse temperate ecoregion, the Appalachian Mountains of eastern North America.

Our first aim was to quantify gastrointestinal and craniodental morphology in the regional species pool. We report a substantial number of new GI measurements from eastern North American mammals, including seven species that have, to our knowledge, never had measurements of the GI tract reported. The three dietary guilds represented in our species pool were not strongly discriminated in terms of the relative GI tract length, which is consistent with prior studies (Duque-Correa et al., 2021; Schieck & Millar, 1985; Appendix S2: Figure S1). However, stronger patterns emerge when comparing the ratio of large- to small-intestine lengths, a proxy for relative degree of herbivory (Chivers & Langer, 2002; Snipes, 1994; Appendix S2: Figure S2A). Those data show that a majority of omnivores and the one carnivore had relatively longer small intestines and shorter large intestines, while a majority of herbivores had relatively shorter small intestines but longer large intestines. Schieck and Millar (1985) also found morphology of the lower digestive tract (cecum and large intestine) to be a much better predictor of diet than the small intestine alone or the total GI tract. Outliers in this LI:SI pattern were *Tamiasciurus hudsonicus* (red squirrel) and

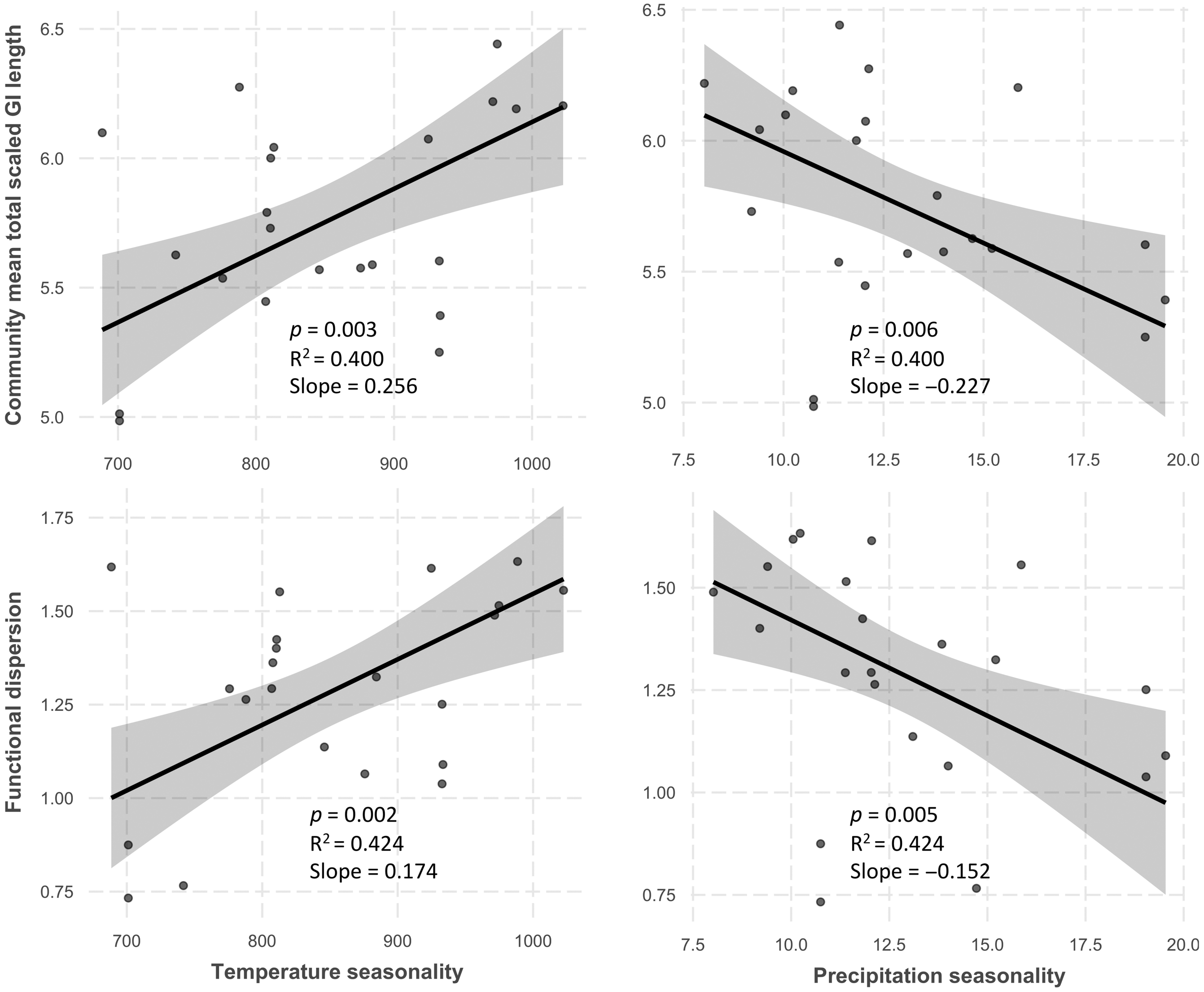

FIGURE 4 Effect plots from the environmental regressions of community gastrointestinal (GI) tract metrics. Top: community mean GI tract length versus temperature seasonality (left) and precipitation seasonality (right). Bottom: functional dispersion of GI tract length versus temperature seasonality (left) and precipitation seasonality (right). All regressions are for 22 total communities.

P. maniculatus (North American deer mouse); however, several studies indicate that both species consume seeds, nuts, fungi, and arthropods (Teron & Hutchison, 2013; Weigl & Hanson, 1980; Wolff et al., 1985), suggesting they are omnivorous rather than true herbivores as classified here. While *Rattus norvegicus* is classified as a carnivore and fits the pattern of carnivores having the lowest LI:SI ratio, many studies suggest it has an animal dominated omnivorous diet (Guiry & Gaulton, 2016; Major et al., 2006). Although these dietary guilds are coarse and may not necessarily reflect the true diet of a species, our observations of relative GI section lengths and the results of classification analyses (see below) still suggest there is dietary signal in GI proportions within our regional species pool. Since each GI section has somewhat specialized function, future work should consider section-specific metrics as well.

Our second aim was to compare the efficacy of GI measurements with more traditional craniodental measurements in predicting dietary guild within our regional context. Craniodental proportions are a gold-standard functional proxy in mammalian evolutionary biology; here, we utilized eight craniodental metrics that capture functional aspects of the mammalian feeding apparatus. Craniodental proportions of 32 species were reasonably accurate (68.75%) at predicting whether a species was a carnivore, omnivore, or herbivore, confirming that these measurements are moderately effective functional dietary traits. Notably, we used the same craniodental measurements as Kohli and Rowe (2019), and our dietary classification accuracy was similar to theirs, despite the fact that most species differ between their regional study system (Great Basin of western United States) and ours.

Considering the GI traits newly assembled for our study, an LDA of the 26 species we obtained data for was slightly more accurate (73.08%) than the aforementioned craniodental data at predicting dietary guild (Figure 1, Table 2). These results suggest that GI morphology is as good, if not slightly better, than craniodental data at predicting species dietary strategy as currently classified using guilds. Extending such comparisons to additional mammal faunas will help to further test this finding, and doing so at regional scales will help refine the usefulness of both trait sets in community ecology and conservation studies.

It is notable that the above patterns exist despite the fact that not all GI sections (specifically, the cecum) could be included in our classification analyses (Figure 1). The cecum is a unique digestive structure that allows herbivores to capture energy from poor quality diets characterized by high plant content, and it reaches maximum proportions in predominant herbivores such as lagomorphs and arvicolines. We therefore predicted that inclusion of cecum measurements would increase functional signal in GI data. We explored this by excluding the carnivores (and one omnivorous mole lacking a cecum) and performing a functionally reduced LDA of the remaining 18 species using all 12 GI traits (lengths, wet masses, and dry masses of four sections including cecum). However, this LDA was only 72.22% accurate at guild classification, performing slightly worse than the GI classifications above and worse than in a functionally reduced LDA based on craniodental traits for the same 18 species from two guilds (83.33%; Table 2; Appendix S2: Figure S3).

While all of our classification analyses assumed accurate assignment of species to dietary guild, this is unlikely the case. Given that GI proportions reported here do correspond with guild-level categorizations (e.g., Appendix S2: Figure S2), and because of the well-demonstrated correlation of GI morphology with diet across Mammalia, we suggest that some guild-level classifications are inaccurate or simply too coarse to fully capture the dietary diversity in wild mammals. We probed this possibility by performing a combined LDA that contained all GI and craniodental traits ($N = 17$ total), which we ran to determine if we could obtain more accurate classifications than either trait did alone. Classifications to guild were 69.23% accurate (Table 2), similar to most single-trait LDAs, and suggesting that there is an upper limit on guild classification accuracy regardless of trait set used. Future ecological research would benefit by a renewed focus on natural history and diet studies, which could generate more quantitative diet metrics such as percent fiber thresholds or percent dietary composition (e.g., from GI contents or fecal analysis) that GI anatomy could be cross-linked with.

Our third aim in this study was to evaluate community functional structure across a major seasonality gradient to provide insight into if and how diet mediates small mammal community assembly in the Appalachian Mountains ecoregion. At higher latitudes and elevations, shorter growing seasons and lower annual productivity (Linderholm, 2006) result in fewer absolute quantities of resources and a shorter temporal window in which those resources are available (e.g., productivity metrics in Table 1). Our prediction was that small mammal communities in these areas should have a higher proportion of species with relatively longer GI tracts (possibly driven by relatively longer large intestines or ceca), aiding in processing low-quality foods for more of the year. We also predicted that functional diversity would be higher in these same environments, as fewer resources drive increased niche partitioning among species and require more diverse GI tract morphologies for coexistence.

Both predictions were supported in our analyses. Considering community mean GI tract length, we found that this metric was positively correlated with latitude (Figure 3). Community mean values for scaled GI length at the highest latitudes are roughly 11% larger than at the lowest latitudes (model average). Our top-ranked environmental model similarly revealed that temperature seasonality (TS) was a significant positive predictor of GI lengths. Conversely, precipitation seasonality was a significant negative predictor of GI length (Figure 4).

While it is hard to make a direct comparison of the craniodental and GI regressions because the top-ranked regressions contained different predictors (raw vs. ordination data), craniodental regressions did not follow the same trends as GI regressions and most predictors were nonsignificant. Further, most craniodental trends had shallower slopes versus climatic variables (Figure 4, Appendix S3: Figures S1 and S2), suggesting minimal predictive capacity. It is especially noteworthy that both craniodental and GI proportions are related to dietary guild, yet only GI tract lengths were found to predict community dietary diversity. Additional work will be required to better understand the dietary signal in the small mammal craniodental apparatus within local community contexts, and future studies should incorporate other craniodental traits that may reflect diet, such as cheek tooth crown height (Samuels & Hopkins, 2017; Schap et al., 2021).

Considering community dispersion in GI traits, our regression of functional dispersion in GI length against latitude was significant and positive (Figure 3), consistent with predictions that lower absolute resource availability in more seasonal environments requires greater dietary niche partitioning (Cisneros et al., 2014; Josué et al., 2019). Environmental regressions likewise showed that both TS and PS predict functional dispersion, although in opposite directions (Figure 4). Species from sites that were more seasonal in terms of temperature were more dispersed in trait space, while species from sites that were less seasonal in terms of precipitation were more dispersed in trait space. In summary, regions of higher temperature seasonality appear to be a filter for species with short GI lengths, supporting small mammal communities with longer relative GI lengths (on average), but the greater diversity in GI form also supports a role for more intense niche partitioning at these sites.

We explored functional trends in more detail to understand what species drive community patterns. Increases in GI mean length and functional dispersion with increasing temperature seasonality were attributable to the addition of a few species with extremely long GI tracts, as well as loss of species with short- or intermediate-length GI tracts (Appendix S2: Figure S4). The herbivorous *Glaucomys sabrinus* (Northern flying squirrel) had the longest relative GI tract length (scaled value of 9.29) of any of species and, with the exception of site LTER2, was only found in the three highest-latitude (and highest TS) sites. All four of the highest-latitude sites (and the four with highest TS) also contained *T. hudsonicus* (red squirrel), another species with a long relative GI length (scaled value 8.39; Appendix S2: Figure S2). *Tamiasciurus hudsonicus* was only present in one low latitude site and one mid-latitude site. Conversely, the insectivorous *Sorex longirostris* (southeastern shrew) had the shortest relative GI length (3.65) and was not present in any of the high latitude sites, although other shrews are. Two other southeastern species—*Ochrotomys nuttalli* (golden mouse) and *P. gossypinus* (cotton mouse)—as well as *Sorex palustris* (American water shrew), had GI tracts of intermediate relative length (4–7; Appendix S2: Figure S2) and were only found in low latitude communities as well. The increased species richness characteristic of lower-latitude sites (Figure 2) is thus accompanied by higher functional redundancy in GI form, specifically of species with intermediate GI tract lengths, suggesting greater community convergence in these areas.

Our observations are consistent with evolutionary explanations for why herbivorous species (and therefore species with relatively longer GI tracts) may be more common at higher latitude, more seasonal sites. Endothermic organisms in colder environments must generate more heat than ones in warmer environments to counter higher temperature differentials, and one way they can do this is by maintaining larger energetically expensive tissues (i.e., the GI tract; Luna et al., 2017; Naya et al., 2013). Naya et al. (2013) found that this greater amount of "obligatory heat" favors increased metabolically expensive tissues, which leads to a bias of herbivores in high latitude, highly seasonal sites. Our findings are consistent with this bias of herbivorous species at higher latitudes and provides further evidence to support the proposed evolutionary explanation.

While patterns of GI functional diversity in the Appalachian Mountains are clear despite the heterogeneous community data available to us, future studies would benefit from more comprehensive within-site sampling that utilizes multiple trap types. For example, some community datasets that met our criteria for inclusion had thousands of trap nights of effort but only used Sherman live traps, which are not well-suited for targeting shrews, moles, and even arboreal squirrels. In these cases, we judged sites to have reliable species lists but unreliable abundance data, as some species are encountered more rarely than their true abundance on the landscape. Indeed, we saw no correlation between the number of trap nights or trap types and the number of species recorded at a site (Appendix S1: Figure S2), suggesting species lists were not biased by sampling effort. Still, we were unable to adopt a community-weighted framework to make inferences about community assembly processes given the difficulties in accurately estimating species abundances, so full inclusion of abundance data in trait-based analyses of mammals is a key next step.

Small mammals can be difficult to monitor in the wild, placing a premium on functional trait proxies that can inform about community assembly processes and guide biodiversity assessments. We showed that GI and craniodental traits possess similar dietary signal within the constraints of available dietary guild assignments; nevertheless, measurements of the GI tract have several unique and desirable characteristics. For example, it is unlikely that skeletal proportions such as the cranium respond to short term environmental shifts at the population level in ways that are directly interpretable as indicative of dietary response. In contrast, the GI tract is highly plastic and has been shown to respond to changes in season, reproductive activity, and dietary quality within individuals and populations (Derting & Hornung, 2003; Derting & Noakes III, 1995; Naya, 2008; Schieck & Millar, 1985). In addition, the GI tract has a central role not just in processing foods, but also in maintaining energetic balance and individual health. More work is therefore warranted to collect GI traits from freshly euthanized specimens and to identify which traits (i.e., total GI tract, specific sections, or ratios) are most illuminating with respect to diet. For this goal, we urge ecologists to continue to work with museums, the NEON biorepository, and other researchers to continue expanding the database of GI traits available, both within and among species and sites.

In conclusion, GI morphology is an effective continuous trait reflective of dietary ecology and predictive of dietary functional structure in Appalachian Mountains small mammal communities. Positive correlations of both (1) GI mean length and (2) GI functional dispersion with latitude and/or temperature seasonality supported our predictions that sets of species coexisting in seasonal environments should have longer relative GI tracts and greater variation in GI length. Conversely, while species in northern assemblages appear to partition dietary resources more finely, southern sites are characterized by increased functional redundancy from the addition of species with short to intermediate GI lengths. Our work provides substantial new natural history and soft tissue trait data linked to museum specimens to explore additional trends in the future. Critical next steps are more integrative process-based investigations into how GI morphology mediates individual fitness and species persistence, perhaps via links with gut microbiome composition, resistance to toxins, or other health-related outcomes.

AUTHOR CONTRIBUTIONS

Olivia S. Chapman and Bryan S. McLean conceived the ideas and designed the methodology. Olivia S. Chapman and Bryan S. McLean collected the data. Olivia S. Chapman analyzed the data. Olivia S. Chapman led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

We thank the researchers who sent us gastrointestinal tracts for this study, including Dr. Amanda Cheeseman, Dr. Nancy Moncrief, Dr. Susan Hoffman, Dr. Brooks Kohli, as well as everyone at the NEON Biorepository at Arizona State University (especially Laura Steger). We also thank the North Carolina Museum of Natural Sciences and the University of Michigan Museum of Zoology for allowing us into their collections to obtain our craniodental measurements. We thank Dr. John Orrock, Dr. John Pagels, and Dr. William McShea for providing us with small mammal capture data for one Virginia site described in McShea et al. (2003). This work was funded by a W. John O'Brien Award for Field Research (to Olivia S. Chapman), an Annie M. Alexander Award from the American Society of Mammalogists (to Olivia S. Chapman), UNCG Department of Biology faculty startup funds (to Bryan S. McLean), and NSF DBI 2233467 (BRC-BIO) award (to Bryan S. McLean). Finally, we thank the many graduate and undergraduate students who helped with fieldwork as well as laboratory work.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (bryansmclean, 2024) are available on Zenodo at https://doi.org/10.5281/zenodo.13837769. Materials utilized for this research include McLean (2023) and National Ecological Observatory Network (2023) datasets available in the Global Biodiversity Information Facility at https://doi.org/10.15468/nujf6d and https://doi.org/10.15468/25vq9q, respectively, and the NEON (National Ecological Observatory Network) (2023) small mammal box trapping release available in the NEON Data Portal at https://data.neonscience.org by searching for Product ID DP1.10072.001.

ORCID

Olivia S. Chapman https://orcid.org/0000-0003-1793-1656

Bryan S. McLean https://orcid.org/0000-0002-1293-5298

REFERENCES

Antonelli, A., W. D. Kissling, S. G. A. Flantua, M. A. Bermúdez, A. Mulch, A. N. Muellner-Riehl, H. Kreft, et al. 2018. "Geological and Climatic Influences on Mountain Biodiversity." *Nature Geoscience* 11(10): 718–725.

Badgley, C., T. M. Smiley, R. Terry, E. B. Davis, L. R. G. DeSantis, D. L. Fox, S. S. B. Hopkins, et al. 2017. "Biodiversity and Topographic Complexity: Modern and Geohistorical Perspectives." *Trends in Ecology & Evolution* 32(3): 211–226.

Biorepository, Arizona State University Biodiversity Knowledge Integration Center. 2023. "Biodiversity Occurrence Data." NEON (National Ecological Observatory Network). NEON Biorepository Data Portal. https://biorepo.neonscience.org/.

Bodmer, R. E. 1991. "Influence of Digestive Morphology on Resource Partitioning in Amazonian Ungulates." *Oecologia* 85(3): 361–65.

Brown, J. H. 1973. "Species Diversity of Seed-Eating Desert Rodents in Sand Dune Habitats." *Ecology* 54(4): 775–787.

Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. "Granivory in Desert Ecosystems." *Annual Review of Ecology and Systematics* 10(1): 201–227.

Bruggeman, J., J. Heringa, and B. W. Brandt. 2009. "PhyloPars: Estimation of Missing Parameter Values Using Phylogeny." *Nucleic Acids Research* 37(suppl_2): W179–W184.

bryansmclean. 2024. "Bryansmclean/Community-Dietary-Traits: Initial Release (v1.0)." Zenodo. https://doi.org/10.5281/zenodo.13837769.

Castleberry, S. B., M. T. Mengak, and W. M. Ford. 2006. "Neotoma magister." *Mammalian Species* 789(May): 1–5.

Chapman, O. S., and B. S. McLean. 2023. "Seasonal and Sex-Specific Changes in the Gastrointestinal Tracts of *Peromyscus maniculatus*." *Journal of Mammalogy* 104(6): 1364–76.

Chivers, D. J., and P. Langer. 2002. *The Digestive System in Mammals: Food Form and Function*. Cambridge: Cambridge University Press.

Cisneros, L. M., K. R. Burgio, L. M. Dreiss, B. T. Klingbeil, B. D. Patterson, S. J. Presley, and M. R. Willig. 2014. "Multiple

Dimensions of Bat Biodiversity along an Extensive Tropical Elevational Gradient." *Journal of Animal Ecology* 83(5): 1124–36.

Codron, D., J. S. Brink, L. Rossouw, M. Clauss, J. Codron, J. A. Lee-Thorp, and M. Sponheimer. 2008. "Functional Differentiation of African Grazing Ruminants: An Example of Specialized Adaptations to Very Small Changes in Diet: Differentiation of African Grazers." *Biological Journal of the Linnean Society* 94(4): 755–764.

Coweeta, L. T. E. R. 2016. "Mammal Species Commonly Present at Coweeta LTER ver 5." Environmental Data Initiative. https://doi.org/10.6073/pasta/2ec6e2ed77ddf3a5a3d06f5a288ef98a.

Crooks, K. R., L. Burdett, D. M. Theobald, S. R. B. King, M. D. Marco, C. Rondinini, and L. Boitani. 2017. "Quantification of Habitat Fragmentation Reveals Extinction Risk in Terrestrial Mammals." *Proceedings of the National Academy of Sciences of the United States of America* 114(29): 7635–40.

Damien, M., and K. Tougeron. 2019. "Prey–Predator Phenological Mismatch under Climate Change." *Current Opinion in Insect Science* 35: 60–68.

Davis, M., and S. Pineda-Munoz. 2016. "The Temporal Scale of Diet and Dietary Proxies." *Ecology and Evolution* 6(6): 1883–97.

Demers, C. 2018. "Small Mammals Surveys, 1981–1996, Adirondack Long-Term Ecological Monitoring Program Project No. 10 by Adirondack Ecological Center of the State University of New York College of Environmental Science and Forestry, Newcomb, New York." Environmental Data Initiative ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/5fbb6e06b7a5a059446c749a289a7030.

Derting, T. L., and C. A. Hornung. 2003. "Energy Demand, Diet Quality, and Central Processing Organs in Wild White-Footed Mice (*Peromyscus leucopus*)." *Journal of Mammalogy* 84(4): 1381–98.

Derting, T. L., and E. B. Noakes, III. 1995. "Seasonal Changes in Gut Capacity in the White-Footed Mouse (*Peromyscus leucopus*) and Meadow Vole (*Microtus pennsylvanicus*)." *Canadian Journal of Zoology* 73(2): 243–252.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345(6195): 401–6.

Duque- Correa,, M. J., D. Codron, C. Meloro, A. McGrosky, C. Schiffman, M. S. Edwards, and M. Clauss. 2021. "Mammalian intestinal allometry, phylogeny, and trophic level." *Proceedings of the Royal Society B: Biological Sciences* 288(1994): 1–9.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37(12): 4302–15.

Ford, W. M. 2000. "Woodland Salamander and Small Mammal Responses to Alternative Silvicultural Practices in the Southern Appalachians of North Carolina." *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 54: 241–250 https://www.fs.usda.gov/research/treesearch/14731.

Ford, W. M., M. A. Menzel, D. W. McGill, J. Laerm, and T. S. McCay. 1999. "Effects of a Community Restoration Fire on Small Mammals and Herpetofauna in the Southern Appalachians." *Forest Ecology and Management*, 114(2–3): 233–243.

Francl, K. E., S. B. Castleberry, and W. M. Ford. 2004. "Small Mammal Communities of High Elevation Central Appalachian Wetlands." *The American Midland Naturalist* 151(2): 388–398.

Francl, K. E., and C. J. Small. 2013. "Temporal Changes and Prescribed-Fire Effects on Vegetation and Small-Mammal Communities in Central Appalachian Forest, Creek, and Field Habitats." *Southeastern Naturalist* 12(1): 11–26.

French, T. W. 1980. "Natural History of the Southeastern Shrew, *Sorex longirostris Bachman*." *American Midland Naturalist* 104(1): 13.

Gainsbury, A. M., O. J. S. Tallowin, and S. Meiri. 2018. "An Updated Global Data Set for Diet Preferences in Terrestrial Mammals: Testing the Validity of Extrapolation." *Mammal Review* 48(3): 160–67.

Galetti, M., R. Guevara, C. L. Neves, R. R. Rodarte, R. S. Bovendorp, M. Moreira, J. B. Hopkins, III, and J. D. Yeakel. 2015. "Defaunation Affects the Populations and Diets of Rodents in Neotropical Rainforests." *Biological Conservation* 190: 2–7.

Goulson, D. 2019. "The Insect Apocalypse, and why it Matters." *Current Biology* 29(19): R967–R971.

Greiman, S. E., J. A. Cook, V. V. Tkach, E. P. Hoberg, D. M. Menning, A. G. Hope, S. A. Sonsthagen, and S. L. Talbot. 2018. "Museum Metabarcoding: A Novel Method Revealing Gut Helminth Communities of Small Mammals across Space and Time." *International Journal for Parasitology* 48(13): 1061–70.

Guiry, E. J., and B. C. Gaulton. 2016. "Inferring Human Behaviors from Isotopic Analyses of Rat Diet: A Critical Review and Historical Application." *Journal of Archaeological Method and Theory* 23(2): 399–426.

Hall, R. E. 1981. *The Mammals of North America*, 2nd ed. New York: John Wiley and Sons.

Han, J., H. Dai, and Z. Gu. 2021. "Sandstorms and Desertification in Mongolia, an Example of Future Climate Events: A Review." *Environmental Chemistry Letters* 19(6): 4063–73.

IPCC. 2023. "Summary for Policymakers." In *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Core Writing Team, H. Lee, and J. Romero, 1–34. Geneva: IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647.001.

Jezkova, T., V. Olah-Hemmings, and B. R. Riddle. 2011. "Niche Shifting in Response to Warming Climate after the Last Glacial Maximum: Inference from Genetic Data and Niche Assessments in the Chisel-Toothed Kangaroo Rat (*Dipodomys microps*)." *Global Change Biology* 17(11): 3486–3502.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, et al. 2009. "PanTHERIA: A Species-Level Database of Life History, Ecology, and Geography of Extant and Recently Extinct Mammals." *Ecology* 90(9): 2648.

Josué, I. I. P., S. J. Cardoso, M. Miranda, M. Mucci, K. A. Ger, F. Roland, and M. M. Marinho. 2019. "Cyanobacteria Dominance Drives Zooplankton Functional Dispersion." *Hydrobiologia* 831(1): 149–161.

Kaminski, J. A., M. L. Davis, M. Kelly, and P. D. Keyser. 2007. "Disturbance Effects on Small Mammal Species in a Managed Appalachian Forest." *The American Midland Naturalist* 157(2): 385–397.

Kellner, K. F., N. A. Urban, and R. K. Swihart. 2013. "Short-Term Responses of Small Mammals to Timber Harvest in the United States Central Hardwood Forest Region: Small Mammal Responses to Timber Harvest." *The Journal of Wildlife Management* 77(8): 1650–63.

Kelt, D. A., J. H. Brown, E. J. Heske, P. A. Marquet, S. R. Morton, J. R. W. Reid, K. A. Rogovin, and G. Shenbrot. 1996. "Community Structure of Desert Small Mammals: Comparisons across Four Continents." *Ecology* 77(3): 746–761.

Kingston, A. K. 2018. "Longitudinal Study of Rat Volar Fat Pad Fixation and Ethanol Storage: Implications for the Use of Fluid-Preserved Specimens in Morphological Studies." *Journal of Anatomy* 233(5): 607–617.

Kissling, W. D., L. Dalby, C. Fløjgaard, J. Lenoir, B. Sandel, C. Sandom, K. Trøjelsgaard, and J. Svenning. 2014. "Establishing Macroecological Trait Datasets: Digitalization, Extrapolation, and Validation of Diet Preferences in Terrestrial Mammals Worldwide." *Ecology and Evolution* 4(14): 2913–30.

Kohli, B. A., and R. J. Rowe. 2019. "Beyond Guilds: The Promise of Continuous Traits for Mammalian Functional Diversity." *Journal of Mammalogy* 100(2): 285–298.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91(1): 299–305.

Lancaster, L. T., G. Morrison, and R. N. Fitt. 2016. "Life History Trade-Offs, the Intensity of Competition, and Coexistence in Novel and Evolving Communities under Climate Change." *Philosophical Transactions of the Royal Society B: Biological Sciences* 372(1712): 20160046.

Linderholm, H. W. 2006. "Growing Season Changes in the Last Century." *Agricultural and Forest Meteorology* 137(1–2): 1–n214.

Luna, F., H. Naya, and D. E. Naya. 2017. "Understanding Evolutionary Variation in Basal Metabolic Rate: An Analysis in Subterranean Rodents." *Comparative Biochemistry and Physiology Part A* 206: 87–94.

Major, H. L., I. L. Jones, M. R. Charette, and A. W. Diamond. 2006. "Variations in the Diet of Introduced Norway Rats (*Rattus norvegicus*) Inferred Using Stable Isotope Analysis." *Journal of Zoology* 271(4): 463–68.

Malhi, Y., J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, and C. A. Nobre. 2008. "Climate Change, Deforestation, and the Fate of the Amazon." *Science* 319(5860): 169–172.

McLean, B. S. 2023. "University of North Carolina at Greensboro Mammal Collection (Arctos)." Version 1.7. University of North Carolina at Greensboro. Occurrence Dataset. https://doi.org/10.15468/nujf6d.

McShea, W. J., J. Pagels, J. Orrock, E. Harper, and K. Koy. 2003. "Mesic Deciduous Forest as Patches of Small-Mammal Richness within an Appalachian Mountain Forest." *Journal of Mammalogy* 84(2): 627–643.

Merritt, J. 2019. "Long Term Mammal Data from Powdermill Biological Station 1979-1999 (Reformatted to ecocomDP Design Pattern) ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/4b33f15a95b323bf80fd0584a615dffa.

Mitchell, J. C., S. C. Rinehart, J. F. Pagels, K. A. Buhlmann, and C. A. Pague. 1997. "Factors Influencing Amphibian and Small Mammal Assemblages in Central Appalachian Forests." *Forest Ecology and Management* 96(1–2): 65–76.

National Ecological Observatory Network. 2023. "NEON Biorepository Mammal Collection (Vouchers [Standard Sampling])." Occurrence Dataset. https://doi.org/10.15468/25vq9q.

Naya, D. E. 2008. "Gut Size Flexibility in Rodents: What We Know, and Don't Know, after a Century of Research." *Revista Chilena de Historia Natural* 81(4): 599–612.

Naya, D. E., F. Bozinovic, and W. H. Karasov. 2008. "Latitudinal Trends in Digestive Flexibility: Testing the Climatic Variability Hypothesis with Data on the Intestinal Length of Rodents." *The American Naturalist* 172(4): E122–E134.

Naya, D. E., L. Spangenberg, H. Naya, and F. Bozinovic. 2013. "How Does Evolutionary Variation in Basal Metabolic Rates Arise? A Statistical Assessment and a Mechanistic Model." *Evolution* 67(5): 1463–76.

Nelson, D. L., K. F. Kellner, and R. K. Swihart. 2019. "Rodent Population Density and Survival Respond to Disturbance Induced by Timber Harvest." *Journal of Mammalogy* 100(4): 1253–62.

NEON (National Ecological Observatory Network). 2022. "Small Mammal Box Trapping, RELEASE-2022 (DP1.10072.001)." https://doi.org/10.48443/h3dk-3a71. https://data.neonscience.org.

NEON (National Ecological Observatory Network). 2023. "Small Mammal Box Trapping (DP1.10072.001)." https://data.neonscience.org.

Quay, W. B. 1974. "Bird and Mammal Specimens in Fluid-Objectives and Methods." *Curator: The Museum Journal* 17(2): 91–104.

Samuels, J. X. 2009. "Cranial Morphology and Dietary Habits of Rodents." *Zoological Journal of the Linnean Society* 156(4): 864–888.

Samuels, J. X., and S. S. B. Hopkins. 2017. "The Impacts of Cenozoic Climate and Habitat Changes on Small Mammal Diversity of North America." *Global and Planetary Change* 149: 36–52.

Sassi, P. L., C. E. Borghi, M. A. Dacar, and F. Bozinovic. 2011. "Geographic and Seasonal Variability in Feeding Behaviour of a Small Herbivorous Rodent." *Acta Theriologica* 56(1): 35–43.

Schap, J. A., J. X. Samuels, and T. A. Joyner. 2021. "Ecometric Estimation of Present and Past Climate of North America Using Crown Heights of Rodents and Lagomorphs." *Palaeogeography, Palaeoclimatology, Palaeoecology* 562: 110144.

Schieck, J. O., and J. S. Millar. 1985. "Alimentary Tract Measurements as Indicators of Diets of Small Mammals." *Mammalia* 49(1): 93–104.

Schmeller, D. S., J.-B. Mihoub, A. Bowser, C. Arvanitidis, M. J. Costello, M. Fernandez, G. N. Geller, et al. 2017. "An Operational Definition of Essential Biodiversity Variables." *Biodiversity and Conservation* 26(12): 2967–72.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. "2016 Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research and Education." *Journal of Mammalogy* 97(3): 663–688.

Snipes, R. L. 1994. "Morphometric Methods for Determining Surface Enlargement at the Microscopic Level in the Large Intestine and their Application." In *The Digestive System in Mammals: Food Form and Function*, edited by D. J. Chivers and P. Langer, 234–286. Cambridge: Cambridge University Press.

Stewart, R. L., Jr., C. M. Kindlin, and P. R. Delis. 2008. "An Inventory of the Small Mammals of Letterkenny Army Depot, Franklin County, Pennsylvania." *Penn State University Press* 81(2/3): 59–65.

Teron, J. N., and L. J. Hutchison. 2013. "Consumption of Truffles and Other Fungi by the American Red Squirrel (*Tamiasciurus hudsonicus*) and the Eastern Chipmunk (*Tamias striatus*)

(Sciuridae) in Northwestern Ontario." *The Canadian Field-Naturalist* 127(1): 57.

Thibault, K. M., C. M. Laney, K. M. Yule, N. M. Franz, and P. M. Mabee. 2023. "The US National Ecological Observatory Network and the Global Biodiversity Framework: National Research Infrastructure with aGlobal Reach." *Journal of Ecology and Environment* 47(21): 1–9.

Ungar, P. S. 2015. "Mammalian Dental Function and Wear: A Review." *Biosurface and Biotribology* 1(1): 25–41.

Upham, N. S., J. A. Esselstyn, and W. Jetz. 2019. "Inferring the Mammal Tree: Species-Level Sets of Phylogenies for Questions in Ecology, Evolution, and Conservation." *PLoS Biology* 17(12): e3000494.

Urban, N. A., and R. K. Swihart. 2011. "Small Mammal Responses to Forest Management for Oak Regeneration in Southern Indiana." *Forest Ecology and Management* 261(3): 353–361.

Valdivia, N., V. Segovia-Rivera, E. Fica, C. C. Bonta, M. A. Aguilera, and B. R. Broitman. 2017. "Context-Dependent Functional Dispersion across Similar Ranges of Trait Space Covered by Intertidal Rocky Shore Communities." *Ecology and Evolution* 7(6): 1882–91.

Venables, B. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*, 4th ed. New York: Springer.

Verde Arregoitia, L. D., and G. D'Elía. 2021. "Classifying Rodent Diets for Comparative Research." *Mammal Review* 51(1): 51–65.

Wang, D.-H., Y.-X. Pei, J.-C. Yang, and Z.-W. Wang. 2003. "Digestive Tract Morphology and Food Habits in Six Species of Rodents." *Folia Zoologica-Praha* 52(1): 51–55.

Weigl, P. D., and E. V. Hanson. 1980. "Observational Learning and the Feeding Behavior of the Red Squirrel *Tamiasciurus hudsonicus*: The Ontogeny of Optimization." *Ecology* 61(2): 213–18.

Wolff, J. O., R. D. Dueser, and K. S. Berry. 1985. "Food Habits of Sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*." *Journal of Mammalogy* 66(4): 795–98.

Wood, C. M., J. W. Witham, and M. L. Hunter. 2016. "Climate-Driven Range Shifts Are Stochastic Processes at a Local Level: Two Flying Squirrel Species in Maine." *Ecosphere* 7(2): 1–9.

Yule, K. M., E. E. Gilbert, A. P. Husain, M. A. Johnston, L. R. Prado, L. Steger, and N. M. Franz. 2020. "Designing Biorepositories to Monitor Ecological and Evolutionary Responses to Change." Zenodo. https://doi.org/10.5281/zenodo.3880411.

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: Chapman, Olivia S., and Bryan S. McLean. 2024. "Gastrointestinal Morphology is an Effective Functional Dietary Proxy that Predicts Small Mammal Community Structure." *Ecology* e4454. https://doi.org/10.1002/ecy.4454