Trait-specific patterns of community ecospace occupancy in an insular mammal radiation

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Abstract

Communities that vary in the richness of closely related species but occupy similar environments provide a powerful system to investigate how trait variation and species richness interact to fill ecological space. In tropical mountain habitats on the island of Sulawesi, Indonesia, local murine rodent community richness ranges from 7 to 23 species. We measured 17 morphological, ecological, and isotopic traits to test for the expansion or packing of community ecospace among nine murine communities. Traits related to cranial shape (but not jaw shape), trophic level, and body shape showed the strongest evidence of expansion. Locomotion emerged as a fundamental axis of ecological variation, expanding ecospace and enabling niche packing of other traits such as diet and body size. Though trait divergence often explains functional diversity in island communities, we found that phylogenetic diversity facilitates community ecospace expansion in some conserved traits such as cranial shape, while more labile traits are overdispersed both within and between island clades. Our results evoke competition, trait evolvability, and the independent evolutionary trajectories of each of Sulawesi's murine clades as central to generating the exceptional functional diversity and species richness in this insular radiation.

Komunitas-komunitas dengan variasi kekayaan spesies berkerabatan dekat tetapi menempati lingkungan yang serupa menyediakan sistem yang kuat untuk menyelidiki bagaimana variasi sifat dan kekayaan spesies berinteraksi untuk mengisi ruang ekologi. Kami mengukur 17 karakter morfologi, ekologi, dan sifat isotop untuk menguji perluasan atau pengemasan volume ruang ekologi komunitas di antara sembilan komunitas hewan pengerat yang terdiri dari 7 hingga 23 spesies di pulau Sulawesi. Sifat-sifat yang berhubungan dengan bentuk tengkorak (tetapi tidak bentuk rahang), tingkat trofik, dan bentuk tubuh menunjukkan bukti ekspansi yang kuat. Sistem penggerak muncul sebagai sumbu fundamental dari variasi ekologi, mengembangkan ruang ekologi, dan memungkinkan pengemasan relung pada sifat lain seperti makanan dan ukuran tubuh. Meskipun divergensi sifat dianggap melampaui konservatisme ceruk di komunitas pulau, kami menemukan bahwa keragaman filogenetik memfasilitasi ekspansi ruang ekologi komunitas dalam beberapa sifat yang dilestarikan seperti bentuk tengkorak, sementara sifat yang lebih labil tersebar secara berlebihan baik di dalam maupun di antara klad pulau. Hasil kami menunjukkan persaingan, sifat evolvabilitas, dan lintasan evolusi independen dari setiap klad murinae Sulawesi sebagai pusat untuk menghasilkan keragaman fungsional yang luar biasa dan kekayaan spesies dalam radiasi insular ini.

Introduction

Local species richness is often positively correlated with the complexity of habitat structure and the diversity of available resources. Different localities with similar habitat structure, resource availability, and historical access often contain ecologically similar communities. These observations precipitated the study of species assembly (Hutchinson 1957, MacArthur and May 1972, Brown and Lieberman 1973, Brown 1975) and gave rise to the prediction that species only co-occur if they partition niche space along some axis, otherwise one will be excluded through competition (May and MacArthur 1972, Pianka 1974, M'Closkey 1978). In areas with high species richness, individual species may use a narrower breadth of resources than in lower species richness communities, thereby limiting niche overlap with co-occurring species, and producing a more densely packed community niche space ("Niche Packing", Figure 1, MacArthur 1970). Among animal communities, this prediction has found support with a variety of phenotypic and behavioral proxies for resource use, such as body size and proportions, wing shape, skull shape, time of activity, and microhabitat use (Brown 1975, Karr and James 1975, M'Closkey 1978, MacArthur and MacArthur 1961, Pianka 1974, Pigot et al. 2016, Van de Perre et al. 2020). However, individual species in the richest communities may exploit habitats or resources that are unused or non-existent in low-resource, species-poor communities. In this case, estimates of community niche space should be positively correlated with species richness ("Niche Expansion", Figure 1; MacArthur 1965, 1970, Pigot et al. 2016, Oliveira et al. 2020). This mode of resource partitioning has also found support, including in isolated communities of many closely related species (Lister 1976). Importantly, individual traits can reflect distinct

processes (Pigot et al. 2016), with packing on one axis (e.g., body size) and expansion on another (e.g., diet, see Spasojevic and Suding, 2012).

The foundational work describing competition's role in community assembly relied on empirical data from continental communities with equal biogeographic accessibility but variation in primary productivity or habitat complexity (Brown and Lieberman 1973, Brown 1975, M'Closkey 1978, Karr and James 1975, Pianka 1974, Weiher and Keddy 1995), or from archipelagos where island size or geographic complexity determines resource availability and habitat area, both of which influence overall species richness (Wilson 1961, Diamond 1975, Lister 1976, Gillespie 2004, Losos 2009, Losos and Ricklefs 2009). Less explored are insular areas of similar habitat structure and resource availability, but with discrete communities that vary widely in species richness ("species richness anomalies", Swenson et al. 2016 pg. E83). Such areas often house many closely related species and provide an opportunity to investigate the role of competition in the evolution of functional diversity and community structure.

Insular settings such as oceanic islands often contain high levels of endemism. Lineages that arrive and diversify in isolated locations regularly undergo ecological shifts that result in behaviors or phenotypes that are uncommon or non-existent in source communities (Pinto et al. 2008, Esselstyn et al. 2012, 2015, Stroud and Losos 2016). However, the degree to which closely related species in isolated locations share similar life history traits may vary (Losos et al. 2003, Hiller et al. 2019, Dorey et al. 2020, Stroud 2021). The strength of phylogenetic niche conservatism, or the tendency for similar niche requirements or trait values to be clustered within clades, mediates the impact of phylogenetic diversity on community niche space. If traits are

conserved within clades, then increasing phylogenetic diversity inevitably expands community niche space. However, high trait lability means that community phylogenetic diversity can be decoupled from functional diversity. Multiple lineages evolving in sympatry in isolated settings may reduce the degree of niche conservatism and promote niche divergence (Losos et al. 2003), thereby limiting the impact of phylogenetic diversity on community niche breadth. Testing the effects of trait conservatism and lability on community ecological space in insular settings requires replicated communities assembled from the same clades, but that vary in species richness.

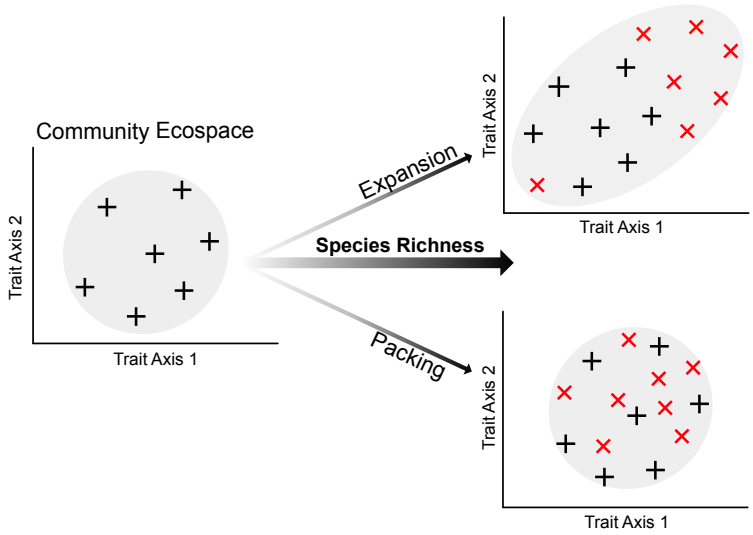


Figure 1: Conceptual diagram of expected patterns from community niche expansion (upper) and packing (lower). Expansion results in a larger ecospace area with the same density of points as the low-richness community, while packing results in a higher ecospace density in the same ecospace area.

We investigate the patterns of niche occupancy among communities of murine rodents (Murinae: Muridae: Rodentia) from the oceanic island of Sulawesi, Indonesia, a mountainous, tropical island (Figure 2) at the center of the Wallacean biodiversity hotspot. The murine diversity of Sulawesi is exceptional, with 41 endemic species stemming from seven colonist ancestors that arrived from circa 6 Ma to < 1 Ma (Figure S1, Rowe et al. 2019, Handika et al.

2021, Nations et al. 2021). While some colonists spawned small radiations of species and others are evidenced by only a single living species (Table 1, Figure S1), each clade is widespread on Sulawesi and most contribute to species richness of all local murine communities on the island. These local communities, defined as the murine species living on a mountain from lowlands to peak, range from 7 to 23 species, with the upper limit being perhaps the most diverse local community of closely related terrestrial small mammals on Earth. Importantly, variation in local community richness does not appear to be determined by environmental or habitat differences, suggesting that environmental filtering, a central process of community assembly (Webb et al. 2002, Cavender-Bares et al. 2004), does not affect community functional diversity. Maximum elevation, which may affect the area occupied by different habitats, appears to play only a minor role (Figure 2A), and net primary productivity is nearly constant across the island's montane regions (Imhoff et al. 2004). Instead, it appears that biogeography is the strongest predictor of local diversity, as richness for many taxa is highest in the central part of the island and generally lower on the peninsulas (Iskandar & Nio 1996, Musser 2014, Esselstyn et al. 2021). Such a disparity in species richness between geographically and ecologically similar mountains provides a natural experiment for testing alternative hypotheses of how communities fill ecological space.

Functional traits, or properties that quantify an organism's performance, microhabitat use, or dietary preferences, are often evaluated as niche axes in vertebrate communities (M'Closky 1978, Ricklefs and Travis 1980, McGill et al. 2006, Pianka et al. 2017). Gathering direct functional data can be difficult in communities of motile, nocturnal, or secretive species. In these cases, functional morphology provides a window into the ecological niche (Ricklefs and Travis 1980, Pigot et al. 2016, 2020). Differences in head shape (Lister 1976, Maestri et al. 2016,

Kohli and Rowe 2019, Van de Perre 2020), body size (Woodward and Hildrew 2002), and body proportions (Karr and James 1975, Ricklefs and Travis 1980, Nations et al. 2019, Nations et al. 2021) indicate differences in dietary and locomotor niches. Other indirect measures of resource use, such as trophic dimensions revealed through stable isotope ratios and estimates of locomotor mode, offer a quantitative assessment of diet and microhabitat use (Baltensperger et al. 2015, Galetti et al. 2016). The murine fauna of Sulawesi is an intriguing system for sampling functional disparity, as it includes some of the most unusual rodent forms (Figure 2B, Esselstyn et al. 2012, 2015, Rowe et al. 2014) living in sympatry with more typical "rat-like" morphologies and ecologies. Sulawesi murines have an array of cranial shapes that likely reflect their dietary preferences (Esselstyn et al. 2012, 2015, Martinez et al. 2018), have body sizes ranging from 10 to 500g, occupy a variety of locomotor modes, and consume a broad range of foods such as fruit, seeds, fungi, leaves, roots, and earthworms (Rowe et al. 2016a).

Table 1: Ages of six clades descended from Sulawesi colonists.

Clade	Crown Age	Species Sampled
Echiothrix	5.11 (4.49-5.69)	10 (10)
Maxomys	3.72 (3.21-4.29)	5 (5)
Bunomys	3.45 (3.09-3.81)	15 (15)
Margaretamys	2.92 (2.29-3.51)	2 (4)
Rattus*	1.57 (1.22-1.95)	6 (6)
Haeromys†	Indeterminate	1 (1)

NOTE.- Median age in millions of years is reported with 95% credible intervals in parentheses. Species sampled reports the number of species in this study with overall clade richness in parentheses and demonstrates near complete sampling. The two unsampled *Margaretamys* species were not detected in the localities in this study. All ages taken from Rowe et al. 2019. *There were likely two colonizations by the ancestors of native *Rattus* spp., the second of which occurred 1.16-0.6 Ma (Rowe et al. 2019), however, all *Rattus* in this study form a clade relative to other Sulawesi murines. Two human-commensal *Rattus* spp. found on Sulawesi were excluded. †The age of arrival of the Haeromys clade is unknown as other species of Haeromys from Borneo have yet to be included in phylogenetic analyses.

Here, we test niche packing and niche expansion as alternative explanations of how trait variation relates to species richness among nine montane communities of murine rodents on

Sulawesi. We quantify both the volume and density of community ecological space ("ecospace"), which we define as the sum of the n-dimensional niches of the species therein, from 12 individual functional and ecological traits and five multivariate trait complexes. Together, these traits reflect the full complexity of biotic interactions. Additionally, we examine the mode of niche filling in these nine montane communities by quantifying the influence of phylogenetic diversity and inter-clade variation on ecospace occupancy.

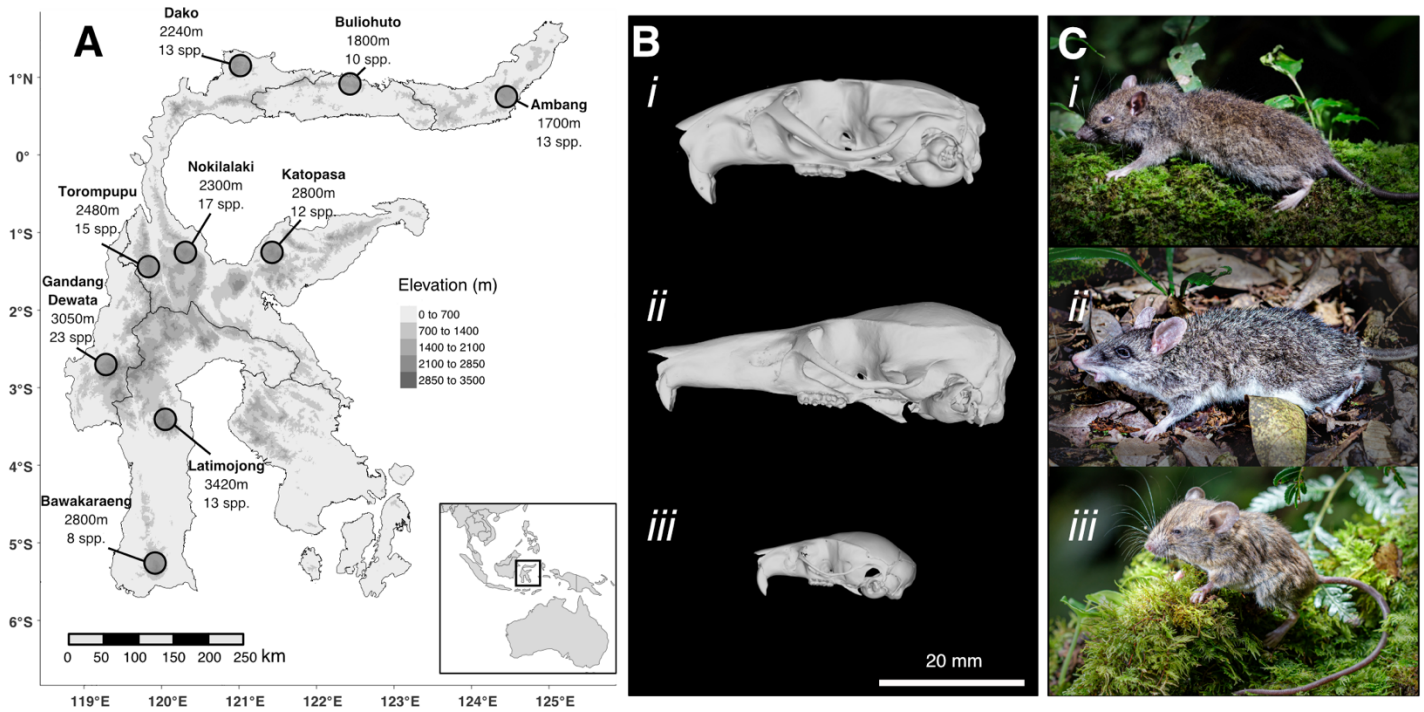


Figure 2: Small mammals surveys of nine mountains A) on the oceanic island of Sulawesi revealed varying murine rodent species richness across the island. Each mountain on the map contains the maximum elevation and the number of murine rodent species present. All but Latimojong were surveyed within 600m of the summit. B) The diversity of Sulawesi murines is exceptional and includes unique forms that live alongside species with more "typical" ecologies and morphologies, as demonstrated from surfaces of cranial µCT scans of *i – Rattus hoffmanni,* a "typical" murine morphology and ecology, *ii* – the shrew rat *Echiothrix leucura* of the Echiothrix Division with its extremely elongate rostrum and soft invertebrate diet, *iii* – the arboreal *Haeromys minahassae*, with a short rostrum and very small size. C) Photographs: *i – Rattus hoffmanni*, *ii –Echiothrix leucura*, and *iii – Haeromys minahassae*.

Materials and Methods

The distribution of species- We compiled small mammal inventories based on surveys of nine mountain regions on Sulawesi, Indonesia. These included one well-documented mountain surveyed from 1973 to 1976 by Guy Musser and colleagues (Mt. Nokilalaki; Musser, 2014) and eight mountains surveyed from 2011 to 2016 (Ambang, Bawakaraeng, Buliohuto, Dako, Gandang Dewata, Katopasa, Latimojong, and Torompupu; Figure 2A). All surveys began in lower primary forest, typically near the line of anthropogenic forest clearing, and extended to montane forests. All surveys extended to within 600m elevation of the summit except for Latimojong (highest survey site at 2535m, summit at 3400m). Historical surveys by Musser lasted several months and were conducted over four years, employing a mix of snap traps and live traps. Modern surveys (2011-16) lasted an average of 17 days (11-25) and employed similar collection methods, including a mix of snap traps, live traps, and 20-30L pitfall buckets. All the murine rodent species known from the sampled localities (Musser 2014, Wilson et al. 2019) were collected during these modern surveys, indicating a thorough sampling effort. Five new taxa that were discovered during these expeditions have been described (Musser 2014, Esselstyn et al. 2012, Rowe et al. 2014, Esselstyn et al. 2015, Rowe et al. 2016b) and several new locality records resulted (Achmadi, et al., 2014; Handika, et al., 2021). Specimens from all surveys were deposited in the Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia; the American Museum of Natural History (AMNH), New York, USA; Museums Victoria (MV), Melbourne, Australia; the Museum of Vertebrate Zoology (MVZ), Berkeley, USA; the Field Museum of Natural History (FMNH), Chicago, USA; and the Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge, USA.

Functional trait data collection and processing- We compiled or generated functional trait values for 11 continuous traits and one discrete trait for all available Sulawesi murines from each of the nine communities. Detailed information on traits, sample sizes, data processing, and multivariate trait composition are available in Table S1. All data, models, and output files are available in Dryad Repository (to be added prior to publication).

Morphological data collection- We assembled external measurement data from 630 specimens, including head-body length (mm), tail length (mm), hind-foot length (mm), ear length (mm), and mass (g), from previously published sources (Wilson et al. 2019, Nations et al. 2021) and online museum databases. Measured specimens were from the nine surveyed mountains and other localities on Sulawesi. To obtain ecologically relevant features of external measurements and mitigate the influence of size in some of our analyses, we calculated three commonly used ratios: Relative tail length (tail length / (head-body length + tail length)), relative hind-foot length (hind-foot length / head-body length), and relative ear length (ear length / head-body length) (Nations et al. 2021, Table S1).

We used a 3-dimensional geometric morphometric approach to calculate the variation in skull shape for each species. We generated μCT scans of the cranium of 64 specimens from 38 species (Table S1) and the mandible of 61 specimens from 36 species (Table S1). Scans were generated from specimens collected in the nine surveys, as well as from previously collected museum materials. Stacks of 2D Tiff files were imported to MorphoDig, where 3D landmarks were placed on cropped volume renderings (Lebrun, 2018). We placed 67 cranial landmarks

(Figure S2) on the left side of the skull, unless damage caused us to use the right side, in which case we reversed the rendering on the Z-axis. In separate renderings, we placed 20 landmarks on the left dentary of the mandible (Figure S2). Landmarks were exported from MorphoDig as .stv files and imported into the R package geomorph v.4.0.3 for processing (Adams et al. 2021, Baken et al. 2021). Missing landmarks (11 of 4288 cranial and three of 1220 mandible landmarks) were imputed with estimate.missing() , a generalized Procrustes analysis (GPA) superimposition was performed using gpagen(), and shape coordinates were subjected to a principal components analysis with gm.prcomp(). We retained the centroid size (an estimate of total size) and the scores from the first 36 principal components of the cranium and 20 axes of the mandible, each representing >95% of the shape variation of the element.

Stable isotope data collection- Approximately 1-2 grams of hairs were plucked from the rump of 286 dry museum specimens collected on six focal surveys. Isotopic values can vary regionally (Fry 2006), therefore we collected hair samples from multiple individuals of each species from each locality (mean = 4.6 specimens/species/locality, range = 1-14). Nitrogen stable isotope values ($\delta^{15}N$) act as a proxy for consumer trophic position as they generally increase by 3–5% per trophic level (DeNiro and Epstein 1981). Carbon isotope values ($\delta^{13}C$) generally exhibit little to no change with trophic position, and are commonly used as proxies of consumer's basal carbon resource use (e.g. use of differing primary production energy pathways; DeNiro and Epstein 1978). Combined, these two metrics are commonly used to quantify the "isotopic niche" of consumers, which can act as a useful proxy of species dietary niche (Newsome et al. 2007, Ben-David and Flaherty 2012). Stable isotope values are reported in delta notation in per mil units. Samples were processed at the Stable Isotope Ecology Laboratory, Department of

Oceanography & Coastal Sciences, Louisiana State University. Details on sample cleaning, processing, and stable-isotope analysis are in the Supporting Methods.

Locomotor mode data collection- Nations et al. (2019, 2021) classified Sulawesi murines into one of four discrete locomotor modes: Arboreal, which means climbing is integral to survival; General, or known to navigate a variety of substrates and habitat strata; Terrestrial, or only known to be on the ground surface; and Amphibious, or a dependence on aquatic habitats for foraging. Nations et al. (2021) showed that locomotor transitions in murines occur in a set order (Arboreal ↔ General ↔ Terrestrial ↔ Amphibious) and therefore we treat these modes as ordinal categories.

Combined traits – We combined our 11 continuous traits into five multivariate traits that represent biologically meaningful groupings: (1) head shape (cranium shape PC 1-36 and mandible shape PC 1-20); (2) isotopic niche space ($\delta^{15}N$ and $\delta^{13}C$ stable isotope values); (3) body proportions (head-body length, relative tail length, relative hind-foot length, and relative ear length); (4) body size (log(mass) and head-body length); and (5) total morphological shape (all nine morphological traits). We did this by combining the predicted trait values for each community (see below), each represented as a column, into a single dataframe of multiple columns (Table S1).

Estimating species' trait values- The sample size of morphological and isotopic data varied between species and mountain communities, and in some cases was limited to one individual, such as with the amphibious *Waiomys mammasae*, a species known from a single specimen

225 (Rowe et al. 2014). To mitigate uneven sampling, we estimated a probability distribution of
226 species trait values using partial-pooling in a multilevel Bayesian model. Unlike complete
227 pooling (one global mean estimated for all combined samples) or no-pooling (one mean
228 estimated per species, independent of all others), partial-pooling estimates a mean for each
229 species as well as the variation among species, which serves as an adaptive prior that is common
230 to all the species' means (McElreath 2020). The Bayesian partial-pooling modeling allowed us to
231 incorporate intraspecific variation in trait value predictions while avoiding point estimates such
232 as averages, which discard valuable information, and prevent unbalanced estimates by using the
233 trait-variance probability estimates from well-sampled species to inform variance estimates of
234 species with fewer samples (Gelman and Hill 2006, McElreath 2020). All analyses were
235 conducted in the probabilistic programming language Stan (Carpenter et al. 2017) within the R
236 library brms v. 2.17.0 (Bürkner 2018). Subsequent data processing and figuring relied on the R
237 libraries tidyverse v. 1.3.1 (Wickham et al. 2020), furrr v. 0.3.0 (Vaughan 2021), and tidybayes
238 v. 3.0.2 (Kay 2020). All data, scripts, and output files are available in Dryad Repository (to be
239 added prior to publication).
240
241 Model, prior, and chain-estimation details are described in the Supporting Methods.
242 Briefly, for each continuous trait (Table S1), we used the trait value as the response variable, and
243 used species as a group-level predictor. All traits were scaled to unity prior to analyses. We used
244 the student-*t* distribution to describe the response variable to minimize the influence of rare,
245 extreme observations (a.k.a. 'robust regression', Kruschke 2013, McElreath 2020). Each model
246 included four chains with 4000 iterations of warm-up and 1000 sampling iterations. Posterior
247 predictions from the four chains were combined, resulting in 4000 samples per trait per species.

248 To mitigate the potential geographic signal in stable isotope values (Fry 2006), and facilitate
249 randomization (see below), the posterior estimates of the $\delta^{15}N$ and $\delta^{13}C$ stable isotope values
250 were estimated with models that included an additional 'community' group-level effect, but
251 otherwise were identical to the models described above (Supporting Methods). These stable
252 isotope models generated posterior values of species' isotopic measurements conditioned on the
253 locality, enabling comparisons among communities and randomized sampling for null models
254 (Table S1, Figure S3).
255
256 *Estimating ecospace volume* – We defined ecospace volume as the total volume of n-
257 dimensional trait space occupied by species in a community, and for consistency and clarity we
258 used the term 'ecospace volume' for all individual and multivariate traits, regardless of
259 dimension. We used the sum of the variance of each trait value, which outperforms other
260 commonly used metrics such as ellipse or convex hull volumes (Guillerme et al. 2020), to
261 estimate ecospace volume. We estimated a posterior distribution of variance of each trait for
262 each community by first grouping the species' trait value estimates by community. Then, for
263 each of the 4000 posterior draws (one draw ranging between 7-23 values, depending on the
264 richness of the community), we estimated the variance of the trait, resulting in a distribution of
265 4000 variance values for each trait for each community. We estimated the combined multivariate
266 trait space variance by summing the variances of each trait, then dividing by the number of traits.
267 To estimate a total community variance for head shape traits (cranium and mandible), we
268 estimated the variance of each axis for each draw, as above, then calculated a weighted value of
269 each PC axis by multiplying the value by the contribution of each axis to the multivariate
270 variation of the PCA, and then summed the normalized values (Cooney et al. 2017). This

avoided both overestimating the impact of PC axes with low importance and arbitrarily dropping PC axes that may contain valuable information (Cooney et al. 2017, Uyeda et al. 2015). We estimated the 89% probability values for the variance of each individual and combined trait space. We estimated the size of locomotor-mode space by calculating the variance of each community.

Estimating ecospace density- We define ecospace density as the density of species within trait space. We used the mean nearest neighbor (NN) to estimate the density of trait values among species (Guillerme et al. 2020) and estimated the density of species in trait space in a similar manner to estimating the variance. First, we grouped species' trait values by community, then estimated the individual trait density for each posterior draw using the NN metric in the disparity() function of the R library dispRity (Guillerme 2018), resulting in a distribution of 4000 NN values for each trait. As NN can be calculated for any number of dimensions, we performed the same steps for the combined trait spaces. All axes in an NN estimate are considered equally, and we were unable to weigh cranial and dentary PC axes by their variances as we did above. Therefore, we conducted a broken stick analysis on the principal components using the R package PCDimension v.1.1.11 (Coombs & Wang 2019) and found the first two principal components of the cranial dataset and the first three components of the dentary dataset to be significant. We used the significant axes in NN estimates of cranial shape, dentary shape, and head shape density. To estimate locomotor mode density, we dummy coded locomotor mode into four binary columns (one per mode) and performed a redundancy analysis (Legendre and Legendre 2012) with the rda() function in the vegan package (Oksanen et al. 2019). We then extracted the PC scores for each species, grouped the species by community, and estimated the

294 NN value for each community as with the continuous traits above, in this case generating only a
295 single NN value per community rather than a distribution.
296
297 *Null models of ecospace volume and density*- We used null models to determine the difference
298 between the ecospace of our nine communities and randomly assembled communities. For each
299 community we created 1000 lists of $n_{community}$ species of Sulawesi murines with the
300 independent swap algorithm, which draws samples using species-occurrence frequency and
301 community species richness (Gotelli 2001, Swenson 2014), resulting in 1000 randomized null
302 communities for each of the nine localities. Each null community vector was equal in length to
303 the richness of the community it represented. We then calculated both volume and density as
304 above for each individual (n=12) and combined (n=5) trait for each of the 1000 randomized
305 community samples. We determined the standardized effect size (SES) of each individual and
306 combined trait value for each community using the formula:

307 $$SES = \frac{Trait_{observed} - Mean(Trait_{Random})}{SD(Trait_{Random})},$$

308 where $Trait_{observed}$ is the vector of 4000 samples of the density or volume of the given trait,
309 $Mean(Trait_{Random})$ and $SD(Trait_{Random})$ are the mean and standard deviation of the density
310 or volume values of the given trait from the 1000 random species assemblies. This method
311 produced distributions of SES values for both the density and volume of each individual and
312 combined trait for each community. Positive SES values indicate greater than random ecospace
313 volume or lower than random ecospace density (overdispersion), meaning that species in that
314 community are occupying ecospace outside the range of other communities and/or their niches
315 are farther apart in ecospace (niche expansion). Negative SES values indicate lower than random
316 ecospace volume and greater than random ecospace density (underdispersion or clustering),

317 meaning that species in that community are occupying less ecological space than other
318 communities and/or their niches are closer together in ecospace (niche packing; Oliveria et al.
319 2020).
320
321 *Effect of species richness on community ecospace volume and density*- If niche expansion is the
322 primary mode of resource partitioning in Sulawesi murine communities, then we expected that
323 ecospace volume will increase with increasing species richness, and that ecospace density will
324 remain stable as richness increases. Whereas if niche packing is occurring, we expected that
325 ecospace density will increase with species richness, and that there will be no effect of richness
326 on ecospace volume (Figure 1). To quantify the effect size of richness ($\beta_{richness}$) on ecospace
327 volume and density, we used Bayesian linear regression models that include the measurement
328 error of the predictor variable to estimate the effect size of species richness on volume or density.
329 Measurement error models contain vastly more information per observation than a single point
330 observation and provide robust estimates despite the small number of sampled communities
331 (Bürkner 2018, McElreath 2020). The models, priors, and chain estimations are detailed in the
332 Supporting Methods. Briefly, we used species richness as the response variable, and the mean
333 and standard error of the trait estimates for each community as the predictor. We ran one model
334 for the SES volume or density of each individual and combined trait space. We also calculated
335 the Bayesian R^2 value for each regression (Gelman et al. 2019).
336
337 *Phylogenetic diversity as a path to trait disparity*- The ecological space occupied by a
338 community may depend on which lineages or clades are present (Webb 2000). Trait disparity
339 appears to vary among clades of Sulawesi murines, and if so, then the volume and densities of

ecospaces may be more influenced by phylogenetic diversity than ecological factors. To determine how phylogenetic diversity mediates ecospace occupancy in the nine murine communities, we estimated the phylogenetic diversity (PD) of each community using Faith's metric of branch length (Faith 1996). We removed all but the Sulawesi species (n = 35) from a time-calibrated phylogenetic hypothesis of Murinae (Nations et al. 2021). For the analyses described above, we had trait data for four species that are not included in this phylogeny: *Maxomys wattsi, Rattus bontanus*, *Rattus mollicomulus*, and *Rattus marmosurus*. We manually added these four species into the tree using the bind.tip() function in phytools (Revell 2012). Details on the phylogenetic positioning of these species is found in the Supplemental Methods. We estimated Faith's metric of PD and, because PD is not independent of species richness, the SES value of PD using the ses.pd() function in picante (Kembell et al. 2010). As previously described, we used the independent swap algorithm to sample 1000 random communities and used linear modeling in brms to estimate the effect size of species richness on SES PD. *Haeromys minahassae* is the only representative of its genus on Sulawesi, and, due to its large phylogenetic distance from other Sulawesi murines, may have an oversized impact on estimates on community PD. Therefore, we repeated the estimates of SES PD and effect size above without including *Haeromys minahassae* to ensure unbiased results. To quantify the trait disparity within and among Sulawesi murine clades, we grouped the posterior distributions of the species' predicted trait values by clade, then estimated the variance of each of the 12 univariate traits. We plotted the trait value variance for each community along with the species' predicted trait values (Figure S4)

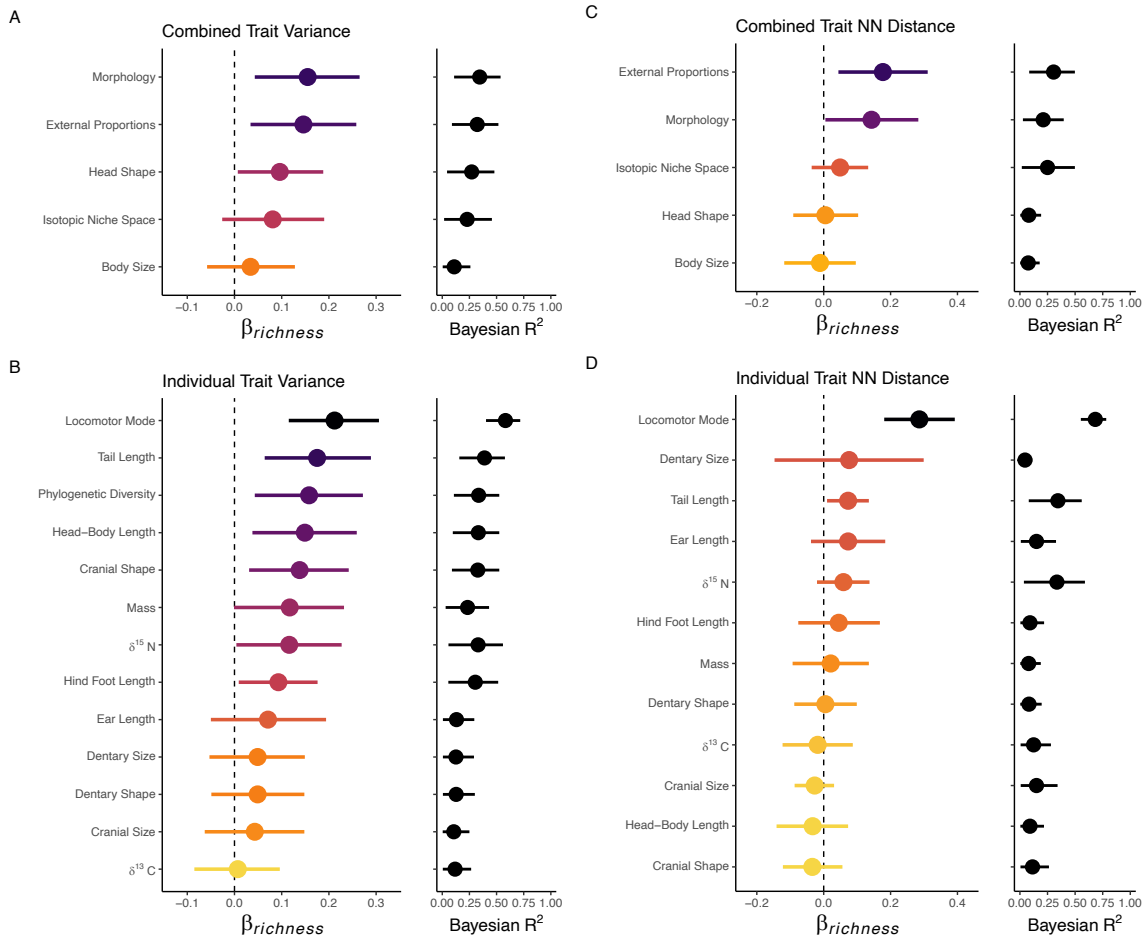


Figure 3: Most estimates of community ecospace volume increase with species richness. X-axes show the $\beta_{richness}$ estimates (effect sizes) for each trait space (y-axis) on the left and the Bayesian R^2 for each $\beta_{richness}$ estimate on the right. Colored point intervals show 89% probability of $\beta_{richness}$ estimates (effect size), with color varying by $\beta_{richness}$ value. Black point intervals show 50% posterior estimations of Bayesian R^2 for each trait space. Four of the five combined traits (A) and seven of the 11 individual traits (B), show an increase in volume with increased richness (i.e., positive $\beta_{richness}$). Phylogenetic diversity also increases with species richness (B). All combined traits (C) and individual traits (D) show a stable or, surprisingly, decreasing ecospace density (increased NN distance) with increased species richness.

Results

Models of trait values- All parameters in the Bayesian multilevel model estimates of trait-value distributions and measurement-error estimates of the species richness effect on trait values had ESS > 1000 and a Gelman-Rubin diagnostic $\hat{R} \leq 1.01$, indicating convergence. Raw size and density values differed from the size and density of SES. To avoid the confounding influence of species richness in our size and density estimates we only report and discuss the SES values (Swenson 2014).

Effects of Species Richness on Ecospace Volume and Density- Ecospace volume is positively correlated with species richness in seven of the 12 traits (locomotor mode, tail length, head-body length, cranium shape, mass, $\delta^{15}N$, and hind foot length), as shown by the positive effect sizes from the Bayesian linear models (Figures 3, Table S3) and the greater variance with higher community richness (Figure 4). The remaining five traits (ear length, cranium size, dentary size, dentary shape, and $\delta^{13}C$) do not substantially increase in volume with increased species richness. The SES values of three of the five combined traits increased substantially with species richness (total morphological shape, external proportions, and head shape) whereas body size and isotopic niche space showed a moderate probability of increasing with species richness (Figures 3, 4, Table S2, S3).

Linear regression showed that species richness had little to no effect on ecospace density (NN SES values) for 10 of the 12 individual traits and three of five multivariate traits (Figures 3, S4, Table S2). The exceptions were a positive effect size (i.e., decreased density with richness)

on locomotor mode, tail length, total morphological shape, and external proportions, suggesting an overdispersion of morphology and locomotor diversity in the richest communities.

Phylogenetic Diversity and Ecospace- Phylogenetic diversity (PD) increased with species richness (Figures 3, 4, Table S2). Including *Haeromys minahassae* in the estimates of PD changed the PD SES values of the individual communities but had a very small impact on the linear regressions (Table S4). Results including *Haeromys minahassae* had a slope ($\beta_{richness}$) of 0.158 (89% C.I. of 0.043, 0.272) while excluding *H. minahassae* generated a slope of 0.168 (0.039, 0.297), and we therefore present the results that include *H. minahassae*. Katopasa, a community of 12 murines on Sulawesi's Eastern Peninsula, has the lowest PD SES value followed by Bawakaraeng on the Southwestern Peninsula (seven species). Gandang Dewata, the richest community, has the highest PD SES value (Figure 4A, Table S2). As we suspected, ecospace volumes vary between clades, though not consistently (Figure S5). For example, the Echiothrix clade has the highest variance in cranial shape, dentary shape, and dentary size but low trait variance for hind-foot length and $\delta^{15}N$. In contrast, the Maxomys clade has low variance for all trait values except tail length and $\delta^{15}N$ (Figure S5). This results in different densities of ecospace occupation among traits, where some trait volumes are strongly influenced by phylogeny, such as cranial space, while other traits such as isotopic niche space have high and low values distributed among clades (Figure 5).

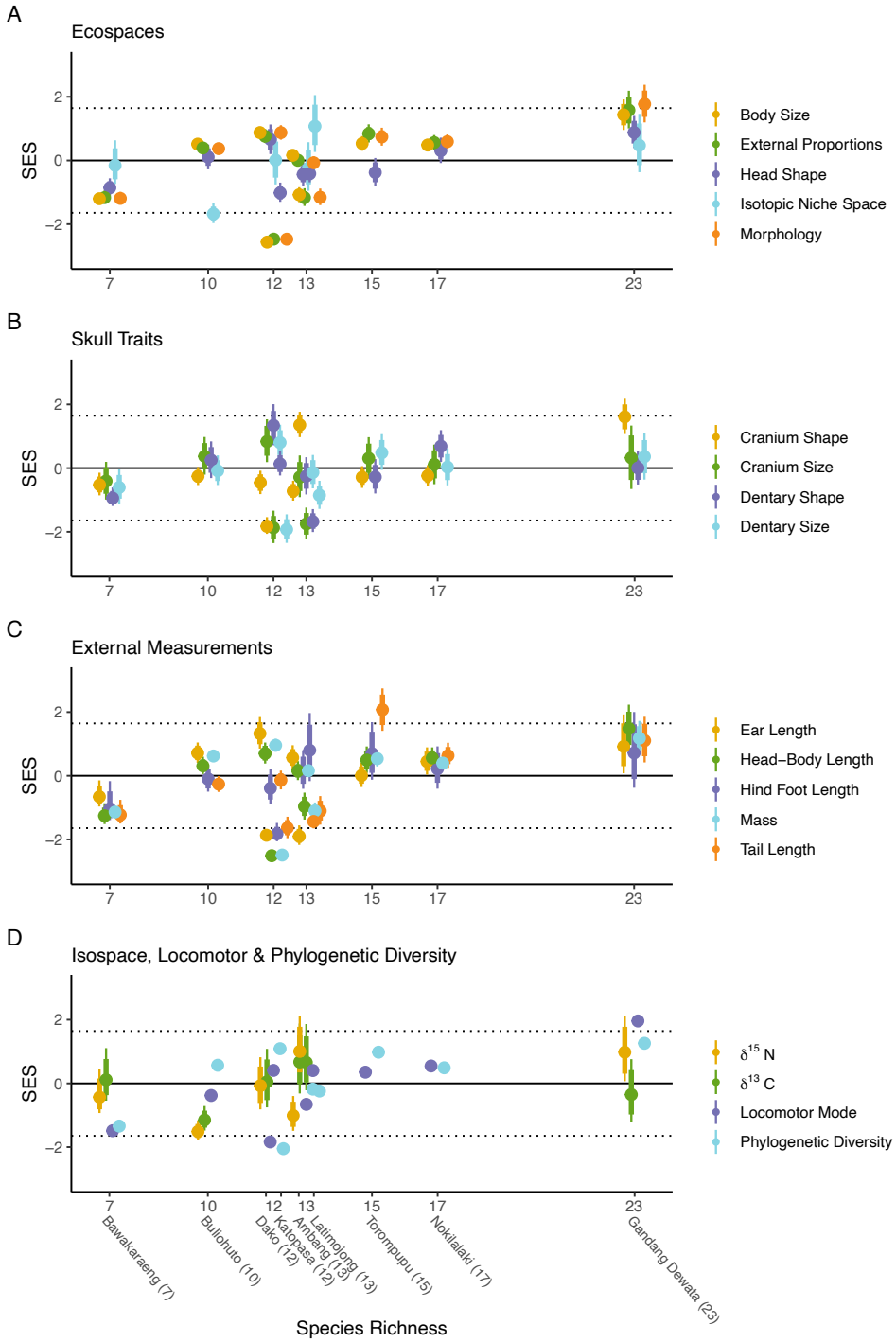
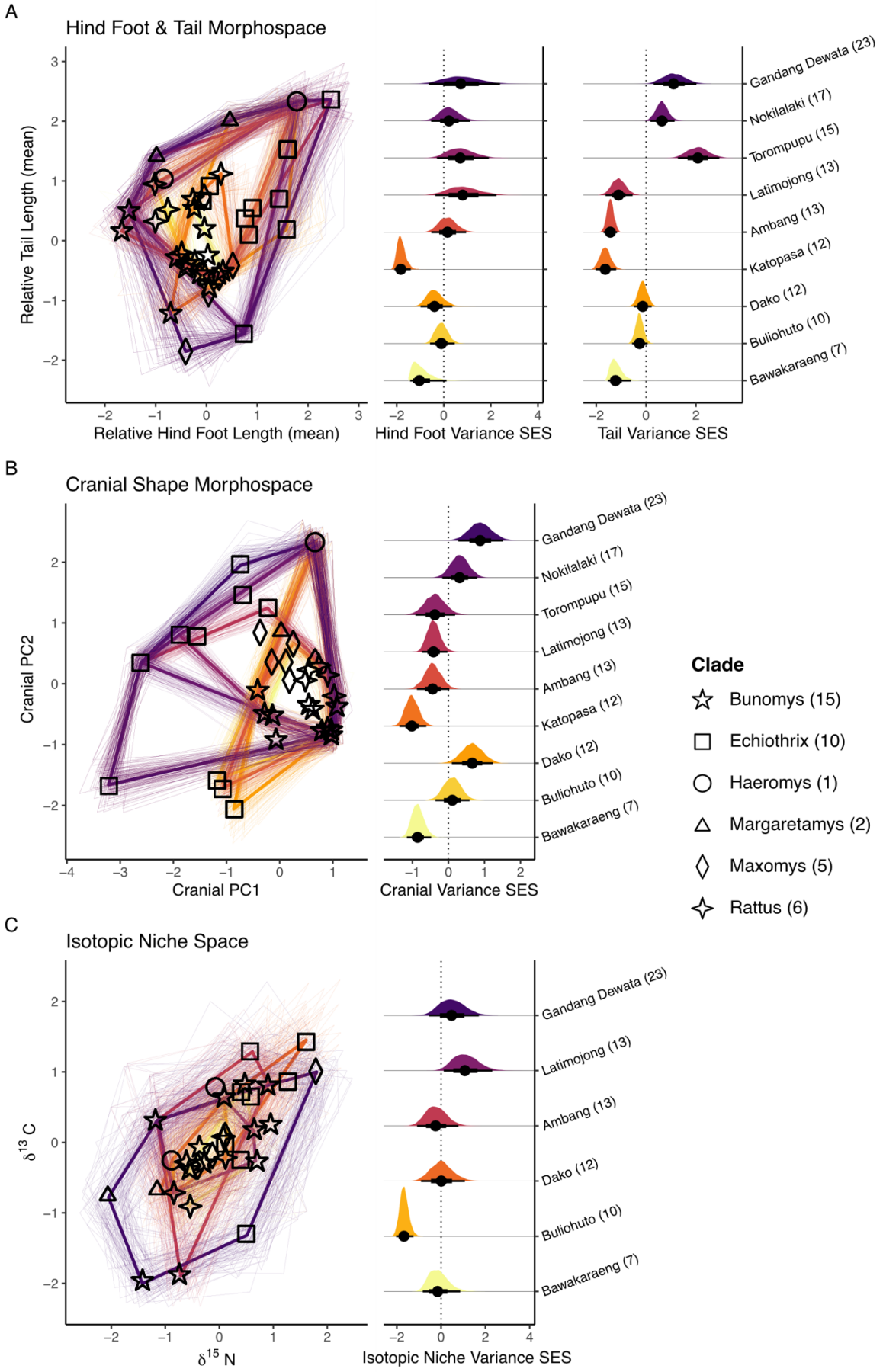


Figure 4: Estimated trait volume SES plotted against species richnesss: A) Combined trait space volumes, B) Skull traits, C) External measurements, and D) Isotopic measures, locomotor mode, and phylogenetic diversity. Points represent the mean SES values and error bars indicate the 89% credible intervals. X-axis tick marks show the species richness values for each of the communities by mountain. Values equal to zero are consistent with null expectations, positive values indicate overdispersion, and negative values show underdispersion (trait clustering). Dotted lines depict the 89% interval of the null distribution. The plot of trait densities is shown in the supporting information (Figure S4)


A
Hind Foot & Tail Morphospace
Relative Tail Length (mean)
Relative Hind Foot Length (mean)
Hind Foot Variance SES
Tail Variance SES
Gandang Dewata (23)
Nokilalaki (17)
Torompupu (15)
Latimojong (13)
Ambang (13)
Katopasa (12)
Dako (12)
Buliohuto (10)
Bawakaraeng (7)
B
Cranial Shape Morphospace
Cranial PC2
Cranial PC1
Cranial Variance SES
Clade
Bunomys (15)
Echiothrix (10)
Haeromys (1)
Margaretamys (2)
Maxomys (5)
Rattus (6)
C
Isotopic Niche Space
δ13 C
δ15 N
Isotopic Niche Variance SES

427

Figure 5: The mode of ecospace filling varies between traits. The bivariate plots in the left-hand columns depict the 2D ecospaces. Each black shape within the ecospace is the mean value of a particular species in each clade (shown in legend). The convex hull colors match the color of the community variance SES distributions in the right-hand columns. The thick convex hull lines are mean values, and 100 random samples from the posterior of each trait are shown in thin hull lines. The number of species in each community and each clade used in this study is shown next to the SES distributions in parentheses. A) Large values of hind foot length belong to members of two clades, while large and small tail length values are dispersed among all six clades, reducing the influence of phylogenetic diversity on tail length disparity. B) Cranial morphospace values are mostly clustered tightly near the mean of each axis, apart from Echiothrix species and the single Haeromys species. Intraspecific variance is also relatively low on these axes. C) Intraspecific variance is high in isotopic niche space. High and low $\delta^{15}N$ values are distributed among clades, though $\delta^{13}C$ values less so.

Discussion

The recognition that species richness often covaries with habitat complexity and resource availability gave rise to the theory of limiting similarity, which suggests that the degree of niche overlap governs the intensity of interspecific competition (MacArthur and Levins 1967, Brown 1975). In the richest communities, the narrowing of species' niches and the packing of resource space appears to be a common form of resource partitioning and is particularly evident at high taxonomic levels and broad spatial scales (Karr and James 1975, Pigot et al. 2016, Cooney et al. 2017, McClain et al. 2018, Hughes et al. 2022). However, interpreting the distribution of functional richness across large resource gradients may be difficult due to covarying factors such as environmental changes or taxonomic turnover (Swenson et al. 2016). Communities of closely related species that inhabit similar environments provide a unique window to explore how interspecific competition may affect community functional richness absent confounding factors like taxonomic or environmental variation (Roughgarden 1976, Swenson et al. 2016), but such communities are rare in nature (Swenson et al. 2016, Van de Perre et al. 2020). Here we use a large dataset of ecological and morphological variables along with a novel probabilistic approach to estimate the changes in community ecospace occupancy across a richness gradient. Our results

from nine murine communities living on similar tropical mountains revealed that the relationship between ecospace volume and density with species richness varies among traits. The most common relationship was an increase of ecospace volume with increasing richness, consistent with niche expansion. The cranial shape, body shape, body size, and locomotor mode ecospaces, all thought to be ecologically important traits in murines and vertebrates in general (Peters 1986, Losos 2009, Martinez et al. 2018, Nations et al. 2021), increase with richness (Figure 3). Measurements of skull size, dentary shape and size, ear length, and $\delta^{13}C$ values all demonstrate either a weak signal of niche packing, or no signal. While the size of many trait ecospaces increase with richness, ecospace density shows little correlation with species richness and in some cases, surprisingly, decreases with increased richness. These results, along with a general underdispersion of trait values in low-richness communities and overdispersion in high-richness communities (Table S2, Figures 4 & S4), suggest that species in rich communities mitigate competition by occupying underused niche space. Our results contrast theoretical predictions on resource partitioning in insular communities. On remote islands, niche packing is expected to occur with increased species richness if resources are constant across communities, as in our Sulawesi localities, but if resources covary with species richness, expansion is expected to occur (Roughgarden 1976). We also found that phylogenetic diversity increases with species richness and ecospace volume beyond random expectation. Combined, these results point to species interactions as a mechanism for both phenotypic and phylogenetic overdispersion (Webb et al. 2002, Cavender-Bares et al. 2004), and suggest that, given adequate resources, structural complexity, and evolutionary time, species can adapt to unique regions of ecospace, often far from the average trait value, which minimizes niche overlap and cultivates exceptional richness.

481 Whether in a single desert valley (Brown 1975), or across continental (Maestri and
482 Patterson 2016) and global latitudinal gradients (Karr and James 1975, Pellissier et al. 2018),
483 structurally complex habitats are thought to foster higher species diversity. High plant diversity,
484 in particular, creates a more complex, vertically structured habitat matrix for other plant and
485 animal species to occupy and has long been tied to higher animal richness (Hutchinson 1959,
486 MacArthur and MacArthur 1961, Scheffers et al. 2013, Oliveira and Scheffers 2018). Our
487 estimates of locomotor-mode occupancy clearly demonstrate that vertical habitat partitioning is
488 critical to maintaining high species richness in Sulawesi murines (Figure 3, Table S2). Strikingly,
489 the density of locomotor trait space decreases along the richness gradient, indicating a very high
490 level of trait value overdispersion (Figures 3C & S4). Arboreal, Terrestrial, and Amphibious
491 locomotor modes each provide access to different microhabitats that contain similar resources.
492 On Mt. Gandang Dewata, the richest community with 23 species, the amphibious *Waiomys*
493 *mamasae*, the terrestrial *Paucidentomys vermidax*, and the arboreal *Sommeromys macrorhinos*,
494 all consume invertebrates and have similar $\delta^{15}N$ values, yet they are unlikely to compete for
495 resources due to their distinct microhabitat use, a pattern observed in other insular communities
496 of closely related vertebrates (e.g., Jamaican *Anolis*; Shoener 1974). Morphological
497 measurements are often used to infer locomotor mode in a variety of eco-evolutionary contexts
498 (Ricklefs and Travis 1980, Samuels and Van Valkenburgh 2009, Pianka et al. 2017, Verde-
499 Arregoitia et al. 2019), and our estimates of tail-length variance, a trait correlated with
500 locomotion in murines (Nations et al. 2021), increases with richness at nearly the same rate as
501 locomotor mode (Figure 3). However, we demonstrate that categorical locomotor modes
502 themselves, especially if shown to be structured in an ordinal manner, can be used directly to
503 estimate community locomotor variance and provide a simple way to test hypotheses of niche

structure and variance across wide taxonomic levels and geographic scales where continuous trait data are lacking.

Combining many traits into one multivariate measure of functional diversity is a common approach in evolutionary ecology. Ordination techniques were especially promoted to overcome pitfalls from early community ecology studies that used few, largely subjective measures of resource use (Ricklefs and Travis 1980). However, merging traits into multivariate axes masks trait-specific processes related to functional space (Spasojevic and Suding 2012, Astor et al. 2014). Indeed, our trait volume and density estimates reveal distinct patterns between individual and combined traits. For example, isotopic niche space, a combined signal of $\delta^{15}N$ and $\delta^{13}C$ values commonly used in terrestrial ecological studies, exhibits an equivocal signal of niche packing and expansion (Figure 3B), but individual isotopic values reveal that the packing signal originates from the static $\delta^{13}C$ value variance along the species richness gradient. The $\delta^{15}N$ value, a signal of trophic level, expands along the richness gradient, a result that would be overlooked in multivariate analyses. In contrast to $\delta^{15}N$, dentary shape exhibits an equivocal signal of packing and expansion, despite its presumed relationship to dietary niche (Maestri et al. 2016, Kohli et al. 2019). These opposing patterns are only illuminated by analyzing differences in the functional diversity of individual traits (Spasojevic and Suding 2012). If we performed this study using only cranial size and dentary shape, which are thought to capture the important axes of size and diet in murine rodents (Rowsey et al. 2019, 2020) and mammals in general (Prevosti et al. 2012, Grossnickle 2020), our results would support niche packing as the dominant pattern.

The theory of limiting similarity is based on both the mean and variance of species' niche space (MacArthur and Levins 1967), and intraspecific trait value variation may equal or exceed interspecific variation (Des Roches et al. 2017). Ignoring the differences between individuals of a species may taint inferences of functional richness within communities (Violle et al. 2012). Here we demonstrate a multilevel approach (Bürkner 2018) to model species' trait distributions and estimate richness and disparity metrics that fully incorporates intraspecific variation, thereby circumventing the typical concerns associated with point estimates or undersampling (Des Roches et al. 2017). We then used those values to estimate distributions of ecospace volume and density. This approach has several favorable properties. First, it allows for any level of intraspecific variation, and seamlessly incorporates this variation in predictions of community ecospace volume and density. Additionally, including uncertainty in ecospace values provides information about the trait itself. Using isotopic niche space as an example, the measure of uncertainty in species-level stable isotope values is far greater than the intraspecific variation estimated for other traits such as tail length or cranial shape (Figures 4 and 5). This result suggests substantial flexibility within species' diets, demonstrating how diversifying dietary items may aid niche partitioning within communities (Grant 1986).

The disparity of traits within a clade can mediate the impact of phylogenetic diversity on community ecospace volume. For example, if trait values are phylogenetically clustered, then increasing phylogenetic diversity, such as through invasion by new clades, is necessary for community niche expansion to occur. But if trait values are phylogenetically overdispersed, niche packing or expansion could result from increased phylogenetic diversity. This phenomenon is especially important for communities that are assembled through a mix of island colonization

549 and in situ speciation such as Sulawesi murines, Caribbean anoles, or Hawaiian spiders
550 (Gillespie 2004, Losos 2009, Rowe et al. 2019; Handika et al 2022). Niche divergence has been
551 hypothesized to overcome niche conservatism in communities with an extended history of
552 coevolution, such as those on oceanic islands, likely diminishing the signal of phylogenetic trait
553 clustering (Losos et al. 2003). Contrarily, we found that for most traits ecospace volume
554 increases with species richness and phylogenetic diversity. For example, the distinct skull
555 features of species in the Echiothrix division, the descendants of the first murine colonists on
556 Sulawesi, set them apart from other clades in skull shape and, despite their relatively low
557 abundance, these species overcontribute to community cranial and dentary shape volumes
558 (Figures 4B, 5B, S5). However, we also found that the effect of phylogenetic diversity on
559 ecospace size and density varies between traits. Unlike cranial shape, trophic level estimates
560 from $\delta^{15}N$ values are notably dispersed (Figures 5C, S5), and high phylogenetic diversity is not
561 necessary for high isotopic niche space estimates. Are there innate differences in these traits that
562 could lead to opposing patterns of niche conservatism?
563
564 The evolutionary lability of ecologically important traits determines the rate of
565 convergence and divergence possible in a given time frame and can directly influence dispersion
566 of trait values among species (Cavender-Bares et al. 2004). The traits with the highest within-
567 clade variance — $\delta^{15}N$, tail length, body size — are all thought to be evolutionarily labile.
568 Changes in tail length, body size, and intestinal tract morphology can occur on brief evolutionary
569 time scales (Powell and King 1997, Naya et al. 2008, Kingsley et al. 2017, 2021), whereas
570 morphological changes in cranial shape, such as substantial rostral elongation and the reduction
571 of molar grinding area, may take much longer. Indeed, insular species are known to have rapidly

expanded breadths of diet and labile morphological traits following colonization (Stuart et al. 2014) and subsequent speciation (Wilson 1959, 1961, Lister 1976, Rowe et al. 2016a). Yet the extreme morphologies of some Sulawesi murines, particularly those of the oldest radiation on the island (Echiothrix division), are likely the result of a long process of in-situ evolution (Rowe et al. 2019). Our results point toward evolvability of traits as a determinant of patterns of trait value dispersion (Webb et al. 2002, Cavender-Bares et al. 2004), which directly relates to our inferences of niche expansion and packing in Sulawesi murines. Less understood is how varying evolutionary lability affects dispersion of trait values. The theory of niche complementarity suggests that a pair of species that are similar in one trait should diverge in another trait (Schoener 1974). Therefore, similarities in some slowly evolving traits may lead to higher divergences in more labile traits, or vice versa. Linking the degree of trait lability with niche complementarity in an island system has important implications for the generation of functional and taxonomic diversity and may further illuminate the process of niche filling in endemic radiations.

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