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Body size and abundance are decoupled from species richness in Australian marine bivalves

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Abstract

The "more individuals hypothesis" suggests that increases in the total number of individuals per species leads to increases in community richness. Abundance, body size distributions and richness do vary with latitude in several taxonomic groups. However, support for this hypothesis has otherwise been mixed. In this paper, we investigate latitudinal changes in all three variables for marine bivalves along the eastern coastline of Australia. We utilise a large, uniformly sampled field dataset of 5670 shells representing 157 species that spans 20º of latitude and crosses a major biogeographic transition. For each of 15 field sites, 10 quadrats were randomly placed and completely sampled, making it possible to quantify total abundance. Species richness was calculated using a new estimator based on the geometric series distribution. Body size was computed as the geometric mean of length and width. Despite uncovering a strong latitudinal gradient in species richness, we found no significant gradient in total abundance and body size at any taxonomic level. Although previous work found family-level trends in bivalve size, it was done at a larger spatial scale and therefore did not pertain to individual communities. Environmental variables do correlate with both abundance and richness, but they are not directly related. Because we find no gradient in abundance and no relationship between abundance and richness, we reject the "more individuals hypothesis" for our system. Instead, latitudinal richness trends in coastal Australia may result from an environmental gradient in dispersal constraint.

Highlights

- The "more individuals" hypothesis relates species richness gradients to population sizes, but it has rarely been tested using counts of individuals within actual communities.

- We test this hypothesis using an extensive and rigorously standardised set of 15 field collections of bivalve shells spanning 20º of latitude along the east coast of Australia.

- We introduce a new richness estimator with high precision and low sample size bias.

- We relate richness and abundance to environmental variables in a structural equation model.

- Because richness and abundance do not correlate directly with each other, the "more individuals" hypothesis can be rejected.

Introduction

Latitudinal diversity gradients are among the most fundamental, intriguing, and heavily debated patterns in ecology. The "more individuals" hypothesis is a leading explanation for diversity gradients (Currie and Fritz, 1993, Currie et al. 2004, Storch et al. 2018). It suggests that productivity increases species richness by increasing the number of viable

populations and therefore lowering extinction rates. Indeed, the number of individuals has been shown to increase with diversity in several groups, across taxa and environments (Siemann et al. 1999, Yee and Juliano, 2007, Seoane et al. 2017, Müller et al. 2018). Meanwhile, the presence of a latitudinal abundance gradient in terrestrial invertebrates is largely supported by the literature, as with gradients in other taxa (Storch et al. 2018).

Nonetheless, evidence for the "more individuals" pattern has been indecisive at every turn. First, it has been suggested to be an instantiation of the species-energy effect (Currie et al. 2004, Evans et al. 2005), but the connection is not direct. The reason is that a variety of mechanisms linking energy to diversity gradients have been proposed other than just increases in total abundance (Allen et al. 2002, Allen et al. 2006, Storch, 2016), such as increased mutation rates. Also, the effects of local disturbances alter the nature of richness-abundance relationships (McGlynn et al. 2010). Overall, recent reviews have yielded mixed support for the "more individuals" hypothesis (Storch et al. 2018).

Trends in the body size of organisms with increasing latitude have also been of key interest to biologists for over a century (Bergmann, 1847, Cushman et al. 1993, Blackburn et al. 1999). The directionality and even the existence of these gradients has been shown to be inconsistent between groups and at different taxonomic levels (McNab, 1971, Blackburn et al. 1999, Roy and Martien, 2001, Meiri and Dayan, 2003, Ashton, 2004, Linse et al. 2006, Adams and Church, 2008). Nonetheless, researchers starting with Bergmann (1847) have illustrated a general trend of larger body sizes with increasing latitude. This trend has been extensively documented in endothermic tetrapods (Meiri and Dayan, 2003, Ashton, 2004).

Because body size changes with latitude, it has been thought that there might be a link to the latitudinal diversity gradient (Hillebrand and Azovsky, 2001, Cardillo, 2002, Barneche et al. 2019). Some larger-bodied organisms have been shown to have stronger latitudinal diversity gradients (Hillebrand and Azovsky, 2001, Weiser et al. 2018), and body size has been directly matched to global diversity patterns in reef fish (Barneche et al. 2019). However, inverse latitudinal body size relationships exist for many groups (Pincheira-Donoso et al. 2008, Moles et al. 2009, Angielczyk et al. 2015). In marine animals, similar gradients have been found with depth (Smith and Brown, 2002), but these general patterns are not consistent within smaller taxonomic units (Berke et al. 2013) and body size can vary more with geographic location than latitude (Linse et al. 2006).

Because support for all of these hypotheses have been mixed, well-designed, field-based tests of these relationships at a large scale are needed. In this paper we investigate the relationship between body size, total abundance, and species richness in marine bivalves along the eastern Australian coastline. Marine invertebrates are not often examined in abundance gradient studies, despite the species-energy relationship having long been known to be present in marine systems and across taxa (Tittensor et al. 2010). Globally, marine bivalves have been shown to have latitudinal body size gradients (Berke et al. 2013), but the exact relationships differ among groups and cannot be generalised. We utilise a systematically collected field dataset, rather than an ad hoc observational dataset. It covers 20.5º of latitude spanning the temperate and tropical zones and crosses a major biogeographical boundary. Thus, any link between these variables should be easy to detect if it exists. We estimate richness using a new estimator based on the geometric series distribution. Latitudinal trends in body size and total abundance are described, and the relationships between abundance, body size and richness are tested and discussed. Finally, we investigate how environmental conditions relate to total abundance, body size and species richness along the coastline.

Materials & Methods

Field collection

Dead bivalve shell assemblages were collected from 15 beaches across the eastern coastline of Australia (Fig. 1, Appendix S1) in August of 2018 and 2019. Beaches were selected to be evenly distributed along the eastern coastline, eastwards facing, and completely open to the ocean.

Ten samples were taken from each beach by putting down 50 x 50cm (0.25 m^2) quadrats: five samples were taken north of the beach midpoint and five were taken to the south. Quadrats were placed haphazardly, but with a minimum of 10m distance between each quadrat ensured. Sampling was only carried out during clear days not following a storm to avoid artefacts of changes in depositional mode. Quadrats were randomly placed along the beach between the high and low tide marks, again ensuring they were ≥ 10 m apart. Sediment recovered down to a 5 cm depth within each sample was processed through 16, 8, and 4 mm sieves, with all shell material retained and identified. Our dataset totalled 5,670 shells representing 157 species (Appendix S2). All shells from the same site were combined to form each site assemblage, from which total abundance and richness were calculated. In other words, total abundance was taken as the total number of valves at each site.

Body size was calculated as in Berke et al. (2013) by taking the geometric mean of shell length and height on a log$_2$ scale. This statistic correlates well with other size metrics (Kosnik et al. 2006). Because the majority
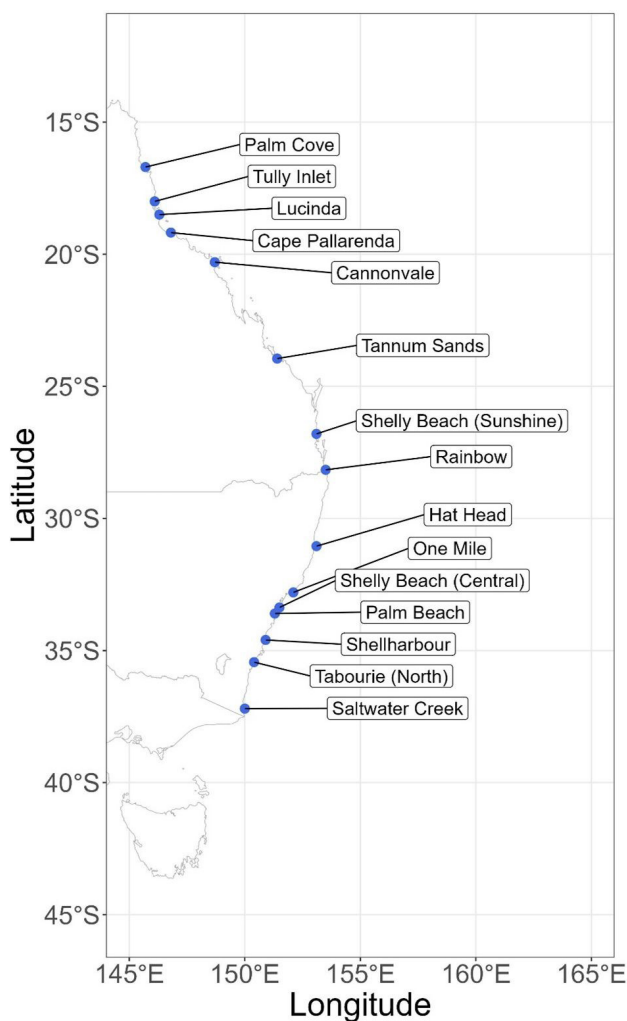
Figure 1. Location of the 15 sites sampled for dead bivalve shell assemblages, along the eastern coast of Australia, during field collection in August of 2018 and 2019. Sites are labelled using names taken from Short et al (2006) and Short et al (2007).

body size of each species. Our measurement dataset contained 350 shells from 12 sites, composed of 126 species from 26 families (Appendix S3) – this number is lower than the total number of the species in the dataset due to many species not being represented by complete valves.

Analysis

We focused our analysis on species richness as a diversity measure, estimating it for each full site-level collection using a new estimator. It is based on the geometric series (GS) distribution, as opposed to the unrealistic uniform distribution tacitly assumed by Chao 1 and related measures (Chao 1984; Alroy 2017). The expected mean of the well-known GS is $1/(1-p)$ where (1) the actual counts are all non-zero and (2) p is the governing parameter of the distribution, and also equal to the proportion of species that have been sampled. We assume that each count n is an independent estimator of p: $n \sim 1/(1-p)$, so $p \sim 1 - 1/n \sim (n-1)/n$. We then take the mean of the $(n-1)/n$ ratios to derive an overall estimate of p, and finally divide this ratio into the number of observed species to estimate the total size of the community. This index performs with high accuracy in simulation (Supplemental Text S1, Fig. S2) when different underlying distributions such as the negative binomial, Poisson log normal, and Weibull are assumed to generate counts in samples. We obtained similar results using Chao 1 (Chao 1984) and a variety of other measures (Table S1), but consider them less reliable because of the new method's conceptual properties and performance in simulation. We include R code for the geometric series index, as well as for these analytical tests, in the supplementary material (Appendix S4).

We first examined latitudinal trends in species richness, the number of individuals at each site, and the body size of species present at a site. Species richness and the number of individuals were log transformed in each analysis. Size was analysed on both a species basis, where only one measurement per species was included, and an individual basis, where size was weighted by the number of individuals of each species at the site. Additionally, we investigated the relationship between body size and latitudinal range for species within our dataset.

We further assessed spatial patterns of body size and total abundance in different environmental conditions. Values for environmental variables were downloaded from the CSIRO Atlas of Regional Seas (Ridgway et al. 2002, Condie and Dunn, 2006) on 4th November 2020. We downloaded values for eight variables at each of our sites: mean annual sea surface temperature, annual temperature standard deviation, mean annual salinity, annual salinity standard deviation, mean annual dissolved oxygen

of the shells were incomplete, the largest complete valve for each species at each site was measured using traditional linear measurements (length and height of the valve: Fig. S1). Other studies that investigate the latitudinal body size trend in bivalves have focused on the largest specimen as a proxy for the body size of a species (e.g., Roy and Martien, 2001 and Berke et al. 2013). By allowing for the maximum to change between sites we are able to account for geographical changes in body size within species as well as among communities. Species present at a site that could not be measured due to the lack of complete valves of the relevant species were assigned the geometric mean of all other occurrences of that species as a proxy value. Although only the largest specimen was measured, species identity significantly explained 64.3% of the variation in maximum size in a one-way ANOVA ($p < 0.001$) and therefore is a suitable proxy for the

content and mean annual concentrations for nitrate, phosphate, and silica.

We tested the relationship between the environmental variables, body size, total abundance and richness using structural equation modelling (SEM), which quantifies the relationships between response variables and latent variables that are constructed from sets of predictor variables. Environmental variables were assigned to latent variables based on the results of an exploratory factor analysis rather than using predetermined sets of variables. The number of latent variables was determined by a parallel analysis run on the abiotic variables. This method compares the scree of the data with that of a randomised table with the same dimensions (Horn, 1965), thereby returning an objective number of factors to use. For this analysis, the number of factors was determined to be three. Each abiotic variable was then assigned to a latent variable by identifying the factor it loaded most strongly upon (Table S2).

The final model was run using the environmental variables and data for species richness, the geometric mean of body size, and total abundance derived for each site from the field collections. Species richness and abundance were logged when carrying out the SEM. All functions for the exploratory factor analysis were drawn from the R package *psych* (Revelle, 2019). We implemented the final model using the R package *lavaan* (Rosseel, 2012).

In order to investigate whether or not the complexity of the ecological community was related to the patterns we uncovered, we used the alpha gambin parameter (Matthews et al. 2014). This is a representation of the shape of the species abundance distribution and therefore the inequality between rare and common species. It has been used in macroecological studies to assess spatial variation in species abundance distributions (e.g. Arellano et al. 2017, Matthews et al. 2019). We calculated the alpha parameter for each site and investigated whether there was a relationship with richness or the number of individuals. This study does not address the question of whether the gambin distribution is particularly representative of the current data set; other distributions may prove to be more relevant.

Finally, a subsampling routine was performed to investigate whether any trends in the within-site spacing of body size distributions might reflect random assembly from the regional species pool. For each site, the pool of all measured species was randomly sampled down to the number of species present in that site. A random measurement was taken from the measured shells for each species and the median nearest neighbour distance for each measured species was computed from the subsampled measurements. This routine was carried out 10,000 times to generate a null distribution, which was then compared to the true median distances between species within the samples. The position of the true median along the null distributions was used to draw conclusions about the assembly of the community from the regional pool.

Results

Our data show a strong species richness gradient along the eastern coastline of Australia (Spearman's rank-order correlation $\rho = 0.851$, $p < 0.001$: Fig. 2a).
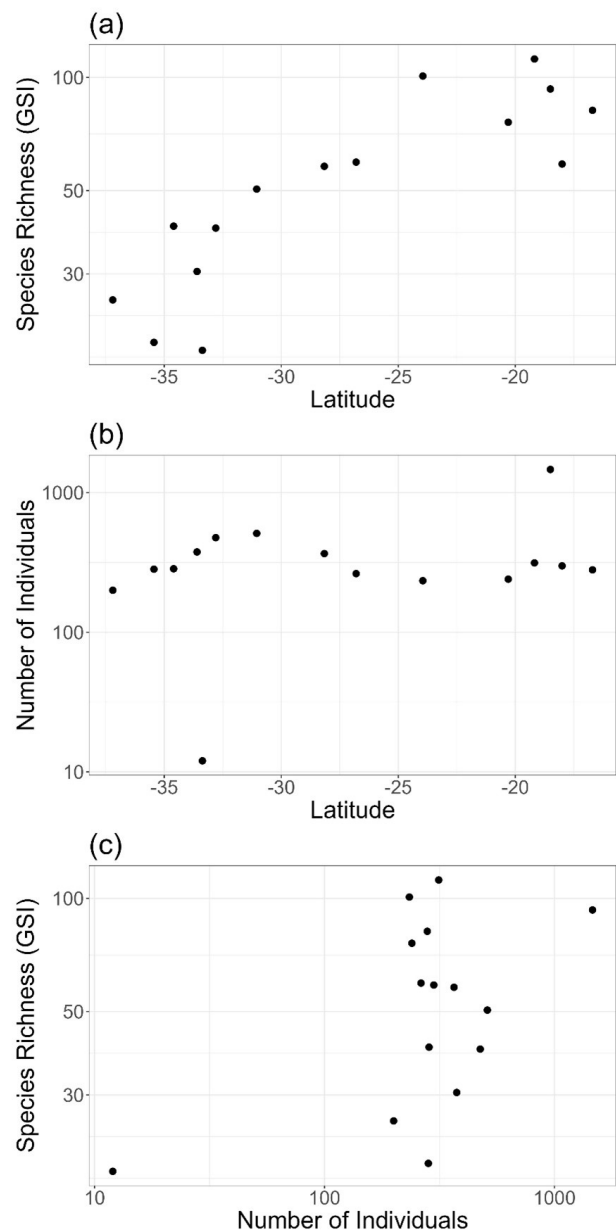

Figure 2. Latitudinal gradients in bivalve richness (a) and the number of individuals (b) observed in samples spanning the eastern coastline of Australia. The lack of a relationship between species richness and the number of individuals is shown in (c). Species richness is calculated using the geometric series index (GSI), but similar patterns are seen when other measures are used. Axes other than latitude are log transformed.

However, the number of individuals present at a site does not significantly change with latitude ($\rho = 0.086$, $p = 0.773$: Fig. 2b) or with species richness ($\rho = -0.046$, $p = 0.880$: Fig 2c).

Mean body size at a site does not significantly change with latitude either when unweighted ($\rho = 0.441$, $p = 0.154$: Fig. 3a) or weighted by relative abundance ($\rho = 0.224$, $p = 0.485$: Fig. 3b). This pattern also holds true at the family level (Fig. S3, Table S3). However, species with larger geographic ranges in our

dataset do have larger maximum body sizes (slope = 1.55, $p < 0.01$, $R^2 = 0.067$: Fig. 4).

We considered a strong relationship in the SEM analysis to correspond with an absolute path coefficient higher than 0.6, a medium-strength relationship to correspond with an absolute path coefficient higher than 0.3, and all other relationships to be weak. There was a medium-strength relationship between latent variable 1 and both species richness and abundance (Fig. 5). Only weak relationships were seen between all
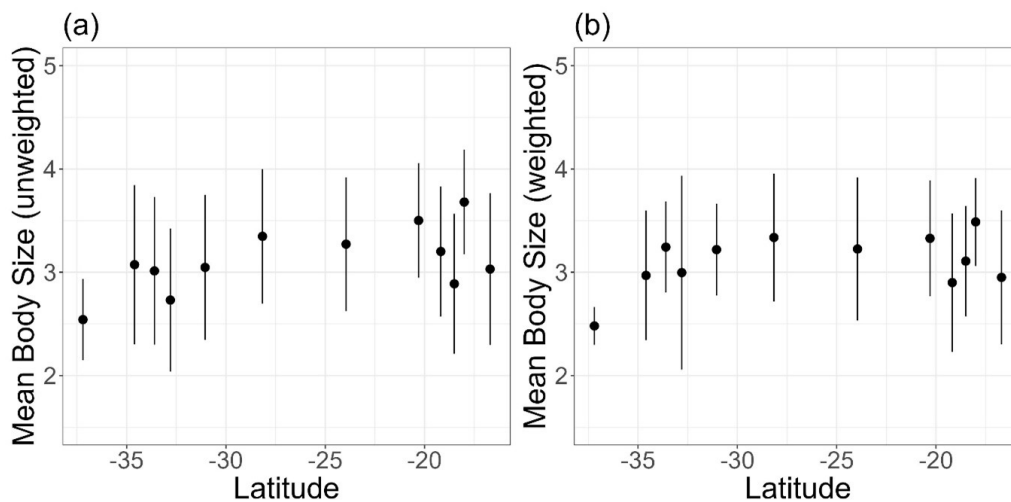

Figure 3. Lack of a latitudinal gradient of body size in east coast Australian marine bivalves. Points represent mean body sizes for species at each site, unweighted in panel (a) and weighted by the species abundance at sites in panel (b). Error bars are one standard deviation around the mean.
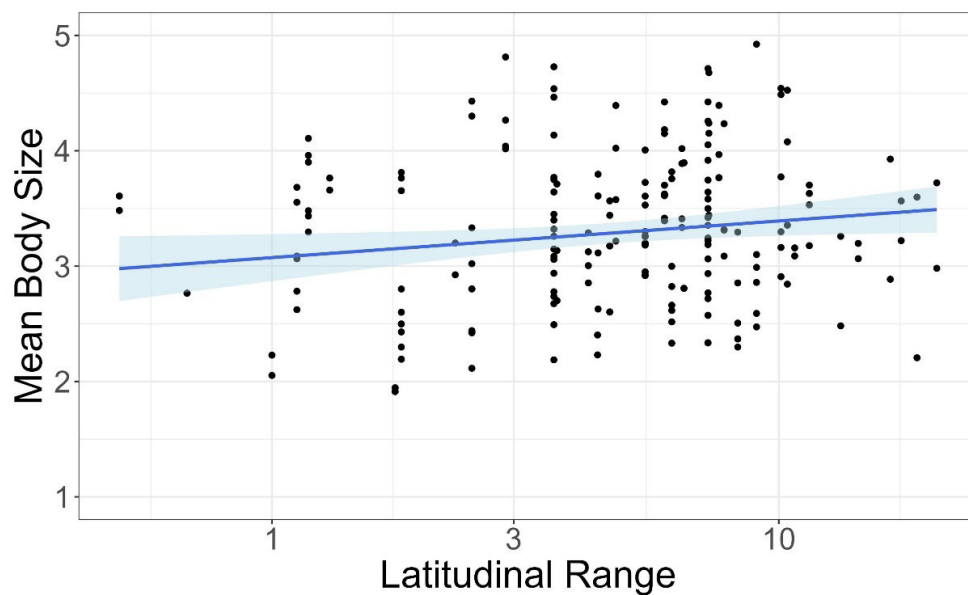

Figure 4. The weak relationship between mean body size and latitudinal range for marine bivalve species (n = 104) sampled along the eastern coastline of Australia. Larger-bodied organisms have slightly larger latitudinal ranges (slope = 0.628, $p < 0.05$, $R^2 = 0.025$). Body size is calculated as the geometric mean of length and height (see Materials & Methods). Only species that appear in more than one site are included.
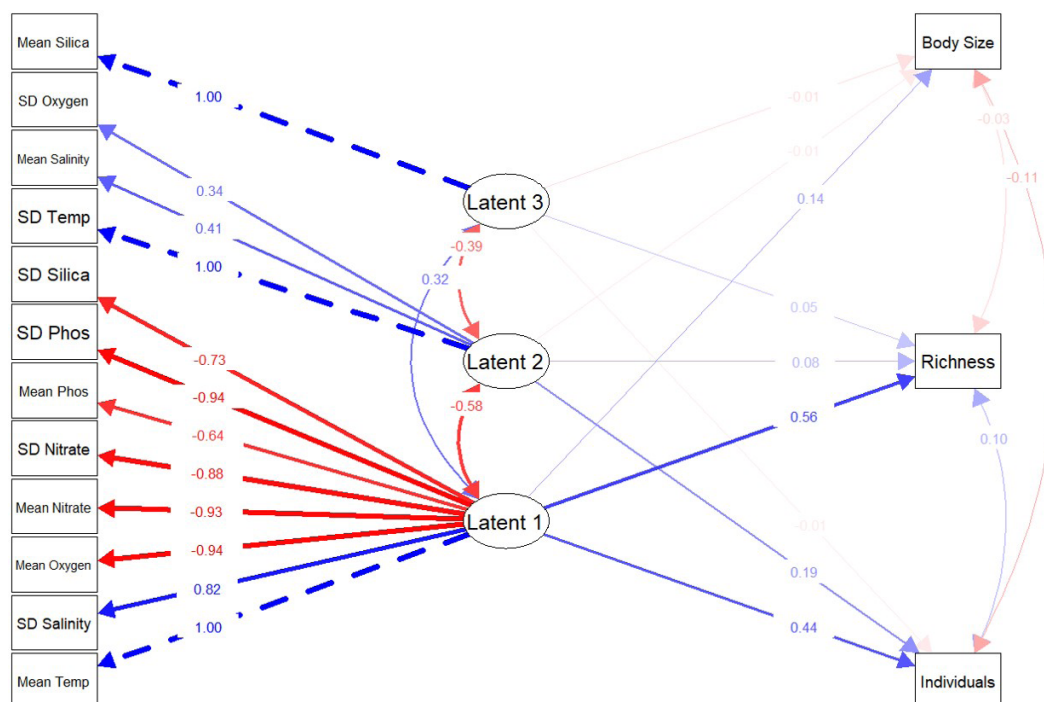
Figure 5. A structural equation model relating marine bivalve total abundance (the number of individuals), mean body size, and species richness to environmental correlates. Body size doesn't relate to abundance, richness, or any environmental factor. Richness (calculated using the geometric series index) and the number of individuals (abundance) are not related to each other, but are linked to a latent variable composed of mean sea surface temperature ("temp"), annual standard deviation (SD) of salinity, mean dissolved oxygen content, and both the mean and standard deviation of nitrate and phosphate ("phos"). Path coefficients normally range between −1 and 1 and are placed on the relevant arrows. Red arrows show negative relationships, blue arrows show positive relationships. The width and transparency of the arrows indicate the strength of the path. Environmental correlates are expressed as three latent variables: the number was determined by a factor analysis prior to the path analysis. Plot was generated using the R package *semPlot* (Epskamp, 2019).

other latent variables and our response variables, and a weak relationship was observed between richness and abundance. We found no relationship between the alpha gambin parameter and richness, the number of individuals, or latitude (Fig. S4). We take no position on whether this indicates either the gambin's lack of realism or the true lack of any predictable variation in abundance distribution shape. The nearest neighbour analysis yielded no pattern in the locations of the true medians, with the true median falling almost exactly on or near the median of the null distribution every time (Fig. S5–8). There was also no latitudinal pattern in the position of the true medians (Fig. S9).

Discussion

Despite a strong latitudinal gradient in bivalve richness along the eastern coastline of Australia (Fig. 2), we find no real support for the "more individuals" hypothesis. Although we do find a medium-strength relationship between environmental variables and total abundance in our study area, similar to the relationship between environmental variables and richness, we do not find a relationship between richness and abundance. The lack of a particularly

strong environmental relationship with richness in this system has been noted in a larger-scale study (Kerr and Alroy, 2021). The number of individuals present in a community within standardised sampling areas also does not significantly correspond to latitude across our entire study area (Fig. 1b) despite a strong latitudinal richness gradient (Fig. 1a). We also find no relationship between the shape of the species abundance distribution, quantified using the alpha gambin parameter, and richness, total abundance, or latitude (Fig. S4).

Recent studies addressing the more individuals hypothesis are largely based on literature reviews or simulated data (e.g., Storch et al. 2018, Vagle and McCain, 2020). As we employed standardised field collection over a large spatial scale, it is more likely that the support for this relationship would have been found if such a relationship existed.

Additionally, there is no significant gradient in the average body size of species (Fig. 3). The lack of a body size gradient here is not surprising, as prior research into bivalves has shown no general trends (Linse et al. 2006, Berke et al. 2013). However, this result persists (Table S2) even if the dataset is broken

into family groupings: no gradient is found in any family – contrary to the results of Berke et al. (2013), an analysis containing the geographic area we covered. Although our analysis used only the largest specimen of each species at a site, Berke et al. (2013) used the largest specimen in their dataset. In contrast, our methodology allows for geographic variation within a species. Additionally, our study used site-specific information across a biogeographical break rather than aggregating size information in five bands. Thus, we allowed for geographic changes in body size. As a result, this study may capture more ecologically meaningful information and may explain the family-level differences between the studies.

Despite covering a major biogeographical transition along coastal Australia (Wilson and Gillett, 1974, Spalding et al. 2007, Costello et al. 2017, Kerr and Alroy, 2021), we still did not observe any trends in total abundance or body size linking the two quite distinct provinces sampled here. Although another analysis of biogeographical effects on body size trends covered a broader latitudinal range (Roy and Martien, 2001), ours nonetheless documents the lack of a pattern at a continental scale. Body size trends in our dataset are also not observed even when the data are weighted for species abundance, showing that changes in distributions are also small. Similarly rigorous analyses could not have featured in previous studies because they did not employ uniformly collected field data and instead used published measurements of the maximum body size of each species (for example, Berke et al. 2013, Barneche et al. 2019).

Given our sampling regime, there is every reason to think that trends in the number of individuals, and body size, would have been found if any factor relevant to molluscan biology had an impact. First, with respect to body size, our nearest-neighbour analysis shows that communities do not diverge from randomly assembled ones having the same species richness. This shows that site-level communities are not overly clumped or highly disparate with respect to the regional species pool, and that the size relationships within sites are stable. This result applies to both temperate and tropical sites. Second, most of the families represented here fall within a similar functional grouping: although some subtidal and rocky shore bivalves were returned, our sampling regime largely represented intertidal families. Third, strong latitudinal trends in beach geomorphology across our sites (Short et al. 2000, Short et al. 2007) did not influence our results. Specifically, the dataset contrasts predominantly wave-dominated beaches in the south with tide-dominated beaches in the north (Short 2006). Finally, although our sampling was based on dead shell assemblages, taphonomic effects are unlikely to change total abundances (Martinelli et al.

2016) and our field sampling can therefore be inferred to reflect living conditions.

Here we have shown that both body size and total abundance of marine bivalves do not significantly relate to latitude or across a recorded biogeographic boundary, despite a strong gradient in richness. Additionally, there was no evidence showing a change in the shape of the species abundance distribution. Species richness is therefore decoupled from these variables, contrary to older studies documenting relationships between them and supporting newer work refuting the "more individuals hypothesis" (Storch et al. 2018, Weiser et al. 2018). Both species richness and abundance are somewhat linked to environmental variables, particularly temperature and nutrient availability, but this relationship is not strong.

This is also not to say body size is unimportant. Body size could be important if it controls geographic range, which in turn drives richness. However, although we do find a relationship between body size and geographic range in our dataset (Fig. 4), any such relationship seems indirect and therefore likely weak.

We hypothesise that species richness trends in coastal Australia result from a gradient in demographic stochasticity that favours the tropics, therefore allowing rare species to persist, and not from changes in body size or population size. Specifically, the major biogeographic break in our dataset is consistent with offshore changes in reef area, and subsequently a change in the potential for dispersal of populations resulting from changes in current regimes (Church et al. 1985, Martel and Chia, 1991). Thus, broader dispersal may stabilise populations in the tropics. On a related note, changes in environmental stochasticity have been shown to impact population dynamics for low-abundance sites in other taxa (Feldman et al. 2015). As more species can therefore be viable, we predict that higher net diversification rates, due to less prevalent extinction, are present in the tropics (Rabosky and Huurlbert, 2015). Therefore, bivalves in temperate zones should have longer phylogenetic branch lengths. As general evolutionary data on bivalves are lacking, a fruitful area of future research would be to further test these relationships using an extensive, highly-resolved phylogenetic dataset.

Acknowledgements

Author Contributions

Matthew R Kerr: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation, Project administration, Funding acquisition.
John Alroy: Conceptualization, Methodology, Software, Resources, Writing – Review and Editing, Supervision, Project administration, Funding acquisition.

Data Accessibility Statement

All data collected during this study is available as supplemental material. Specimens are presently housed in the Palaeobiology Laboratory at Macquarie University. Functions defined in this study are available as supplemental material, along with supplementary text detailing additional analytical tests carried out.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Text S1. A description of the richness estimator and analytical tests.
Figure S1. Diagrammatic representation of valve measurements taken for the study.
Figure S2. Plots of estimated richness against true richness in analytical tests performed on the geometric series richness index described in both the main text and the supplement.
Figure S3. Latitudinal body size trends for bivalve families in this study.
Figure S4. Relationships between the alpha gambin parameter and richness, total abundance, and latitude.
Figure S5. Results of a nearest neighbour analysis comparing the true median body size to generated null distributions for three individual sites.
Figure S6. Results of a nearest neighbour analysis comparing the true median body size to generated null distributions for three individual sites.

Figure S7. Results of a nearest neighbour analysis comparing the true median body size to generated null distributions for three individual sites.
Figure S8. Results of a nearest neighbour analysis comparing the true median body size to generated null distributions for three individual sites.
Figure S9. Latitudinal trend in true median body size generated by a nearest neighbour analysis.
Table S1. The strength of the latitudinal gradient in marine bivalves on the eastern coastline of Australia for several diversity metrics.
Table S2 The results of a factor analysis of the ten environmental variables used in the study, showing which latent variable each one is associated with.
Table S3. Latitudinal trends in body size for marine bivalve families on the eastern coastline of Australia.
Appendix S1. Site locations of bivalve occurrence data collected in this study.
Appendix S2. Bivalve occurrence data collected in this study.
Appendix S3. Bivalve measurements taken for this study.
Appendix S4. R code for the geometric series index and code for the analytical test described in Text S1.

References

Adams, D. C. & Church, J. O. (2008) Amphibians do not follow Bergmann's rule. Evolution, 62, 413-420. https://doi.org/10.1111/j.1558-5646.2007.00297.x

Allen, A. P., Brown, J. H. & Gillooly, J. F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science, 297, 1545-1548. https://doi.org/10.1126/science.1072380

Allen, A. P., Gillooly, J. F., Savage, V. M. & Brown, J. H. (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences USA, 103, 9130-9135. https://doi.org/10.1073/pnas.0603587103

Alroy, J. (2017) The effects of habitat disturbance of on tropical forest biodiversity. Proceedings of the National Academy of Sciences USA, 114, 6056-6062. https://doi.org/10.1073/pnas.1611855114

Angielczyk, K. D., Burroughs, R. W. & Feldman, C. R. (2015) Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world's turtles. Journal of Experimental Zoology B: Molecular and Developmental Evolution, 324, 270-294. https://doi.org/10.1002/jez.b.22602

Arellano, G., Umaña, M. N., Macía, M. J., Loza, M. I., Fuentes, A., Cala, V. & Jørgensen, P. M. (2017), The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon–Andes gradient. Global Ecology and Biogeography, 26, 191-202. https://doi.org/10.1111/geb.12531

Ashton, K. G. (2004) Sensitivity of Intraspecific Latitudinal Clines of Body Size for Tetrapods to Sampling, Latitude and Body Size. Integrative and Comparative Biology, 44, 403-412. https://doi.org/10.1093/icb/44.6.403

Barneche, D., Rezende, E., Parravicini, V., Maire, E., Edgar, G., Stuart-Smith, R., Arias-González, J., Ferreira, C., Friedlander, A. & Green, A. (2019) Body size, reef area and temperature predict global reef-fish species richness across spatial scales. Global Ecology and Biogeography, 28, 315-327. https://doi.org/10.1111/geb.12851

Bergmann, C. (1847) Uber die Verhaltnisse der warmeokonomie der Thiere zu uber Grosso. Gottinger Studien, 3, 595-708.

Berke, S. K., Jablonski, D., Krug, A. Z., Roy, K. & Tomasovych, A. (2013) Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. Global Ecology and Biogeography, 22, 173-183. https://doi.org/10.1111/j.1466-8238.2012.00775.x

Blackburn, T. M., Gaston, K. J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions, 5, 165-174. https://doi.org/10.1046/j.1472-4642.1999.00046.x

Cardillo, M. (2002) Body size and latitudinal gradients in regional diversity of New World birds. Global Ecology and Biogeography, 11, 59-65. https://doi.org/10.1046/j.1466-822X.2001.00265.x

Chao, A. (1984) Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics, 11, 265-270. https://doi.org/10.1080/01621459.1992.10475194

Church, J. A., Andrews, J. C. & Boland, F. M. (1985) Tidal currents in the central Great Barrier Reef. Continental Shelf Research, 4, 515-531. https://doi.org/10.1016/0278-4343(85)90008-1

Condie, S. A., & J. R. Dunn (2006), Seasonal characteristics of the surface mixed layer in the Australasian region: Implications for primary productivity and biogeography. Marine and Freshwater Research, 57, 569-590. https://doi.org/10.1071/MF06009

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z. & Chaudhary, C. (2017) Marine biogeographic realms and species endemicity. Nature Communications, 8, 1057. https://doi.org/10.1038/s41467-017-01121-2

Currie, D. J. & Fritz, J. T. (1993) Global patterns of animal abundance and species energy use. Oikos, 67, 56-68. https://doi.org/10.2307/3545095

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T. & O'brien, E. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters, 7, 1121-1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x

Cushman, J. H., Lawton, J. H. & Manly, B. F. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia, 95, 30-37. https://doi.org/10.1007/BF00649503

Epskamp, S. (2019) semPlot: Path diagrams and visual analysis of various SEM packages. Available at https://CRAN.R-project.org/package=semPlot

Evans, K. L., Warren, P. H. & Gaston, K. J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews, 80, 1-25. https://doi.org/10.1017/s1464793104006517

Feldman, R. E., Anderson, M. G., Howerter, D. W. & Murray, D. L. (2015) Where does environmental stochasticity most influence population dynamics? An assessment along a regional core-periphery gradient for prairie breeding ducks. Global Ecology and Biogeography, 24, 896-904. https://doi.org/10.1111/geb.12323

Hillebrand, H. & Azovsky, A. I. (2001) Body size determines the strength of the latitudinal diversity gradient. Ecography, 24, 251-256. https://doi.org/10.1034/j.1600-0587.2001.240302.x

Horn, J. L. (1965) A rationale and test for the number of factors in factor analysis. Psychometrika, 30, 179-185. https://doi.org/10.1007/BF02289447

Kerr, M. R. & Alroy, J. (2021) Marine diversity patterns in Australia are filtered through biogeography. Proceeding of the Royal Society B. 288, 20211534. https://doi.org/10.1098/rspb.2021.1534

Kosnik, M. A., Jablonski, D., Lockwood, R. & Novack-Gottshall, P. M. (2006) Quantifying molluscan body size in evolutionary and ecological analyses: maximizing the return on data-collection efforts. Palaios, 21, 588-597, 10. https://doi.org/10.2110/palo.2006.p06.012r

Linse, K., Barnes, D. K. A. & Enderlein, P. (2006) Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. Deep Sea Research Part II: Topical Studies in Oceanography, 53, 921-931. https://doi.org/10.1016/j.dsr2.2006.03.006

Matthews, T. J., Sadler, J. P., Kubota, Y., Woodall, C. W. & Pugh, T. A. M. (2019) Systematic variation in North American tree species abundance distributions along macroecological climatic gradients. Global Ecology and Biogeography, 28, 601– 611. https://doi.org/10.1111/geb.12879

Matthews, T. J., Borregaard, M. K., Ugland, K. I., Borges, P. A.V., Rigal, F., Cardoso, P. & Whittaker, R. J. (2014), The gambin model provides a superior fit to species abundance distributions with a single free parameter: evidence, implementation and interpretation. Ecography, 37, 1002-1011. https://doi.org/10.1111/ecog.00861

Martel, A. & Chia, F.-S. (1991) Drifting and dispersal of small bivalves and gastropods with direct development. Journal of Experimental Marine Biology and Ecology, 150, 131-147. https://doi.org/10.1016/0022-0981(91)90111-9

Martinelli, J. C., Madin, J. S. & Kosnik, M. A. (2016) Dead shell assemblages faithfully record living molluscan assemblages at One Tree Reef. Palaeogeography, Palaeoclimatology, Palaeoecology, 457, 158-169. https://doi.org/10.1016/j.palaeo.2016.06.002

Mcglynn, T. P., Weiser, M. D. & Dunn, R. R. (2010) More individuals but fewer species: testing the more individuals hypothesis in a diverse tropical fauna. Biology Letters, 6, 490-493. https://doi.org/10.1098%2Frsbl.2010.0103

Mcnab, B. K. (1971) On the Ecological Significance of Bergmann's Rule. Ecology, 52, 845-854. https://doi.org/10.2307/1936032

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. Journal of Biogeography, 30, 331-351. https://doi.org/10.1046/j.1365-2699.2003.00837.x

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A. & Leishman, M. R. (2009) Global patterns in plant height. Journal of Ecology, 97, 923-932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Müller, J., Brandl, R., Brändle, M., Förster, B., De Araujo, B. C., Gossner, M. M., Ladas, A., Wagner, M., Maraun, M. & Schall, P. (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos, 127, 814-824. https://doi.org/10.1111/oik.04972

Pincheira-Donoso, D., Hodgson, D. J. & Tregenza, T. (2008) The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? BMC Evolutionary Biology, 8, 68-68. https://doi.org/10.1186/1471-2148-8-68

Rabosky, D. L & Hurlbert, A. H. (2015) Species richness at continental scales is dominated by ecological limits. The American Naturalist, 185, 572-583. https://doi.org/10.1086/680850

Revelle, W. (2019) psych: procedures for personality and psychological research. Available at https://CRAN.R-project.org/package=psych

Ridgway, K. R., Dunn, J. R. & Wilkin, J. L (2002) Ocean interpolation by four-dimensional weighted least squares—application to the waters around Australasia. Journal of Atmospheric and Oceanographic Technology, 19, 1357-1375. https://doi.org/10.1175/1520-0426(2002)019%3C1357:OIBFDW%3E2.0.CO;2

Rosseel, Y. (2012) lavaan: an R Package for Structural Equation Modelling. Journal of Statistical Software, 48, 1-36.

Roy, K. & Martien, K. K. (2001) Latitudinal distribution of body size in north-eastern Pacific marine bivalves. Journal of Biogeography, 28, 485-493. https://doi.org/10.1046/j.1365-2699.2001.00561.x

Seoane, J., Laiolo, P. & Obeso, J. R. (2017) Abundance leads to more species, particularly in complex habitats: a test of the increased population size hypotheses in bird communities. Journal of Biogeography, 44, 556-566. https://doi.org/10.1111/jbi.12877

Short, A. (2006) Australian beach systems—nature and distribution. Journal of Coastal Research, 22, 11-27. https://doi.org/10.2112/05A-0002.1

Short, A. D., Mcleod, K. A., Safety, A. B., Program, M., Australia, S. L. S. & Unit, U. O. S. C. S. (2000) Beaches of the Queensland Coast: Cooktown to Coolangatta: a guide to their nature, characteristics, surf, and safety. Sydney University Press, Australia.

Short, A. D., Safety, A. B., Program, M., Australia, S. L. S. & Unit, U. O. S. C. S. (2007) Beaches of the New South Wales Coast: a guide to their nature, characteristics, surf and safety (2nd edn). Sydney University Press, Australia.

Siemann, E., Tilman, D. & Haarstad, J. (1999) Abundance, diversity and body size: patterns from a grassland arthropod community. Journal of Animal Ecology, 68, 824-835. https://doi.org/10.1046/j.1365-2656.1999.00326.x

Smith, K. F. & Brown, J. H. (2002) Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. Global Ecology and Biogeography, 11, 313-322. https://doi.org/10.1046/j.1466-822X.2002.00286.x

Spalding, M. D., Fox, H. E., Allen, G. R., et al. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience, 57, 573-583. https://doi.org/10.1641/B570707

Storch, D. (2016) The theory of the nested species–area relationship: geometric foundations of biodiversity scaling. Journal of Vegetation Science, 27, 880-891. https://doi.org/10.1111/jvs.12428

Storch, D., Bohdalková, E. & Okie, J. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecology Letters, 21, 920-937. https://doi.org/10.1111/ele.12941

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. Nature, 466, 1098. https://doi.org/10.1038/nature09329

Vagle, G. L. & McCain, C. M. (2020) Natural population variability may be masking the more-individuals hypothesis. Ecology, 101, e03035. https://doi.org/10.1002/ecy.3035

Weiser, M. D., Michaletz, S. T., Buzzard, V., Deng, Y., He, Z., Shen, L., Enquist, B. J., Waide, R. B., Zhou, J. & Kaspari, M. (2018) Toward a theory for diversity gradients: the abundance–adaptation hypothesis. Ecography, 41, 255-264. https://doi.org/10.1111/ecog.02314

Wilson, B. R. & Gillett, K. (1974) Australian Shells. Reed Press, Sydney, Australia.

Yee, D. A. & Juliano, S. A. (2007) Abundance matters: a field experiment testing the more individuals hypothesis for richness–productivity relationships. Oecologia, 153, 153-162. https://doi.org/10.1007/s00442-007-0707-1