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Increased energy differentially increases richness and abundance of optimal body sizes in deep-sea wood falls

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Abstract. Theoretical and empirical studies suggest that the total energy available in natural communities influences body size as well as patterns of abundance and diversity. But the precise mechanisms underlying these relationships or how these three ecological properties relate remain elusive. We identify five hypotheses relating energy availability, body size distributions, abundance, and species richness within communities, and we use experimental deep-sea wood fall communities to test their predicted effects both on descriptors describing the species-richness–body-size distribution, and on trends in species richness within size classes over an energy gradient (size-class–richness relationships). Invertebrate communities were taxonomically identified, weighed, and counted from 32 *Acacia* sp. logs ranging in size from 0.6 to 20.6 kg (corresponding to different levels of energy available), which were deployed at 3,203 m in the Northeast Pacific Ocean for 5 and 7 yr. Trends in both the species-richness–body-size distribution and the size-class–richness distribution with increasing wood fall size provide support for the Increased Packing hypothesis: species richness increases with increasing wood fall size but only in the modal size class. Furthermore, species richness of body size classes reflected the abundance of individuals in that size class. Thus, increases in richness in the modal size class with increasing energy were concordant with increases in abundance within that size class. The results suggest that increases in species richness occurring as energy availability increases may be isolated to specific niches, e.g., the body size classes, especially in communities developing on discrete and energetically isolated resources such as deep sea wood falls.

Key words: body size; community assembly; competition; diversity; energy; niche packing; productivity; species–energy relationship.

Introduction

Increases in available energy frequently translate into increases in species richness (Rosenzweig and Abramsky 1993, Waide et al. 1999, Clarke and Gaston 2006, Cusens et al. 2012) although the existence of this relationship is not universal and often weak (Mittelbach et al. 2001). The processes generating this greater diversity potentially stem from the transformation of this increased energy into maintenance, work, growth, and reproduction at the individual and population levels, thereby enabling opportunities for biodiversity maintenance and growth at the community level (Rosenzweig and Abramsky 1993). For example, chemical energy translated into individual reproduction and population growth may buffer against local extinctions, thereby leading to higher community diversity (Wright 1983, Wright et al. 1993, Srivastava and Lawton 1998). Chemical energy translated into greater individual growth and population numbers can lead to greater prey biomass supporting increased abundances and diversity of higher trophic levels (Post et al. 2000, Post 2002). Greater availability of chemical energy may also allow for greater species richness by allowing phenotypes with greater metabolic demands (c.f. the resource-ratio hypothesis [Tilman 1982, McClain et al. 2004, 2012b, 2014]).

Increases in energy availability could also translate into growth leading to alterations of species-richness–body-size distributions and ultimately impacting overall diversity. Hypotheses linking diversity and body size are prominent in ecology (Hutchinson 1959, Hutchinson and MacArthur 1959, May 1988). Many biological rates and outputs scale with body size, leading to the potential for substantial variation in species traits within a community (Peters 1983, Kerr and Dickie 2001, Brown et al. 2004). Consequently, body size is often viewed as a major axis of niche segregation and an important determinant of community structure (Hutchinson and MacArthur 1959, Grant 1968, Wilson 1975, Kozlowski and Gawelczyk 2002, Simberloff and Dayan 2005). However, the role of body size in community assembly remains controversial and processes are poorly understood. Hutchinson (1959) documented a consistent ratio in mammals and birds between contiguously sized species within a trophic level, which he hypothesized results from competitive size displacement. Although the notion of a fixed ratio is now

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largely discredited (Simberloff and Boeklin 1981), terrestrial mammal community structure is still often considered to reflect competitive exclusion between species of similar sizes (Brown and Nicoletto 1991) unless size-based competitive interactions are mitigated (e.g., habitat heterogeneity; Bakker and Kelt 2000). However non-competitive neutral mechanisms (Etienne and Olff 2004, Vergnon et al. 2009) have also been proposed to explain community body size distributions.

Prior hypotheses that link body size and diversity may also be related to energetic processes. Specific body size classes may be more speciose because they represent energetic optima, i.e., a balance of energetic trade-offs, or allow greater access to food resources (Sebens 1982, 2002, Brown et al. 1993, Rex and Etter 1998, Roy et al. 2000, Ernest 2005). Across both terrestrial and marine communities, greater richness in a body size class is often coupled to a greater number of individuals (Marquet et al. 1995, Siemann et al. 1996, 1999, Marquet and Taper 1998, Fa and Fa 2002, McClain 2004, McClain and Nekola 2008). This implies that more energy may be available to these size classes and diversity increases reflect species–energy processes (Wright 1983, Wright et al. 1993, Siemann et al. 1996, Srivastava and Lawton 1998). However, other work has found that the overall metabolic demand of size class does not correlate with species richness (Ernest 2005). Alternatively, increased richness in certain size classes may reflect the availability of energy to that size class (Ernest 2005). For example, Ritchie and Olff (1999) propose that the fractal geometry of resource concentrations allows greater species richness within a size class slightly greater than the mean, producing left-skewed body size distributions. This geometry of resource concentrations also relates back to the habitat architecture hypothesis of Holling (1992).

Here we build on this work relating body size and species richness by presenting and testing five alternative hypotheses of how this relationship responds to increase in energy (Fig. 1). Each hypothesis makes specific predictions regarding how descriptors of the species-richness–body-size distribution (i.e., mean, standard deviation, kurtosis, number of modes) will change with increase in energy, and how change (i.e., slope) in the species richness vs. energy relationship within discrete body size classes (size-class–richness relationships), will vary among size classes.

H1: Increased packing into optimal body size

Greater energy availability leads to increased species richness through increased packing of species into the optimal body size class(es). This optimal body size class may reflect a series of energetic constraints (Sebens 1982, 2002, Brown et al. 1993, Rex and Etter 1998, Roy et al. 2000, Ernest 2005). This implies that increases of energy do not impact the optimal body size nor affect in which size class resources are available (Brown et al. 1993, 1996, Roy et al. 2000). The consequences for the species-richness–body-size distribution of adding more species at or around the optimal body size include a small decrease in variance and a pronounced increase in kurtosis, but no systematic change in mean or modality (Fig. 1, top row). Richness within optimal size classes will increase with increasing energy but richness in other size classes will be unaffected (Fig. 1, top row). Increased energy into the community should translate into increased abundance of only the optimal size class.

H2: Relaxed pressure for optimal body size

Increased energy availability relaxes pressure for species to be at the energetic optimum allowing for the additional species to be added at larger or smaller body sizes (McClain et al. 2006, 2012b). A simple relaxation of pressure will be evidenced by increased variance of the species-richness–body-size distribution and increases in richness across all size classes (Fig. 1, second row) over a gradient of energy availability. As more energy becomes available into the community, energy will be directed toward the smallest and largest size classes resulting in disproportionate increases in abundance of these size classes.

H3: Shifts in optimal body size

Increased energy affects the energetic trade-offs that determine the optimal body size, thus the modal size class changes (Sebens 1982, 2002, Rex and Etter 1998, McClain 2004, Collins et al. 2005). This will result in a systematic trend in mean body size over the energy gradient and by increases within larger size classes and decreases in smaller size classes (Fig. 1, third row) or vice versa, depending on the direction of the shift. Regardless of the direction of shift, a relative decrease in the original modal class is expected. Increased representation in large-sized species with increased energy may reflect relaxation of metabolic constraints (McClain et al. 2006, 2012b,b). Decreased representation in small-sized species may result from decreased pressure for larger foraging areas and starvation resistance (McClain et al. 2006, 2012b,b). As energy increases, the size class with the highest abundance will shift to the new optimum body size. No predicted changes are expected in the other descriptors of the species-richness–body-size distribution. For the size-class–richness relationship, peak abundances are predicted to track shifts in the optimal body size class.

H4: Multimodal distributions with increased rare resources

Increased energy increases availability of rare resources (Schoener 1976, DeAngelis 1994, Evans et al. 1999, 2005). These rare resources make energy available to additional size bins allowing for multi-modal species-richness–body-size distributions (Thibault et al. 2011). Trends in most descriptors of the species-richness–body-size distribution will be idiosyncratic, depending on the order in which

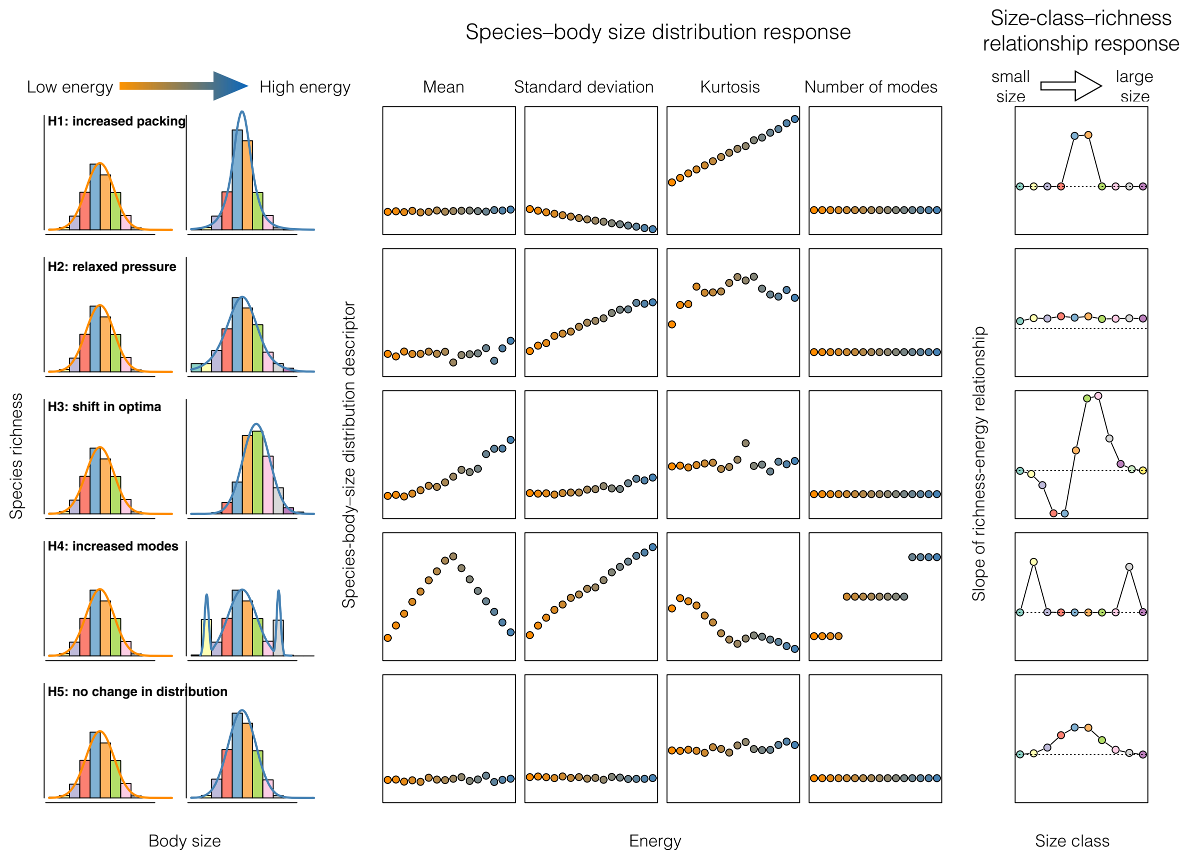

FIG. 1. Schematic representation of the consequences of increased environmental energy for species–body-size distributions and size-class–richness relationships under each of the five hypotheses outlined in the *Introduction*. Each hypothesis begins with the same species–body-size distribution (left-hand histograms), and an increase in energy results in the addition of an identical number of species, but the position of these new species on the body size axis varies according to each hypothesis (right-hand histograms). The effects of adding species according to each hypothesis on the species-richness–body-size distribution are shown by plotting four descriptors of the distribution (mean, standard deviation, kurtosis, number of modes) as more species are added (i.e., across a gradient of energy; species-richness–body-size distribution response, central four columns of scatter plots). Consequences for the size-class–richness relationship are shown by plotting the slope of the relationship between species richness and energy separately for each size class (size-class–richness relationship response, right-hand scatter plots; points are colored according to the size classes represented by bars in the species–body-size histograms). The y-axis scales are held constant for each plot within a column to illustrate the relative magnitude of expected effects. Note that the patterns in H4 are illustrative of one particular way of adding species (first to a large mode, then to a small mode); patterns in mean, variance, and kurtosis in this hypothesis are expected to be idiosyncratic, the main diagnostic features of H4 are the increase in number of modes, and peaks in the slope of the richness–energy relationship at smaller- and larger-than-modal size classes.

species are added to different modes (one example, where first a larger size class and then a smaller size class is favored, is shown in Fig. 1, fourth row). However, variance will typically increase, and a systematic increase in the number of modes is detected as energy availability increases, with pronounced increases also within the size classes closest to the new modes (Fig. 1, fourth row). Increased number of modes with increased energy should be concordant with increases of abundance in these same size classes.

H5: Size invariance

Under this scenario, although overall species richness increases with increased energy, the descriptors of the species–energy relationship remain essentially unchanged (Fig. 1, fifth row), i.e., abundance increases equitably across size classes, and richness increases in proportion to original richness across all size classes as energy increases. The primary descriptor distinguishing this from H1 is lack of change in kurtosis that characterizes H1.

As Fig. 1 shows, these hypotheses can be distinguished by using statistical properties of empirical species-richness–body-size distributions and size-class–richness relationships. However, this requires data on body sizes across replicate communities over a gradient of energetic settings that are not confounded by factors such as varying temperature, regional pools, connectivity between communities, and community ages. Deep-sea ecosystems provide opportunities for macroecological analyses where environmental variables that are tightly correlated in terrestrial and shallow marine systems (e.g., temperature and productivity) become decoupled (Tittensor et al. 2011, McClain et al. 2012*a*, Webb 2012, Woolley et al. 2016). This is particularly pronounced for the communities developing on resource-rich patches such as wood falls, which occur ephemerally on the typically resource-poor deep-sea floor. Wood is transported to the oceans via rivers, and after drifting and becoming saturated with water, eventually sinks to the ocean floor. On the deep-sea floor, wood falls develop largely endemic and highly diverse communities consisting of wood and sulfide obligates, and associated predators (Voight 2007, McClain and Barry 2014, McClain et al. 2016). The endemicity of wood falls reflects an energetic isolation because of the specific nutritional requirements for wood (xylophagy), sulfide, and/or methane produced at the wood fall, or predator specificity for endemic wood-fall species.

Wood-fall communities in the deep sea are thus an ideal system for testing hypotheses about community assembly and energetic theory because we can precisely and experimentally control the total amount of energy available to the community, i.e., the size of a single wood fall (McClain and Barry 2014, McClain et al. 2016). Increasing energy may increase habitat heterogeneity (Chase and Leibold 2002). Deploying single wood logs of varying sizes allows for testing of increases in energy without increasing habitat heterogeneity that may confound the results. Each wood log, no matter size, is identical in shape, structure, and heterogeneity. Increasing the size of wood falls risks conflating increased energy with increased area. However, species–area and species–energy relationships are known to be intrinsically linked (Storch et al. 2005, Hurlbert 2006, Hurlbert and Jetz 2010, McClain et al. 2016), with species–area relationships a special case of the more general species–energy relationship (Wright 1983). On ecological timescales, increasing area only increases species richness if resources increase proportionally (Hurlbert 2006), and in the energetically isolated wood fall communities we study it is ultimately the energetic content of the resource that drives community dynamics (reviewed in McClain et al. 2016). Thus, by modeling how the statistical properties of species-richness–body-size distributions and size-class–richness relationships change over wood-fall communities developing on wood falls of different sizes, we are able to specifically tie changes in size-based community assembly to variation in energy availability.

Wood falls afford an additional opportunity to examine how connectivity between communities affects the diversity–size–energy relationship. Research on freshwater systems (Chase and Ryberg 2004) demonstrated that the strength of productivity–diversity relationships was in part determined by the connectivity among sites along the productivity gradient. With heightened connectivity, the diversity of low-productivity and low-diversity sites is augmented by recruitment in from high-productivity and high-diversity sites. In early community development, community structure is greatly influenced by larval recruitment from the regional larval pool (Webb et al. 2017). As wood fall communities develop, connectivity between nearby wood falls increases as the populations of species become mature enough to contribute to the larval pool (Webb et al. 2017), which has the effect of suppressing the productivity–diversity relationship (McClain et al. 2016). Dispersal ability, and its scaling with body size, also serves as a key parameter in some models that predict the unimodal size distribution (Etienne and Olff 2004). All of the species on wood falls, despite size class, have similar dispersal ability, recruitment to the wood fall occurs from a highly dispersive larval phase with limited motility in adults. Thus wood falls provide an important test of the role of dispersal in generating species-richness–body-size distributions. First, we hypothesize if dispersal scaling with body size is important, the overall species-richness–body-size distribution should be unimodal as predicted by Etienne and Olff (2004). If the species had limited dispersal ability or body size and dispersal ability are uncoupled, then the distribution should be uniform. Second, we hypothesize that, as connectivity increases between wood falls, this should mitigate energetic relationships that establish the species-richness–body-size distribution, i.e., communities that have been established for longer should move toward the distribution of size invariance (H5). Although it might be predicted that, with all species having long dispersal distance, a regional larval pool may overwhelm the effects of proximate wood falls, the number of larval recruits generated locally should far exceed the regional pool of larvae diminished by mortality and dilution.

Here, we test the effects of varying environmental energy on the distribution of body sizes between species by fitting empirical species-richness–body-size distributions and size-class–richness relationships to complete communities collected from 32 experimentally deployed, naturally colonized wood falls differing in size from <1 to >20 kg, and established for either 5 or 7 yr. This allows us to test the five hypotheses outlined above over a productivity gradient and with minimal variation in confounding factors.

Methods

Experimental systems and communities

Wood falls on the deep-sea floor are unique and diverse communities consisting of xylophages, sulfide obligates, predators of these two groups, and, to rare extent, opportunists (Appendix S1). Xylophages ingest wood and rely on heterotrophic bacteria to aid digestion and assimilation. Certain species of wood-fall inhabiting echinoids harbor wood-digesting microbiota in their guts (Becker et al. 2009). One species of galatheid crab appears to prefer wood falls and is regularly found with wood-filled guts (Hoyoux et al. 2009). Several species of ostracods from the genus *Xylocythere* are also only known to inhabit wood falls (Maddocks and Steineck

1987) and may potentially be wood obligates. The most notable and abundant xylophagous species are members of the bivalve subfamily Xylophagainae (Knudsen 1961, Turner 2002, Voight 2007). Sulfide obligates rely nutritionally on chemoautotrophic bacteria, e.g., bivalves in genus *Idas*, which colonize wood falls and benefit from chemoautotrophic endosymbionts (but see Ockelman and Dinesen 2011, Bienhold et al. 2013). Predators feed on xylophages, sulfide obligates, and opportunists. Certain acotylean polyclad flatworms, for example, likely feed on wood-boring bivalves (Voight 2007). Opportunists have less specialized diets but are numerically rare. Only four of 39 wood-associated species in the wood falls here were also found in the background sediment or nearby hard substrates (McClain et al. 2009, 2010, 2011, 2016, McClain and Barry 2010, 2014). All of these generalist habitat species are rare and represented by one to four individuals and as such do not make up a significant component of the wood-fall community. The remaining wood-fall specialists all have abundances that range from ~10 to 1,000 individuals on a single wood fall.

Succession at wood-fall communities begins at 1–2 months with wood-boring bivalves and opportunists such as amphipods (Bienhold et al. 2013). At 3–6 months, Xylophagainae begin to serve as ecosystem engineers of wood falls; their boreholes generate various spaces for inhabitation by other species and they offer biomass for predators (Turner 1973, 1977, Schander et al. 2010, Appendix S1). At 6–12 months, the enhanced respiration leads to the development of sulfidic niches attracting animals that rely nutritionally on chemolithoautotrophic bacteria (Bienhold et al. 2013). Successional stage is driven by the rate at which wood-boring bivalves make carbon available for other species and by the total amount of wood available (McClain and Barry 2014). Once the complete wood-fall community assembles, the complete community includes a variety of epifaunal and infaunal species inhabiting the surface and interior of the wood fall.

In November 2006, 32 *Acacia* sp. logs were deployed at 3,203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W, Appendix S1: Fig. S1). Each wood fall was comprised of a single *Acacia* log. These individual wood falls ranged in size from 0.6 to 20.6 kg and correspond to different levels of energy available to the invertebrate communities assembling on wood falls, with approximately one-half of the woodfalls being <3 kg and half being >3 kg to ensure good representation of contrasting energy levels. Each log was sewn into a synthetic fiber mesh bag (5 mm mesh, large mesh size ensured larval settlement was not hindered, Appendix S1: Figs. S2 and S3). Mesh bags allowed for collection at the end of the experiment of highly degraded wood falls (Voight 2007).

Wood falls were dispersed over a ~160-m^2 area with ~5 m between wood falls in four rows 10 m apart from one another, with each row including wood falls from across the range of available sizes (Appendix S1: Fig. S1). The distance between rows reflect the distance needed to allow the remotely operated vehicle (ROV) to operate without disturbing the next row. The distance between wood falls in the row also allowed for quick deployment and retrieval while keeping ROV transit time minimal. The close proximity of the wood falls also ensured regional pools of larvae were similar. Species occurring on the wood falls primarily have larval dispersal phases that allow for colonization. Adults because of either both their size and limited or complete lack of motility complete their lives on individual wood falls. Thus, the distance between individual wood falls here is sufficient to isolate the communities except through larval exchange. As an example, if larger wood falls support higher trophic levels these predators would not be able to move to a smaller nearby wood fall and crop prey.

Sixteen *Acacia* logs ranging across available sizes were collected in October 2011 (Set 1, 5 yr), and the additional 16 *Acacia* logs were collected in October 2013 (Set 2, 7 yr; Appendix S1: Fig. S1). Set 2 demonstrates exhibited evidence of increased connectivity between individual wood falls (McClain et al. 2016, Webb et al. 2017) that did not occur in Set 1 (McClain and Barry 2014). Thus differences in patterns between Sets 1 and 2 likely reflect these differences in connectivity.

Collection and processing

Logs were deployed and collected with the Monterey Bay Aquarium Research Institute's ROVs *Doc Ricketts* and *Tiburon* aboard the RV *Western Flyer.* Logs were placed into 300-μm mesh bags with sealable closing lids during ROV retrieval, ensuring no loss of individuals and/or cross contamination among different samples. All individuals occurring on the wood fall exterior and interior were collected. The size ranges of organisms in this study thus range in length from those organisms retained by the 300-μm mesh up to the largest sized organisms occurring on the surface of the wood fall.

All specimens were picked from wood, preserved in either 95% ethanol or formalin. All of the taxa were identified to the species level except *Actinaria* spp. Species names were assigned to taxa when possible. All individuals from each wood fall were counted and assigned to species. For each species, the total wet mass (mg) was taken of all individuals on a wood fall. Individuals were allowed to dry for two minutes on paper towels. Average mass for species on an individual wood fall was taken from the total wet mass for the species divided by the number of individuals per wood fall. For each wood fall, we recorded the initial mass (kg), location, and surface area (m^2). We used initial wood fall mass (kg), a measure of available energy, as our productivity gradient in all analyses.

Analyses

For each individual wood fall, the species–body-size distribution was defined as the distribution of $\log_{10}$-transformed mean species-level body sizes calculated for that specific community. We calculated for each wood fall the mean, variance, and kurtosis of the species–body-size distribution. We used the unbiased (type 3) estimate of kurtosis given by the kurtosi function in the psych package (Revelle 2015). We estimated the optimal number of modes that best fit the species–body-size distribution on each wood fall using Bayesian information criterion (BIC) values initialized by hierarchical clustering for parameterized Gaussian mixture models using the mclust package (Fraley and Raftery 2002, Fraley et al. 2012). We set the maximum number of modes to 4, although results are not sensitive to this choice. A size-class–richness relationship was also calculated for each community, using size classes ranging from -5.5 to 1 $\log_{10}$ mass units in 0.5 $\log_{10}$ unit steps, resulting in 14 size classes. Each species was assigned to the relevant size class for a given community based on its mean wet mass in that community, and total richness within each size class for each community was used as a basis to model changes in richness within size classes over the productivity gradient.

We tested the hypotheses outlined in Fig. 1 by modeling each species-richness–body-size distribution descriptor (mean, standard deviation, kurtosis, number of modes) as a function of $\log_{10}$-transformed wood fall size. To test for differences between communities collected after 5 and 7 yr (i.e., between less and more connected communities), Set (two-level factor, 1 or 2) was included as a covariate in all models. The four models were thus all linear models of the form species–body-size distribution descriptor ~ log(wood fall mass) × Set, although we fitted the number of modes model as a Poisson GLM as number of modes is a count variable response. To facilitate interpretation of the model results, we removed any non-significant interactions between log(wood fall mass) and Set to focus instead on the main effects of each predictor. The slopes of these relationships were then used to assess support for each hypothesis following Fig. 1.

All data manipulation, summary statistics, analyses, and figures were produced using R 3.3.3 (R Core Development Team 2017) and additional packages dplyr (Wickham and Francois 2015), tidyr (Wickham 2015), ggplot2 (Wickham 2009), gridExtra (Auguie 2015), and lme4 (Bates et al. 2015). Data and R code are available on Dryad at www.datadryad.org/.

Results

Species-richness–body-size distributions

Across all communities, the distribution of body sizes is unimodal with a modal class centered at -1.75 $\log_{10}$ mass units (Fig. 2). Testing specifically how the species-richness–body-size distribution varied over the energy gradient, there was no interaction between wood-fall size and collection Set in any of the models: ($\log_{10}$(wood fall size) × Set interaction in mean body size model = -0.05 ± 0.214, $t = 0.25$, $P = 0.808$; in standard deviation of body size model = 0.24 ± 0.142, $t = 1.68$, $P = 0.105$;

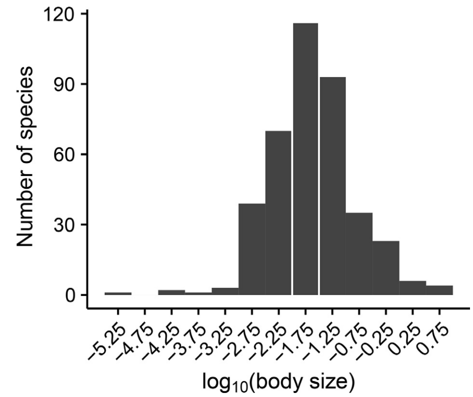

FIG. 2. Overall species-richness–body-size distribution across all communities combined. Bin widths correspond to the 0.5 $\log_{10}$ mass unit size classes used to analyze size-class–richness relationships, and the modal size class (centered on -1.75 $\log_{10}$ mass units) is outlined in white.

in kurtosis of body size model = -0.07 ± 0.990, $t = 0.07$, $P = 0.942$; in number of modes model = 0.06 ± 0.259, $z = 0.234$, $P = 0.815$). Models were therefore refitted as additive models only. There was no significant change in either the mean ($\log_{10}$(wood fall size) coefficient = 0.09 ± 0.105, $t = 0.84$, $P = 0.408$, Fig. 3A) or the standard deviation ($\log_{10}$(wood fall size) coefficient = -0.03 ± 0.073, $t = 0.42$, $P = 0.680$, Fig. 3B) of the species–body-size distribution with increasing wood fall size. There was a tendency for kurtosis to increase with increasing wood fall size ($\log_{10}$(wood fall size) coefficient = 0.84 ± 0.482, $t = 1.74$, $P = 0.092$). Examining both the data (Fig. 3C) and model diagnostic plots, two logs (Logs 7 and 23) had very high standardized residuals (>3) in this model. We do not have a clear explanation for this, but excluding these two logs results is sufficient to drive the relationship to significance while having minimal effect of the slope estimate ($\log_{10}$(wood fall size) coefficient = 0.85 ± 0.267, $t = 3.16$, $P = 0.0038$, Fig. 3C). The number of modes of the species–body-size distribution is not related to wood fall size ($\log_{10}$(wood fall size) coefficient = -0.22 ± 0.299, $t = 0.75$, $P = 0.455$, Fig. 3D). Set did not have a significant effect on any of these relationships (mean, $t = 1.43$, $P = 0.162$; SD, $t = 0.68$, $P = 0.504$; kurtosis, $t = 1.13$, $P = 0.269$; kurtosis excluding logs 7 and 23, $t = 1.66$, $P = 0.109$; number of modes, $z = 0.23$, $P = 0.815$).

Size-class–richness relationships

Relationships between species richness and $\log_{10}$(wood fall size) are shown for each of the 12 size classes present in our data set in Fig. 4A. There was never a significant $\log_{10}$(wood fall size) × Set interaction ($P > 0.25$ for all size classes in which an interaction term could be fitted). Removing the interactions, species richness was higher in Set 2 than in Set 1 for size classes -2.75 (Set 2 vs. Set 1 contrast = 0.90 ± 0.296, $t = 3.04$, $P = 0.006$) and -1.25

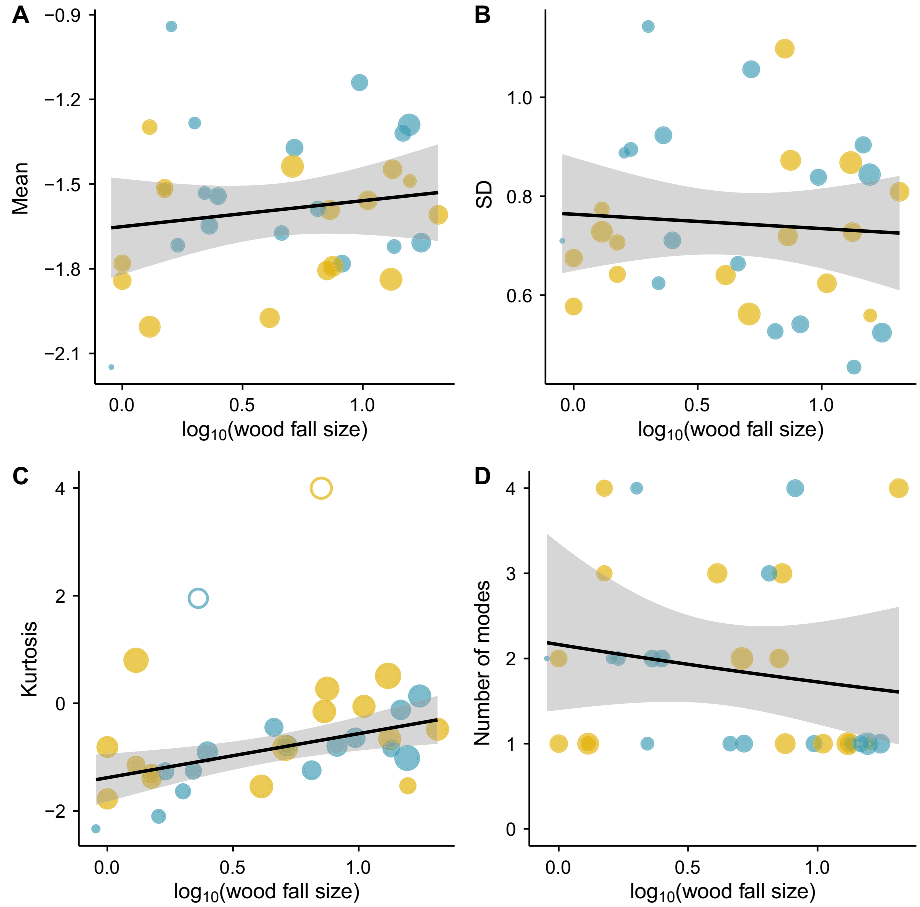

Fig. 3. (A) The mean, (B) the standard deviation, (C) the kurtosis, and (D) the number of modes of the species-richness–body-size distribution over a gradient of energy availability, as quantified by the size of wood fall. Blue points indicate Set 1 communities and orange points are Set 2 communities, but as slopes never varied between sets, a single relationship across all communities is illustrated. In panel C, communities identified as outliers (high standardized residual) are shown as open symbols, and the fitted model excludes these (slope = 0.85 ± 0.267, t = 3.16, P = 0.0038). Black lines indicate significant linear regressions with gray shaded areas indicating standard error.

(Set 2 vs. Set 1 contrast = 1.49 ± 0.525, t = 2.83, P = 0.010), and in all other size classes for which a meaningful model could be fitted (i.e., where there was variation in richness between wood falls) the Set 2 vs. Set 1 contrast was also positive. The only significant relationship between species richness and $\log_{10}$(wood fall size) was found in the size class centered on −1.75 $\log_{10}$ mass units (Fig. 4B, 0.01 to 0.032 g; $\log_{10}$(wood fall size) coefficient = 1.70 ± 0.753, t = 2.26, P = 0.031), the modal size class when all species and wood falls are considered together (Fig. 2).

Discussion

The body size of the constituent species is often heralded as vital to community assembly, either through energetic (Ernest 2005), competitive (Hutchinson and MacArthur 1959), habitat/textural (Schwinghamer 1981, Ritchie and Olff 1999), dispersal (Etienne and Olff 2004), or other mechanisms (reviewed in Allen et al. 2006), but an understanding of the precise role, importance, and generality of these mechanisms remains incomplete. Here, we use an experimental system directly controlling the energy available to the community to explore how body size and energy availability interact to regulate community richness. The main finding is that increased energy availability and the resulting increase in species richness results from packing species into a modal size class (H1 in Fig. 1). Despite strong theoretical and empirical reasons to expect increases in the range, modality, and mean of the species-richness–body-size distribution (Fig. 1), none of these patterns occurred with increased energy availability (Fig. 3) in these wood fall communities. Surprisingly, we also find that duration of the community does not modify any of these results, indicating that the increased connectivity present in Set 2 (Webb et al. 2017), which should impact diversity–productivity relationships (Chase and Ryberg 2004, McClain et al. 2016) has less effect on the energetic rules determining the species-richness–body-size distribution. Likewise, we find that,

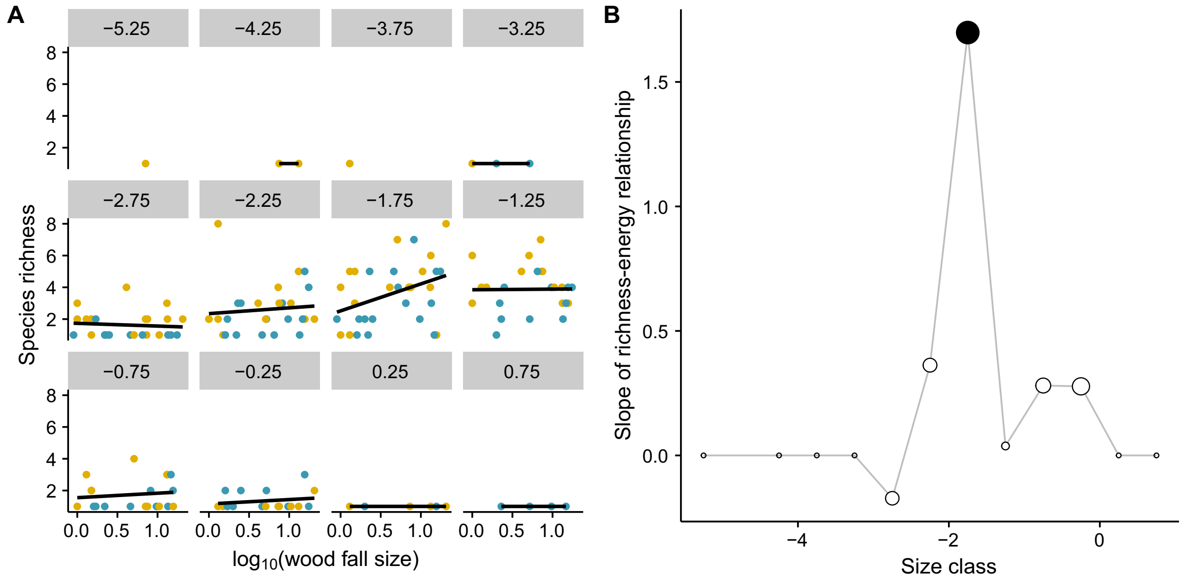

FIG. 4. (A) Species richness as a function of wood fall size shown separately for each body size class. Size classes are identified above each plot by their midpoint on a $\log_{10}$ body mass scale. Blue points indicate Set 1 communities, orange points are Set 2 communities, but as slopes never varied between sets, a single relationship across all communities for each size class is illustrated. (B) The slopes of the relationships illustrated in panel A as a function of body size class. Points are scaled to reflect the correlation between richness and wood fall size (larger points indicate higher absolute values of the correlation coefficient). Solid points represent slopes that differ significantly from 0 ($P < 0.05$).

despite similar dispersal abilities, we still recover a unimodal body size distribution contrary to some theoretical expectations (Fig. 2; Etienne and Olff 2004).

The increased packing of species in the modal size class appears to be tied to increases in abundance, i.e., size classes with the highest abundances possess the most species (Figs. 4 and 5). At least at local scales, the increases in richness of certain size classes appears to reflect a species–energy mechanism (Wright 1983, Wright et al. 1993, Srivastava and Lawton 1998, Hurlbert 2006, Hurlbert and Jetz 2010) as proposed by Siemann et al. (1996, 1999) in which increases in abundance buffer local populations against local stochastic extinction thereby increasing overall community richness. This match between abundance and species richness among size classes within communities has been found in deep-sea gastropods (McClain 2004, McClain and Nekola 2008), terrestrial gastropods (McClain and Nekola 2008), coastal gastropods (Fa and Fa 2002), and grassland insects (Siemann et al. 1996, 1999, 1999).

These results imply that, as energy to the community increased, this additional energy was either not available to every size class or alternatively a single size class monopolized increases in energy. Because wood-fall community energy usage or availability is not even across size classes, we find an overall breakdown in the energetic-equivalence rule (EER) in this system. Briefly, because the average mass of a species scales similarly with abundance and metabolic rate, this suggests that energy use is equivalent across size classes (Damuth 1981, Ernest et al. 2003). This pattern is clearly a macroecological phenomenon occurring at broad phylogenetic and spatial scales (Brown 1995). However, EER's support within communities is mixed (Blackburn et al. 1990, 1993, 1994, Marquet et al. 1990, Blackburn and Lawton 1994, Silva and Downing 1995, Blackburn and Gaston 1996, Russo et al. 2003, Ernest 2005).

What determines the size class in which abundance, richness, and energy is the highest? One, energy may only be more environmentally available to a specific size class or classes. This is an expansion of the textural discontinuity hypothesis of Holling (1992) with an emphasis on the aspects of resource concentration, availability, and fractality as opposed to habitat complexity (reviewed in Allen et al. 2006). Ritchie and Olff (1999) theoretically and mathematically formalized this view that in fractal resources, species perceive the resource at a scale of resolution that is determined by body size. This generates a prediction of species richness peaking at a size class slightly larger than the intermediate. Evans et al. (2005) propose that as energy increases preferable resources also increase. Joining these hypotheses, a greater diversity of energy/resource types may be available to specific size classes. Second, certain size classes may be more energetically efficient (Sebens 1982, Brown et al. 1993, Rex and Etter 1998, Roy et al. 2000, Sebens 2002, Ernest 2005, reviewed in Allen et al. 2006) allowing more species to coexist in the same size class. Third, certain size classes are able to monopolize greater proportions of total available energy. Monopolization of energy resources by larger size classes is known in marine invertebrates (McClain and Barry 2010).

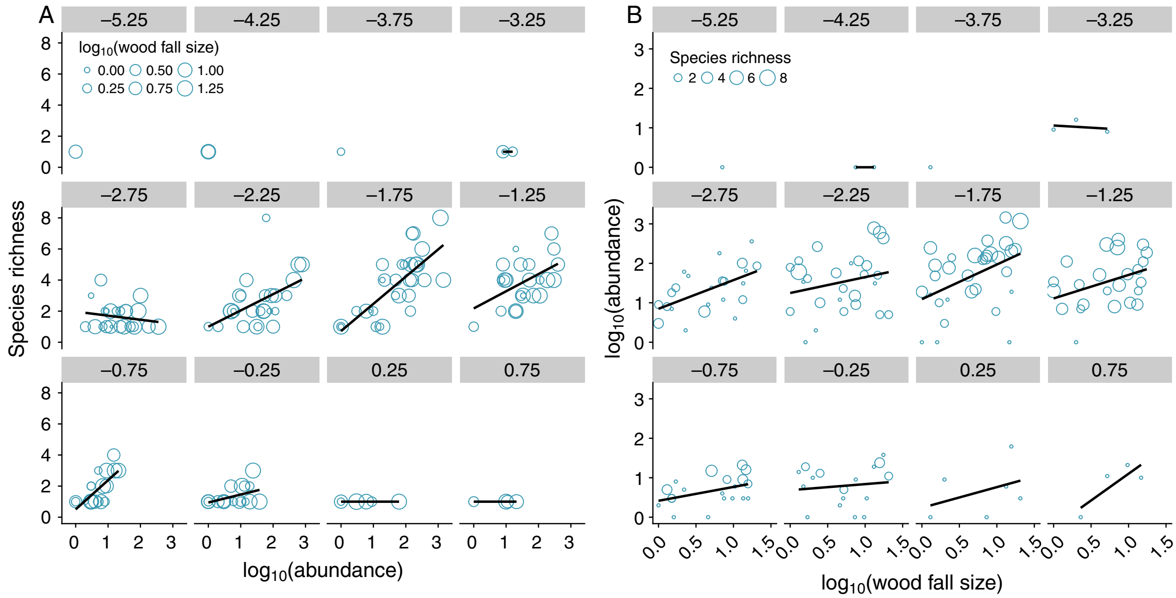

FIG. 5. (A) Species richness as a function of abundance shown separately for each body size class across all wood falls. Size of the circles denotes size of the wood fall. (B) Abundance as a function of wood fall size shown separately for each body size class across all wood falls. Size of the circles denotes size of the species richness on individual wood falls. Size classes are identified above each plot by their midpoint on a $\log_{10}$ body mass scale.

Distinguishing among these different processes proves difficult. The modal size class among wood falls occurs at 0.01 to 0.032 g, which incorporates a broad set of organisms including the limpet *Caymanabyssia vandoverae*; an undescribed isopod species; an undescribed bivalve species of the genus *Yodiella*; four gastropods, *Provanna* sp. 1, *Provanna pacifica*, *Hyalogyra* sp. 1, *Dillwynella (Ganesa) panamesis*; and three undescribed species of polychaetes from the families Eucylmeninae and Opheliidae. It is hard to envision a single optimal body size that spans across these broad phylogenetic groups, ecologies, and body plans. These species are utilizing different trophic niches, ranging from microbial mat grazers to predators and scavengers. In addition, those species that are microbial grazers are partitioning the gradients in the concentration of reduced sulfur compounds that occur from the degradation of the wood (*unpublished data*). This does seem to provide some support for textural discontinuity hypothesis (Holling 1992, Ritchie and Olff 1999) and that as energy increases this textural discontinuity, in the form of resource gradients, also increases (Evans et al. 2005) providing more niche space for species packing of this body size class.

The lack of patterns for body size range, mean, or modality across wood-fall sizes is surprising given the strong theoretical expectations for the existence of these relationships. At large spatial scales, increases in mean body size (Stemberger and Gilbert 1985, Gliwicz 1990, Aava 2001, McClain et al. 2006, 2012b,b, Olson et al. 2009, Terribile et al. 2009) and body size range (McClain et al. 2006, 2012b,b) are expected with increased energy availability. McClain et al. (2012b) proposed that increases in body size range with increasing energy availability at oceanic scales reflects increased niche opportunity and diversity afforded with increasing energy (sensu Evans et al. 2005). Given the invoked niche processes, this pattern should be observable at the community level. The findings of these studies incorporating large spatial scale and productivity ranges may simply not translate to local scale processes over more moderate spatial scales or confounded by other major drivers of diversity, e.g., habitat heterogeneity. Although multimodal species-richness–body-size distribution are prevalent among wood falls (Fig. 3D), replicating the constancy of multimodal distributions across small mammal habitats (Ernest 2005), there is no consistent change in modality with increasing energy availability. This provides some evidence against the idea that increased energy changes the patchiness, type, and distribution of resources that would make them available to new size classes (sensu Evans et al. 2005). Rather, if this mechanism occurs, it only expands niche space in a specific size class.

The extent to which our results are specific to the unique setting of deep-sea wood-fall communities is hard to gauge. In particular, the dependence of these communities on a single type of resource, wood falls, and the fact that community development is dependent on the ecosystem engineering activity of Xylophagainae bivalves, may mean that the availability of increased energy is less equitably distributed across size classes than in other ecological settings. However, the existence of positive abundance–richness relationships across a much broader range of size classes than energy–richness relationships (compare Figs. 4A and 5A), together with increases in abundance with energy within most size classes (Fig. 5B), suggests that energy is available to organisms outside the modal size class, it is just not translated into increased richness. In addition, the taxonomic and functional diversity of species occurring within the modal size class suggests that the increased energy is not restricted to species with particular traits or occupying a single specialized niche. Finally, any priority effects (Connell 1961) should decrease in significance through time, yet support for increased packing is seen across communities sampled at both time periods (Figs. 3 and 4), even though these represent different stages of succession (McClain et al. 2016, Webb et al. 2017). Thus we do not consider there to be strong a priori reasons why increased packing should be preferred in these communities over and above the other hypotheses listed in Fig. 1.

Conclusions

Among the experimental wood-fall communities studied here, certain size classes are more speciose, concordant with increases in abundance. Indeed, the relationship between abundance and species richness among sizes classes within a community is strikingly similar to the relationship of abundance and species richness among wood-fall communities, suggesting that the more-individuals hypothesis (or species-energy theory) scales across levels of ecological complexity. As energy to the wood-fall community increased, increases in abundance and species richness occurred. However, these increases in abundance and richness did not occur equitably across size classes. As richness increased in a community with increased energy, species were just packed into the modal size class. The modal size class saw disproportionally stronger increases in both abundance and richness. This suggests that increases in richness occurring as energy availability increases may be isolated in specific niches, e.g., the body size classes. A clear need exists for further investigation of these patterns in other taxa, communities, and ecosystems, and for identification of the precise mechanisms underlying these phenomena.

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