Received: 10 January 2023 | Revised: 8 June 2023 | Accepted: 30 June 2023

DOI: 10.1002/ecs2.4667

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Disentangling mechanisms of species–energy relationships in experimental deep-sea wood falls

Craig R. McClain[1] | **S. River D. Bryant**[1] | **Granger Hanks**[1] | **Jarrett Byrnes**[2]

[1]Department of Biology, University of Louisiana, Lafayette, Louisiana, USA

[2]Department of Biology, University of Massachusetts, Boston, Massachusetts, USA

Correspondence
Craig R. McClain
Email: craig.mcclain@louisiana.edu

Funding information
NSF, Grant/Award Number: 1744048

Handling Editor: Robert J. Miller

Abstract

A multitude of hypotheses have been invoked to explain increases in richness with increases in energy availability. Experiments have the potential to reveal causality, and species–energy experiments have yielded substantial insights into energetic community assembly. Here, we examine six mechanisms underlying species–energy relationships in an experimental wood fall system in the deep Gulf of Mexico. Twenty-four wood falls were deployed in the deep Gulf of Mexico for 21 months. To test for differences in total energy availability, individual wood falls ranged in size from 0.91 to 24 kg, corresponding to different levels of energy available to the wood-obligate invertebrate communities assembling on wood falls. To test for differences in total energy accessibility, we chose a softwood (pine, $n = 12$) and soft hardwood (sugarberry, $n = 12$). Structural equation models were used to disentangle the multiple hypothesized pathways by which changes in wood fall type and mass correlated with richness. Whereas we find support for the more individuals hypothesis, we also find that niche dynamics and competition play important roles as well linking energy and diversity. Furthermore, we find that not only the total energy but also the accessibility of that energy, dictating rates of energy flow, leads to differences in community structure. Using structural equation modeling (SEM), we evaluate seven hypotheses to demonstrate that no single hypotheses alone can predict the species–energy relationship.

KEYWORDS
body size, diversity, energetics, niche, productivity, resource availability, structural equation modeling (SEM)

INTRODUCTION

In part, diversity is set by the resources available to individuals and species (McGlynn et al., 2010; Rabosky & Hurlbert, 2015). Hutchinson's (1959) foundational paper was one of the earliest to draw a link between productivity and limitations to diversity, "If the fundamental productivity of an area is limited…then the rarer species in a community may be so rare that they do not exist." Since insightful papers over half a century ago (Connell & Orias, 1964; Hutchinson, 1959; MacArthur & Pianka, 1966; Pianka, 1966), ecologists have continued to document a relationship between diversity and productivity (e.g., Currie, 1991; Cusens et al., 2012; Evans et al., 1999; Hurlbert, 2004; Kaspari et al., 2000; Woolley et al., 2016). Extending island-biogeography theory, Wright (1983) formalized species–energy theory, predicting that species richness changes as the amount of available energy increases, with the underlying mechanism reflecting energetic controls on immigration and extinction rates, with richness ultimately reflecting scaling with abundance. Note recent authors have used the term species-energy to refer any general reelationship of richness to energy availbility, while others see the species-energy as a posited mechanism to explain the overall productivity-diversity relationship (Rosenzweig & Abramsky, 1993). Here, we follow recent nomenclature of species–energy to describe the general relationship of richness with energy availability. To explain species–energy relationships, multiple mechanisms have been posited relying on environmental heterogeneity, community stability, food web dynamics, changes in competitive structure, disturbance, variation in population sizes, area, among others (Cardinale et al., 2009; Chase & Leibold, 2002; Chase & Ryberg, 2004; Cusens et al., 2012; DeAngelis, 1994; Evans et al., 1999, 2005; Hurlbert & Stegen, 2014; McCain, 2021; Rosenzweig & Abramsky, 1993; Wright, 1983).

However, no single hypothesis appears to explain the species–energy relationship successfully and the overall mechanism "remains somewhat mysterious" (Evans et al., 1999; Rosenzweig & Abramsky, 1993). Moreover, many of the hypotheses for species–energy relationships reflect multiple and intertwined processes (Cardinale et al., 2009; Evans et al., 1999; Hurlbert & Jetz, 2010; McCain, 2021; McClain et al., 2016; McClain & Barry, 2010; Yee & Juliano, 2007). For example, many hypotheses share similar subcomponents such as minimizing competitive mechanisms or alterations to population dynamics, leading to similar changes in trait distributions, abundance, and evenness. A structural equation modeling (SEM) approach (Bollen, 1989; Grace, 2006; Lefcheck, 2016), previously utilized in studies related to species–energy theory (McCain, 2021; Yee & Juliano, 2007), provides a powerful tool to disentangle and reveal multiple interaction pathways connecting energy availability to species richness. Here, we use SEM to disentangle seven contending and overlapping hypotheses within six mechanisms linking energy availability to species richness. Using an experimental system, we can focus on a subset of hypotheses focusing on community dynamics while controlling processes working over evolutionary time, impacting regional pools, or reflecting habitat heterogeneity.

More individuals

Species richness increases with energy through influences on population size (Srivastava & Lawton, 1998; Wright, 1983). Low productivity reduces population sizes and increases the risk of stochastic local extinction (Srivastava & Lawton, 1998; Wright, 1983). As energy and population sizes increase, Allee effects are reduced and local coexistence increases (Srivastava & Lawton, 1998; Wright, 1983). Thus, increased energy availability leads to increases in abundance, which in turn increases diversity.

$$\text{Energy availability} \rightarrow \text{abundance} \rightarrow \text{richness.}$$

Niche-mediated more individuals

Greater energy availability may not be equitably distributed across all niches. For example, certain niches, as measured by size classes, may be more energetically efficient (Allen et al., 2006; Brown et al., 1993; Ernest, 2005; Sebens, 2002). Increases in energy may allow for greater coexistence of species within only certain functional traits (DeAngelis, 1994; Evans et al., 2005; Marquet et al., 1995; McClain, Heim, et al., 2018). Thus, increases in energy leading to increases in abundance and ultimately richness may happen only in specific niches (McClain, Barry, et al., 2018; McClain, Nunnally, et al., 2018). If composition reflects the functional traits in the community, then compositional differences should correlate with changes in abundance and ultimately changes in diversity.

$$\text{Energy availability} \rightarrow \text{traits/composition} \rightarrow \text{abundance} \rightarrow \text{richness.}$$

Metabolic adaptation/more specialization/niche position

Increased energy offers more niches and subsequent higher diversity, because more species can meet their minimum energetic requirements (McClain et al., 2020; McNaughton & Wolf, 1970). Low-metabolic-need taxa may survive on patches of low quality, quantity, or density of resources that are not monopolized by high-metabolic-need taxa within these high-energy habitats. In low-energy habitats, high-metabolic-need taxa are lost because minimum energetic requirements cannot be met. Thus, if high-energy habitats support more energetic niches, species richness may increase at higher energy availability because species are able to specialize on preferred resources, for example, a predator consuming a single prey species or a herbivore consuming a single plant, reducing competitive interactions and allowing for greater species coexistence (Evans et al., 2005). The more specialization hypothesis (DeAngelis, 1994;

Schoener, 1976) and niche position hypothesis (Evans et al., 1999, 2005) are related theories in which a minimum amount of energy is needed to support specialist species. At low energy, some resources are too rare to support these species. At high energy, greater specialization is allowable and prevents competitive exclusion. A high metabolic individual replaces one low metabolic rate individual, so no changes in abundance occur, distinguishing it from the previous hypothesis.

Energy availability → traits/composition → richness.

Competitive evenness

Many hypotheses accounting for increases in richness with increased energy invoke competition models (Huston, 1979; Rosenzweig & Abramsky, 1993; Tilman, 1982). The prediction of how energy impacts evenness is complex. In one scenario, high-energy and high-richness communities reflect the addition of rare species (Evans et al., 2005). As the number of rare species at a site increases, the evenness of that community declines because of the increased mix of common and rare species. However, according to the more individuals hypothesis, increases in population sizes, particularly previously numerically rare species, buffer against local extinction events, thus increasing species richness. If numerically dominant species are already limited by their population growth rates, then evenness would increase. If numerically dominant species also increase, then no change in evenness would occur. More even relative distributions of relative abundances are documented as energy increases (Hurlbert, 2004), but in other studies, such distributions were found to be weak to nonexistent (Symonds & Johnson, 2008).

Energy availability → abundance → evenness → richness.

Body size–diversity

Hypotheses linking diversity and body size are prominent in ecology (Hutchinson, 1959; May, 1988) and are often related to energy availability (Fa & Fa, 2002; Marquet et al., 1995; McClain, 2004; McClain et al., 2011; Siemann et al., 1996, 1999). Greater richness in a body size class is often coupled to a greater number of individuals (Fa & Fa, 2002; Marquet et al., 1995; McClain, 2004; McClain et al., 2011; Siemann et al., 1996, 1999). This implies that more energy may be available to these size classes and diversity increases reflect species–energy processes (Siemann et al., 1996; Srivastava & Lawton, 1998; Wright, 1983; Wright et al., 1993).

Energy availability → body size → abundance → richness.

Alternatively, the linkage between body size and diversity may not occur through an abundance mechanism if body size alters competitive interactions, occurrence, or persistence in the community.

Energy availability → body size → richness.

Energy accessibility

While total available energy may be high, the rate in which energy flows into the community or is accessible to the community may be low. In addition, energy availability may increase within the community but not be accessible to all species (Evans et al., 2005). Thus, increases in energy accessibility, irrespective of availability, should increase species richness. This mechanism may occur through changes in traits, compositions, or abundances.

Energy accessibility → ... → richness.

Because energy availability correlates with many other important ecological variables, correlations alone between energy and species richness may not ultimately reveal causality (Rosenzweig, 1995). Experiments have the potential to reveal causality, and species–energy experiments have yielded substantial insights into energetic community assembly (Chase, 2010; Hurlbert, 2006; McClain et al., 2016; McClain, Barry, et al., 2018; Schuler et al., 2015; Srivastava & Lawton, 1998). Here, we examine mechanisms underlying species–energy relationships in an experimental wood fall system in the deep Gulf of Mexico. On the deep seafloor, sunken wood, that is, wood falls, develop endemic and diverse communities comprising wood and sulfide obligates and associated predators (Bienhold et al., 2013; Kalenitchenko et al., 2018; McClain et al., 2016). The endemicity of wood fall communities reflects energetic isolation because of their specific nutritional requirements for wood, produced sulfide and/or methane, or predator specificity for endemic wood fall species (Bienhold et al., 2013; Kalenitchenko et al., 2018; Romano et al., 2020). Deep-sea wood falls provide a unique opportunity to examine community assembly and energetic theory because the amount of energy available to the community can be experimentally controlled (i.e., the size of a single wood fall) while holding other correlated variables, for example, temperature, heterogeneity, and age, constant. Moreover, due to the low deposition rates of phytodetritus and weaker currents in the deep sea, there is minimal risk of deep-sea wood falls being buried by sediment. This may not be the case for certain shallow water (continental-shelf) settings.

We expand on our previous work (McClain et al., 2016) in this new experiment by utilizing an SEM approach to disentangling and evaluating specific species–energy pathways. The overall productivity in a region may determine the strength of species–energy relationships, being stronger in more productive regions, because the regional pool is likely to have species adapted to both high and low productivity (Cornell & Harrison, 2014). Our previous work was limited to relatively low richness communities (25 vs. 76 co-occurring species in the current study) likely through a limited regional pool, a feature of the depth, locations, and hard wood use in the previous experiment. Here, by focusing on communities in the Gulf of Mexico, which are regularly fed wood by the Mississippi River, we can explore how a larger regional pool, from a more productive area, impacts the species–energy relationships. Finally, by altering wood type (hard vs. soft), we are also able to vary the rate at which energy form the wood is available to the community, that is, xylophagous species will bore slower through harder wood.

METHODS

In May 2017, 24 wood falls were deployed at 2171 m in the northern Gulf of Mexico (27.135° N, 89.924° W). Individual wood falls (logs) were taken from the same tree individual. Trees were freshly cut and logs were dried for a minimum of three months to get wood moisture to ~15%. Weights were taken before deployment. Each wood fall was quartered and then zipped tied back together to allow for easier post-deployment processing. Logs were sewn into a synthetic fiber mesh bag (5-mm mesh, large mesh size ensured larval settlement was not hindered). Mesh bags allowed for collection at the end of the experiment of highly degraded wood falls. To test for differences in total energy availability, individual wood falls ranged in size from 0.91 to 24 kg, corresponding to different levels of energy available to the wood-obligate invertebrate communities assembling on wood falls. To test for differences in total energy accessibility, we chose a softwood *Pinus elliotti* (pine, $n = 12$) and a soft hardwood *Celtis laevigata* (sugarberry, $n = 12$). The Jenka Hardness, the force required to imbed a 11.28-mm-diameter steel ball into the wood to half the ball's diameter, is 3910 N for sugarberry and 3380 N for pine. The harder sugarberry thus reduced the access by limiting burrowing and feeding of xylophagous species. Remaining constituents of the community, for example, predators, thus are energetically limited by the rates in which xylophagous species make this energy available. Also worth noting is that among boring terrestrial invertebrates, for example, termites, wood consumption is largely controlled by wood density and not secondary compounds (Dodji Kasseney et al., 2011). An unpublished work (McClain et al.) demonstrates that wood hardness correlates with abundance (Pearson's product–moment correlation: $\mathrm{df} = 41$, $r = -0.34$, $p = 0.006$) and richness (Pearson's product–moment correlation: $\mathrm{df} = 41$, $r = -0.47$, $p = 0.0001$) of xylophagous bivalves across controlled experiment of 11 wood species. Given this empirical evidence and prior literature demonstrating the primacy of density in boring rates suggest that this is a feasible test of energy delivery rates on community assembly.

Wood falls were individually deployed and collected with Oceaneering's remotely operated vehicle (ROV) *Global Explorer* aboard LUMCON's RV *Pelican*. Wood falls were randomly dispersed in two species-specific lines, with ~5 m between wood falls and 500 m between the two lines. Wood falls were collected in February of 2019 and after 21 months. Wood falls 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 range of organisms in this study varies from those retained by the 300-μm mesh to the largest organisms found on the surface of the wood fall. All wood falls were preserved in 80% ethanol after quarters were separated.

All specimens were picked from wood and preserved in ethanol. All taxa were identified to the morpho-species level and confirmed with taxonomists. Species names were assigned to taxa when possible in consultation with taxonomists. All individuals from each wood fall were counted and assigned to species. For each species, the total wet mass (in milligrams), including shells, was taken of all individuals on a wood fall. Individuals were allowed to dry for 2 min on paper towels. The 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.

To quantify compositional differences, a principal components analysis (PCA) was conducted on the Hellinger pre-transformed data (Legendre et al., 2005), calculated using the adespatial package (Dray et al., 2018), with the functions decostand and rda in the vegan package (Oksanen et al., 2013) in R (R Development Core Team, 2021). The Hellinger transformation was implemented to preserve Euclidean distances between transects as advocated for when in use with redundancy (RDA) or PCA (Legendre & Gallagher, 2001). Hellinger distance also offered a better compromise between linearity and resolution than some other distance metrics (Legendre & Gallagher, 2001).

Structural equation models were used to explore the pathways by which changes in wood fall type (pine vs. sugarberry) and mass correlated with richness. General linear models (GLMs), with Gaussian distributions, were used to build individual models for species richness, evenness (Pielou's J'), compositional differences (proxied by principal component 1 [PC1] and principal component 2 [PC2]), $\log_{10}$ abundance, and skewness of the community $\log_{10}$ body size distribution. We then assembled these GLMs into a structural equation model and evaluated the resulting model to determine whether it was missing any paths via Fisher's C (i.e., any paths or hypotheses not considered in our current model; if they were important, our model would not fail our test of fit). Fitting and evaluation of the piecewise structural equation models occurred in the piecewiseSEM package (version 2.12; Lefcheck, 2016) in R (R Development Core Team, 2021). While our sample size was low (ideally $n = 5\text{–}10$ per parameter), piecewise SEM for hypothesis evaluation, rather than simulation, has the advantage of only needing to require sample size requirements for individual pieces. A full model (Appendix S1: Figure S1A) was constructed of all possible predictive connections assuming the predictive hierarchy of richness > evenness > abundance > composition > body size > wood type and accessibility. A full model was constructed to account for mechanisms and pathways not explicit in hypothesized paths. We then constructed a reduced model that removed pathways not different from 0 at the $\alpha = 0.05$ level. While it is likely some of those paths could be important, we believed that this approach was a better way to test theory than to explore the thousands of possible model topologies with different combinations of initially unsupported paths included. Finally, we fit an ecological model with the hypothesized paths predicted by the more-individuals, niche-mediated more individuals, metabolic adaptation/more specialization/niche position, competitive evenness, body size–diversity, and energy accessibility mechanisms (Appendix S1: Figure S1B). Models were compared against one another with Akaike information criterion (AIC) values to evaluate difference in model fit given model complexity. We then calculated standardized coefficients for all paths (Grace & Bollen, 2005) to compare the relative strength of different paths to one another. We note that, given suppression effects of some of the variables, some standardized paths were greater than 1, indicating that the effects of some variables would have been masked by others without adopting a multivariate approach (Bollen, 1982).

RESULTS

In total, 58,883 individuals from 162 morphospecies were identified across all wood falls. Species richness ($S \sim 45.9 + 18.7 \times \log_{10}$ wood fall mass, $F_{1,22} = 10.39$, $p = 0.0049$, $R^2 = 0.30$) and abundance ($\log_{10}$ abundance $\sim 3.0 + 0.6 \times \log_{10}$ wood fall mass, $F_{1,22} = 24.22$, $p < 0.0001$, $R^2 = 0.52$) both significantly increase with increasing wood fall mass (Figure 1). Wood type did not significantly affect either relationship (richness: t value$_{21}$ = 0.976, $p = 0.3810$; abundance: t value$_{21}$ = 0.619, $p =$ 0.5420). Species richness scaled with

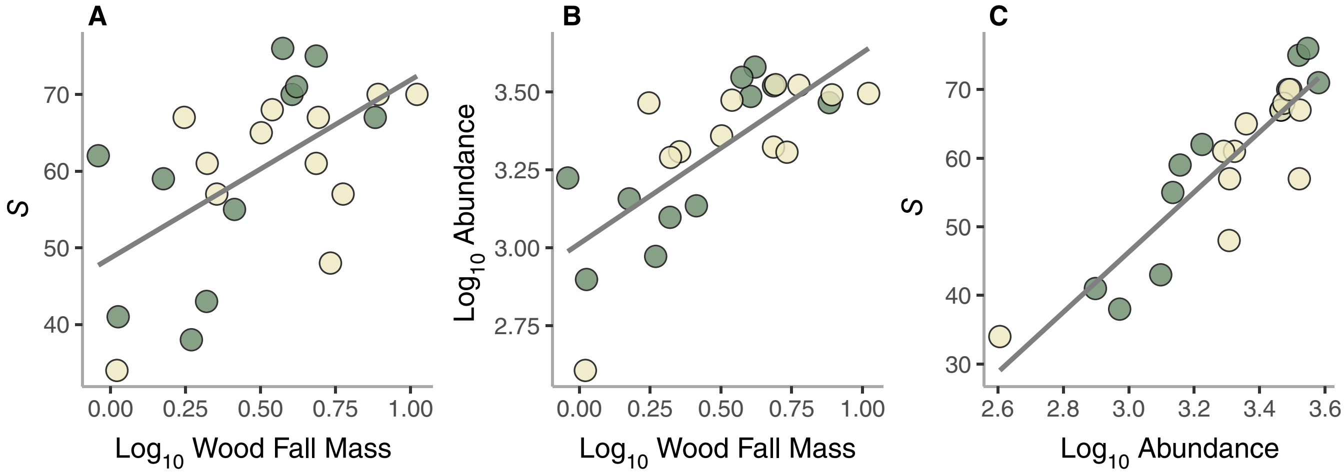

FIGURE 1 Linear fits of relationships predicted by the more-individuals hypothesis. (A) Number of species as a function of $\log_{10}$ wood fall mass (in kilograms), a measure of total energy (B) $\log_{10}$ abundance as a function of $\log_{10}$ wood fall mass, and (C) the scaling of species richness as a function of $\log_{10}$ abundance across wood falls. In plots, green color denotes wood falls of the softwood *Pinus elliotti* and cream color denotes wood falls of the soft hardwood *Celtis laevigata*. Wood hardness here serves as a proxy for energy accessibility.

abundance ($S = -74.8 + 39.1 \times \log_{10}$ abundance, $F_{1,22} = 98.68$, $p < 0.0001$, $R^2 = 0.82$; Figure 1).

PC1 and PC2 cumulatively described 60% of the variation in composition of wood falls (Figure 2). Compositional shifts were related to changes in both wood fall type and mass (Figures 2 and 3; Appendix S1: Table S1), with PC1 driven by wood type and PC2 driven by wood mass.

A full structural equation model with all possible connections yielded an AIC of 77.2 while the ecological structural equation model resulted in a higher AIC (93.0). A reduced model, removing nonsignificant effects

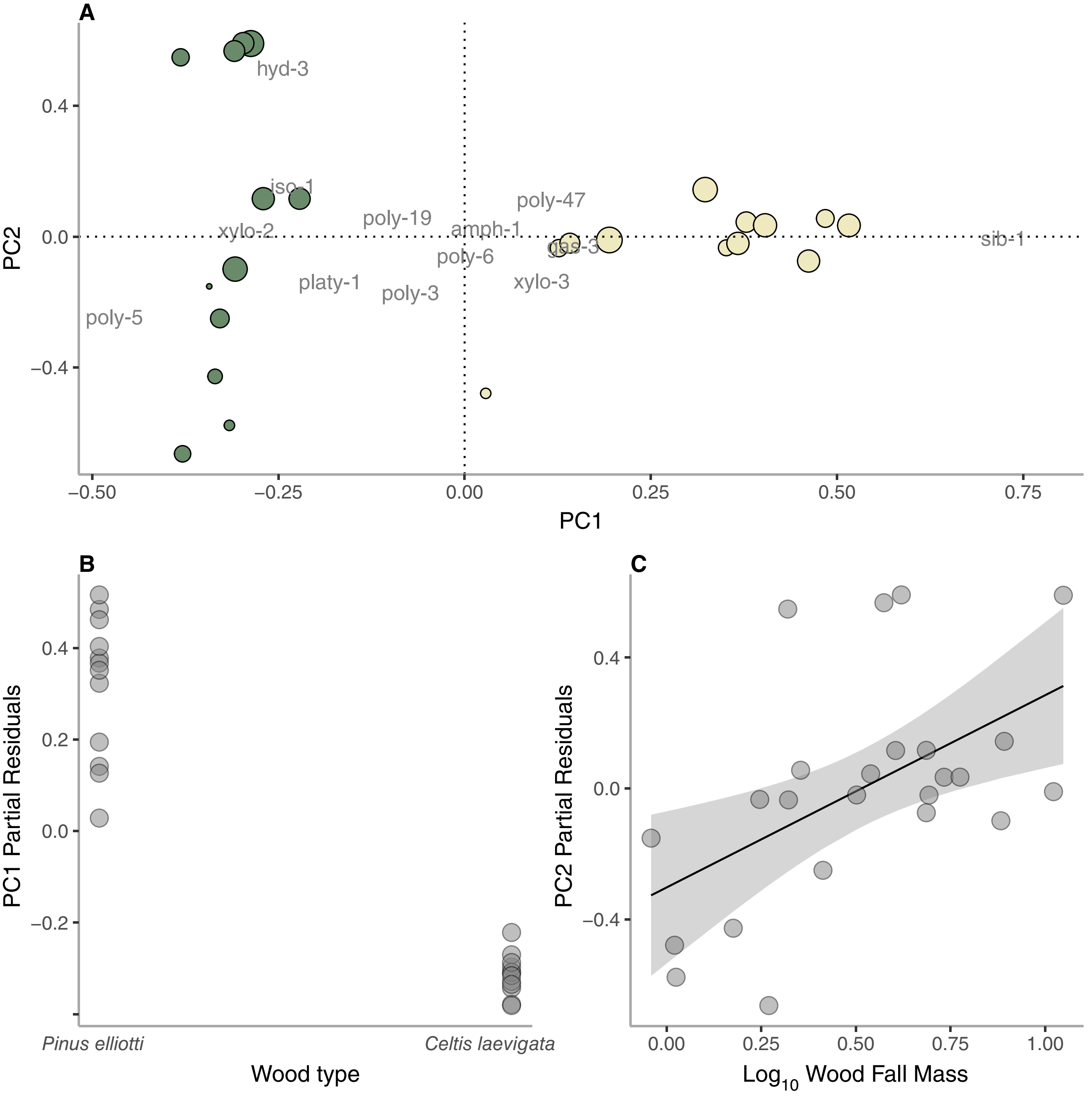

FIGURE 2 (A) Principal components analysis on the Hellinger pre-transformed data. In plot, green color denotes wood falls of the softwood *Pinus elliotti* and cream color denotes wood falls of the soft hardwood *Celtis laevigata*. Gray text in plot indicates species loadings, with abbreviations indicating taxonomic affiliation and a species identification number: amp, amphipod; gas, gastropod; hyd, hydrodzoan; iso, isopod; poly, polychaete; platy, platyhelminthes; sib, sibloglonid; xylo, xylophagous bivalve. Significant relationships emerging from the reduced structural equation model. Partial residuals of principal component 1 (PC1) as a function of (B) wood type (a measure of energy accessibility) and (C) principal component 2 (PC2) as a function of $\log_{10}$ wood fall mass (in kilograms, measure of total energy). Solid lines indicate model fit. Shaded gray areas denote 95% CIs.

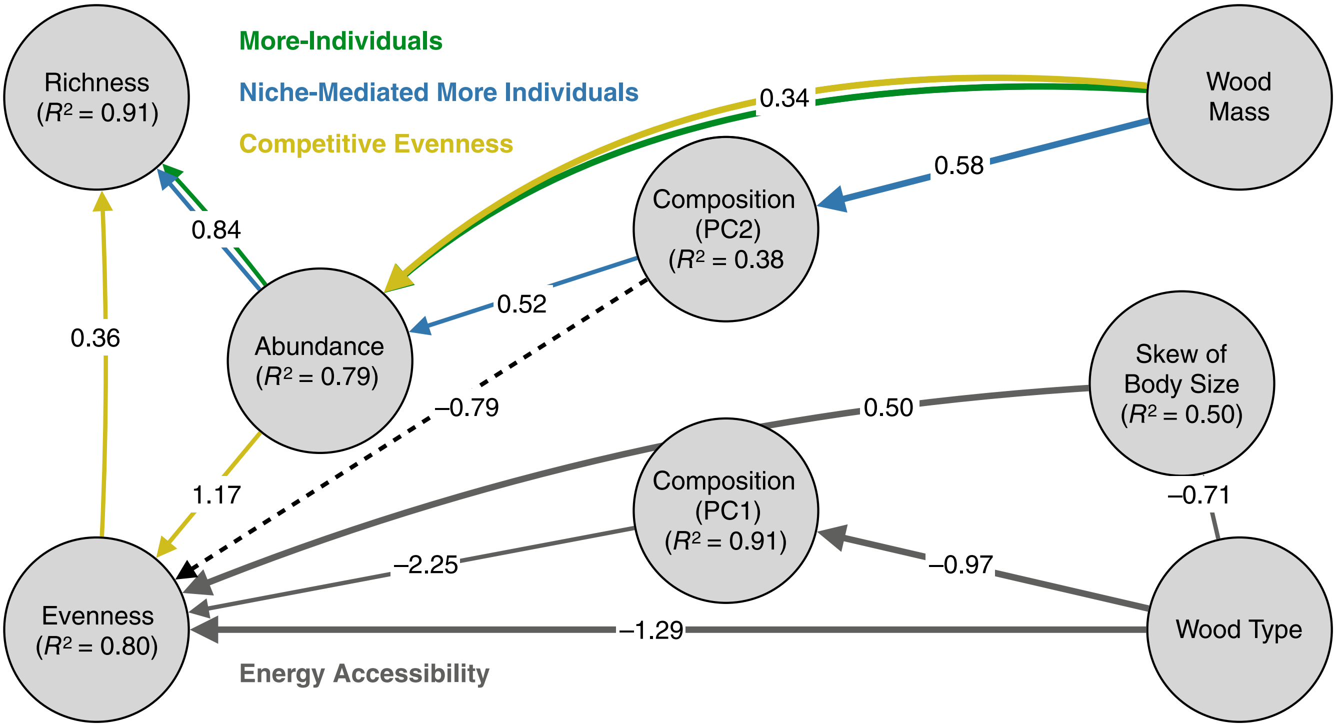

FIGURE 3 Structural equation model path diagram for reduced model where paths not different from zero were removed. Colors indicate paths predicted by individual species–energy hypotheses. Values are standardized coefficients. Dashed line refers to path included in the reduced model but not in the hypothesized mechanisms. PC1, principal component 1; PC2, principal component 2.

of the full model, produced the best AIC (75.6, Figure 3), comparable to the full structural equation model, that is, the ΔAIC < 2. In both the full and reduced models, the p value for Fisher's C was not significant (full: Fisher's $C_2 = 1.175$, $p = 0.55$; reduced: Fisher's $C_{30} = 26.163$, $p = 0.67$), indicating no missing paths. A total of 14 direct relationships were dropped in the reduced structural equation model (Appendix S1: Table S1). Coefficients for the remaining paths were not qualitatively different.

Species richness was more positively correlated with abundance than evenness (Figures 3 and 4A,B; Appendix S1: Table S1), with increases in both abundance and evenness correlated with increases in richness. Many of these dropped direct relationships were predictors of species richness, including wood type, wood mass, composition, and skewness of body size (Appendix S1: Table S1).

Abundance was positively correlated with shifts in species compositions along PC axis 2 as well as wood mass (Figures 3 and 4C,D; Appendix S1: Table S1). Standardized coefficients were relatively similar for both factors on abundance.

The strongest relationships in the structural equation model were with evenness, including wood type, composition, abundance, and skew of body size all exhibiting significant relationships (Figures 3 and 5; Appendix S1: Table S1). Of these, wood type, abundance, and composition (PC1) were the strongest. Greater abundances and an increase in the skew of body sizes concurrently contributed to enhanced evenness (Figures 3 and 5; Appendix S1: Table S1). Evenness also decreased on sugarberry wood falls. While increases in abundance and skew of body size both increased evenness.

Finally, wood type also impacted the skew of body size distribution, with invertebrates on sugarberry being skewed toward smaller sizes (Figure 3; Appendix S1: Figure S2, Table S1).

We find strong support using the reduced model for the more individuals hypothesis,

$$\text{Energy availability} \rightarrow \text{abundance} \rightarrow \text{richness}\,(\text{relative overall path strength} = 0.28),$$

the niche-mediated more individuals hypothesis,

$$\text{Energy availability} \rightarrow \text{composition} \rightarrow \text{abundance} \rightarrow \text{richness}\,(\text{strength} = 0.29),$$

the energy accessibility hypothesis,

$$\text{Energy accessibility/availability} \rightarrow \ldots \rightarrow \text{evenness} \rightarrow \text{richness}\,(\text{strength} = 1.02),$$

and compelling support for the competitive evenness hypothesis.

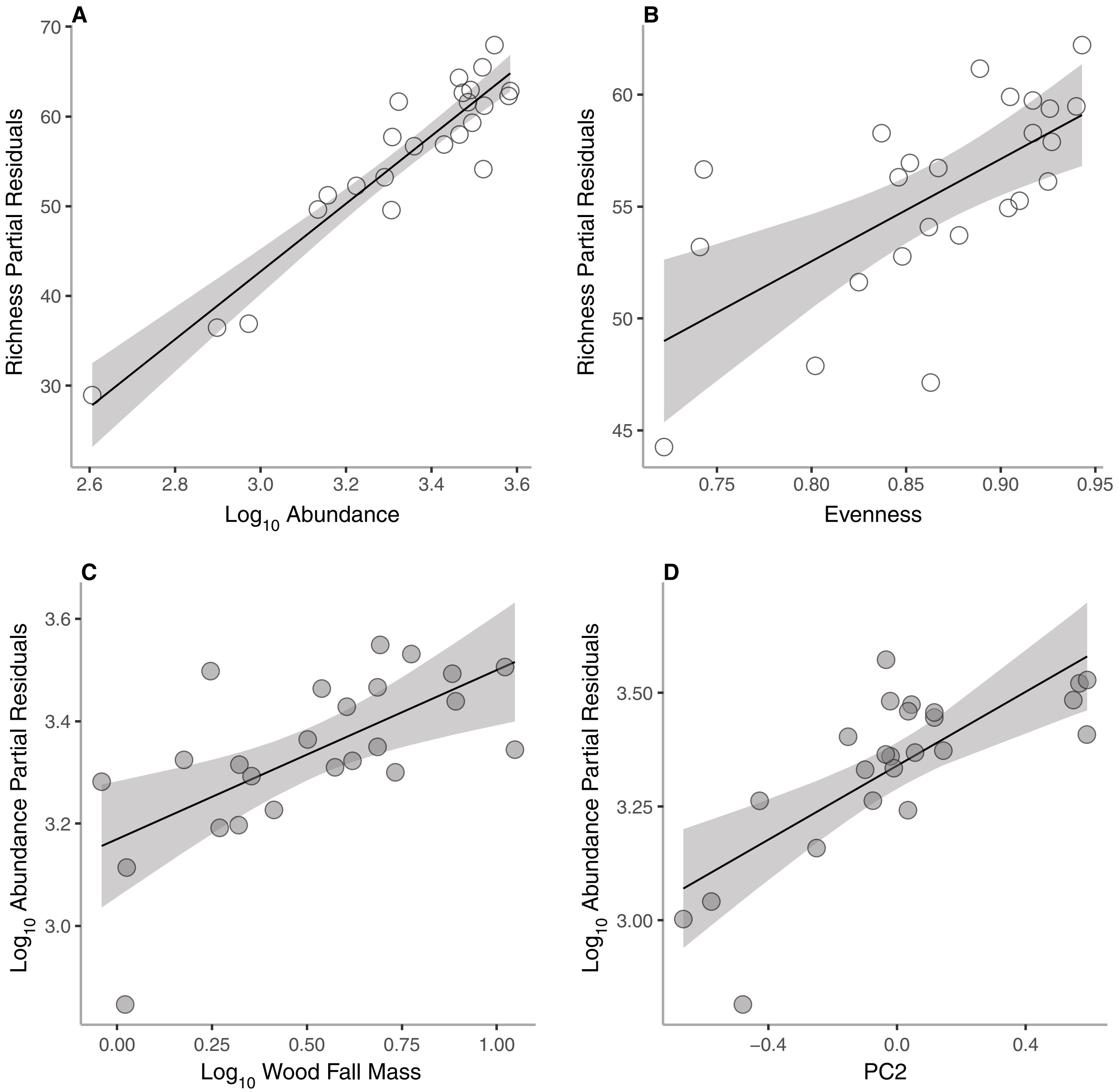

FIGURE 4 Significant relationships emerging from the reduced structural equation model. Partial residuals of species richness (open circles) as a function of (A) $\log_{10}$ abundance and (B) evenness. Partial residuals of $\log_{10}$ abundance (filled circles) as a function of (C) $\log_{10}$ wood fall mass (in kilograms, measure of total energy) and (D) principal component 2 (PC2) (a measure of species composition). Solid lines indicate model fit. Shaded gray areas denote 95% CIs.

$$\text{Energy accessibility/availability} \rightarrow \ldots \rightarrow \text{evenness} \rightarrow \text{richness}\ (\text{strength} = 0.14).$$

Two hypotheses were not supported or had weak effects, including the body size–diversity hypothesis:

$$\text{Energy availability} \nrightarrow \text{body size} \nrightarrow \text{abundance} \rightarrow \text{richness}\ (\text{strength} = 0.01),$$

$$\text{Energy availability} \nrightarrow \text{body size} \nrightarrow \text{richness}\ (\text{strength} = 0.00),$$

and the metabolic adaptation hypothesis.

$$\text{Energy availability} \rightarrow \text{traits/composition} \nrightarrow \text{richness}\ (\text{strength} = 0.06).$$

DISCUSSION

While a strong relationship (Figure 1) existed among the experiments here in support of the more-individuals relationship (Srivastava & Lawton, 1998; Wright, 1983; Wright et al., 1993), our findings suggest that how niche dynamics and competitive processes distribute individuals in a community is equally important in limiting or bolstering diversity. In the structural equation model, richness was related to evenness and abundance (Figures 3 and 4; Appendix S1: Table S1). Thus, richness in part reflects the classic species–abundance power relationship (May, 1975; Preston, 1962) but also how that abundance is distributed among species. We also find a complex and multifaceted set of relationships supported by the structural equation model linking richness to metrics of total energy availability and accessibility, yielding a high prediction fidelity of species richness ($R^2 = 0.91$; Figure 3).

Abundance is well described in the structural equation model by energy availability ($R^2 = 0.79$, energy availability → abundance [strength = 0.37, energy availability → composition → abundance, strength = 0.34]). The result is supportive of the more-individuals hypothesis that predicts a strong positive relationship between energy and abundance, as well as between abundance and diversity. We also observe that abundance is controlled by species composition of the community. High values of PC2 correspond with increases in abundance (Figure 2) and dominated in part by undescribed hydroid and isopod species from lower metabolic demand groups (McClain et al., 2020). If species composition in the community largely reflects shifts in traits, the findings indicate that certain sets of species and traits may be able to translate energy more effectively into abundance and ultimately richness. To restate, certain species have lower energetic demands (Brown et al., 2004; McClain et al., 2020), so more energy may translate into population growth. Previous work (McClain, Barry, et al., 2018; McClain, Nunnally, et al., 2018) has found that increases in energy may affect only certain size classes and ecological traits, with subsequent changes in abundance only in these groups.

Species richness is not directly related to the species composition of the community (Figure 3; Appendix S1: Table S1). This lack of a direct relationship, independent of abundance, suggests, as energy increases, that energy is put into an additional individual irrespective of metabolic demand or species identity, increasing abundance, not into replacing that individual with one with a greater metabolic demand. The more specialization hypothesis (DeAngelis, 1994; Schoener, 1976) or niche position hypothesis (Evans et al., 1999, 2005, 2006) also indicates a minimum amount of energy is needed to support specialist species, but this may occur largely by abundance additions not replacements. Additionally, at high productivity, specialization is facilitated and prevents competitive exclusion (DeAngelis, 1994; Schoener, 1976). This increased energy may increase overall niche availability by allowing either novel resource niches at the edge of niche space, that is, niche expansion, or filling of previously unfilled “holes” in niche space, that is, niche packing.

A lack of direct or indirect connections from total energy to body size and ultimately richness is surprising. Across both terrestrial and marine communities, greater richness in a body size class is often coupled to a greater number of individuals (Fa & Fa, 2002; Marquet et al., 1995; McClain, 2004; Siemann et al., 1996, 1999), implying that more energy may be available to these size classes and diversity increases reflect more individual processes (Siemann et al., 1996; Srivastava & Lawton, 1998; Wright, 1983; Wright et al., 1993). Our previous work has found connections through abundance, that is, more individuals, and niche packing between body size and diversity on wood falls (McClain, Barry, et al., 2018). Given the short duration of the wood falls (21 months) versus (>60 months) and slow growth rates of deep-sea species (McClain et al., 2012), there may not have been sufficient time for growth and subsequent impacts on the body size distribution. However, a connection exists in which energy accessibility → body size → evenness → richness. The relative hardness of *C. laevigata* slows the potential rate of energy acquisition by individuals. Larger sized species may not be able to acquire energy quickly enough, that is, boring through the wood, to meet metabolic demands. This forced energy regulation thus favors smaller sized species, leading to uneven communities and preventing competition from larger sized species (Appendix S1: Figure S2).

Competitive exclusion of species is often invoked in species–energy hypotheses, particularly to account for the negative part, increased energy leading to decreased richness, of unimodal species–energy relationships (Huston, 1979; Rosenzweig & Abramsky, 1993; Tilman, 1982), leading to decreases in evenness. Empirical work has also demonstrated high evenness, abundance, and richness occur in concert (Hurlbert, 2004). We find a direct relationship exists between richness and species evenness and both direct and indirect linkages between energy → evenness → richness. While energy accessibility directly and indirectly linked to evenness, energy availability only indirectly correlated with evenness. Changes in both energy availability and accessibility change the composition, traits, and abundance of species, which ultimately may impact competitive interactions

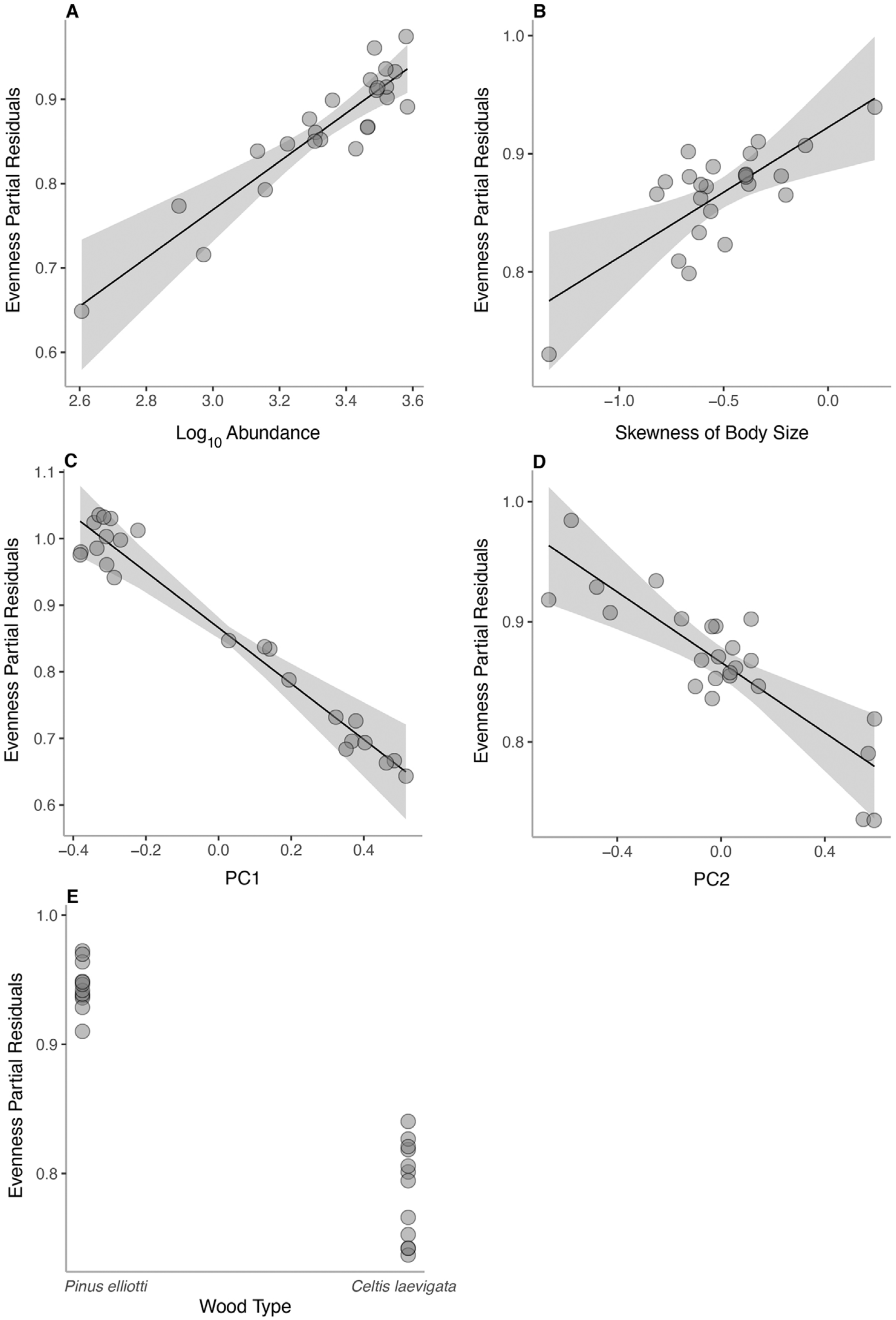

FIGURE 5 Significant relationships emerging from the reduced structural equation model. Partial residuals of evenness as a function of (A) $\log_{10}$ abundance, (B) skewness of the body size distribution, (C) principal component 1 (PC1) (a measure of species composition), (D) principal component 2 (PC2) (a measure of species composition), and (E) wood type (a measure of energy accessibility). Solid lines indicate model fit. Shaded gray areas denote 95% CIs.

and evenness. In other words, decreases in richness occur when a few species with key traits dominate available energy.

Accessibility of energy may not directly affect richness but does control structure through evenness of the community, that is, which species are getting energy. The strongest relationships in the structural equation model were with wood type and compositional relationships with evenness (Figure 3). Pine possessed more even distributions than those on sugarberry (Figure 4E). On average, among sugarberry wood falls, the top eight species possessed abundances greater than 100 individuals, with the bottom 30 possessing abundances less than 20. This unevenness on sugarberry likely reflects that few species were able to flourish given the relative inaccessibility of carbon on the wood fall (Romano et al., 2013). The hardwood likely restricted and slowed growth and colonization of the wood-boring bivalves (Romano et al., 2013). This allowed for more time for a sulfidic habitat to develop (Kalenitchenko et al., 2018). Indeed, sugarberry wood fall surfaces were covered in yellow microbial sulfur biofilms. This produced a habitat favorable to the siboglinid annelid *Sclerolinum* often associated with decaying organic materials like sunken wood or sulfidic sediments, which relies on endosymbiotic bacteria for nutrition (Georgieva et al., 2015). Much of the unevenness in sugarberry wood falls is attributed to the numerical dominance by *Sclerolinum*. Abundances of *Sclerolinum* on pine were below 10 on average, while on sugarberry, abundances were frequently above 1000. The other dominant species was a new species of *Xyloredo* that obtain larger sizes and dig deeper burrows than the other species on wood falls (McClain et al., unpublished manuscript). This suggests a capacity for greater wood-boring ability compared with other species.

Worth noting is that the wood falls in this experiment represent hyperdiverse communities. The richness in individual wood falls ranged from 34 to 76 co-occurring species. This is substantially larger than the maximum of 24 co-occurring species on wood falls in a similar experiment off the Central California Coast (McClain et al., 2016). The overall species pool on the 24 Gulf of Mexico wood falls ($S = 162$) is also an order of magnitude greater than that for the 32 California wood falls ($S = 48$). The experimental site in this study lies in close proximity to the Mississippi River outfall, which generates a considerable input of organic carbon, including woody debris, into the deep ocean (Schlünz & Schneider, 2000; Wei et al., 2012). In the northern Gulf, wood debris can reach densities of over one piece of wood debris per hectare (Wei et al., 2012). In addition, the Gulf of Mexico represents a hot spot of chemosynthetic communities due to its unique geological history (Cordes et al., 2009). This considerable woody input and chemosynthetic habitats likely generated considerable evolutionary opportunity for diversification of wood- and chemosynthetic-obligate species leading to a large regional pool of species in the Gulf of Mexico (Romano et al., 2013). In comparison, the California experimental site is not near a major river input. This increased regional pool in the Gulf of Mexico is likely to impact overall community structure. For example, the larger regional pool will allow local ecological dynamics to become more important in setting species richness (Cornell & Lawton, 1992). In the case of wood falls, the wood fall size, a metric for local productivity, determines the number of species from the regional pool that colonize (Chase & Myers, 2011). In more productive regions, the strength of species–energy relationships is stronger, reflecting the regional pool containing species adapted to both high and low productivity (Cornell & Harrison, 2014). Indeed, the Gulf of Mexico species–energy relationship for wood falls is higher in both slope and intercept than that of California (GoM: $S \sim 45.9 + 18.7 \times \log_{10}$ wood fall mass; California: $S \sim 5.2 + 8.3 \times \log_{10}$ wood fall mass).

Larger areas inherently contain larger numbers of individuals, and thus, because wood fall area is also increasing in this experiment, the relationships may reflect species–area mechanisms versus species–energy. However, adding additional individuals into the community requires a concordant increasing in energy to meet their metabolic demand. Many of the species are xylophagous, or predators on xylophagous species, requiring the wood as nutritional and energy source rather than just as a substrate. Because of this, the species–area relationship may be seen as specific case of a more general species–energy relationship (Wright, 1983). Abundance and species richness also depend on the total quantity of resource available, regardless of the density and area of that resource (Hurlbert, 2006). Larger areas may also have received greater larval recruitment in our experiment; however, growth and persistence of that individual still require energy. In our previous work, simulated relationships (McClain et al., 2016), drawing individuals at random from the regional pool, overpredicted the number of species on wood falls. The predicted rate of increase in richness with increasing wood fall was also much less than predicted. The lack of fit between predicted and empirical reflects the species in experiments were more aggregated distributions, that is, did not occur across all wood falls with equal probability, suggesting the species had energy-specific requirements.

The complexity of ecological processes underlying the more-individuals relationship may be why the theory has found limited support (Hurlbert, 2004; Hurlbert & Jetz, 2010; McCain, 2021; McClain et al., 2016;

McClain, Barry, et al., 2018). Here, we show that while there is a tight coupling between available energy, the number of individuals, and the number of species in a community, the underlying mechanics of this relationship is also regulated by the composition of species in the community and the traits they possess. Some ecological groups may be able to monopolize much of the available energy. Increases in energy then translate to increases in individuals and ultimately species in those ecological groups. However, the more-individuals hypothesis is not sufficient to explain the totality of richness increases with increasing energy, and understanding the distribution of individuals and energy among species is vital. Overall, this points to a potential for complex reactions to anthropogenic changes in productivity.

ACKNOWLEDGMENTS

We would like to thank the captain, crew, and marine technicians of the R/V *Pelican*. The work by the expert pilots and the ROV *Global Explorer* from Oceaneering greatly facilitated the deployment and retrieval of the experiments. Special thanks to Jason Tripp, Lead Pilot and ROV Superintendent, for his work in facilitating our technical work on the sea floor. We thank C. Nunnally for his tremendous efforts with experimental deployments, retrieval, and processing. This research was supported through NSF Grant No. 1744048 to Craig R. McClain.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (McClain, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.8212720.

ORCID

Craig R. McClain https://orcid.org/0000-0003-0574-428X

S. River D. Bryant https://orcid.org/0000-0002-1712-6158

Jarrett Byrnes https://orcid.org/0000-0002-9791-9472

REFERENCES

Allen, C. R., A. S. Garmestani, T. D. Havlicek, P. A. Marquet, G. D. Peterson, C. Restrepo, C. A. Stow, and B. E. Weeks. 2006. "Patterns in Body Mass Distributions: Sifting among Alternative Hypotheses." *Ecology Letters* 9: 630–643.

Bienhold, C., P. P. Risotva, F. Wenzhofer, T. Dittmar, and A. Boetius. 2013. "How Deep-Sea Wood Falls Sustain Chemosynthetic Life." *PLoS One* 8: e53590.

Bollen, K. A. 1982. "A Confirmatory Factor Analysis of Subjective Air Quality." *Evaluation Review* 6(4): 521–535.

Bollen, K. A. 1989. *Structural Equations with Latent Variables*. Hoboken, NJ: John Wiley & Sons.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–89.

Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. "Evolution of Body Size: Consequences of an Energetic Definition of Fitness." *American Naturalist* 142: 573–584.

Cardinale, B. J., H. Hillebrand, W. S. Harpole, K. L. Gross, and R. Ptacnick. 2009. "Separating the Influence of Resource 'Availability' from Resource 'Imbalance' on Productivity–Diversity Relationships." *Ecology Letters* 12: 475–487.

Chase, J. M. 2010. "Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments." *Science* 328: 1388–91.

Chase, J. M., and M. A. Leibold. 2002. "Spatial Scale Dictates the Productivity-Biodiveristy Relationship." *Nature* 416: 427–430.

Chase, J. M., and J. A. Myers. 2011. "Disentangling the Importance of Ecological Niches from Stochastic Processes across Scales." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–63.

Chase, J. M., and W. A. Ryberg. 2004. "Connectivity, Scale-Dependence, and the Productivity-Diversity Relationship." *Ecology Letters* 7: 676–683.

Connell, J. H., and E. Orias. 1964. "The Ecological Regulation of Species Diversity." *The American Naturalist* 98: 399–414.

Cordes, E. E., D. C. Bergquist, and C. R. Fisher. 2009. "Macro-Ecology of Gulf of Mexico Cold Seeps." *Annual Review of Marine Science* 1: 143–168.

Cornell, H. V., and S. P. Harrison. 2014. "What Are Species Pools and When Are They Important?" *Annual Review of Ecology, Evolution, and Systematics* 45: 45–67.

Cornell, H. V., and J. H. Lawton. 1992. "Species Interactions, Local and Regional Processes, and Limits to the Richness of Ecological Communities: A Theoretical Perspective." *Journal of Animal Ecology* 61: 1–12.

Currie, D. J. 1991. "Energy and Large-Scale Patterns of Animal- and Plant-Species Richness." *American Naturalist* 137: 27–49.

Cusens, J., S. D. Wright, P. D. McBride, and L. N. Gillman. 2012. "What Is the Form of the Productivity-Animal-Species-Richness Relationship? A Critical Review and Meta-Analysis." *Ecology* 2012: 2241–52.

DeAngelis, D. L. 1994. "Relationships between the Energetics of Species and Large-Scale Species Richness." In *Linking Species and Ecosystems*, edited by C. G. Jones and J. H. Lawton, 263–272. New York: Chapman & Hall.

Dodji Kasseney, B., T. Deng, and J. Mo. 2011. "Effect of Wood Hardness and Secondary Compounds on Feeding Preference of *Odontotermes formosanus* (Isoptera: Termitidae)." *Journal of Economic Entomology* 104: 862–67.

Dray, S., G. Blanchet, D. Borcard, S. Clappe, G. Guenard, T. Jombart, G. Larocque, P. Legendre, N. Madi, and H. H. Wagner. 2018. "despatial: Multivariate Multiscale Spatial Analysis." https://github.com/sdray/adespatial.

Ernest, S. K. M. 2005. "Body Size, Energy Use, and Community Structure of Small Mammals." *Ecology* 86: 1407–13.

Evans, K. L., J. J. D. Greenwood, and K. J. Gaston. 2005. "Dissecting the Species-Energy Relationship." *Proceeding of the Royal Society B: Biological Sciences* 272: 2155–63.

Evans, K. L., N. A. James, and K. J. Gaston. 2006. "Abundance, Species Richness and Energy Availability in the North American Avifauna." *Global Ecology and Biogeography* 15: 372–385.

Evans, K. L., P. H. Warren, and K. J. Gaston. 1999. "Species–Energy Relationships at the Macroecological Scale: A Review of the Mechanisms." *Biological Reviews* 80: 1–25.

Fa, D. A., and J. E. Fa. 2002. "Species Diversity, Abundance and Body Size in Rocky-Shore Mollusca: A Twist in Siemann, Tilman, and Haarstads's Parabola?" *Journal of Molluscan Studies* 68: 95–100.

Georgieva, M. N., H. Wiklund, J. B. Bell, M. H. Eilertsen, R. A. Mills, C. T. Little, and A. G. Glover. 2015. "A Chemosynthetic Weed: The Tubeworm *Sclerolinum contortum* Is a Bipolar, Cosmopolitan Species." *BMC Evolutionary Biology* 15: 1–17.

Grace, J. B. 2006. *Structural Equation Modeling and Natural Systems*. Cambridge: Cambridge University Press.

Grace, J. B., and K. A. Bollen. 2005. "Interpreting the Results from Multiple Regression and Structural Equation Models." *Bulletin of the Ecological Society of America* 86: 283–295.

Hurlbert, A. H. 2004. "Species-Energy Relationships and Habitat Complexity in Bird Communities." *Ecology Letters* 7: 714–720.

Hurlbert, A. H. 2006. "Linking Species–Area and Species–Energy Relationships in *Drosophila* Microcosms." *Ecology Letters* 9: 287–294.

Hurlbert, A. H., and W. Jetz. 2010. "More than "More Individuals": The Nonequivalence of Area and Energy in the Scaling of Species Richness." *The American Naturalist* 176: E50–E65.

Hurlbert, A. H., and J. C. Stegen. 2014. "When Should Species Richness Be Energy Limited, and How Would We Know?" *Ecology Letters* 17: 401–413.

Huston, M. 1979. "A General Hypothesis of Species Diversity." *American Naturalist* 113: 81–101.

Hutchinson, G. E. 1959. "Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals." *American Naturalist* 93: 145–159.

Kalenitchenko, D., E. Péru, L. Contreira Pereira, C. Petetin, P. E. Galand, and N. Le Bris. 2018. "The Early Conversion of Deep-Sea Wood Falls into Chemosynthetic Hotspots Revealed by In Situ Monitoring." *Scientific Reports* 8: 907.

Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. "Energy, Density, and Constraints to Species Richness: Ant Assemblages along a Productivity Gradient." *American Naturalist* 155: 280–293.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modelling in r for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–79.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. "Analyzing Beta Diversity: Partitioning the Spatial Variation of Community Composition Data." *Ecological Monographs* 75: 435–450.

Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformation for Ordination of Species Data." *Oecologia* 129: 271–280.

MacArthur, R. H., and E. R. Pianka. 1966. "On Optimal Use of a Patchy Environment." *The American Naturalist* 100: 603–9.

Marquet, P. C., S. A. Navarrete, and J. C. Castilla. 1995. "Body Size, Population Density, and the Energetic Equivalence Rule." *Journal of Animal Ecology* 64: 325–332.

May, R. M. 1975. "Patterns of Species Abundance and Diversity." In *Ecology and Evolution of Communities*, edited by M. Cody and J. Diamond, 81–120. Cambridge, MA: Belknap Press. https://www.hup.harvard.edu/catalog.php?isbn=9780674224445.

May, R. M. 1988. "How Many Species Are There on Earth?" *Science* 241: 1441–49.

McCain, C. M. 2021. "Another Rejection of the More-Individuals-Hypothesis: Carrion Beetles (Silphidae, Coleoptera) in the Southern Rocky Mountains." *Frontiers of Biogeography* 13: 20210303.

McClain, C. R. 2004. "Connecting Species Richness, Abundance, and Body Size in Deep-Sea Gastropods." *Global Ecology and Biogeography* 13: 327–334.

McClain, C. R. 2023. "crmcclain/gom_woodfall: Release 1.0 for Community Ecology Data (v1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.8212720.

McClain, C. R., A. P. Allen, D. P. Tittensor, and M. A. Rex. 2012. "The Energetics of Life on the Deep Seafloor." *Proceedings of the National Academy of Sciences of the United States of America* 109: 15366–71.

McClain, C. R., and J. P. Barry. 2010. "Habitat Heterogeneity, Biogenic Disturbance, and Resource Availability Work in Concert to Regulate Biodiversity in Deep Submarine Canyons." *Ecology* 91: 964–976.

McClain, C. R., J. P. Barry, D. Eernisse, T. Horton, J. Judge, K. Kakui, C. L. Mah, and A. Waren. 2016. "Multiple Processes Generate Productivity-Diversity Relationships in Experimental Wood-Fall Communities." *Ecology* 97: 885–898.

McClain, C. R., J. P. Barry, and T. J. Webb. 2018. "Increased Energy Differentially Increases Richness and Abundance of Optimal Body Sizes in Deep-Sea Wood Falls." *Ecology* 99: 184–195.

McClain, C. R., N. A. Heim, M. L. Knope, and J. L. Payne. 2018. "Is Biodiversity Energy-Limited or Unbounded? A Test in Fossil and Modern Bivalves." *Paleobiology* 44: 385–401.

McClain, C. R., J. C. Nekola, L. Kuhnz, and J. P. Barry. 2011. "Local-Scale Turnover on the Deep Pacific Floor." *Marine Ecology Progress Series* 442: 193–200.

McClain, C. R., C. Nunnally, A. S. Chapman, and J. P. Barry. 2018. "Energetic Increases Lead to Niche Packing in Deep-Sea Wood Falls." *Biology Letters* 14: 20180294.

McClain, C. R., T. J. Webb, C. C. Nunnally, S. Dixon, S. Finnegan, and J. A. Nelson. 2020. "Metabolic Niches and Biodiversity: A Test Case in the Deep Sea Benthos." *Frontiers in Marine Science* 7: 216.

McGlynn, T. P., M. D. Weiser, and R. R. Dunn. 2010. "More Individuals but Fewer Species: Testing the 'More Individuals Hypothesis' in a Diverse Tropical Fauna." *Biology Letters* 6: 490–93.

McNaughton, S., and L. Wolf. 1970. "Dominance and the Niche in Ecological Systems." *Science* 167: 131–39.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, and H. Wagner. 2013. "vegan: Community Ecology Package." https://cran.r-project.org/web/packages/vegan/index.html.

Pianka, E. R. 1966. "Latitudinal Gradients in Species Diversity: A Review of Concepts." *American Naturalist* 100: 33–46.

Preston, F. W. 1962. "The Canonical Distribution of Commonness and Rarity." *Ecology* 43(185–214): 410–432.

R Development Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rabosky, D. L., and A. H. Hurlbert. 2015. "Species Richness at Continental Scales Is Dominated by Ecological Limits." *American Naturalist* 185: 572–583.

Romano, C., A. Nunes-Jorge, N. Le Bris, G. W. Rouse, D. Martin, and C. Borowski. 2020. "Wooden Stepping Stones: Diversity and Biogeography of Deep-Sea Wood Boring Xylophagaidae (Mollusca: Bivalvia) in the North-East Atlantic Ocean, with the Description of a New Genus." *Frontiers in Marine Science* 7: 579959.

Romano, C., J. Voight, J. B. Company, M. Plyuscheva, and D. Martin. 2013. "Submarine Canyons as the Preferred Habitat for Wood-Boring Species of Xylophaga (Mollusca, Bivalvia)." *Progress in Oceanography* 118: 175–187.

Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M. L., and Z. Abramsky. 1993. "How Are Diversity and Productivity Related?" In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, edited by R. E. Ricklefs and D. Schluter, 52–65. Chicago, IL: University of Chicago Press.

Schlünz, B., and R. R. Schneider. 2000. "Transport of Terrestrial Organic Carbon to the Oceans by Rivers: Re-Estimating Flux-and Burial Rates." *International Journal of Earth Sciences* 88: 599–606.

Schoener, T. W. 1976. "Alternatives to Lotka-Volterra Competition: Models of Intermediate Complexity." *Theoretical Population Biology* 10: 309–333.

Schuler, M. S., J. M. Chase, and T. M. Knight. 2015. "More Individuals Drive the Species Energy–Area Relationship in an Experimental Zooplankton Community." *Oikos* 124: 1065–70.

Sebens, K. P. 2002. "Energetic Constraints, Size Gradients, and Size Limits in Benthic Marine Invertebrates." *Integrative and Comparative Biology* 42: 853–861.

Siemann, E., D. Tilman, and J. Haarstad. 1996. "Insect Species Diversity, Abundance, and Body Size Relationships." *Nature* 380: 704–6.

Siemann, E., D. Tilman, and J. Haarstad. 1999. "Abundance, Diversity and Body Size: Patterns from a Grassland Arthropod Community." *Journal of Animal Ecology* 68: 824–835.

Srivastava, D. S., and J. H. Lawton. 1998. "Why More Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities." *The American Naturalist* 152: 510–529.

Symonds, M. R., and C. N. Johnson. 2008. "Species Richness and Evenness in Australian Birds." *The American Naturalist* 171: 480–490.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Wei, C.-L., G. T. Rowe, C. C. Nunnally, and M. K. Wiksten. 2012. "Anthropogenic "Litter" and Macrophyte Detritus in the Deep Northern Gulf of Mexico." *Marine Pollution Bulletin* 64: 966–973.

Woolley, S. N. C., D. P. Titternsor, P. K. Dusntan, G. Guillera-Arroita, J. J. Lahoz-Monfrort, B. A. Wintle, B. Worm, and T. D. O'Hara. 2016. "Deep-Sea Diversity Patterns Are Shaped by Energy Availability." *Nature* 533: 393–96.

Wright, D. H. 1983. "Species-Energy Theory: An Extension of Species-Area Theory." *Oikos* 41: 496–506.

Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. "Energy Supply and Patterns of Species Richness on Local and Regional Scales." In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, edited by R. E. Ricklefs and D. Schluter, 66–74. Chicago, IL: University of Chicago Press.

Yee, D. A., and S. A. Juliano. 2007. "Abundance Matters: A Field Experiment Testing the More Individuals Hypothesis for Richness–Productivity Relationships." *Oecologia* 153: 153–162.

SUPPORTING INFORMATION

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

How to cite this article: McClain, Craig R., S. River D. Bryant, Granger Hanks, and Jarrett Byrnes. 2023. "Disentangling Mechanisms of Species–Energy Relationships in Experimental Deep-Sea Wood Falls." *Ecosphere* 14(10): e4667. https://doi.org/10.1002/ecs2.4667