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Article:

McClain, C.R., Barry, J.P. and Webb, T.J. orcid.org/0000-0003-3183-8116 (2018)
Increased Energy Differentially Increases Richness and Abundance of Optimal Body Sizes in Deep-Sea Wood-Falls. *Ecology*, 99 (1). pp. 184-195. ISSN 0012-9658

<https://doi.org/10.1002/ecy.2055>

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Increased Energy Differentially Increases Richness and Abundance of Optimal Body Sizes in Deep-Sea Wood-Falls

Journal:	<i>Ecology</i>
Manuscript ID	ECY17-0380.R1
Wiley - Manuscript type:	Articles
Date Submitted by the Author:	27-Jul-2017
Complete List of Authors:	McClain, Craig; Louisiana Universities Marine Consortium, Barry, James; Monterey Bay Research Institute Webb, Thomas; University of Sheffield
Substantive Area:	Community Ecology < Substantive Area, Experimental Microcosms/Mesocosms < Community Ecology < Substantive Area
Organism:	Invertebrates < Animals
Habitat:	Bathyal < Marine < Aquatic Habitat < Habitat
Geographic Area:	Pacific Ocean < Geographic Area
Additional Keywords:	diversity, energy, competition, body size, species-energy, niche packing, productivity, community assembly
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 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 <i>Acacia</i> sp. logs ranging in size from 0.6 to 20.6 kg (corresponding to different levels of energy available) which were deployed at 3203 m in the Northeast Pacific Ocean for between 5 and 7 years. 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.

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energy and body size in wood falls

1 **Increased Energy Differentially Increases Richness and Abundance of**
2 **Optimal Body Sizes in Deep-Sea Wood-Falls**

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10 *Short running title: energy and body size in wood falls*

11

12 *Keywords: diversity, energy, competition, species-energy, body size, niche packing, productivity,*

13 *community assembly*

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3 **Abstract**

4 Theoretical and empirical studies suggest that the total energy available in natural communities
5 influences body size as well as patterns of abundance and diversity. But the precise mechanisms
6 underlying relationships or how these three ecological properties relate remain elusive. We
7 identify five hypotheses relating energy availability, body size distributions, abundance, and
8 species richness within communities, and we use experimental deep sea wood fall communities
9 to test their predicted effects both on descriptors describing the species richness-body size
10 distribution, and on trends in species richness within size classes over an energy gradient (size
11 class-richness relationships). Invertebrate communities were taxonomically identified, weighed,
12 and counted from 32 *Acacia* sp. logs ranging in size from 0.6 to 20.6 kg (corresponding to
13 different levels of energy available) which were deployed at 3203 m in the Northeast Pacific
14 Ocean for between 5 and 7 years. Trends in both the species richness-body size distribution and
15 the size class-richness distribution with increasing wood fall size provide support for the
16 Increased Packing hypothesis: species richness increases with increasing wood fall size but only
17 in the modal size class. Furthermore, species richness of body size classes reflected the
18 abundance of individuals in that size class. Thus, increases in richness in the modal size class
19 with increasing energy were concordant with increases in abundance within that size class. The
20 results suggest that increases in species richness occurring as energy availability increases may
21 be isolated to specific niches, e.g. the body size classes, especially in communities developing on
22 discrete and energetically isolated resources such as deep sea wood falls.

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3 **Introduction**

4 Increases in available energy frequently translate into increases in species richness (Rosenzweig
5 and Abramsky 1993, Waide et al. 1999, Clarke and Gaston 2006, Cusens et al. 2012) although
6 the existence of this relationship is not universal and often weak (Mittelbach et al. 2001). The
7 processes generating this greater diversity potentially stem from the transformation of this
8 increased energy into maintenance, work, growth, and reproduction at the individual and
9 population levels, thereby enabling opportunities for biodiversity maintenance and growth at the
10 community level (Rosenzweig and Abramsky 1993). For example, chemical energy translated
11 into individual reproduction and population growth may buffer against local extinctions thereby
12 leading to higher community diversity (Wright 1983, Wright et al. 1993, Srivastava and Lawton
13 1998). Chemical energy translated into greater individual growth and population numbers can
14 lead to greater prey biomass supporting increased abundances and diversity of higher trophic
15 levels (Post et al. 2000, Post 2002). Greater availability of chemical energy may also allow for
16 greater species richness by allowing phenotypes with greater metabolic demands (c.f. the
17 resource-ratio hypothesis of Tilman 1982, McClain et al. 2004, McClain et al. 2012b, McClain et
18 al. 2014).

19 Increases in energy availability could also translate into growth leading to alterations of species
20 richness-body size distributions and ultimately impacting overall diversity. Hypotheses linking
21 diversity and body size are prominent in ecology (Hutchinson 1959, Hutchinson and MacArthur
22 1959, May 1988). Many biological rates and outputs scale with body size, leading to the

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1 potential for substantial variation in species traits within a community (Peters 1983, Kerr and
2 Dickie 2001, Brown et al. 2004). Consequently, body size is often viewed as a major axis of
3 niche segregation and an important determinant of community structure (Hutchinson and
4 MacArthur 1959, Grant 1968, Wilson 1975, Kozłowski and Gawelczyk 2002, Simberloff and
5 Dayan 2005). However, the role of body size in community assembly remains controversial and
6 processes are poorly understood. Hutchinson (1959) documented a consistent ratio in mammals
7 and birds between contiguously sized species within a trophic level, which he hypothesized
8 results from competitive size displacement. Although the notion of a fixed ratio is now largely
9 discredited (Simberloff and Boeklin 1981), terrestrial mammal community structure is still often
10 considered to reflect competitive exclusion between species of similar sizes (Brown and
11 Nicoletto 1991) unless size-based competitive interactions are mitigated (e.g. habitat
12 heterogeneity, Bakker and Kelt 2000). However non-competitive neutral mechanisms (Etienne
13 and Olff 2004, Vergnon et al. 2009) have also been proposed to explain community body size
14 distributions.

15 Prior hypotheses that link body size and diversity may also be related to energetic processes.
16 Specific body size classes may be more speciose because they represent energetic optima, i.e. a
17 balance of energetic tradeoffs, or allow greater access to food resources (Sebens 1982, Brown et
18 al. 1993, Rex and Etter 1998, Roy et al. 2000, Sebens 2002, Ernest 2005). Across both terrestrial
19 and marine communities, greater richness in a body size class is often coupled to a greater
20 number of individuals (Marquet et al. 1995, Siemann et al. 1996, Marquet and Taper 1998,
21 Siemann et al. 1999, Fa and Fa 2002, McClain 2004, McClain and Nekola 2008). This implies
22 that more energy may be available to these size classes and diversity increases reflect species-
23 energy processes (Wright 1983, Wright et al. 1993, Siemann et al. 1996, Srivastava and Lawton

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1 1998). However, other work has found that the overall metabolic demand of size class does not
2 correlate with species richness (Ernest 2005). Alternatively, increased richness in certain size
3 classes may reflect the availability of energy to that size class (Ernest 2005). For example,
4 Ritchie and Olff (1999) propose that the fractal geometry of resource concentrations allows
5 greater species richness within a size class slightly greater than the mean, producing left-skewed
6 body size distributions. This geometry of resource concentrations also relates back to the habitat
7 architecture hypothesis of Holling (1992).

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

14 **H1: Increased packing into optimal body size** Greater energy availability leads to increased
15 species richness through increased packing of species into the optimal body size class(es) This
16 optimal body size class may reflect a series of energetic constraints (Sebens 1982, Brown et al.
17 1993, Rex and Etter 1998, Roy et al. 2000, Sebens 2002, Ernest 2005). This implies that
18 increases of energy do not impact the optimal body size nor affect in which size class resources
19 are available (Brown et al. 1993, Brown et al. 1996, Roy et al. 2000). The consequences for the
20 species richness–body size distribution of adding more species at or around the optimal body size
21 include a small decrease in variance and a pronounced increase in kurtosis, but no systematic
22 change in mean or modality (Fig. 1, top row). Richness within optimal size classes will increase
23 with increasing energy but richness in other size classes will be unaffected (Fig. 1, top row).

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1 Increased energy into the community should translate into increased abundance of only the
2 optimal size class.

3 **H2: Relaxed pressure for optimal body size:** Increased energy availability relaxes pressure for
4 species to be at the energetic optimum allowing for the additional species to be added at larger or
5 smaller body sizes (McClain et al. 2006, McClain et al. 2012b). A simple relaxation of pressure
6 will be evidenced by increased variance of the species richness-body size distribution and
7 increases in richness across all size classes (Fig. 1, second row) over a gradient of energy
8 availability. As more energy becomes available into the community, energy will be directed
9 toward the smallest and largest size classes resulting in disproportionate increases in abundance
10 of these size classes.

11 **H3: Shifts in optimal body size:** Increased energy affects the energetic tradeoffs that determine
12 the optimal body size thus the modal size class changes (Sebens 1982, Rex and Etter 1998,
13 Sebens 2002, McClain 2004, Collins et al. 2005). This will result in a systematic trend in mean
14 body size over the energy gradient and by increases within larger size classes and decreases in
15 smaller size classes (Fig. 1, third row) or vice versa, depending on the direction of the shift.

16 Regardless of the direction of shift, a relative decrease in the original modal class is expected.
17 Increased representation in large-sized species with increased energy may reflect relaxation of
18 metabolic constraints (McClain et al. 2006, McClain et al. 2012b). Decreased representation in
19 small-sized species may result from decreased pressure for larger foraging areas and starvation
20 resistance (McClain et al. 2006, McClain et al. 2012b). As energy increases, the size class with
21 the highest abundance will shift to the new optimum body size. No predicted changes are
22 expected in the other descriptors of the species richness-body size distribution. For the size class-
23 richness relationship, peak abundances are predicted to track shifts in the optimal body size class.

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1 **H4: Multimodal distributions with increased rare resources:** Increased energy increases
2 availability of rare resources (Schoener 1976, DeAngelis 1994, Evans et al. 1999, Evans et al.
3 2005). These rare resources make energy available to additional size bins allowing for multi-
4 modal species richness-body size distributions (Thibault et al. 2011). Trends in most descriptors
5 of the species richness-body size distribution will be idiosyncratic, depending on the order in
6 which species are added to different modes (one example, where first a larger size class and then
7 a smaller size class is favored, is shown in Fig. 1, fourth row). However, variance will typically
8 increase, and a systematic increase in the number of modes is detected as energy availability
9 increases, with pronounced increases also within the size classes closest to the new modes (Fig.
10 1, fourth row). Increased number of modes with increased energy should be concordant with
11 increases of abundance in these same size classes.

12 **H5: Size Invariance:** Under this scenario, although overall species richness increases with
13 increased energy, the descriptors of the species–energy relationship remain essentially
14 unchanged (Fig. 1, 5th row), i.e. abundance increases equitably across size classes, and richness
15 increases in proportion to original richness across all size classes as energy increases. The
16 primary descriptor distinguishing this from H1 is lack of change in kurtosis that characterizes
17 H1.

18 As Figure 1 shows, these hypotheses can be distinguished by using statistical properties of
19 empirical species richness-body size distributions and size class–richness relationships. However,
20 this requires data on body sizes across replicate communities over a gradient of energetic settings
21 that are not confounded by factors such as varying temperature, regional pools, connectivity
22 between communities, and community ages. Deep-sea ecosystems provide opportunities for
23 macroecological analyses where environmental variables that are tightly correlated in terrestrial

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1 and shallow marine systems (e.g. temperature and productivity) become decoupled (Tittensor et
2 al. 2011, McClain et al. 2012a, Webb 2012, Woolley et al. 2016). This is particularly pronounced
3 for the communities developing on resource-rich patches such as wood falls which occur
4 ephemerally on the typically resource-poor deep-sea floor. Wood is transported to the oceans via
5 rivers, and after drifting and becoming saturated with water, eventually sinks to the ocean floor.
6 On the deep-sea floor, wood falls develop largely endemic and highly diverse communities
7 consisting of wood and sulfide obligates, and associated predators (Voight 2007, McClain and
8 Barry 2014, McClain et al. 2016). The endemism of wood falls reflects an energetic isolation
9 because of the specific nutritional requirements for wood (xylophagy), sulfide, and/or methane
10 produced at the wood fall, or predator specificity for endemic wood-fall species.

11 Wood-fall communities in the deep sea are thus an ideal system for testing hypotheses about
12 community assembly and energetic theory because we can precisely and experimentally control
13 the total amount of energy available to the community, i.e. the size of a single wood fall
14 (McClain and Barry 2014, McClain et al. 2016). Increasing energy may increase habitat
15 heterogeneity (Chase and Leibold 2002). Deploying single wood logs of varying sizes allows for
16 testing of increases in energy without increasing habitat heterogeneity that may confound the
17 results. Each wood log no matter size is identical in shape, structure, and heterogeneity.

18 Increasing the size of wood falls risks conflating increased energy with increased area. However,
19 species–area and species–energy relationships are known to be intrinsically linked (Storch et al.
20 2005, Hurlbert 2006, Hurlbert and Jetz 2010, McClain et al. 2016), with species-area
21 relationships a special case of the more general species-energy relationship (Wright 1983). On
22 ecological timescales, increasing area only increases species richness if resources increase
23 proportionally (Hurlbert 2006), and in the energetically isolated wood fall communities we study

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1 it is ultimately the energetic content of the resource that drives community dynamics (reviewed
2 in McClain et al. 2016). Thus, by modeling how the statistical properties of species richness-
3 body size distributions and size class-richness relationships change over wood-fall communities
4 developing on wood falls of different sizes, we are able to specifically tie changes in size-based
5 community assembly to variation in energy availability.

6 Wood falls afford an additional opportunity to examine how connectivity between communities
7 affects the diversity-size-energy relationship. Research on freshwater systems (Chase and
8 Ryberg 2004) demonstrated that the strength of productivity-diversity relationships was in part
9 determined by the connectivity among sites along the productivity gradient. With heightened
10 connectivity, the diversity of low-productivity and low-diversity sites is augmented by
11 recruitment in from high-productivity and high-diversity sites. In early community development,
12 community structure is greatly influenced by larval recruitment from the regional larval pool
13 (Webb et al. 2017). As wood fall communities develop, connectivity between nearby wood falls
14 increases as the populations of species become mature enough to contribute to the larval pool
15 (Webb et al. 2017), which has the effect of suppressing the productivity-diversity relationship
16 (McClain et al. 2016). Dispersal ability, and its scaling with body size, also serves a key
17 parameter in some models that predict the unimodal size distribution (Etienne and Olf 2004).
18 All of the species on wood falls, despite size class, have similar dispersal ability, recruitment to
19 the wood fall occurs from a highly dispersive larval phase with limited motility in adults. Thus
20 wood falls provide an important test of the role of dispersal in generating species richness-body
21 size distributions. First, we hypothesize if dispersal scaling with body size is important, the
22 overall species richness-body size distribution should be unimodal as predicted by Etienne and
23 Olf (2004). If the species had limited dispersal ability or body-size and dispersal ability are

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1 uncoupled then the distribution should be uniform. Second, we hypothesize that as connectivity
2 increases between wood falls this should mitigate energetic relationships that establish the
3 species richness-body size distribution, i.e. communities that have been established for longer
4 should move towards the distribution of size invariance (H5). Although it might be predicted that
5 with all species having long dispersal distance, a regional larval pool may overwhelm the effects
6 of a proximate wood falls, the number of larval recruits generated locally should far exceed the
7 regional pool of larvae diminished by mortality and dilution.

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

14 Methods*15 Experimental Systems and Communities*

16 Wood falls on the deep-sea floor are unique and diverse communities consisting of xylophages,
17 sulfide obligates, predators of these two groups, and, to rare extent, opportunists (Supplemental
18 Figures). Xylophages ingest wood and rely on heterotrophic bacteria to aid digestion and
19 assimilation. Certain species of wood-fall inhabiting echinoids harbor wood-digesting microbiota
20 in their guts (Becker et al. 2009). One species of galatheid crab appears to prefer wood falls and
21 is regularly found with wood-filled guts (Hoyoux et al. 2009). Several species of ostracods from
22 the genus *Xylocythere* are also only known to inhabit wood falls (Maddocks and Steineck 1987)

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1 and may potentially be wood obligates. The most notable and abundant xylophagous species are
2 members of the bivalve subfamily Xylophaginae (Knudsen 1961, Turner 2002, Voight 2007).
3 Sulfide obligates rely nutritionally on chemoautotrophic bacteria, e.g. bivalves in genus *Idas*,
4 which colonize wood falls and benefit from chemoautotrophic endosymbionts (but see Ockelman
5 and Dinesen 2011, Bienhold et al. 2013). Predators feed on xylophages, sulfide obligates, and
6 opportunists. Certain acotylean polyclad flatworms, for example, likely feed on wood-boring
7 bivalves (Voight 2007). Opportunists have less specialized diets but are numerically rare. Only 4
8 of 39 wood-associated species, in the wood falls here were also found in the background
9 sediment or nearby hard substrates (McClain et al. 2009, McClain and Barry 2010, McClain et
10 al. 2010, McClain et al. 2011, McClain and Barry 2014, McClain et al. 2016). All of these
11 generalist habitat species are rare and represented by 1-4 individuals and as such do not make up
12 a significant component of the wood-fall community. The remaining wood-fall specialists all
13 have abundances that range from ~10-1000 individuals on a single wood fall.

14 Succession at wood-fall communities begins at 1-2 months with wood-boring bivalves and
15 opportunists such as amphipods (Bienhold et al. 2013). At 3-6 months, Xylophaginae begin to
16 serve as ecosystem engineers of wood falls; their boreholes generate various spaces for
17 inhabitation by other species and they offer biomass for predators (Turner 1973, 1977, Schander
18 et al. 2010)(Supplemental Figures). At 6-12 months, the enhanced respiration leads to the
19 development of sulfidic niches attracting animals that rely nutritionally on chemolithoautotrophic
20 bacteria (Bienhold et al. 2013). Successional stage is driven by the rate at which wood-boring
21 bivalves make carbon available for other species and by the total amount of wood available
22 (McClain and Barry 2014). Once the complete wood-fall community assembles, the complete

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1 community includes a variety of epifaunal and infaunal species inhabiting the surface and
2 interior of the wood fall.

3 In November 2006, 32 *Acacia* sp. logs were deployed at 3203 m in the Northeast Pacific Ocean
4 (Station Deadwood: 36.154098° N, 122.40852° W, Fig. S1). Each wood fall was comprised of a
5 single *Acacia* log. These individual wood falls ranged in size from 0.6 to 20.6 kg and correspond
6 to different levels of energy available to the invertebrate communities assembling on wood falls,
7 with approximately half of the woodfalls being <3 kg and half being >3kg to ensure good
8 representation of contrasting energy levels. Each log was sewn into a synthetic fiber mesh bag
9 (5 mm mesh, large mesh size ensured larval settlement was not hindered, Fig. S2&S3). Mesh
10 bags allowed for collection at the end of the experiment of highly degraded wood falls (Voight
11 2007).

12 Wood falls were dispersed over a ~160m² area with ~5 meters between wood falls in 4 rows 10
13 m apart from one another, with each row including wood falls from across the range of available
14 sizes (fFig. S1). The distance between rows reflect the distance needed to allow the remotely
15 operated vehicle (ROV) to operate without disturbing the next row. The distance between wood
16 falls in the row also allowed for quick deployment and retrieval while keeping ROV transit time
17 minimal. The close proximity of the wood falls also ensured regional pools of larvae were
18 similar. Species occurring on the wood falls primarily have larval dispersal phases that allow for
19 colonization. Adults because of either both their size and limited or complete lack of motility
20 complete their lives on individual wood falls. Thus, the distance between individual wood falls
21 here is sufficient to isolate the communities except through larval exchange. As an example, if
22 larger wood falls support higher trophic levels these predators would not able to move to a
23 smaller nearby wood fall and crop prey.

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1 Sixteen *Acacia* logs ranging across available sizes were collected in October 2011 (Set 1, 5
2 years), and the additional 16 *Acacia* logs were collected in October 2013 (Set 2, 7 years; figure
3 S#). Set 2 demonstrates exhibited evidence of increased connectivity between individual wood
4 falls (McClain et al. 2016, Webb et al. 2017) that did not occur in Set 1 (McClain and Barry
5 2014). Thus differences in patterns between Set 1 and 2 likely reflects these differences in
6 connectivity.

Collection and Processing

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

14 All specimens were picked from wood, preserved in either 95% ethanol or formalin. All of the
15 taxa were identified to the species level except *Actinaria* spp. Species names were assigned to
16 taxa when possible. All individuals from each wood fall were counted and assigned to species.

17 For each species, the total wet weight (mg) was taken of all individuals on a wood fall.

18 Individuals were allowed to dry for two minutes on paper towels. Average weight for species on
19 an individual wood fall was taken from the total wet weight for the species divided by the
20 number of individuals per wood fall. For each wood fall, we recorded the initial weight (kg),
21 location, and surface area (m^2). We used initial wood fall weight (kg), a measure of available
22 energy, as our productivity gradient in all analyses.

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1 *Analyses*

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

16 We tested the hypotheses outlined in Figure 1 by modeling each species richness-body size
17 distribution descriptor (mean, standard deviation, kurtosis, number of modes) as a function of
18 \log_{10} -transformed wood fall size. To test for differences between communities collected after 5
19 and 7 years (i.e. between less and more connected communities), Set (two level factor, 1 or 2)
20 was included as a covariate in all models. The four models were thus all linear models of the
21 form *species-body size distribution descriptor* $\sim \log(\text{wood fall weight}) \times \text{Set}$ although we fitted
22 the *number of modes* model as a Poisson GLM as number of modes is a count variable response.
23 To facilitate interpretation of the model results, we removed any non-significant interactions

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1 between $\log(\text{wood fall weight})$ and Set to focus instead on the main effects of each predictor.
2 The slopes of these relationships were then used to assess support for each hypotheses following
3 Figure 1.

4 All data manipulation, summary statistics, analyses and figures were produced using R 3.3.3
5 (2017) and additional packages dplyr (Wickham and Francois 2015), tidyr (Wickham 2015),
6 ggplot2 (Wickham 2009), gridExtra (Auguie 2015), and lme4 (Bates et al. 2015). Data and R-
7 code are available on Dryad at www.datadryad.org/xxx

8 **Results**

9 **Species Richness-Body Size distributions**

10 Across all communities, the distribution of body sizes is unimodal with a modal class centered at
11 $-1.75 \log_{10}$ mass units (Fig 2). Testing specifically how the species richness-body size
12 distribution varied over the energy gradient, there was no interaction between wood-fall size and
13 collection Set in any of the models ($\log_{10}(\text{wood fall size}) \times \text{Set}$ interaction in mean body size
14 model = -0.05 ± 0.214 , $t = 0.25$, $P = 0.808$; in standard deviation of body size model = $0.24 \pm$
15 0.142 , $t = 1.68$, $P = 0.105$; in kurtosis of body size model = -0.07 ± 0.990 , $t = 0.07$, $P = 0.942$; in
16 number of modes model = 0.06 ± 0.259 , $z = 0.234$, $P = 0.815$). Models were therefore refitted
17 as additive models only. There was no significant change in either the mean ($\log_{10}(\text{wood fall}$
18 $\text{size})$ coefficient = 0.09 ± 0.105 , $t = 0.84$, $P = 0.408$, Fig 3A) or the standard deviation
19 ($\log_{10}(\text{wood fall size})$ coefficient = -0.03 ± 0.073 , $t = 0.42$, $P = 0.680$, Fig 3B) of the species-
20 body size distribution with increasing wood fall size. There was a tendency for kurtosis to
21 increase with increasing wood fall size ($\log_{10}(\text{wood fall size})$ coefficient = 0.84 ± 0.482 , $t = 1.74$,
22 $P = 0.092$). Examining both the data (Fig 3C) and model diagnostic plots, two logs (Logs 7 and

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1 23) had very high standardized residuals (>3) in this model. We do not have a clear explanation
2 for this, but excluding these two logs results is sufficient to drive the relationship to significance
3 whilst having minimal effect of the slope estimate ($\log_{10}(\text{wood fall size})$ coefficient = $0.85 \pm$
4 0.267 , $t = 3.16$, $P = 0.0038$, Fig 3C). The number of modes of the species-body size distribution is
5 not related to wood fall size ($\log_{10}(\text{wood fall size})$ coefficient = -0.22 ± 0.299 , $t = 0.75$, $P =$
6 0.455 , Fig 3D). Set did not have a significant effect on any of these relationships (mean: $t = 1.43$,
7 $P = 0.162$; standard deviation: $t = 0.68$, $P = 0.504$; kurtosis: $t = 1.13$, $P = 0.269$; kurtosis
8 excluding logs 7 and 23: $t = 1.66$, $P = 0.109$; number of modes: $z = 0.23$, $P = 0.815$).

9 Size class-richness relationships

10 Relationships between species richness and $\log_{10}(\text{wood fall size})$ are shown for each of the 12
11 size classes present in our dataset in figure 4A. There was never a significant $\log_{10}(\text{wood fall}$
12 $\text{size}) \times \text{Set}$ interaction ($P > 0.25$ for all size classes in which an interaction term could be fitted).
13 Removing the interactions, species richness was higher in Set 2 than in Set 1 for size
14 classes -2.75 (Set 2 v Set 1 contrast = 0.90 ± 0.296 , $t = 3.04$, $P = 0.006$) and -1.25 (Set 2 v Set 1
15 contrast = 1.49 ± 0.525 , $t = 2.83$, $P = 0.010$), and in all other size classes for which a meaningful
16 model could be fitted (i.e., where there was variation in richness between wood falls) the Set 2 v
17 Set 1 contrast was also positive. Slopes of the relationships between species richness and wood
18 fall weight are plotted against size class in figure 4B. The only significant relationship between
19 species richness and $\log_{10}(\text{wood fall size})$ was found in the size class centered on $-1.75 \log_{10}$
20 mass units (0.01 to 0.032g; $\log_{10}(\text{wood fall size})$ coefficient = 1.70 ± 0.753 , $t = 2.26$, $P = 0.031$),
21 the modal size class when all species and wood falls are considered together (Fig 2).

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1 **Discussion**

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

20 The increased packing of species in the modal size class appears appears to be tied to increases
21 in abundance, i.e. size classes with the high abundances possess the most species (Figs. 4&5). At
22 least at local scales, the increases in richness of certain size classes appears to reflect a species-
23 energy mechanism (Wright 1983, Wright et al. 1993, Srivastava and Lawton 1998, Hurlbert

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1 2006, Hurlbert and Jetz 2010) as proposed by Siemann et al. (1996, 1999) in which increases in
2 abundance buffer local populations against local stochastic extinction thereby increasing overall
3 community richness. This match between abundance and species richness among size classes
4 within communities has been found in deep-sea gastropods (McClain 2004, McClain and Nekola
5 2008), terrestrial gastropods (McClain and Nekola 2008), coastal gastropods (Fa and Fa 2002),
6 and grassland insects (Siemann et al. 1996, 1999).

7 These results imply that, as energy to the community increased, this additional energy was either
8 not available to every size class or alternatively a single size class monopolized increases in
9 energy. Because wood-fall community energy usage or availability is not even across size
10 classes, we find an overall breakdown in the energetic-equivalence rule (EER) in this system.
11 Briefly, because the average mass of a species scales similarly with abundance and metabolic
12 rate this suggests that energy use is equivalent across size classes (Damuth 1981, Ernest et al.
13 2003). This pattern is clearly a macroecological phenomenon occurring at broad phylogenetic
14 and spatial scales (Brown 1995). However, EER's support within communities is mixed
15 (Blackburn et al. 1990, Marquet et al. 1990, Blackburn et al. 1993, Blackburn et al. 1994,
16 Blackburn and Lawton 1994, Silva and Downing 1995, Blackburn and Gaston 1996, Russo et al.
17 2003, Ernest 2005).

18 What determines the size class in which abundance, richness, and energy is the highest? One,
19 energy may only be more environmentally available to a specific size class or classes. This is an
20 expansion of the textural discontinuity hypothesis of Holling (1992) with an emphasis on the
21 aspects of resource concentration, availability, and fractality as opposed to habitat complexity
22 (reviewed in Allen *et al.* 2006). Ritchie and Olf (1999) theoretically and mathematically
23 formalized this view that in fractal resources, species perceive the resource at a scale of

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1 resolution which is determined by body size. This generates a prediction of species richness
2 peaking at a size class slightly larger than the intermediate. Evans et al. (2005) propose that as
3 energy increases preferable resources also increase. Joining these hypotheses, a greater diversity
4 of energy/resource types may be available to specific size classes. Second, certain size classes
5 may be more energetically efficient (Sebens 1982, Brown et al. 1993, Rex and Etter 1998, Roy et
6 al. 2000, Sebens 2002, Ernest 2005, reviewed in Allen et al. 2006) allowing more species to
7 coexist in the same size class. Third, certain size classes are able to monopolize greater
8 proportions of total available energy. Monopolization of energy resources by larger size classes
9 is known in marine invertebrates (McClain and Barry 2010).

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

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

19 The extent to which our results are specific to the unique setting of deep-sea, wood-fall
20 communities is hard to gauge. In particular, the dependence of these communities on a single
21 type of resource—wood falls—and the fact that community development is dependent on the
22 ecosystem engineering activity of Xylophaginae bivalves, may mean that the availability of
23 increased energy is less equitably distributed across size classes than in other ecological settings.

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1 However, the existence of positive abundance-richness relationships across a much broader
2 range of size classes than energy-richness relationships (compare Figs. 4A and fig 5A), together
3 with increases in abundance with energy within most size classes (Fig. 5B), suggests that energy
4 is available to organisms outside the modal size class, it is just not translated into increased
5 richness. In addition, the taxonomic and functional diversity of species occurring within the
6 modal size class suggests that the increased energy is not restricted to species with particular
7 traits or occupying a single specialized niche. Finally, any priority effects (Connell 1961) should
8 decrease in significance through time, yet support for increased packing is seen across
9 communities sampled at both time periods (Figs. 3, 4), even though these represent different
10 stages of succession (McClain et al. 2016, Webb et al. 2017). Thus we do not consider there to
11 be strong *a priori* reasons why increased packing should be preferred in these communities over
12 and above the other hypotheses listed in Figure 1.

13 Conclusions

14 Among the experimental wood-fall communities studied here, certain size classes are more
15 speciose, concordant with increases in abundance. Indeed, the relationship between abundance
16 and species richness among sizes classes within a community is strikingly similar to the
17 relationship of abundance and species richness among wood-fall communities, suggesting that
18 the more-individuals hypothesis (or species-energy theory) scales across levels of ecological
19 complexity. As energy to the wood-fall community increased, increases in abundance and
20 species richness occurred. However, these increases in abundance and richness did not occur
21 equitably across size classes. As richness increased in a community with increased energy,
22 species were just packed into the modal size class. The modal size class saw disproportionately
23 stronger increases in both abundance and richness. This suggests that increases in richness

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1 occurring as energy availability increases may be isolated in specific niches, e.g. the body size
2 classes. A clear need exists for further investigation of these patterns in other taxa, communities,
3 and ecosystems, and for identification of the precise mechanisms underlying these phenomena.

4 **Acknowledgements**

5 The crew of the R/V *Western Flyer* and ROV *Doc Ricketts* and *Tiburón* were invaluable for their
6 help in deployment and retrieval. We also thank C. Lovera, K. Buck, P. Whaling, and D. Honig
7 for providing help with processing of the retrieved logs. CRM was supported by the National
8 Evolutionary Synthesis Center (NSF # EF-0905606). This work was also supported by the
9 Monterey Bay Aquarium Research Institute (projects 200002, 900703, 900608) and the David
10 and Lucile Packard Foundation. TJW is a Royal Society Research Fellow. Michelle Gaither-
11 McClain provided editorial assistance and loving patience with the first author.

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7 richness on local and regional scales. Pages 66-74 *Species Diversity in Ecological*
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9 Chicago.
- 10 **Figure 1.** Schematic representation of the consequences of increased environmental energy for
11 species-body size distributions and size class-richness relationships under each of the five
12 hypotheses outlined in the text. Each hypothesis begins with the same species-body size
13 distribution (left-hand histograms), and an increase in energy results in the addition of an
14 identical number of species, but the position of these new species on the body size axis varies
15 according to each hypothesis (right-hand histograms). The effects of adding species according to
16 each hypothesis on the species richness-body size distribution are shown by plotting four
17 descriptors of the distribution (mean, standard deviation, kurtosis, number of modes) as more
18 species are added (i.e. across a gradient of energy; *species-richness body size distribution*
19 *response*, central four columns of scatter plots). Consequences for the size class-richness
20 relationship are shown by plotting the slope of the relationship between species richness and
21 energy separately for each size class (*size class-richness relationship response*, right-hand scatter
22 plots; points are colored according to the size classes represented by bars in the species-body size
23 histograms). Y-axis scales are held constant for each plot within a column to illustrate the

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1 relative magnitude of expected effects. Note that the patterns in H4: Increased modes are
 2 illustrative of one particular way of adding species (first to a large mode, then to a small mode);
 3 patterns in mean, variance, and kurtosis in this hypothesis are expected to be idiosyncratic, the
 4 main diagnostic features of H4 are the increase in number of modes, and peaks in the slope of the
 5 richness ~ energy relationship at smaller- and larger-than-modal size classes.

6

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

10

11 **Figure 3.** **A** The mean, **B** the standard deviation, **C** the kurtosis, and **D** the number of modes of
 12 the species richness-body size distribution over a gradient of energy availability, as quantified by
 13 the size of wood fall. Blue points indicate Set 1 communities, orange points are Set 2
 14 communities, but as slopes never varied between Sets a single relationship across all
 15 communities is illustrated. In **C**, communities identified as outliers (high standardized residual)
 16 are shown as open symbols, and the fitted model excludes these (slope = 0.85 ± 0.267 , $t = 3.16$,
 17 $P = 0.0038$).

18

19 **Figure 4.** **A** Species richness as a function of wood fall size shown separately for each body size
 20 class. Size classes are identified above each plot by their midpoint on a \log_{10} body mass scale.

21 Blue points indicate Set 1 communities, orange points are Set 2 communities, but as slopes never
 22 varied between Sets a single relationship across all communities for each size class is illustrated.

23 **B** The slopes of the relationships illustrated in **A** as a function of body size class. Points are

energy and body size in wood falls

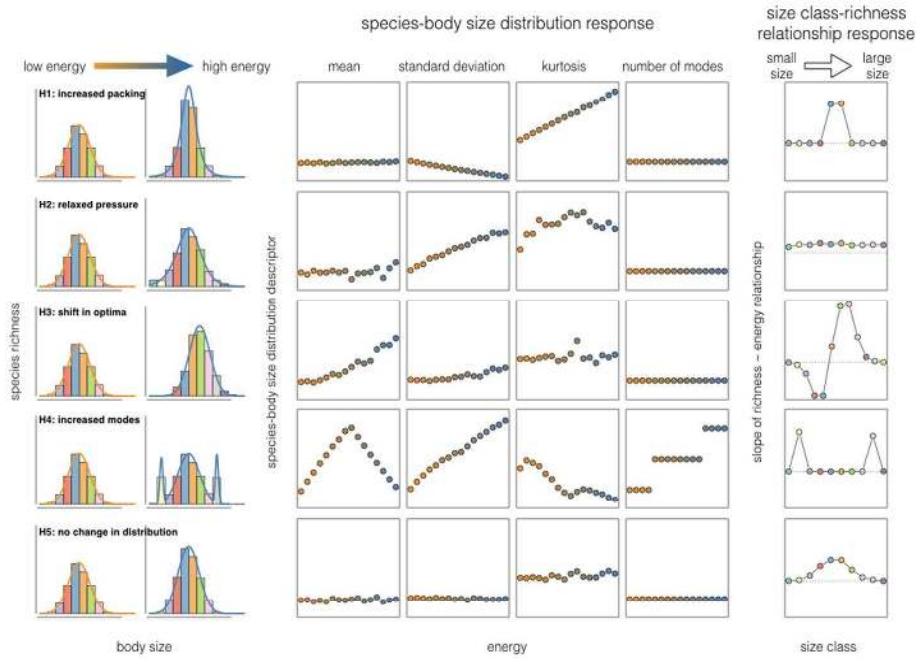
1 scaled to reflect the correlation between richness and wood fall size (larger points = higher
2 absolute values of the correlation coefficient). Filled points represent slopes that differ
3 significantly from 0 ($P < 0.05$).

4

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

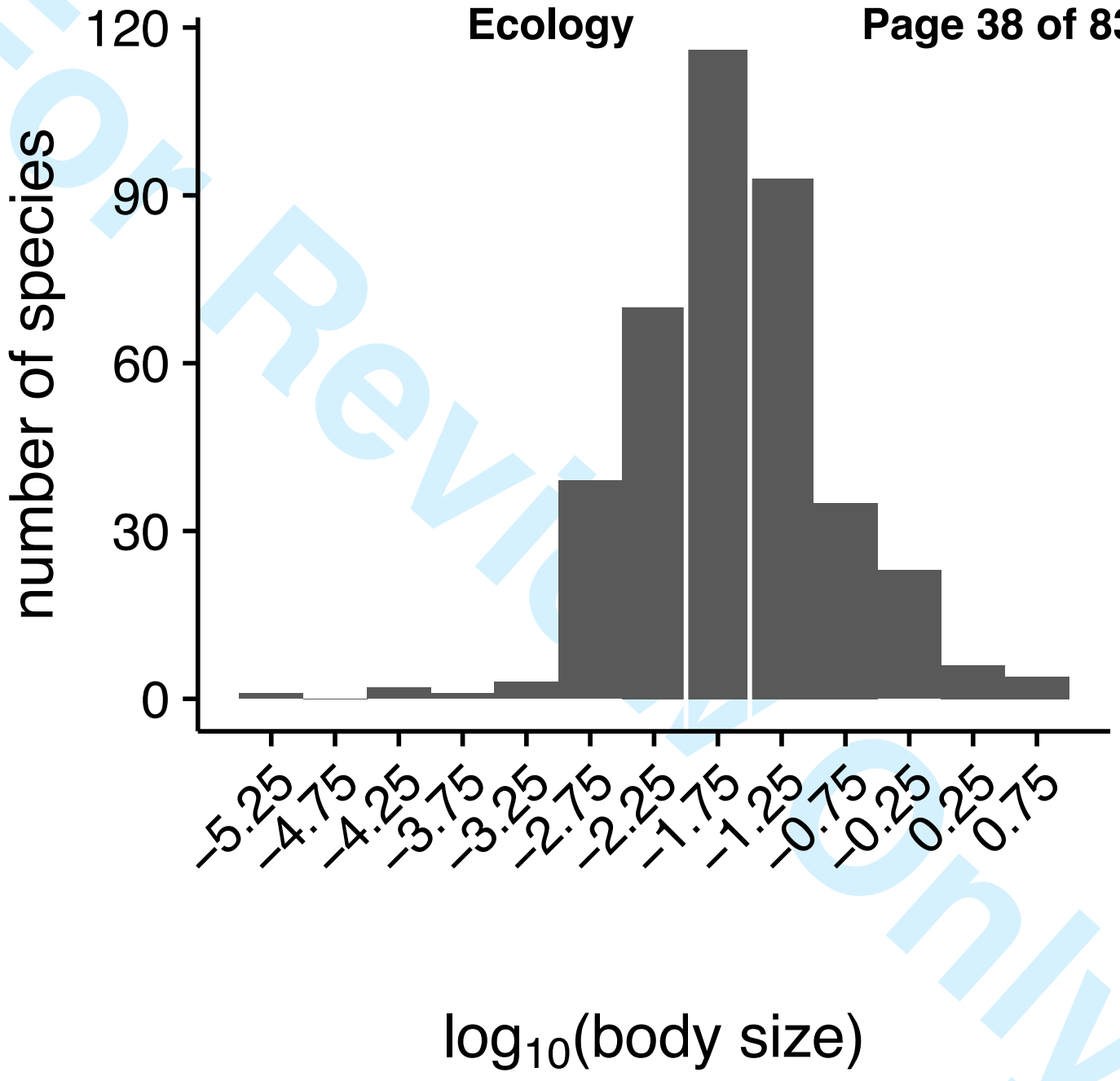
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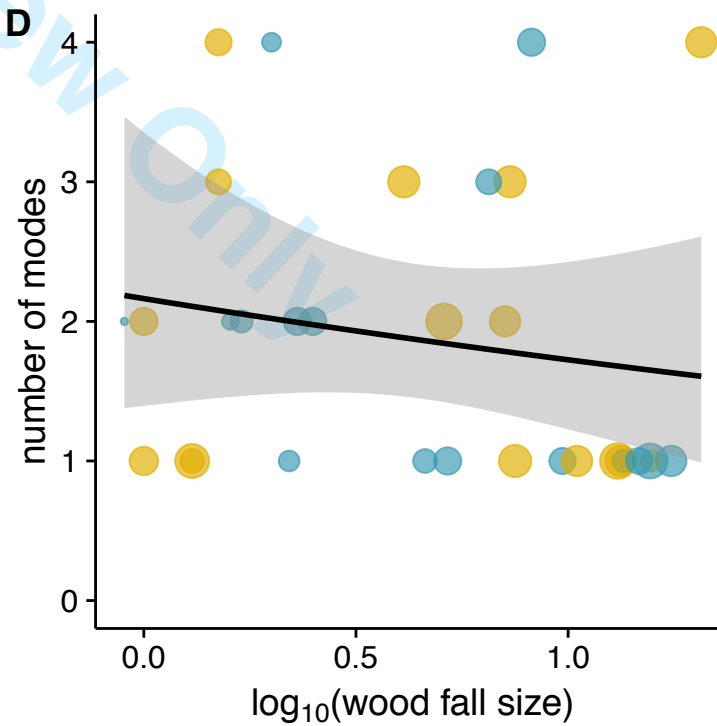
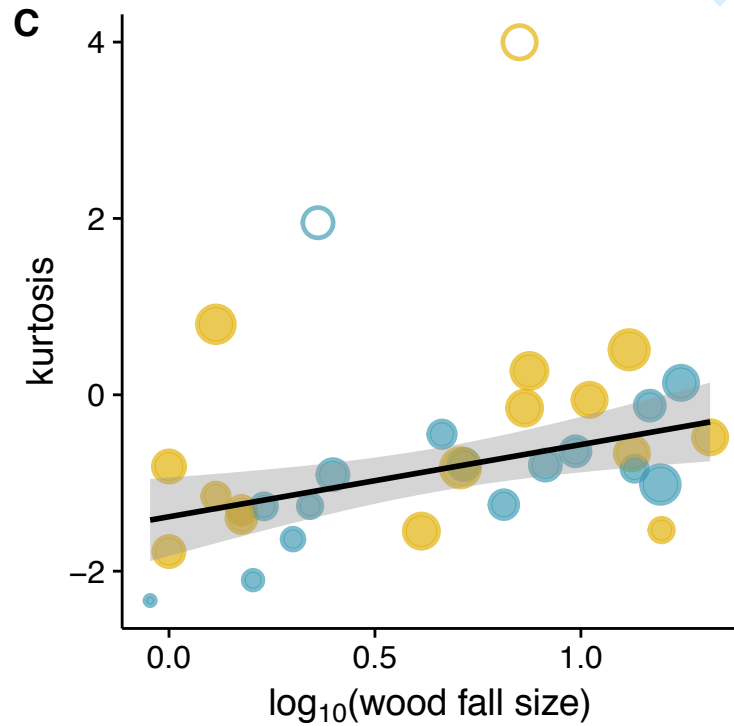
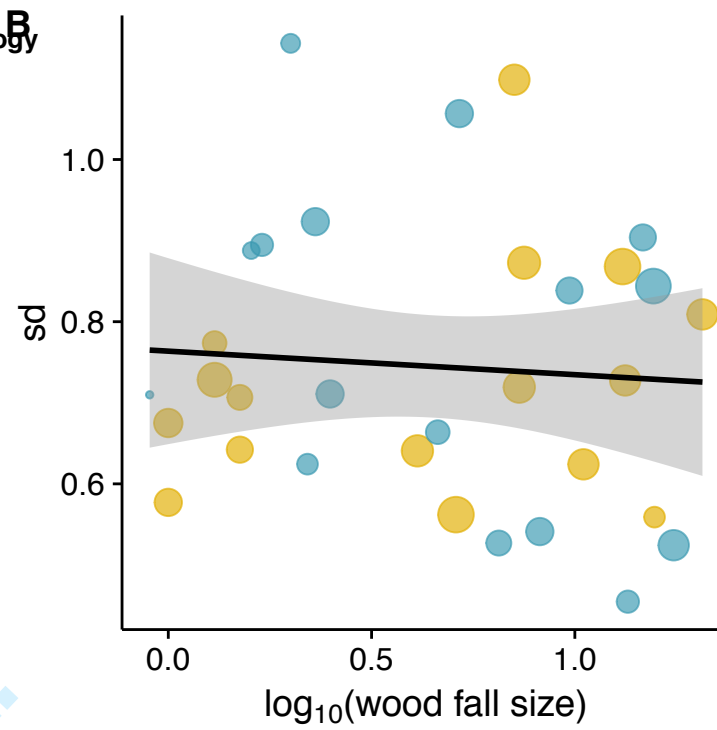
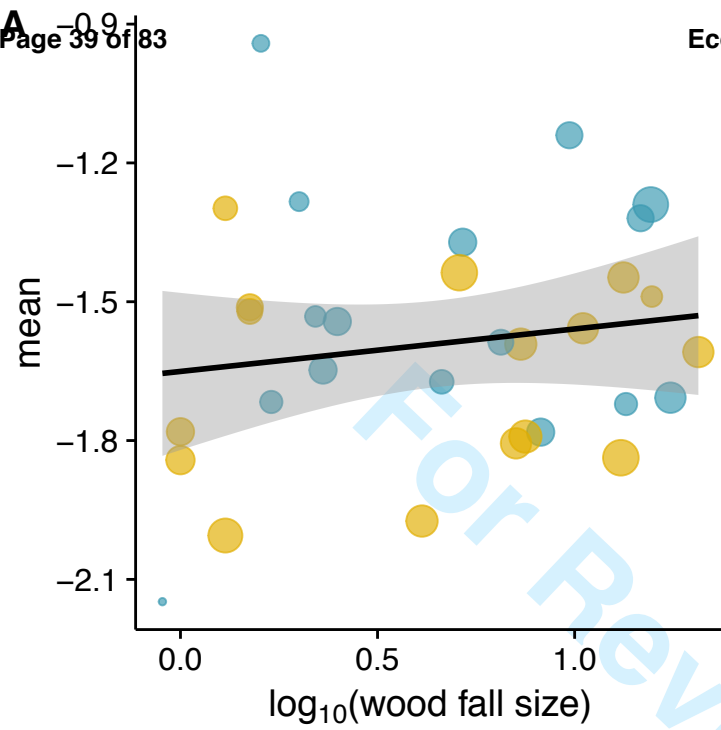
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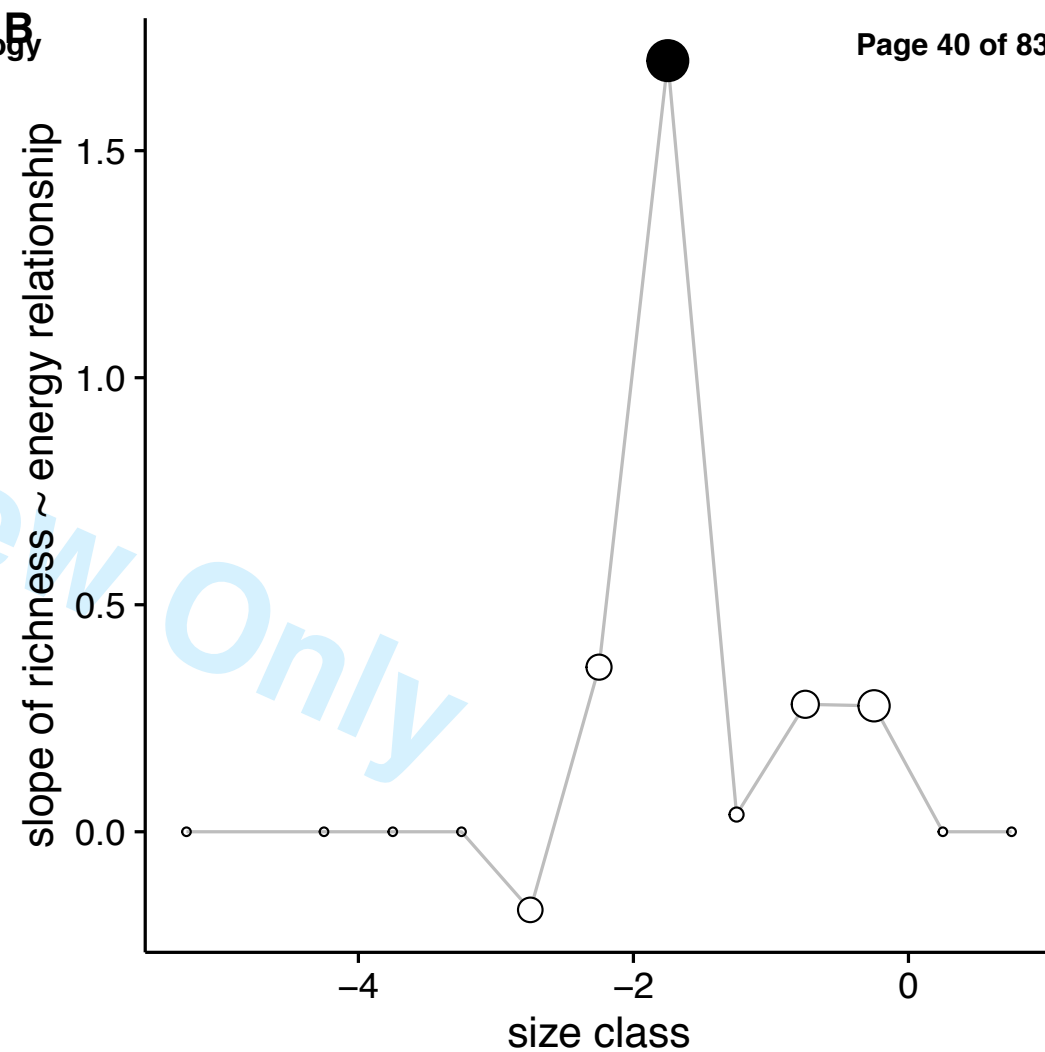
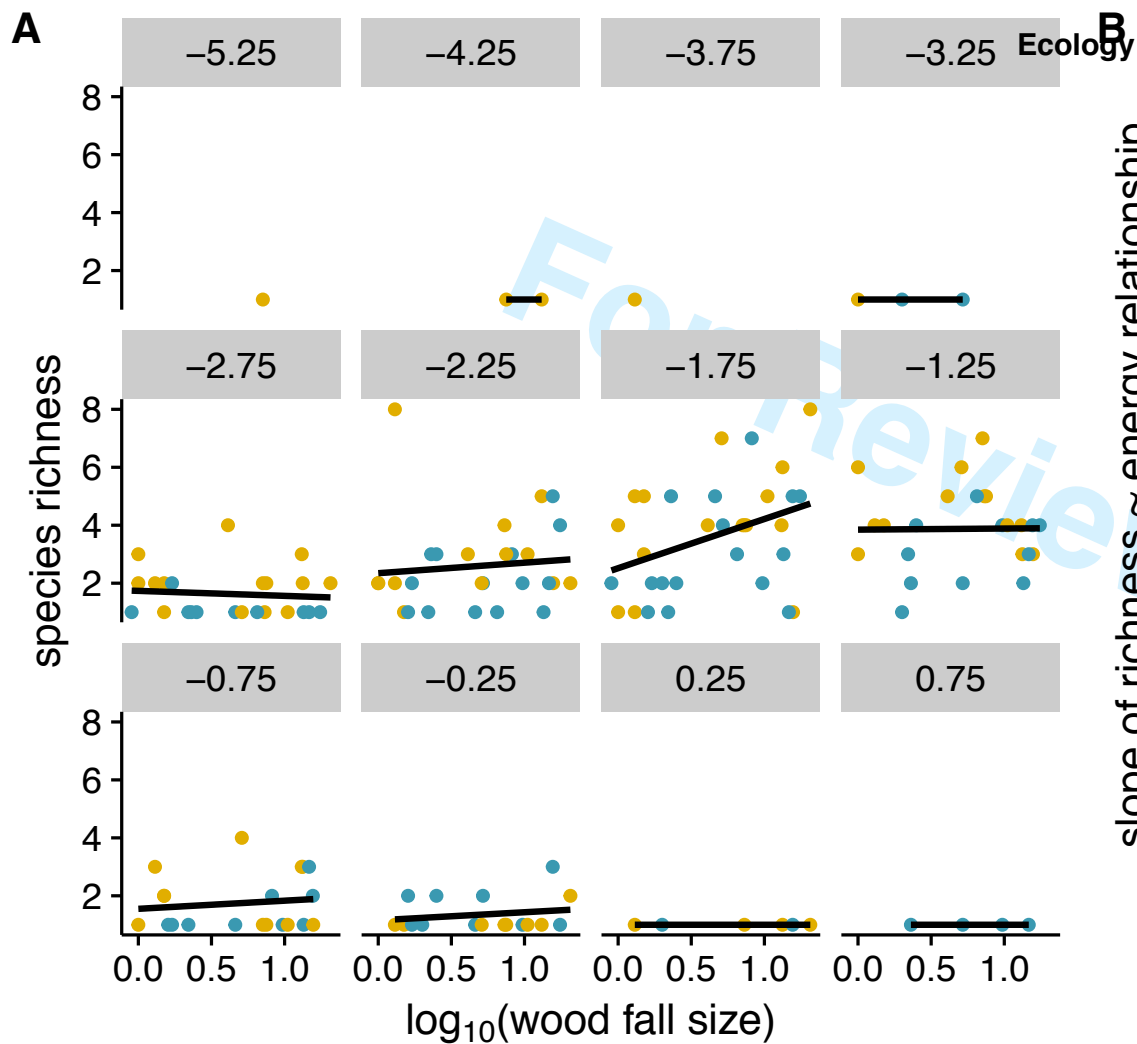


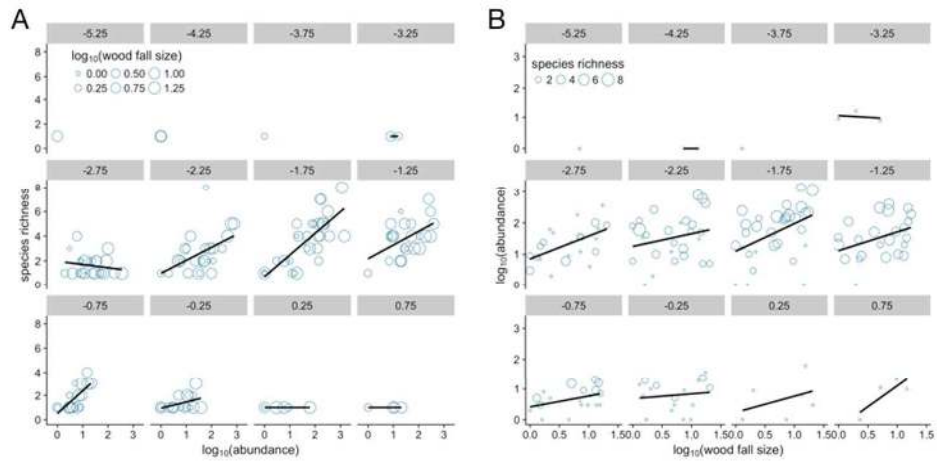
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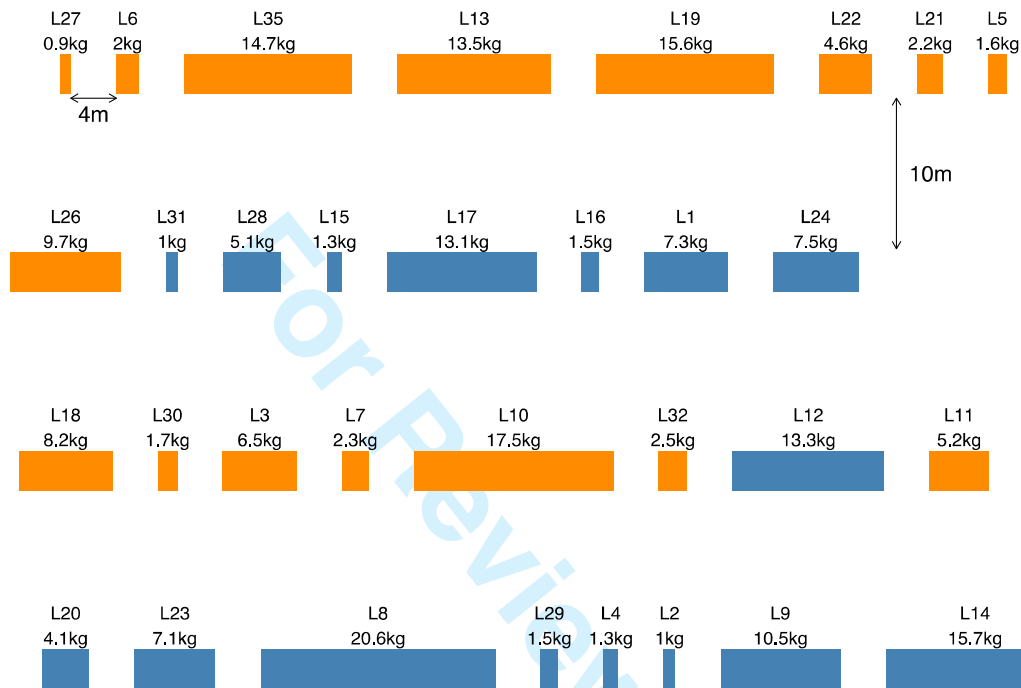




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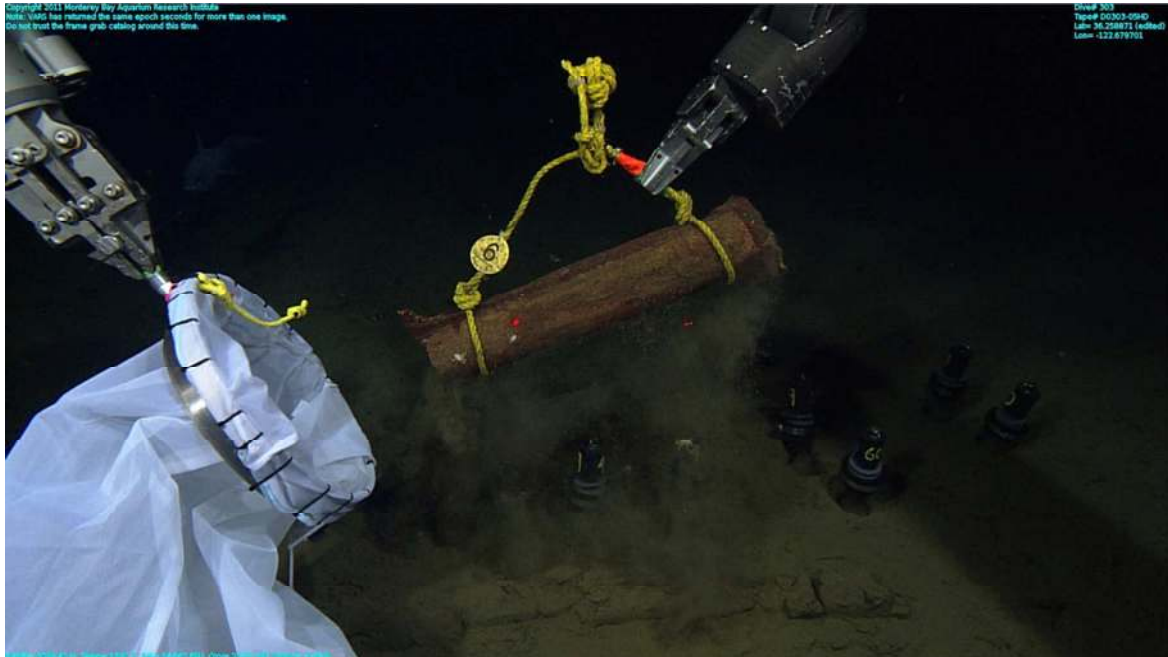
Supplemental for Increased Energy Differentially Increases Richness and Abundance of Optimal Body Sizes in Deep-Sea Wood-Falls



Supplemental Figure 1: Schematic of the deployment of 32 *Acacia* sp. logs at 3203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W) in November 2006. Logs were deployed in 4 rows of 8, each row 10m apart from one another with ~4-5m between individual logs within a row. The total area of deployment was c. 160m². In this schematic, each log is represented by its unique identifying number, followed by its mass in kg (thus L27, 0.9kg indicates log #27, which was 0.9kg). Logs collected after 5y (Set 1) are shown in orange, those collected after 7y (Set 2) are shown in blue.



Supplemental Figure 2: Deployed wood fall at 3203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W). The wood fall is covered with several galatheids, grubs, and scaled predatory polychaetes. A halo of darkened sediment around the wood fall denotes carbon enrichment and bacterial growth. Large mobile holothurans can be also seen surrounding the wood falls. For the study here only species occurring on the wood fall itself are examined and treated as the wood-fall assemblage. Image © 2017 MBARI



Supplemental Figure 3: ROV video frame grab demonstrating collection of individual wood fall at the end of the experiment. Logs were placed into 300 μ m mesh bags with sealable closing lids during ROV retrieval, ensuring no loss of individuals and/or cross contamination among different samples. Material coming off bottom of wood fall is the anoxic and thus azoic sediment from underneath the wood fall. Image © 2017 MBARI



Supplemental Figure 4: Wood fall after retrieval and processing. All organisms have been removed. Exhibited are the wood boring tracks formed by the bivalve species of the subfamily Xylophaginae. Image by Craig McClain

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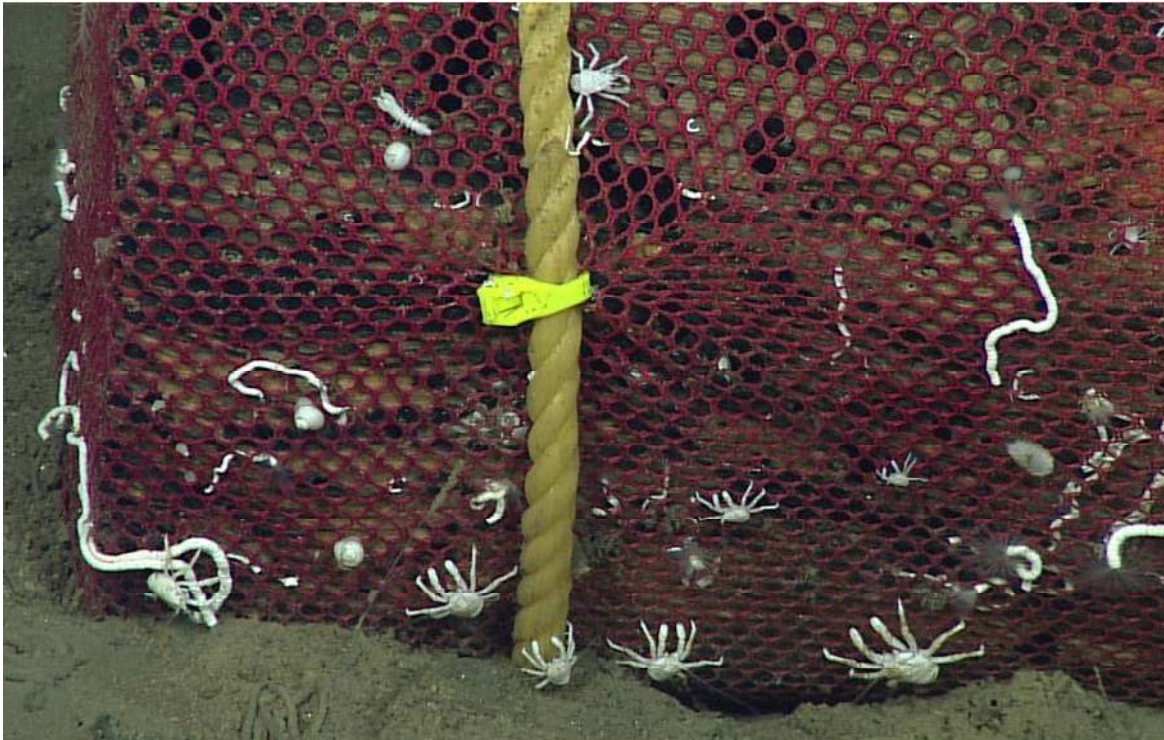


Supplemental Figure 5: Wood fall after retrieval and during processing. Exhibited are the wood boring tracks formed by the bivalve species of the subfamily Xylophaginae. Image by Craig McClain



Supplemental Figure 6: Close up of a wood fall, not from this experiment, showing the settlement and boring of juvenile Xylophaginae. Image by Craig McClain

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Supplemental Figure 7: Close up of a wood fall exhibiting a variety of species including a tanaid, gastropods, galatheid crabs, tube-building polychaetes, and a scaled polychaete. Note individuals of the species also occur within the cavities on the interior of the wood fall and beneath the mesh netting. Image © 2017 MBARI