

1 **Energetic Increases Lead to Niche Packing in Deep-Sea Wood Falls**

2 Craig R. McClain¹, Clifton Nunnally¹, Abbie S. A. Chapman², James P. Barry³,

3 1. *Louisiana Universities Marine Consortium, 8124 Hwy. 56, Chauvin, LA 70344,*

4 cmclain@lumcon.edu

5 2. *Ocean and Earth Science, University of Southampton Waterfront Campus, National*
6 *Oceanography Centre, European Way, Southampton, U.K.*

7 3. *Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd., Moss Landing, CA*
8 *95039*

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10

11 Abstract

12 Mechanisms leading to variation in diversity over energetic gradients continue to challenge
13 ecologists. Changes in diversity may reflect the environmental capacity to support species'
14 coexistence through increased niche packing or niche space expansion. Current ecological
15 theory predicts increases of energy may lead to both scenarios but not their relative strengths.
16 We use experimental deep-sea, wood-fall communities, where energy supply can be controlled,
17 to test for the importance of niche expansion and packing in functional space over an energetic
18 gradient. Invertebrate communities were identified and counted from 16 *Acacia* sp. logs ranging
19 in size from 0.6 to 20.6 kg in mass (corresponding to energy availability) deployed at 3203 m in
20 the Pacific Ocean for 5 years. We use four fundamental energetic species-level functional traits--
21 -food source, trophic category, motility, and tiering--to characterize species niches. Increases in
22 energy on wood falls lead to increases of species richness. This higher species richness
23 resulted from a substantial increase in mean niche overlap, suggesting that increases in energy
24 may afford reduced competition.

25 Introduction

26 Species diversity often increases as more energy becomes available to a community [1-4].
27 Although the form and strength of this relationship vary, this species and energy relationship
28 appears to be pervasive among taxa and systems [1-4]. The processes creating this pattern
29 remain elusive, with numerous hypotheses proposed and supported [1]. Many of these
30 hypotheses share two common mechanisms; positing greater species diversity is afforded with
31 increased energy through either greater niche diversity or greater niche packing [1, 5, 6]. With
32 niche space expansion, increased energy allows for novel, and potentially energetically
33 expensive, traits to persist [7]. Niche packing occurs if increased energy promotes

34 specialization as resources become abundant [6, 8]. Although research into this area has
35 occurred for several decades under labels of ecological/trait/functional diversity and
36 morphological disparity [9-13], the development of new functional diversity metrics has sparked
37 renewed interest [14-16]. Recent studies in diverse systems find that niche space expansion is
38 not as important as niche packing for increases in diversity in general [17, 18] and over
39 energetic gradients [19].

40 Here, we examine the process underlying increases in energy and species richness, by
41 quantifying niche space expansion and packing, in experimental deep-sea, wood-fall
42 communities. On the deep seafloor, sunken wood, i.e. wood falls, develop endemic and diverse
43 communities comprising wood and sulfide obligates, and associated predators [17, 20]. The
44 endemism of wood-fall communities reflects an energetic isolation because of their specific
45 nutritional requirements for wood, produced sulfide and/or methane, or predator specificity for
46 endemic wood-fall species [17, 20]. Deep-sea wood falls provide a unique opportunity to
47 examine community assembly and energetic theory because the amount of energy available to
48 the community can be experimentally controlled (i.e. the size of a single wood fall) [17, 20, 21].
49 Further details on the natural history of wood falls is in the Supplemental Information.

50 Our previous work on wood-falls documented rises in energy and species diversity concordant
51 with increased packing around an optimal body size, implying energy increases are experienced
52 only in this size class [21]. Here, we examine four additional functional traits, reflecting how
53 species contribute to wood-fall functioning and perform themselves, which should track energy
54 availability. Three of these traits are based on previous functional trait metrics [22, 23] and
55 include feeding, motility, and tiering (Supplemental). Feeding type is theoretically and
56 empirically connected to energy availability, including in marine invertebrates using these
57 metrics [24]. Likewise, increases in motility are associated with higher metabolic demand [25].
58 Increases in energy availability may therefore allow for increased motility types, promoting niche

59 space expansion. Additionally, epifaunal species are predicted to have adaptive advantages as
60 they can better compete for available food, suggesting patterns of tiering (e.g., epifaunal versus
61 infaunal) likely exist over energy gradients; e.g. deeper infaunal species are associated with
62 higher energy [26]. We also add energy source, based on published literature for each taxa, as
63 a metric, to capture whether species rely on xylophagous or sulphur pathways within the wood
64 fall (Supplemental). Increased energy is hypothesized to either: i) increase abundance of
65 preferred food resources, leading to specialization and niche packing; or ii) increase novel food
66 items, allowing for niche space expansion.

67 Methods

68 The methods of the wood-fall experiments are described in detail in previous work [17, 20, 21]
69 and Supplemental. Briefly, 32 *Acacia* sp. logs were deployed with a remotely operated vehicle
70 at 3203 m in the Northeast Pacific Ocean. Each wood fall was comprised of a single *Acacia* log,
71 ranging in size from 0.6 to 20.6 kg, corresponding to different levels of energy available to the
72 wood-fall assemblage. Wood falls were dispersed over a ~160m² area with ~5 meters between
73 wood falls in 4 rows 10 m apart, with each row including sizes across the range. For each wood
74 fall, we recorded the initial weight (kg), location, and surface area (m²). We used initial wood fall
75 weight (kg), a measure of available energy, as the energy metric in all analyses.

76 Logs were placed into 300 µm mesh bags, the standard mesh size for deep-sea macrofauna
77 [27], with sealable closing lids during retrieval, ensuring no loss of individuals and/or cross
78 contamination among samples. All individuals occurring on the wood-fall exterior and interior
79 were collected. Species were identified to morphospecies and traits were assigned based on
80 published natural histories for species [28].

81 For each wood fall, we calculated Unique Trait Combinations (UTC), as a metric of niche space
82 expansion, and functional overlap (raw simple, mean, median, max, and min MVO), as a metric

83 of niche packing, using the `multirich` [16] in the R-package (ver. 3.5.0). We also calculated, for
84 each wood fall, functional richness (FRic), functional evenness (FEve), functional divergence
85 (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (Rao's Q) using the FD R-
86 package [14, 15]. An overview, including the strengths and weaknesses of the each of these
87 metrics is provided in the supplemental.

88 A variety of functional diversity metrics were employed to ensure patterns were ecological,
89 rather than a result of metric selection. As opposed to *a priori* selecting metrics and given the
90 ease of which these can be calculated, we instead choose to quantify several metrics examining
91 which quantify unique aspects of functional diversity and implement these in the final analysis.
92 Several of these functional diversity metrics actually demonstrate high correlations
93 (Supplemental). High correlations were found between: Rao's Q and functional dispersion;
94 functional richness and unique trait combinations; and between various metrics of functional
95 overlap (Supplemental Figure 1). Functional evenness and functional divergence poorly
96 correlated with the other metrics. Thus for the analyses, we only report those results of
97 functional dispersion, functional richness, mean functional overlap, functional evenness, and
98 functional divergence as each quantifies a unique attribute of functional diversity.

99 Results

100 With increased wood fall size, only meanMVO, a measure of niche overlap, increased
101 concordantly (Figure 1, Supplemental Table 1, p -value=0.0037). Functional evenness
102 decreased with increasing wood fall size but was not significant (Figure 1, Supplemental Table
103 1, p -value=0.0720). A Shapiro-Wilk Normality Test indicates that all variables were not
104 significantly different from normal distributions (p =0.2436-0.9636). Likewise, a Shapiro-Wilk
105 Normality Test on the residuals from the models were not significantly different from normal
106 distributions (p =0.1634-0.9668).

107 With increased species richness, meanMVO also increased (Figure 1, Supplemental Table 2, p-
108 value=0.0002). Functional richness also increased with increasing species richness but was not
109 significant (Figure 1, Supplemental Table 2, p-value=0.0507). A Shapiro-Wilk Normality Test
110 indicates that all variables were not significantly different from normal distributions ($p=0.4972$ -
111 0.9636). A Shapiro-Wilk Normality Test on the residuals from the models were not significantly
112 different from normal distributions ($p=0.0631$ - 0.9427).

113 A full generalized linear model was constructed with functional dispersion, functional richness,
114 mean functional overlap, functional evenness, and functional divergence, and \log_{10} wood-fall
115 mass to explain species richness. The best-fit model to predict changes in species richness
116 contains mean functional overlap and functional richness only (Full model: AIC= -35.97;
117 Reduced model: AIC= -37.58, Supplemental Table 3). Together mean functional overlap and
118 functional richness predict 81% of the variation in species richness. However, mean functional
119 overlap explains 63.8% of the variation alone. Variance inflation factors were low in both the full
120 (1.25 - 2.60) and reduced models (1.01). A Shapiro-Wilk Normality Test on the residuals from
121 both models were not significantly different from normal distributions ($p= 0.6389$ and 0.8049).

122 Discussion

123 In investigating the relative influences of niche space expansion and niche packing on diversity
124 in experimental deep-sea, wood-fall communities, we find that chemical energy availability is
125 concordant with increases in functional overlap and niche packing. With increased chemical
126 energy available for experimental wood fall-communities, species richness also increases
127 ($\rho=0.75$) [20]. However, when changes in niche packing are accounted for, wood-fall size is
128 no longer a significant predictor of richness (Supplemental Table 3). This pattern corresponds
129 with the observed pattern of increased niche packing of optimal size bins [1] with increasing
130 wood-fall size [17].

131 Only weak evidence of niche space expansion exists. Most functional traits present on large
132 sized wood-falls are also present on smaller wood-falls. This suggests that functional diversity
133 of either the regional pool or the total range ecologies supported at the local wood fall is limited,
134 regardless of total energy availability. Functional richness (Figure 1) appears to reach an
135 asymptote, implying the regional pool contains functionally redundant species. This pattern may
136 be expected in wood-fall ecosystems, as species must be specialized to colonize and persist on
137 these unique habitats. However, the relationship between functional volume space and species
138 richness may be a spurious statistical relationship based on sampling number [29].

139 Current and previous results [17] suggest that energy may not be distributed equitably across
140 traits. Certain traits show increased abundance on larger wood-falls (Figure 2). This could occur
141 because increases in energy allow for greater coexistence of species with certain functional
142 traits [24, 30-32]. For example, increased energy allows for greater dominance of more mobile
143 fauna. Alternatively, species with certain functional traits may have more resource available to
144 them [24]. Here, larger wood-falls allow for increased wood degradation and production of
145 sulfur niches increasing the availability of diverse energy resources (Figure 2). At small-wood
146 fall sizes, these resources may be too rare to support a wealth of species similar, i.e. resource
147 concentration mechanism of [33, 34]. Conversely, species with certain functional traits might be
148 able to monopolize a greater proportion of total available energy. Both certain tiering and
149 feeding traits may provide a greater spatial access to the bacterial mats or wood itself (Figure
150 2). Distinguishing between these, while difficult, provides fertile ground for future investigation.

151

152 **Figure 1:** Metrics of functional diversity with \log_{10} wood-fall mass and species richness.

153 Regression lines are provided for p-values <0.05 (Supplemental Table 1 and Supplemental
154 Table 2).

155 **Figure 2:** Dominance, as determined by abundance, of ecological traits over wood-fall size.

156 Width of grey violin plot reflects numerical dominance of the trait at that wood-fall size.

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239

240 Author Contributions

241 All authors contributed substantially to the design, acquisition, analysis, and interpretation of the
 242 data. All authors contributed to drafting and revising the article and gave final approval of the
 243 version to be published. All authors agree to be accountable for all aspects of the work in

244 ensuring that questions related to the accuracy or integrity of any part of the work are
245 appropriately investigated and resolved.

246 Data Accessibility

247 Data available at <https://doi.org/10.5061/dryad.8q2kg02>

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250 Competing interests

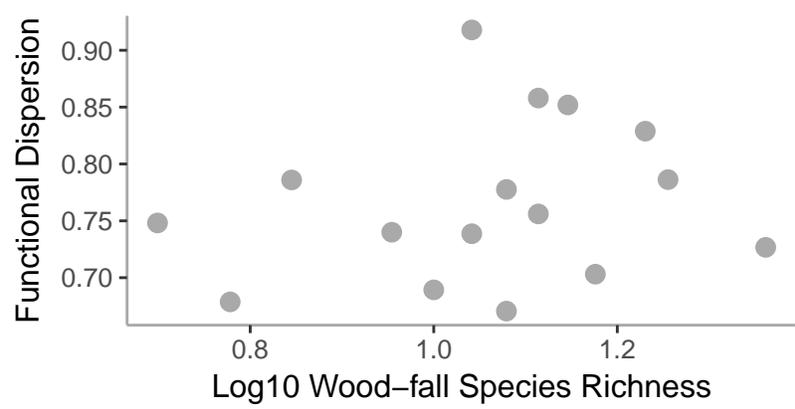
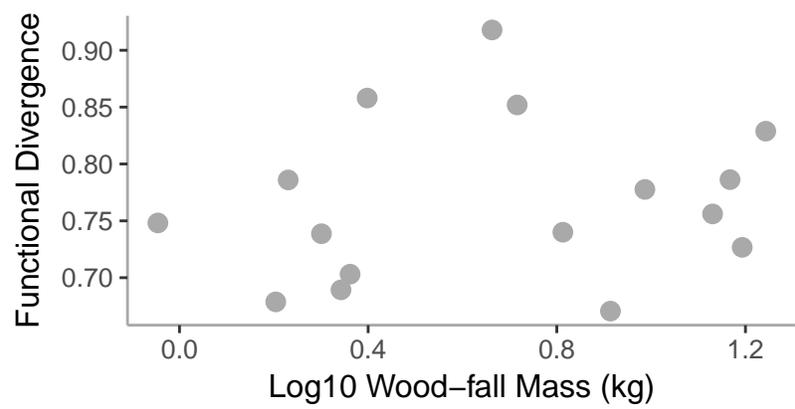
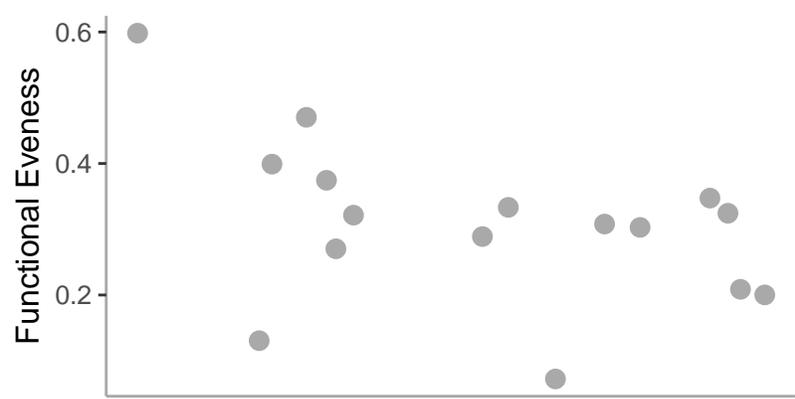
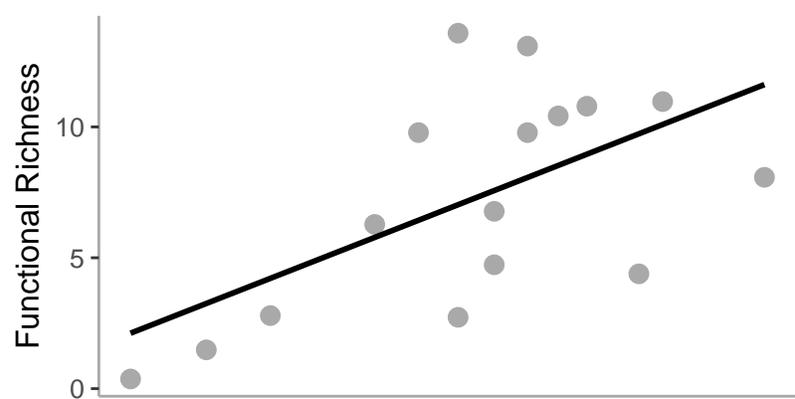
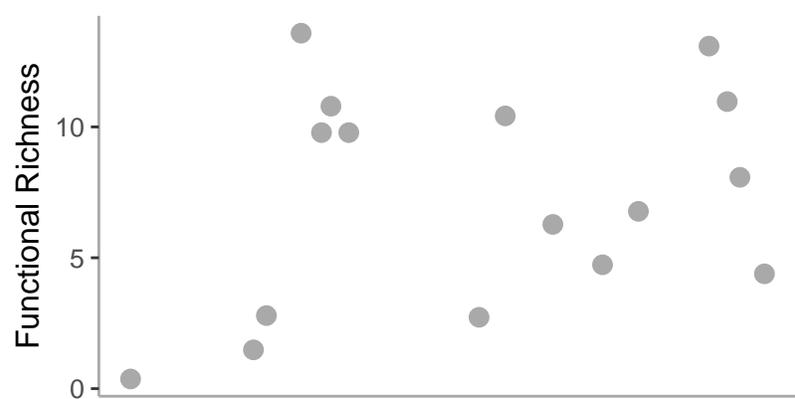
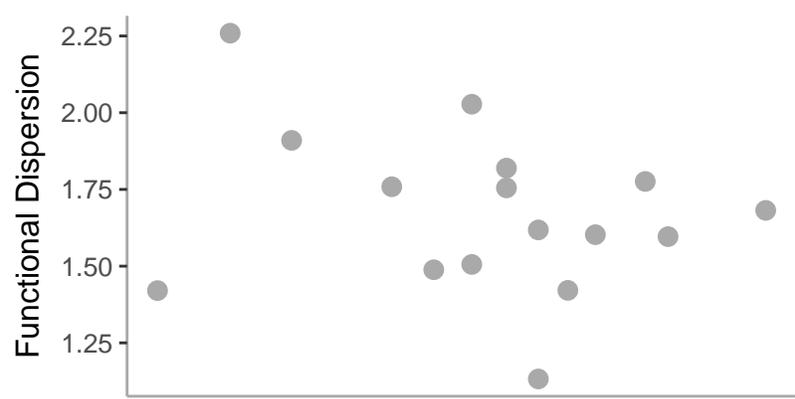
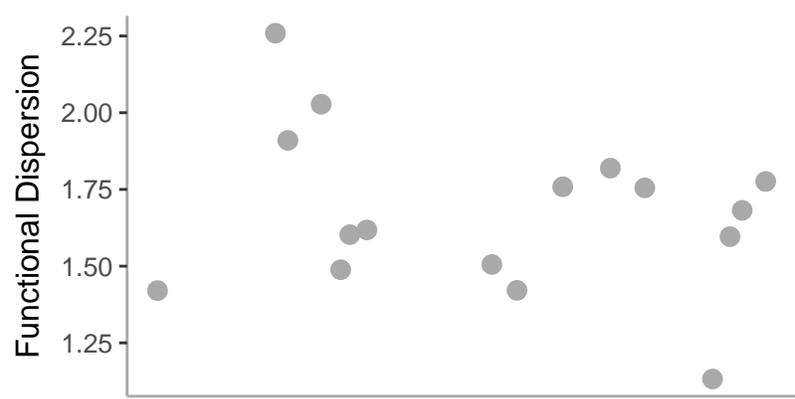
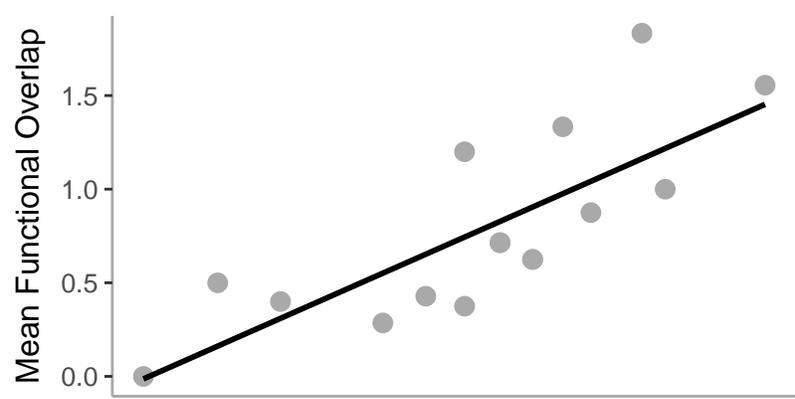
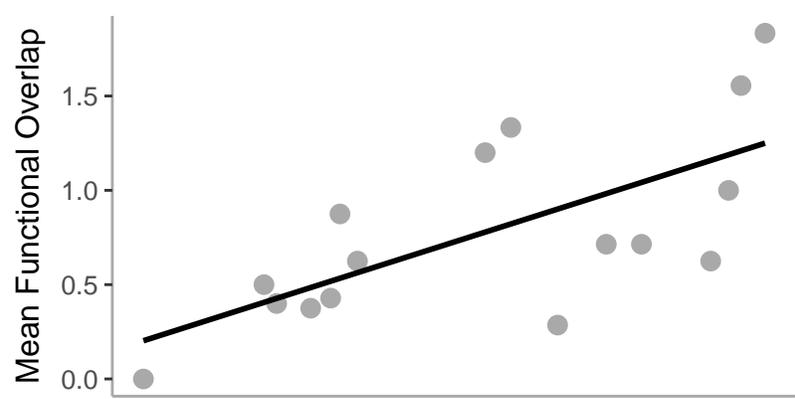
251 We have no competing interests.

252 Ethical statement

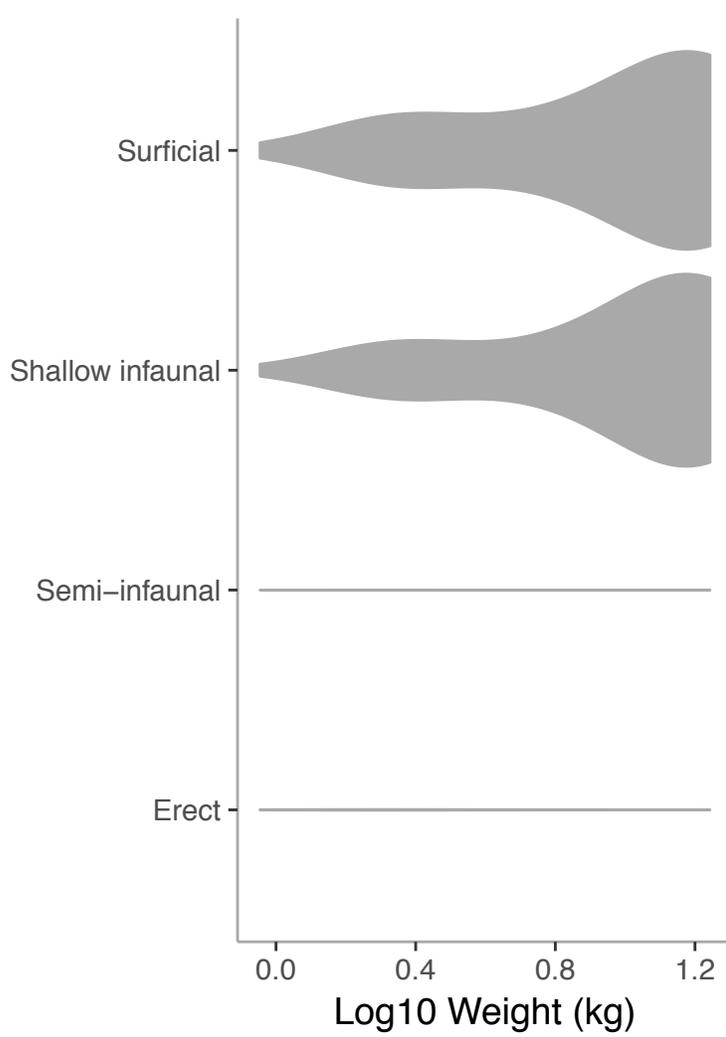
253 No licenses or permits were required for this research.

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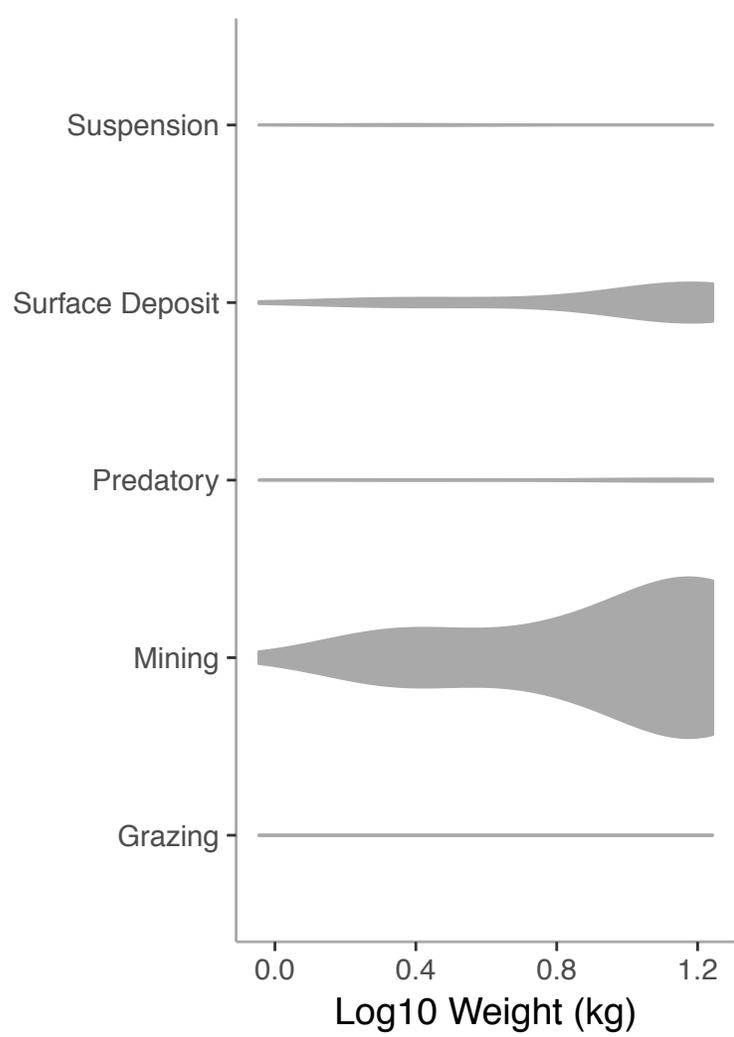
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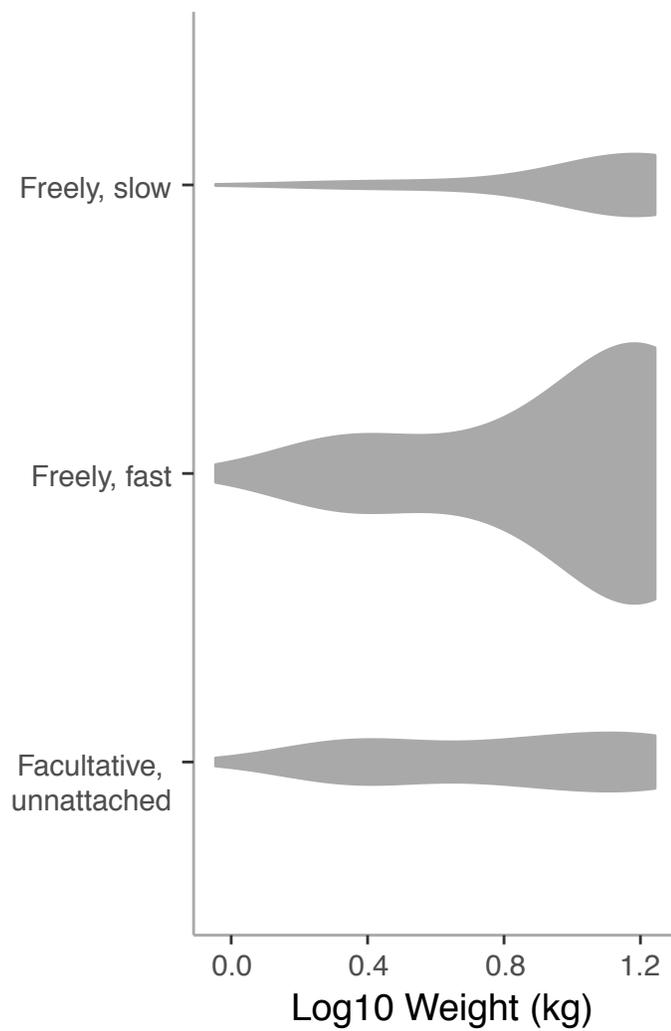
Tiering



Feeding Type



Motility



Food Source

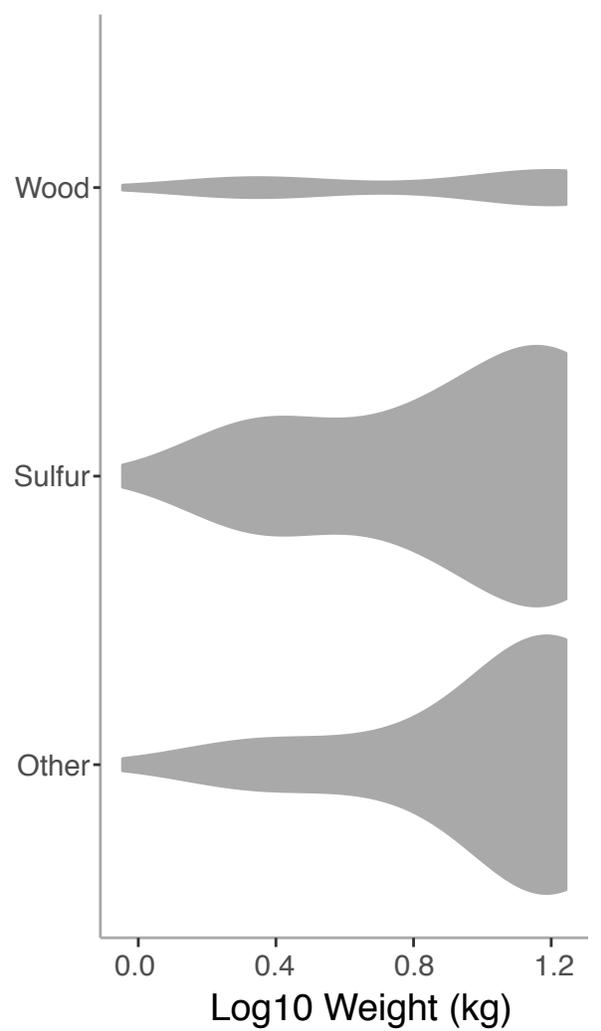


Table 1: Linear fit models between various functional diversity metrics with wood-fall size (log10 mass)

	<i>Dependent variable:</i>				
	meanmvo	FDis	FRic	FEve	FDiv
	(1)	(2)	(3)	(4)	(5)
log10mass	0.813*** (0.233)	-0.151 (0.167)	2.804 (2.582)	-0.140* (0.072)	0.029 (0.045)
Constant	0.240 (0.181)	1.774*** (0.130)	5.393** (2.002)	0.402*** (0.056)	0.747*** (0.035)
Observations	16	16	16	16	16
R ²	0.464	0.055	0.078	0.213	0.029
Adjusted R ²	0.426	-0.012	0.012	0.157	-0.040
Residual Std. Error (df = 14)	0.375	0.268	4.145	0.115	0.072
F Statistic (df = 1; 14)	12.118***	0.819	1.179	3.789*	0.424

Note:

*p<0.1; **p<0.05; ***p<0.01

Table 2: Linear fit models between various functional diversity metrics with wood-fall species richness

	<i>Dependent variable:</i>				
	meanmvo	FDis	FRic	FEve	FDiv
	(1)	(2)	(3)	(4)	(5)
log10(richness)	2.213*** (0.473)	-0.391 (0.395)	14.335** (5.107)	-0.220 (0.183)	0.082 (0.105)
Constant	-1.560*** (0.507)	2.087*** (0.423)	-7.902 (5.468)	0.542** (0.196)	0.679*** (0.113)
Observations	16	16	16	16	16
R ²	0.610	0.066	0.360	0.094	0.042
Adjusted R ²	0.582	-0.001	0.314	0.029	-0.027
Residual Std. Error (df = 14)	0.320	0.267	3.453	0.124	0.071
F Statistic (df = 1; 14)	21.854***	0.982	7.878**	1.448	0.610

Note:

*p<0.1; **p<0.05; ***p<0.01

Table 3: Linear fit models between various functional diversity metrics and log10 wood-fall mass with wood-fall species richness

	<i>Dependent variable:</i>	
	log10(richness)	
	(1)	(2)
meanmvo	0.210*** (0.052)	0.256*** (0.034)
FRic	0.019*** (0.004)	0.022*** (0.004)
FDis	0.008 (0.079)	
FEve	0.040 (0.175)	
FDiv	-0.181 (0.287)	
log10mass	0.112 (0.064)	
Constant	0.791** (0.309)	0.699*** (0.041)
Observations	16	16
R ²	0.920	0.881
Adjusted R ²	0.867	0.863
Residual Std. Error	0.064 (df = 9)	0.065 (df = 13)
F Statistic	17.331*** (df = 6; 9)	48.241*** (df = 2; 13)

Note: *p<0.1; **p<0.05; ***p<0.01

Supplemental Information

Energetic Increases Increase Richness Through Niche Space Packing in Deep-Sea Wood Falls

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Ecological Traits

Table 1. Basic ecological categories for tiering, motility level, and feeding mechanism from [1, 2]. Numbers after include the number of bivalve species in the modern range dataset, modern point dataset, and the number of bivalve genera in the fossil dataset.

Tiering	
1. Pelagic	Living in the water column, free of the bottom
2. Erect	Benthic, extending into the water mass
3. Surficial	Benthic, not extending significantly upwards
4. Semi-infaunal	Partly infaunal, partly exposed to the water column
5. Shallow infaunal	Infaunal, living in the top c. 5 cm of the sediment
6. Deep infaunal	Infaunal, living more than c. 5 cm deep in the sediment

Motility level	
1. Freely, fast	Regularly moving, unencumbered (walking, swimming)
2. Freely, slow	Regularly moving, intimate contact maintained with substrate
3. Facultative, unattached	Moving only when necessary, free-lying
4. Facultative, attached	Moving only when necessary, attached
5. Non-motile, unattached	Not capable of self-propulsion, free-lying
6. Non-motile, attached	Not capable of self-propulsion, attached

Feeding mechanism	
1. Suspension	Capturing food particles from the water
2. Surface deposit	Capturing loose particles from a substrate
3. Mining	Recovering buried food
4. Grazing	Scraping or nibbling food from a substrate
5. Predatory	Capturing prey capable of resistance
6. Other	Varies, includes photo- or chemosymbiosis, parasitism

Natural History Information

Wood falls on the deep-sea floor are unique and diverse communities consisting of xylophages, sulfide obligates, predators of these two groups, and, occasionally, opportunists. Xylophages ingest wood and rely on heterotrophic bacteria to aid digestion and assimilation [3]. Certain species of wood-fall inhabiting echinoids harbor wood-digesting microbiota in their guts

[4]. One species of galatheid crab appears to prefer wood falls and is regularly found with wood-filled guts [5]. Several species of ostracods from the genus *Xylocythere* are also only known to inhabit wood falls [6] and may potentially be wood obligates. The most notable and abundant xylophagous species are members of the bivalve subfamily Xylophaginae [7-9]. Sulfide obligates rely nutritionally on chemoautotrophic bacteria, e.g. bivalves in genus *Idas*, which colonize wood falls and benefit from chemoautotrophic endosymbionts [10, but see 11]. Predators feed on xylophages, sulfide obligates, and opportunists. Certain acotylean polyclad flatworms, for example, likely feed on wood-boring bivalves [9]. Opportunists have less specialized diets but are numerically rare. Only 4 of 39 wood-associated species, in the wood falls here were also found in the background sediment or nearby hard substrates [12-17]. All of these generalist habitat species are rare and represented by 1-4 individuals and as such do not make up a significant component of the wood-fall community. The remaining wood-fall specialists all have abundances that range from ~10-1000 individuals on a single wood fall.

Succession at wood-fall communities begins with bacteria degradation of the wood [18, 19]. Bacterial degradation can generate sulfide within a month and these sulfidic niches attracting animals that rely nutritionally on chemolithoautotrophic bacteria [18, 19]. Additionally, and as early as 3-6 months, Xylophaginae can serve as ecosystem engineers of wood falls; their boreholes generate various spaces for inhabitation by other species and they offer biomass for predators [20-22]. Successional stage may be driven by the rate at which wood-boring bivalves make carbon and space available for other species and by the total amount of wood available [12]. Once the complete wood-fall community assembles, the complete community includes a variety of epifaunal and infaunal species inhabiting the surface and interior of the wood fall.

Functional Diversity Metrics

Table 2. Metrics used to measure functional diversity of wood-fall communities. The calculation of these metrics is described in detail in the references cited in the ‘Reference’ column. Note that this table is split into two, to represent the R packages used to compute these indices (UTC and associated metrics are computed using ‘multirich’, while FRic and other indices are calculated using the ‘FD’ package). We selected metrics from both of these ‘groups’, as all can be computed using categorical traits as well as continuous.

Metric(s)	Details	Strengths	Weaknesses	How weaknesses are addressed in our study	Reference
Unique Trait Combinations (UTC); scaled UTC (sUTC); functional overlap	UTC represent the functional richness of a community in multivariate trait space, by looking at the trait combination of each species in a community and establishing whether it is unique, relative to all other species the species is found with in a community. UTC is the total number of unique trait combinations in a community, whilst sUTC is this number, divided by the maximum number of combinations that could have been possible, given the number of species and traits. Functional overlap (shown as mean-, max-, c-, and med- mvo in Figure 1) represents the number of species that overlap in trait space by identifying duplicate trait combinations.	<ul style="list-style-type: none"> - Easy to calculate and interpret, without need for further multivariate analyses. - Identifies the amount of filled and unfilled trait space (the hypervolume containing all possible trait combinations), which can be interpreted as the amounts of niche space filled and unfulfilled. 	<ul style="list-style-type: none"> - Sensitive to trait selection (e.g., level of binning, or number of trait categories). For example, if many traits were used to calculate this metric, the potential number of UTC would be larger. - Sensitive to missing values. - Trait space can be increased by ecologically-impossible trait combinations. 	<ul style="list-style-type: none"> - Only include relevant traits and the minimal number of traits that could capture important ecological processes. - Do not have missing values in our study. - Do not have ecologically impossible trait combinations in our trait matrix. 	[23]
Functional richness (FRic)	Functional richness is the amount of functional trait space (calculated as the minimum convex hull volume) that a community fills. FRic tends to increase with the number of species in a community (species richness), unless there is functional redundancy	<ul style="list-style-type: none"> - Higher values equate to higher values of this component of functional diversity (easy to interpret). - Can be combined with species richness 	<ul style="list-style-type: none"> - Cannot incorporate information on the relative abundances of species and is therefore sensitive to species with extreme trait values (e.g., rare, 	<ul style="list-style-type: none"> - Used a variety of functional diversity metrics to capture different components of diversity. - Only include relevant traits and the minimal 	[24-26]

	(i.e. a species in the community shares the same traits, and the same trait space, as another species).	information to assess functional redundancy.	specialist species). - Often correlated with species richness. - Sensitive to trait selection (and scores).	number of traits that could capture important ecological processes.	
Functional evenness (FEve)	Functional evenness captures how the abundances of species are spread in the convex hull they occupy (e.g., where dominant and rare species are found, based on their relative abundances). FEve is 1 when species are equally distributed in the convex hull, based on their traits and abundances; it is 0 when species are clustered in a particular area of the convex hull, given their traits and abundances.	- Higher values equate to higher values of this component of functional diversity (easy to interpret). - Independent of species richness and functional richness.	- Does not look at the distribution in the convex hull with respect to its volume. - Sensitive to trait selection (and scores).	- Also calculated FDis, which can account for the convex hull volume. - Only include relevant traits and the minimal number of traits that could capture important ecological processes.	[24, 25]
Functional divergence (FDiv)	Functional divergence is similar to functional evenness, but accounts for dissimilarities in abundance distributions within the convex hull volume. It is calculate relative to the centre of trait space.	- Higher values equate to higher values of this component of functional diversity (easy to interpret). - Independent of species richness and functional richness.	- Does not look at the distribution in the convex hull with respect to its volume. - Sensitive to trait selection (and scores).	- Also calculated FDis, which can account for the convex hull volume. - Only include relevant traits and the minimal number of traits that could capture important ecological processes.	[24, 25]
Functional dispersion (FDis)	This metric measures the mean distance of a species to the centroid of trait space. The centroid is calculated using all species in the community. FDis captures the dispersion of species within available trait space. The centroid and the mean distance are both weighted using species relative abundances.	- Independent of species richness. - Can have more traits than species. - Can incorporate abundance information. - Not strongly	- Not constrained between 0 and 1. - Sensitive to trait selection (and scores).	- Kept this feature of this metric (unconstrained values) in mind during interpretation. - Only include relevant traits and the minimal number of traits that could capture important ecological	[24]

influenced by outliers.

processes.

Rao's quadratic entropy (Rao's Q)

Rao's Q is another measure of functional divergence. It incorporates information on the pairwise differences between species in terms of their traits and relative abundances.

- Independent of species richness.
- Captures dissimilarity among species given abundance and/or traits.

- Sensitive to trait selection (and scores) through covariance.

- Only include relevant traits and the minimal number of traits that could capture important ecological processes.

[24, 27, 28]

Supplemental Methods

In November 2006, 32 *Acacia* sp. logs were deployed at 3203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W, Fig. S1). Each wood fall was comprised of a single *Acacia* log. These individual wood falls ranged in size from 0.6 to 20.6 kg and correspond to different levels of energy available to the invertebrate communities assembling on wood falls, with approximately half of the wood falls being <3 kg and half being >3kg to ensure good representation of contrasting energy levels. Each log was sewn into a synthetic fiber mesh bag (5 mm mesh, large mesh size ensured larval settlement was not hindered. Mesh bags allowed for collection at the end of the experiment of highly degraded wood falls [9]. Sixteen *Acacia* logs ranging across available sizes were collected in October 2011 (Set 1, 5 years), and the additional 16 *Acacia* logs were collected in October 2013 (Set 2, 7 years; figure S1). Set 2 demonstrates exhibited evidence of increased connectivity between individual wood falls [13, 29] that did not occur in Set 1 [12]. This increased connectivity between wood falls removed the relationship between wood-fall diversity and wood-fall size. For the study here we only analyze Set 1 where the productivity gradient occurs.

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

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

Correlations of Functional Metrics

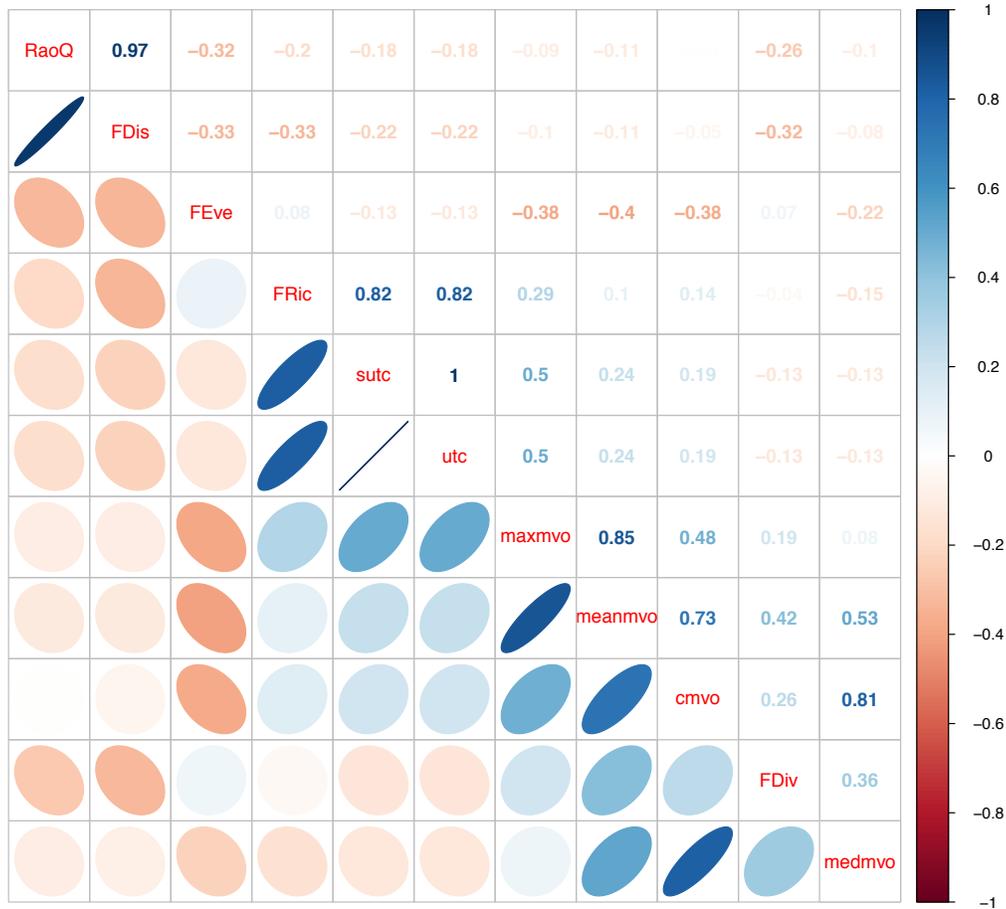


Figure 1: Upper diagonal reports correlations between functional metrics used in this study.

The lower diagonal displays those correlations as clouds of the data. Metrics include Unique Trait Combinations (UTC and Standardized UTC), as a metric of niche space expansion, and functional overlap (MVO including maximum, mean, median, and raw (c) MVO). We also calculated, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDIs), and Rao's quadratic entropy (Rao's Q). Colors correspond to the strength and sign of the correlation with red be negative and blue being positive.

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Table 3: Linear fit models between various functional diversity metrics with wood-fall size (log10 mass)

	<i>Dependent variable:</i>				
	meanmvo	FDis	FRic	FEve	FDiv
	(1)	(2)	(3)	(4)	(5)
log10mass	0.813*** (0.233)	-0.151 (0.167)	2.804 (2.582)	-0.140* (0.072)	0.029 (0.045)
Constant	0.240 (0.181)	1.774*** (0.130)	5.393** (2.002)	0.402*** (0.056)	0.747*** (0.035)
Observations	16	16	16	16	16
R ²	0.464	0.055	0.078	0.213	0.029
Adjusted R ²	0.426	-0.012	0.012	0.157	-0.040
Residual Std. Error (df = 14)	0.375	0.268	4.145	0.115	0.072
F Statistic (df = 1; 14)	12.118***	0.819	1.179	3.789*	0.424

Note:

*p<0.1; **p<0.05; ***p<0.01

Table 4: Linear fit models between various functional diversity metrics with wood-fall species richness

	<i>Dependent variable:</i>				
	meanmvo	FDis	FRic	FEve	FDiv
	(1)	(2)	(3)	(4)	(5)
log10(richness)	2.213*** (0.473)	-0.391 (0.395)	14.335** (5.107)	-0.220 (0.183)	0.082 (0.105)
Constant	-1.560*** (0.507)	2.087*** (0.423)	-7.902 (5.468)	0.542** (0.196)	0.679*** (0.113)
Observations	16	16	16	16	16
R ²	0.610	0.066	0.360	0.094	0.042
Adjusted R ²	0.582	-0.001	0.314	0.029	-0.027
Residual Std. Error (df = 14)	0.320	0.267	3.453	0.124	0.071
F Statistic (df = 1; 14)	21.854***	0.982	7.878**	1.448	0.610

Note:

*p<0.1; **p<0.05; ***p<0.01

Table 5: Linear fit models between various functional diversity metrics and log10 wood-fall mass with wood-fall species richness

	<i>Dependent variable:</i>	
	log10(richness)	
	(1)	(2)
meanmvo	0.210*** (0.052)	0.256*** (0.034)
FRic	0.019*** (0.004)	0.022*** (0.004)
FDis	0.008 (0.079)	
FEve	0.040 (0.175)	
FDiv	-0.181 (0.287)	
log10mass	0.112 (0.064)	
Constant	0.791** (0.309)	0.699*** (0.041)
Observations	16	16
R ²	0.920	0.881
Adjusted R ²	0.867	0.863
Residual Std. Error	0.064 (df = 9)	0.065 (df = 13)
F Statistic	17.331*** (df = 6; 9)	48.241*** (df = 2; 13)

Note:

*p<0.1; **p<0.05; ***p<0.01