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

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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 resulted from a substantial increase in mean niche overlap, suggesting that increases in energy 23 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

specialization as resources become abundant [6, 8]. Although research into this area has
occurred for several decades under labels of ecological/trait/functional diversity and
morphological disparity [9-13], the development of new functional diversity metrics has sparked
renewed interest [14-16]. Recent studies in diverse systems find that niche space expansion is
not as important as niche packing for increases in diversity in general [17, 18] and over
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 endemicity of wood-fall communities reflects an energetic isolation because of their specific nutritional requirements for wood, produced sulfide and/or methane, or predator specificity for 45 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 items, allowing for niche space expansion. 66

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 wood-fall assemblage. Wood falls were dispersed over a $\sim 160 \text{m}^2$ area with ~ 5 meters between 72 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.

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

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

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

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

With increased species richness, meanMVO also increased (Figure 1, Supplemental Table 2, pvalue=0.0002). Functional richness also increased with increasing species richness but was not
significant (Figure 1, Supplemental Table 2, p-value=0.0507). A Shapiro-Wilk Normality Test
indicates that all variables were not significantly different from normal distributions (p=0.49720.9636). A Shapiro-Wilk Normality Test on the residuals from the models were not significantly
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 log₁₀ 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 concertation 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.

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Figure 1: Metrics of functional diversity with log₁₀ wood-fall mass and species richness.
Regression lines are provided for p-values <0.05 (Supplemental Table 1 and Supplemental 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.

157

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240 Author Contributions

- 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
- appropriately investigated and resolved.

246 Data Accessibility

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

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- 251 We have no competing interests.
- 252 Ethical statement
- 253 No licenses or permits were required for this research.
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		Dependent variable:							
	meanmvo	FDis	FRic	FEve	FDiv				
	(1)	(2)	(3)	(4)	(5)				
log10mass	$\begin{array}{c} 0.813^{***} \\ (0.233) \end{array}$	-0.151 (0.167)	2.804 (2.582)	-0.140^{*} (0.072)	$0.029 \\ (0.045)$				
Constant	$0.240 \\ (0.181)$	$\begin{array}{c} 1.774^{***} \\ (0.130) \end{array}$	5.393^{**} (2.002)	$\begin{array}{c} 0.402^{***} \\ (0.056) \end{array}$	$\begin{array}{c} 0.747^{***} \\ (0.035) \end{array}$				
Observations	16	16	16	16	16				
\mathbb{R}^2	0.464	0.055	0.078	0.213	0.029				
Adjusted \mathbb{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				

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

Note:

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

		Depe	endent varial	ole:				
	meanmvo	FDis	FRic	FEve	FDiv			
	(1)	(2)	(3)	(4)	(5)			
log10(richness)	2.213***	-0.391	14.335^{**}	-0.220	0.082			
	(0.473)	(0.395)	(5.107)	(0.183)	(0.105)			
Constant	-1.560***	2.087***	-7.902	0.542^{**}	0.679***			
	(0.507)	(0.423)	(5.468)	(0.196)	(0.113)			
Observations	16	16	16	16	16			
\mathbb{R}^2	0.610	0.066	0.360	0.094	0.042			
Adjusted \mathbb{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 2: Linear fit models between various functional diversity metrics with wood-fall species richness

	Dependent variable:					
	log10(1	richness)				
	(1)	(2)				
meanmvo	0.210***	0.256***				
	(0.052)	(0.034)				
FRic	0.019***	0.022***				
	(0.004)	(0.004)				
FDis	0.008					
	(0.079)					
FEve	0.040					
	(0.175)					
FDiv	-0.181					
	(0.287)					
log10mass	0.112					
Ű	(0.064)					
Constant	0.791^{**}	0.699***				
	(0.309)	(0.041)				
Observations	16	16				
\mathbb{R}^2	0.920	0.881				
Adjusted \mathbb{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<().1; **p<0.05; ***p<0.01				

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

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, modernpoint dataset, and the number of bivalve genera in the fossil dataset.

Tiering						
	the interview of the second second second second second					
	Living in the water column, free of the bottom					
2. Erect	Benthic, extending into the water mass					
3. Surficial	Benthic, not extending significantly upwards					
 Semi-infaunal 	Partly infaunal, partly exposed to the water column					
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.	Moving only when necessary, free-lying					
unattached	, , , , , , , , , , , , , , , , , , ,					
4. Facultative, attached	Moving only when necessary, attached					
5. Non-motile,	Not capable of self-propulsion, free-lying					
unattached						
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 prev 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 Xylophagainae [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]. Additionlaly, and as early as 3-6 months, Xylophagainae 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 Combinatio ns (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.	 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. 	 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. 	 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	 Higher values equate to higher values of this component of functional diversity (easy to interpret). Can be combined with species richness 	- Cannot incorporate information on the relative abundances of species and is therefore sensitive to species with extreme trait values (e.g., rare,	 Used a variety of functional diversity metrics to capture different components of diversity. Only include relevant traits and the minimal 	[24-26]		

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

	influenced by outliers.		processes.				
Rao'sRao's Q is another measure of functional divergence. It incorporates information on the pairwise (Rao's Q)(Rao's Q)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 individual 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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		Dependent variable:							
	meanmvo	FDis	FRic	FEve	FDiv				
	(1)	(2)	(3)	(4)	(5)				
log10mass	0.813***	-0.151	2.804	-0.140^{*}	0.029				
	(0.233)	(0.167)	(2.582)	(0.072)	(0.045)				
Constant	0.240	1.774^{***}	5.393**	0.402***	0.747***				
	(0.181)	(0.130)	(2.002)	(0.056)	(0.035)				
Observations	16	16	16	16	16				
\mathbb{R}^2	0.464	0.055	0.078	0.213	0.029				
Adjusted \mathbb{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				

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

Note:

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

		Dependent variable:							
	meanmvo	FDis	FRic	FEve	FDiv				
	(1)	(2)	(3)	(4)	(5)				
$\log 10(\text{richness})$	2.213***	-0.391	14.335**	-0.220	0.082				
	(0.473)	(0.395)	(5.107)	(0.183)	(0.105)				
Constant	-1.560^{***}	2.087***	-7.902	0.542^{**}	0.679***				
	(0.507)	(0.423)	(5.468)	(0.196)	(0.113)				
Observations	16	16	16	16	16				
\mathbb{R}^2	0.610	0.066	0.360	0.094	0.042				
Adjusted \mathbb{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 4: Linear fit models between various functional diversity metrics with wood-fall species richness

	Dependent variable:						
	log10(1	richness)					
neanmvo FRic FDis FEve FDiv og10mass	(1)	(2)					
meanmvo	0.210***	0.256^{***}					
	(0.052)	(0.034)					
FRic	0.019***	0.022***					
	(0.004)	(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^{**}	0.699***					
	(0.309)	(0.041)					
Observations	16	16					
\mathbb{R}^2	0.920	0.881					
Adjusted \mathbb{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					

Table 5	Linear f	fit models	hetween	various	functional	diversity	metrics and	log 10	wood-f	² a11	mass wit	h woo	d_fa	ll sne	ries	rich	ness
rable 0.	Lincari	in mouchs	DCUWCCII	various	runceionai	urverbruy	mounds and	10510	woou-i	an	mass wro	II WOU	nu nu	n spc	CICB	110IL	noop