

Research



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Community ecology

Energetic increases lead to niche packing in deep-sea wood falls

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

1. Introduction

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

Here, we examine the process underlying increases in energy and species richness, by quantifying niche space expansion and packing, in experimental deep-sea, wood-fall communities. On the deep seafloor, sunken wood, i.e. wood falls, develop endemic and diverse communities comprising wood and sulfide obligates, and associated predators [17,20]. The endemism 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 endemic wood-fall species [17,20]. Deep-sea wood falls provide a unique opportunity to examine community assembly and energetic theory because the amount of energy available to the community can be experimentally controlled (i.e. the size of a single wood fall) [17,20,21]. Further details on the natural history of wood falls are in the electronic supplementary material.

Our previous work on wood falls documented rises in energy and species diversity concordant with increased packing around an optimal body size, implying energy increases are experienced only in this size class [21]. Here, we examine four additional functional traits, reflecting how species contribute to wood-fall functioning and perform themselves, which should track energy availability. Three of these traits are based on previous functional trait metrics [22,23] and include feeding, motility, and tiering (electronic supplementary material). Feeding type is theoretically and empirically connected to energy availability, including in marine invertebrates, using these metrics [24]. Likewise, increases in motility are associated with higher metabolic demand [25]. Increases in energy availability may therefore allow for increased motility types, promoting niche space expansion. Additionally, epifaunal species are predicted to have adaptive advantages as they can better compete for available food, suggesting patterns of tiering (e.g. epifaunal versus infaunal) likely exist over energy gradients; e.g. deeper infaunal species are associated with higher energy [26]. We also add energy source, based on published literature for each taxa, as a metric, to capture whether species rely on xylophagous or sulfur pathways within the wood fall (electronic supplementary material). Increased energy is hypothesized to either: (i) increase abundance of preferred food resources, leading to specialization and niche packing; or (ii) increase novel food items, allowing for niche space expansion.

2. Methods

The methods of the wood-fall experiments are described in detail in previous work [17,20,21] and electronic supplementary material. Briefly, 32 *Acacia* sp. logs were deployed with a remotely operated vehicle at 3203 m in the Northeast Pacific Ocean. Each wood fall comprised a single *Acacia* log, 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 an approximately 160 m² area with approximately 5 m between wood falls in four rows 10 m apart, with each row including sizes across the range. For each wood fall, we recorded the initial weight (kilogram), location and surface area (square metre). We used initial wood fall weight (kilogram), 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 (v. 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 R-package [14,15]. An overview,

including the strengths and weaknesses of the each of these metrics, is provided in the supplementary material.

A variety of functional diversity metrics were employed to ensure patterns were ecological, rather than a result of metric selection. As opposed to *a priori* selecting metrics and given the ease of which these can be calculated, we instead choose to quantify several metrics examining which quantify unique aspects of functional diversity and implement these in the final analysis. Several of these functional diversity metrics actually demonstrate high correlations (electronic supplementary material). High correlations were found between: Rao's *Q* and functional dispersion; functional richness and unique trait combinations; and between various metrics of functional overlap (electronic supplementary material, figure S1). Functional evenness and functional divergence poorly correlated with the other metrics. Thus for the analyses, we only report those results of functional dispersion, functional richness, mean functional overlap, functional evenness and functional divergence as each quantifies a unique attribute of functional diversity.

3. Results

With increased wood fall size, only meanMVO, a measure of niche overlap, increased concordantly (figure 1; electronic supplementary material, table S1, $p = 0.0037$). Functional evenness decreased with increasing wood fall size but was not significant (figure 1; electronic supplementary material, table S1, $p = 0.0720$). 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 indicates that the residuals from the models was not significantly different from normal distributions ($p = 0.1634$ – 0.9668).

With increased species richness, meanMVO also increased (figure 1; electronic supplementary material, table S2, $p = 0.0002$). Functional richness also increased with increasing species richness but was not significant (figure 1; electronic supplementary material, table S2, $p = 0.0507$). A Shapiro–Wilk normality test indicates that all variables were not significantly different from normal distributions ($p = 0.4972$ – 0.9636). A Shapiro–Wilk normality test indicates that the residuals from the models were not significantly different from normal distributions ($p = 0.0631$ – 0.9427).

A full generalized linear model was constructed with functional dispersion, functional richness, mean functional overlap, functional evenness and functional divergence, and log₁₀ wood-fall mass to explain species richness. The best-fit model to predict changes in species richness contains mean functional overlap and functional richness only (full model: AIC = -35.97 ; reduced model: AIC = -37.58 , electronic supplementary material, table S3). Together mean functional overlap and functional richness predict 81% of the variation in species richness. However, mean functional overlap explains 63.8% of the variation alone. Variance inflation factors were low in both the full (1.25–2.60) and reduced models (1.01). A Shapiro–Wilk normality test indicates that the residuals from both models were not significantly different from normal distributions ($p = 0.6389$ and 0.8049).

4. Discussion

In investigating the relative influences of niche space expansion and niche packing on diversity in experimental deep-sea,

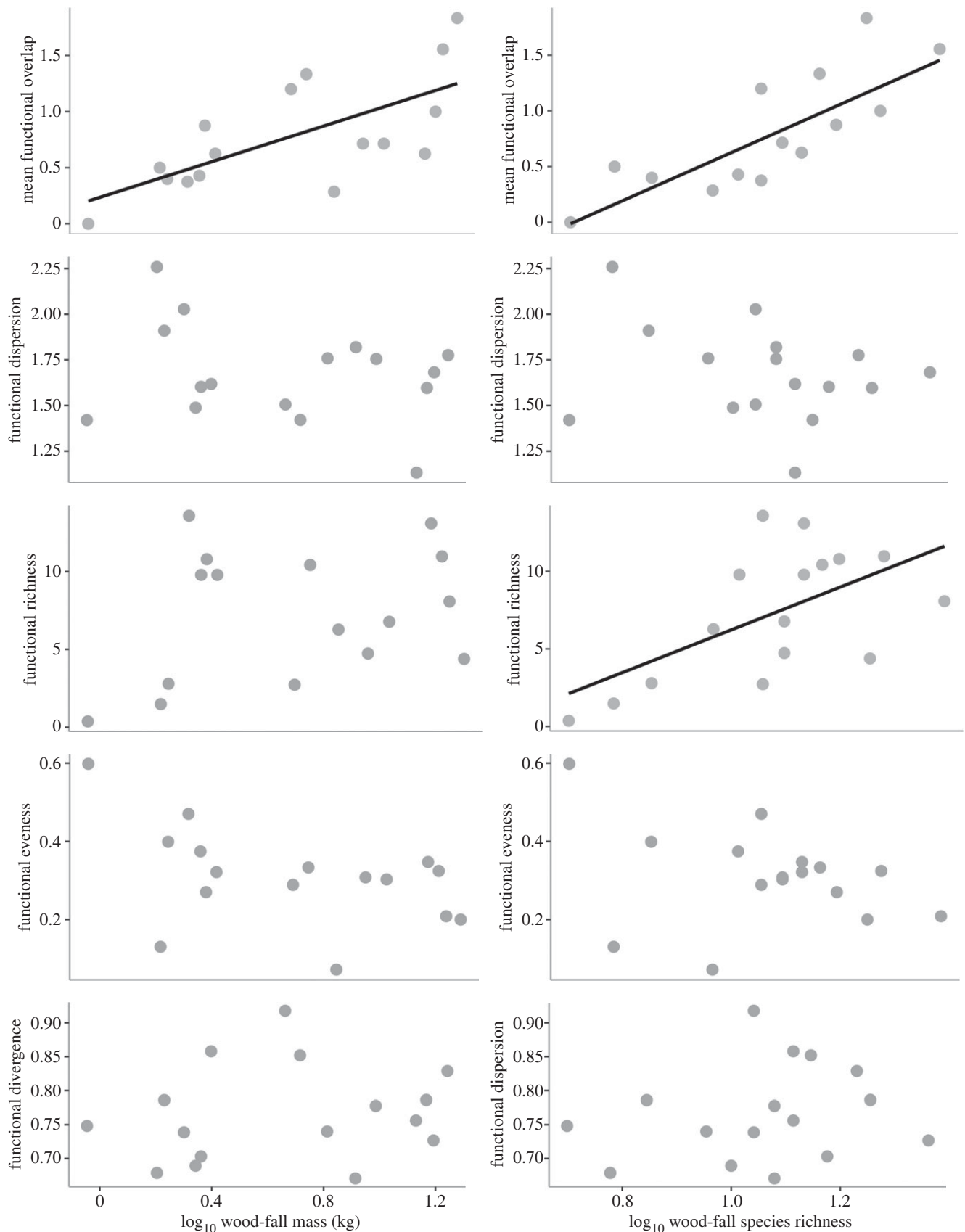


Figure 1. Metrics of functional diversity with $\log_{10}$ wood-fall mass and species richness. Regression lines are provided for p -values < 0.05 (electronic supplementary material, tables S1 and S2).

wood-fall communities, we find that chemical energy availability is concordant with increases in functional overlap and niche packing. With increased chemical energy available for experimental wood-fall communities, species richness also increases ($\rho = 0.75$) [20]. However, when changes in niche packing are accounted for, wood-fall size is no longer a

significant predictor of richness (electronic supplementary material, table S3). This pattern corresponds with the observed pattern of increased niche packing of optimal size bins [1] with increasing wood-fall size [17].

Only weak evidence of niche space expansion exists. Most functional traits present on large-sized wood falls

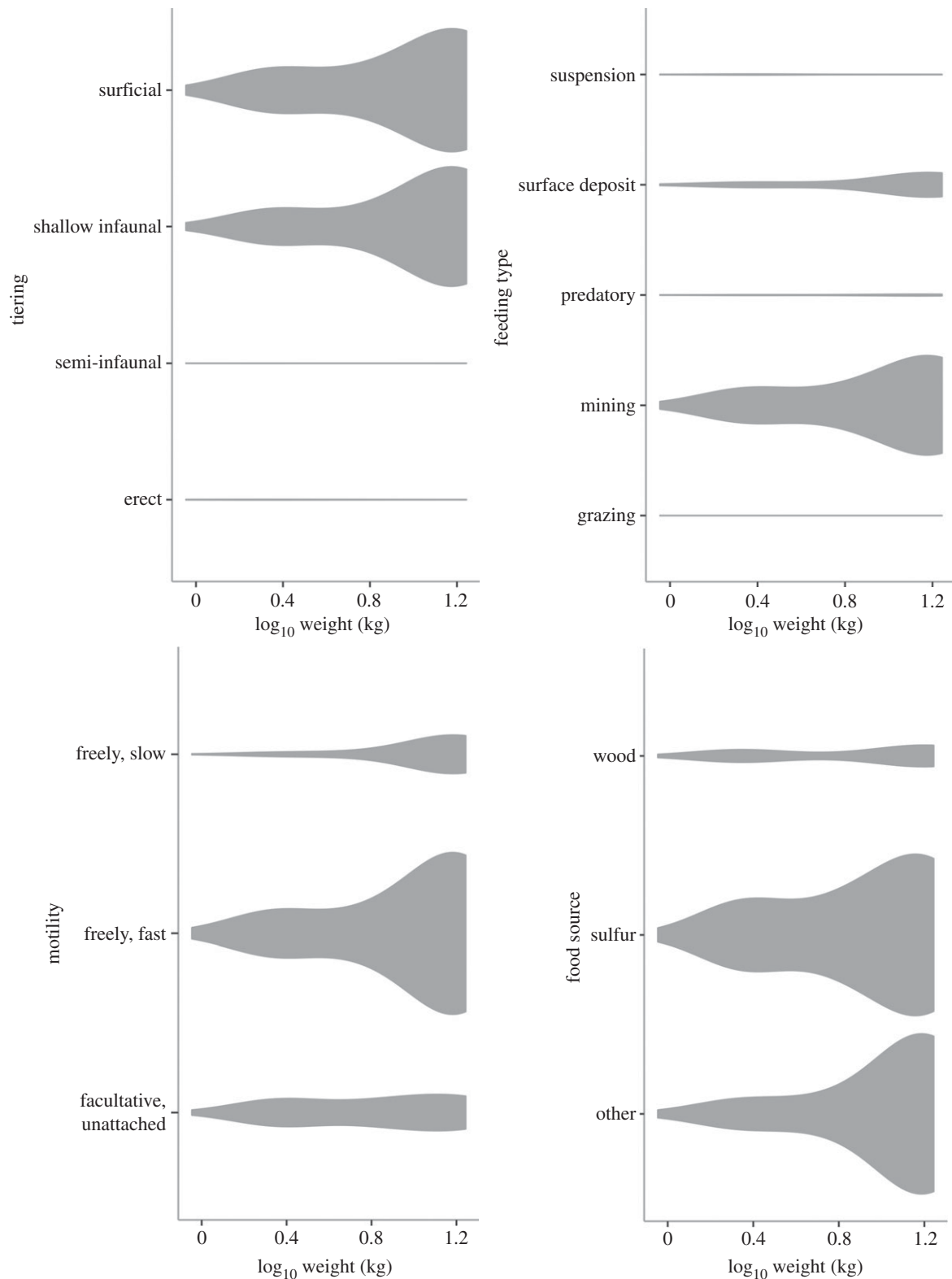


Figure 2. Dominance, as determined by abundance, of ecological traits over wood-fall size. Width of grey violin plot reflects numerical dominance of the trait at that wood-fall size.

are also present on smaller wood falls. This suggests that functional diversity of either the regional pool or the total range ecologies supported at the local wood fall is limited, regardless of total energy availability. Functional richness (figure 1) appears to reach an asymptote, implying the regional pool contains functionally redundant species. This pattern may be expected in wood-fall ecosystems, as species must be specialized to colonize and persist on these unique habitats. However, the relationship between functional volume space and species richness may

be a spurious statistical relationship based on sampling number [29].

Current and previous results [17] suggest that energy may not be distributed equitably across traits. Certain traits show increased abundance on larger wood falls (figure 2). This could occur because increases in energy allow for greater co-existence of species with certain functional traits [24,30–32]. For example, increased energy allows for greater dominance of more mobile fauna. Alternatively, species with certain functional traits may have more resources available to them [24].

Here, larger wood falls allow for increased wood degradation and production of sulfur niches increasing the availability of diverse energy resources (figure 2). At small wood-fall sizes, these resources may be too rare to support a wealth of species similar, i.e. resource concentration mechanism of [33,34]. Conversely, species with certain functional traits might be able to monopolize a greater proportion of total available energy. Both certain tiering and feeding traits may provide a greater spatial access to the bacterial mats or wood itself (figure 2). Distinguishing between these, while difficult, provides fertile ground for future investigation.

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Data accessibility. Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8q2kg02> [28].

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