Abundance and Functional Roles, Not Richness, Govern Wood-Fall Degenerative Ecosystem Function in the Deep Sea

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ABSTRACT: Biological diversity is widely recognized as a key driver of ecosystem function, yet the mechanisms underlying biodiversity-ecosystem function (BEF) relationships in natural systems, particularly for regenerative processes, remain poorly understood. We examined the BEF relationship in deep-sea xylophagous bivalve communities using 63 experimental wood falls deployed ~2,000 m deep in the Gulf of Mexico. This system allowed us to combine natural community assembly with controlled wood-fall deployments to examine how trophic partitioning, species dominance, and community-level properties influence total wood consumption, our metric of ecosystem function. We identified 26,324 individuals from 12 xylophagous bivalve species, which occupied complementary trophic niches, although their contributions to wood consumption varied substantially. Wood consumption increased with total abundance and, to a lesser extent, species richness, but richness effects largely reflected underlying variation in abundance. Analyses using the Price equation and species randomization approaches revealed that ecosystem function was primarily driven by a core group of abundant species, with occasional nonrandom contributions from rare species. These results indicate that in naturally assembled deep-sea communities, total abundance and key species' functional capacity outweigh species richness or phylogenetic diversity as predictors of ecosystem function, emphasizing the importance of individual species roles in shaping BEF relationships.

Keywords: assembly, biodiversity, complementarity, ecosystem function, isotopic niche, Price equation

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Introduction

Biological diversity has long been recognized as a critical component of healthy and resilient ecosystems (McCann 2000; Loreau et al. 2001; Tilman et al. 2014). Numerous experiments have demonstrated that ecosystems with high levels of biological diversity are more productive, more stable in the face of disturbances, and better able to provide important ecosystem services such as nutrient cycling and pollination (McCann 2000; Loreau et al. 2001; Tilman et al. 2014). The relationship between biological diversity and enhanced ecosystem function, the biodiversity-ecosystem function (BEF) relationship, is also pervasive across scales of space (Thompson et al. 2018; Qiu and Cardinale 2020), ecosystem processes (Byrnes et al. 2014; Gross et al. 2017), taxonomy (Solan et al. 2004; Tilman et al. 2006; Little and Altermatt 2018), and habitats (Field et al. 1998; Haas et al. 2002; Hu et al. 2020) as well as in both empirical (Fargione et al. 2007; Eisenhauer et al. 2016) and theoretical (Fox 2005; Connolly et al. 2013; Mokany et al. 2016) contexts.

However, whether the drivers of generative BEF relationships (those resulting in increased biomass and diversity and which are relatively well studied) differ from

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the drivers of regenerative BEF relationships (such as nutrient cycling and decomposition) remains poorly understood (Godbold et al. 2009; van der Plas 2019). Previous research on experimental and naturally assembled communities is dominated by primary production in terrestrial plant communities and focuses on primary production. Work on regenerative processes, especially in the marine realm, is relatively rare (Cardinale et al. 2011; Des Roches et al. 2018; van der Plas 2019). Prior research indicates that generally the BEF relationship for regenerative processes is neutral in natural systems (van der Plas 2019), suggesting that regenerative BEF relationships may be weaker or nonexistent compared with generative BEF relationships. One of the few studies focused on regenerative processes found that differences in ecosystem functioning across sites were more strongly influenced by shifts in species' effects than by changes in species composition at most sites, potentially reflecting underlying variation in unmeasured abiotic conditions (Mateo-Tomás et al. 2017). In many studies of regenerative processes, the effects of abiotic conditions were more important than biodiversity (van der Plas 2019). However, the relatively small number of studies of regenerative processes underscores the need for further investigation of the relative importance of abiotic and biotic factors in regenerative ecosystem functions.

Another unresolved issue in BEF research concerns the extent to which results from experimental manipulations of biodiversity capture the processes that govern ecosystem functioning in naturally assembled observational systems. Despite BEF research dating back to Elton (1958) and the rapid expansion of the field since the 1990s, many questions remain about the processes that generate BEF relationships, particularly in natural systems (Cardinale et al. 2011; Tilman et al. 2014; van der Plas 2019). This uncertainty has led to a long-running discussion about the extent to which experimental results can inform the factors that drive ecosystem function in nature (Srivastava and Vellend 2005; Duffy 2009; Winfree et al. 2015; Wardle 2016; van der Plas 2019; Jochum et al. 2020). This discussion has emphasized the value of experimental systems, such as laboratory or mesocosm studies, because they provide the ability to manipulate variables and control environmental conditions. Yet there remains a concern that experimental systems may not fully capture the complexity and interactions present in natural systems (Winfree et al. 2015; van der Plas 2019). On the other hand, natural systems, such as field studies or long-term ecological research sites, may provide a more realistic representation of ecosystem function and biodiversity dynamics. However, natural systems have their own drawbacks: they are often complex and dynamic, which makes it challenging to disentangle the effects of different factors. Furthermore, causal inference based on observational data is speculative and must be done carefully. Therefore, a significant challenge in ecosystem function and biodiversity research is bridging the gap between natural and experimental systems (Cardinale et al. 2012). More robust insights could be gained by combining approaches. Here, we present a study of deep-sea wood-fall communities. These provide a setting in which we can combine the control of experimental studies with the realism provided by natural colonization and community assembly while also exploring a regenerative function, namely, wood consumption by xylophagous bivalves.

One consequence of the contrast between experimental and observational systems is that the mechanisms inferred to underlie ecosystem functioning may differ between the two. In experimental systems, ecosystem function seems to be largely driven through complementarity rather than selection effects, especially for experiments run for many years (Fargione et al. 2007; Reich et al. 2012). Despite the clear importance of richness in experiments, there are several reasons to suspect that richness may be disconnected from ecosystem function in observational data. Here, we focus on two trends present in observational data but (generally) not in experiments: variation in total community abundance among sites and ubiquitous high dominance. First, in observational data, sites vary dramatically in total abundance. As such, sites with more individuals can have higher function even if redundancy (similar traits/niches among species) is high, leading to ecosystem function being driven by the identity and population sizes of species in a community as much as richness per se (McCann 2000; Wardle et al. 2000; Bruno et al. 2005; van der Plas 2019). Complementarity (different traits/niches among species) can also affect ecosystem function in observational data, although we may expect its role to be limited relative to experiments that control initial total abundance across replicates. At one end of a continuum, complementarity among species allows for a wider scope of ecosystem-level effects (Loreau and Hector 2001; Zuppinger-Dingley et al. 2014), while functional redundancy may provide resilience against local extinctions of any one species (Biggs et al. 2020).

Second, biodiversity experiments generally maximize evenness among species (e.g., equal seeding rates), such that species that would be rarer in natural communities are more common—at least initially—in experiments. However, all known ecological communities have few dominant and many rare species (McGill et al. 2007), and these dominant species may have disproportionate roles in ecosystem functioning (see the "selection" effect in both Fox [2005] and Loreau and Hector [2001]). Outsized effects of some species can be anticipated in the

case of keystone, foundational, dominant, or invasive species (Des Roches et al. 2018), and there is increasing evidence that among-site variation in the populations sizes of dominant species can be a major driver of variation in ecosystem function in observational data (Winfree et al. 2015; Lohbeck et al. 2016; Genung et al. 2020).

Experiments and observational BEF studies also differ in the types of analyses commonly used. A foundational analysis for experimental BEF research is Loreau and Hector's (2001) approach, based on evolutionary biology's Price equation (Frank 2012). This approach was a key advance but requires monocultures that are impossible (or at least very rare) in nature, and thus the complementarity versus selection framework does not apply as easily with observational data in natural systems. A different ecological adaptation of the Price equation, one that does not require monocultures, can also be used to attribute variation in ecosystem function into three components: species richness, species identity, and a "context dependence" term (Fox 2006; Fox and Kerr 2012; Harrison et al. 2022), which is often driven by the population size of dominant species. This approach is easily applied to observational data, and there is a growing body of research that has leveraged it to gain insight about what determines variation in ecosystem function across time or space (Winfree et al. 2015; Genung et al. 2017; Genung et al. 2020; Lefcheck et al. 2021). However, the Price equation has been used only once to study regenerative processes (Mateo-Tomás et al. 2017) and has not been applied to deep-sea communities.

Here, we investigate BEF relationships in xylophagous bivalve communities on experimental deep-sea wood falls. Wood is transported to the oceans via rivers and eventually sinks, creating isolated habitats on the sea floor (McClain et al. 2016). This process can transport a considerable amount of energy to the deep sea (Schlünz and Schneider 2000). This dead wood in the deep oceans is a key contributor to biodiversity, providing dynamic habitats and resources for a huge variety of endemic invertebrates across several invertebrate phyla (Turner 1977; Bienhold et al. 2013; McClain and Barry 2014). Only ~10% of wood-associated species are found in the background sediment or nearby hard substrates (McClain et al. 2016), and most of these are rare, with fewer than five individuals per wood fall. This endemicity reflects trophic dependence on the wood fall. Xylophages ingest wood and rely on heterotrophic bacteria to aid digestion and assimilation (Maddocks and Steineck 1987; Becker et al. 2009; Hoyoux et al. 2009), with the most notable and abundant xylophagous species being members of the bivalve family Xylophagaidae (Knudsen 1961; Turner 2002; Voight 2007). These wood-boring and consuming bivalves ultimately dominate the consumption and decomposition of deep-sea wood falls, serving as ecosystem engineers and foundational species creating habitat for other species (Turner 1973) while also serving as a conduit of terrigenous organic material entering into deep-sea food webs. The distinctive xylophagous bivalve communities developing on wood falls are dependent on ephemeral and spatially unpredictable resources and are thus made up of strong colonizers, establishing in 1 to 2 years (McClain et al. 2016). Communities developing on individual wood falls are also clearly distinct from surrounding deep-sea sediment communities and largely exhibit independent community composition, even over quite small spatial scales (McClain et al. 2016). This enables experiments that include multiple communities at tractable spatial and temporal scales.

To mimic natural wood falls, we seeded the deep-sea floor with wood upon which a diverse set of xylophagous bivalves naturally assembled. To examine the importance of biotic factors in regenerative ecosystem processes, the wood falls were deployed at sites with comparable abiotic conditions. Regenerative ecosystem function was quantified for each wood fall as the biomass of wood consumed by xylophagous bivalves. To test for redundancy versus complementarity in traits and niches, we quantified isotopic (i.e., trophic) niches and population sizes of each xylophagous species. We focused on key traits expected to influence wood consumption, population size, and trophic position, which are likely to affect the rate and efficiency of decomposition. We then tested for dominance effects by quantifying whether each individual species was positively correlated with wood consumption. Next, we examined the relative importance of different community attributes—total abundance, species diversity, functional/trait diversity, and phylogenetic diversity—for wood consumption. Finally, we dissected changes in species gains and losses and the functionality of those species in the community on ecosystem function using Fox and Kerr's (2012) modification of the Price equation.

Methods

Experiments and Collections

In May 2017, 63 wood falls were deployed at two sites (site 1: $N = 23$, 2,171 m; site 2: $N = 40$, 1,970 m) in the northern Gulf of Mexico (further details are provided in table S1; tables S1–S5 are available online). All analyses were conducted at the wood-fall scale with analyses including all 63 wood falls; however, isotopic analyses, which required intensive sampling, were performed on a subset of 10 logs. Sites were chosen on the basis of similarity in depth and comparable environmental conditions

(particulate organic carbon [POC]: 0.88–1.99 gC/m/yr; current speed: 0.001–0.002 m/s; temperature: 3.9°C–4.1°C; oxygen: 191.3–193.5 mol/m^3; salinity: 35 ppt). These depths also ensured that wood, as opposed to POC, was the dominant energy source for xylophagous bivalves while remaining within the operational limits of the remotely operative vehicle. Eleven tree species were used, including *Carya illinoensis* (4), *Celtis laevigata* (16), *Magnolia grandiflora* (4), *Pinus echinata* (4), *P. elliottii* (15), *Quercus alba* (4), *Q. rubra* (3), *Q. virginiana* (3), *Salix nigra* (4), *Taxodium distichum* (3), and *Ulmus americana* (3). At site 1, 11 *P. elliotti* and 12 *C. laevigata* were deployed, with remaining wood falls deployed at site 2. Individual wood falls (logs) were taken from the same individual tree. Trees were fresh cut, and logs were dried to a moisture of ~15%. Wood falls were debarked, quartered, and then zip-tied back together to allow for processing upon collection. Wood falls were sewn into a synthetic fiber mesh bag to enable subsequent collection of highly degraded wood falls (5-mm mesh, ensuring that larval settlement was not hindered). At each site, wood falls were dispersed ~5 m apart and deployed by a remotely operated vehicle. The first set of wood falls (site 1: $N = 23$; site 2: $N = 20$) were collected in February/April 2019 after 21/23 months. The remaining 20 wood falls at site 2 were collected in February 2020 after 33 months. After collection, wood falls were immediately preserved in 80% EtOH after quarters were separated.

All xylophagous bivalves were subsequently removed and identified. Twelve distinct types of wood-boring bivalves were distinguished by both morphology and phylogenetic analysis of histone H3 DNA sequences, except for *Xylophaga* sp. 9, which was only morphologically identified; the distinct morphological and genetic units are referred to as "species" herein. The minimum interspecific genetic distance was 2.7%. Voucher specimens of sequenced species were deposited at the Scripps Institution of Oceanography's Benthic Invertebrate Collection; unique voucher numbers are displayed on the supplementary phylogenetic tree figure. The phylogenetic tree (fig. S1; figs. S1–S12 are available online) used in this study was generated specifically from this dataset, following the procedure outlined in the supplemental PDF. Due to natural variation in community composition, individual wood falls contained between one and nine of these species across the 63 wood falls. For the isotopic analyses, which focused on the six most abundant species, individual wood falls contained between one and five species.

Finally, wood consumed weights (CWs) for each wood fall were calculated as dry initial weight minus final weight after drying and returning the moisture to ~15%. All analyses were conducted using R (ver. 4.2.3; R Development Core Team 2024).

Redundancy versus Complementarity in Isotopic Niches

To assess the relationship among trophic diversity, complementarity, and ecosystem function, we quantified isotopic niches for the six most abundant xylophagous bivalve species (table 1; $N = 567$) for each wood fall. These analyses were conducted across 10 wood falls representing a gradient in species richness (one to five species per wood fall), reflecting natural variation in community assembly (table S2). The 10 wood falls spanned across both sites and three tree species. We measured bulk tissue carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values, where δ^{13}C traces variation in basal resources (e.g., wood) and δ^{15}N indicates trophic position (Newsome et al. 2007); details of the isotopic analyses are provided in the "Isotopic Analysis Methods" section of the supplemental PDF. We calculated three proxies for trophic structure: (1) the isotopic niche of each species on each wood fall, measured as the standard ellipse area of isotopic values (SEA_{Sp}); (2) the total isotopic niche of the community on each wood fall (TNW); and (3) the relative niche index (i.e., degree of specialization) per species per log (RNI_{Sp}). We tested the relationship between trophic niches and species diversity using a series of linear regressions. Complementarity should decrease trophic niche overlap, but we could also see this pattern for a range of reasons. Therefore, we used null models to test whether trophic niche overlap was higher than expected. A detailed description of these null models can be found in the "Null Models for Isotopic Niches" section of the supplemental PDF.

Redundancy versus Complementarity in Population Size

Population size was quantified for each species on each wood fall as the total number of individuals present. We used an ANOVA with population size as the dependent variable and species identity as the independent variable to determine whether population size varied across species. We computed estimated marginal means for species pairs using the emmeans package (Russell 2019).

Dominance Effects

We implemented a randomization test (Gotelli et al. 2011) to quantify the average positive and negative associations of xylophagous bivalve species with wood consumption. In the first test, a presence-absence matrix of wood falls versus species was constructed along with the vector of wood consumed. The empirical distance value was calculated for each species as the difference in wood consumed when the species was present versus when it was absent. We also regressed wood consumption by abundance for each species and noted the empirical

Table 1: Summary statistics for xylophagous bivalve species

	Population size				Presence/absence				Slope			
Species name	Summed	Average	No. wood falls	Mass (g)	Empirical	Simulated	*Z*	*P*	Empirical	Simulated	*Z*	*P*
Xyloredo sp. 1	17,000	274.2	62	125.9	.925	−.006	*3.00*	*.0020*	.001	1.848	−.02	.4860
Spiniapex sp. 3	5,316	91.7	58	28.0	.274	−.001	*2.39*	*.0080*	.005	−.181	.02	.4980
Xylopholas sp. 5	2,277	162.6	14	1.1	.439	−.006	*2.32*	*.0060*	.002	1.086	−.03	.4980
Abditoconus cf. *brava*	1,604	69.7	23	28.5	.384	−.004	*2.92*	*.0010*	.001	−1.145	.03	.4940
Xylonora sp. 10	747	27.7	27	67.4	.440	.001	*3.48*	*.0000*	.072	.031	.05	.4930
Xylophagidae sp. 11	713	29.7	24	12.9	−.088	.039	−.29	.3120	−.088	.003	**−2.52**	**.0240**
Xylonora sp. 12	137	4.3	32	18.4	.187	−.004	1.68	.0420	.002	−.360	.04	.4890
Xylophagidae sp. 16	70	23.3	3	.6	.106	.000	.94	.1710	.004	−.185	.03	.4980
Bankia sp. 7	62	3.6	17	2.2	.299	−.001	*2.69*	*.0010*	.030	−.060	.12	.4640
Xylonora sp. AC78	16	3.2	5	151.7	1.054	−.020	*2.52*	*.0000*	.351	−.005	*3.35*	*.0000*
Xylonora sp. 13	3	3.0	1	82.8	−.599	−.007	**−2.63**	**.0040**	−.077	−.014	−.20	.3960
Xylophaga sp. 9	1	1.0	1	15.9	.065	.014	.20	.4420	−.003	.094	−.04	.4290

Note: Summed population size and average population size are taken across all wood falls. Mass is wet weight of a random subset of individuals ($N = 20$), or all individuals when $N < 20$, for each species, weighing them together and calculating average size. The last eight columns are the results of randomization tests for quantifying species importance to ecosystem function. The empirical distance value was calculated for each species as the difference in wood consumed when the species was present versus absent in both empirical and simulated relationships. The intercept and slopes for regression between abundance and wood consumed for each species are given for empirical and simulated relationships. The standardized effect sizes (SES or *Z* scores) were calculated by subtracting the mean randomized values from the empirical values and dividing by the standard deviation of randomized values. Italic versus bold *Z* scores and *P* values indicate positive versus negative relationships, respectively.

intercept and slope. We randomized the wood consumption vector 1,000 times and recalculated distance, intercept, and slope to get null distributions for each variable. The standardized effect sizes (SES or Z scores) were calculated by subtracting the mean randomized values from the empirical values and dividing by the standard deviation of randomized values. If $|\text{SES}| > 2$, then the observed value is approximately in the 5% tail of a normal distribution. Pseudo P values are reported as the number of randomized values greater than or less than empirical values.

Community Attributes: Abundance and Diversity

Ecosystem function was measured for each wood fall as the total wood consumed by xylophagous bivalve species, calculated as the loss of weight of the entire wood fall between pre- and postdeployment. We constructed linear models to predict total wood consumed by xylophagous bivalves based on richness, total abundance across all species, wood type, and population sizes of individual wood-boring species. Species richness, Shannon-Weiner's H', and Simpson's J were quantified with the vegan package (Oksanen et al. 2013). Faith's phylogenetic diversity (PD) was calculated with the picante package (Kembel et al. 2010) based on the constructed phylogeny (supplemental PDF). Because wood hardness could impact boring rates of xylophagous species, we accounted for differences between wood species using Janka hardness as a metric for wood hardness. Janka hardness values were taken from http://wood-database.com.

Generalized linear models (GLMs) were assembled to analyze how consumed wood weight (in kilograms and $\log_{10}$ transformed) was dependent on total xylophagous bivalve abundance, richness, Faith's PD, wood hardness, deployment site, and deployment time for each wood fall. Nagelkerke's pseudo R^2 was calculated with the performance package (Lüdecke et al. 2021) for each GLM. We used the dredge function in the MuMIn package (Bartoń 2011) to determine which linear model best predicted consumed wood weight (using the Akaike information criterion [AIC]). The dredge function conducted an automated model search using all subsets of the provided global model. Top models with AIC $< \Delta 2$ were kept, and coefficients were model averaged. Partial ϵ^2 (ϵ^2p) was calculated with the effectsize package (Ben-Shachar et al. 2020) to quantify the proportion of partial variance uniquely explained by the associated effects in models. For a subset of 10 wood falls for which we were able to build isotopic niche data, we compared AICs of single-parameter GLMs of total abundance, richness, Faith's PD, and total isotopic niche width.

Community Attributes: Species Gains and Losses

We quantified the cumulative effects of community assembly (i.e., species gains and losses) and individual species' contribution (i.e., relative population size and per capita species function) to ecosystem function using an ecological application of the Price equation (Fox 2006; Fox and Kerr 2012; Harrison et al. 2022). An in-depth explanation of our ecological application of the Price equation is provided in the supplemental PDF. In brief, our method partitions differences in ecosystem function into three components: the species richness effect (SRE), the species identity effect (SIE), and the context-dependent effect (CDE). The SRE is a null expectation if species were gained (SRE_{gain}) and lost (SRE_{loss}) at random with respect to function, whereas the SIE represents the gain (SIE_{gain}) or loss (SIE_{loss}) of species that are functionally above or below average. The SIE terms can either cancel the corresponding SRE terms (if low-function species are lost) or augment them (if high-function species are lost).

Last, the CDE represents the changes in functional contribution of species that are shared across communities. This is essentially the net difference in contribution to ecosystem function of core species shared among communities—for example, species X consumed 10 mg in community A versus 20 mg in community B, then repeated and summed across all species. If the CDE is high relative to the SRE and SIE, it suggests that ecosystem function is driven more by variation in population size of common species, with the addition and loss of rare species playing a comparatively small role. To do this, the Price equation incorporates the number of species in two communities (baseline and comparison), the number of shared species, the average species-level function, and the function of species shared by both communities.

Here, because we could not measure species-specific per capita effects, we assumed that all individuals contributed equally to CW by dividing total mass loss by xylophagous bivalve total abundance for each wood fall. While this approach potentially underestimates species-specific differences in per capita function, it captures patterns in species total and relative populations sizes that are likely important for species-level effects.

We compared CW between all pairwise communities and partitioned differences in ecosystem function among the three Price components using the priceTools R package (Bannar-Martin et al. 2018; Kremer 2020). For pairwise comparisons, we designated the baseline community as the community with the lower CW. To summarize the relative importance of each process captured by the Price components, we normalized them by dividing by the absolute value of the largest Price component within each comparison. To compare the absolute effects of each

component, we standardized each to the baseline ecosystem function and reported percent change in CW relative to the baseline (positive effects = more wood consumed). We used generalized additive models (GAMs) to describe the relationship among Price components and increased xylophagous bivalve total abundance using the brms (Bürkner 2017) and mgcv packages (Wood 2006). The quality of the GAM fit for each Price component–abundance relationship was assessed through comparison of the estimated predictive accuracy between itself and a null model with leave-one-out cross validation using the loo package (Vehtari et al. 2015). When predictive differences exceeded a cutoff of four, models were considered different if predictive differences (elpd) exceeded twice the calculated standard error in predictive difference.

Results

We found diverse and abundant assemblages of wood-boring bivalves on the deep-sea wood falls. A total of 26,324 individuals were classified into morphospecies, with their identification confirmed through DNA sequencing (fig. S1). In total, 11 species of xylophagaid (Xylophagaidae) bivalves and one species of *Bankia* (Teredinidae) were present across the assemblages, resulting in diverse xylophagous bivalve communities with species belonging to six genera (table 1).

Redundancy versus Complementarity in Isotopic Niches

Species-level trophic niches (table S1; raw data are presented in figs. S2–S5) were relatively static, as there was no relationship between species' isotopic niches measured as standard ellipse areas (SEA_{Sp}) and richness ($F_{1, 22} = 1.88$, $P = .18$), species identity ($F_{5, 22} = 0.48$, $P = .79$), or sample size ($F_{1, 22} = 0.04$, $P = .85$; multiple $R^2 = 0.16$). In contrast, the TNW, consisting of all xylophagous bivalves present on the wood fall, increased significantly with species richness ($F_{1, 8} = 7.42$, $P = .03$, $R^2 = 0.48$; fig. 1). Relative niche index (i.e., degree of specialization; RNI_{Sp}) decreased with richness ($F_{1, 22} = 21.68$, $P < .01$; fig. 1), but we found no effect of species identity ($F_{5, 22} = 0.65$, $P = .66$) or sample size ($F_{1, 22} = 0.52$, $P = .48$; multiple $R^2 = 0.54$). Within cross sections of individual wood falls from 10 of 11 species (*Salix nigra* was not sampled), subsamples at three locations (innermost core, outer edge, midpoint) varied by 1.0‰–3.2‰ for $\delta^{13}C$ and by 0.1‰–3.1‰ for $\delta^{15}N$ (table S3).

Because niche metrics can change as a consequence of richness and total abundance alone, independent of niche complementarity, we evaluated whether the observed patterns differed from expectations under a null model. For both SEA_{Sp} and TNW, slope estimates for the effect of richness were almost indistinguishable from null model expectations (fig. S6). In contrast, the observed decline in RNI_{Sp} with richness was in the negative tail of the null distribution, suggesting a tendency toward enhanced niche subdivision. However, we stress that this pattern did not exceed null expectations with high confidence. Details of the null model and associated figures are provided in the supplemental PDF.

Redundancy versus Complementarity in Population Size

Average population sizes of bivalves varied significantly among species $F_{11, 255} = 1.86$, $P < .0001$; figs. 2, S7), as did total summed population size (i.e., summed across wood falls; table 1). *Xyloredo* sp. 1 exhibited the highest population sizes, being significantly higher than five other species. *Abditoconus* cf. *brava*, *Spiniapex* sp. 3, and *Xylopholas* sp. 5 had the next three highest populations sizes, respectively, with each species being significantly different from two least abundant species, *Xylonora* sp. 12 and *Bankia* sp. 7. In contrast, *Xylonora* sp. AC78 and *Xylophaga* sp. 9 yielded nonsignificant post hoc comparisons with other species because of their low total population sizes ($N = 3$, $N = 1$).

Dominance Effects

Of the 12 bivalve species, eight species yielded significant results for the presence-absence analysis (table 1). The randomization tests revealed seven positive and one negative associations between species presence and wood consumption (CW). In contrast, the regression analyses using population size as the predictor yielded only one positive and one negative association with CW. In general, positive effects in the presence-absence analysis (high positive *Z* scores) were correlated with both a species' overall population size (Pearson's $r = 0.61$, $P = .0332$) and occupancy (Pearson's $r = 0.69$, $P = .0119$) among wood falls.

Community Attributes: Abundance and Diversity

As consumer total abundance and species richness increased, so did CW. Wood falls that possessed more abundant and diverse bivalves were more fully consumed (fig. 3*A*, 3*B*; total abundance: $\log_{10}CW = -0.40 + 0.001 \times$ total abundance, $R^2 = 0.39$, $P \leq .0001$; richness: $\log_{10}CW = -0.61 + 0.03 \times$ richness, $R^2 = 0.25$, $P < 0.0001$). However, evenness did not exhibit a significant effect on CW (fig. 3*C*; $P = .19$). CW was also strongly correlated with community phylogenetic distance (fig. 3*D*; $\log_{10}CW = -0.80 + 2.82 \times$ Faith's PD, $R^2 = 0.31$, $P \leq .0001$).

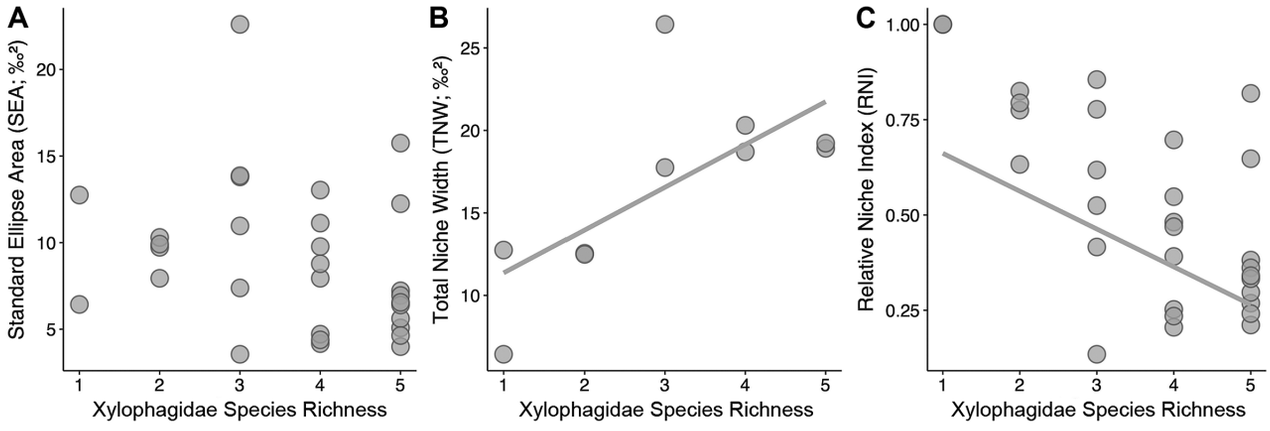


Figure 1: Relationships between xylophagous bivalve species richness and isotope-based trophic niche metrics. *A*, Species-level isotopic niche width, quantified as the standard ellipse area (SEA_{Sp}), representing the trophic niche occupied by each species on a wood fall. *B*, Community-level total isotopic niche width (TNW), calculated from all species present on a wood fall and representing the overall trophic niche space of the community. *C*, Relative niche index (RNI_{Sp}), which measures the degree of trophic specialization of each species relative to the total community niche space.

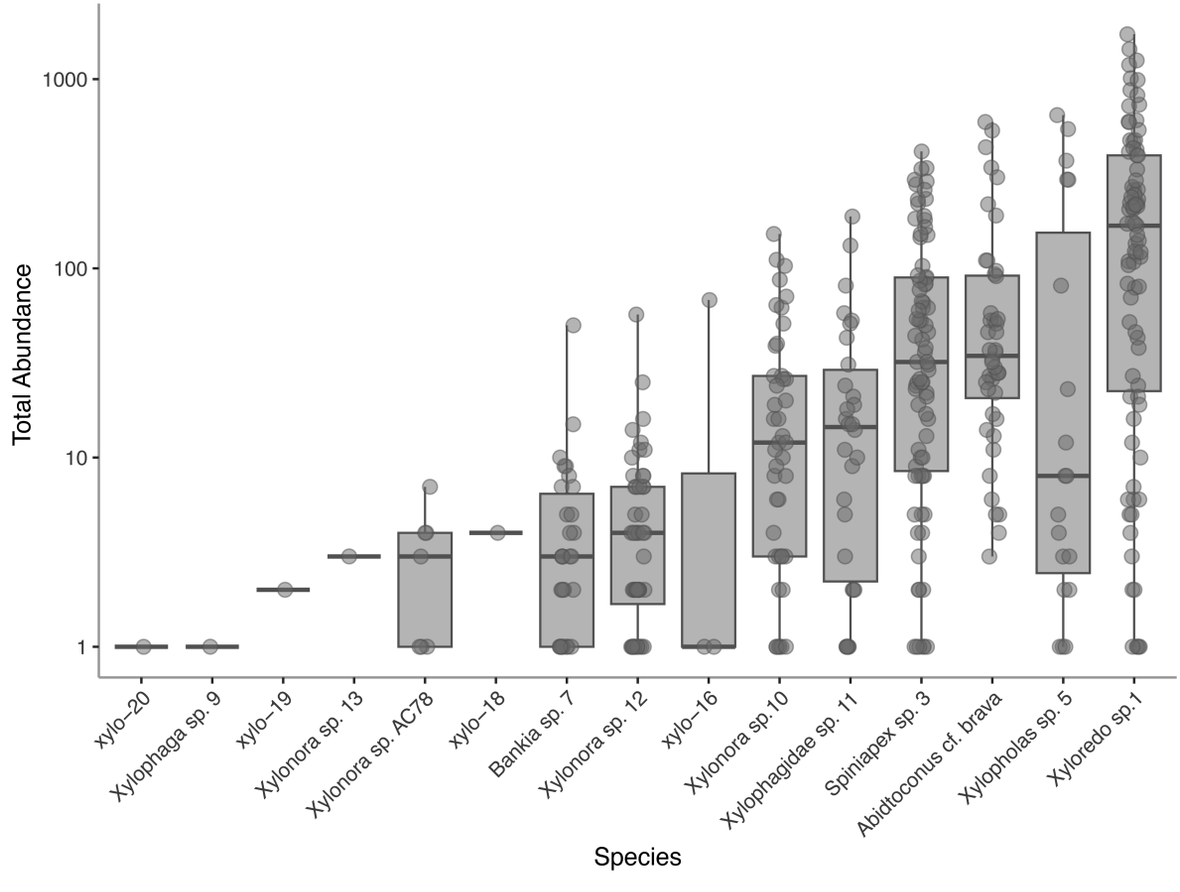


Figure 2: Boxplots of population size for each xylophagous bivalve species across wood falls. Boxes indicate the median and first and third quartiles, with whiskers extending to 1.5 times the interquartile range.

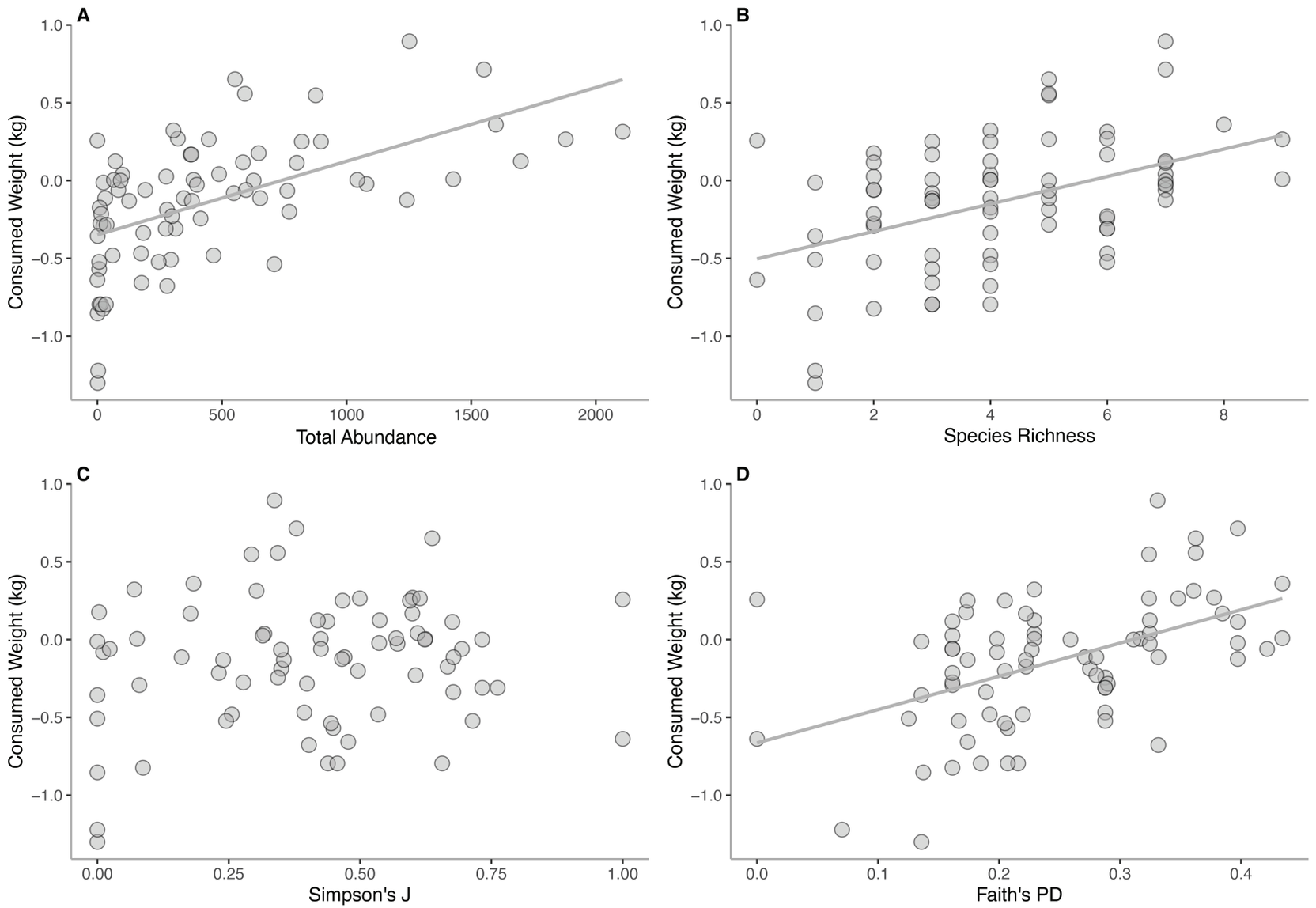


Figure 3: Log_{10}-transformed consumed wood weight (kg) as a function of xylophagous bivalve (*A*) total abundance, (*B*) species richness (*S*), (*C*) evenness (Simpson's *J*), and (*D*) community phylogenetic diversity (Faith's PD). Gray lines represent individual linear regression fits for each relationship.

The dredge analysis recovered two models with AIC < Δ2. The best fit, based on AIC values, was for a model that included just total abundance, site, deployment time, and phylogenetic diversity, explaining 64.7% of the variance of CW (table S3). The second-best model excluded site, and the third-best excluded phylogeny. Wood type, hardness, or species richness were not included in any of the top models. Neither phylogenetic diversity nor site were significant in the averaged model (table S3). The largest partial variance was explained by total abundance ($\epsilon^2 p = 0.46$) and deployment time ($\epsilon^2 p = 0.46$). Site and phylogenetic diversity had lower explanatory power ($\epsilon^2 p = 0.37$ and 0.13, respectively).

For the subset of 10 wood falls with data for isotopic niche width, the total abundance-only general linear model produced both the lowest AIC and highest pseudo R^2 (table S4). Total isotopic niche width explained 37% of the variance in CW and was the next-best model per AIC values. Richness and phylogenetic distance both performed poorly compared with the other parameters, producing both the lowest pseudo R^2 and highest AICs.

Community Attributes: Species Gains and Losses

Across wood-fall comparisons, the Price equation components showed a wide range of relative importance (fig. 4*A*). Functional roles of the core shared species (CDE: 0.72 ± 0.36) were the most important contribution to differences in CW. This effect was followed by the loss (SRE_{loss}: 0.51 ± 0.41) and gain (SRE_{gain}: 0.36 ± 0.38) of functionally average species. Loss (SIE_{loss}) and gains (SIE_{gain}) of species above or below average had the smallest effects (0.30 ± 0.34 and 0.29 ± 0.30, respectively). While the functional roles of the core shared species (CDE) were most often the Price component with the highest relative importance, its absolute contribution to CW varied qualitatively between positive and negative effects (fig. 4*B*). In general, the CDE contributed to an increase of ~7% in CW (7.2% ± 95.2% [median ± median absolute deviation]). In comparison, random species loss (SRE_{loss}) decreased CW by 42% ± 26.5%, and random gains (SRE_{gain}) increased CW by 17% ± 25.5%. Species loss was generally attributed to low-functioning species, as shown by the positive SIE_{loss} (18.8% ± 27.9%), which partially cancelled the negative SRE_{loss}. In contrast, species gains were generally below average to average (0% ± 13.6%), as ~90% of the nonrandom species gain effects (SIE_{gain}) were zero or negative (fig. 4*B*).

The contribution of Price components showed varying effects with increasing bivalve abundances (fig. 4*C*). With increasing total abundance, the CDE and SRE_{gains} had larger effects on differences in CW among wood falls. This was especially true as total abundance increased above 1,500 individuals. In contrast, SIE_{gains} increasingly depressed CW differences within increasing total abundance, suggesting that new species added were generally rare and/or functionally below average (fig. 4*C*). Furthermore, the relationship between the CDE and loss components (SRE_{loss} and SIE_{loss}) suggested that the function provided by shared species (those not lost or gained between sites) did not compensate for species losses. Instead, random and nonrandom species loss was associated with lower function of shared species (fig. S8).

Discussion

In general, xylophagous bivalve species possessed different trophic niches on wood falls. Across wood falls, TNW increased with species richness in the empirical data, but this relationship almost exactly matched null expectations. This suggests that any correlation between higher richness and expanded community-level niche space can be accounted for as a statistical consequence of adding species, rather than as a clear ecological signal of niche expansion. Instead, a potential role for richness was most evident in the relative distribution of niche space among species (RNI_{Sp}), which decreased with richness in the empirical data. This decline was more negative than the null model's mean expectation, although the observed slope remained within the null model's confidence interval. Taken together, these results provide at most modest evidence for richness-dependent niche subdivision beyond null assembly. To the extent that RNI_{Sp} declines faster than expected, it would be consistent with increasing subdivision of a conserved community niche space among coexisting species (MacArthur 1958; MacArthur and Levins 1967; Chesson 2000). However, this analysis, and the corresponding null model, was limited to only 10 wood falls; the observed patterns—or apparent lack thereof—may also reflect limited statistical power rather than a true absence of ecological signal. Together, these results, if not due to low power, indicate that if richness drives changes in community structure, it is unlikely to do so via niche expansion but rather through how existing niche space is apportioned among species.

Some species appear to have a greater impact on wood consumption. *Xyloredo* sp. 1 creates deeper, wider burrows than other species, implying that individuals of this species are consuming more wood per capita, along with having greater overall abundance and occupancy among wood falls (table 1). As xylophagous bivalves grow they bore more deeply; as such, the deeper burrows of *Xyloredo* sp. 1 may reflect its comparatively larger body size. These results indicate a significant role for this species in the total wood consumed by the community—our measure of regenerative ecosystem function.

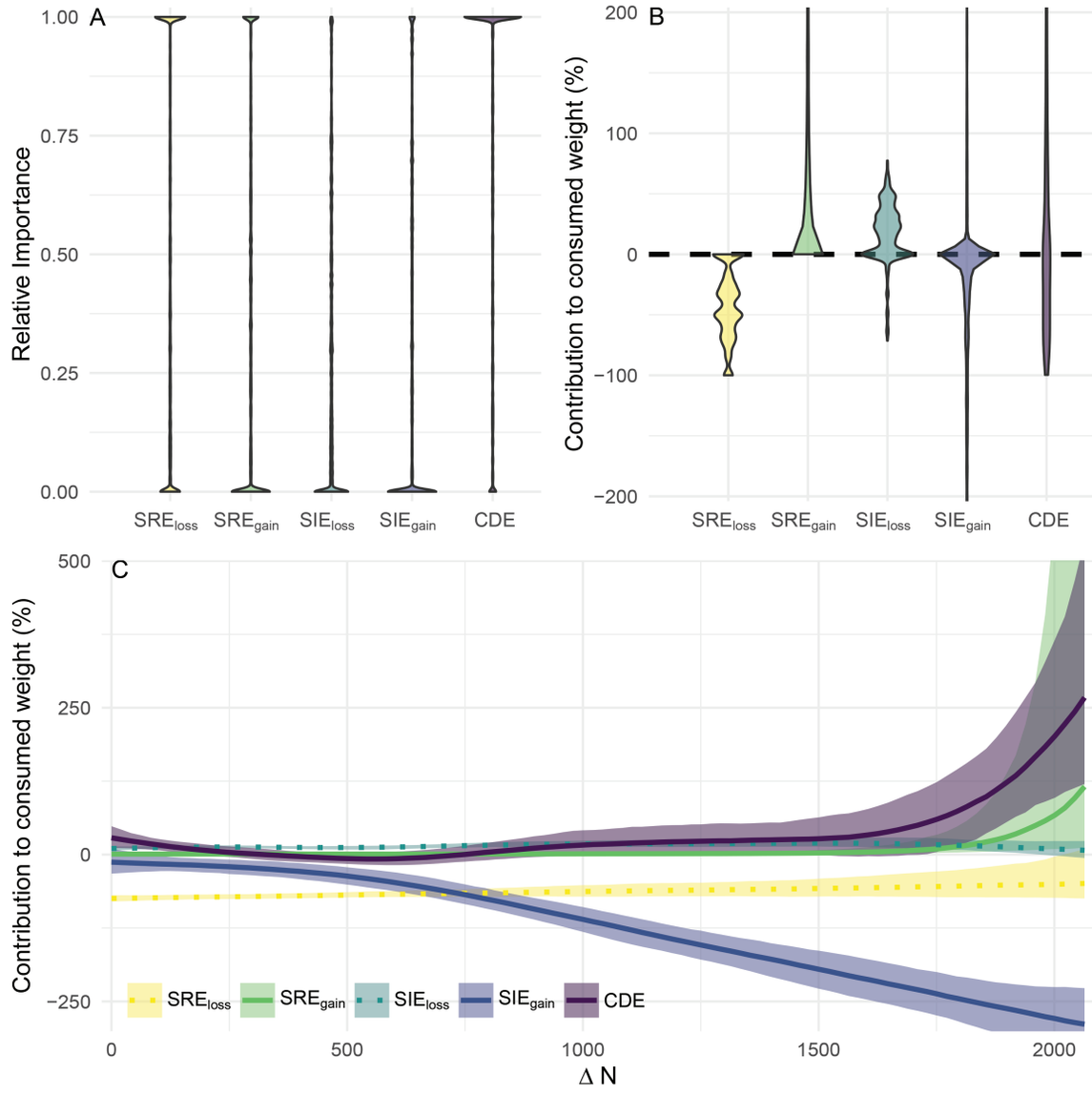


Figure 4: *A*, Relative importance of the four components of the Price equation for all pairwise comparisons of wood falls: SRE_{gain} (random gains of species with average function), SRE_{loss} (random losses of species with average function), SIE_{gain} (nonrandom gains of species with above- or below-average function), SIE_{loss} (nonrandom losses of species with above- or below-average function), and CDE (changes in the functional contribution of species shared between communities). Each component quantifies a distinct process contributing to differences in total wood consumed (ecosystem function) between communities. The vertical axis represents the mean relative contribution of each component across all pairwise comparisons. *B*, Contribution of each Price component to differences in wood mass loss, standardized as a percentage of baseline ecosystem function (100% represents a doubling of function). The *y*-axis is limited to ±200% for clarity, capturing >80% of values for all Price components. *C*, Contribution of Price components to differences in wood mass loss in relation to differences in xylophagous bivalve abundance between wood falls. Lines indicate mean predictions from generalized additive models, and ribbons represent the 2.5% and 97.5% percentiles of the posterior distributions. Dashed lines for SRE_{loss} and SIE_{loss} indicate that these models had predictive accuracy similar to intercept-only null models.

Redundancy versus Complementarity in Isotopic Niches

These trophic patterns suggest that syntopic xylophagous bivalves partition resources to maximize energy extraction from their environment. This could be accomplished in two ways. First, potential spatial partitioning of species within a wood fall can be reflected by isotopic complementarity when different portions

of the wood fall vary in isotopic composition. Indeed, individual wood falls systematically varied by up to ~3‰ in both $\delta^{13}C$ and $\delta^{15}N$, depending on tree species (table S2). We quantified the spatial positions and burrow characteristics of four xylophagous bivalve species within a single wood fall and found evidence consistent with spatial niche partitioning across multiple dimensions, including burrowing depth, surface preference, and location along the wood fall. These differences appear to be associated with species-specific morphologies and behaviors, supporting the plausibility of spatial partitioning despite the lack of replication across multiple wood falls (supplemental PDF, "Spatial Niches," figs. S9–S11).

Second, there could be species-level variation in how xylophagous bivalves assimilate nutrients, influenced by the symbiotic gill microbiome communities they host and perhaps even the sources of nitrogen (Distel and Roberts 1997; Fagervold et al. 2014; Voight et al. 2020). In the case of low-nitrogen diets (here, wood-boring bivalves; this applies to many herbivores), symbioses can allow animals to obtain nitrogen via pathways of nutrient input that would otherwise not be available. We found that bivalve $\delta^{15}N$ was 1‰ lower to 9‰ higher than the $\delta^{15}N$ of the species of wood on which they were found (because of the challenge in measuring $\delta^{15}N$ in wood, bivalves were not necessarily compared to samples of their exact wood fall). Bivalves with low $\delta^{15}N$ that was similar to wood may have assimilated wood nitrogen with little isotopic fractionation, as well as possibly supplementing this resource with newly fixed nitrogen from symbionts, which would have a $\delta^{15}N$ value of ~0‰ (Somes et al. 2010). Bivalves with high $\delta^{15}N$ that was substantially greater than that of the wood may have also digested the symbionts themselves (causing a nitrogen isotope fractionation of ~3‰, associated with a trophic level), as well as possibly assimilating an alternative nitrogen source, such as particulate organic matter. Voight et al. (2020) found similar $\delta^{15}N$ variation among wood-boring bivalves and likewise concluded that mixotrophy must be occurring. Regardless of the exact pathways employed by each species, the variation in isotopic values and niches indicates a partitioning of resources. This may also be supported by the fact that some xylophagous species may preferentially colonize one type of wood over others (Romano et al. 2013).

Redundancy versus Complementarity in Population Size and Dominance Effects

Variation in population sizes and occupancy across wood falls translated into species varying in their importance to ecosystem function. In general, the presence of a numerically dominant species increased ecosystem function (positive effects for the four most abundant species; table 1). These four species may also possess other traits that maximize functionality beyond numerical dominance because they possess unique morphological characteristics not captured in the study here (Sasaki and Lauenroth 2011). Changes in population sizes across wood falls for most species (i.e., other than the four most abundant) were not associated with changes in ecosystem function. This result may reflect the lack of variation in populations sizes as relative ranks remained the same among wood falls. However, the presence of three rare species was also associated with increased total wood consumption. Overall, the results suggest a synergy between dominant and rare species in contributing to ecosystem function, reflective of findings that species on opposite ends of the dominance-to-rarity spectrum contribute to functional diversity that enhances ecosystem function (Mateo-Tomás et al. 2017; Chapman et al. 2018). The presence of rare species may reflect greater larval attraction to wood falls highly consumed by the four dominant species that may have created stronger settlement cues through wood degradation.

Community Attributes: Total Abundance and Diversity

The species-level findings of trophic complementarity, along with significant species presence effects, suggest that a BEF relationship could exist. Indeed, wood falls that possessed more abundant and diverse xylophagous bivalve communities were more fully consumed. The least diverse wood falls with just a single species had on average 17% of the wood consumed by the end of the experiment, while the most diverse wood falls with seven or eight species had on average 44% consumed, a 2.6-fold increase in ecosystem function. However, the relationship with richness was likely driven by changes in total abundance, as the best models did not include richness when abundance was included (tables S3, S4). This finding suggests that the first-order richness-function relationship of BEF may be reflective of the classic species-abundance power relationship (Preston 1962). In this context, BEF may be a spurious correlation simply reflecting that more individuals translates into both greater function and greater species richness (Bengtsson 1998). This strong and consistent correlation between total abundance and ecosystem function suggests that the total abundance of common species, not species richness, is driving ecosystem function (Winfree et al. 2015).

Overall, species and phylogenetic diversity were poor proxies for capturing the actual functional diversity present within the community occurring in these communities and for predicting ecosystem function. Niche axes

of the species—whether population size or isotopic partitioning—were more important than richness or phylogeny per se. This result has also been found in other naturally assembled communities (Teixidó et al. 2018; van der Plas 2019; Genung et al. 2020). Importantly, the BEF relationship here reflects more than the simple effect of the total abundance of common species, suggesting complex underlying relationships dependent on traits. While the greatest amount of wood consumed occurred in the most abundant communities, variation isotopic niche width outperformed species or phylogenetic diversity in predicting function.

Community Attributes: Species Gains and Losses

Ecosystem function was mediated by the population sizes of a core group of species. The Price analysis revealed that functional changes within shared species (CDE) were more important (0.72 mean relative importance) than other components, such as random species losses and gains (SRE: 0.51 and 0.36) and nonrandom species losses and gains (SIE: 0.29 and 0.30). CDE became greater at higher xylophagous bivalve total abundance, while the effects of nonrandom species gains were increasingly negative, suggesting that new species were rare and/or functionally lower on average. The estimated effect of the CDE component increased approximately fourfold, as differences in total abundance between wood falls increased from 0 to 2,000 individuals. As species were lost, core species were also less abundant and consumed less wood, further reducing ecosystem function. In general, ecosystem function was primary driven by changes in the abundance of numerically abundant core species. In the ecological Price equation approach we use, it is possible that positive effects of rare species on the dominant species could allow dominant species to be more abundant on some logs; in this case, the rarer species would be contributing to the CDE. However, we did not see any obvious evidence for this in the site-by-species abundance patterns, which showed no correlation between wood-fall-level abundance and richness.

Conclusion

The deep sea is strongly food limited, and this scarcity of energy fundamentally shapes ecological processes (Smith et al. 2008; McClain et al. 2020). In this context, wood-fall habitats represent localized "oases," supporting higher biomass and greater species diversity than the surrounding environment (McClain et al. 2025). However, these resources are ephemeral: the available energy declines over time as the wood is consumed and the habitat itself degrades (McClain et al. 2025). This temporal and energetic limitation may influence the relative roles of abundance and diversity in driving decomposition. When energy is the primary constraint, communities may not reach saturation, and ecosystem function is dominated by the total abundance of consumers rather than species richness per se. Consequently, it is perhaps unsurprising that abundance emerged as the strongest predictor of decomposition in our study. These dynamics likely extend to other ephemeral resource habitats where regenerative processes are dominant—such as carrion, fallen forest trees, and other temporally constrained nutrient patches—emphasizing that energy limitation and resource ephemerality can modulate the relationships between biodiversity and ecosystem functioning in decomposition-driven systems (Butterworth et al. 2023).

Our work adds to the limited number BEF studies in metazoans, marine systems, and particularly the deep ocean (Danovaro et al. 2008; Leduc et al. 2013; Thurber et al. 2014) through a novel field experiment with realistic abundance distributions and natural community assemblies on the deep-sea floor. Overall, we find that while there is a significant relationship between species richness and ecosystem function, the underlying processes that drive this pattern are more complex and the BEF relationship was driven by changes in total abundance—specifically, the populations sizes of key species, including both dominant and rare taxa. This result is supported by both the Price equation analysis and the species randomization models. The relationship between abundance and function is consistent with theoretical predictions for systems with variable abundances and weak interactions among species (Harrison et al. 2022). This is modestly supported by isotopic partitioning among species that could potentially limit interactions as well as xylophagous total abundance spanning four orders of magnitude across wood falls. Together, these results suggest that diversity per se is less important than the presence and population sizes of functionally important species (Huston and Gilbert 1996; Huston 1997; Wardle et al. 2000). We also demonstrate that many of the species in this system are complementary, possessing unique functional roles in the community. In communities with limited functional redundancy, ecosystem function is particularly vulnerable to biodiversity loss.

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Statement of Authorship

C.R.M. and S.D.N. conceptualized the study, secured funding, developed the methods, collected and analyzed data, performed coding and simulations, wrote the original draft, revised the manuscript, and supervised the project. M.G. contributed to methods development, data analysis, coding and simulation, and writing of both the original draft and revisions. G.W.H. assisted with data collection and writing of the original draft. P.J.M. contributed to methods development, data collection, data analysis, coding and simulation, and writing of the original draft. C.M.B., A.S.H., and C.R. contributed to data collection, with C.R. also assisting in drafting the original manuscript. S.R.D.B. contributed to data collection, data analysis, and writing of the original draft. J.R.J. contributed to methods development, data analysis, coding and simulation, writing of the original draft, revisions, and supervision. C.N. contributed to conceptualization, methods development, and data collection. G.W.R. contributed to methods development, data collection, data analysis, writing of the original draft and revisions, and supervision. J.P.W. contributed to methods development, data collection, data analysis, and writing of both the original draft and revisions.

Data and Code Availability

Data and code are available from GitHub (https://github.com/crmcclain/gom_ecosystemfunction) and Zenodo (https://doi.org/10.5281/zenodo.18853739; McClain 2026).

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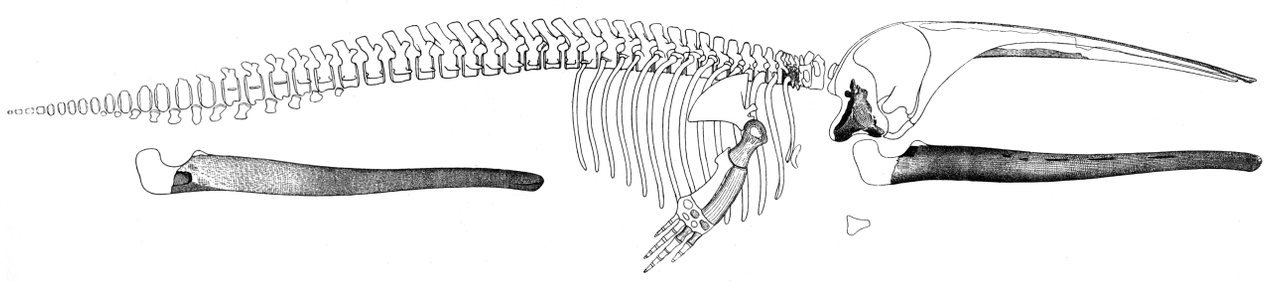
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"*Cetotherium cephalus* Cope. . . . The portions shaded are the actual specimens of one individual found in the Miocene of Maryland, and now in the Museum of the Academy of Natural Sciences of Philadelphia." From "The Cetacea" by E. D. Cope (*The American Naturalist*, 1890, 24:599–696).