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Metabolic Niches and Biodiversity: A Test Case in the Deep Sea Benthos

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The great anthropogenic alterations occurring to carbon availability in the oceans necessitate an understanding of the energy requirements of species and how changes in energy availability may impact biodiversity. The deep-sea floor is characterized naturally by extremely low availability of chemical energy and is particularly vulnerable to changes in carbon flux from surface waters. Because the energetic requirements of organisms impact nearly every aspect of their ecology and evolution, we hypothesize that species are adapted to specific levels of carbon availability and occupy a particular metabolic niche. We test this hypothesis in deep-sea, benthic invertebrates specifically examining how energetic demand, axes of the metabolic niche, and geographic range size vary over gradients of chemical energy availability. We find that benthic invertebrates with higher energetic expenditures, and ecologies associated with high energy demand, are located in areas with higher chemical energy availability. In addition, we find that range size and location of deep-sea, benthic species is determined by geographic patterns in chemical energy availability. Our findings indicate that species may be adapted to specific energy regimes, and the metabolic niche can potentially link scales from individuals to ecosystems as well as adaptation to patterns in biogeography and biodiversity.

Keywords: energetic, metabolism, adaptation, diversity, niche

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INTRODUCTION

As demonstrated by several environmental indicators anthropogenic impacts on the environment continue to exhibit a long-term, post-industrial rise (Steffen et al., 2015). This human induced environmental degradation has led to significant declines in global biodiversity including increasing numbers of endangered species and decreasing abundances of key taxa (Lotze et al., 2006; Butchart et al., 2010). Alarmingly, this decline of species diversity in response to climate change is a factor of four greater in marine systems as compared to terrestrial systems (Blowes et al., 2018). Much research has been dedicated to alterations of the marine environment as

a function of several key parameters – including temperature, acidification, oxygen, and pollution – and how these have and will impact marine communities (Kennish, 1997; Harley et al., 2006; Vaquer-Sunyer and Duarte, 2008; Kordas et al., 2011; Doney et al., 2012). Much less research exists in characterizing how marine ecosystems will respond to the immense anthropogenic alterations to carbon cycling and availability, especially in the deep oceans, the largest habitat on Earth and the key in long-term sequestration of carbon.

We propose an eco-evolutionary adaptive theory of the metabolic niche (Wilson et al., 2011) where species are adapted to specific energy regimes which scale with biodiversity patterns. We hypothesize that the species observed in a locality are dependent on the energy content of that habitat. Here, we develop this hypothesis through a series of 10 linked propositions, from first principles of metabolic ecology through to biogeographic patterns in metabolic adaptation. For each of these propositions, we review current support and theory from a general eco-evolutionary viewpoint and specifically with a deep-sea perspective. The deep-sea benthos provides an ideal test system for metabolic hypotheses because the system is productivity limited, experiences little temperature variation, and has documented clines over productivity gradients (Gage and Tyler, 1991; Tittensor et al., 2011; McClain et al., 2012a; McClain and Barry, 2014; Woolley et al., 2016). The deep seafloor, which encompasses depths below 200 m, covers most of Earth and is an especially energy-deprived system (Gage and Tyler, 1991). Primary production is virtually absent in these dark depths. The carbon that sustains most deep-sea seafloor life is sequestered from sinking particulate organic carbon (POC) derived from primary production in the euphotic zone (Gage and Tyler, 1991). However, temperature is relatively constant over the deep seafloor varying between -1 and 4°C (Gage and Tyler, 1991), allowing us to examine the role of productivity largely independent of the role of temperature. Previous studies have also demonstrated that biodiversity patterns in the deep ocean are controlled primarily by productivity with a weaker or non-existent effect of temperature (Tittensor et al., 2011; McClain et al., 2012a; McClain and Barry, 2014; Woolley et al., 2016). For many of the propositions, we bring new data from deep-sea, benthic invertebrates to bear to quantify and specifically test the hypotheses.

PROPOSITION 1: LIFE REQUIRES ENERGY

Premise

Energy is the currency of life, intrinsically linked to ecological (Brown et al., 2004) and evolutionary (Van Valen, 1976; Bambach, 1993) processes and driving fitness through growth, maintenance, and reproduction (Van Valen, 1976). Four basic forms of energy affect biological systems – photosynthetically active radiation; thermal kinetic energy as indexed by temperature; mechanical energy in the form of movement of air, water, and earth; and chemical potential energy stored in reduced carbon compounds (Denny, 1999; Clarke and Gaston, 2006) – encompassing the fundamental axes which together form an organism's energetic niche.

Metabolic rate is the rate of chemical energy uptake, transformation, and allocation (Brown et al., 2004). In heterotrophs, this energy is obtained by oxidizing carbon compounds; the respiration rate of chemical energy is the metabolic rate (Brown et al., 2004). Thus, the energetic needs of an organism are its total organic carbon demand. We define carbon availability as the amount of organic carbon available for an organism to consume and in part can be viewed analogous to the more general term of food.

Here, we restrict our use of the term *energy* to chemical potential energy, or organic carbon, following the conventions of species-energy theory (Wright, 1983; Wright et al., 1993; Hurlbert, 2004, 2006). For terrestrial and shallow-water systems, productivity, e.g., net primary production, is often used as a metric for chemical energy. For the deep-sea benthos, organic carbon availability is often quantified as either POC flux or organic carbon in the sediment. Note that organic carbon may also arrive to the seafloor through large food parcels such as whale carcasses, macroalgae, jellyfish, and wood. However, these larger food falls are isolated and scarce both in time and space, due to the immense scale of ocean basins, so while they are locally important at certain times, background levels of organic carbon availability are more general drivers of deep-sea diversity. Promisingly, previous studies have demonstrated that macroecological patterns in the deep-sea benthos are highly correlated with POC flux (Tittensor et al., 2011; McClain et al., 2012a; McClain and Barry, 2014; Woolley et al., 2016). This suggests that POC represents a reasonable metric for understanding the chemical energy available to deep-sea benthic organisms.

Consequence

This basic requirement of energy can be quantified for each organism and potentially inform about biological patterns from the individual up to the ecosystem.

PROPOSITION 2: AGAINST A BACKDROP OF GLOBAL CHANGE IN ORGANIC CARBON AVAILABILITY, UNDERSTANDING THE ENERGETIC NEEDS OF ORGANISMS IS VITAL

Premise

In the oceans, the combination of global phytoplankton production declines over century to decadal timescales (Behrenfeld et al., 2006; Boyce et al., 2010), with more varied responses at regional and local scales (Harding and Perry, 1997; Boyce et al., 2010; McQuatters-Gollop et al., 2011; Rousseaux and Gregg, 2015), indicates significant heterogeneity of anthropogenic impacts and a major reworking of carbon cycling. This alteration of organic carbon availability is predicted to increase with continued anthropogenic disturbance (Chust et al., 2014; Bryndum-Buchholz et al., 2019) potentially leading to

15–30% decreases in biomass in some ocean basins and 20–80% increases in others (Bryndum-Buchholz et al., 2019).

Consequence

The metabolic niche and its relationship to biodiversity is important because of these immense anthropogenic alterations to carbon cycling and availability. Against this backdrop of global change in organic carbon availability, understanding how organisms respond to a changing energetic environment is critical. Changing organic carbon availability can affect aggregate properties of ecological communities such as the number of individuals and species (Wright, 1983; Wright et al., 1993; Brown et al., 2004), but the extent to which species with different carbon requirements and adaptations will vary in their responses to a novel energetic environment is not well known. This has consequences for how we expect ecological communities to be structured, and for predicting winners and losers as we progress into the Anthropocene.

PROPOSITION 3: THE DEEP-SEA BENTHOS IS PARTICULARLY VULNERABLE TO ALTERATIONS IN ORGANIC CARBON AVAILABILITY

Premise

As previously stated, below 200 m the oceans are chemical energy-deprived systems (Gage and Tyler, 1991; McClain et al., 2012a), with deep-sea floor communities reliant on primary production occurring in surface waters sinking in the form of POC (Gage and Tyler, 1991). This supply of chemical energy to the benthos varies as a function of depth because of remineralization and surface primary production, also often decreasing with distance from productive coastal regions (Gage and Tyler, 1991). On the abyssal plains, one of the largest habitats on Earth, with an average depth of 4.4 km, the downward flux of POC represents less than 1% of surface production (Lampitt and Anita, 1997) resulting in an extremely food-limited environment, albeit one with considerable energetic patchiness at a range of spatial scales. The decrease in environmental energy availability is mirrored by substantial decreases in biomass and abundance with depth (often used as a proxy for total energy availability) in benthic faunal groups ranging from bacteria to large mobile fish and invertebrates (Rex et al., 2006; Wei et al., 2010b; McClain et al., 2012a).

Consequence

Nearly every aspect of deep-sea benthic ecology and evolution is driven by this flux of carbon from the sea surface (Smith et al., 2008), and "[t]he presence and persistence of life itself on the ocean-floor can be viewed as a response to organic inputs" (Gooday, 2002). In contrast to shallower ecosystems (Tittensor et al., 2010), deep-sea diversity is primarily driven by patterns of chemical energy and not by other forms of energy such as thermal energy, indexed by temperature (Woolley et al., 2016). As noted by Smith et al. (2008) "Many aspects of ecosystem structure and function in the abyss are strongly modulated by the rate and nature of food flux to the seafloor. Climate change and human activities will alter patterns of sinking food flux to the deep ocean, substantially impacting the structure, function and biodiversity of abyssal ecosystems."

PROPOSITION 4: SUBSTANTIAL VARIATION EXISTS IN METABOLIC NEED, I.E., ENERGETIC NEEDS, ACROSS TAXA EVEN AFTER ACCOUNTING FOR TEMPERATURE AND BODY SIZE

Premise

Under the Metabolic Theory of Ecology (MTE) (Brown et al., 2004), energy is an allocated resource translated into work and mass and further allocated into the fitness-enhancing processes of survival, growth, and reproduction. The energy demand, i.e., the metabolic niche, of an organism in the MTE is largely set by first principles governing the distribution of materials and temperature-related kinetics as indexed by temperature and body size (Gillooly et al., 2001). Metabolic rate can be described by the power-law relationship between organismal size, temperature, and metabolic rate:

$$B = \beta_0 M^b e^{-E/kT}$$

where B is the metabolic rate, β_0 is a normalizing constant, M is mass, b is the scaling coefficient, T is temperature, E the activation energy of the respiratory complex, and k is Boltzmann's constant (Gillooly et al., 2001). Substantial variation–at least 1–2 orders of magnitude–exists in metabolic rates even when standardized for organismal mass and temperature (Glazier, 2005) even among deep-sea organisms (McClain et al., 2012a).

Data and Analysis

We analyze the global dataset of Brey et al. (2010) on relationships between mass, elemental composition and energy content for marine invertebrates to quantify the relationship between mass and respiration rate. We limited the dataset to include only benthic, marine, adult measurements. This includes data for 13,478 individuals from 444 species, 336 genera, 46 orders, 29 classes, and 14 phyla ranging in depths from 1 to 4,420 meters. Complete details on the construction of the database can be found in Brey et al. (2010). Original respiration and mass data from the literature included a wide array of measurement units. All of these were converted into respiration into the energy unit of Joules per day and all masses were converted from dry, ash free dry, wet, or carbon content into Joules. From the database, we analyze log10 of respiration rate (J) as a function of log10 of mass (J) and the inverse of temperature (°K) using a linear model in R Package (R Development Core Team, 2019). The general relationship was visualized utilizing ggplot (Wickham, 2009). Residuals from the linear model were further analyzed with ANOVA to test for significant

differences in the residuals among taxa. Residuals were visualized with ggridges (Wilke, 2018). We then test whether different phyla vary in their typical departure from this relationship by testing for significant differences in the residuals between phyla using ANOVA.

Consequence

Respiration rate is strongly and positively related to mass (**Figure 1**, $p < 0.0001$) across the 13,478 marine invertebrate individuals in our dataset. Even after correcting for mass and temperature, metabolic rate residuals exhibit considerable variation (**Figures 1**, **2**). Moreover, this variation is in part related to ecological and evolutionary differences in higher level taxa (**Figure 2**, ANOVA: $p < 0.0001$, $R^2 = 0.24$). This implies that the energetic need of organisms is set by factors beyond the first principles of distribution of materials and temperature-related kinetics (Gillooly et al., 2001). We thus propose an adaptive model of the metabolic niche where species are *adapted to specific energy regimes* to explain this residual variation.

PROPOSITION 5: THIS VARIATION IN METABOLIC NEED IS ADAPTIVE, I.E., SPECIES HAVE A METABOLIC NICHE

Premise

The metabolic niche represents a series of energetic tradeoffs within an organism that sets overall metabolic need, and is comprised of axes that govern the anatomy, physiology, and behaviors of an organism that increase or decrease these energetic costs. Under this model, we propose that species occur on a continuum of energetic need, from "high-energy taxa" (HET) to "low-energy taxa" (LET), and are thus adapted specifically for temporally and spatially varying levels of carbon availability.

Consequence

This variation in energetic need spans evolution across the tree of life (Uyeda et al., 2017). Major clades of vertebrates exhibit significant differences in scaling, suggesting fundamental evolutionary shifts in the adaptation of metabolic need (Uyeda et al., 2017), and comparative studies have revealed other generalities too, e.g., between endotherms and ectotherms (Nagy, 1987), trophic levels (Carbone et al., 2007), passerines and non-passerines (McNab, 2016), foraging (Childress, 1995), locomotory (Voight and Speakman, 2007; Shen et al., 2010) and predator avoidance strategies (McNab, 1986). Overall, this variation suggests that metabolic rates, while in part controlled by first-order principles, vary considerably within and across clades (Makarieva et al., 2008), and that this reflects trade-offs in energetic demand. Importantly, the links between metabolic rates and well-studied ecological traits or other well-understood mechanisms could be generalized to set up testable predictions in other groups and environmental settings.

PROPOSITION 6: A RELATIONSHIP EXISTS BETWEEN ENVIRONMENTAL AVAILABILITY OF CARBON AND METABOLIC NICHE

Premise

Given this variation in energy needs across the tree of life, we might also expect to observe a relationship between the environmental availability of carbon and the metabolic niche. However, previous research indicates that temperature- and mass-corrected basal metabolic rates do not appear to vary over carbon gradients (Childress, 1995). One possibility to reconcile our theory with this finding would be if basal metabolic rates themselves, as the lowest basic need of organism, were governed by fundamental first principles (Brown et al., 2004) and evolutionarily conserved. In this scenario, field metabolic rates or active metabolic rates indicating work and fitness beyond maintenance may more strongly map onto environmental availability of carbon.

Alternatively, total metabolic demand, accounting for differences in organismal mass, may vary with carbon availability, even if per unit mass metabolic rates do not. To restate, the primary ecological and evolutionary energetic response of species to changes in carbon availability is alterations in body size. Indeed, reductions in body size, and thus total metabolic demand, with declining POC are well documented in the deep sea (Thiel, 1975, 1979; Rex et al., 2006; Wei et al., 2010a; McClain et al., 2012b).

Data and Analysis

Allen (2008) compiled and taxonomically standardized bivalve data from samples collected with an epibenthic sledge during research cruises from 1962 to 1979. The dataset includes 204,068 individuals representing 527 bivalve species from 11 basins and 255 sites ranging in depth from 68 to 5875 m (McClain et al., 2012c). Species-level maximum body size (biovolume) was collected from the literature and biovolume was calculated as length*width^2 (details can be found in McClain et al., 2012b). Intraspecific variation in biovolume is much less than interspecific variation and the choice of using median or maximum body size in mollusks is unlikely to mask ecological patterns (McClain, 2004). Biovolume was converted to wet weight utilizing the conversions in Powell and Stanton (1985). Utilizing published scaling equations for bivalve families and orders (Vladimirova et al., 2003), we calculated metabolic rate (mW). Body size data was not available for all species, reducing the final analyzed dataset down to 475 bivalve species. We estimated POC flux (gC/m^2/yr) from Lutz et al. (2007) for each site. For each species, we calculated the mean POC across all station occurrences for that species. The Lutz et al. (2007) study uses empirically derived sediment trap POC flux estimates compared to remotely sensed estimates of net primary production and sea surface temperature. These data were used to develop an algorithm with coefficients predicting annual POC flux at a given depth from remotely sensed data. We analyzed the log10 of respiration rate (mW) as a function of log10 of POC

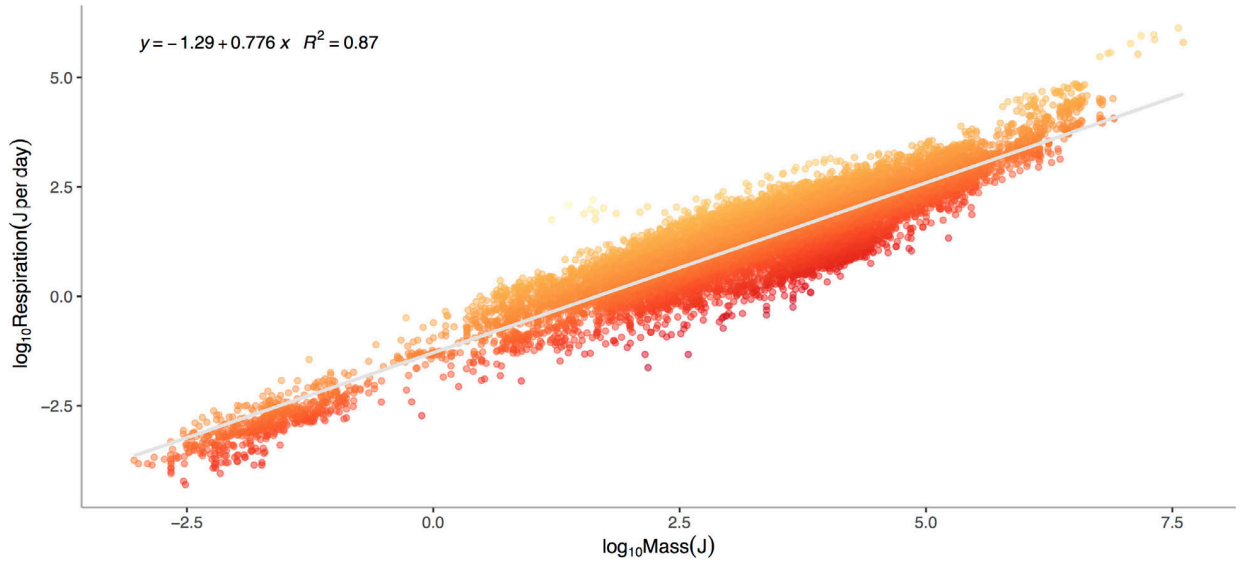

FIGURE 1 | Log_{10} Metabolic Rate (Joules per Day) verses Log_{10} Mass (Joules) for marine invertebrates. Data represent a global database from Brey et al. (2010) on relationships between mass, elemental composition and energy content for marine invertebrates. This includes data for 13,478 individuals from 444 species, 336 genera, 46 orders, 29 classes, and 14 phyla ranging in depths from 1 to 4,420 meters. Colors denote large negative (red) to large positive (orange) residuals of the relationship between respiration and mass.

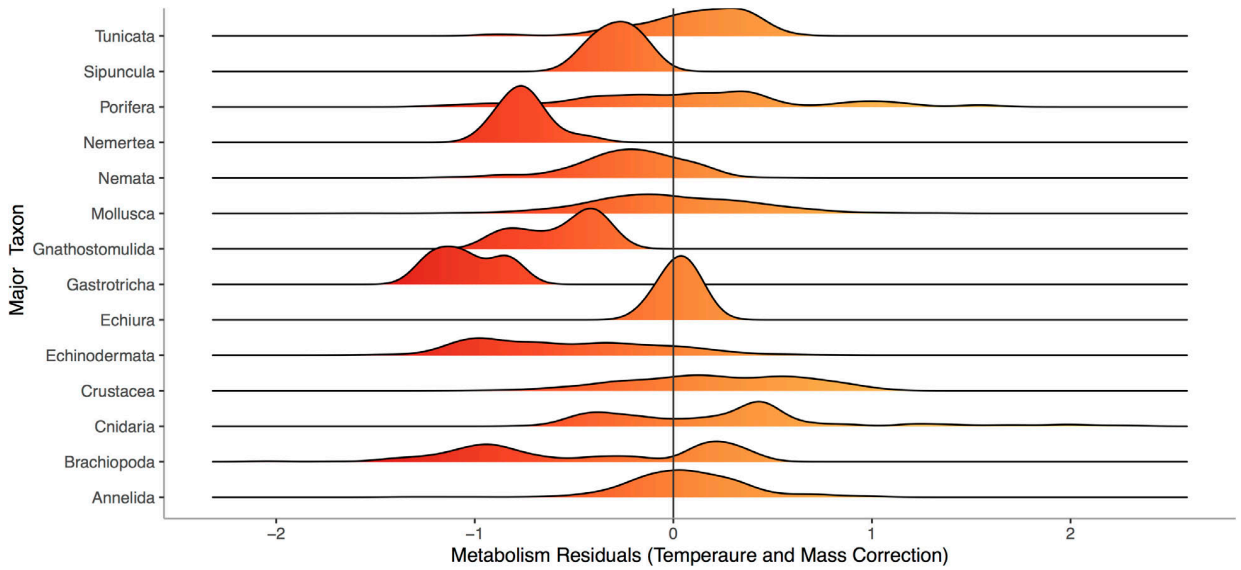

FIGURE 2 | Distribution of residuals for each of 14 phyla from a model fitting Log_{10} Metabolic Rate (Joules per Day) as a function of Log_{10} Mass (Joules) and 1/Temperature (°K), using data from the same 13,478 individuals from 444 species shown in **Figure 1**. Colors denote large negative (red) to large positive (orange) residuals of the relationship between respiration and mass.

flux and using a linear model in R Development Core Team (2019). The general relationship was visualized utilizing ggplot (Wickham, 2009).

Consequence

POC is a significant predictor of total bivalve metabolism ($p < 0.0001$) among 475 deep-sea bivalve species across the Atlantic Ocean (**Figure 3**). The intercepts ($p < 0.0001$) but not the slopes ($p = 0.0627$) of this relationship vary among bivalve orders. These results suggest that a species' total energetic demand, as set by body size, is concordant with energy available in the environment. Additional evolutionary history and ecology associated with higher taxonomic levels also sets additional energetic needs. Thus while body size is a major axis of the metabolic niche, different intrinsic factors of taxa define the other axes.

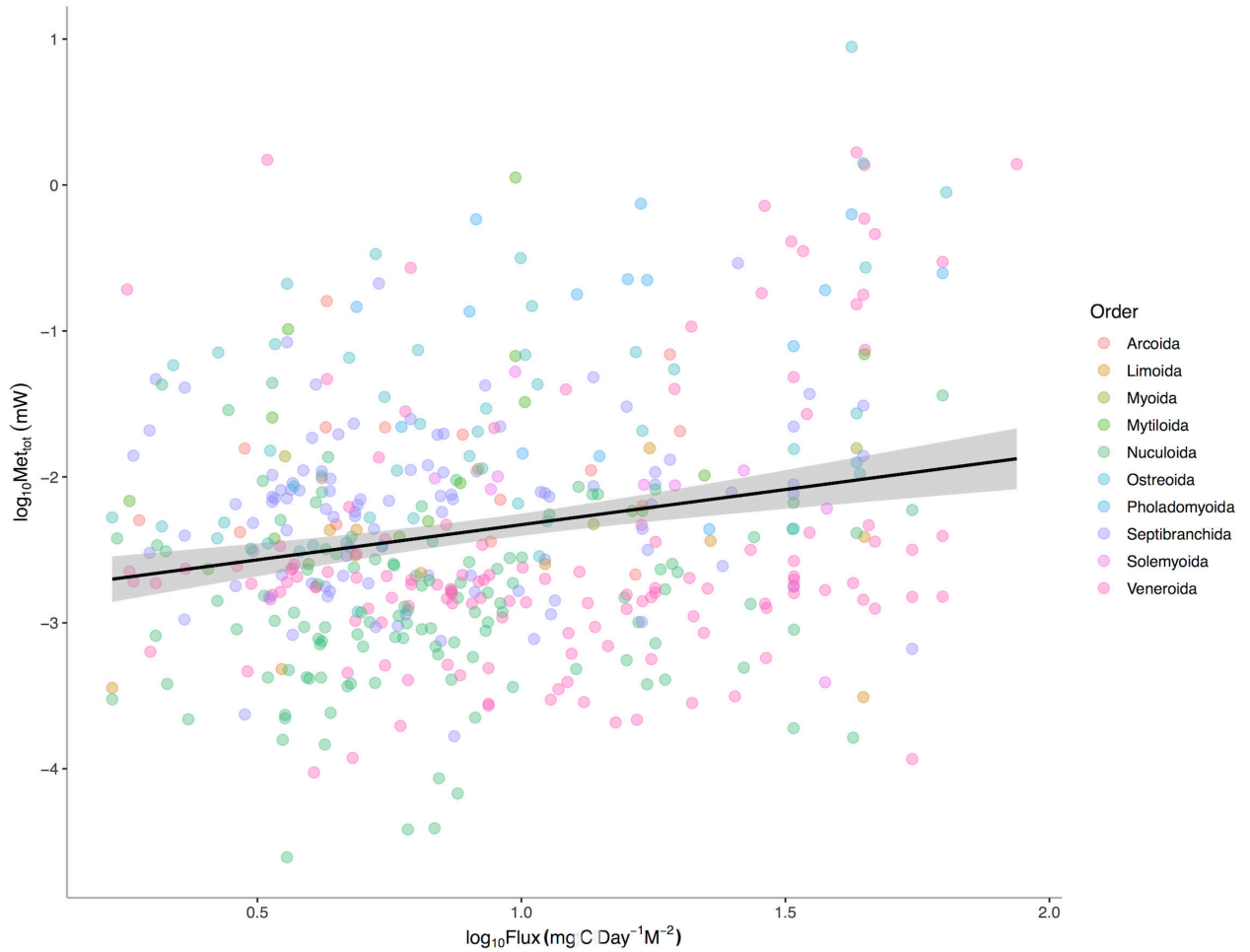

FIGURE 3 | Log_{10} Maximum Metabolic Rate (mW) verses Log_{10} Mean Standardized Carbon Flux (gC m^{-2} d^{-1}) for 475 species of deep-sea bivalves across the Atlantic Ocean. Black line represents linear regression for all species and gray area represents the 95% confidence interval around the linear fit.

PROPOSITION 7: THE METABOLIC NICHE IS THE SUM OF A SERIES OF ENERGETIC TRADEOFFS, THUS THE REPRESENTATION OF ECOLOGICAL TRAITS, AS SET BY THEIR METABOLIC REQUIREMENTS, SHOULD VARY WITH ENVIRONMENTAL AVAILABILITY OF CARBON

Premise

Energetic niche axes can be defined as specific functional traits that dictate overall energetic demand. Thus, quantifying the underlying functional traits and tradeoffs that impact the balance between metabolic intake and demand can be used to define the energetic niche. We can quantify these functional trait tradeoffs and begin to identify the traits of HET and LET, by either exploring how they impact metabolic demand or exploring how functional traits vary over a carbon energy gradient.

We know that energy demand is impacted by the functional traits of the organisms. For example, metabolic rates are higher in endotherms due to the increased costs of maintaining homeostasis (Nagy, 1987). Metabolic rates increase with increasing trophic level (McNab, 1986; Nagy, 1987) in vertebrates (Carbone et al., 2007) and invertebrates (Vladimirova, 2001; Vladimirova et al., 2003) alike, potentially reflecting the increased need for locomotor capacity and range to capture and search for resources at lower densities for carnivores versus herbivores (Tamburello et al., 2015). In the deep sea, temperature- and mass-corrected metabolic rates among species decline with depth in pelagic fish and crustaceans because the attenuation of light leads to a switch from visual-base foraging and a subsequent decline in need for locomotor capacity (Childress, 1995). Prior research indicates that at broad levels, physiological and trophic adaptations lead to a LET to HET spectrum.

A number of traits are known to co-vary with spatial clines in carbon availability. Metabolically expensive morphological characteristics, such as the production and maintenance of complex shells (McClain et al., 2004; McClain, 2005), may

be precluded in low energy environments. The environmental energy availability is also reflected in the trophic niches with, for example, suspension feeders and specialist carnivores declining in importance with decreasing carbon availability (Sokolova, 1960; Gage and Tyler, 1991). In some circumstances, lower carbon availability and resource competition may drive species to exploit and specialize on new carbon resources (Sanders, 1977), as observed in deep-sea polychetes (Jumars et al., 1990) and, anecdotally, in the occurrence of wood- and bone-eating deep-sea specialists (Turner, 1973; Rouse et al., 2004; Johnson et al., 2010). In general, as carbon availability increases, so too does the prevalence of direct development, while the prevalence of planktonic larval stages decreases (McClain et al., 2014). These findings suggest that some reproductive strategies are too energetically expensive at low carbon availabilities, or arise only when energy is available, and thus may be restricted to HET.

Data and Analysis

Methods and data are from McClain et al. (2018). Data, including carbon flux, were originally taken from McClain et al. (2012b). In brief, data on the taxonomy, maximum and minimum water depth in meters, maximum and minimum longitude, and maximum and minimum latitude were compiled for bivalves in the Northeast Pacific and Northwest Atlantic through an extensive search of the primary literature and online databases. The final dataset includes complete information for 1578 species from 75 families.

Over each species' biogeographic range, we estimated POC flux (gC/m2/yr) from Lutz et al. (2007) model (equal-area grid of 9 km resolution) as described above. These values were previously determined as part of another study (McClain et al., 2012b). For each species, McClain et al. (2012b) quantified the mean, median, and standard deviation of carbon flux over their known latitudinal and depth ranges. For the analyses here, we used mean carbon flux only as mean and median fluxes are highly correlated (Spearman's rho = 0.94, $p < 0.0001$). We created a range map for each species based on its latitudinal range. This range map was then overlain onto a bathymetry layer (GEBCO 08, 30 arc-second grid, September 2010 release)[1] and cropped to regions between the minimum and maximum reported depth. We assumed a species' range represents an elongated band with North/South limits set by maximum and minimum reported latitude. East/West limits were set by depth, instead of longitude, because North American coasts run approximately south to north with species occurring in depth bands along the continental margins. POC flux values were pulled for each cell within a species' biogeographic range as defined minimum and maximum latitude and depth.

We classified species according to a framework for ecological modes that is based on the first principles of functional morphology and developed by Bambach et al. (2007) and Bush et al. (2007). The ecological mode of a species is defined by three axes: tiering, motility, and feeding. Each axis consists of six categorical states. The tiering axis consists of pelagic, erect, surficial, semi-infaunal, shallow infaunal, and deep infaunal. The motility axis consists of freely motile/fast; freely motile/slow; facultatively motile/unattached; facultatively motile/attached; non-motile/unattached; and non-motile/attached. The feeding axis consists of suspension feeding, surficial deposit feeding, mining, grazing, predatory, and other (for feeding strategies that do not fit into the previous five feeding modes). Bush et al. (2007) provide a full description of this ecospace model. Ecological mode assignments were made at the genus level. Huber (2010) describes the life habits of individual bivalve families, and in the cases where genera within families are known to differ from one another, notes which genera differ and how they differ from other genera in the family. All ecological assignments were based on the life habits of the adult form. In the exceedingly rare cases where a genus occupied more than one ecological category for a given axis as an adult, the single ecological category that describes the majority of species in the genus was chosen. For the modern bivalve range dataset, we were able to assign ecological modes to 1,477 of 1,578 species by matching species to genera.

We conducted a correlation analysis of mean POC fluxes among ecological modes, to elucidate which modes were associated with HET and LET, comparing the mean POC values determined with the Atlantic data to those determined with the Pacific data using Spearman's *rho* statistic to estimate a rank-based measure of association. This allowed us to examine whether high-energy or low-energy ecological modes were consistently found in high- or low-energy settings using independent lists of species and independent ocean basins. We also tested whether the representation of ecological modes differs between the overall higher productivity Pacific Ocean and lower productivity Atlantic Ocean. For the Atlantic and Pacific oceans separately, we calculated the proportion of each species within each ecological mode. We then calculated the difference in the proportion of species within each ecological mode between the Atlantic and Pacific oceans and compare that to the mean carbon flux of the ecological mode. We predict that ecological modes more strongly tied to higher POC fluxes will occur at higher proportions in the Pacific compared to the Atlantic Ocean due to the overall higher productivity in the Pacific. We tested this relationship using a general linear regression model with mean POC flux of the ecological mode as the independent and the Atlantic/Pacific ratio of the proportion of species as the dependent variable. Linear models were performed in R Development Core Team (2019). The general relationship was visualized utilizing ggplot (Wickham, 2009).

Consequence

Ecological niche axes in modern bivalves over oceanic scales are correlated with the available environmental energy (McClain et al., 2018; **Figures 4**, **5**). More specifically, the basic functional traits of feeding mode, tiering level, and motility level are associated with their relative prevalence in low- or high-energy settings (McClain et al., 2018). The strong consistency between the rank orders of ecological modes based on carbon flux between the Atlantic and Pacific Oceans, observed across independent lists of endemic species, implies that the association between ecological mode and carbon flux is also not an artifact of indirect connections but, rather, a fundamental aspect of these ecological

[1] www.gebco.org

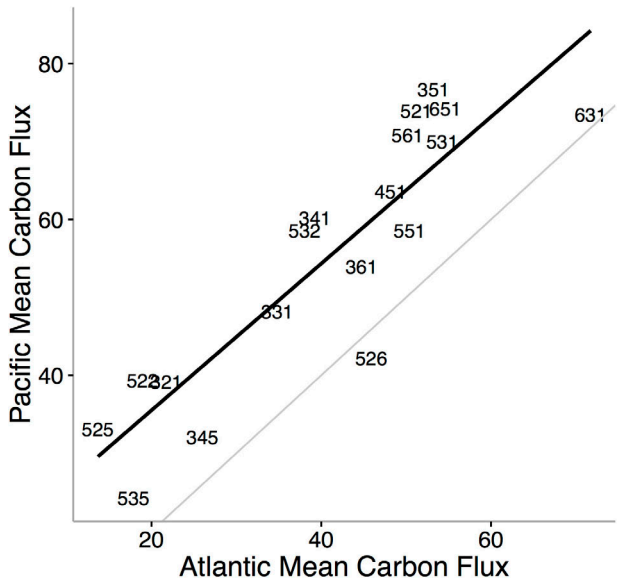

FIGURE 4 | Mean carbon flux of bivalve ecological modes in the Pacific Ocean versus the mean carbon flux of ecological modes in the Atlantic Ocean. Black line denotes the rank order correlation and the gray line represents the one-to-one value line. Numbers refer to unique functional combinations on three ecological mode axes: tiering, motility, and feeding. Each axis consists of six categorical states. The tiering axis consists of 1 pelagic, 2 erect, 3 surficial, 4 semi-infaunal, 5 shallow infaunal, and 6 deep infaunal. The motility axis consists of 1 freely motile/fast; 2 freely motile/slow; 3 facultatively motile/unattached; 4 facultatively motile/attached; 5 non-motile/unattached; and6 non-motile/attached. The feeding axis consists of 1 suspension feeding, 2 surficial deposit feeding, 3 mining, 4 grazing, 5 predatory, and 6 other (for feeding strategies that do not fit into the previous five feeding modes). Using independent values of mean carbon flux for ecological modes by restricting the analysis to species endemic to either the Atlantic or the Pacific, we find striking consistency in the ranking of carbon flux requirements in bivalve ecological modes. The finding that most ecological modes are typically associated with higher flux values in the Pacific Ocean is not surprising; the Pacific is on average more productive than the Atlantic (Marra et al., 1987; Lutz et al., 2007). From McClain et al. (2018).

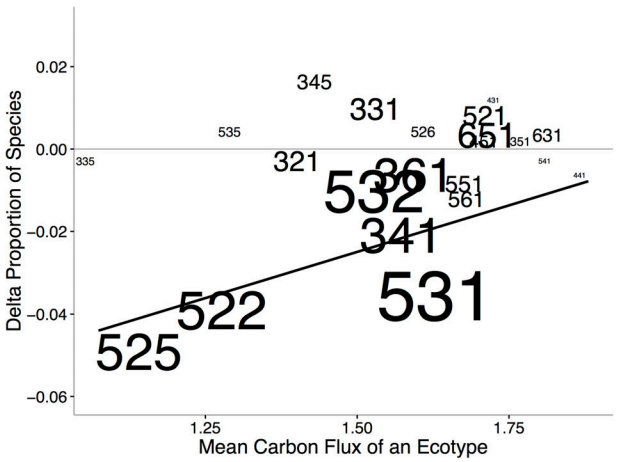

FIGURE 5 | Changes in the proportion of ecological modes between the Atlantic and Pacific Oceans verses the mean carbon flux of the ecological mode. Increases in values indicate increased representation in the Pacific and decreased representation in the Atlantic. Size of text indicates ecological-mode proportion in the data set. Numbers refer to unique functional combinations on three ecological mode axes, tiering, motility, and feeding (see **Figure 4** caption for details of numbers). We find that HET associated with higher POC fluxes occur in greater proportion in the Pacific Ocean and, conversely, LET occur in greater proportion in the Atlantic. From McClain et al. (2018). Dashed line represents in proportions in the Atlantic and Pacific Oceans. Solid line indicates significant regression line.

modes (**Figure 4**). Ecological differences among ocean basins, correlated with differences in POC, provide evidence that overall food availability at broad scales can shape the ecology of the regional to global biota (**Figure 5**). The differences in total carbon flux between the Atlantic and Pacific Ocean determine the relative proportion of specific bivalve ecologies (**Figure 5**). In the more productive Pacific, HET ecologies are numerically dominant, and conversely, in the less productive Atlantic, LET ecologies are numerically dominant (**Figure 5**).

In many cases, empirical results are surprising and contrary to theoretical predictions. Simultaneous hermaphroditism, predicted to increase with decreasing environmental carbon availability as low populations sizes would decrease the chance of finding a mate, actually show the opposite pattern in deep-sea mollusks (McClain et al., 2014). These kinds of counter-theory findings suggest that much work is required in order to elucidate patterns of functional tradeoffs and adaptation over energetic gradients. Emerging research does support the presence of certain metabolically expensive traits that can be tied to low-energy and high-energy taxa (LET vs. HET) such that their relative representations vary over energetic gradients. We analyzed the Atlantic deep-sea bivalve database with a general additive model (GAM) to examine how two common traits, suspension and deposit feeding, vary with POC flux. We find (**Figure 6**) that the proportion of species of suspension feeding increases ($p < 0.0001$, $R^2 = 0.19$) and deposit feeding decreases ($p = 0.0030$, $R^2 = 0.11$) with increasing POC flux. Suspension feeders require a continuous supply of suspended particulate matter at a density high enough to offset the energetic costs of filter feeding; thus, the link to regional carbon fluxes is predictable (McClain and Lundsten, 2015).

PROPOSITION 8: METABOLIC NICHE WIDTH INCREASES WITH INCREASING ENVIRONMENTAL AVAILABILITY OF CARBON

Premise

To the extent that biogeographic range is the realization of a species' niche (Slayter et al., 2013), processes controlling the metabolic niche should impact the size and placement of species distributions. For example, energetically expensive traits such as large body sizes may be confined to high energy regions (Fernández and Vrba, 2005; McClain et al., 2012b). In addition, within a given environmental setting

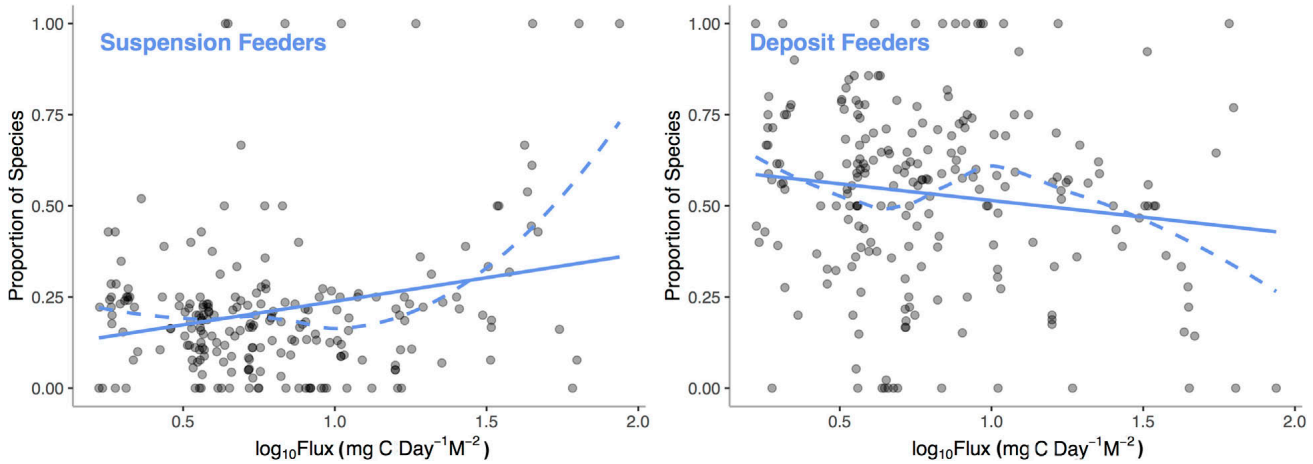

FIGURE 6 | Proportion of deep-sea, bivalve species that are suspension feeders and deposit feeders among sampling stations across the Atlantic Ocean verses Log_{10} Standardized Carbon Flux (gC m^{-2} d^{-1}) for the sampling station. Dashed line represent LOESS smooths and the solid lines represent general additive model fits.

HET are predicted to possess larger biogeographic ranges as home range sizes increase to incorporate the increased food resources required (McNab, 1963; Brown and Maurer, 1987). Energetics may also impact biogeographic range size because of the connections with niche breadth (Slatyer et al., 2013): higher energy availability can lead to smaller ranges because species become resource specialists (Sircom and Walde, 2010; Whitton et al., 2012). Range size is also impacted by the degree of environmental variability in both time and space. For instance, marine bivalves achieve broad geographic ranges across broad, contiguous isotherms (Jablonski et al., 2013; Tomasovych et al., 2015); widespread biogeographic ranges could also be constructed through large and homogenous chemical energetic landscapes. Environmental variables associated with habitat productivity, especially temperature and precipitation, are typically important predictors of species occurrence across taxonomic groups (Bradie and Leung, 2017), supporting the contention that the biogeographic ranges of many species are set, at least in part, by chemical energy availability.

Two different hypotheses relate niche width more generally to carbon availability: (1) Increased carbon availability increases the amount of a preferred resource allowing species to decrease their consumption of less optimal resources, i.e., specialization (Evans et al., 1999). Lower food availability may favor generalists, e.g., scavengers, so that any carbon resources can be utilized, expanding the niche. These hypotheses predict that niche width, or generalism, exhibits a negative relationship with carbon availability. (2) Alternatively, low carbon availability could favor specialization on previously underutilized carbon sources as energy sources become limited, leading to narrow niche widths (Sanders, 1977).

Measuring niche breadth directly is difficult. However, we can use geographic range as proxy, allowing us to test hypotheses. Geographic range is known to reflect niche width such that specialization is associated with smaller geographic ranges (Slayter et al., 2013).

Data and Analyses

We examine this relationship between geographic range size, as a proxy for niche width, and mean POC across the geographic range for gastropod species across the Atlantic Ocean. Data were compiled by McClain et al. (2018) in an extensive search of the primary literature and online databases resulting in complete information a 3,162 species from 100 families. Data include taxonomic information from subclass to species, synonymies, maximum and minimum water depth in meters, maximum and minimum longitude, and maximum and minimum latitude. Biogeographic range and POC were quantified for each gastropod species by the methods described in the Proposition 6 for bivalves. Total range size was calculated as the number of 1° by 1° cells assuming that a species occurs at all sites across its latitudinal and depth range. For the range size verses mean carbon flux, we utilized a GAM to account for potential non-linear effects. The full model also includes other known variants of range size including temperature, mean latitude, mean depth, and species biovolume. The GAM was implemented using the mgcv package in R (Wood, 2011).

Consequence

After accounting for temperature, body size, latitude and depth, we find a significant and positive relationship between geographic range size of Atlantic gastropods and mean POC ($p < 0.0001$, **Figure 7**). Increasing temperature, body size, depth, and latitude also correlated with increases in range size ($p < 0.0001$ for all independent factors) with the overall model accounting for 41.9% of the variation.

Lower carbon availabilities produce smaller geographic range sizes and potentially narrow niche widths. Increases in food availability correlate with larger ranges. This positive correlation is in contrast to most theories suggesting that higher carbon availability should lead to smaller ranges (Evans et al., 1999;

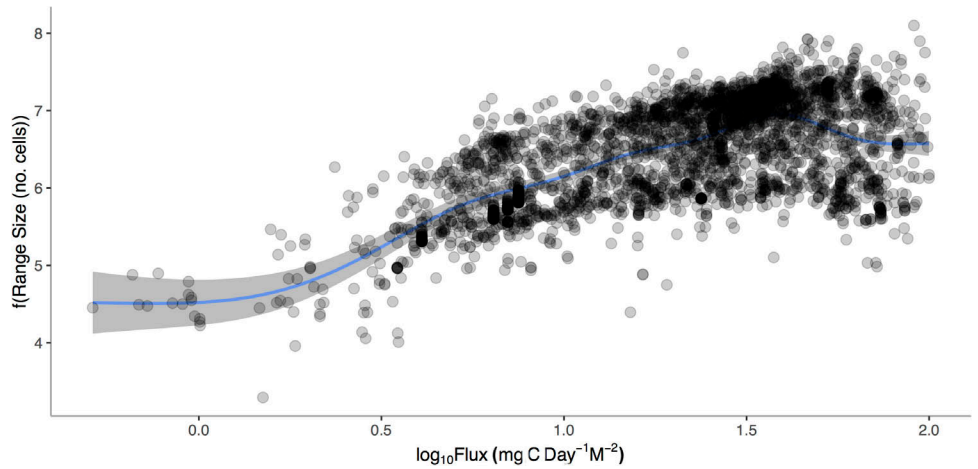

FIGURE 7 | Geographic range size (1°cells) of marine gastropods from the Atlantic Ocean verses Log_{10} Mean Carbon Flux (gC m^{-2} d^{-1}). General additive model relationship is shown for the conditional relationship once body size, mean depth, mean latitude, and temperature are accounted for.

Bonn et al., 2004; Sircom and Walde, 2010; Whitton et al., 2012). One possible reason for this result is that the analyses here control for a variety of other geographic, environmental, and biological factors correlated with body size. Thus, the negative pattern between productivity and range size may reflect other factors correlated with productivity. For example, body size increases with increasing productivity (McClain et al., 2012b). Sanders (1977) originally proposed that low productivity would favor specialization to consume previously underutilized carbon sources. Indeed, the low productivity encountered in the deep sea appears to select for specialization on exotic carbon sources (Van Dover, 2000; Braby et al., 2007; Bienhold et al., 2013).

PROPOSITION 9: IF METABOLIC NICHES, AND ENERGETIC REQUIREMENTS, VARY AMONG SPECIES THEN COMPOSITIONAL CHANGES ARE EXPECTED OVER SPATIAL OR TEMPORAL GRADIENTS OF ENERGY

Premise

Beta diversity (β-diversity) is "the extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments" (Whittaker, 1960, p. 320). β-diversity patterns therefore emerge from the interaction between the environment and the varying metabolic niche requirements (indexed by biogeographic range and patchiness of occupancy within that range) of all species in an assemblage. If metabolic niches, and energetic requirements, do indeed vary among species then compositional changes are expected over spatial or temporal gradients of energy.

Consequence

In support of this, clines of β-diversity over energy gradients have been documented among bacteria (Zinger et al., 2011), invertebrates (McClain and Barry, 2010, 2014; McClain et al., 2011, 2012c, 2016; Andrew et al., 2012), and vertebrates (He and Zhang, 2009; Melo et al., 2009; Qian and Xiao, 2012), on land (He and Zhang, 2009; Melo et al., 2009; Andrew et al., 2012; Qian and Xiao, 2012) and in the ocean (McClain and Barry, 2010, 2014; McClain et al., 2011, 2012c, 2016; Zinger et al., 2011), with the rate of this turnover set by both niche width and the intensity of the environmental gradient in energy availability. At a taxonomic level, species or clades with comparatively higher metabolic demands should exhibit higher rates of turnover (Soininen et al., 2007a,b), because HET will be more sensitive to changes in environmental energy. Any reduction in energy should push HET increasingly near to their energetic minimum requirements. β-diversity does vary greatly among taxa with different body masses, trophic levels, and thermoregulation as predicted from energetic theory based on how these factors control metabolic demand (Soininen et al., 2007a,b).

Despite the overall paucity of energy, the deep seafloor supports high alpha diversity, which may be comparable to much more productive ecosystems such as coral reefs or tropical rainforests. This paradox of seemingly high diversity in a low-energy system is well treated in the deep-sea literature (McClain and Schlacher, 2015) but the most influential idea is the patch-mosaic hypothesis (Grassle and Sanders, 1973). Grassle posited that interactions between the spatially heterogeneous fall of POC and microscale topography such as burrows and mounds, or feeding trails of large mobile deposit feeders, create a mosaic of centimeter scale patches of high and low energy availability (Grassle, 1989) which – unlike in shallow water where patches are homogenized quickly (days to weeks) due to frequent bioturbation and currents – can persist for years (Etter and Mullineaux, 2001). Species are highly specialized in microhabitat preference which leads to an overall diverse mosaic

of assemblages, each with a unique set of species. To restate, species have a metabolic niche that contributes to high small-scale beta diversity increasing local alpha-diversity.

This patchiness is reflected in high species turnover at small scales (Etter and Mullineaux, 2001; Snelgrove and Smith, 2002), and experimental work enriching nutrients in deep-sea colonization trays has underlined the key role that energy plays, with species that are rare or absent in the background environment reaching high abundances in enriched patches (Levin and Smith, 1984; Snelgrove et al., 1992, 1994, 1996; Bernardino et al., 2010; McClain et al., 2011).

PROPOSITION 10: METABOLIC NICHES, AND ENERGETIC REQUIREMENTS, CAN BE USED TO MAKE SPECIFIC PREDICTIONS OF BIODIVERSITY PATTERNS OVER SPATIAL OR TEMPORAL GRADIENTS OF ENERGY

Premise

Increases in available carbon frequently translate into increases in species richness or alpha-diversity (Rosenzweig and Abramsky, 1993; Waide et al., 1999; Clarke and Gaston, 2006; Cusens et al., 2012), either linearly or as a unimodal relationship with richness peaking at intermediate levels of energy. Although a variety of mechanisms exist to explain the relationship between species richness and energy (Rosenzweig and Abramsky, 1993), here we explore only how understanding species metabolic niches may inform about diversity gradients. We envision two different scenarios for patterns of β- and a-diversity over gradients in energy availability in the context of the metabolic niche (**Figure 8**). These differ in whether β-diversity occurs because of the replacement of some species with others (species turnover) or because species loss leads to smaller communities forming ordered subsets of larger communities (nestedness) (Baselga, 2010, 2012). It is worth noting, across energy gradients there is evidence of both nestedness (Baselga et al., 2012; Brault et al., 2013; McClain et al., 2016; Stuart et al., 2016) and turnover (Andrew et al., 2012; Brault et al., 2013; Wagstaff et al., 2014). These two scenarios lead to different predictions of alpha-diversity over a productivity gradient as well.

PROPOSITION 10A: HIGH METABOLIC DEMAND TAXA ARE LOST FROM COMMUNITIES WHEN ENVIRONMENTAL ENERGY DROPS BELOW THEIR METABOLIC NEED

The first scenario predicts nestedness will occur as energy availability falls below the minimum metabolic requirement of certain taxa (**Figure 8**, top). At ecological scales, high-energy habitats offer more niches because more species can meet their minimum energetic requirements, and both LET and HET can persist. LET may survive on patches of low quality, quantity, or density of resources that are not monopolized by HET within these high-energy habitats, i.e., no competitive exclusion occurs. In low-energy habitats, HET are lost because minimum energetic requirements cannot be met. While empirical tests for this idea are lacking, the test is relatively straightforward – the diversity of interspecific metabolic rates should increase with greater energy availability.

If high-energy habitats support more energetic niches, species richness may increase at higher energy availability because species are able to specialize on preferred resources, e.g., a predator consuming a single prey species or a herbivore consuming a single plant, reducing competitive interactions and allowing for greater species coexistence (Evans et al., 2005). Again, empirical tests of this hypothesis are rare but easily conducted: the trophic niche, measured for instance as the variance in $\delta^{13}C$ (a measure of the variability in consumed carbon sources), and the variance in $\delta^{15}N$ (a measure of trophic specialization), should both decrease with increasing energy availability.

PROPOSITION 10B: LOW METABOLIC DEMAND TAXA ARE LOST FROM COMMUNITIES FROM COMPETITIVE EXCLUSION WHEN ENVIRONMENTAL ENERGY IS HIGH

In the second scenario, over a decreasing gradient of carbon availability, the expectation is for LET to replace HET, i.e., turnover (**Figure 8**, bottom). As before, the minimum metabolic demands of HET cannot be met when environmental energy declines, but this scenario additionally assumes that LET do not exist in higher energy availability habitats, because they are competitively excluded by HET that can monopolize resources. To restate, HETs with faster growth rates, population growth rates, increased mobility, and larger sizes may prove to be superior competitors to LETs in high energy environments. This is essentially the second half of the dynamic equilibrium model (Huston, 1979) and is in some aspects very similar to the resource ratio hypothesis in that it invokes competition under high energy availability (Tilman, 1982). The competitive exclusion of LET in high energy habitats predicts a unimodal relationship between α-diversity and energy availability, similar to the interaction competition hypothesis (Rosenzweig and Abramsky, 1993), where all increases in energy go to a competing taxon.

Data and Analyses

We analyze the Allen (2008) bivalve data as described in Proposition 6. We decomposed β-diversity over the POC gradient into two distinct components: species turnover and species loss leading to nestedness using the *betapart* package (Baselga et al., 2013) in R to decompose Sørensen's dissimilarity index $\beta_{SØR}$ into dissimilarity due to turnover measured as Simpson's index β_{SIM} and a new index of dissimilarity due to species loss leading to nestedness β_{NES}. We computed dissimilarity between pairs of sites against the difference in

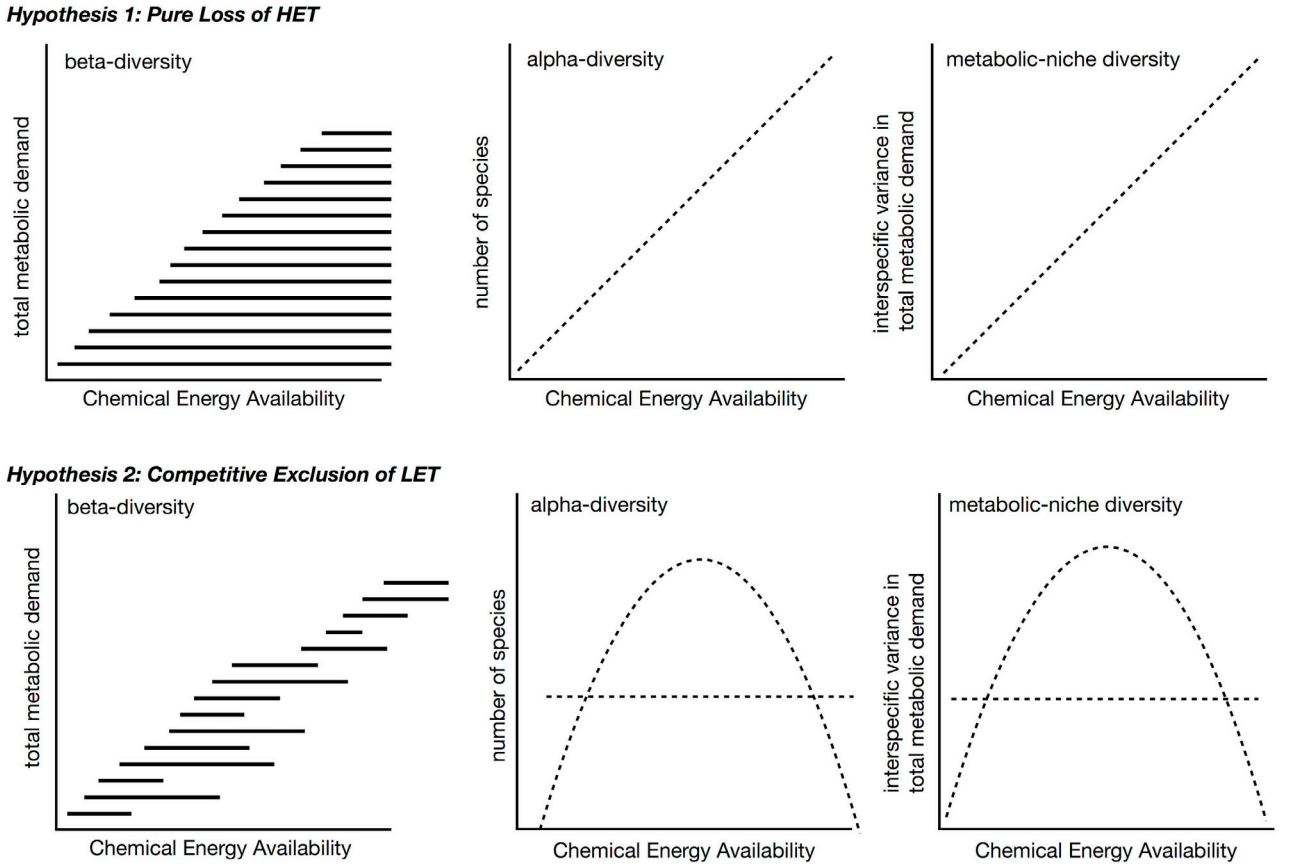

FIGURE 8 | Two hypotheses for beta- and alpha-diversity patterns in the context of metabolic niches. In both scenarios, high energy taxa (HET) are lost from communities as chemical energy availability decreases across a gradient. In the second hypothesis, high chemical energy availability LET are additionally outcompeted, e.g., due to slower populations rates, and are lost from these communities. The competitive exclusion in LET in second hypothesis leads to a unimodal species-energy relationship as opposed to a linear pattern. In both hypotheses, metabolic niche diversity, e.g., interspecific variation in metabolic rate, should mirror the species richness pattern.

depth for each pair (Baselga, 2010). We used a Mantel test with 1,000 replicates (Pearson correlation) to assess whether the components of β-diversity changed among sites along the gradient of POC flux.

Consequence

In our analysis of bivalves from the deep-sea of the Atlantic Ocean, we find that turnover (Mantel Test: $r = 0.1141, p < 0.0001$) rather than nestedness (Mantel Test: r = -0.258, p = 0.904) is prevalent (**Figure 9**) implying that both metabolic competition and limits are important in shaping compositional changes.

In the context of the two scenarios illustrated in **Figure 8**, turnover appears to be prevalent in deep-sea invertebrates over a depth gradient, implying LET are replacing HET and that LET are outcompeted at higher energy availabilities (Brault et al., 2013). Equally, in deep-sea canyons areas with increased POC support only a small subset of species, with the loss coming from competitive exclusion (McClain and Barry, 2010). At larger scales, patterns of taxonomic, functional, and phylogenetic beta-diversity are tied to POC (McClain et al., 2012c), implying that the changes in beta-diversity have an adaptive origin tied to species traits. From local to oceanic spatial scales, a pattern is emerging that the metabolic niche of deep-sea species and its relations to energy availability sets beta-diversity.

However at very low energy values, like those occurring on the abyssal plains, nestedness occurs, reflecting the loss of even LET when energy availability falls below minimum metabolic needs (Rex et al., 2005). Low-energy communities on deep-sea wood falls are also nested taxonomic subsets of high-energy communities (McClain et al., 2016). This switch from turnover to nestedness implies that at extreme energy limitation, evolutionary novelty and adaptation may not be possible; rather, a source-sink system emerges in which populations from higher energy availability regions of the deep sea sustain through emigration populations of abyssal low-energy sites mitigating Allee effects (Rex et al., 2005). This combination of nestedness and turnover is reflected in a general unimodal pattern of alpha-diversity which typically peaks at intermediate depths and levels of POC (Rex and Etter, 2010): in low-energy habitats, HET are lost because minimum energetic requirements cannot be met (Rex et al., 2005), whereas LETs may not be able to survive at the highest energy availabilities because they are outcompeted

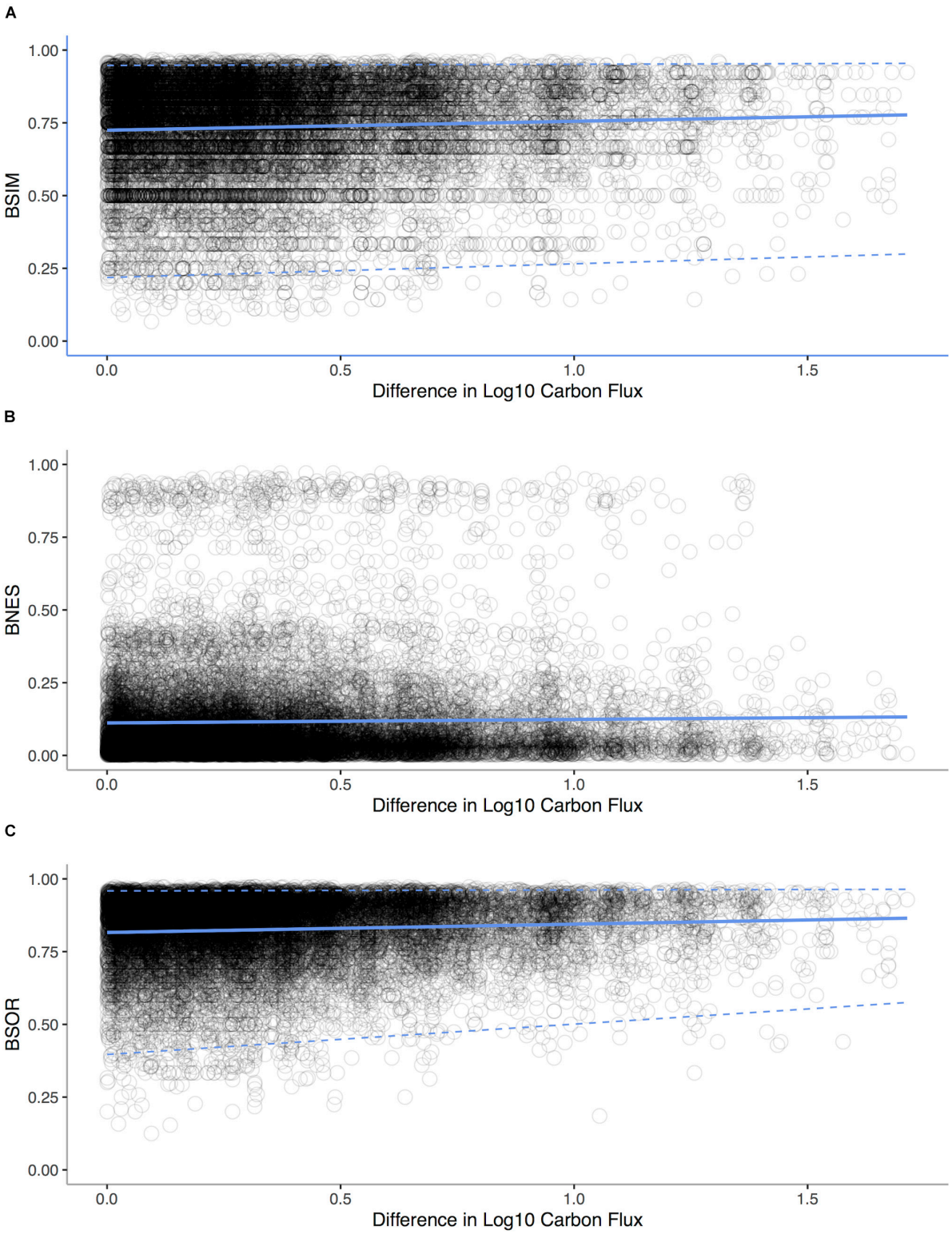

FIGURE 9 | Standard environmental distance-decay plots representing pairwise comparisons of bivalve community similarity verses differences in POC flux for each sampling station in the Atlantic Ocean. **(A)** Simpson's index β_{SIM} of dissimilarity due to turnover vs. difference in Log_{10} Carbon Flux (gC m^{-2} d^{-1}, Mantel statistic r: 0.08, $p < 0.0001$). **(B)** Dissimilarity due to species loss leading to nestedness β_{NES} verses Log_{10} Carbon Flux (Mantel statistic r: -0.03, $p = 0.904$). **(C)** Sørensen's dissimilarity index $\beta_{SØR}$ verses differences Log_{10} Carbon Flux (Mantel statistic r: 0.11, $p < 0.0001$). Regression lines (solid lines) and quantile regressions lines (1 and 99%, dashed lines) are shown.

by HETs that can monopolize resources, as observed in deep-sea canyons (McClain and Barry, 2010).

CONCLUSION

Van Valen (1976) stated that "Potential energy in the form of reduced carbon is the fuel of the fire of life. All other resources, even when regulatory, can be considered surrogates, when they are competed for." This perhaps represents an extreme view, but every aspect of an animal's existence requires carbon. We propose from this simple concept that understanding and quantifying the metabolic niche can potentially link scales from individuals to ecosystems and link adaptation to patterns in biogeography and biodiversity. Energy and the metabolic niche also allow for explicit links between ecological and evolutionary theory. Future avenues of research include addressing the following questions:

(1) Do intraspecific metabolic rates vary over energy gradients?
(2) What is the diversity of and energetic adaptations among organisms and how do these vary over energy gradients? Is a greater diversity of metabolic niches and adaptations afforded at greater energy availability?
(3) Do generalists or specialists prevail at high and low energy habitats?
(4) To what extent are range limits and biogeographic patterns set by the metabolic niche?
(5) Do patterns of α- and β-diversity differ among high and low energy taxa?
(6) Are low energy taxa competitively excluded at high energy availability?

We have outlined how the unique features of deep-sea benthos that make them an ideal testbed for many of these questions, but linking data on the occurrences and biological traits of species with their energetic environmental settings in a range of extreme systems, including deep-sea pelagic systems, will help to generalize the metabolic niche concept.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

CM led writing, theory development, and analyses. SD, TW, and SF contributed to the analyses. All authors contributed to theory development, writing, and editing.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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