Project Summary

Overview

Over 50 years of research reveals a common pattern across ecosystems in which abundance (N) declines with increasing body mass (M). The shape of this relationship is described by a power law, $N \sim M^b$, known as the abundance size-spectrum, and the exponent b varies in relation to changes in energy flow through the food web. The value of b is almost always negative, indicating a remarkably consistent ecological pattern. However, the value of b also varies among ecosystems. Climate change is expected to alter size-spectra, based in part on shifts in body size with temperature that are predicted from macroecological temperature-size rules. Despite a seemingly simple relationship of body size and temperature, experimental and field studies demonstrate disparate results for size spectra-temperature relationships, finding positive, negative, and neutral shifts in size-spectra across temperature regimes. These studies largely consist of single samples across relatively small spatial scales, making it difficult to predict how size-spectra varies with temperature at the macroecological scale. In addition, deviations from theoretical predictions of the b-temperature relationship may be resolved by accounting for variation in resource supply, but the effect of resource supply at large scales is also unknown. The goal of this proposal is to quantify the natural variation of b in streams across the broad geographical areas represented by NEON sites and to test the hypothesis that b scales with temperature and resource supply.

Intellectual Merit

There is a clear expectation that future warmer temperatures will generate reductions in body size, particularly for ectotherms in aquatic environments. Whether that reduction will alter energy flow through food webs is critical to understand because it will allow ecologists to predict energy flux through food webs under future climate scenarios, including the amount fish biomass that could be produced for human consumption. Uncertainty in the temperature-b relationship is driven by two primary challenges, which this proposal overcomes. First, while temperature induces higher metabolic costs, leading to reduced transfer efficiency, this reduction can be counteracted by increases in resource supply, but these are rarely considered simultaneously. Second, understanding how temperature and resource supply interact at macroecological scales requires large logistical efforts that were previously not possible without programs like NEON. Thus, this proposal will move ecology forward by providing a critical test of how ecosystem function might respond to future temperature scenarios at macroecological scales, while critically accounting for co-variation in resource supply.

Broader Impacts

The primary broader impact of this proposal is to remove a technological barrier for studying size spectra with NEON data. To do this, we will develop an R package that calculates size spectra for NEON fish and macroinvertebrate data using maximum likelihood estimation. This will allow future researchers to examine patterns in size spectra automatically using NEON data. This proposal will also improve public knowledge of NEON data by incorporating the R package into a large undergraduate Biology class taught bi-annually by the PI.

Project Description

Over 50 years of research reveals a common pattern across ecosystems in which abundance (N) declines with increasing body mass (M) (Sheldon, Prakash, and Sutcliffe 1972; Blanchard et al. 2009, 2017). The shape of this relationship is described by a power law, $N \sim M^b$, known as the size-spectrum. The exponent b varies as a function of the efficiency of energy flow through the food web (Dickie, Kerr, and Boudreau 1987; Jonsson, Cohen, and Carpenter 2005; Sprules and Barth 2015; O'Gorman et al. 2017). Shallower slopes (less negative values of b) indicate more efficient energy flow due to lower loss in energy transfer between consumers and their resources (Jonsson, Cohen, and Carpenter 2005; Sprules and Barth 2015). The exponent b is almost always negative and typically ranges from ~ -1 to -2 for the abundance size spectrum, indicating a remarkably consistent pattern (Cyr 2000; Brown and Gillooly 2003; Sprules and Barth 2015; Blanchard et al. 2017). Because of this apparent consistency, ecologists have begun using size spectra changes to indicate fundamental shifts in ecosystem functioning in response to environmental disturbances (Jennings and Blanchard 2004). For example, macroinvertebrate size spectra were used in New Zealand streams to document shifts in stream community structure (Pomeranz, Warburton, and Harding 2019) and function (Pomeranz, Wesner, and Harding 2020) in response to acid mine drainage. Similar shifts are documented in response to land use (Martínez et al. 2016) and resource subsidies (Perkins et al. 2018). The direction of change in slope depends on the relative impact of disturbances to large versus small organisms.

Many fundamental aspects of an organism's biology are controlled by body size, including metabolic rate, life history characteristics, diet breadth, and trophic position (Brown et al. 2004; Woodward et al. 2005; White et al. 2007). As a result, changes in size spectra reflect changes in ecosystem function, providing a simple but powerful way to measure variation in ecosystem function across large spatial and temporal scales (Woodward et al. 2010; Edwards et al. 2017; Sprules and Barth 2015; Blanchard et al. 2017; O'Gorman et al. 2017). Temperature is thought to alter body size distributions in ecosystems, forming a central core of macroecological theory (Brown et al. 2004; Baiser et al. 2019). Bergmann's Rule predicts that small species are more common than large species at warmer temperatures (Bergmann 1848). It was originally devised for homeotherms but has since found support in poikilotherms including fishes (Rypel 2014) and insects (Shelomi 2012; Zeuss, Brunzel, and Brandl 2017). James' Rule predicts that populations within species have smaller average body sizes at warmer temperatures (James 1970; O'Gorman et al. 2012). At the individual level, the Temperature-Size rule predicts that individuals mature at smaller sizes at warmer temperatures (Atkinson 1994), a prediction that is well-supported in aquatic ecosystems, driven in part by a reduction in oxygen availability at high temperatures (Forster, Hirst, and Atkinson 2012).

While these macroecological rules all predict reductions in body size with temperature, from individuals to communities, they also share a common theme in which the empirical shape of these relationships varies widely across studies and taxa (Rypel 2014; Shelomi 2012; Zeuss, Brunzel, and Brandl 2017; Baiser et al. 2019). The relationship between body size and temperature is often negative (Daufresne, Lengfellner, and Sommer 2009), but can also be positive (Rypel 2014; Zeuss, Brunzel, and Brandl 2017). Even within those taxa that show a negative relationship between body size and temperature, the magnitude of change varies widely (Forster, Hirst, and Atkinson 2012), in part due to trait-based responses to temperature (Zeuss, Brunzel, and Brandl 2017). This makes it exceedingly difficult to know how an emergent property like size-spectra will scale with temperature, even if the individual taxa comprising the food webs generally show negative temperature-size relationships (Figure 1).

Uncertainty in the scaling of size spectra with temperature is compounded by contrasting results in studies that have directly tested it. Warming either makes exponents steeper (i.e., b becomes more negative, (Yvon-Durocher et al. 2011), (Dossena et al. 2012), shallower (i.e., b becomes more positive, (O'Gorman et al. 2017)), or has no effect (Mazurkiewicz et al. 2020). An intriguing explanation for these variable results is that temperature effects on size spectra are mediated by resource supply (i.e., nutrients or
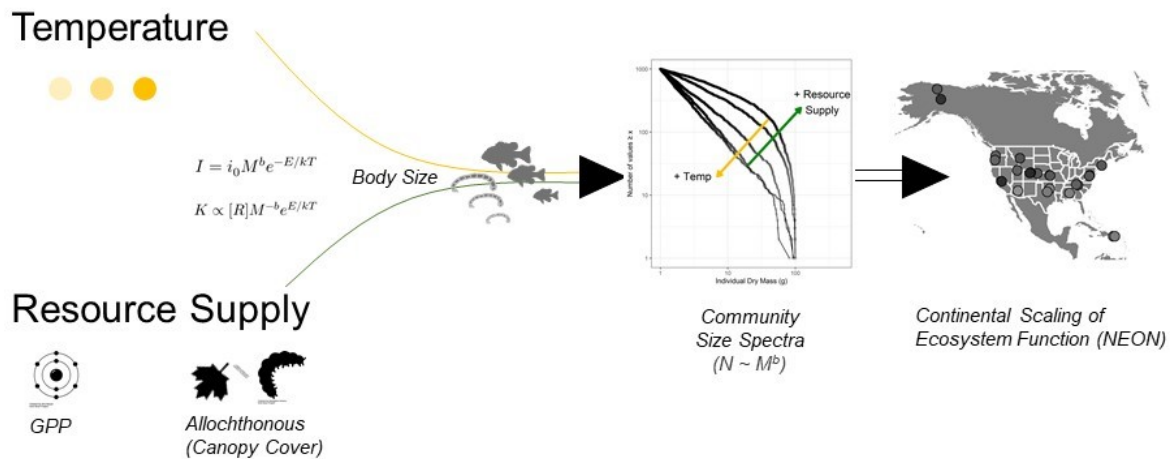
Figure 1. Conceptual schematic of proposal. Size spectra are influence in opposite directions by temperature and resource supply. We will measure size spectra responses to these variables across North American streams.

primary productivity), in which increased metabolic demand of lower trophic levels at high temperatures is offset by increased resource supply at the base of the food chain (O'Gorman et al. 2017). This allows food webs to support larger organisms at high temperatures than would be expected under constant rates of resource supply (O'Gorman et al. 2017). Resource supply is a fundamental concept in predictions of the metabolic theory of ecology (Brown et al. 2004). It helps to explain previous apparent contradictions to MTE theory (Junker et al. 2020) but its implications have generally been less explored relative to temperature (Cross et al. 2015).

The goal of this proposal is to quantify natural variation in community size spectra across space and time and resolve the relationship between temperature, resource supply, and size spectra.

Underlying the uncertainty in how size spectra scales with temperature is a lack of understanding of the natural variation of size spectra exponents over time and space. Due to the large logistical efforts needed to collect, identify, count, and measure 1,000's or 10,000's of individuals for a single size spectrum, studies are limited to a small number of replicates and typically a single sample per site. This increases the risk that reported changes in size spectra exponents are transient, making it difficult to draw conclusive inferences about the response of size spectra to ecological stressors. In addition, the magnitude of changes reported are difficult to place into context due to the lack of knowledge of background variation. Using single samples to indicate shifts in size spectra is akin to using abundance shifts between samples of a population to indicate species decline without accounting for natural variation in abundance of that species (Didham et al. 2020). A shift in slope by ~0.1 units is typically reported in the literature (Table 1). Whether that reflects a concerning shift in ecosystem function depends on placing it in the context of natural background variation (Jennings and Blanchard 2004). For example, the slopes of normalized abundance size spectra in Virginia streams varied seasonally by ~0.2 units, but not in direct response to temperature (McGarvey and Kirk 2018). In contrast, slopes for normalized biomass size spectra from polar marine benthic communities were similar among seasons, although the ambient temperature change in this system was slight (~1.14 deg C) (Mazurkiewicz et al. 2019).

Why spatiotemporal variation is currently difficult to quantify

Meta-analysis would offer an obvious solution to quantifying natural variation in *b*. This is made difficult by the disparate analytical approaches used to compute size spectra (White, Enquist, and Green 2008; Sprules and Barth 2015; Edwards et al. 2017). A common approach is to sum the number (or biomass) of organisms within logarithmic bins and estimate *b* as the slope of a log-log linear regression.

Table 1. Contrasting results of studies testing the relationship between size spectra exponents and temperature. b Change is the magnitude of slope change (in units of b), between the lowest and highest temperatures in each study.

Hypothesis	Author	b change	System	Temp Range
H1 Steeper	Dossena et al. 2012	0.11	FW mesocosms	4°C above ambient
H2 Shallower	Dossena et al. 2012	-0.08	FW mesocosms	4°C above ambient
H1 Steeper	Yvon Durocher et al. 2011	0.08	FW mesocosms	4°C above ambient
H1 Steeper	Yvon Durocher et al. 2011	0.13	FW mesocosms	4°C above ambient
H2 Shallower	O'Gorman et al. 2017	-0.15	Streams	5 to 25°C
H3 No Change	Mazurkiewicz et al. 2020	-0.03	Marine	-0.2 to 8°C
H3 No Change	McGarvey and Kirk	-0.19	Streams	Seasonal
H3 No Change	Mazurkiewicz et al. 2020	0.16	Marine	Seasonal (1.14°C range)

Unfortunately, even with the same dataset, this approach can generate very different estimates of b depending on the choice of logarithm base and other pre-analysis choices, like normalization (Edwards et al. 2017). Binning also removes important information on body sizes by collapsing all individuals in a bin to a single value. Binning methods can provide important information when compared within studies, but the different approaches make it nearly impossible to draw broader inference about variation in b among studies, because the different methods are not estimating the same parameter (White, Enquist, and Green 2008; Sprules and Barth 2015; Edwards et al. 2017, 2020). Further complicating meta-analysis is that some approaches use a biomass size spectrum and other estimate an abundance spectrum. Both are valid, but by multiplying two quantities (biomass vs abundance) by at least eight methods, there are at least 16 types of size spectra reported in the literature, and they cannot be reconciled by simple transformations. In this proposal, we will estimate b using maximum likelihood estimation, which does not require binning, thus providing an unbiased estimate of b (White, Enquist, and Green 2008; Unwin et al. 2020).

Why NEON data are essential for this project

Quantifying natural background variation of community size spectra over space and time and resolving the relationship between temperature, resource supply, and size spectra requires a large network of consistently collected and analyzed data that are repeatedly collected over time (Figure 2, Table 2). NEON samples provide such data. We propose to use NEON data from streams (fish and invertebrates) to 1) Characterize the natural variation in community size spectra, and 2) resolve competing hypotheses about the influence of temperature on community size spectra.

Theoretical Background

The theoretical basis for size abundance scaling in ecosystems is underpinned by a number of fundamental "rules" in ecology. First, all organisms take in, transform, and expend energy through metabolic processes. The rate of metabolism is intimately linked to organism size and can be described by the allometric relationship between body size and individual energy use:

$$I = i_0 M^b$$

where, I is individual metabolic rate, i_0 is a body size independent normalization constant, M is individual body mass, and b is an allometric exponent, often ~0.75 (Kleiber 1932). We can extend these predictions to include temperature by scaling its effect on subcellular kinetics to individual metabolism, through the inclusion of an Arrhenius relationship, whereby the initial description of I is modified to:
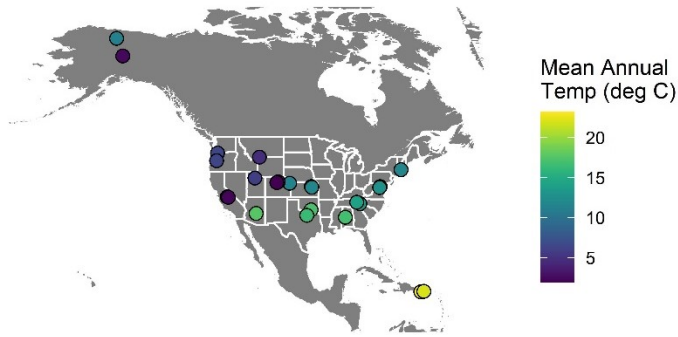
$$I = i_0 M^b e^{-E/kT}$$

Figure 2. NEON stream sites with 2019 mean annual temperatures.

here, i_0 is a body size and temperature independent normalization constant, E is the activation energy of the metabolic process (usually 0.6 - 0.7 for heterotrophic metabolism (Gillooly et al. 2001)), K is Boltzmann's constant, and T is absolute temperature in Kelvin (Gillooly et al. 2001). The simple observation that larger and/or hotter organisms require more energy can be extended to predict patterns of collections of organisms (e.g., populations, communities) within an ecosystem. For example, a finite amount of energy can support many small, cool individuals or fewer large, warm individuals because energy use per individual is higher for larger or warmer organisms. As such, it is predicted that the carrying capacity, K, of some resource, $[R]$, decreases with body size and temperature in an equal and opposite pattern as individual metabolic rate:

$$K \propto [R]M^{-b}e^{E/kT}$$

This formulation predicts the equivalence in population energy use with body size and temperature supported by empirical and theoretical work (e.g., energy equivalence) (Damuth 1987; Junker et al. 2020; Cross et al. 2015), if we assume energy supply is constant. Therefore, for communities within a trophic level that share a common, equitably distributed energy source, the value of the exponent b is predicted to be ~ -0.75, following the 3/4 scaling of individual energy use with body size and E is predicted ~0.65 based on the activation energy of heterotrophic metabolism (Jennings and Mackinson 2003; Brown et al. 2004).

However, in size structured communities trophic level is positively related to individual body size, therefore, individuals do not share a common energy source which leads to modified expectations of size-abundance scaling across trophic levels. First, inefficient energy transfer reduces the amount of energy available to larger organisms, leading to steeper slopes with typical values between ~ -1 to -2 (Cyr 2000; Jennings and Mackinson 2003; Blanchard et al. 2017). The rate of this reduction is governed by the predator:prey mass ratio (PPMR), often measured as the mean of M_{pred_i}/M_{prey_j} for predator species i and prey species j, and by the trophic transfer efficiency (TTE) P_{pred}/P_{prey} where P_x is production of prey or predator. The ratio reflects the proportion of prey production converted to predator production (Jennings and Mackinson 2003). As described earlier from temperature-size rules, the biomass of larger organisms is expected to decline with increasing temperature, which should reduce the PPMR. In addition, warmer temperatures can reduce TTE through a number of mechanisms: 1) the biological rates determining consumer energy intake (e.g., attack rate, handling time, consumption, etc.) may not increase as quickly as metabolic demand with warming (Vucic-Pestic et al. 2011), 2) stoichometric theory predicts a decline in organism nutrient content with increased temperatures, which should cause a decline in TTE due to a reduction in the nutritional value of individual prey (Woods et al. 2003; Cross et al. 2015). These shifts (reduced PPMR and reduced TTE) yield steeper size spectra slopes (Jennings and Mackinson 2003) by limiting the amount of energy available to larger organisms. As a result, increased temperatures are predicted to create steeper size-spectra slopes (more negative values of b) (Figure 3a).

The overall size abundance relationship and the role of declining PPMR and TTE at higher temperatures can be modified by species-specific (Twomey et al. 2012) and ecosystem-specific (O'Gorman et al. 2017)

responses to warming and how these modify the supply of resources to different trophic levels (Brose et al. 2012). For example, in geothermally influenced watersheds in Iceland [], increased biological nitrogen fixation countered the negative effects of increasing temperature on basal resource carrying capacity (Welter et al. 2015; O'Gorman et al. 2017; Bernhardt, Sunday, and O'Connor 2018). Thus, higher values of [R] lead to increased carrying capacity, an effect which, if large enough, is predicted to reverse the sign of the b-Temperature relationship (O'Gorman et al. 2017) (Figure 3c). Further, allochthonous inputs of prey can increase the K of larger top predators resulting in less negative b (Perkins et al. 2018). Currently, theoretical frameworks and data sets accounting for resource supply, with comparable methodology that span a large temperature gradient, are needed to test the theoretical relationship between temperature and b. We propose to address these issues in this work.

Hypotheses

We will test four main hypotheses, and the mechanisms underlying them, describing the scaling of b with environmental temperature (Figure 3).
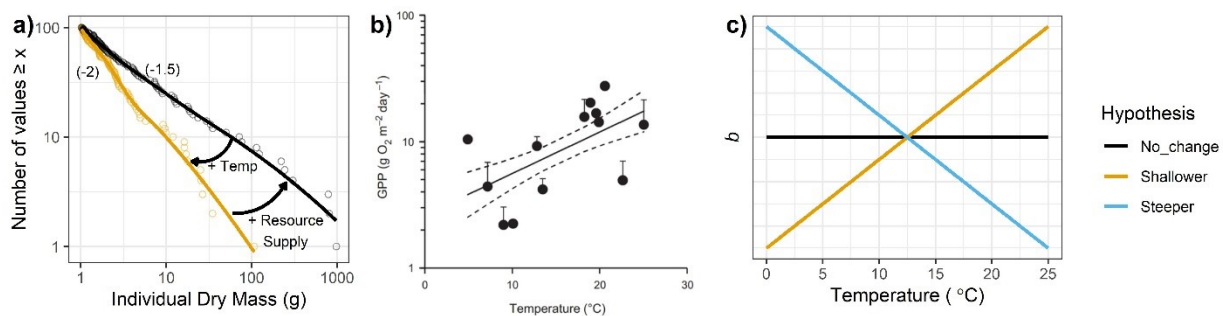

Figure 3. Hypotheses. a) Two simulated size spectra showing hypothesized shifts in opposite directions due to increased temperature or resource supply. Values for the size spectrum exponent b are shown in parentheses. b) Resource supply (as GPP) is loosely positively related to temperature in streams (from Demars et al. 2011). c) Hypotheses tested in this proposal. At the macroecological scale, size spectra slopes can increase, decrease, or stay the same with temperature depending on the relative effects of resource supply.

H1: Size spectra exponents become steeper (exponents become more negative) with increasing temperatures, because larger organisms become rarer relative to smaller organisms at higher temperatures.

Theoretical support for this hypothesis is driven by ecological rules that describe temperature-size relationships at different levels of organization (Daufresne, Lengfellner, and Sommer 2009; Forster, Hirst, and Atkinson 2012; O'Gorman et al. 2012) and expected decline in trophic transfer efficiency with warming (Vucic-Pestic et al. 2011). Empirical support comes from mesocosm studies with zooplankton and phytoplankton, in which a 4°C increase in temperature caused slopes to become steeper at elevated temperatures (Yvon-Durocher et al. 2011), though the effect was also seasonally dependent (Dossena et al. 2012) (Table 1).

H2: Size spectra exponents become shallower (exponents become less negative) with increasing temperatures, because resource supplies increase at warmer temperatures, thereby making up for increased metabolic/nutrient demand of primary producers. Community biomass at lower trophic levels declines but increases at intermediate and top trophic levels.

Empirical support for this hypothesis comes from a study of 13 Icelandic streams that vary from 5-25°C due to different supplies of naturally heated groundwater. Across this gradient, size-spectra exponents increased from ~-0.89 to -0.67 (O'Gorman et al. 2017). This unexpected result was explained by increasing rates of nitrogen fixation at higher temperatures in these nitrogen limited streams. As a result, resource production at lower trophic levels overcame an expected decline in resource standing stock,

allowing higher trophic levels (fish) to persist when macroecological theory suggested they should decline (O'Gorman et al. 2017).

H3: Size spectra exponents are unrelated to environmental temperature, because body size scaling with temperature is inconsistent among taxa.

This hypothesis is not expected under macroecological theory, nor by the mechanisms of increasing nutrient supply described above. However, it is supported by a study of marine benthic macroinvertebrates, in which size spectra exponents did not change across sites with mean temperatures ranging from -2 to 8°C (Mazurkiewicz et al. 2020). While community composition across the gradient changed, the relative abundance of size classes did not, resulting in consistent size spectra exponents. This hypothesis is also supported implicitly by (Dossena et al. 2012), who found opposite effects of temperature on size spectra exponents in winter and spring, which would cancel each other out on average, generating no long-term shift in size spectra over time.

H4: Size spectra exponents change in response to environmental temperature, but the change is mediated by resource supply.

This hypothesis is non-mutually exclusive with H1-H3 in the sense that any of the univariate relationships with temperature described above could be masked by non-constant rates of resource supply. This is supported from metabolic theory which suggests that increases in resource supply can compensate for expected increases in metabolic rates at higher temperatures (Cross et al. 2015; Perkins et al. 2018). The importance of resource supply for size spectra relies on the expectation of reduced efficiency of trophic transfer to larger consumers. This would generally lead to a reduction or extinction of large consumers, but that can be mediated if the production of lower trophic levels is increased due to increases in resource supply or larger organisms can access allochthonous energy sources. We will test this by estimating gross primary production and canopy cover (as a proxy for allochthonous inputs) at each site and including these as covariates in candidate models.

Characterizing Natural Variation: In addition to testing the above hypotheses, our analysis will characterize natural variation in abundance size spectra among seasons, sites, and years. We estimate generating a minimum of ~576 abundance size spectra (3 samples per year (for macroinvertebrates) x 24 sites x 4 years). To our knowledge, this is the largest collection of size spectra time-series to date. We will use this collection to produce a reference distribution of natural variation in stream size spectra across North America.

Methods

To test these hypotheses, we will compile data from the 24 NEON stream sites (Table 2). Across these broad environmental gradients, we will calculate community size spectra relationships using fish and macroinvertebrates (see details below). All types of data are collected at least twice per year since 2017, allowing us to account for seasonal and yearly variation at each site and to test models based on their ability to predict future size spectra. Below we briefly describe the data sets, the analytical approach to calculate size spectra, the statistical approach to compare hypotheses, and preliminary data.

Datasets

Fish - Fish are sampled twice per year - once in spring and once in fall - using backpack electrofishing along a 1000 m reach at each stream site. During collection, the reach is split into six equally spaced sub-reaches. Each reach is sampled with at least a single pass and three reaches are sampled with three passes. Individual fish are identified to species and the first 50 individuals collected in each sub-reach are measured for total length and wet weight and then released. This generates up to 300 measures of individual body size for each sampling event. Because size spectra analysis with MLE depends only on

the distribution of measured body sizes (not abundance *per se*), we will use all reported body size measures during a collection event (i.e. collection date and site), regardless of which electrofishing pass they were derived from (Figure 4a).

In some cases, electrofishing techniques can be size-biased against small individuals (Sutton and Jones 2020). Preliminary plots suggest this bias in a few sites (as indicated by a sharp uptick on the y-axis for small fish). To determine whether this affects our conclusions, we will run each analysis twice: once with all samples and once with the potentially biased samples removed. The cutoffs for removal will be chosen by visually assessing the data for abrupt increases in y-values for small fish and removing those data prior to analysis (Sutton and Jones 2020).

Macroinvertebrates - Benthic macroinvertebrates are sampled three times per year at each stream from a known area using the sampling method most suited to a site. Taxa are typically identified to the genus or species and a subset of individuals measured for length to the nearest mm. Lengths will be converted to individual dry mass (M, in mg) using published length-weight regression coefficients (Benke et al. 1999). Based on our preliminary analysis, the data sets available through 2019 include length measurements for >87,000 individuals and counts that total >21 million individuals (Figure 4b).
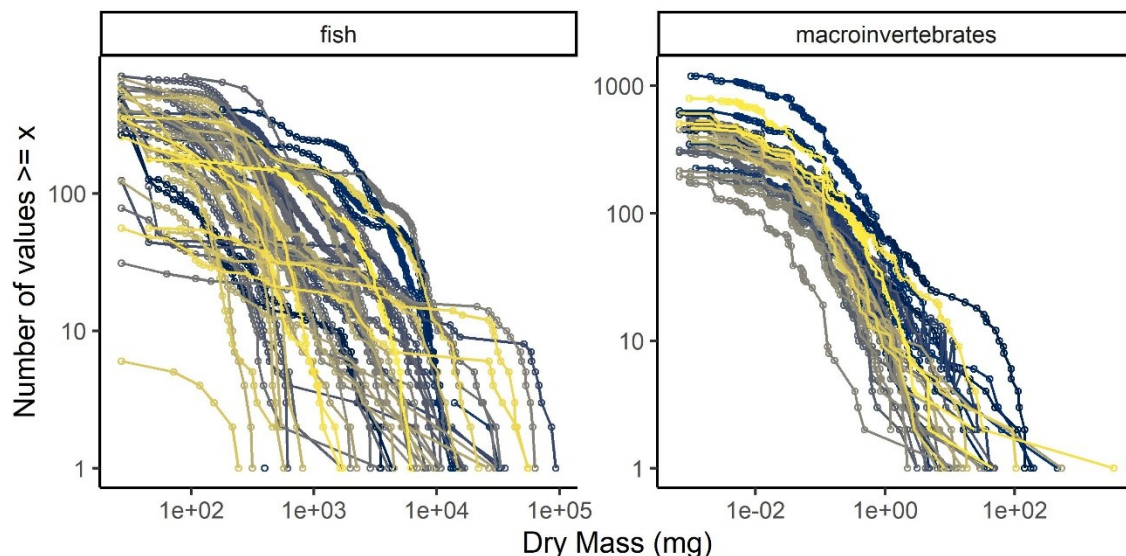

Figure 4. Preliminary data. Size spectra of fish and macroinvertebrates from 24 NEON stream sites (2017-2019). Each color is a different site.

Temperature - Surface water temperature is collected in 30-minute intervals from fixed stations at each stream. We will use these data to calculate mean temperature in each year. In general, mean annual temperatures vary from -4 to 25C (Table 2). The stream sites span 18 to 68 deg N (Figure 2).

Resource Supply - We will leverage and integrate existing NEON data products to estimate resource supply to ecosystems from both autochthonous and allochthonous sources. Gross primary production (GPP) will be estimated as a measure of autochthonous resource supply. Daily GPP will be estimated using single-station open channel methods (Odum 1956). Estimates of reached-averaged GPP can be made from subdaily measurements of dissolved oxygen concentration (DO; from in situ sensors, DP1.20288.001), water temperature (DP1.20053.001), average depth (DP1.20016.001, DP1.20267.001), air pressure (DP1.00004.001), and photosynthetically active radiation (DP1.20042.001). We will also use empirical rearation measurements (DP1.20190.001) to help constrain this parameter within the model. To model GPP, we will employ open source tools available in the *StreamMetabolizer* R package (Appling et al. 2018). *StreamMetabolizer* integrates recent advances in ecosystem metabolism modeling (e.g.,

Bayesian hierarchical models, simultaneous modeling of multiple parameters, etc.) to estimate GPP in a unified framework (Appling et al. 2018). GPP will be estimated to characterize differences in autochthonous resource supply across sites and seasonally within a site. To capture allochthonous resource supply, we will use canopy cover as an indirect measure of terrestrial subsidy input. Canopy cover is associated with increased terrestrial invertebrate and leaf litter input (Nakano, Miyasaka, and Kuhara 1999; England and Rosemond 2004). Neither of those direct inputs are measured by NEON, so canopy cover was chosen as a proxy. Percent canopy cover is obtained with replicate readings in the center and 0.3 meters from the left and right banks of each stream (Scott 2017) using a convex densiometer following methods of (Ode, Fetscher, and Busse 2016).

Caveats and considerations - In a closed system, GPP represents the total energy available to support metabolic activities (e.g., autotrophic and heterotrophic respiration, secondary production, etc.) and as such may be a better measure of resource availability than static measures such as chlorophyll *a* which are more easily collected and extensively available. Data availability of subdaily DO varies considerably across and within sites (~60 complete days to >1500 days among sites and ~60 to >1000 continuous days within sites). Despite the multiple necessary data sets and the increased difficulty of collection, cursory analyses show 19 sites with >275 continuous days of DO in at least one year and ~160 unique site-date combinations with concurrent DO, fish, and macroinvertebrate sampling. Yet GPP, may only represent a small portion of total energy availability in some streams (Webster and Meyer 1997) , canopy cover provides a broad measure of the potential for allochthonous inputs as more densely covered streams have higher particulate organic matter inputs than less forested streams (Golladay 1997; Hagen et al. 2010).

Data Quality Control - To ensure that the data are not biased by misreadings or data entry errors, we will remove data errors identified through NEON's QA/QC process, which are included as notes in the raw data. We will also use scatterplots to identify any remaining potential data errors. If found, we will consult with NEON experts to ensure that the data used for analysis are free from data entry errors or errors in sensors.

Size Spectra Analysis

We will estimate the mean and confidence interval of abundance size spectra exponents using maximum likelihood estimation from a bounded power law (Edwards et al. 2017). NEON sites contain two samples per year of fish and three samples per year of macroinvertebrates (Goodman et al. 2015). Data analysis will be limited to the two samples per year that include both fish and macroinvertebrates.

Quantitative samples of benthic macroinvertebrates and fish from all 24 NEON wadeable-stream sites are currently available from 2017-2019 and will be obtained up to the most recent completed year (NEON 2020).

The maximum likelihood of the slope *b* will be estimated using the bounded power law with probability density function:

$$f(x) = Cx^b, x_{min} \leq x \leq x_{max}$$

where *x* is body mass, *b* is the scaling exponent (size spectra exponent), and the distribution is bounded by the minimum and maximum body sizes observed in a collection. Estimates will be made using R code provided in the *sizeSpectra* R package (Edwards et al. 2017). To determine how relationships vary depending on grouping, we will estimate *b* for both the pooled data set (fish and macroinvertebrates together) and for fish and macroinvertebrates separately (Cyr 2000; O'Gorman et al. 2017). The analyses below will be conducted on each of these three groups.

Table 2. Variation in physical and chemical characteristics of NEON stream sites. All values are averages across from repeated collections over at least one year. 'Chl *a*' is chlorophyll a. 'Q' represents mean stream discharge. 'TDN' and 'TDP' represent total dissolved nitrogen and total dissolved phosphorus, respectively.

Site	Temp (C)	Chl *a*	Canopy (%)	Q (cfs)	TDN (mg/L)	TDP (mg/L)
OKSR	-4	5	0	38.1	0.24	0.008
CARI	-1	1	76	15.6	0.45	0.008
COMO	-0.3	5	82	2.3	0.16	0.007
WLOU	-0.3	5	82	5.8	0.09	0.006
BLDE	0.2	17	29	18.7	0.19	0.029
BIGC	7	8	82	3.2	0.14	0.014
TECR	7	7	94	1.8	0.08	0.007
HOPB	8	12	76	5.6	0.17	0.007
MART	8	3	85	9.9	0.05	0.019
REDB	9.5	11	88	3.2	0.12	0.016
MCRA	10	3	91	6.9	0.09	0.018
ARIK	11	8	18	1	0.32	0.022
KING	12	20	88	1.8	0.21	0.02
LEWI	12	113	94	3.2	2.74	0.008
MCDI	12	25	88	2.8	0.53	0.027
POSE	13	48	88	0.9	0.46	0.015
LECO	13.4	17	94	7.8	0.22	0.008
WALK	15.3	9	94	0.9	0.09	0.01
BLUE	16	80	41	86.3	0.51	0.014
MAYF	17	1	91	6.3	0.13	0.006
PRIN	18	8	65	1	0.38	0.028
SYCA	21	5	53	7.6	1.07	0.113
CUPE	25	29	82	4.1	0.41	0.011
GUIL	25	54	53	6.9	0.5	0.021

Statistical Analysis and Model Selection

After obtaining size spectra exponents for each collection, we will create a suite of Bayesian generalized linear mixed models to determine the combination of temperature, GPP, and canopy cover that best explain size spectra exponents and total community biomass. We will fit different versions of the following models: 1) intercept only, 2) temperature only, 3) temperature and GPP main effects and interaction, 4) temperature and canopy cover main effects and interaction, and 5) temperature, GPP, and canopy cover main effects and interactions. The different versions will vary in how GPP is summarized by averaging it over different time intervals: 1 month prior to the sample date, 6 months prior to the sample date, and averaged over the year of the sample dates. Including these three levels of GPP will allow us to account for the possibility that an individual size spectra exponent may respond more strongly to enhanced GPP prior to collection rather than average GPP over the year. Model likelihoods will be Gaussian for size spectra exponents because the exponents are continuous measures that can take on positive or negative values and a Gamma likelihood for biomass estimates because biomass is strictly positive and continuous (Hobbs and Hooten 2015). Each model will include random intercepts for site and year to account for multiple measures within site and year and to account for uncertainty in prediction of exponents in future years. Priors will be chosen via prior predictive simulation (Gelman, Simpson, and

Betancourt 2017; Gabry et al. 2019) and checked via posterior predictive checking and prior sensitivity analysis (Hobbs and Hooten 2015).

An exciting feature of our analysis approach is that we can use out-of-sample validation to select the top model(s) instead of relying only on the data set used to fit the models (Hooten and Hobbs 2015). To do this, we will fit our models using data released through 2021 and use those models to predict size spectra exponents for data released in 2022. In addition, we will use the models to *hindcast* by predicting exponents collected prior to 2017. Model performance will be assessed using the log predictive density (Hobbs and Hooten 2015):

$$log[\text{y\_}oos|\text{y}] \approx log \left(\frac{\sum_{k=1}^{K}[\,\text{y}_{oos}|\text{y}, \theta^{(k)}]}{K} \right)$$

where y_{oos} is an out-of-sample size spectra exponent, and y is the posterior prediction of the size spectra exponent for that sample generated by solving from a single iteration k across the parameters θ. Repeating this calculation across each iteration of the posterior and each out-of-sample size spectra exponent, dividing by the total number of iterations K, and taking the log generates a predictive score for a given model. Models with better predictive capability have higher scores (Hobbs and Hooten 2015).

Mechanisms - To determine how much shifts in size spectra are driven by changes to large versus small organisms, we will use linear regression to assess how the mean body size of the largest quantile and smallest quantile in each population changes as a function of temperature (Figure 5, Pomeranz, Warburton, and Harding 2019). Differences in the slopes of these two lines will reveal whether a change in b is caused by a larger relative decline in body size of the largest organisms compared to smaller organisms across the temperature gradient.
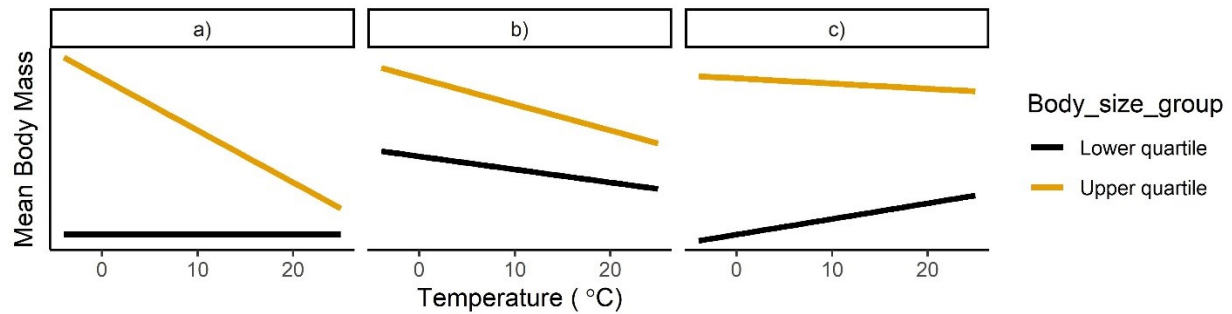

Figure 5. Hypothetical mechanisms that could cause reductions in size spectra exponents across temperature. a) Biomass reduction in only large individuals (upper quartile), b) biomass reduction in large and small (lower quartile) individuals, but stronger reduction in large, c) biomass reduction in large individuals and biomass increase in small individuals.

Preliminary Data

Using the methods described above, we estimated size spectra exponents for macroinvertebrate samples from 2017-2019 and modeled them as a function of mean annual temperature (Figure 6a). The slope in general is negative, indicating that for every unit increase in temperature the average exponent declines by ~0.003 units of b.

The preliminary analysis generally supports the prediction from the MTE that size spectra exponents should get steeper as temperatures increase due to reductions in trophic transfer efficiency. However, these data are limited to macroinvertebrates only and do not account for variation in resource supply (i.e., GPP, litter input). The magnitude of change is also fairly weak, with exponents declining by ~ 0.1 units
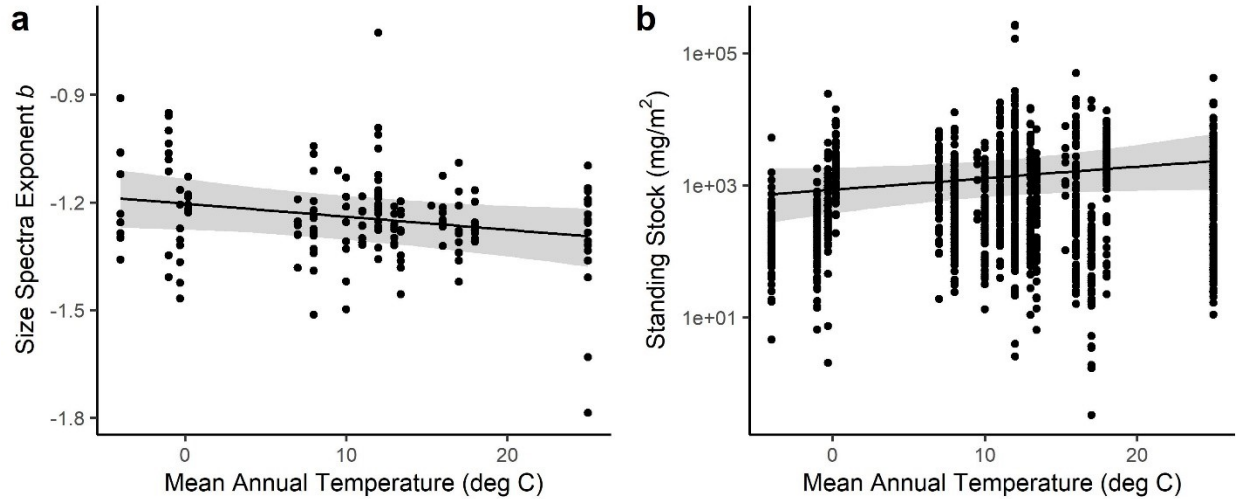
Figure 5. Preliminary data. Macroinvertebrate size spectra and standing stock dry mass as a function of mean annual temperature. Data are from 2017-2019 across 24 NEON streams

across the 25°C temperature gradient and lots of unexplained variation in size spectra exponents. For example, the modeled rate of change in *b* for every unit of temperature C is -0.003. In Icelandic streams, modeled values of the rate of change of *b* with temperature C ranged from -0.01, to +0.02 (O'Gorman et al. 2017), with low values (e.g. -0.01) associated with low resource supply and high values (e.g. 0.02) associated with high resource supply levels. Based on this comparison our preliminary value of -0.003 suggest an influence of resource supply, since the estimated slope in Figure 3a could plausibly by ~3 times steeper without the influence of resource supply. Thus, even though the rate of change in *b* is negatively related to temperature, that does not suggest that resource supply is not contributing to these preliminary patterns.

Intriguingly, while size spectra exponents decline with temperature, standing stock biomass *increases* with temperature (Figure 6b). This is the opposite of predictions from MTE, which predict a decline in standing stock biomass with temperature due to reductions in individual body sizes and increased rates of individual energy use (Brown et al. 2004; Yvon-Durocher et al. 2010). Crucially, this prediction also relies on the assumption of constant resource supply, such that standing stock biomass B_{tot} scales with temperature as follows: $B_{tot} = [R]M^{1/4}e^{E/kT}$ where $[R]$ is resource supply, $e^{E/kT}$ is the Boltzmann factor with E equal to the activation energy of metabolism and k and T as Boltzmann's constant and absolute temperature in Kelvin, respectively. Importantly, in this formulation positive values of E relate to a negative relationship between B_{tot} and temperature (Brown et al. 2004). This demonstrates that resource supply–via GPP, litter or terrestrial invertebrates–could counteract expectations from temperature alone, perhaps indicating the influence of temperature on size spectra may be fairly strong but is moderated by increasing resource supply at higher temperatures. Further support for this hypothesis comes from a similar mechanism - interaction of resource supply and temperature - that explained secondary production in arctic streams (Junker et al. 2020). There is likely wide variation in resource supply among streams. Available data show ~2 orders of magnitude variability in chlorophyll *a* standing stock and total dissolved nutrient concentrations (Table 2).

Intellectual Merit

Continued human disruption of ecosystems threatens to not only alter species distributions and composition, but also the structure and function of ecosystems (Brose et al. 2017). One important ecosystem function, the flux of energy through food webs (Barnes et al. 2018), is reflected by the size distribution of individuals within ecosystems (Jennings and Blanchard 2004; Petchey and Belgrano 2010;

Blanchard et al. 2017). There is a clear expectation that future warmer temperatures will generate reductions in body size, particularly for ectotherms in aquatic environments (Forster, Hirst, and Atkinson 2012). Whether that reduction will alter the distribution of body sizes in ecosystems is unclear. Understanding this relationship is critical for predicting changes in ecosystem function under future climate scenarios (Yvon-Durocher et al. 2010; O'Gorman et al. 2012, 2017).

Uncertainty in the temperature-size spectra relationship is driven by two primary challenges, which this proposal overcomes. First, while temperature induces higher metabolic costs, leading to reduced transfer efficiency, this reduction can be counteracted by increases in resource supply (Brown et al. 2004; O'Gorman et al. 2017; Junker et al. 2020). Second, understanding how temperature and resource supply interact at macroecological scales requires large logistical efforts that were previously not possible without programs like NEON. Thus, this proposal will move ecology forward by providing a critical test of how ecosystem function might respond to future temperature scenarios at macroecological scales, while critically accounting for co-variation in resource supply (Cross et al. 2015).

An additional benefit of this proposal is that it will provide the largest (to our knowledge) reference database of size spectra in streams. By estimating size spectra over multiple seasons and years across a broad geographical gradient, we will generate a range of size spectra that can be expected in relatively unimpaired streams. This is important given the increasing use of size spectra to infer degradation of ecological systems (Jennings and Blanchard 2004; Petchey and Belgrano 2010; Sprules and Barth 2015; Perkins et al. 2018; Pomeranz, Warburton, and Harding 2019). By providing a posterior distribution of expected size spectra slopes, our results will serve as a reference to interpret whether size spectra exponents in impaired systems exceed the expected natural variation from comparable streams in the NEON network. This complements traditional monitoring of freshwater ecosystems, which has focused on population or diversity metrics that track the abundance and richness of species. While these studies are critical, a taxonomic approach alone does not account for the large trophic changes that occur across ontogeny (Miller and Rudolf 2011; Brose et al. 2017). Size-spectra approaches complement taxonomic approaches by quantifying ecological communities in terms of their distribution of individual body sizes, rather than the distribution of individual species or trophic groups (Sheldon, Prakash, and Sutcliffe 1972; Blanchard et al. 2017).

Broader Impacts

This proposal will address priorities of NSF by improving public awareness and understanding of science and engaging a diverse community of learners in the use of NEON. These goals will be achieved through two complementary sources: 1) development of an R package that automates estimation of size spectra exponents using NEON data, and 2) incorporation of NEON data into an undergraduate course for Biology majors titled "Inquiry and Analysis in Biology".

R package - We will convert our functions for this project into an R package that merges the functionality of two existing packages - *sizeSpectra* (Edwards et al. 2017) and *neonUtilities* (Lunch et al. 2019). The *sizeSpectra* package contains functions to estimate the mean and confidence intervals of the size spectra exponent using maximum likelihood estimates (MLE) (White, Enquist, and Green 2008; Edwards et al. 2017). To apply this technique to NEON data, we will combine the calculations from the *sizeSpectra* package to automatically calculate size spectra exponents for fish and macroinvertebrate datasets from NEON, accessed through the *neonUtilities* package. The functions to compute this are developed in scripts by the PI's (used to analyze data for Figure 6, for example), but have not been converted to a publicly available R package. For the developed package, the functions to calculate maximum likelihood estimates rely only on base R code, so will be included directly without relying on dependency of the *sizeSpectra* package itself. It will rely on the *tidyverse* (Wickham et al. 2019) and *neonUtilities* (Lunch et al. 2019) to produce tibbles of the data and take advantage of the functionality of the *tidyverse*. Initial development will focus on calculating size spectra with fish and invertebrate data because of our

experience with those data and their size spectra. However, any data from NEON that contain individual measures of body size can be included.

Undergraduate Course - NEON data will be made available to a large undergraduate course taught each semester by PI Wesner. The course is required of all Biology majors at the University of South Dakota and includes ~140 students per year. Currently, students analyze large datasets in public health available through *https://gapminder.org* (Rosling and Zhang 2011). Previous attempts to give students the option of using ecological data have been hampered by the disparate styles of data presentation that are available on common data archives (e.g. Zenodo, Data Dryad, etc). NEON data overcome this limitation by providing a single source of commonly-formatted data. The students in the course are beginners at R, so full use of *neonUtilities* or *ecocomDP* (Smith 2020) is too advanced. Therefore, PI Wesner will make available, in simplified form, all datasets used in this project - *fish (abundance and body size), macroinvertebrates (abundance and body size), temperature, nutrients, GPP, etc)* - or will work with interested students to obtain any additional data sets. In addition, students will be given the option to conduct projects using the R package. This will aid both in testing new hypotheses of size spectra exponents that the students derive, and in stress testing the R package as it develops.

Results from Prior Support

Jeff Wesner (PI) - PI, #1837233, 2018-2021, *EAGER: Stage-structured predation between fish and aquatic insects*. *Intellectual Merit*: Quantified stage-structured feeding in > 600 fish samples. Built large database of fish diet information from literature. Compared the effects of fish on ecosystem subsidies according to stage-structure of diet. *Broader Impacts*: Recruited postdoc. Mentored two underrepresented REU students. >5 presentations to date. Conducted outreach events for local high schools. MS student graduated and is in a Ph.D. program with first publication from MS in advanced prep (Kanz 2020). Publications: Wesner 2019. *Freshwater Science*, 38, 928-935. Wesner et al. 2020. *Ecosystems*, 23, 111-123. Pomeranz et al. 2020. *Ecology*. All data and code associated with published papers is available with DOI on Zenodo (jsw 2019; Jpomz 2020). Data and code from theses or unpublished work is available on GitHub: *https://github.com/Abrahamkanz, https://github.com/jswesner*.

Jim Junker (PI) - New Investigator. No prior NSF support.

Justin Pomeranz (Senior Personnel, Postdoc) - No prior NSF support.

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