

Temperature effects on community size structure: The value of large-scale biomonitoring programs

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The effects of climate warming on individuals and populations are becoming increasingly apparent (e.g. changes in body mass, species range shifts); however, impacts at higher levels of biological organization (i.e. communities and ecosystems) are less understood (Heneghan et al., 2019). Ecological communities comprise many small- and few large-sized individuals. The individual size distribution—the frequency distribution of individual body sizes (White et al., 2007; Figure 1)—represents a key measure of community structure, signifying the relative number of large versus small organisms (Perkins et al., 2019). Where organisms occupy different trophic levels, the power-law exponent that underpins the individual size distribution (ISD exponent, *henceforth*) represents the efficiency of energy transfer from small, abundant prey to fewer large predators (Brown et al., 2004). As such, the individual size distribution provides a lens through which to understand the effects of multiple aspects of climatic (and general environmental) change on energy flow in natural systems (Heneghan et al., 2019; Petchey & Belgrano, 2010). A study by Pomeranz et al. in this issue provides clear focus on how this measure of community size structure varies with temperature at the continental scale.

There is growing evidence that warming 'benefits the small' with a decrease in the mean individual body mass within a community, driven by various temperature-size 'rules' (Daufresne et al., 2009). These include a decrease in individual body size within populations (James's rule) and an increase in the proportion of small species within a community (Bergmann's rule) at higher temperature. It is therefore expected that ISD exponents should change with environmental temperature (Heneghan et al., 2019; Saito et al., 2021). However, testing this across natural gradients of temperature has been hampered by a lack of detailed, standardized data collected across sufficiently large spatio-temporal scales to encompass a biologically meaningful temperature range. Pomeranz et al. utilize superb open-source data from the National Ecological Observatory Network (NEON) funded by the National Science Foundation (USA). These data come from standardized aquatic invertebrate sampling performed in 81 wadeable stream sites across a broad climatic gradient: from Alaska to Puerto Rico (<https://data.neonscience.org/home>). The monitoring program

regularly collects samples in which individuals are measured and counted across seasons and years in each site. This allowed the authors to compare variation in individual size distributions attributed to temperature to that associated with 'background' intra- and inter-annual variability. The data set used by Pomeranz et al. includes the individual sizes of a truly impressive 13 million stream invertebrates.

Using a series of elegant statistical models and fits to empirical data, Pomeranz et al. demonstrate that ISD exponents decreased (slopes became steeper; Figure 1a) across a 29°C gradient in (mean annual) temperature. The authors show that warmer sites had a relatively lower proportion of large-sized individuals (e.g. predatory invertebrates), but more small individuals (e.g. primary consumers) compared to colder sites (Figure 1b). This work adds to a growing body of research demonstrating that body-size distributions are sensitive to a host of environmental variables (Petchey & Belgrano, 2010). Results from this space-for-time substitution approach indicate that environmental warming could be associated with inefficient energy transfer, changing community size structure. The observed shift towards more small individuals with increasing temperature is consistent with expectations based on temperature-size rules; although the relative role of changes in the individual body size within populations, compared to the proportion of different sized species, is unclear in this study.

How large is the effect of temperature on community size structure? Pomeranz et al. show that the observed changes in the magnitude of ISD exponents across the 29°C gradient in stream temperature is comparable to previously reported temperature-driven changes in size structure. These include a significant steepening of invertebrate size spectra in response to 3–5°C warming in pond mesocosms (Dossena et al., 2012), and an unexpected pattern found in Icelandic geothermal streams whereby size spectra became shallower across a 20°C gradient in stream temperature (O'Gorman et al., 2017). Pomeranz et al. show that ISD variation with temperature is dwarfed in comparison to changes in ISD exponents reported in response to human disturbances, such as commercial fishing or acid mine drainage. Furthermore, seasonal and annual variation in ISD exponents in their study sites was similar in magnitude compared to the variation observed across the full 29°C gradient. The authors therefore argue that the effect of temperature change on

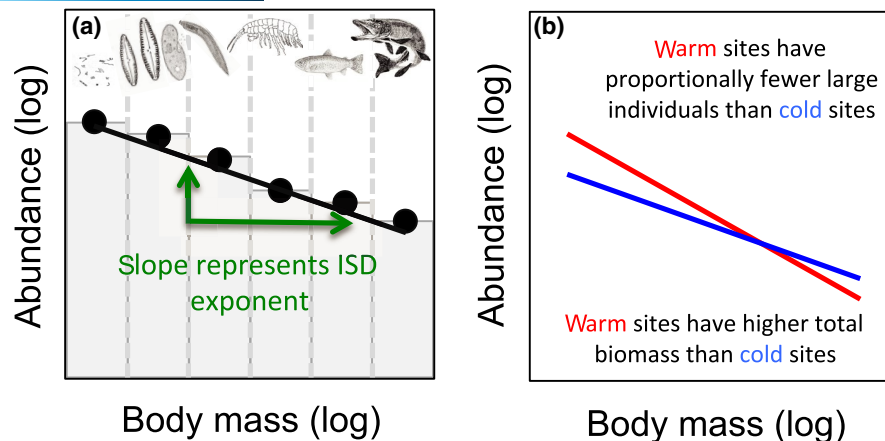


FIGURE 1 Temperature effects on community size structure. (a) The individual size distribution can be depicted by constructing the 'size spectrum', plotting the sum of all individuals (regardless of taxonomic identity) within logarithmically spaced size bins (e.g. 1, 10, 100 mg etc.) on log–log axes. (b) Summarized results from Pomeranz et al. show how the exponent of the individual size distribution (i.e. size spectrum slope) and community biomass (analogous to the size spectrum intercept) of stream invertebrate communities respond to changes in mean annual temperature [Colour figure can be viewed at wileyonlinelibrary.com]

the individual size distribution is relatively small and community size structure appears to be a somewhat stable and conserved pattern across large spatial scales (e.g. Perkins et al., 2019).

I would agree in principle, but there are a couple of cautionary points to consider. First, this study lacks the experimental control of potentially confounding variables that also vary biogeographically (such as seasonality). Therefore the singular effects of temperature on community size structure could be masked to some unknown extent and therefore might be conservative. Second, individual size distributions in this study are confined to macroinvertebrates, and considering a broader range of trophic levels in these stream food webs (e.g. Figure 1a) might magnify the changes in the exponent. With these caveats in mind, even these 'subtle' effects on community size structure could correspond to pronounced impacts on community metabolic capacity and ecosystem-level processes (such as ecosystem respiration and gross primary production; Yvon-Durocher & Allen, 2012) given the sublinear relationship between organism body size and metabolic rate (Brown et al., 2004). It is clear that further work is required to help assess the relative impacts of temperature (and other global change drivers) on community size structure.

The authors also found that total community biomass—the combined body mass of all invertebrates within each site—increased with local stream temperature. This empirical pattern conflicts with predictions from metabolic scaling theory that, given a fixed supply of resources, standing biomass should decline with temperature (Brown et al., 2004). That is, the faster biomass-specific respiration at higher temperature should decrease the amount of biomass that can be supported for a given amount of energy. What might therefore explain this unexpected pattern? Perhaps an insight into this comes from recent research from geothermal stream ecosystems (O'Gorman et al., 2017), which found a similar increase in total community biomass with temperature. Here, the temperature dependence of basal resource carrying capacity

was suggested to account for these previously unexpected results. That is, if nutrient supply increases with temperature to offset the rising metabolic demand of primary producers, there will be sufficient resources to sustain more consumers (such as macroinvertebrates). Whether this applies across the streams studied by Pomeranz et al. is unclear, but given that low-order streams receive regular replenishment of nutrients from surface to subsurface exchanges, the assumption of fixed resource supply might not hold in these systems.

Pomeranz et al. demonstrate how significant new insights can be gained when high-quality data are available to test general ecological theory. Data from large-scale biological monitoring programs (such as NEON) are laborious to collect, requiring skilled researchers with many years of experience in taxonomic identification. Open-source data such as these are therefore unfortunately rare, but are invaluable for investigating the potential impacts of climate warming at large spatial-temporal scales. Body-size distributions integrate the response of biota to environmental change and provide a simple, yet general, framework for understanding the effects of global change in natural ecological communities (Petchey & Belgrano, 2010). The significance of this approach calls for additional systematic collection of appropriate data to help reveal the effects of global change at high levels of biological organization.

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