

1 **Temperature effects on community size structure: the value of large-**
2 **scale biomonitoring programs**

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Daniel M. Perkins¹

¹School of Life and Health Sciences, Whitelands College, University of Roehampton,
London, SW15 4JD, UK.

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

25 There is growing evidence that warming ‘benefits the small’ with a decrease
26 in the mean individual body mass within a community, driven by various
27 temperature-size ‘rules’ (Daufresne *et al.*, 2009). These include a decrease in
28 individual body size within populations (James’s rule) and an increase in the
29 proportion of small species within a community (Bergmann’s rule) at higher
30 temperature. It is therefore expected that ISD exponents should change with
31 environmental temperature (Heneghan *et al.*, 2019; Saito *et al.*, 2021). However,
32 testing this across natural gradients of temperature has been hampered by a lack of
33 detailed, standardized data collected across sufficiently large spatio-temporal scales to

34 encompass a biologically meaningful temperature range. Pomeranz et al. utilize
35 superb open-source data from the National Ecological Observatory Network (NEON)
36 funded by the National Science Foundation (USA). These data come from
37 standardized aquatic invertebrate sampling performed in 81 wadeable stream sites
38 across a broad climatic gradient: from Alaska to Puerto Rico (<https://data.neonscience.org/home>). The monitoring program regularly collects samples in which
39 individuals are measured and counted across seasons and years in each site. This
40 allowed the authors to compare variation in individual size distributions attributed to
41 temperature to that associated with ‘background’ intra- and inter- annual variability.
42 The dataset used by Pomeranz et al. includes the individual sizes of a truly impressive
43 13 million stream invertebrates.
44

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

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60 <INSERT FIG HERE >

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63 **Figure 1** Temperature effects on community size structure. (a) The individual size
64 distribution can be depicted by constructing the ‘size spectrum’, plotting the sum of
65 all individuals (regardless of taxonomic identity) within logarithmically spaced size
66 bins (e.g. 1mg, 10mg, 100mg etc.) on log-log axes. (b) Summarised results from
67 Pomeranz et al. show how the exponent of the individual size distribution (i.e. size

68 spectrum slope) and community biomass (analogous to the size spectrum intercept) of
69 stream invertebrate communities respond to changes in mean annual temperature.

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71 How large is the effect of temperature on community size structure? Pomeranz
72 et al. show that the observed changes in the magnitude of ISD exponents across the
73 29°C gradient in stream temperature is comparable to previously reported
74 temperature-driven changes in size structure. These include a significant steepening of
75 invertebrate size spectra in response to 3-5°C warming in pond mesocosms (Dossena
76 *et al.*, 2012), and an unexpected pattern found in Icelandic geothermal streams
77 whereby size spectra became shallower across a 20°C gradient in stream temperature
78 (O’Gorman *et al.*, 2017). Pomeranz et al. show that ISD variation with temperature is
79 dwarfed in comparison to changes in ISD exponents reported in response to human
80 disturbances, such as commercial fishing or acid mine drainage. Furthermore,
81 seasonal and annual variation in ISD exponents in their study sites was similar in
82 magnitude compared to the variation observed across the full 29°C gradient. The
83 authors therefore argue that the effect of temperature change on the individual size
84 distribution is relatively small and community size structure appears to be a somewhat
85 stable and conserved pattern across large spatial scales (e.g. Perkins *et al.*, 2019).

86 I would agree in principle but there are a couple of cautionary points to
87 consider. First, the present study lacks the experimental control of potentially
88 confounding variables that also vary biogeographically (such as seasonality).
89 Therefore the singular effects of temperature on community size structure could be
90 masked to some unknown extent and therefore might be conservative. Second,
91 individual size distributions in this study are confined to macroinvertebrates, and
92 considering a broader range of trophic levels in these stream food webs (e.g. Fig. 1a)
93 might magnify the changes in the exponent. With these caveats in mind, even these
94 ‘subtle’ effects on community size structure could correspond to pronounced impacts
95 on community metabolic capacity and ecosystem-level processes (such as ecosystem
96 respiration and gross primary production; Yvon-Durocher & Allen, 2012) given the
97 sub-linear relationship between organism body size and metabolic rate (Brown *et al.*,
98 2004). It is clear that further work is required to help assess the relative impacts of
99 temperature (and other global change drivers) on community size structure.

100 The authors also found that total community biomass - the combined body
101 mass of all invertebrates within each site - increased with local stream temperature.

102 This empirical pattern conflicts with predictions from metabolic scaling theory that,
103 given a fixed supply of resources, standing biomass should decline with temperature
104 (Brown *et al.*, 2004). That is, the faster biomass-specific respiration at higher
105 temperature should decrease the amount of biomass that can be supported for a given
106 amount of energy. What might therefore explain this unexpected pattern? Perhaps an
107 insight into this comes from recent research from geothermal stream ecosystems
108 (O’Gorman *et al.*, 2017), which found a similar increase in total community biomass
109 with temperature. Here, the temperature dependence of basal resource carrying
110 capacity was suggested to account for these previously unexpected results. That is, if
111 nutrient supply increases with temperature to offset the rising metabolic demand of
112 primary producers, there will be sufficient resources to sustain more consumers (such
113 as macroinvertebrates). Whether this applies across the streams studied by Pomeranz
114 *et al.* is unclear but given that low-order streams receive regular replenishment of
115 nutrients from surface to sub-surface exchanges, the assumption of fixed resource
116 supply might not hold in these systems.

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

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