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1	Temperature effects on community size structure: the value of large-
2	scale biomonitoring programs
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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 <i>et al.</i> 2007: Figure 1) - represents a key

15 measure of community structure, signifying the relative number of large versus small organisms (Perkins et al., 2019). Where organisms occupy different trophic levels, the 16 power-law exponent that underpins the individual size distribution (ISD exponent, 17 *henceforth*) represents the efficiency of energy transfer from small, abundant prey to 18 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.neons 39 cience.org/home). The monitoring program regularly collects samples in which 40 individuals are measured and counted across seasons and years in each site. This 41 allowed the authors to compare variation in individual size distributions attributed to 42 temperature to that associated with 'background' intra- and inter- annual variability. 43 The dataset used by Pomeranz et al. includes the individual sizes of a truly impressive 44 13 million stream invertebrates.

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 demonstrating that body-size distributions are sensitive to a host of environmental 51 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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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. 1mg, 10mg, 100mg etc.) on log-log axes. (b) Summarised 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) ofstream 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 skilled researchers with many years of experience in taxonomic identification. Open-120 121 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 (Petchev & 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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## 129 **References**

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Brown J, Gillooly J, Allen A, Savage V, West G (2004) Toward a metabolic theory of
ecology. *Ecology*, 85, 1771–1789.

Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in
aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106,
12788–12793.

136	Dossena M, Yvon-Durocher G, Grey J, Montoya JM, Perkins DM, Trimmer M,
137	Woodward G (2012) Warming alters community size structure and ecosystem
138	functioning. Proceedings. Biological sciences / The Royal Society, 279, 3011–
139	3019.
140	Heneghan RF, Hatton IA, Galbraith ED (2019) Climate change impacts on marine
141	ecosystems through the lens of the size spectrum. Emerging Topics in Life
142	<i>Sciences</i> , <b>3</b> , 233–243.
143	O'Gorman EJ, Zhao L, Pichler DE et al. (2017) Unexpected changes in community
144	size structure in a natural warming experiment. Nature Climate Change, 7, 659-
145	663.
146	Perkins DM, Perna A, Adrian R et al. (2019) Energetic equivalence underpins the size
147	structure of tree and phytoplankton communities. Nature Communications, 10.
148	Petchey OL, Belgrano A (2010) Body-size distributions and size-spectra: universal
149	indicators of ecological status? Biology letters, 6, 434-437.
150	Saito VS, Perkins DM, Kratina P (2021) A Metabolic Perspective of Stochastic
151	Community Assembly. Trends in Ecology & Evolution.
152	White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body
153	size and abundance in ecology. Trends in ecology & evolution, 22, 323-30.
154	Yvon-Durocher G, Allen AP (2012) Linking community size structure and ecosystem
155	functioning using metabolic theory. Philosophical transactions of the Royal
156	Society of London. Series B, Biological sciences, 367, 2998–3007.
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