

# Spatiotemporal variability of abundance size-spectra in streams across North America

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## Abstract

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The distribution of abundance and biomass within ecological communities is related to trophic transfer efficiency from prey to predators. While it is considered to be one of the few consistent patterns in ecology, spatiotemporal variation of this relationship across continental-scale environmental gradients is unknown. Using a database of stream communities collected across North America (18-68° N latitude, -4 to 25°C mean annual temperature) over 3 years, we constructed 162 mass-abundance relationships (i.e. size spectra). Size-spectra slopes declined (became steeper) with increasing temperature. However, the magnitude of change was relatively small, with median slopes changing from -1.2 to -1.3 across a 29°C range in mean annual temperature. In contrast, total community biomass increased 3-fold over the temperature gradient. Our study suggests strong conservation of abundance size-spectra in streams across broad natural environmental gradients. This supports the emerging use of size-spectra deviations as indicators of ecosystem health.

## Spatiotemporal variability of abundance size-spectra in streams across North America

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**Data accessibility:** Upon article acceptance, all data and code used in the present study will be archived in Data Dryad and Zenodo, respectively.

## Abstract

The distribution of abundance and biomass within ecological communities is related to trophic transfer efficiency from prey to predators. While it is considered to be one of the few consistent patterns in ecology, spatiotemporal variation of this relationship across continental-scale environmental gradients is unknown. Using a database of stream communities collected across North America (18-68° N latitude, -4 to 25°C mean annual temperature) over 3 years, we constructed 162 mass-abundance relationships (i.e. size spectra). Size-spectra slopes declined (became steeper) with increasing temperature. However, the magnitude of change was relatively small, with median slopes changing from -1.2 to -1.3 across a 29°C range in mean annual temperature. In contrast, total community biomass increased 3-fold over the temperature gradient. Our study suggests strong conservation of abundance size-spectra in streams across broad natural environmental gradients. This supports the emerging use of size-spectra deviations as indicators of ecosystem health.

## Introduction

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). Communities, particularly in aquatic environments, are often size structured and characterized by a strong negative relationship between the abundance or biomass of individuals and body size, known as the size spectrum (White *et al.* 2007; Blanchard *et al.* 2009). The slope of this relationship is related to trophic transfer efficiency (Trebilco *et al.* 2013; Sprules & Barth 2015). Therefore, understanding the distribution of biomass within communities connects individual- and population-level traits to community structure, function, and ecosystem dynamics (Dossena *et al.* 2012; O'Gorman *et al.* 2012; Yvon-Durocher & Allen 2012; Trebilco *et al.* 2013).

Size spectra are one of the few well documented organizing principles in ecology. A large body of literature has demonstrated the consistency of size-spectra relationships in diverse ecosystems (Jennings & Blanchard 2004; Trebilco *et al.* 2013; Blanchard *et al.* 2017; Mazurkiewicz *et al.* 2019, 2020). A strongly negative relationship between the abundance or biomass of individuals for a given body size range has been consistently documented in aquatic communities, to the point that size-spectra parameters have been recommended as a potential "universal" indicator of ecological health (Petchey & Belgrano 2010).

However, while estimated slope coefficients are universally consistent in sign (i.e. always negative), their specific values can vary in response to both natural and anthropogenic environmental drivers (Yvon-Durocher *et al.* 2011; Dossena *et al.* 2012; O'Gorman *et al.* 2012; McGarvey & Kirk 2018; Pomeranz *et al.* 2019). For example, because metabolic rates increase with both body size and temperature, environmental warming may have asymmetrical effects on community structure and biomass distributions (Brown *et al.* 2004; Brose *et al.* 2012). Bergmann's and James' rule predict that warmer regions will tend to have smaller species, or smaller-sized populations within a species, respectively (Bergmann 1847; James 1970). Further, the temperature-size rule states that warmer temperatures cause smaller individual body sizes in ectotherm species (Atkinson 1994). Finally, small body size is a predicted response to global warming (Daufresne *et al.* 2009; Gardner *et al.* 2011). Therefore, temperature is hypothesized to be one of the main drivers of variation in size spectra

(O’Gorman *et al.* 2012, 2017). Other anthropogenic impacts, including land use (Martínez *et al.* 2016), acid mine drainage (Pomeranz *et al.* 2019), as well as natural variation, including seasonal variation (McGarvey & Kirk 2018), and resource subsidies (Perkins *et al.* 2018), have also caused slope estimates to vary.

While these and other studies suggest that environmental conditions can alter size spectra relationships, it is difficult to know how those effects scale up to broader patterns in size-spectra at the continental scale and across multiple years. A major limiting factor in large-scale studies of size spectra is the logistical challenge of obtaining consistently collected, processed, and analyzed data across a large spatiotemporal scale. As a result, empirical studies of size spectra share a fundamental limitation of small geographic scales and limited sampling through time (typically a single sample). To overcome this limitation, we estimated size spectra across stream sites in the National Ecological Observatory Network (NEON). We had two primary objectives in this study: 1) assess the broad geographical consistency of size spectra across North American streams, 2) test the hypothesis that size spectra vary as a function of temperature (measured as mean annual temperature).

## Materials and Methods

Quantitative samples of benthic macroinvertebrates from NEON Wadeable-stream sites from 2017-2019 were downloaded to determine size-spectra relationships (National Ecological Observatory Network 2020). NEON is a National Science Foundation (USA) funded program which collects standardized samples from 81 sites (24 streams) across a variety of terrestrial and aquatic ecosystems in North America. Repeat collections include automated instrument recordings and observational field sampling throughout the year, and data are available as open source data products (<https://data.neonscience.org/home>). The stream sites range across a broad environmental gradient (Figure 1), spanning from 18 to 68° N latitude (majority between 33 to 45° N), mean annual temperatures of -4 to 25° C, and mean annual precipitation of 331 to 2530 mm (Table 1). Additionally, sites are in varying biomes and terrestrial plant communities, and subject to different local geologies and flow regimes.

Sites were sampled 1-4 times each year across the local growing season. Most sites had at least two years with three samples, except for COMO which only had one year with three samples (2018), and two samples collected in both 2017 and 2019. Additionally, three sites only had data available from a single collection in a single year; REDB in 2018, WALK and WLOU both in 2019. Details of sample collection and processing protocols are available at the NEON website. Briefly, macroinvertebrate samples were collected from a known area using the sampling method most suited to a site. Laboratory processing included subsampling for taxonomic identification and size class measurement (nearest mm) and estimating the total count per sample. Estimated total counts were standardized to individuals per m<sup>2</sup> by dividing by the area sampled (Chesney 2019). Macroinvertebrate size classes (mm) were converted to individual dry mass (M, in mg) using published length-weight regression coefficients. Most (96%) taxa had taxon-specific length-weight regressions and these were used for model development and assessment. Approximately 8% of the observations were flagged by NEON as being damaged, affecting their length measurements, and were removed from the data. The final data set included length measurements for >82,000 individuals and counts that totaled >17 million individuals.

Size spectra slopes have been estimated using a variety of methods, with binning methods being common in the published literature (White *et al.* 2008; Sprules & Barth 2015; Edwards *et al.* 2017). However, recent comparative studies have shown binning methods to be inaccurate, providing biased slope estimates, and recommend using maximum likelihood methods (Edwards *et al.* 2017). We fitted body size data (dry weight estimated from length-weight regressions) of macroinvertebrates from each collection to a bounded power law distribution with a probability density function:

$$f(x) = \frac{(b+1)x^b}{x_{\max}^{b+1} - x_{\min}^{b+1}}, \quad b \neq 1$$

$$f(x) = \frac{1}{\log x_{\max} - \log x_{\min}}, \quad b = 1$$

Where  $x$  is body mass,  $b$  is the scaling exponent (size spectra slope), and the distribution is bounded by the minimum ( $x_{\min}$ ) and maximum ( $x_{\max}$ ) body sizes observed in a collection. Maximum likelihood methods were used to estimate the exponent,  $b$ , using code modified from Edwards et al. (2017). Using these methods, a more negative  $b$  exponent represents a steeper slope of the size spectra. Slopes can be steeper due to either a relative increase in the abundance of small body sizes, or a relative decrease in the abundance of large body sizes, or a combination of the two. Regardless, steeper slopes represent a relatively smaller proportion of large individuals compared to small individuals within a community.

In addition to the size spectra slopes, we also examined how total community biomass varied across the collections. First, we multiplied the estimated biomass of individuals by their estimated density to calculate mg of dry mass per m<sup>2</sup> for each sample within a collection ( $n = 8$  samples per collection). The 8 samples per collection were used as individual observations in the hierarchical Bayesian analyses (see *Statistical Analyses*).

Macroinvertebrates were generally sampled three times within the growing season from each site. However, due to the wide geographical distribution of sites, there was significant variation in the sample dates. For example, samples in Alaska (latitude 65-68° N) were collected between May and August, whereas samples in Alabama (latitude 33° N) were collected between February and November. Because we are interested in the effects of temperature on size spectra, we used the mean annual temperature in degrees Celsius for each site.

### *Statistical Analyses*

To estimate the effect of temperature on size spectra slopes ( $b$  exponent) and standing stock community biomass, we fit separate hierarchical models with varying intercepts across sites and year (McElreath 2020). We chose a Bayesian approach because it easily incorporates prior information and hierarchical model structures (Hobbs & Hooten 2015; Dietze 2017). Because the exponent  $b$  is continuous and can be positive or negative, we used a Gaussian likelihood to model size spectra slopes. The predictor variable was mean annual temperature. To account for unexplained variation among sites and years, we included random intercepts of *site* and *year*. Priors for the intercept were set as *Normal* (-1.5, 1). This puts low prior probabilities on positive exponents and on exponents with extreme negative values (e.g.,  $< -4$ ), reflecting a wide range of possible values reported in the size spectra literature (White et al. 2007, Blanchard et al. 2009, Edwards et al. 2017). Prior distributions for the effect of mean annual temperature were set as *Normal* (0,0.1), and *Exponential* (2) for sigma and the standard deviation of the random intercepts. To ensure that the prior distributions contained reasonable prior prediction but did not overwhelm the posterior inference, we used prior predictive simulation (see Supplemental Information, Fig. S1; Gabry et al. 2019).

For community biomass, we used a Gamma likelihood with a log link, because biomass is a continuous and positive measure (Hobbs & Hooten 2015). The model structure for biomass was the same as the model structure for size spectra slopes. The prior for the intercept was set as *Normal* (7,1). This reflects a prior expectation that community biomass values of ~150 to ~9000 mg dry mass/m<sup>2</sup> are reasonable, with a mean of ~1000. These point estimates are obtained by exponentiating, due to the log-link, the prior mean (i.e. 7) plus and minus two standard deviations (7-2 or 7+2). These values are compatible with the range of values reported in the literature (Benke et al. 1984; Grimm 1988; Warmbold & Wesner 2018). The remaining priors were *Normal* (0,0.1) for the slope, *Exponential* (2) for the standard deviation of the random intercepts, and *Gamma* (0.01, 0.01) for the shape parameter of the Gamma likelihood. As before, these priors were specified using prior predictive simulation (Supplemental Information, Fig. S1). Our prior and posterior distributions for parameter coefficients are plotted in SI Figures S2 and S3. A sensitivity analysis of our priors indicated our parameter coefficient estimates were robust to halving and doubling the SD value (Fig. S6). The full hierarchical model structure can be found in Supplemental Information S1.

Models were specified using the *brms* package (Bürkner 2018) in R (R Development Core Team 2017), with posterior distributions derived using Hamiltonian Monte Carlo in *rstan* (Stan Development Team 2018). The models were run using 4 chains each with 6000 iterations, in which the first half were discarded as warmup, resulting in 12000 posterior draws. Convergence was checked by ensuring that all  $\hat{r}$ -hats were  $<1.1$ , and by visually assessing trace plots (Gelman & Rubin 1992). To assess model fit, we used posterior predictive checks in which we simulated ten data sets from the posterior distribution and graphically compared them to the original data set (Gelman et al. 2013; Gabry et al. 2019; Figure S4 and S5). Strong visual discrepancies between the original data and simulated data indicate poor model fit (Gabry et al. 2019). In our simulations, both models produced data that were qualitatively similar to the original data, indicating good model fit (SI, Figures S4 & S5).

### Data availability

All of the data and R code to reproduce our results and figures will be archived upon article acceptance. The data will be archived in an appropriate repository (i.e., Dryad) and the code will be archived on Zenodo.

## Results

### Size Spectra slopes

The maximum likelihood estimates of the power law exponent (e.g., size spectra slopes) for individual collections ranged from -0.73 to -1.80. The median of the posterior distribution of size spectra slopes from the hierarchical Bayesian model was -1.25 (95% CrI (-1.39, -1.11); Table 2). Size-spectra slopes had a 98% probability of being negatively related to mean annual temperature (coefficient estimate = -0.004, 95% CrI (-0.007, 0.0004); Table 2), meaning that increasing temperature was associated with relatively fewer larger body sizes compared to small body sizes within a community (Figure 2A). However, the magnitude of this decline was small, with median slopes changing from -1.2 to -1.3 across the 29°C temperature gradient. This range was smaller than the among-sample range in measured slopes within sites (Figure 2A). Using the posterior predictive distribution from our model to estimate variation among sites, median slopes ranged from a low of -1.33 at site GUIL (mean annual temperature = 25°C) to a high of -1.15 at site CARI (mean annual temperature = -1°C; Figure 3A).

### Community biomass

Community biomass showed higher variation among sites (Figure 2B) with collection-specific medians ranging from 22.3 to 6,729 mg dry mass per m<sup>2</sup>. The global median of the posterior samples from the hierarchical Bayesian model was 1,333 mg dry mass per m<sup>2</sup> (95% CrI (247, 10 929)). Community biomass had a 95% probability of being positively related to mean annual temperature (coefficient estimate = 0.04 (CrI (-0.008, 0.09); Table 2). After exponentiating, this indicates that each unit increase in mean annual temperature causes an average of a 4% increase in biomass. From the posterior predictive distribution, median biomass values ranged from a low of 285 mg dry mass per m<sup>2</sup> at site CARI (mean annual temperature = -1°C) to a high of 11,309 mg dry mass per m<sup>2</sup> at site LEWI (mean annual temperature = 12°C, Figure 3B).

## Discussion

We analyzed the largest collection of size spectra relationships in stream communities that we are aware of, and we found that slope estimates varied in response to a broad temperature gradient. Size-spectra slopes represent the efficiency of energy transfer from small, abundant, individuals to fewer large predators (Trebilco *et al.* 2013) with clear implications for ecosystem functioning (O’Gorman *et al.* 2012; Cross *et al.* 2015). Shallow slopes indicate efficient transfer of energy by supporting a relatively higher proportion of larger individuals, while steeper slopes indicate inefficient energy transfer with relatively fewer large individuals. The steeper slopes reported here with increasing mean annual temperatures implies that warmer sites have fewer large individuals relative to the number of small individuals within a site compared to colder sites.

These results help to resolve previous uncertainty in how size spectra slopes scale with temperature. Variation in size spectra slopes is driven by variation in body size distributions and body size is in turn altered by

temperature, either through reductions in taxon-specific body size, species turnover, or through changes in community structure (Bergmann 1847; Atkinson 1994; Daufresne *et al.* 2009; Winder *et al.* 2009; O’Gorman *et al.* 2012). Thus, it is widely expected size-spectra slopes should vary across temperature gradients, though the direction of change is uncertain (Daufresne *et al.* 2009; Dossena *et al.* 2012; O’Gorman *et al.* 2012). Theory predicts that warm environments should favor smaller individuals, and this is supported by empirical (James 1970; Atkinson 1994; Daufresne *et al.* 2009) and experimental observations (Yvon-Durocher *et al.* 2011; Dossena *et al.* 2012). However, O’Gorman *et al.* (2017) found that warmed Icelandic streams had shallower slopes, perhaps due to increased nutrient availability and changes in trophic transfer efficiency, leading to increased top-down effects of consumers on diatoms. In contrast, Dossena *et al.* (2012) found that slopes declined with temperature, but the effect varied over seasons. Mazurkiewicz *et al.* (2020) found no relationship between marine benthic size spectra and temperatures in arctic systems. These contrasting outcomes, derived from different experimental approaches, generate uncertainty in how size spectra slopes should scale with temperature across large spatial gradients. The results presented here support the hypothesis that slopes become steeper in response to increasing temperature.

However, while size spectra slopes scaled with temperature, the overall change was relatively small, with median slopes declining by only  $\sim 0.1$  units across the temperature gradient. Direct comparisons of this effect size with previous studies of size spectra responses to temperature (e.g., Yvon-Durocher *et al.* 2012, O’Gorman *et al.* 2017) are hampered by the different approaches to estimating size spectra exponents (Edwards *et al.* 2017). However, in a 30-year dataset from the International Bottom Trawl Survey (ICES 2015), Edwards *et al.* (2020) found that size spectra slopes calculated using maximum likelihood varied  $\sim 0.4$  units among years. In addition, among sample variation at NEON sites in this study was  $\sim 0.3$  to  $0.8$  units, with measured slopes at one site varying from  $-1$  to  $-1.8$  among sample dates. Placing our results into this context, the influence of temperature appears small relative to variation due to other factors, including natural variation over time.

In contrast to the negative relationship of temperature with size-spectra slopes, community biomass was positively related to mean annual temperature. This is also in agreement with predicted effects of increasing environmental temperature supporting more small-bodied individuals. For example, an increase in community biomass could be driven by small-bodied individuals alone, if their increase was larger than the relative decrease in larger-bodied individuals. It is important to account for community biomass, as increased biomass at lower trophic levels may be able to support biomass at higher trophic levels (O’Gorman *et al.* 2012), even if trophic transfer efficiency is affected by temperatures (Trebilco *et al.* 2013). However, the magnitude of the random effects of *site* were large, and the effect of temperature was relatively small. Including additional predictor variables thought to affect community biomass, such as productivity or nutrient availability at the base of the food web (Morin *et al.* 2001; Daan *et al.* 2005), may help explain additional variation.

Given the relatively small influence of temperature and the overlap in site-specific averages of size spectra (Figure 3A), our results provide an opportunity to use our range of size-spectra as a baseline indicator in studies of disturbance. Size-spectra relationships have been proposed as a universal indicator of ecological health, with deviations from “natural” size spectra representing disturbed systems (Jennings & Blanchard 2004; Petchey & Belgrano 2010; Trebilco *et al.* 2013). Defining “natural” is difficult without accounting for variation among broad spatial and temporal scales. By accounting for the effect of temperature on size spectra slopes in relatively undisturbed systems across 50 degrees of latitude over three years, our results reveal bounds that could help to gauge the severity of size spectra change in response to disturbance. For example, one approach would be to compare size spectra from disturbed sites to the posterior predictive distribution of size-spectra at a similar site in our study, with deviations outside of the expected range of natural variation indicating the level of disturbance. This may represent a powerful tool for assessing ecological condition. Indeed, as NEON data continues to be collected, it will be possible to compare our predictions to size-spectra collected after intense disturbances, such as extremely high or low flow events, temperature anomalies due to climate change, wildfires, flow debris, etc. This represents an exciting opportunity to test responses to disturbances at higher levels of organization, which has typically been difficult or impossible due to the large logistical efforts needed to collect community-wide data across broad spatial scales. Furthermore, data on post-disturbance size spectra within the NEON sites will provide valuable information on community

recovery, and the magnitude, direction, and expected duration of altered size spectra.

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## Tables and Figures

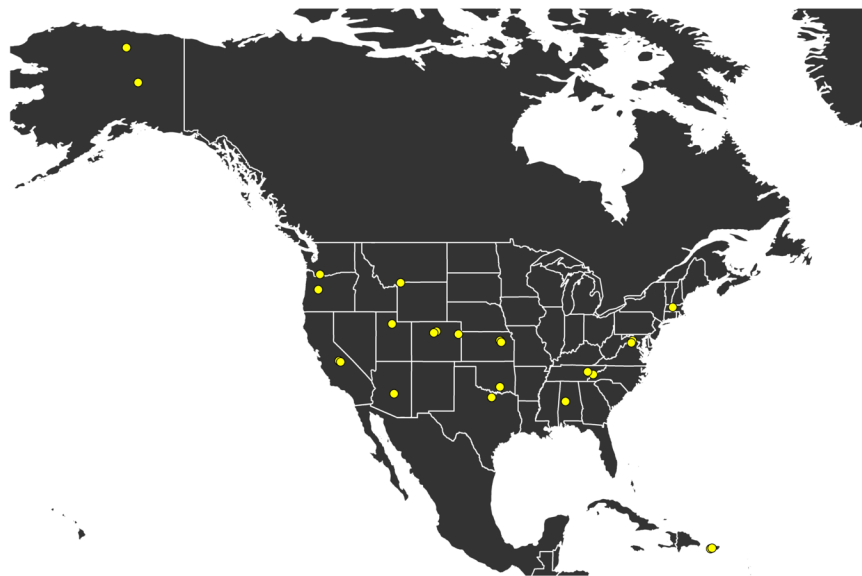
**Table 1.** Site-level information for stream sites in the National Ecological Observatory Network.

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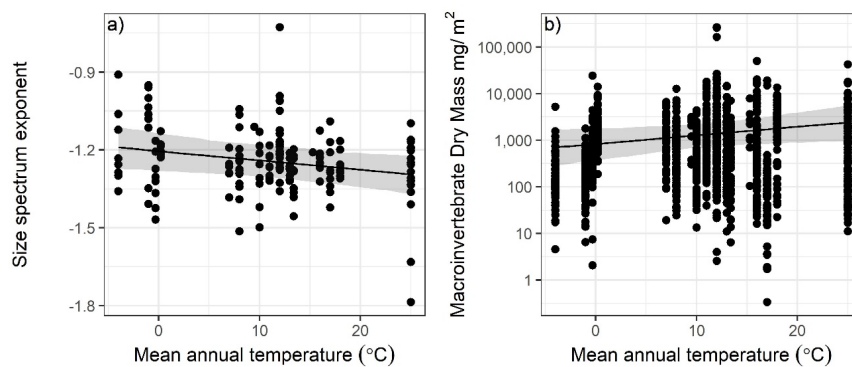
image1.emf available at <https://authorea.com/users/367796/articles/487073-spatiotemporal-variability-of-abundance-size-spectra-in-streams-across-north-america>

**Table 2.** Population-level coefficient estimates and 95% credible intervals for the effects of degree days on size spectra slopes ( $b$  exponent) and community biomass.

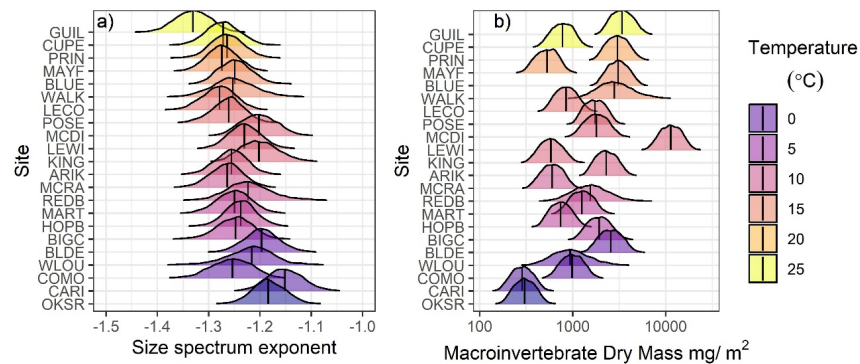
Model	Coefficient	Estimate	Q2.5	Q97.5	R-hat
$b$ exponent	y-intercept	-1.2	-1.3	-1.1	1
	degree days	-0.003	-0.007	0.0004	1
Biomass	y-intercept	6.7	6.2	7.5	1
	degree days	0.04	-0.008	0.08	1



**Figure 1.** Map of site locations across North America.



**Figure 2 .** Effect of mean annual temperature on the slope and intercept of normalized size-spectra relationships. Horizontal lines and shading indicate the median and 95% CrI of the change in slopes or intercepts across degree day values. Dots indicate individual collections.



**Figure 3** . Posterior distributions of slope (a) and biomass (b) across sites where color corresponds to mean annual temperature. Black vertical lines within density distributions show the median value for a given collection. Sites are ordered by decreasing mean annual temperature, e.g., GUIL is the warmest site at 25°C, while OKSR is the coldest at -4°C.