

Thermal traits of freshwater macroinvertebrates vary with feeding group and phylogeny

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Abstract

1. Functional traits of organisms, especially feeding traits, influence how organisms mediate ecosystem processes. As climate change, landscape modification and industrial waste heat release continue to increase water temperatures, shifts in the composition of feeding traits within aquatic macroinvertebrate communities may alter ecosystem processes. However, it is unclear whether thermal traits of macroinvertebrates vary systematically across functional feeding groups (FFGs; i.e., categories based on feeding ecology such as herbivores, shredders, predators, etc.) or phylogeny.
2. We used previously published datasets on hundreds of macroinvertebrate taxa to evaluate how thermal traits differed across FFGs. We also examined the strength of phylogenetic signal in both FFG and thermal traits, using a new phylogeny of insect taxa. Then, we tested whether phylogenetic patterns offered a plausible explanation for differences in thermal traits among FFGs by comparing phylogenetic and non-phylogenetic regressions.
3. Shredders tended to have lower temperature preferences, optima and maxima (three of five of the thermal traits evaluated) than other FFGs. Patterns for other FFGs differed by thermal trait, but predators, collector-gatherers and filterers had some of the highest thermal trait values. FFG explained 40% of the variation in critical thermal maximum, but <12% of the variation in the four other thermal traits.
4. Phylogeny explained 26%–88% of the variation in thermal and feeding traits. For the subset of taxa and trait data that were available, phylogeny explained more than double the variation in thermal traits relative to FFG, but comparison of phylogenetic and non-phylogenetic regressions highlighted that FFG explained variation in thermal traits that was independent of phylogeny.
5. Our results highlight phylogeny and FFG as predictors of thermal traits in aquatic macroinvertebrates. Our results suggest that warmer water temperatures could favour predators, filterers and collector-gatherers over shredders. Furthermore, our results confirm that certain orders of macroinvertebrates,

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such as Diptera, may be better suited to warmer temperatures than other orders, such as Plecoptera.

KEYWORDS

climate change, critical thermal maxima, temperature preference, temperature sensitivity, upper lethal temperature

1 | INTRODUCTION

Functional traits mediate how organisms interact with their environment (Shipley et al., 2016; Martini et al., 2021) and may determine how organisms influence ecosystem processes (Vaughn, 2010; Wallace & Webster, 1996). Some functional traits can be highly correlated with climate variables (Ahrens et al., 2020), suggesting that climate warming may alter the distribution of traits within a community (Bjorkman et al., 2018; Debouk et al., 2015). Thus, changes in ecosystem processes in response to warming can result from both direct physiological responses to increased temperature (Enquist et al., 2003; Song et al., 2018) and associated changes in the distribution of functional traits (Dorji et al., 2013). Therefore, understanding how thermal traits differ across functional groups is important for predicting future changes in ecosystem function.

In aquatic ecosystems, macroinvertebrates are critical drivers of ecosystem processes (Cuffney et al., 1990; Wallace et al., 1982). In this context, one of the most important traits of macroinvertebrates is how they consume food, referred to as their “functional feeding group” (FFG). Macroinvertebrate FFGs describe their main food source and are based on gut contents, mouthpart morphology, enzymatic activity analysis and/or stable isotopes (Cummins & Klug, 1979; Dodds et al., 2014; López-Rodríguez et al., 2012; Wallace & Webster, 1996), although some taxa employ more generalised feeding strategies (Descroix et al., 2010). If different FFGs are differentially sensitive to temperature, then changing thermal regimes will lead to predictable changes in invertebrate community composition (Bjorkman et al., 2018), demand for resources (Schramski et al., 2015), and fluxes of energy and material (Cuffney et al., 1990).

Previous studies have found mixed results regarding the relative temperature sensitivity of different FFGs. One study, which used species distribution models to predict future distributions of 86 insect taxa, found that shredding (i.e., leaf-consuming) and algal-grazing aquatic insects were particularly sensitive to climate change, with 30%–40% of taxa projected to be extirpated across some ecoregions of the western United States (Pyne & Poff, 2017). Corroborating the notion that shredders may be sensitive to temperature, studies have reported less alpha diversity and lower biomass of insect shredders at warm tropical sites compared to cool temperate sites (Boyer et al., 2012; Dobson et al., 2002). The results of Pyne and Poff (2017) also are similar to the results of a long-term, space-for-time study in Sweden that demonstrated a reduction in grazer biomass and a shift in species composition due to warming (Salo et al., 2020). While this body of work has shed light on the potential relationship between macroinvertebrate FFGs and thermal traits, these analyses have been limited taxonomically – either

studying relatively few taxa or focusing on a single order of insects – making generalisations difficult (e.g., Hering et al., 2009; Pyne & Poff, 2017). Furthermore, it has been suggested that an evolutionary correlation between thermal traits and FFG is the ultimate cause of relationships between aquatic macroinvertebrate FFGs and thermal traits (Boyer et al., 2012). However, links between thermal and feeding traits have not been thoroughly evaluated in the context of modern phylogenies, even though there have been previous phylogenetic analyses of aquatic macroinvertebrates (Poff et al., 2006).

Determining the degree to which thermal and feeding traits are phylogenetically constrained can inform predictions about how macroinvertebrates will respond to a warming climate. Examining trait distributions across a phylogeny can provide important information about the evolutionary lability of traits (Blomberg et al., 2003). Traits that are evolutionarily labile and have diverged many times throughout evolutionary history will show patterns that appear more random across a phylogeny, while traits that are more evolutionarily conserved will show greater similarity among closely related taxa (Blomberg et al., 2003). Furthermore, traits that are more evolutionarily labile are expected to be more responsive to environmental and ecological pressures, and thus may be more flexible in the face of environmental change, such as warming temperatures (Liu et al., 2015). Many macroinvertebrate traits show a strong phylogenetic signal, but in one analysis, temperature preference and feeding mode were less aligned with phylogeny and were considered among the most evolutionarily labile traits (Poff et al., 2006). This suggests that these traits may be more adaptable to environmental conditions and less constrained by taxonomic identity. However, the evolutionary lability of temperature preference and feeding mode merits further analysis in light of new phylogenetic and trait data (Chesters, 2017; Chown et al., 2015; Schmidt-Kloiber & Hering, 2015).

Here, we test whether the functional feeding group of aquatic macroinvertebrates influences their thermal traits using multiple large datasets. We use data that include: (a) maximum observed temperature in the field (*OMax*) and estimates of thermal optima (*TOpt*) informed by species range models from the United States; (b) thermal preference (*TPref*) data from across the European Union; and (c) laboratory measurements of critical thermal maxima (*CTMax*) and upper lethal temperature (*ULT*) compiled by Chown et al. (2015). For each of these datasets, we evaluate differences in thermal parameters among FFGs. We hypothesise that shredders and herbivores will prefer cooler temperatures and have lower optimum and maximum temperatures than other groups of aquatic macroinvertebrates (H1). Then, we use phylogenetic comparative methods to evaluate the degree of correlation of both feeding mode and thermal sensitivity with the phylogeny of aquatic insects (an important subset

of macroinvertebrates). We hypothesise that both feeding traits and thermal traits will have a low degree of phylogenetic signal – indicative of evolutionarily labile traits (H2). Finally, if differences in thermal traits among FFGs are caused primarily by an evolutionary correlation, then we hypothesise that accounting for phylogenetic relationships with phylogenetic regressions will eliminate any effect of FFG on thermal parameters (H3).

2 | MATERIALS AND METHODS

2.1 | Evaluating thermal traits of functional feeding groups across the United States

We tested whether there was variation in temperature preferences among FFGs with data compiled from across the United States using the Freshwater BioTraits database, which is maintained by the United States Environmental Protection Agency. From this database (US EPA, 2012), we evaluated estimates of $TOpt$ for taxa compiled from eight different studies which estimated thermal optima using species distribution models of biomonitoring data. We used data on the maximum temperature at which a given taxon was observed in the field ($OMax$), which are compiled from 53 studies. We used the classification of FFGs from this dataset listed under the trait values for “Primary functional feeding group abbreviated” and “Primary feeding mode.” We recoded the values of these traits to fit into the six FFGs (i.e., “Herbivore”, “Collector-gatherer”, “Predator”, “Shredder”, “Filterer” and “Generalist”). The diet of some taxa changes throughout their life cycle, and across seasons or space (Tierno de Figueroa et al., 2019), resulting in variation that may be represented by conflicting records in the database. We assigned taxa that had conflicting records for their FFG assignment to the “Generalist” category. When data included both larval and adult stages we used only the data from the larval stage. After merging temperature preference data with FFG data by taxon name, we had 623 taxa with estimates of $TOpt$ and 212 taxa with estimates of $OMax$, although some taxa had multiple estimates of their thermal parameters (e.g., from different source studies).

We tested whether $TOpt$ and $OMax$ varied among FFGs using linear mixed-effects models. We accounted for non-independence at the taxon and data source level using random intercepts. We fitted models using the *lme4* package, estimated contrasts among FFGs using the *emmeans* package, and estimated the portion of variation explained by the fixed effects alone (marginal R^2) and the full model (conditional R^2) using the *MuMIn* package (Bartoń, 2020; Bates et al., 2014; Lenth et al., 2021), all within the R (R Core Team, 2021). project.org

2.2 | Evaluating thermal traits of functional feeding groups across the European Union

We used macroinvertebrate trait data from across the European Union to test the same hypothesis as above (that thermal traits vary across FFGs) (Schmidt-Kloiber & Hering, 2015). We reduced the

FFG data in this dataset down to the same six categories as above by combining “Active-filterer” and “Passive-filterer” into “Filterers”, changing “Grazers” to “Herbivores” and dropping the relatively uncommon groups “Parasites”, “Xylophagous”, “Miners” and “Other”. For each taxon, this dataset assigns each feeding group a weight, which sums to 10 across all feeding groups. If any single feeding group had a weight greater than five, we designated the taxa as specialists in that feeding group (most specialist taxa were very clear, ~65% of taxa designated as specialist had a score of 10 in one category). Taxa with weights assigned more evenly across FFGs (weights of five or less in all feeding groups) were designated as “Generalists.” We used information on temperature preferences ($TPref$) from across the EU which were generated from models of summer stream temperatures and macroinvertebrate occurrence (Schmidt-Kloiber & Hering, 2015). After merging these two data sources, we had 332 taxa with values for $TPref$ and FFG. We evaluated differences in $TPref$ among FFGs using an ANOVA and used a Tukey *post hoc* comparison to evaluate which differences were significant.

2.3 | Laboratory measurement of thermal traits

We also evaluated differences in thermal parameters across FFGs using data compiled by Chown et al. (2015) on the ULT and $CTMax$ of aquatic insects. Both ULT and $CTMax$ are measurements of acute temperature sensitivity obtained by gradually increasing temperatures and recording the temperature of either death (ULT) or a behavioural response (e.g., loss of righting response for $CTMax$). While both of these metrics reflect temperature tolerance over only a short time, they have the advantage of being somewhat independent of environmental temperature. To identify the FFG of these taxa, we first merged the thermal trait data from Chown et al. (2015) with the FFG data from the EU trait dataset. Then, for taxa that did not have an FFG assigned in the EU trait dataset, we looked for assignments in the Freshwater BioTraits dataset. Many of the taxa in the data compiled by Chown et al. (2015) were identified only to genus level. Thus, we assigned some FFGs at the genus level by summarising the Freshwater BioTraits dataset at genus level, and restricting our analysis to taxa that had a unanimous assignment of FFG. We fitted linear mixed-effects models to evaluate the differences among FFGs and included a random effect to account for non-independence at the level of the source study.

2.4 | Evaluating the evolutionary hypothesis for FFG specific thermal traits

We evaluated the phylogenetic signal, or the tendency for more closely related taxa to have similar traits, of $TPref$ and FFG by merging these trait values with a recent phylogenetic tree of insect taxa (Chesters, 2017). The only thermal trait that we evaluated was $TPref$ from the EU dataset, as the other datasets have structures which make phylogenetic mapping difficult (i.e., conflicting results

for many taxa representing different source studies). We evaluated phylogenetic signal using Pagel's λ , which varies from one when the distribution of a trait matches expectations based on evolution according to a model of Brownian motion, to zero when a trait is distributed randomly with respect to phylogeny (Pagel, 1999). We used the numerical trait values in the EU dataset to evaluate the signal in each FFG independently, and graphed data using R/ggtree (Yu, 2020). We estimated λ using the *phylosig* function from R/phytools (Revell, 2012). Additionally, we report the portion of the variation in the trait data explained by this phylogeny-only model using a pseudo- R^2 calculated with R/MuMIn (Bartoń, 2020).

Finally, we used a subset of the data (94 taxa) which have information on FFG, *TPref* and phylogenetic relationships to evaluate the effect of accounting for phylogeny on relationships between FFG and thermal parameters. With this subset of data, we evaluated the effect of FFG on *TPref* without controlling for phylogeny using an ANOVA. Then we fitted two generalised least squares models with a phylogenetic covariation structure to the data, one of which included a parameter for FFG and one which had no fixed effects. We report the *p*-value associated with the FFG term, the R^2 and the Akaike information criteria adjusted for small samples sizes (*AICc*) of these models to evaluate how controlling for phylogeny influences the relationships between FFG and *TPref*.

3 | RESULTS

Differences in *TPref*, *OMax*, *TOpt*, *CTMax* and *ULT* were related to the FFG of macroinvertebrates (Figure 1; Table 1). There were many differences in *TPref* among FFGs (Figure 1a). Shredders had an average *TPref* value that was lower than that of collector-gatherers, predators, filterers and generalists by 2.1, 1.6, 1.3 and 1.3°C, respectively (Figure 1a). Collector-gatherers had the highest *TPref*, greater than that of herbivores and generalists by 0.8°C. Shredders had lower *TOpt* than predators by 1.9°C, and shredders had a lower *OMax* than filterers by 4.1°C (Figure 1b, c). Predators had a higher *CTMax* than generalists by 6.9°C (Figure 1d). Predators also had a higher *ULT* than both shredders and generalists by 6.4 and 5.5°C respectively. While each of these models estimated effects of FFG on thermal parameters (Table 1), the amount of variation in the data that was explained by FFG typically was small, only exceeding 11% in the case of *CTMax*. Furthermore, when random effects were included in the models (for either source study or repeated measurement of taxa), the random effects generally explained a much larger portion of the variation in the thermal trait data than FFG, again with the exception of *CTMax* (Table 1).

We found that there was a strong phylogenetic signal in both FFG and *TPref* of aquatic insects (Table 2; Figures 2 and 3). Each of the FFGs and *TPrefs* had estimated values of Pagel's λ that were different from zero, and many were close to one (Table 2). Furthermore, phylogeny typically explained a large portion of the variation in each of these traits, with R^2 values all >0.25 and as high as 0.88 (Table 2). In the subset of data where we evaluated the effect of controlling

for phylogeny on the observed relationship between FFG and *TPref* we found that the observed effect of FFG was only mildly diminished by controlling for the phylogenetic relationship among taxa. Specifically, we found that while the phylogenetic model with only an intercept term explained a substantial portion of the variation in the *TPref* data ($R^2 = 0.26$), this increased when an FFG term was added ($R^2 = 0.34$), which was similar to the portion of variation in the *TPref* data explained by FFG alone (Table 3). We found a similar pattern in *AICc* among the models, which indicated that the addition of the FFG term explained additional variation beyond phylogeny alone ($\Delta AICc = 4.3$; Table 3).

4 | DISCUSSION

We found that the FFG of macroinvertebrates explained some of the difference in thermal traits among taxa. In each of the field-collected thermal parameters (*TPref*, *TOpt* and *OMax*), shredders had lower values than at least one other FFG. However, in the laboratory-collected data (*ULT* and *CTMax*) shredders had similar thermal parameter values to other FFGs, with the exception of a difference between the *ULT* of predators and shredders, which was caused by an unusually high values for predators not low values for shredders. While there were many other differences among FFGs for various thermal parameters, the effects were more mixed across datasets with differences in one dataset not present in others. We found strong evidence for a phylogenetic signal in both FFG and *TPref* of aquatic insects, and the phylogenetic models typically explained a large portion of the variation in the trait data. However, while the phylogenetic models explained much of the variation in both functional feeding group and thermal traits, our results suggest that phylogenetic similarity among taxa is not a sufficient explanation for differences in thermal traits among FFGs.

Although we found effects of FFG on several of the thermal parameters that we studied, the design of our analysis probably inflated the probability of type-1 errors (Blomberg et al., 2003). Because the union of the thermal trait, feeding trait and phylogenetic data provided only a small sample size, we were not able to control for the effect of phylogeny on the relationship between FFG and thermal traits in our primary analysis. More closely related species are more likely to have similar trait values, which was confirmed by our phylogenetic analysis. This similarity among closely related taxa represents an important form of non-independence that was unaccounted for in many of the contrasts that we made. However, in the subset of data in which we controlled for phylogeny, we still detected an effect of FFG on *TPref*, which suggests that similarity among closely related taxa is not the sole cause of the relationships which we observed between FFG and thermal traits. Furthermore, we argue that the ecological consequences of variation in thermal traits across FFGs are meaningful, regardless of whether the underlying cause has to do with phylogenetic similarity or an ecological tradeoff between thermal traits and feeding mode (Boyero et al., 2012).

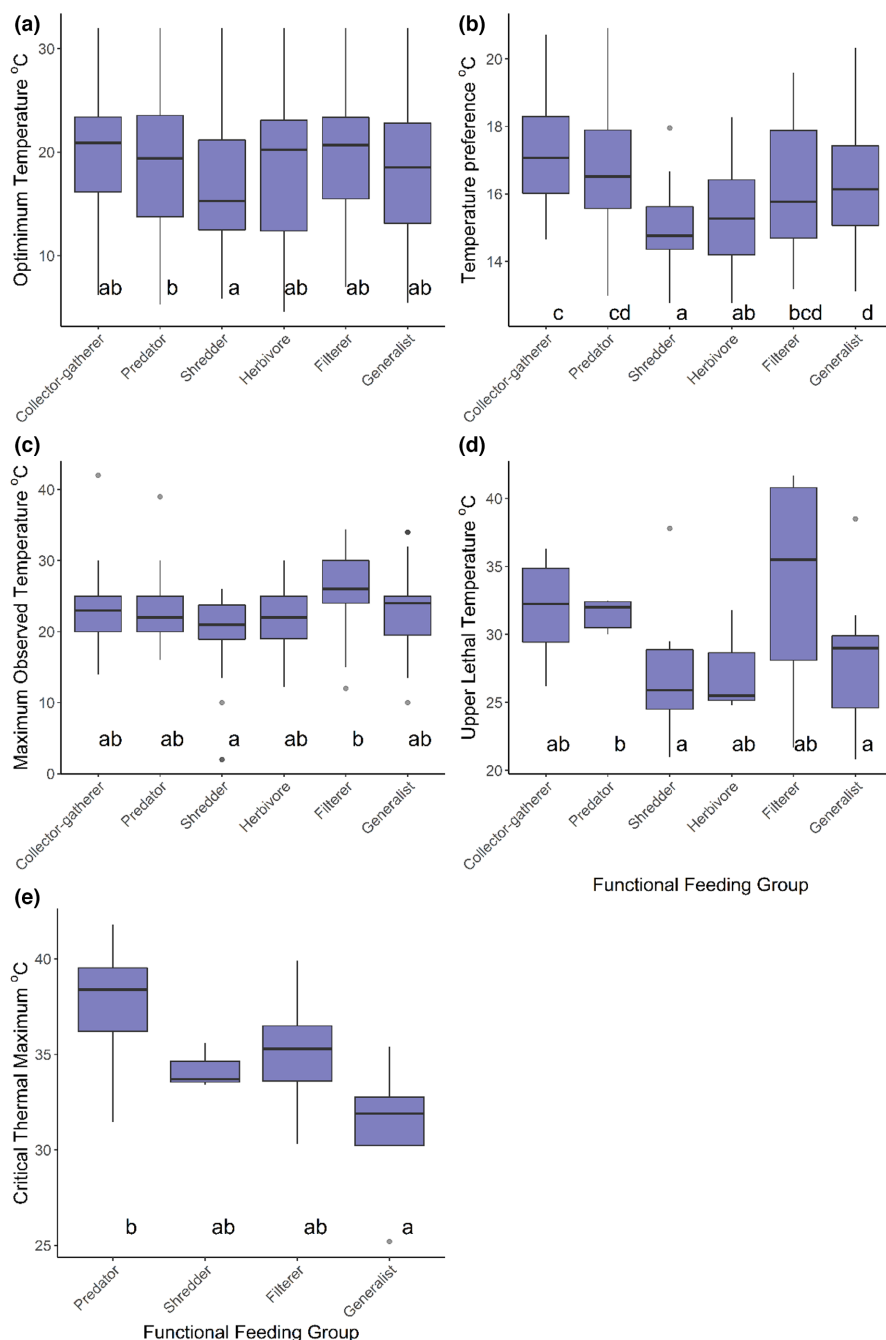


FIGURE 1 Boxplots of thermal parameters across functional feeding groups. We present the optimum temperature (a), temperature preference (b), maximum observed temperature (c), upper lethal temperature (d) and critical thermal maximum (e). Shaded boxes cover the middle 50% of the trait distribution, and lines within represent the means. Boxplot whiskers extend to the largest and smallest values, unless those values are <1.5 IQR from the middle of the 50% of the distribution, in which case points are plotted individually as outliers

This study highlights that shredders appear to be more sensitive to temperature than other FFGs, yet our data are not sufficient to understand the ultimate cause of this sensitivity. We highlight three non-exclusive mechanisms that could contribute to the observed lower thermal trait values of shredders. Firstly, a diet of leaves may make organisms more sensitive to warm temperatures. Leaves are a nutrient-poor resource (Villanueva et al., 2011), and are made up of carbon compounds that are difficult to access and digest (e.g., lignin and cellulose). This low-quality diet may make it difficult for shredders to maintain the high rates of metabolism required at higher temperatures. Experimental evidence demonstrates that more nutrient-dense food is required to optimise growth at higher environmental temperatures (Kutz et al., 2019). This effect has been

demonstrated in microcosms where shredders fed higher-quality food had greater survival at warm temperatures (Fenoy et al., 2020). Secondly, variation in resource supply may contribute to patterns of shredder abundance, and these patterns may be misinterpreted as effects of temperature. In addition to providing food to shredders, riparian vegetation can play an important role in the thermal regime of stream ecosystems (Caissie, 2006). For instance, selective removal of 66% of the riparian canopy resulted in a 5°C increase in mean summer stream temperatures in one study (Feller & Kimmins, 1984). Thus, covariation in temperature and resource supply may cause some of the variation observed in the data collected from the field (Vannote et al., 1980), independent of underlying physiological thermal traits (Junker et al., 2020). This notion

TABLE 1 Model results for tests of variation in thermal traits among functional feeding groups (FFGs)

Parameter	Number taxa	<i>p</i> -value	Marginal R^2	Conditional R^2
<i>TOpt</i>	623	0.02	0.01	0.67
<i>TPref</i>	332	<0.0001	0.11	NA
<i>OMax</i>	212	0.006	0.04	0.85
<i>ULT</i>	39	0.02	0.09	0.84
<i>CTMax</i>	28	0.01	0.40	0.41

Note: We modelled the thermal optima (*TOpt*), temperature preference (*TPref*), maximum observed temperature (*OMax*), upper lethal temperature (*ULT*) and temperature preference (*TPref*) as a function of FFG. We present the number of taxa, the *p*-value, the marginal R^2 (just the effect of FFG) and the conditional R^2 which describes the portion of variation explained by the full model which has random effects accounting for non-independence at the study and taxa level.

TABLE 2 Estimates of phylogenetic signal for temperature preference (*TPref*) and functional feeding groups (FFG)

Trait	Number of taxa	Pagel's λ	<i>p</i> -value	Pseudo- R^2
<i>TPref</i>	137	0.59	<0.00001	0.26
FFG: Shredder	579	1.0	<0.00001	0.88
FFG: Herbivore	579	0.97	<0.00001	0.62
FFG: Collector-filterer	579	0.88	<0.00001	0.64
FFG: Collector-gather	579	0.92	<0.00001	0.60
FFG: Predator	579	0.95	<0.00001	0.80

Note: We report estimates of Pagel's λ , *p*-values associated with the estimate of λ , and the R^2 of a model that only incorporates phylogenetic signal. Estimates of Pagel's $\lambda \approx 1$ imply that a trait follows a pattern that would be expected based on evolution according to Brownian motion. Each FFG was modelled separately, using the 1–10 fuzzy coding scheme of the raw data.

is somewhat supported by our data, as shredders appear to have lower values of thermal parameters in the field data (*TPref*, *OMax* and *TOpt*), although this pattern is not as clear in the laboratory data (*CTMax* and *ULT*). Thirdly, shredders may be outcompeted by microbes and generalist consumers at warmer temperatures. Warming is expected to favour organisms with smaller body sizes (Daufresne et al., 2009), and one aspect of the relationship between microbes and shredders is resource competition (Marks, 2019). At warmer temperatures, microbes may consume leaves too quickly for robust populations of specialised shredders to develop or persist (Irons et al., 1994). However, our analysis focuses primarily on insects, and thus may not generalise to other shredding/detritivorous organisms in streams such as fish and decapods.

Predators often had higher values of thermal traits than other taxa. Predatory taxa are in a unique position relative to other FFGs as shifts in the traits of their food also are likely to occur with warming (Nelson et al., 2016). Furthermore, the temporal relationships

between predators and prey (e.g., oscillations and feedbacks) can influence site-level persistence (Uszko et al., 2017; Vucic-Pestic et al., 2011). However, Pyne and Poff (2017) did not find predators to have a lower risk of local extirpation in their analysis. The more complex interactions involved in predator persistence may imply that their responses to temperature are more idiosyncratic than other FFGs.

Although we found significant differences among FFGs in many of these thermal parameters, we observed large ranges in thermal parameters within each FFG and particularly *TOpt*. This large range suggests that any local assemblage, which includes only a small fraction of the number of species included in our analysis, may idiosyncratically have different patterns of thermal parameters among FFGs. This is highlighted by the large explanatory power of the random effects in our models of the effect of FFG on thermal parameters. For instance, FFG explained 1% of the variation in *TOpt* whereas the random effects (species and study) explained 66% of the variation, much of which was explained by the different studies being conducted in different regions of the United States. An additional factor that is important to consider in the application of these data is the flexibility that organisms can have in their actual feeding strategies. Tierno de Figueroa et al. (2019) demonstrate that organisms can have diets that differ from their commonly assigned FFG, that also are variable in space and time. The use of a 'Generalist' category helps account for this, but variation in diets still represents uncertainty in our analysis, and may explain some of the relatively low R^2 values we found in parts of our analysis.

Our results demonstrate a high degree of phylogenetic signal in both *TPref* and FFG, suggesting that these traits are evolutionarily constrained. The traits of animals, and interactions among animals in a community (TerHorst et al., 2018), can affect the fitness of animals which leads to evolutionary pressure on functional traits (Laughlin et al., 2020). Although it is broadly understood that there are evolutionary tradeoffs to thermal traits (Clarke, 2003), the only previous analysis of the evolutionary lability of aquatic insect traits found that thermal preferences and feeding traits were among the most labile (Poff et al., 2006). This is congruent with other findings that behavioural or ecological traits tend to be more labile than morphological traits (Blomberg et al., 2003). Poff et al. (2006) estimated trait lability by counting the minimum number of trait state changes required to fit the observed phylogenetic distribution of a trait and taking the ratio of this observed number to the minimum number of trait changes to fit any phylogeny (i.e., the consistency index). This method is useful for comparing different traits mapped onto the same phylogenetic tree, but both metrics used by Poff et al. (2006) are sensitive to total tree size, which makes quantitative comparison with the present results difficult. Thus, although morphological traits may have an even higher degree of phylogenetic signal than feeding or thermal traits, our data indicated that similarity in thermal and feeding traits among taxa is still an important pattern in aquatic insects.

The high degree of phylogenetic correlation that we observed in both feeding and thermal traits suggests these traits may be

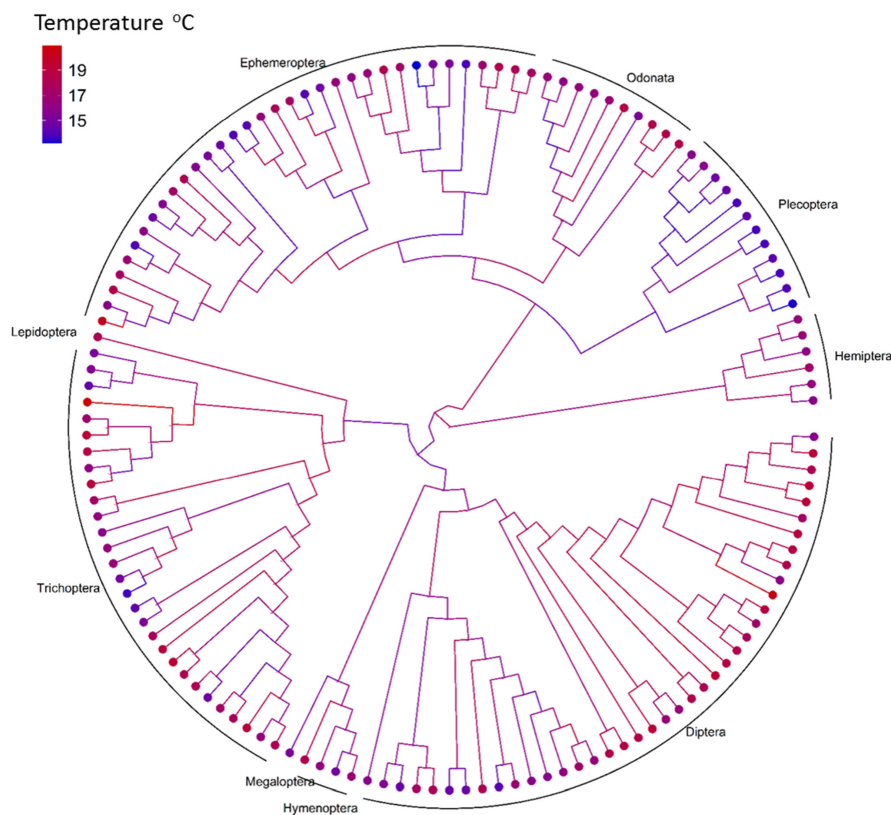


FIGURE 2 Temperature preferences of aquatic insect taxa presented with phylogenetic relationships. Colour indicates temperature preference, with red indicating high temperatures and blue indicating low. Lines and labels denote insect orders. See Figure S1 for a high-resolution version with species labelled

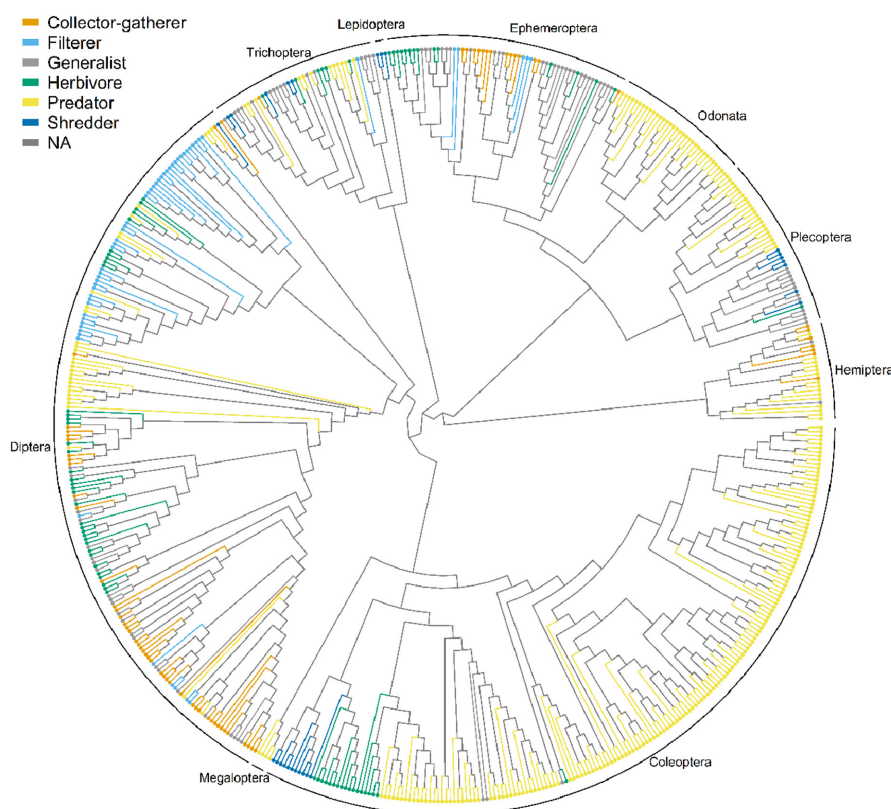


FIGURE 3 Functional feeding groups of aquatic insects represented in a phylogenetic tree by colour. Lines and labels denote insect orders. Categorical values are used for representation here, but fuzzy coding values were used in some analyses of feeding group data, and those data are represented graphically in Figures S2–S6

highly predictable. Our analysis of macroinvertebrate traits covered many taxa, yet we still had data for only a small fraction of the total aquatic macroinvertebrate taxa in each dataset. For instance, in the

EU dataset, we analysed records that had both feeding group and temperature preferences identified for 332 taxa, but this represented <8% of the taxa in the dataset. Likewise, we only had records

TABLE 3 Results of models comparing effects of functional feeding group (FFG) on temperature preferences of aquatic macroinvertebrates

Model	p-value	R ²	AICc
No Phylogenetic relationship (ANOVA)	0.03	0.10	488.9
GLS – FFG and phylogenetic	0.02	0.34	450.0
GLS – phylogenetic only	NA	0.26	454.33

Note: We compared models with no phylogenetic structure (ANOVA), to a generalised least squares (GLS) model with a covariance structure representing the phylogenetic relationship among taxa and a GLS model with only the phylogenetic relationships (not estimating an effect of FFG). We report the *p*-value of the effect of FFG, the *R*² and the corrected Akaike Information Criterion (AICc) of each model. Each model is fit to the same subset of 94 taxa.

of feeding group and *TOpt* or *OMax* for <15% of the 3,835 taxa in the Freshwater BioTraits dataset. With the current interest in understanding how environmental stressors alter the distribution of traits (Barnum et al., 2017; Statzner & Bêche, 2010), the paucity of information on traits presents a major challenge. However, the high degree of phylogenetic correlation that we observed in this study suggests that it may be possible to predict trait status based on phylogenetic relationships, particularly as more resolved phylogenetic trees become available. Additionally, the largest databases of trait data that we were able to access only covered the United States and European Union. Furthering our understanding of universal patterns in macroinvertebrate traits requires the creation of a global trait database (Maasri, 2019), and efforts to understand species traits outside of the US and EU (Camacho et al., 2009). The development of a larger universal database of macroinvertebrate trait data could make trait-based approaches to biomonitoring and management more tractable and powerful.

AUTHOR CONTRIBUTIONS

Conceptualization: NT, AR, CC, PR. Developing methods, data analysis, preparation of figures and tables, conducting the research: NT, PR. Data interpretation, writing: NT, AR, PR, CC.

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All authors contributed to the design of this study and preparation of the final manuscript. N.J.T. conducted the analysis and wrote the initial draft of the manuscript. All data used in this study were collected from public databases or published literature. This work has benefited greatly from discussions and comments from Kelsey Solomon, Phillip Bumpers, Laura Naslund, Carol Yang, Craig Osenberg and Seth Wenger.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Github at https://github.com/nathantomczyk/MI_Thermal_Traits.

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REFERENCES

- Ahrens, C. W., Andrew, M. E., Mazanec, R. A., Ruthrof, K. X., Challis, A., Hardy, G., Byrne, M., Tissue, D. T., & Rymer, P. D. (2020). Plant functional traits differ in adaptability and are predicted to be differentially affected by climate change. *Ecology and Evolution*, 10, 232–248. <https://doi.org/10.1002/ece3.5890>
- Barnum, T. R., Weller, D. E., & Williams, M. (2017). Urbanization reduces and homogenizes trait diversity in stream macroinvertebrate communities. *Ecological Applications*, 27, 2428–2442. <https://doi.org/10.1002/eap.1619>
- Bartoń K. (2020). Package: MuMIn: multi-model inference
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562, 57–62. <https://doi.org/10.1038/s41586-018-0563-7>
- Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>
- Boyer, L., Pearson, R. G., Dudgeon, D., Ferreira, V., Graça, M. A. S., Gessner, M. O., Boulton, A. J., Chauvet, E., Yule, C. M., Albariño, R. J., Ramírez, A., Helson, J. E., Callisto, M., Arunachalam, M., Chará, J., Figueroa, R., Mathooko, J. M., Gonçalves Jr, J. F., Moretti, M. S., ... Barmuta, L. A. (2012). Global patterns of stream detritivore distribution: Implications for biodiversity loss in changing climates. *Global Ecology and Biogeography*, 21, 134–141. <https://doi.org/10.1111/j.1466-8238.2011.00673.x>
- Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, 51, 1389–1406. <https://doi.org/10.1111/j.1365-2427.2006.01597.x>
- Camacho, R., Boyero, L., Cornejo, A., Ibáñez, A., & Pearson, R. G. (2009). Local variation in shredder distribution can explain their oversight in tropical streams. *Biotropica*, 41, 625–632. <https://doi.org/10.1111/j.1744-7429.2009.00519.x>
- Chesters, D. (2017). Construction of a species-level tree of life for the insects and utility in taxonomic profiling. *Systematic Biology*, 66, 426–439. <https://doi.org/10.1093/sysbio/syw099>
- Chown, S. L., Duffy, G. A., & Sørensen, J. G. (2015). Upper thermal tolerance in aquatic insects. *Current Opinion in Insect Science*, 11, 78–83. <https://doi.org/10.1016/j.cois.2015.09.012>

- Clarke, A. (2003). Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution*, 18, 573–581. <https://doi.org/10.1016/j.tree.2003.08.007>
- Cuffney, T. F., Wallace, J. B., & Lughart, G. J. (1990). Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biology*, 23, 281–299. <https://doi.org/10.1111/j.1365-2427.1990.tb00272.x>
- Cummins, K. W., & Klug, M. J. (1979). Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, 10, 147–172. <https://doi.org/10.1146/annurev.es.10.110179.001051>
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 12788–12793. <https://doi.org/10.1073/pnas.0902080106>
- Debouk, H., De Bello, F., & Sebastia, M. T. (2015). Functional trait changes, productivity shifts and vegetation stability in mountain grasslands during a short-term warming. *PLoS One*, 10, 1–17. <https://doi.org/10.1371/journal.pone.0141899>
- Descroix, A., Bec, A., Bourdier, G., Sargos, D., Sauvanet, J., Misson, B., & Desvillettes, C. (2010). Fatty acids as biomarkers to indicate main carbon sources of four major invertebrate families in a large river (the Allier, France). *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 177, 39–55. <https://doi.org/10.1127/1863-9135/2010/0177-0039>
- Dobson, M., Magana, A., Mathooko, J. M., & Ndegwa, F. K. (2002). Detritivores in Kenyan highland streams: More evidence for the paucity of shredders in the tropics? *Freshwater Biology*, 47, 909–919. <https://doi.org/10.1046/j.1365-2427.2002.00818.x>
- Dodds, W. K., Collins, S. M., Hamilton, S. K., Tank, J. L., Johnson, S., Webster, J. R., Simon, K. S., Whiles, M. R., Rantala, H. M., McDowell, W. H., Peterson, S. D., Riis, T., Crenshaw, C. L., Thomas, S. A., Kristensen, P. B., Cheever, B. M., Flecker, A. S., Griffiths, N. A., Crowl, T., ... Martí, E. (2014). You are not always what we think you eat: Selective assimilation across multiple whole-stream isotopic tracer studies. *Ecology*, 95, 2715–2722. <https://doi.org/10.1890/13-2276.1>
- Dorji, T., Totland, Ø., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, 19, 459–472. <https://doi.org/10.1111/gcb.12059>
- Enquist, B. J., Economo, E. P., Huxman, T. E., Allen, A. P., Ignace, D. D., & Gillooly, J. F. (2003). Scaling metabolism from organisms to ecosystems. *Nature*, 423, 639–642. <https://doi.org/10.1038/nature01671>
- Feller, M. C., & Kimmins, J. P. (1984). Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. *Water Resources Research*, 20, 29–40. <https://doi.org/10.1029/WR020i001p00029>
- Fenoy, E., Moyano, F. J., & Casas, J. (2020). Warming and nutrient-depleted food: Two difficult challenges faced simultaneously by an aquatic shredder. *Freshwater Science*, 39, 393–404. <https://doi.org/10.1086/709023>
- Hering, D., Schmidt-Kloiber, A., Murphy, J., Lücke, S., Zamora-Muñoz, C., López-Rodríguez, M. J., Huber, T., & Graf, W. (2009). Potential impact of climate change on aquatic insects: A sensitivity analysis for European caddisflies (Trichoptera) based on distribution patterns and ecological preferences. *Aquatic Sciences*, 71, 3–14. <https://doi.org/10.1007/s00027-009-9159-5>
- Irons, J. G. I., Oswood, M. W., Stout, J. R., & Pringle, C. M. (1994). Latitudinal patterns in leaf litter breakdown: Is temperature really important? *Freshwater Biology*, 32, 401–411. <https://doi.org/10.1111/j.1365-2427.1994.tb01135.x>
- Junker, J. R., Cross, W. F., Benstead, J. P., Huryn, A. D., Hood, J. M., Nelson, D., Gislason, G. M., & Ólafsson, J. S. (2020). Resource supply governs the apparent temperature dependence of animal production in stream ecosystems. *Ecology Letters*, 23, 1809–1819. <https://doi.org/10.1111/ele.13608>
- Kutz, T. C., Sgrò, C. M., & Mirth, C. K. (2019). Interacting with change: Diet mediates how larvae respond to their thermal environment. *Functional Ecology*, 33, 1940–1951. <https://doi.org/10.1111/1365-2435.13414>
- Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., & Moore, M. M. (2020). The net effect of functional traits on fitness. *Trends in Ecology and Evolution*, 35, 1037–1047. <https://doi.org/10.1016/j.tree.2020.07.010>
- Lenth, R., Buerkner, P., Herve, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2021). Emmeans: Estimated marginal means, aka least-squares means. *R package version 1*.
- Liu, H., Xu, Q., He, P., Santiago, L. S., Yang, K., & Ye, Q. (2015). Strong phylogenetic signals and phylogenetic niche conservatism in ecophysiological traits across divergent lineages of Magnoliaceae. *Scientific Reports*, 5, 1–12. <https://doi.org/10.1038/srep12246>
- López-Rodríguez, M. J., Trenzado, C. E., Tierno de Figueroa, J. M., & Sanz, A. (2012). Digestive enzyme activity and trophic behavior in two predator aquatic insects (Plecoptera, Perlidae). A comparative study. *Comparative Biochemistry and Physiology - A*, 162, 31–35. <https://doi.org/10.1016/j.cbpa.2012.01.020>
- Maasri, A. (2019). A global and unified trait database for aquatic macroinvertebrates: The missing piece in a global approach. *Frontiers in Environmental Science*, 7, 1–3. <https://doi.org/10.3389/fenvs.2019.00065>
- Marks, J. C. (2019). Revisiting the fates of dead leaves that fall into streams. *Annual Review of Ecology, Evolution, and Systematics*, 50, 547–568. <https://doi.org/10.1146/annurev-ecolsys-110218-024755>
- Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B. E., Bittner, L., Castella, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaud, E., Usseglio-Polatera, P., Vogt, M., ... Ayata, S. D. (2021). Functional trait-based approaches as a common framework for aquatic ecologists. *Limnology and Oceanography*, 66, 965–994. <https://doi.org/10.1002/lno.11655>
- Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., Junker, J. R., Gislason, G. M., & Ólafsson, J. S. (2016). Experimental whole-stream warming alters community size structure. *Global Change Biology*, 23, 2618–2628. <https://doi.org/10.1111/gcb.13574>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Poff, N. L. R., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of north American lotic insects: Traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, 25, 730–755. [https://doi.org/10.1899/0887-3593\(2006\)025\[0730:FTNNA\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)025[0730:FTNNA]2.0.CO;2)
- Pyne, M. I., & Poff, N. L. R. (2017). Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Global Change Biology*, 23, 77–93. <https://doi.org/10.1111/gcb.13437>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for statistical computing. <https://www.R-project.org/>
- Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Salo, T., Mattila, J., & Eklöf, J. (2020). Long-term warming affects ecosystem functioning through species turnover and intraspecific trait variation. *Oikos*, 129, 283–295. <https://doi.org/10.1111/oik.06698>
- Schmidt-Kloiber, A., & Hering, D. (2015). www.freshwaterecology.info - an online tool that unifies, standardizes and codifies more than

- 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53, 271–282.
- Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M., & Brown, J. H. (2015). Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences*, 112, 2617–2622. <https://doi.org/10.1073/pnas.1423502112>
- Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Song, C., Dodds, W. K., Rüegg, J., Argerich, A., Baker, C. L., Bowden, W. B., Douglas, M. M., Farrell, K. J., Flinn, M. B., Garcia, E. A., Helton, A. M., Harms, T. K., Jia, S., Jones, J. B., Koenig, L. E., Kominoski, J. S., McDowell, W. H., McMaster, D., Parker, S. P., ... Ballantyne, F., IV. (2018). Continental-scale decrease in net primary productivity in streams due to climate warming. *Nature Geoscience*, 11, 1–6. <https://doi.org/10.1038/s41561-018-0125-5>
- Statzner, B., & Bêche, L. A. (2010). Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, 55, 80–119. <https://doi.org/10.1111/j.1365-2427.2009.02369.x>
- TerHorst, C. P., Zee, P. C., Heath, K. D., Miller, T. E., Pastore, A. I., Patel, S., Schreiber, S. J., Wade, M. J., & Walsh, M. R. (2018). Evolution in a community context: Trait responses to multiple species interactions. *American Naturalist*, 191, 368–380. <https://doi.org/10.1086/695835>
- Tierno de Figueroa, J. M., López-Rodríguez, M. J., & Villar-Argaiz, M. (2019). Spatial and seasonal variability in the trophic role of aquatic insects: An assessment of functional feeding group applicability. *Freshwater Biology*, 64, 954–966. <https://doi.org/10.1111/fwb.13277>
- U.S. EPA. (2012). Freshwater biological traits database (Final report)
- Uszko, W., Diehl, S., Englund, G., & Amarasekare, P. (2017). Effects of warming on predator–prey interactions – A resource-based approach and a theoretical synthesis. *Ecology Letters*, 20, 513–523. <https://doi.org/10.1111/ele.12755>
- Vannote, R. L., Minshall, W. G., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137.
- Vaughn, C. C. (2010). Biodiversity losses and ecosystem function in freshwaters: Emerging conclusions and research directions. *Bioscience*, 60, 25–35. <https://doi.org/10.1525/bio.2010.60.1.7>
- Villanueva, V. D., Albariño, R., & Canhoto, C. (2011). Detritivores feeding on poor quality food are more sensitive to increased temperatures. *Hydrobiologia*, 678, 155–165. <https://doi.org/10.1007/s10750-011-0837-7>
- Vucic-Pestic, O., Ehnes, R. B., Rall, B. C., & Brose, U. (2011). Warming up the system: Higher predator feeding rates but lower energetic efficiencies. *Global Change Biology*, 17, 1301–1310. <https://doi.org/10.1111/j.1365-2486.2010.02329.x>
- Wallace, J. B., & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 41, 115–139. <https://doi.org/10.1146/annurev.en.41.010196.000555>
- Wallace, J. B., Webster, J. R., & Cuffney, T. F. (1982). Stream detritus dynamics: Regulation by invertebrate consumers. *Oecologia*, 53, 197–200.
- Yu, G. (2020). Using ggtree to visualize data on tree-like structures. *Current Protocols in Bioinformatics*, 69, 1–18. <https://doi.org/10.1002/cpbi.96>

SUPPORTING INFORMATION

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