Quantifying habitable water temperatures and thermal sensitivities among species functional traits of stream invertebrates

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Abstract

Ectothermic species have body temperatures that reflect their environment to varying degrees. Environmental temperature drives all cellular and physiological functions, including metabolism, development, growth, migration, and reproduction. Extreme temperatures are occurring more frequently with climate change, and understanding the thermal tolerance and adaptive traits of species is critical.We hypothesized that 1) geographic location of stream ecosystems, such as elevation and latitude, influence the habitable water temperature of lotic (stream) invertebrates because the thermal habitat of species directly influences their life cycle and consequently fitness and 2) species functional traits (e.g., voltinism and feeding behavior) are influenced by habitable temperature. Here, we tested these hypotheses across diverse taxa and geographic regions using a dataset for stream invertebrates traits across North America. We showed that maximum water temperature in habitats and thermal breadth were significantly lower and narrower across streams ranging in elevation, from 0 to 3000 m, suggesting that invertebrate taxa across various elevations are less tolerant of warmer water temperature. Also, we identified thermal sensitivity differences among species traits, especially functional feeding group traits, as these are related to habitat selection in stream ecosystems. Our synthesis suggests that elevation and species traits can help predict thermal breadth and thermal tolerance for different species under a changing climate.

Introduction

Anthropogenic climate change is having pronounced and accelerated biological impacts on organisms and ecosystems (Pacifici et al., 2015; Sinclair et al., 2016). Biologists are trying to understand and predict these impacts. Inevitably, most of these impacts are mediated by the behavioral and physiological responses of organisms to changing biological variables (Doi et al., 2008; Radchuk et al., 2019). The concept of species habitability with temperature applies community-level understanding of species thermal tolerance using assembly rules that estimate the presence or absence of species as well as their abundance (Menezes et al., 2010). Yet, the need to move beyond descriptive to a predictive understanding of species thermal tolerances is critical given climate-driven increases in temperature (e.g., Pacifici et al., 2015; Sinclair et al., 2016).

Most aquatic species, such as invertebrates, are ecothermic and therefore have body temperatures that reflect their environment to varying degrees (Angilletta, 2009; Sinclair et al., 2016). Extremely high or low temperatures are lethal, and temperature determines all cellular and physiological functions, including metabolism, development, growth, migration, and reproduction and indirectly throughout changes in prey community and environments (Grigaltchik et al., 2012; Ylla et al., 2014; Nelson et al., 2020b; Schofield & Kline, 2018; Shah et al., 2021). Changes in water temperature have serious implications at population, community, and ecological levels (e.g., Grigaltchik et al., 2012; Sinclair et al., 2016), especially given the uncertainty in how stream temperature regimes may change with different climate and land-use changes (Kominoski & Rosemond, 2012).

To date, attempts to measure vulnerability to climate change have largely assessed species responses to temperature challenges, such as lethal and critical thermal limits, i.e., habitable temperature (Deutsch et al., 2008; Pinsky et al., 2019). Metabolic rates of ecotherms can influence individual fitness, and consequently geographic distributions and abundances (Angilletta, 2009; Shah et al., 2020; Terblanche & Chown, 2007; Vannote & Sweeney, 1980), and related to their body temperatures. For example, in aquatic ecosystems increased metabolic demand with higher temperature can outpace the supply of oxygen from the environment causing decreased performance and lowered tolerance to heat stress (Pörtner et al., 2017). Therefore, understanding habitable temperature across different environments would help us to predict geographic variation in fitness, as well as species abundance and distributions in response to global warming (Dillon et al., 2010). Addressing the effects of climate change through the lens of exothermic biology, especially species habitable temperature, will expand understanding of how temperature affects the majority of species on Earth.

Recent experimental temperature manipulations have quantified the habitable temperature ranges of stream invertebrates (Nelson et al., 2017a, 2017b, 2020a, 2020b; Shah et al., 2020). These studies suggested that habitable temperature varied among the geographical location of the habitats, such as elevation and latitude, and species traits, such as feeding mode (Shah et al., 2017, 2020; Sunday et al., 2011). Shah et al. (2017) showed the elevation effects of thermal breadth of many stream macroinvertebrates in the temperate and trophic streams. Also, Nelson et al. (2020a) reported the effect of thermal breadth diversity on energy flux through a stream food web. A global analysis of thermal tolerance among terrestrial and marine ecotherms found thermal tolerance breadths increased with latitude (Sunday et al., 2017). Yet, how habitable temperatures and thermal tolerances range across diverse stream ecotherms from broad geographic regions and along elevation gradients is needed to better predict the effects of changing temperatures on species functional traits of inland waters (Shah et al., 2020).

In this study, we compared how geographic location and species traits vary across North America. First, we hypothesized that geographic location of stream ecosystems, such as elevation and latitude, influence the habitable water temperature of lotic (stream) invertebrates, such that habitats directly influence species' life cycles and consequently their fitness and evolution (Kearney et al., 2020; Shah et al., 2020; Sunday et al., 2011). Second, we hypothesized that species traits (e.g., voltinism and feeding behavior) are influenced by habitable temperature, as these traits are directly related with species adaptations to temperature (Sgrò et al., 2016). Also, thermal performance in the different phylogeny (e.g., taxonomic category) is different, as these traits are directly related with species adaptations to temperature. Numerous tests of the two hypotheses have been performed (e.g., Kong et al., 2019; Nelson et al., 2020b; Shah et al., 2021), but such tests have only been conducted using temperature manipulations in the field and laboratory for a limited number of species. Here, we tested our hypotheses with variable taxa and geographic regions using a dataset of stream invertebrate traits in North America (Vieira et al., 2006). The dataset we used includes thermal preferences, i.e., maximum and minimum water temperature surviving in, and the habitat conditions, such as elevation and latitude of the collected points as well as various species traits, including voltinism and feeding behavior for over$n$ = 2,200 species. The dataset contained data from various taxa, including bivalve, amphipods, and insects in streams across North America, mostly in the United States. Use of a database summarized various related data which allowed us to compare these factors to the habitable water temperature of stream macroinvertebrate taxa across broad geographic ranges in latitude and elevation.

Materials and methods

Database and obtained data

We used "A database of lotic invertebrate traits for North America" (Vieira et al., 2006) provided by the U.S. Geological Survey (USGS). USGS's National Water-Quality Assessment Program in cooperation with Colorado State University compiled the database. A total of N = 14,127 records for over n = 2,200 species, n = 1,165 genera, and n = 249 families have been compiled for the database from n = 967 reports, including journal papers and scientific reports.

In this study, we focused on maximum and minimum water temperature surviving in (°C, hereafter, max.

and min. temperature). The data of max. and min. temperature were from $n = 390$ and $n = 440$ records, respectively. Because species thermal tolerance data (maximum lethal temperature, 5 records, thermal preference, 63 records with various descriptions) records were very limited, we did not use these data in our analyses in our analyses. We obtained the related geographic factors, including maximum and minimum habitat elevation and the U.S. state where the taxa recorded. Because of our testing for species traits hypothesis,we also obtained the biological traits of the species, including the mean and maximum body length (mm), functional feeding guilds, voltinism (i.e., <1, 1, 2 and 3 year of the life cycle), and species order of the taxa, which we obtained from the dataset. We collected mean degree of latitude of the U.S. state where the taxa recorded from the list of US state database (https://www.latlong.net/category/states-236-14.html). We decided to use a single database to summarize all variables in the same manner to directly compare these factors to the thermal preference of the taxa.

Statistical analyses

We calculated the "thermal breadth (°C)" by maximum - minimum habitat temperature (°C). We obtained $n = 306$ data records of thermal breadth (°C).

All statistics and graphics were performed using R ver. 4.0.2 (R Core Team, 2020). We set the significant level, $\alpha = 0.05$. We performed generalized linear models (GLMs) to predict the maximum and minimum temperature and thermal breadth using "glm" function with the degree of latitude N of the collected points, the elevation (above sea level, m), and their mean body length as the body size index. We used the Gaussian distribution as the error distribution for the GLM. We performed the GLMs without the random factor due to too many data source categories from 967 independent reports for the database. Before the GLM analysis, we calculated the variance inflation factor (VIF) to check for co-linearity of among factors. The maximum VIF was 10.2 for the explanatory factors of GLM so we excluded the maximum elevation for all GLMs because of significantly correlated with minimum elevation (Pearson's coefficient by "cor.test" function, r = 0.692, P < 0.0001). After the exclusion, the maximum VIF was 1.34 indicating that co-linearity among the factors would not significantly influence the results of GLMs. We used simple GLM without random factors, because the database does not have the suitable random factors for the analysis.

For categorical data, including voltinism, functional feeding guilds, and taxonomic Order, we performed a three-way analysis of variance (ANOVA) and evaluated interactions using "aov" function. Also, we simply used the ANOVA without the random factor due to 967 independent reports for the database. When the ANOVA was significant, we performed the post-hoc test using Tukey multiple comparisons with "TukeyHSD" function.

Results

Stream temperatures varied across habitats based on latitude and elevation, as expected (Figs. 1, 2). Maximum stream temperatures were lower at latitudes above than latitudes below 35°N, but minimum stream temperatures were similar across latitudes (Fig. 1, Table 1a,b). Thermal breadths were lower at latitudes above compared to latitudes below 35°N (Fig. 1, Table 1c). We did not observe broad categorical elevation trends with any stream temperature metric (Fig. 2, Table 1 d.e, and f). Importantly, geographic information was not included for 74.8% of total$n = 229$ records of stream maximum and minimum temperatures and calculated thermal breadths (Figs. 1, 2). Maximum stream temperature and thermal breadth were linearly related to habitat elevation (Fig. 3a Table 2 s), whereas minimum stream temperature was not related to elevation (Fig. 3a, Table 2). In contrast, stream latitude was not linearly related with any stream habitat temperature variable (Fig. 3b, Table 2).

We found that habitable maximum temperatures varied across voltinism and among functional feeding guilds of species (Table 3, Figs. 4a-4c). Specifically, multivoltine taxa had higher maximum stream temperatures than univoltine and semivoltine taxa (Fig. 4a). Collector-gatherers tended to have higher maximum stream temperatures (Fig. 4b), however, effects of stream temperature among taxonomic Order were not clearly evident (Fig. 4c, Table 3, 4). We detected significant interactions among voltinism and feeding guilds (Table 3), however, we did not detect differences in maximum temperatures and thermal breadth among interactions with functional feeding guilds, voltinism, or taxonomic Order (Figs. 4a-4c).

Discussion

Quantifying the habitable temperature range of ectotherms is critical to predicting how global warming will impact different species (Huey & Kingsolver, 2019) and understanding the influence of temperature on the minimum energy demands. Payne and Smith (2017) suggested that species with narrower temperature ranges may simply reflect the acute effects of temperature on biological rates of organisms living in warmer environments. Water temperatures in shallow mountain streams can dynamically change with changes in air temperature (Birrell et al., 2020; Mohseni & Stefan, 1999; Pilgrim et al., 1998), and water temperatures in mountain streams are rapidly increasing worldwide with air temperatures (e.g., Isaak & Rieman, 2013). For example, in the Pacific Northwest, stream water temperatures have increased by 0.22°C per decade in the last decades (Isaak et al., 2012). We found the invertebrate taxa across various elevations from 0 to 3000 m, with less tolerances of warmer stream temperatures. We specifically tested the thermal tolerance differences among functional feeding guilds and voltinism. Our use of linear models to predict thermal breadth and habitat temperature tolerances among diverse stream macroinvertebrates can be used to better understand how elevation among temperate streams constrains species traits (Shah et al., 2017, 2020). Although our model results provide further inference towards predicting thermal responses of stream communities and ecosystems under temperature increases, holistic integration of dynamic taxon-specific variation to changing temperatures is needed (Nelson et al., 2020b; Shah et al., 2021).

change effects on the fitness and habitats of stream invertebrates, especially higher elevation stream invertebrate communities, are predictable. We found that thermal tolerance was strongly correlated with voltinism among stream taxa. For example, multi-voltinism such as bivoltine and trivoltine taxa were found in streams with higher maximum temperatures. Semi- and univoltine species have thermal tolerance for colder water temperatures. Voltinism was explained by the combined predictions of thermal adaptation (Kong et al., 2019), but typically, semivoltine species generally inhabit in colder waters (Braune et al., 2008; Danks, 2007; Huryn, 1990). Our synthesis, across a large geographic range of temperate streams, suggests that there are tradeoffs between higher thermal tolerance and energy allocation towards growth that are generalizable across taxa with different life history development strategies. In this study, we found the unexpected result that longer-voltinism species may have thermal adaptation for warmer temperatures. Therefore, our results provide further evidence that thermal adaptation for warmer temperatures is a habitable trait of longer-voltinism species.

Thermal ranges varied among stream functional feeding guilds. We found higher maximum temperatures for collector-gatherer taxa than other feeding guilds. Collector-gatherers can feed on various types of food sources, including animal and detrital plant matter (Merritt et al., 2017), and we have identified that they can tolerate a larger temperature range than other feeding guilds. Collectively, this may extend their habitats more than other species, such as shredders and scrapers. Therefore, the apparently higher thermal tolerance of collector-gatherers may be due to their ability to occupy a broader range of habitats with more diverse food resources than other macroinvertebrates. Among the functional feeding guilds, differences in thermal sensitivity, e.g., tolerance and breath, have been observed previously (Gilman et al., 2010; Grigaltchik et al., 2012; Kordas et al., 2011; Pincebourde & Casas, 2019; Shah, 2020; Vucic-Pestic et al., 2011), but have not summarized. Our large-scale synthesis illustrates a phenomenon of thermal tolerance differences among functional feeding guilds, especially for collector-gatherers. These results could have functional consequences for how increasing temperatures interact with stream communities to alter organic matter processing (Ferreira & Canhoto, 2014; Ylla et al., 2014). Further studies needs to consider the effects of thermal tolerance differences among functional feeding guilds on the stream community and ecosystem function with climate change (Pyne & Poff, 2017).

Temperature variability in aquatic ecosystems is changing worldwide with increased air and land surface temperatures and shifts in precipitation, as well as human-driven flow alterations. Although minimum stream temperatures are increasing in winter months in North American streams, regulated streams and rivers can have lower stream water temperatures in summer months compared to unregulated streams and rivers

(Carlisle et al., 2016). As temperature is a primary factor influencing metabolic rates (Nelson et al., 2020b; Shah et al., 2021), organic matter and biogeochemical processes (Ferreira & Canhoto, 2014; Ylla et al., 2014) and stream community composition (Carlisle et al., 2016; Nelson et al., 2017a, 2017b, 2020a), understanding the structural and functional constraints of increasing temperatures on stream ecosystems is critical and likely to be highly variable among taxa (Nelson et al., 2020b; Shah et al., 2021).

Although our synthesis focused on water temperature variation from a large public database (Vieira et al., 2006), we should note that the most extreme biological responses are often triggered by the synchronous occurrence of multiple environmental stressors, e.g., water quality, water flow, and UV radiation (Denny et al., 2011; Jackson et al., 2016). Therefore, the consequences of multiple interacting environmental changes on stream communities and their ecosystem functions is an imperative to understanding climate-induced changes to streams. For example, a study in a mountainous headwater stream in Portugal found complex food web interactions from experimental warming, whereby the presence of a dominant shredder increased fungal biomass and influenced fungal composition on decomposing litter only in the reach with elevated stream temperature (Domingos et al., 2015). Changes in stream temperature from climate and land-use changes have complex effects on stream community composition, biological interactions, and ecosystem functioning. Shifts in food web relationships regardless of changes in temperature or macroinvertebrate community composition can still impact rates of organic matter processing in streams (Demi et al., 2019; Domingos et al., 2015; Kominoski et al., 2011; Kominoski et al., 2013; Rosemond et al., 2015). Understanding how variation in thermal tolerance among stream taxa interacts with other global environmental changes is critical for holistically assessing stream ecosystem integrity. Further, studies that explicitly test for interactive effects of temperature and other environmental changes are needed to elucidate the specific physiological, genetic or environmental drivers behind functional changes in stream ecosystems in a changing world.

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Author contributions

H.D., J.S.K., and I.K. designed the research. H.D. analyzed the data and wrote the first draft. All authors contributed to writing and editing the final manuscript.

Data availability

All data were obtained from USGS data repository of "A database of lotic invertebrate traits for North America" (https://pubs.er.usgs.gov/publication/ds187).

Competing interests

The authors declare no competing financial interests.

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Table 1 The linear model results for latitude and elevation category effects on a, d) Max, b, e) Min temperature and c, f) thermal breadth. Bold factors mean P < 0.05.

a) Max. temperature								
	Estimate	Estimate	SE	SE	t	t	P	P
(Intercept)	**26.2267**	**26.2267**	**0.8504**	**0.8504**	**30.84**	**30.84**	**2.00E^{-16}**	**2.00E**
Latitude >40	**-7.8221**	**-7.8221**	**0.9204**	**0.9204**	**-8.498**	**-8.498**	**2.67E^{-15}**	**2.67E**
Latitude 35-40	**-5.3919**	**-5.3919**	**1.2909**	**1.2909**	**-4.177**	**-4.177**	**4.23E^{-05}**	**4.23E**
R^2	**0.2403**	**0.2403**						
P	**1.38E^{-14}**	**1.38E^{-14}**						
b) Min. temperature								
	Estimate	Estimate	SE	SE	t	t	P	P
(Intercept)	**7.02**	**7.02**	**1.27098**	**1.27098**	**5.523**	**5.523**	**9.15E^{-08}**	**9.15E**
Latitude >40	1.57543	1.57543	1.37562	1.37562	1.145	1.145	0.253	0.253

a) Max. temperature								
Latitude 35-40	-0.05478	-0.05478	1.92936	1.92936	-0.028	-0.028	0.977	0.977
R^2	0.0006497	0.0006497						
P	0.3435	0.3435						
c) Thermal breadth								
	Estimate	Estimate	SE	SE	t	t	P	P
(Intercept)	**19.207**	**19.207**	**1.446**	**1.446**	**13.283**	**13.283**	**2.00E^{-16}**	**2.00E^{-}**
Latitude >40	**-9.398**	**-9.398**	**1.565**	**1.565**	**-6.005**	**-6.005**	**7.62E^{-09}**	**7.62E^{-}**
Latitude 35-40	**-5.337**	**-5.337**	**2.195**	**2.195**	**-2.431**	**-2.431**	**0.0158**	**0.0158**
R^2	**0.1579**	**0.1579**						
P	**0.03748**	**0.03748**						
d) Max. temperature	d) Max. temperature							
		Estimate	Estimate	SE	SE	t	t	P
(Intercept)	**(Intercept)**	**21.05**	**21.05**	**2.037**	**2.037**	**10.332**	**10.332**	**7.10E^{-}**
elevation >2000m	elevation >2000m	-4.09	-4.09	2.881	2.881	-1.42	-1.42	0.165
elevation 1000-2000m	elevation 1000-2000m	-1.944	-1.944	2.597	2.597	-0.748	-0.748	0.46
R^2	**R^2**	0.0004934	0.0004934					
P	**P**	0.3757	0.3757					
e) Min. temperature	e) Min. temperature							
		Estimate	Estimate	SE	SE	t	t	P
(Intercept)	**(Intercept)**	**9.72**	**9.72**	**2.0773**	**2.0773**	**4.679**	**4.679**	**4.73E^{-}**
elevation >2000m	elevation >2000m	0.39	0.39	2.9378	2.9378	0.133	0.133	0.895
elevation 1000-2000m	elevation 1000-2000m	-0.4388	-0.4388	2.6481	2.6481	-0.166	-0.166	0.869
R^2	R^2	-0.05739	-0.05739					
P	P	0.9511	0.9511					
f) Thermal breadth	f) Thermal breadth							
		Estimate	Estimate	SE	SE	t	t	P
(Intercept)	**(Intercept)**	**11.33**	**11.33**	**1.7**	**1.7**	**6.666**	**6.666**	**1.38E^{-}**
elevation >2000m	elevation >2000m	-4.48	-4.48	2.404	2.404	-1.864	-1.864	0.0713
elevation 1000-2000m	elevation 1000-2000m	-1.505	-1.505	2.167	2.167	-0.695	-0.695	0.4922
R2	**R2**	0.04476	0.04476					
P	**P**	0.1779	0.1779					

Table 2 The linear model results for latitude and Min. elevation effects on a) Max, b) Min temperature and c) thermal breadth. Bold factors mean $P < 0.05$.

a) Max. temperature				
	Estimate	SE	t	P
(Intercept)	**18.516248**	**8.675901**	**2.134**	**0.04206**
Latitude	0.038174	0.204745	0.186	0.85349
Min. elevation	**-0.003588**	**0.001269**	**-2.827**	**0.00875**
R^2	**0.1713**			
P	**0.03014**			
b) Min. temperature				
	Estimate	SE	t	P
(Intercept)	9.96	9.08	1.097	0.282
Latitude	-0.0756	0.214	-0.353	0.727
Min. elevation	-4.71E^{-05}	0.00133	-0.035	0.972
R^2	-0.06896			
P	0.9376			

a) Max. temperature				
c) Thermal breadth				
	Estimate	SE	t	P
(Intercept)	8.55361	8.924003	0.958	0.3463
Latitude	0.113774	0.210601	0.54	0.5935
Min. elevation	**-0.003541**	**0.001306**	**-2.712**	**0.0115**
R^2	**0.1579**			
P	**0.03748**			

Table 3 The ANOVA results for voltinism (Volt), functional feeding group (FFG), and species order (Order) on a) Max, b) Min temperature and c) thermal breadth. Bold factors mean $P < 0.05$.

a) Max. temperature	a) Max. temperature				
	Df	Sum Sq	Mean Sq	F	P
Volt	**3**	**474.9**	**158.3**	**7.176**	**0.00046**
FFG	**4**	**524.1**	**131.02**	**5.939**	**0.000594**
Order	5	99	19.8	0.897	0.490664
Volt:FFG	**5**	**590.7**	**118.13**	**5.355**	**0.000563**
Volt:Order	3	52.3	17.44	0.791	0.505147
FFG:Order	4	67.2	16.8	0.762	0.555471
Volt:FFG:Order	1	9.2	9.21	0.418	0.521246
b) Min. temperature	b) Min. temperature				
	Df	Sum Sq	Mean Sq	F	P
Volt	3	109.7	36.56	1.803	0.159
FFG	4	68	17.01	0.839	0.507
Order	5	81.1	16.22	0.8	0.555
Volt:FFG	5	18.3	3.65	0.18	0.969
Volt:Order	3	66	21.98	1.084	0.365
FFG:Order	4	46.1	11.53	0.569	0.687
Volt:FFG:Order	1	0.6	0.6	0.03	0.864
c) Thermal breadth	c) Thermal breadth				
	Df	Sum Sq	Mean Sq	F	P
Volt	3	180.8	60.27	1.266	0.2968
FFG	4	395.8	98.95	2.079	0.0986
Order	5	229.5	45.9	0.964	0.4493
Volt:FFG	5	508.8	101.76	2.138	0.0772
Volt:Order	3	104.5	34.83	0.732	0.5382
FFG:Order	4	35.4	8.84	0.186	0.9447
Volt:FFG:Order	1	14.5	14.52	0.305	0.5834

Table 4 Tukey post-hoc comparison for a) voltinism and b) functional feeding group on Max temperature. Bold factors mean $P < 0.05$.

a) Voltinism		
comparison	differences	P
1-<1	-2.16851	0.71915
2-<1	3.236363	0.4831368
3-<1	-2.26363	0.9621085

a) Voltinism

2-1	**5.404878**	**0.0076061**
3-1	-0.0951	0.9999963
2-3	-5.500	0.6131607

b) FFG

comparison	differences	P
Collector gatherer -Collector filterer	-3.03943	0.0397763
Predator-Collector filterer	**-5.6287**	**0.0000004**
Scraper/grazer-Collector filterer	**-3.93106**	**0.0001579**
Shredder-Collector filterer	**-6.53636**	**0.0000001**
Predator-Collector gatherer	-2.58932	0.1044006
Scraper/grazer-Collector gatherer	-0.89163	0.8866317
Shredder-Collector gatherer	**-3.49693**	**0.0224365**
Scraper/grazer-Predator	1.69769	0.2977081
Shredder-Predator	-0.90760	0.9186897
Shredder-Scraper/grazer	-2.60530	0.0685934

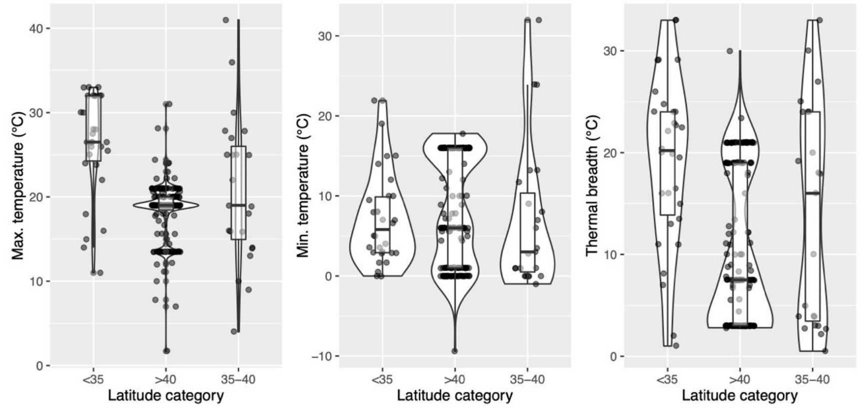


Figure 1. Stream temperature ranges (Max., Min. temperature and thermal breadth) across a categorical grouping of habitat latitude from the Vieira et al. (2006) database.

Boxes and bars in the box plots indicate medians ± inter-quartiles and ± 1.5 × inter-quartiles, respectively. Points represent individual data values. The smooth lines indicate the distribution of the data using violin plots. The violin plot outlines illustrate kernel probability density, i.e., the width of the enclosed area represents the proportion of the data located.

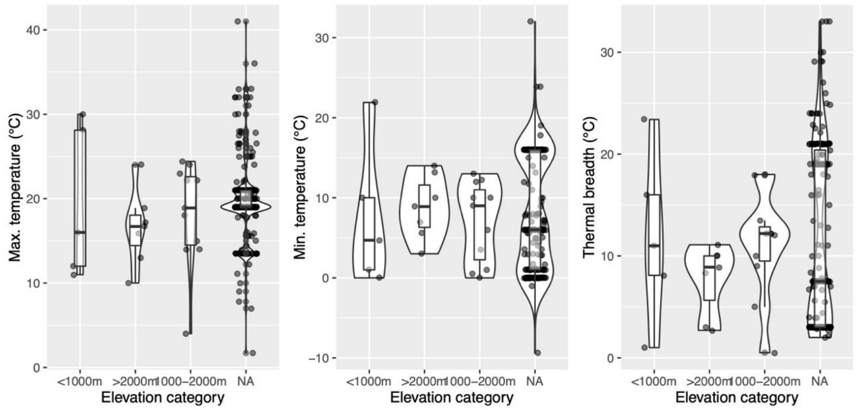


Figure 2. Stream temperature ranges (Max., Min. temperature and thermal breadth) across categorical grouping of habitat elevation from the Vieira et al. (2006) database.

Boxes and bars in the box plots indicate medians ± inter-quartiles and ± 1.5 × inter-quartiles, respectively. Points represent individual data values. The smooth lines indicate the distribution of the data using violin plots. The violin plot outlines illustrate kernel probability density, i.e., the width of the enclosed area represents the proportion of the data located.

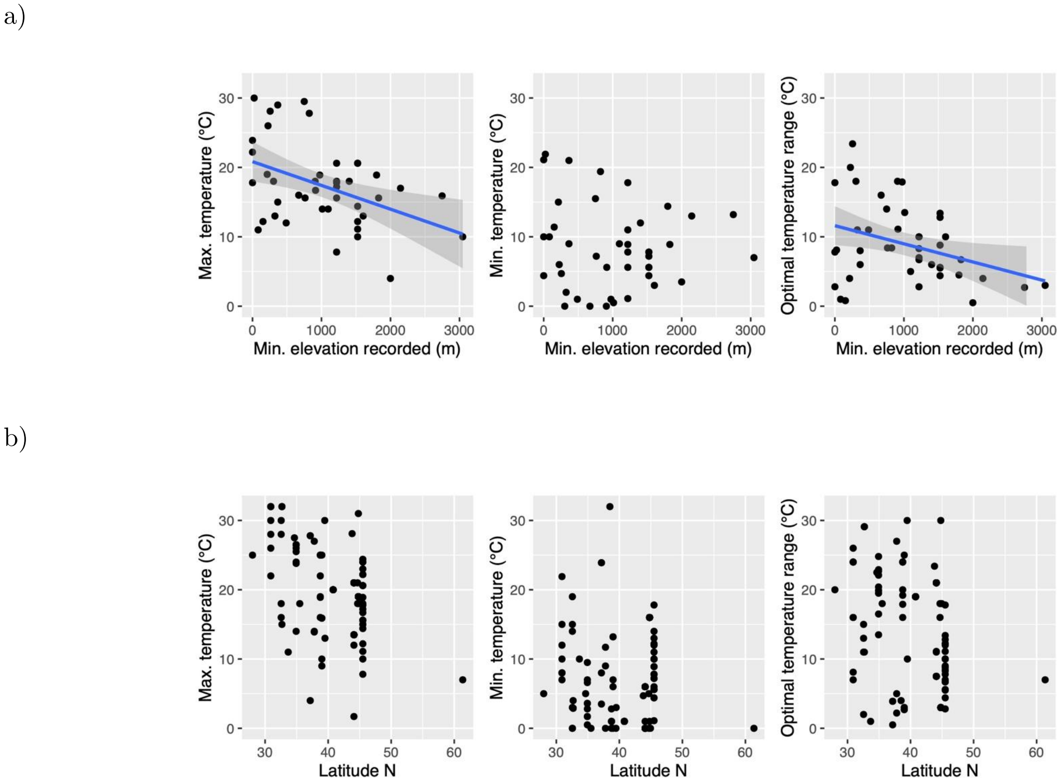
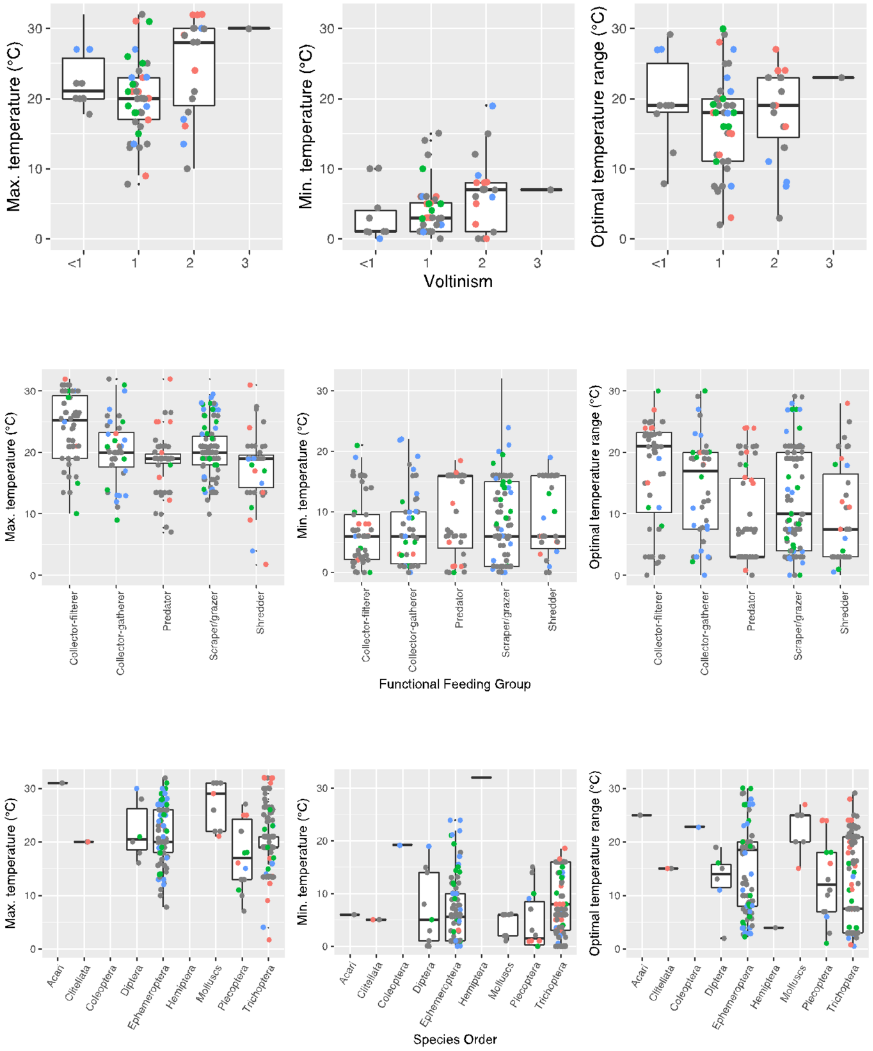


Figure 3. Stream temperature ranges (Max., Min. temperature and thermal breadth) and a) minimum elevation recorded and b) with the degree of latitude N. The blue line with shaded area indicates the results of regression with 95% confidential interval of the significant slope in the GLMs ($P < 0.05$ for the coefficient,

Table S1). The habitat temperature ranges (Max., Min. temperature and optimal range) with maximum elevation recorded showed in Fig. S1.

a)



b)c)

Figure 4. Macroinvertebrates habitat temperature ranges (Max, Min temperature, and thermal breadth) and a) voltinism, b) their functional feeding guilds (FFGs), and c) species order. The boxes and bars in the box plots indicate median ± inter-quartiles and ±1.5 × inter-quartiles, respectively. The points represent individual data values with the colors indicating the body size category (blue= Small (body length < 9 mm), green = Mid (9-16 mm), red= Large (>16 mm), and grey = no data).