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Streams in an uninhabited watershed have predictably different thermal sensitivities to variable summer air temperatures

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Abstract

1. Warming temperatures from climate change are altering the distributions and abundances of many species. Aquatic organisms, however, may be buffered from the immediate impacts of air temperature change due to the thermal inertia of water. The extent of this buffering in freshwater ecosystems will determine the fate and possible management strategies for many ecologically and economically important species.

2. Using 11 years of air and stream temperature data collected from an uninhabited New Hampshire watershed, we investigated the relationship between air and water temperature change throughout the summer months. Maximum daily stream temperatures during the summer months are known to influence the distribution and phenology of aquatic organisms. As such, we built a predictive model of maximum daily stream temperature as a function of air temperature change, discharge and stream order.

3. Diurnal changes in stream temperatures and changes in stream temperature through the summer consistently lagged changes in air temperature, and deviations in daily air temperatures from seasonally predicted means were a strong driver of water temperatures. A mean increase in residual air temperature over the past 5 days of 1.0°C corresponded to a 0.5–0.8°C increase in maximum daily stream temperature. Smaller, headwater streams were colder and less sensitive to changes in air temperature.

4. Although stream temperatures did not increase as much as air temperatures, our results suggest that even small increases in water temperatures will extend the duration of physiologically stressful conditions for biota in this watershed. Thus, preserving thermal heterogeneity and unrestricted access to thermal refuges may be key for species' persistence. We encourage continued use of monitoring data to document within-stream and within-watershed thermal heterogeneity and to generate stream temperature models. These tools will be key for developing management strategies to mitigate the impacts of climate change on streams and their biota.

KEYWORDS
climate change, streams, temperature models, thermal change, thermal heterogeneity

1 | INTRODUCTION

Climate change is altering the ecology of freshwater ecosystems, including changes to the phenology and distributions of aquatic species (e.g., Culler, Ayres, & Virginia, 2015; Domisch et al., 2013; Winder & Schindler, 2004). Increases in water temperature affect the metabolic rates of aquatic organisms (Culler, McPeek, & Ayres, 2014; Gillooly, Brown, West, Savage, & Charnov, 2001) and lead to changes in physiology, behaviour, and mortality (e.g., Araujo, Thuiller, & Pearson, 2006; Dallas & Ross-Gillespie, 2015; Domisch et al., 2013; Lowe & Hauer, 1999; Xu, Letcher, & Nislow, 2010). Many species of invertebrates and coldwater-dependent fish are particularly sensitive to increases in temperature (Ebersole, Liss, & Frissell, 2001; Elliott, 1991; Elliott & Elliott, 1995; Garside, 1973; Huntsman, 1942; Lee & Rinne, 1980; Stewart, Close, Cook, & Davies, 2013), thus giving water temperature both ecological and economic significance (Caissie, 2006). Given the current and projected magnitude of thermal changes occurring globally and that temperatures in some systems have already reached the thermal limits for aquatic organisms (e.g., Comte & Grenouillet, 2013), there is a need for tools to identify and manage thermally threatened aquatic habitats.

As global air temperatures increase and precipitation patterns change, water temperatures and associated factors, such as dissolved oxygen levels, are profoundly affected (Davies, 2010; Morrill, Bales, & Conklin, 2005; Orr et al., 2015). However, most climate warming projections are in units of air temperature increase and are not readily translatable to freshwater environments (Hobday & Lough, 2011). For example, a 2013 NOAA Technical Report for the U.S. National Climate assessment indicated that air temperatures in the north-east U.S.A. are projected to increase by 1.4 to 3.1°C by 2055 (Kunkel et al., 2013), but no such projections are available for water temperatures. Similarly, the most recent Intergovernmental Panel on Climate Change report (AR5 2014) highlights many of the consequences of rising freshwater temperatures in Chapters 3 and 4 of Working Group II (Jiménez Cisneros et al., 2014; Settele et al., 2014), but do not include projections of future water temperature change as they do for air temperatures.

Although water temperatures vary with air temperatures (Cho & Lee, 2012), freshwater systems can exhibit dampened and delayed responses at various spatial and temporal scales to changes in air temperature due to the thermal inertia of water (Erickson & Stefan, 2000). In an analysis of air–water temperature relationships in 43 streams, very few showed a water temperature increase of 1°C for every 1°C increase in air temperatures averaged over daily, 3-day and weekly time periods (Morrill et al., 2005). van Vliet, Ludwig, Zwolsman, Weedon, and Kabat (2011) reported increases in annual mean river temperatures of +1.3, +2.6 and +3.8°C with air temperature increases of +2, +4 and +6°C, respectively. Null, Viers, Deas, Tanaka, and Mount (2013) reported an increase in average annual stream temperature of 1.2–1.9°C for a simulated 2°C increase in average annual air temperature. Isaak et al. (2016) reported warming rates for streams of 0.1°C per decade versus 0.2°C per decade for air temperatures throughout the north-western United States. Thus, stream temperatures will

reflect changes in air temperatures from daily to decadal timescales, but often with a reduced amplitude (Morrill et al., 2005).

In addition to air temperature, other factors influence water temperature or modify the effects of air temperature on water temperature. Smaller and headwater streams, depending on their primary source of water, may be more or less buffered from changes in air temperature. If groundwater-dominated, the water in these streams has had less time to exchange heat with the atmosphere and the greater proportion of direct groundwater input versus larger streams would tend to keep them relatively cooler during the summer months (Power, Brown, & Imhof, 1999; Sweeney, 1993). Changes in precipitation patterns that occur alongside changes in temperature, such as more or less precipitation or more falling as snow versus rain, can also modify water levels via effects on overall watershed discharge. Higher discharge, that is, a greater volume of water flowing through a stream system, could affect stream temperature by increasing the amount of groundwater input into streams (Winter, Harvey, Franke, & Alley, 1998). Furthermore, a greater volume of water will be less sensitive to a unit of air temperature increase due to thermal inertia of water. Additional local factors such as stream orientation, riparian vegetation and canopy cover affect the overall amount of short- and long-wave radiation that enters a stream, which, especially for smaller streams, can substantially change stream temperatures (Davies-Colley, Meleason, Hall, & Rutherford, 2009; Rutherford, Blackett, Blackett, Saito, & Davies-Colley, 1997; Rutherford, Marsh, Davies, & Bunn, 2004).

Considerable efforts have been made to build models of air–water temperature relationships (reviewed in Caissie, 2006), but are hindered by inadequate long-term monitoring of stream temperatures (Lough & Hobday, 2011). Additionally, most locations with long-term data are in highly managed or urban areas (Isaak, Wollrab, Horan, & Chandler, 2012), thereby confounding natural relationships between air and water temperature. As the ability to monitor water temperature in conjunction with air temperature has rapidly improved with the development of inexpensive water temperature loggers, we can now use empirical data sets to develop models that relate changes in air temperature to changes in water temperature. These models can be used to identify areas of conservation or management priority, particularly areas that may act as thermal refuges for species that can move out of more thermally stressful or unstable areas (e.g., Berman & Quinn, 1991; Kaya, Kaeding, & Burkhalter, 1977; Sutton, Deas, Tanaka, Soto, & Corum, 2007).

We analysed 11 years of stream temperature data that covered multiple streams within the largest uninhabited watershed in New Hampshire. Our study site is located in the north-eastern U.S.A., which is considered the fastest warming region in the contiguous U.S.A. and is projected to warm by 3°C by the time that global warming reaches 2°C (Karmalkar & Bradley, 2017). First, we characterised how diurnal and daily changes in air temperature throughout the summer corresponded with changes in water temperatures across the watershed. We then built a model that predicts maximum daily stream temperature as a function of air temperature, while also testing for the importance of factors such as stream order and

discharge on water temperatures. We focused on modelling maximum daily stream temperature because of its potential role in shaping the distribution, abundance and phenology of aquatic invertebrates and brook trout in this watershed.

2 | METHODS

2.1 | Study site and temperature data

We collected temperature data in the Dead Diamond River watershed in northern New Hampshire (44°52′54.3″N, 71° 4′8.4″W, Figure 1). This uninhabited watershed contains the last self-sustaining, native, unstocked population of brook trout in New Hampshire and Vermont (Kelson, Kapuscinski, Timmins, & Ardren, 2015). It lies within Dartmouth College's Second College Grant, a 27,000-acre property characterised by many small (<2 km² drainage) first-order streams of moderate slope (2%–4%, Nislow & Lowe, 2003) that flow into two larger rivers (Figure 1). The forest is composed of mostly Sugar Maple (*Acer saccharum*), Paper Birch (*Betula papyrifera*), Yellow

Birch (*Betula alleghaniensis*), American Beech (*Fagus grandifolia*), Balsam Fir (*Abies balsamea*) and Red Spruce (*Picea rubens*).

From 2001 to 2011, we measured hourly water temperatures using Hobo temperature loggers (TidbiT UTBI-001, Onset, Bourne, MA, U.S.A., resolution = 0.02°C at 25°C) at twelve sites (eight water, four air) during June–September. Five of the water temperature sites were within large streams (>3 m wide, >4th order, open-canopy; Gate, Lower Swift, Lower Dead, Upper Swift, Upper Dead; circles 1–5 in Figure 1), and three of the water temperature sites were within small streams (<2 m wide, 1st–3rd order, closed canopy; Alder, Merrill, Loomis Valley; circles 6–8 in Figure 1). Elevations (above sea level) were ~390 m at Gate, ~415 m at Lower Dead and Lower Swift, ~450 m at Upper Swift, ~430 m at Upper Dead and ~430 m at each Alder, Merrill and Loomis Valley. Loggers were placed in the same locations within each stream consistently across the years, always anchored to a brick placed within 2 m of the stream bank and at a depth of 0.5–1.0 m. Loggers were placed in locations where water was running and well-mixed (not in riffles or pools).

We collected additional water temperature data from 28 June to 8 August 2014 to determine the extent of thermal heterogeneity within a stream. On 20 June 2014, we deployed five pairs of HOBO pendant data loggers within the Dead Diamond River (arrows in Figure 1). Loggers recorded stream temperatures at 30-min intervals. Using aforementioned methods, we placed one "shallow" logger within 2 m of the stream bank at a depth of 0.5–1.0 m. We also placed a paired "deep" logger in a nearby (5–10 m horizontal distance) deep pool (1.8–2.2 m depth). We selected site locations with the a priori goal of choosing locations that would maximise within-site spatial thermal variability, assuming that deeper pools would be colder and thus potential thermal refuges for resident coldwater species such as brook trout.

We measured hourly air temperatures at four locations distributed throughout the study area. Hourly shaded air temperatures at 1.5 m height were recorded at Merrill throughout the study and in some years at Airstrip (2002–2007, 2009, 2011–2012), Hellgate (2001–2005, 2007, 2009–2010, 2012) and Johnson (2007–2008, 2012, see Figure 1). In 4 years at Merrill and 3 years at Airstrip, we collected measurements from replicate temperature sensors. The precision of replicate temperature sensors was good: for average daily air temperatures at two sites: $r^2 > .995$ and average absolute value of differences between replicates <0.30°C. Air temperatures recorded across our study area indicated a relatively homogenous thermal environment ($r^2 = .94$–$.98$ for six pairwise comparisons among four sites, Table S1). Merrill, which was near the geographic centre, had air temperatures typical of the study area (average difference in mean daily air temperature between Merrill and the other three locations = −0.38 to 0.57°C, Table S1, Figure S1). Compared to records from the two nearest long-term weather stations, air temperatures at Merrill were a bit cooler and well correlated (Figure S2). In the light of these patterns, we used average daily air temperatures at Merrill, as the independent variable for developing models of stream temperature as a function of air temperature.

From our raw air and water temperature data, for each day between 22 June and 30 September in each year (2001–2011), we
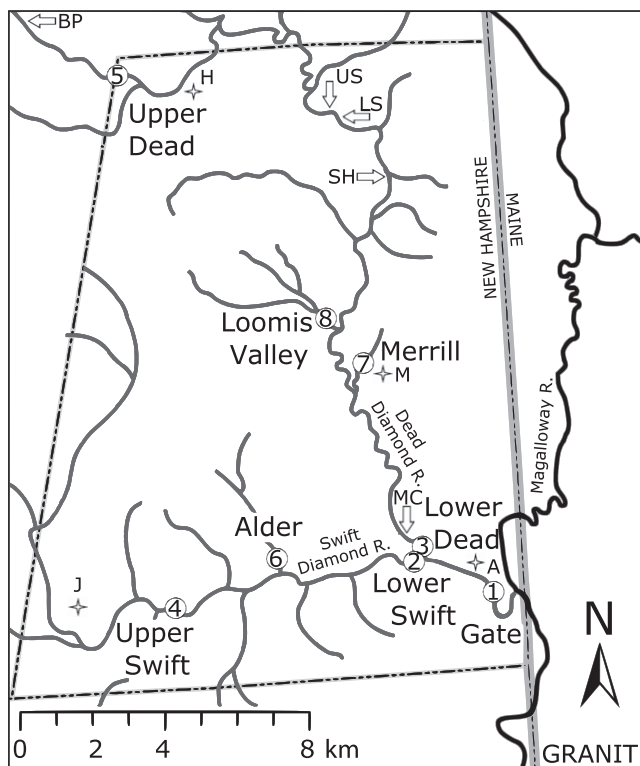

FIGURE 1 Map of streams in the Dead Diamond River Watershed (grey lines). The circles indicate the location of the water temperature loggers at Gate (1), Lower Swift (2), Lower Dead (3), Upper Swift (4), Upper Dead (5), Alder (6), Merrill (7) and Loomis Valley (8). The diamonds indicate the location of the four air temperature loggers (A = Airstrip; H = Hellgate; J = Johnson; and M = Merrill). Arrows indicate the locations of the thermal heterogeneity studies from 2014 (MC = Management Center; SH = Sid Hayward; US = Upper Slewgundy; LS = Lower Slewgundy; BP = Beaver Pond). The dashed lines indicate state borders and the boundary of Dartmouth College's Second College Grant. Map was created using ArcMap 10.3.1

calculated average daily water (W_{avg}) or air (A_{avg}) temperature as the average of the 24 hourly measurements recorded by the temperature loggers. For each water temperature logger (sites 1–8), we also extracted maximum daily stream temperature (W_{max}).

2.2 | Diurnal and summer patterns

To summarise the general patterns in air and water temperatures in the Dead Diamond River watershed during the summer months, we fit cosine functions (Equation 1, Figure S3) to the average daily temperatures at each of the nine sites in each year from 2001 to 2011 (PROC NLIN, SAS v.9.3),

$$W_{avg}, A_{avg} = a + b \times \cos\left(\frac{2\pi}{365.25} \times (\text{solar day} - c)\right) \qquad (1)$$

and calculated the mean solar day of maximum average daily temperature (c) and maximum average daily temperature ($a + b$), as the average across years at each site.

To compare diurnal patterns over the summer, we fit cosine functions (Equation 2, Figure S4) to the hourly temperature data from each of the nine sites (W_{hour}, A_{hour}) in each year from 2001 to 2011 during four time periods (22–28 June, 22–28 July, 22–28 August and 22–28 September; PROC NLIN, SAS v.9.3),

$$W_{hour}, A_{hour} = a + b \times \cos\left(\frac{2\pi}{24} \times (\text{hour} - c)\right) \qquad (2)$$

and calculated mean local time of maximum daily temperature (c), maximum daily temperature ($a + b$) and daily amplitude ($2b$) as the average across years for each site in each time period.

2.3 | Stream–Air Temperature Model

Changes in average daily air temperature (A_{avg}) are driven by the effects of seasonality and changes in weather patterns. We removed the effect of seasonality by calculating an average daily air temperature residual, A_R (Equation 3), that represented how much the average daily air temperature deviated from what was predicted (A_{pred}) based on seasonality.

$$A_R = A_{avg} - A_{pred} \qquad (3)$$

A_{pred} was calculated using the parameters from a sine function (Equation 4) fit to average daily air temperatures (A_{avg}) as a function of solar day (S) across all years (likelihood v.1.5, R):

$$A_{avg} = a + b \times \sin\left(\frac{2\pi}{365.25}(S - c)\right) \qquad (4)$$

The parameters $a = 4.4$, $b = 12.3$ and $c = 136$ were subsequently used to calculate A_{pred} for each solar day.

Although the focus of our study was developing a model relating deviations in air temperatures (A_R) to maximum daily stream temperatures (W_{max}), we included a few additional components that could potentially improve the model (see Introduction), including stream

order as a categorical variable (high for sites 1–5; low for sites 6–8) and daily measurements of discharge (D). Daily discharge data from the Dead Diamond River watershed were downloaded from www.waterdata.usgs.gov (site 01052500) and log-transformed before use in the model. These daily measurements were taken at a location approximately 500 m upstream from site 1 (Gate, see Figure 1) and thus integrate changes in discharge across the studied watershed. Lastly, we included solar day (S) in the model to account for seasonal variation in stream temperatures (Caissie, 2006; see Table S2).

Changes in water temperature often lag changes in air temperature due to thermal inertia of water (Erickson & Stefan, 2000) so we also developed a function that would allow us to evaluate the significance of mean daily air temperatures in the previous days in explaining maximum daily stream temperature. We used the function,

$$A_{RW} = \frac{\sum_{x=1}^{y} \left(A_{R(S-x+1)} * x^{-q}\right)}{\sum_{x=1}^{y} (x^{-q})} \qquad (5)$$

to calculate a mean daily air temperature residual, A_{RW}, over the past y days (from $x = 1$ to $x = y$ days), where A_R is the deviation in daily air temperature from the seasonally predicted mean on a given solar day (S) and q is the decay factor. If $q = 0$, then each previous day's air residual was equally important as today's. If $q = 1$, then yesterday's was half as important as today's, and 2 days ago was one-third as important, etc. Increasing q decreases the importance of days in the past. If $q \approx \infty$, then only today's air residual was important. q was optimised for high and low stream orders (see below), and a range of values for y, that is, the number of previous day's air temperatures included in the model, was tested. The numerator is the sum of the weighted values and the denominator is the sum of the weights, leaving a weighted average daily air temperature residual (A_{RW}) over the past y days (see Table S2). An A_{RW} ($y = 5$) value of 1 indicates that residual air temperatures were 1°C greater than predicted by seasonality over the past 5 days.

We used maximum-likelihood methods to estimate the parameters of the model relating maximum daily stream temperature (W_{max}) to all possible effects and interactions of weighted air residuals over the past 5 days (A_{RW}, $y = 5$), discharge (D) and solar day (S). Each parameter was separately estimated for high- and low-order stream data, nested within one master model (likelihood v.1.5, R). We created a series of models, each of which had one effect or interaction removed. To analyse parameter contribution to model fit, we used a chi-square test on the relative likelihood of the model with versus without each effect or interaction term. We sequentially removed non-significant terms ($p > .05$)—beginning with the term with the greatest p value and updating the model after each removal—until all remaining terms were considered significant ($p < .05$). We confirmed that the removed terms were still non-significant when added back into the reduced model. After reducing the model, we varied y in Equation (5) from 1 to 15 and calculated the AICc and root mean square error (RMSE) for each iteration to determine how adding more days from the past affected model fit.

To visualise the master model and any main or interactive effects of A_{RW}, discharge and solar day, we conducted sensitivity analyses.

We calculated how a sustained 5-day change in air temperature residuals by one standard deviation would change maximum daily water temperatures (at mean levels of discharge), and, conversely, how a one standard deviation change in discharge would change water temperatures (if air temperatures were not deviating from the seasonally predicted daily means).

3 | RESULTS

Sampling of within-site stream temperatures indicated that the water was generally well-mixed and that thermal heterogeneity was minimal. Only 2.3% of the 14,790 paired temperature observations collected in 2014 revealed within-site differences greater than 1°C. Within a location, mean differences between shallow and deep loggers were all less than 0.25°C (Figure S5). We never observed mean within-site differences in temperature of more than 1°C, and there was no pattern of shallow sites tending to be warmer than deep sites (Figure S6).

3.1 | Summer patterns

When averaged across all years, air and water temperatures peaked in July with a 9-day lag in maximum daily water temperatures (maximum air: 17 July, maximum water: 26 July; Table 1). The average maximum air temperature was 16.8°C. Average maximum summer stream temperatures were 18.9°C and 14.6°C for high- and low-order streams, respectively (Table 1).

3.2 | Diurnal patterns

On a daily scale, air and water temperatures were lowest just before sunrise and then increased during the day (Figure S4). Similar to the seasonal patterns, water temperatures reached their daily peak after

air temperatures (local hour 17:45 for water versus local hour 15:30 for air, see Table S3, Figure S4). Maximum daily air temperatures were generally higher or equal to maximum daily stream temperatures in higher order streams (Table S3). Lower order streams had considerably colder maximum daily stream temperatures (13.9°C averaged across all months) versus the higher order streams (18.4°C averaged across all months, Table S3). The daily amplitude in temperature was fairly consistent across the season, but was highest for air, which had an amplitude of 8.2°C (Table S3). High-order streams had a daily amplitude of 3.2°C, but some streams had considerably more than others. For example, daily amplitude in the Lower Dead was only 1.2°C compared with 4.3°C in the Lower Swift. The low-order streams had a daily amplitude on average of 1.5°C, but Merrill Brook only varied by about 0.9°C every day, whereas Alder varied by about 2.0°C. Loomis Valley was intermediate with an amplitude of 1.5°C (Table S3).

3.3 | Modelling stream temperature

Changes in mean daily water temperatures (W_{avg}) corresponded with changes in mean daily air temperature (A_{avg}), but water temperatures often continued to increase a day or more after air temperatures positively deviated from predicted seasonal temperatures (e.g., Figure 2). Average daily water temperatures in the larger streams tended to be higher than average daily air temperatures (Figure 2) due to the high amplitude in daily air temperatures (Table S3); that is, although maximum daily air temperatures exceeded those of the stream (see Figure 2 inset), air temperatures also decreased significantly at night, thereby lowering the calculated average daily air temperature (Figure 2).
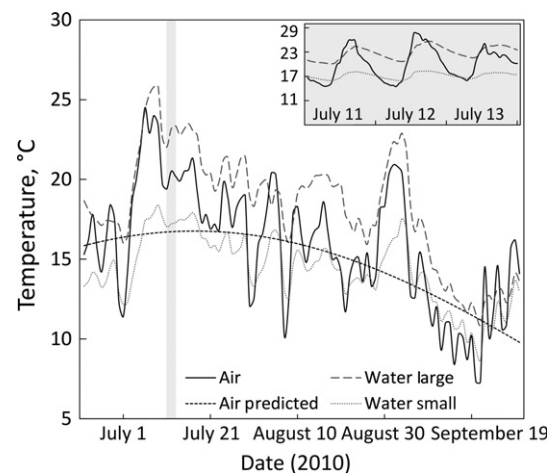

FIGURE 2 As mean daily air temperatures (A_{avg}, solid black line) deviated from predicted mean daily air temperatures (A_{pred}, dotted black line), mean daily water temperatures (W_{avg}) followed a similar pattern [large high-order stream (Gate): grey dashed line; small low-order stream (Loomis Valley): grey dotted line]. Data shown are from 22 June–30 September 2010. Inset shows hourly temperatures corresponding to a 3-day period (11–13 July 2010, shaded in large panel) for air (solid black line), a large stream (Gate, grey dashed line),and a small stream (Loomis Valley, grey dotted line)

TABLE 1 Maximum seasonal summer temperature ($a + b$) and the date of this peak temperature (c) were calculated from the parameter estimates (Equation 1) averaged across all years (2001–2011) during the time period 22 June–30 September

Site	Stream order	Max. summer temp (°C) Mean	SE	Date of peak Mean (date)	SE (days)
Air	n/a	16.8	0.3	17 July	3
Gate	High	19.3	0.4	25 July	2
Lower Swift		19.4	0.6	26 July	4
Lower Dead		19.4	0.5	26 July	3
Upper Swift		17.7	0.2	26 July	3
Upper Dead		18.7	0.5	27 July	3
Merrill	Low	14.4	0.2	27 July	2
Alder		14.7	0.8	24 July	3
Loomis		14.7	0.2	28 July	3

Within the master model (Table 2), maximum daily water temperature (W_{max}) of low-order streams was predicted using the 5-day weighted residual mean air temperature, discharge, solar day and an interactive effect between the 5-day weighted residual mean air temperature and discharge ($R^2 = 0.95$, RMSE = 0.7, Table 2, see Table S2 for sample calculation). The sensitivity (increase in °C) of maximum daily water temperature in low-order streams per 1.0°C increase in residual air temperatures (A_{RW}) over the previous 5 days was 0.58 at mean levels of discharge (~3.8 m³/s), 0.65 at high levels (~15.8 m³/s) and 0.53 at low levels (~1.1 m³/s; Figure 3). At mean levels of discharge, a sustained 5-day increase in air temperature residuals by one standard deviation (3.1°C) would increase maximum daily water temperature by 1.8°C. By comparison, a one standard deviation increase in discharge (6.5 m³/s) would decrease water temperatures by only 0.1°C.

For the high-order streams, maximum daily water temperature (W_{max}) was a function of the 5-day weighted residual mean air temperature and solar day, in addition to all two-way and the three-way interaction ($R^2 = 0.92$, RMSE = 1.6, Table 2, see Table S2 for sample calculation); that is, maximum daily stream temperature varied with residual air temperatures, but the relationship was modified by discharge and solar day (Figure 3). In these streams, W_{max} increased by a maximum of 0.81°C per 1°C increase in 5-day residual air temperature, but this relationship changed based on solar day, discharge and interactive effects between solar day and discharge (see Figure 3 for visualisation of how main effects and interactions affect sensitivity). At mean levels of discharge, a sustained 5-day increase in air temperature residuals by one standard deviation (3.1°C) would increase maximum daily water temperature by 2.3–2.5°C depending on solar day (Table 3). Discharge was markedly more influential in large streams than small streams: a one standard deviation increase in discharge (6.5 m³/s) would decrease water temperatures by 1.5–1.9°C (Table 3).

In a subsequent analysis of the model residuals, there was no apparent effect of day-to-day variation in photosynthetically active radiation (PAR, sunny days versus cloudy days) on water temperatures, even though PAR ranged by over fourfold, from <10 to
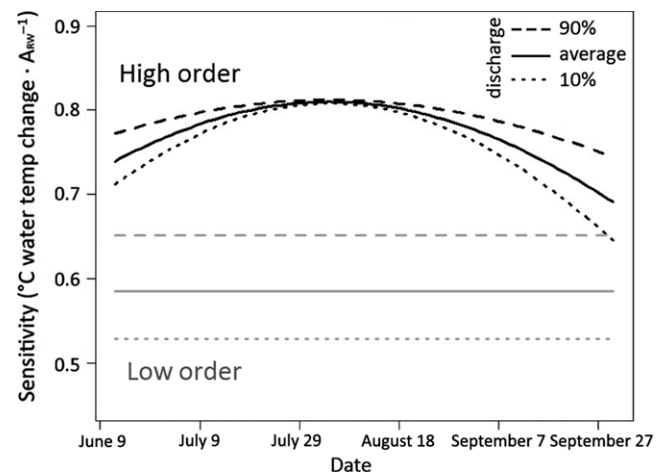

FIGURE 3 The sensitivity (increase in °C) of maximum daily water temperature to a 1.0°C increase in residual air temperatures (A_{RW}) over the previous 5 days ranged from 0.5 to 0.8°C depending on date (x-axis), stream order (high order = black lines; low order = grey lines) and discharge (average discharge = solid lines; 10% discharge = dotted lines; 90% discharge = dashed lines)

>40 moles m⁻² day⁻¹ (measured using Licor Quantum sensors in an open-canopy field at the Airstrip during the summers of 2002, 2003, 2004, 2005 and 2008, Figure 1; Figure S7). There was only a weak positive relationship between PAR and summer air temperatures ($y = 14.0 + 0.047 \cdot$ PAR, $r^2 = .03$).

Increasing the number of previous days of air temperature residuals (y, Equation 5) improved the model fit, more so for the small than for the large streams (Figure S8). q in Equation 5 was estimated as 1.4 ($\pm$ 0.03); that is, yesterday's mean air temperature residual was less than half as important as today's mean air temperature residual.

4 | DISCUSSION

Our results showed a fundamental relationship between air and water temperatures in the Dead Diamond River watershed. This

TABLE 2 Parameter coefficient estimates and standard errors (SE) for maximum-likelihood models predicting maximum daily stream water temperature in high- and low-order streams. *Air temp.* (A_{RW}) is a function that weights residual air temperature (in °C) over the past 5 days (Equation 5); *Discharge* (D) is natural-logarithm transformed discharge (m³/s); and *Seasonality* $g(S)$ is a sine function related to solar day (S) (see eq. ii in Table S2). χ^2 and p values are for the likelihood ratio test when each parameter was removed, performed on one degree of freedom. See Table S2 for example calculations of how to use the models

Parameter	Low order			High order		
	Estimate $\pm$ SE	χ^2	p	Estimate $\pm$ SE	χ^2	p
Intercept	6.1 ± 0.08			7.4 ± 0.1		
Air Temp. (A_{RW})	0.5 ± 0.009	2,150	<.0001	0.4 ± 0.04	5,810	<.0001
Discharge (ln(D))	0.1 ± 0.01	7,030	<.0001			
Seasonality $g(S)$	9.2 ± 0.08	7,040	<.0001	16.0 ± 0.1	6,150	<.0001
$A_{RW} \times$ ln(D)	0.05 ± 0.006	67.0	<.0001	0.08 ± 0.02	12.6	.00038
$A_{RW} \times g(S)$				0.4 ± 0.06	8,430	<.0001
ln(D) $\times g(S)$				-1.9 ± 0.03	1,180	<.0001
$A_{RW} \times$ ln(D) $\times g(S)$				-0.08 ± 0.03	6.49	.011

TABLE 3 Sensitivity of maximum daily water temperature (ΔT = change in°C) in high-order streams to a sustained 5-day increase in air temperature residuals by one standard deviation (σ_A = 3.1°C) and to a one standard deviation increase in ln (discharge) ($\sigma_{\ln(D)}$ = 1.01, ~6.5 m^3/s), calculated for three different dates. Sensitivity was calculated at mean discharge (ln(D) = 1.33) and air temperature residual (A_{RW} = 0). Note that increasing air temperature residuals leads to an increase in water temperatures, whereas an increase in discharge leads to a decrease in water temperatures

Date (Solar day)	$\Delta T/\sigma_A$	$\Delta T/\sigma_{\ln(D)}$
26 June (187)	2.3°C	−1.5°C
26 July (217)	2.5°C	−1.9°C
26 August (248)	2.4°C	−1.8°C

enabled a predictive understanding of how air temperatures alter stream temperatures at daily and seasonal timescales. Many of the observed patterns, such as the time lags of changes in water temperature behind changes in air temperature, reflect the thermal inertia of water; that is, it takes more energy per unit volume to raise the temperature of water versus air. For this reason, we found that stream temperatures increased by less than 1°C for every 1°C increase in air temperatures above the seasonal norms. Somewhat surprisingly, we found no indication that day-to-day variation in photosynthetically active radiation (PAR), for example sunny versus cloudy days, had a meaningful impact on water temperatures in our system. Instead, the main driver of summer stream temperatures in this watershed was air temperature, with additional patterns related to stream discharge.

4.1 | Drivers of stream temperature in an uninhabited watershed

Changes in daily water temperatures corresponded with deviations of air temperatures from seasonally predicted daily means (Figure 2), which is consistent with other studies that show air temperature is a prominent driver of stream temperature (e.g., Isaak et al., 2012). The results from our model indicated that an increase of 1.0°C in residual mean air temperature over the past 5 days corresponded with an increase in maximum daily stream temperature by 0.53–0.81°C. Including previous days' air temperature deviations improved the model, as is typical for models of air and water temperatures (Preud'homme & Stefan, 1993; Webb & Nobilis, 1995). However, the reduction in root mean square error by including 5 days versus just the current day was only ~0.1 or 0.2°C for the large and small streams, respectively. This difference may be biologically negligible, and thus, the additional data, although they improved the model fit (Figure S8), may not be necessary depending on the intended use of the model.

The relationship between air and water temperature was strengthened with basic knowledge about the size and order of the study streams within the watershed. Maximum daily stream temperature in the larger, higher order streams (sites 1–5) corresponded with changes in residual mean air temperature more strongly than

lower order streams; that is, the slopes were higher in the high-order streams across all levels of discharge and solar day (0.65–0.81°C for every 1.0°C increase in residual mean air temperatures). Similar estimates have been found in non-groundwater-dominated streams in Minnesota (slope = 0.82) and Oklahoma (slope = 0.80, Erickson & Stefan, 2000). Groundwater-dominated streams, such as Alder, Merrill and Loomis Valley, had lower slopes than larger streams (0.53–0.65°C for a 1.0°C in residual mean air temperature), similar to what was calculated in a groundwater-dominated stream in England (slope = 0.61°C, Mackey & Berrie, 1991). The lower slope relative to the larger streams is likely due to greater proportions of relatively cool groundwater input that help to cool summer water temperatures (Power et al., 1999) and greater canopy cover that absorbs incoming radiation and reduces heat transfer to the stream (Davies, 2010; Davies-Colley et al., 2009; Lough & Hobday, 2011; McCullough et al., 2009; Rutherford et al., 2004).

Including daily measurements of discharge improved the model and highlighted some general conclusions related to concomitant changes in temperature and precipitation. Across all streams, higher discharge decreased maximum daily stream temperature. This was particularly pronounced in the larger streams, where a heavy rain event would cause greater amounts of cold ground water to flush into the channel, lowering stream temperatures by over 1°C (versus 0.1°C in the small streams). Under ambient conditions, smaller streams already receive a greater proportion of groundwater input; thus, increasing discharge has less of a direct effect. However, high levels of discharge increased the sensitivity of stream temperatures to changes in air temperatures, particularly in the small streams (Figure 3). Cooling water temperatures from high discharge would increase the temperature gradient between air and water, thus affecting how much a one degree increase in residual air temperatures would change stream temperature on a given day. In the small streams, this may be particularly pronounced because temperatures are already colder and it is a smaller volume of water. Conversely, low levels of discharge, representative of drought conditions, will result in higher water temperatures that are less sensitive to increases in air temperature because of a decreased thermal differential.

Similar to other studies (van Vliet et al., 2011), we found that the impacts of discharge on stream temperatures were less than the effects of changes in air temperature (see Table 3). Nonetheless, if precipitation increases (Karmalkar & Bradley, 2017), this could potentially buffer some of the increases in water temperature that will follow increases in air temperature due to the cooling effect of groundwater input. However, an increase in drought frequency, as is also predicted for New England (Frumhoff, McCarthy, Melillo, Moser, & Wuebbles, 2007; Hayhoe et al., 2007), may exacerbate the effects of rising air temperatures on water temperature (Mosley, 1983).

4.2 | Biological consequences of the air–water temperature relationship

Forecasting the response of freshwater organisms to warming requires connecting local physical conditions with key physiological

and ecological processes. When air temperatures were warmer than average in July (the warmest month of the year), we measured stream temperatures that surpassed levels known to cause physiological and behavioural responses in stream organisms. In the large rivers, 38% of our hourly temperature observations in July were above 20°C (Figure S9). These temperatures are known to cause thermal stress and increased mortality in brook trout (Trumbo et al., 2014; Xu et al., 2010). Furthermore, mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera), which are common in this watershed (Culler and Ayres, personal observations), are known to be particularly sensitive to temperatures between 20 and 25°C (reviewed in Stewart et al., 2013; Rogowski & Stewart, 2016; Sweeney, Funk, Camp, Buchwalter, & Jackson, 2018). For example, mayflies experience mortality at sustained temperatures as low as 20.5°C (Stewart et al., 2013) and the mortality of caddisflies in shaded mountain streams in Costa Rica increased with temperatures above 22.3°C (Rogowski & Stewart, 2016). Although temperatures in our streams reached the upper lethal levels for some taxa, diurnal patterns in stream temperatures (Figure S4) likely prevent sustained exposure with lethal consequences.

Beyond direct mortality from high temperatures, we anticipate that warming events will have pronounced sub-lethal effects on stream ectotherms (Dallas & Ross-Gillespie, 2015), including those taxa with broad and high thermal tolerances (e.g., Coleoptera and Odonata, see Stewart et al., 2013). For fish, there are significant energetic costs associated with the behavioural response of searching for a thermal refuge (Selong, McMahon, Zale, & Barrows, 2001). This may be particularly true in our watershed, where the lack of within-stream thermal heterogeneity may require the native brook trout to move considerable distances. For aquatic insects, exposure to elevated but sub-lethal temperatures can alter their body size (e.g., Atkinson, 1995; Sweeney et al., 2018) as well as their growth rates (e.g., Culler et al., 2014; Sweeney et al., 2018), phenology (e.g., Culler et al., 2015; Harper & Peckarsky, 2006; Ross-Gillespie, 2014) and fecundity (e.g., Vannote & Sweeney, 1980; Sweeney & Vannote, 1981; Giberson & Rosenberg, 1992; Elliott, 2013; see Dallas and Ross-Gillespie (2015) for a review of sub-lethal temperature effects on aquatic insects). Taken together, lethal and sub-lethal impacts of temperature help explain why strong associations are found between stream temperatures and community composition (Chinnayakanahalli, Hawkins, Tarboton, & Hill, 2011; Friberg et al., 2009; Lowe & Hauer, 1999; Sweeney & Vannote, 1978).

As air temperatures are predicted to increase in the north-eastern U.S.A. (Horton et al., 2014; Karmalkar & Bradley, 2017), we expect that increased occurrences of high water temperatures will have consequences for both community composition and stream ecosystem function (Kuemmerlen et al., 2015; Pyne & Poff, 2016; Woodward, Perkins, & Brown, 2010). Currently, our smaller streams rarely exceed thresholds for taxa intolerant of water temperatures >20°C (Figure S9, Stewart et al., 2013) because their volume is comprised of a high proportion of ground water that keeps both the mean temperature and amplitude of temperature fluctuations low (Mackey & Berrie, 1991). Groundwater temperatures in the Dead

Diamond River watershed peaked at around 12.2°C in August (M. Ayres, unpublished data), and daily maximum groundwater temperatures were relatively stable, only varying between 9.3 and 12.3°C throughout the summer months. Thus, these habitats will be increasingly important for maintaining populations of thermally intolerant invertebrates and providing thermal refuges for fish that may otherwise have little access to thermal heterogeneity within the larger rivers.

4.3 | Implications for management

Documenting and preserving a diversity of natural stream habitats, including pools and areas with large amounts of groundwater input (Dugdale, Bergeron, & St-Hilaire, 2013, 2015; Kurylyk, MacQuarrie, & Voss, 2014); preventing deforestation and flow alteration; and ensuring unrestricted movement of fish and invertebrates can help maintain thermally suitable habitats required by many cold stenothermic stream biota. Conservation of headwater and smaller streams in particular is important, because, in addition to providing thermal heterogeneity, any changes to the thermal characteristics of smaller streams will be integrated in downstream habitat. Over time, increases in air temperatures will lead to changes in groundwater temperature (Caissie, 2006) that will impact the thermal characteristics of microrefuges and smaller streams. Although this is predicted to take decades (Deitchman & Loheide, 2012), monitoring groundwater temperature in conjunction with stream and air temperature can eventually lead to predictive stream temperature models that can incorporate these longer-term lagged effects.

Thermally suitable habitats in rivers are increasingly threatened by anthropogenic activities such as deforestation (Beschta, 1997; Brown & Krygier, 1970; Johnson & Jones, 2000), flow alteration (Morse, 1972; Sinokrot & Gulliver, 2000) and climate change (Schindler, 2001; Sinokrot, Stefan, McCormick, & Eaton, 1995). In addition to increases in air temperature, climate change is altering precipitation patterns that can potentially affect the ability of a stream to buffer changes in air temperature. Our results indicate that within a watershed, streams differ in their sensitivity to changes in air temperature based on stream size and discharge. Furthermore, it is possible to generate useful models that can identify stream habitat within a watershed that should be of conservation and management priority using data that are relatively easy and inexpensive to collect. We encourage continued monitoring of steam temperatures at the watershed scale, and multidisciplinary team efforts to fully address the conservation of ecologically and economically important aquatic natural resources.

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REFERENCES

Araujo, M. B., Thuiller, W., & Pearson, R. G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, *33*, 1712–1728.

Atkinson, D. (1995). Effects of temperature on the size of aquatic ectotherms: Exceptions to the general rule. *Journal of Thermal Biology*, *20*, 61–74. https://doi.org/10.1016/0306-4565(94)00028-H

Berman, C. H., & Quinn, T. P. (1991). Behavioral thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) in the Yakima River. *Journal of Fish Biology*, *39*, 301–312. https://doi.org/10.1111/j.1095-8649.1991.tb04364.x

Beschta, R. L. (1997). Riparian shade and stream temperature: An alternative perspective. *Rangelands*, *19*, 25–28.

Brown, G. W., & Krygier, J. T. (1970). Effects of clear-cutting on stream temperature. *Water Resources Research*, *6*, 1133–1139. https://doi.org/10.1029/WR006i004p01133

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

Chinnayakanahalli, K. J., Hawkins, C. P., Tarboton, D. G., & Hill, R. A. (2011). Natural flow regime, temperature and the composition and richness of invertebrate assemblages in streams of the western United States. *Freshwater Biology*, *56*, 1248–1265. https://doi.org/10.1111/j.1365-2427.2010.02560.x

Cho, H., & Lee, K. (2012). Development of an air–water temperature relationship model to predict climate-induced future water temperature in estuaries. *Journal of Environmental Engineering*, *138*, 570–577. https://doi.org/10.1061/(ASCE)EE.1943-7870.0000499

Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distributions shifts in recent decades. *Ecography*, *36*, 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Culler, L. E., Ayres, M. P., & Virginia, R. A. (2015). In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 665–673.

Culler, L. E., McPeek, M. A., & Ayres, M. P. (2014). Predation risk shapes thermal physiology of a predaceous damselfly. *Oecologia*, *176*, 653–660. https://doi.org/10.1007/s00442-014-3058-8

Dallas, H. F., & Ross-Gillespie, V. (2015). Sublethal effects of temperature on freshwater organisms, with special reference to aquatic insects. *Water SA*, *41*, 712–726. https://doi.org/10.4314/wsa.v41i5.15

Davies, P. M. (2010). Climate change implications for river restoration in global biodiversity hotspots. *Restoration Ecology*, *18*, 261–268. https://doi.org/10.1111/j.1526-100X.2009.00648.x

Davies-Colley, R. J., Meleason, M. A., Hall, R. M. J., & Rutherford, J. C. (2009). Modelling the time course of shade, temperature and wood recovery in streams with riparian forest restoration. *New Zealand Journal of Marine and Freshwater Research*, *43*, 673–688. https://doi.org/10.1080/00288330909510033

Deitchman, R., & Loheide, S. P. II (2012). Sensitivity of thermal habitat of a trout stream to potential climate change, Wisconsin, United States. *Journal of the American Water Resources Association*, *48*, 1091–1103. https://doi.org/10.1111/j.1752-1688.2012.00673.x

Domisch, S., Araújo, M. B., Bonada, N., Pauls, S. U., Jähnig, S. C., & Haase, P. (2013). Modelling distribution in European stream macroinvertebrates under future climates. *Global Change Biology*, *19*, 752–762. https://doi.org/10.1111/gcb.12107

Dugdale, S. J., Bergeron, N. E., & St-Hilaire, A. (2013). Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. *Remote Sensing of Environment*, *136*, 358–373. https://doi.org/10.1016/j.rse.2013.05.018

Dugdale, S. J., Bergeron, N. E., & St-Hilaire, A. (2015). Spatial distribution of thermal refuges analysed in relation to riverscape hydromorphology using airborne thermal infrared imagery. *Remote Sensing of Environment*, *160*, 43–55. https://doi.org/10.1016/j.rse.2014.12.021

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2001). Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish*, *10*, 1–10. https://doi.org/10.1034/j.1600-0633.2001.100101.x

Elliott, J. M. (1991). Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology*, *25*, 61–70. https://doi.org/10.1111/j.1365-2427.1991.tb00473.x

Elliott, J. M. (2013). Contrasting dynamics from egg to adult in the life cycle of summer and overwintering generations of *Baetis rhodani* in a small stream. *Freshwater Biology*, *58*, 866–879. https://doi.org/10.1111/fwb.12093

Elliott, J. M., & Elliott, J. A. (1995). The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. *Journal of Fish Biology*, *47*, 917–919. https://doi.org/10.1111/j.1095-8649.1995.tb06014.x

Erickson, T. R., & Stefan, H. G. (2000). Linear air/water temperature correlations for streams during open water periods. *Journal of Hydrologic Engineering*, *5*, 317–321. https://doi.org/10.1061/(ASCE)1084-0699(2000)5:3(317)

Friberg, N., Dybkjaer, J. B., Olafsson, J. S., Gíslason, G. M., Larsen, S. E., & Lauridsen, T. L. (2009). Relationships between structure and function in streams contrasting in temperature. *Freshwater Biology*, *54*, 2051–2068. https://doi.org/10.1111/j.1365-2427.2009.02234.x

Frumhoff, P. C., McCarthy, J. J., Melillo, J. M., Moser, S. C., & Wuebbles, D. J. (2007) *Confronting climate change in the U.S. Northeast: Science, impacts, and solutions. Synthesis report of the Northeast Climate Impacts Assessment (NECIA)*. Cambridge, MA: Union of Concerned Scientists (UCS).

Garside, E. T. (1973). Ultimate upper lethal temperature of Atlantic salmon (*Salmo salar* L.). *Canadian Journal of Zoology*, *51*, 898–900. https://doi.org/10.1139/z73-135

Giberson, D. J., & Rosenberg, D. M. (1992). Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia* (Ephemeroptera: Ephemeridae). *Journal of the North American Benthological Society*, *11*, 181–193. https://doi.org/10.2307/1467384

Gillooly, J. E., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*, 2248–2251. https://doi.org/10.1126/science.1061967

Harper, M. P., & Peckarsky, B. L. (2006). Emergence cues of a mayfly in a high-altitude stream ecosystem: Potential response to climate change. *Ecological Applications*, *16*, 612–621. https://doi.org/10.1890/1051-0761(2006)016[0612:ECOAMI]2.0.CO;2

Hayhoe, K., Wake, C. P., Huntington, T. G., Luo, L., Schwartz, M. D., Sheffield, J., . . . Wolfe, D. (2007). Past and future changes in climate

and hydrological indicators in the US Northeast. *Climate Dynamics*, *28*, 381–407. https://doi.org/10.1007/s00382-006-0187-8

Hobday, A. J., & Lough, J. M. (2011). Projected climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, *62*, 1000–1014.

Horton, R., Yohe, G., Easterling, W., Kates, R., Ruth, M., Sussman, E., ... Lipschultz, F. (2014). Ch. 16: Northeast. In J. M. Melillo, T. C. Richmond & G. W. Yohe (Eds.), *Climate change impacts in the United States: The Third National Climate Assessment*. Washington, DC: U.S. Global Change Research Program.

Huntsman, A. G. (1942). Death of salmon and trout with high temperature. *Journal of the Fisheries Research Board of Canada*, *5*, 485–501. https://doi.org/10.1139/f40-051

Isaak, D. J., Wollrab, S., Horan, D., & Chandler, G. (2012). Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. *Climatic Changes*, *113*, 499–524. https://doi.org/10.1007/s10584-011-0326-z

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., ... Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4374–4379. https://doi.org/10.1073/pnas.1522429113

Jiménez Cisneros, B. E., Oki, T., Arnell, N. W., Benito, G., Cogley, J. G., Döll, P., ... Mwakalila, S. S. (2014) Freshwater resources. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the fifth assessment report of the intergovernmental panel on climate change* (pp. 229–269). Cambridge, UK and New York, NY: Cambridge University Press.

Johnson, S. L., & Jones, J. A. (2000). Stream temperature response to forest harvest and debris flows in western Cascades, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(Suppl. 2), 30–39. https://doi.org/10.1139/f00-109

Karmalkar, A. V., & Bradley, R. S. (2017). Consequences of global warming of 1.5°C and 2°C for regional temperature and precipitation changes in the contiguous United States. *PLoS ONE*, *12*, e0168697. https://doi.org/10.1371/journal.pone.0168697

Kaya, C. M., Kaeding, L. R., & Burkhalter, D. E. (1977). Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. *The Progressive Fish-Culturist*, *39*, 37–39. https://doi.org/10.1577/1548-8659(1977)39[37:UOACRB]2.0.CO;2

Kelson, S. J., Kapuscinski, A., Timmins, D., & Ardren, W. (2015). Fine-scale genetic structure of brook trout in a dendritic stream network. *Conservation Genetics*, *16*, 31–42. https://doi.org/10.1007/s10592-014-0637-5

Kuemmerlen, M., Schmalz, B., Cai, Q., Haase, P., Fohrer, N., & Jähnig, S. C. (2015). An attack on two fronts: Predicting how changes in land use and climate affect the distribution of stream macroinvertebrates. *Freshwater Biology*, *60*, 1443–1458. https://doi.org/10.1111/fwb.12580

Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., ... Dobson, J. G. (2013). Regional climate trends and scenarios for the U.S. National Climate Assessment: Part 1. Climate of the Northeast. U.S. NOAA Technical Report NESDIS 142-1, Washington, DC. 87 pp.

Kurylyk, B. L., MacQuarrie, K. T., & Voss, C. I. (2014). Climate change impacts on the temperature and magnitude of groundwater discharge from shallow, unconfined aquifers. *Water Resources Research*, *50*, 3253–3274. https://doi.org/10.1002/2013WR014588

Lee, R. M., & Rinne, J. N. (1980). Critical thermal maximum of five trout species in the southwestern United States. *Transactions of the American Fisheries Society*, *109*, 632–635. https://doi.org/10.1577/1548-8659(1980)109<632:CTMOFT>2.0.CO;2

Lough, J. M., & Hobday, A. J. (2011). Observed climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, *62*, 984–999. https://doi.org/10.1071/MF10272

Lowe, W. H., & Hauer, F. R. (1999). Ecology of two large, net-spinning caddisfly species in a mountain stream: Distribution, abundance, and metabolic response to a thermal gradient. *Canadian Journal of Zoology*, *77*, 1637–1644. https://doi.org/10.1139/z99-146

Mackey, A. P., & Berrie, A. D. (1991). The prediction of water temperatures in chalk streams from air temperatures. *Hydrobiologia*, *210*, 183–189. https://doi.org/10.1007/BF00034676

McCullough, D. A., Bartholow, J. M., Jager, H. I., Beschta, R. L., Cheslak, E. F., Deas, M. L., ... Mesa, M. G. (2009). Research in thermal biology: Burning questions for coldwater stream fishes. *Reviews in Fisheries Science*, *17*, 90–115. https://doi.org/10.1080/10641260802590152

Morrill, J. C., Bales, R. C., & Conklin, M. H. (2005). Estimating stream temperature from air temperature: Implications for future water quality. *Journal of Environmental Engineering*, *131*, 139–146. https://doi.org/10.1061/(ASCE)0733-9372(2005)131:1(139)

Morse, W. L. (1972). Stream temperature prediction under reduced flow. *Journal of the Hydraulics Division*, *98*, 1031–1047.

Mosley, M. P. (1983). Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research*, *17*, 331–342. https://doi.org/10.1080/00288330.1983.9516007

Nislow, K. H., & Lowe, W. H. (2003). Influences of logging history and stream pH on brook trout abundance in first-order streams in New Hampshire. *Transactions of the American Fisheries Society*, *132*, 166–171. https://doi.org/10.1577/1548-8659(2003)132<0166:IOLHAS>2.0.CO;2

Null, S. E., Viers, J. H., Deas, M. L., Tanaka, S. K., & Mount, J. F. (2013). Stream temperature sensitivity to climate warming in California's Sierra Nevada: Impacts to coldwater habitat. *Climatic Change*, *116*, 149–170. https://doi.org/10.1007/s10584-012-0459-8

Orr, H. G., Simpson, G. L., Clers, S., Watts, G., Hughes, M., Hannaford, J., ... Evans, R. (2015). Detecting changing river temperatures in England and Wales. *Hydrological Processes*, *29*, 752–766. https://doi.org/10.1002/hyp.10181

Power, G., Brown, R. S., & Imhof, J. G. (1999). Groundwater and fish-insights from northern North America. *Hydrological Processes*, *13*, 401–422. https://doi.org/10.1002/(ISSN)1099-1085

Preud'homme, E. B., & Stefan, H. G. (1993). Stream temperature estimation from air temperature. *Water Resources Bulletin*, *29*, 27–45.

Pyne, M. I., & Poff, N. L. (2016). 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.

Rogowski, D. L., & Stewart, K. L. (2016). Effects of increased temperature on a Trichoptera (Hydropsychidae) from premontane forest streams in Southern Costa Rica. *Tropical Ecology*, *57*, 57–68.

Ross-Gillespie, V. (2014). *Effects of water temperature on life-history traits of selected South African aquatic insects*. PhD thesis, University of Cape Town, Cape Town.

Rutherford, J. C., Blackett, S., Blackett, C., Saito, L., & Davies-Colley, R. J. (1997). Predicting the effects of shade on water temperature in small streams. *New Zealand Journal of Marine and Freshwater Research*, *31*, 707–721. https://doi.org/10.1080/00288330.1997.9516801

Rutherford, J. C., Marsh, N. A., Davies, P. M., & Bunn, S. E. (2004). Effects of patchy shade on stream water temperature, how quickly do small streams heat and cool? *Marine and Freshwater Research*, *55*, 737–748. https://doi.org/10.1071/MF04120

Schindler, D. W. (2001). The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new

millennium. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 18–29. https://doi.org/10.1139/f00-179

Selong, J. H., McMahon, T. E., Zale, A. V., & Barrows, F. T. (2001). Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society*, *130*, 1026–1037. https://doi.org/10.1577/1548-8659(2001)130<1026:EOTOGA>2.0.CO;2

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., . . . Taboada, M. A. (2014). Terrestrial and inland water systems. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the fifth assessment report of the intergovernmental panel on climate change* (pp. 271–359). Cambridge, UK and New York, NY: Cambridge University Press.

Sinokrot, B. A., & Gulliver, J. S. (2000). In-stream flow impact on river water temperatures. *Journal of Hydraulic Research*, *38*, 339–349. https://doi.org/10.1080/00221680009498315

Sinokrot, B. A., Stefan, H. G., McCormick, J. H., & Eaton, J. G. (1995). Modeling of climate change effects on stream temperatures and fish habitats below dams and near groundwater inputs. *Climatic Change*, *30*, 181–200. https://doi.org/10.1007/BF01091841

Stewart, B. A., Close, P. G., Cook, P. A., & Davies, P. M. (2013). Upper thermal tolerances of key taxonomic groups of stream invertebrates. *Hydrobiologia*, *718*, 131–140. https://doi.org/10.1007/s10750-013-1611-9

Sutton, R. J., Deas, M. L., Tanaka, S. K., Soto, T., & Corum, A. (2007). Salmonid observations at a Klamath River thermal refuge under various hydrological and meteorological conditions. *River Research and Applications*, *23*, 775–785. https://doi.org/10.1002/(ISSN)1535-1467

Sweeney, B. W. (1993). Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in Eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *144*, 291–340.

Sweeney, B. W., Funk, D. H., Camp, A. A., Buchwalter, D. B., & Jackson, J. K. (2018). Why adult mayflies of *Cloeon dipterum* (Ephemeroptera: Baetidae) become smaller as temperature warms. *Freshwater Science*, *37*, 64–81. https://doi.org/10.1086/696611 https://doi.org/10.1086/696611

Sweeney, B. W., & Vannote, R. L. (1978). Size variation and the distribution of hemimetabolous aquatic insects: Two thermal equilibrium hypotheses. *Science*, *200*, 444–446. https://doi.org/10.1126/science.200.4340.444

Sweeney, B. W., & Vannote, R. L. (1981). *Ephemerella* mayflies of White Clay Creek: Bioenergetic and ecological relationships among six coexisting species. *Ecology*, *62*, 1353–1369. https://doi.org/10.2307/1937299

Trumbo, B. A., Nislow, K. H., Stallings, J., Hudy, M., Smith, E. P., Kim, D. Y., . . . Dolloff, C. A. (2014). Ranking site vulnerability to increasing temperatures in southern Appalachian brook trout streams in Virginia: An exposure-sensitivity approach. *Transactions of the American Fisheries Society*, *143*, 173–187. https://doi.org/10.1080/00028487.2013.835282

Vannote, R., & Sweeney, B. W. (1980). Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist*, *115*, 667–695. https://doi.org/10.1086/283591

van Vliet, M. T. H., Ludwig, F., Zwolsman, J. J. G., Weedon, G. P., & Kabat, P. (2011). Global river temperatures and sensitivity to atmospheric warming and changes in river flow. *Water Resources Research*, *47*, W02544. https://doi.org/10.1029/2010WR009198

Webb, B. W., & Nobilis, F. (1995). A long-term perspective on the nature of the air-water temperature relationship: A case study. *Hydrological Processes*, *11*, 137–147.

Winder, M., & Schindler, D. E. (2004). Climate change uncouples trophic interactions in a lake ecosystem. *Ecology*, *85*, 2100–2106. https://doi.org/10.1890/04-0151

Winter, T. C., Harvey, J. W., Franke, O. L., & Alley, W. M. (1998) Ground water and surface water: A single resource. U.S. Geological Survey Circular 1139.

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Xu, C., Letcher, B. H., & Nislow, K. H. (2010). Context-specific influence of water temperature on brook trout growth rates in the field. *Freshwater Biology*, *55*, 2253–2264.

SUPPORTING INFORMATION

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