

Envisioning, Quantifying, and Managing Thermal Regimes on River Networks

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Water temperatures fluctuate in time and space, creating diverse thermal regimes on river networks. Temporal variability in these thermal landscapes has important biological and ecological consequences because of nonlinearities in physiological reactions; spatial diversity in thermal landscapes provides aquatic organisms with options to maximize growth and survival. However, human activities and climate change threaten to alter the dynamics of riverine thermal regimes. New data and tools can identify particular facets of the thermal landscape that describe ecological and management concerns and that are linked to human actions. The emerging complexity of thermal landscapes demands innovations in communication, opens the door to exciting research opportunities on the human impacts to and biological consequences of thermal variability, suggests improvements in monitoring programs to better capture empirical patterns, provides a framework for suites of actions to restore and protect the natural processes that drive thermal complexity, and indicates opportunities for better managing thermal landscapes.

Keywords: water temperature, variability, human impacts, biota, landscape

The study of water temperature in rivers has a long and rich history (Webb et al. 2008). Much of this work has focused on mean temperatures, lethal extremes, and patterns across stream reaches because measurements at a fine temporal (e.g. minutes to days) or spatial (e.g. meters to kilometers) resolution could not be collected over long time periods or extensive areas. The types of data that could be collected efficiently were at a limited series of places and times. Therefore, until recently, researchers have generally been unable to quantify the potential ecological and biological consequences of spatial patterns of water temperature that change over time. Nuanced facets of thermal regimes can be coupled to specific ecological consequences or human activities in order to make effective management decisions; however, these relationships have been difficult to understand without conceptual and quantitative models built from fine-scale data.

Our objectives in this article are (a) to illustrate how advances in data collection and quantitative modeling are refining our vision of the thermal landscape of rivers, including an introduction to the idea of a thermal facet or nuanced aspect of the thermal landscape that is ecologically important; (b) to highlight foundational and new science on the biological importance of thermal variability and on how humans are altering the spatiotemporal complexity of

thermal landscapes; and (c) to synthesize needs and opportunities in riverine management and science resulting from this emerging understanding of variation in thermal landscapes over time and space.

New data and tools

Advances in data collection technology as well as in statistical and mathematical modeling are enabling important refinements in how we think about thermal landscapes.

The recent explosion of water-temperature data. Relatively recently, inexpensive sensors capable of measuring water temperature every hour, minute, or second have been installed extensively (e.g., Isaak et al. 2012). Newer technology allows for instantaneous recording of water temperature every meter along more than a kilometer of fiber-optic cable (Westhoff et al. 2007). Remotely sensed technology for imaging water temperature across the entire two-dimensional water surface has also become widely available. Using these technologies, researchers can quantify thermal variability at multiple spatiotemporal scales. For example, thermal infrared imaging, which measures emitted longwave radiation, can be used to create maps of surface temperature longitudinally and laterally within a stream channel (Dugdale 2016) or across a floodplain (Tonolla et al. 2010). Creative combinations of

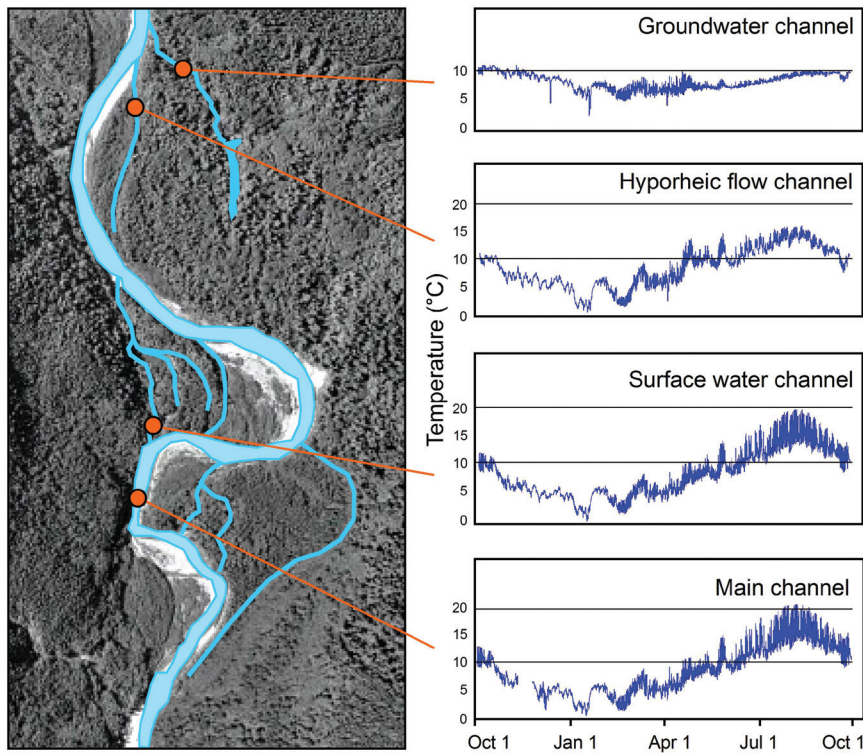


Figure 1. Temporal patterns in water temperature in the main channel and three side channels of a relatively undisturbed floodplain on the Sauk River near Darrington, Washington, United States. Water temperatures measured from October 2004 through September 2005 illustrate that a surface-water side channel has the same seasonal and diel temperature pattern as the main channel, a hyporheic flow channel has a similar seasonal pattern but reduced diel variation in summer, and a groundwater channel has both reduced seasonal and diel variation. Abbreviation: °C, degrees Celsius.

technology are also yielding exciting new data. For example, with a drone and a powered paraglider, Wawrzyniak and colleagues (2013) identified and mapped patterns of diel fluctuations in water temperature between adjacent aquatic habitats. Similarly, using a thermal infrared imaging camera on a helicopter, Dugdale and colleagues (2013) quantified shifts in fine-scale thermal refuges over time. These innovations in data collection and processing have elucidated spatiotemporal complexity that was previously only poorly understood.

Understanding of the natural dynamics of thermal landscapes has been gained from studies of pristine or near-pristine systems (Tonolla et al. 2010, Armstrong et al. 2013, Lisi et al. 2013). Although many of these areas are at high latitudes, observations of relatively undisturbed sites in lower latitudes also suggest that water temperature naturally varies in complex ways across both time (figure 1) and space (figures 1 and 2). A hierarchy of factors such as elevation, aspect, and local groundwater seeps combine to produce patches of cooler water within reaches (Dugdale et al. 2013), complex configurations on networks (Steel et al. 2016), and a wide variety of longitudinal patterns (Fullerton et al. 2015) across river systems. Leach and colleagues (2016), for

example, observed considerable spatial variability across headwater streams in a relatively small area of western Oregon in the United States and also found seasonal differences in the degree of that spatial variability. The recognition of both variety and pattern in the spatial structure of thermal regimes on entire river networks has recently been reinforced through airborne thermal surveys over 1000s of kilometers of river. Fullerton and colleagues (2015) found that water temperature in rivers throughout the Pacific Northwest exhibited highly variable and sometimes unexpected spatial patterns (e.g., cooling in a downstream direction). Temporal dynamics are equally complex, and thermal regimes are often geographically distinct. Maheu and colleagues (2016a) were able to classify rivers across the United States by annual temperature patterns, finding similar patterns among rivers within ecoregions. Our understanding of trends over long time frames is increasing, but it is compromised by the lack of empirical time series of sufficient length (Arisemendi et al. 2012, Isaak et al. 2012).

Envisioning how river temperatures vary over space and time. The enormous quantities of new data provide insights into the complex nature of thermal regimes in

free-flowing rivers. Thermal fluctuations in natural rivers take place minute by minute, day to night, season to season, and across years at every point in the stream network. Thermal diversity also exists across space: surface to subsurface, hyporheic to groundwater, streambank to thalweg, pool to riffle, mainstem to side channel, upstream to downstream, across floodplains (figure 3), and on the entire stream network at every moment in time. The spatial distribution of thermal regimes cannot be explained as simple shifts with elevation, from day to night, or from season to season (Steel et al. 2016). The thermal landscape is therefore difficult to visualize. Creative three-dimensional graphics can portray shifts in daily patterns over space for a single river section (e.g., figure 4), but envisioning changes in water temperature on an entire river network is more difficult.

Animations have advantages over static figures and graphs for illustrating changes in water temperature on the stream network over time. Using data collected every 30 minutes on the Snoqualmie River, Washington, we created movies to describe some of the spatiotemporal complexity of the thermal landscape (supplemental videos S1–S3). Over the hydrologic year 2014–2015 (video S1), seasonal warming and cooling patterns are not consistent across tributaries or

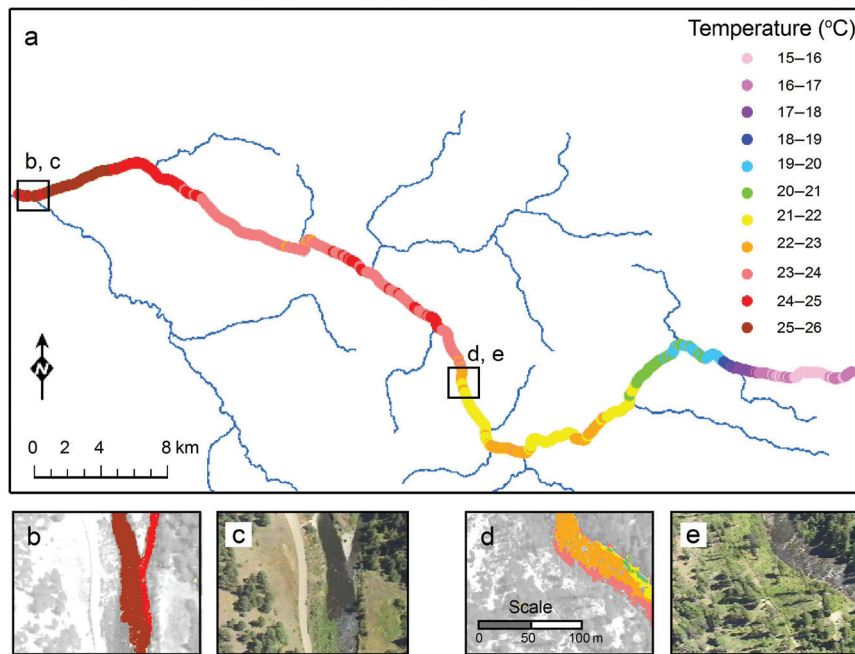


Figure 2. Spatial heterogeneity in summertime stream temperature at broad and fine scales in the North Fork John Day River, Oregon, United States (4 August 1998). Longitudinal patterns at a broad scale (a) illustrate the high degree of patchiness within the overall upstream–downstream gradient of cold to warm temperature in a wilderness stream. Finer-scale thermal patchiness occurs where a cooler tributary (Desolation Creek) enters the river (b and c) and where a cool-water seep flows into the main channel (d and e). Abbreviations: °C, degrees Celsius; km, kilometers; m, meters.

even across the three main river forks; the distribution of mean hourly temperatures on the network is at times fairly homogenous in space and at other times quite variable. On a hot day in summer 2015 (video S2), daily warming and cooling occurred at different rates at each location on the river network. For example, some tributaries warm rapidly, some tributaries begin warming late in the day, and the three forks of the river each have their own daily pattern. We demonstrate a combination of diel and longer-term patterns by displaying diel fluctuations within the month of May (video S3). Further complexity in the thermal landscape could be explored by creating movies that include lateral diversity, vertical gradients, and fine-scale heterogeneity, such as cool-water thermal refuges or warm-water patches.

Advances in modeling stream temperatures. Statistical methods have recently been developed to build models of stream temperature over space and time from new data sources. For instance, Westhoff and colleagues (2007) and Vatland and colleagues (2015) used fine-scale empirical data to create statistical models that predict longitudinal patterns of water temperature within a river and over time (figure 4). Cardenas and colleagues (2014) used time-lapse thermal imaging to explore the thermal dynamics of 2 square kilometers (km²) of a proglacial floodplain in Switzerland over meters and

minutes. McNyset and colleagues (2015) used remotely sensed land-surface temperature to provide spatially and temporally continuous estimates of mean daily stream temperature in the John Day River basin, Oregon, United States. A different way to manage the interaction of space and time is to model variability in time over space. For example, the River Assessment for Forecasting Temperature (RAFT) model (Pike et al. 2013) can predict the magnitude and timing of diel temperature fluctuations over a 100-km-long reach. As longer temporal data sets become available, one might also model the evolution of spatial pattern over time. It may be possible to use air-temperature data, which are more frequently available, to improve models of water temperature by adding daily or seasonal dynamics to spatial models; however, such approaches often rely on questionable assumptions such as a consistent and linear relationship between air and water temperature over time and on river networks. Statistical innovations will be required to manage time lags or for areas with sharp gradients in air temperature (Webb et al. 2003, Letcher et al. 2016).

A particularly powerful development is that of spatial stream-network models (SSNMs; Peterson et al. 2013), which have been applied across the western and eastern United States (www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html; Detenbeck et al. 2016). These models incorporate the spatial covariance present in water-temperature data and allow statistical predictions across whole river networks (e.g., videos S1–S3). SSNMs incorporate the unique branching structure of the river network, flow connectivity, and streamflow volume and directionality, as well as discontinuities associated with tributary confluences. Where SSNMs have been applied, accounting for spatial correlation in the data has significantly improved the accuracy of predictions at unsampled locations (Peterson et al. 2013), and Turschwell and colleagues (2016) found that SSNMs outperformed random forest across a range of thermal metrics. As yet, SSNMs cannot incorporate temporal variability explicitly, but Isaak and colleagues (2015) used time-sensitive covariates—flow and air temperature—to implicitly incorporate time. Another way to explore temporal variability on stream networks is to create summaries of temporal variability that are modeled on the network (Steel et al. 2016). Similarly, Jackson and colleagues (2017) used river network smoothers to build spatial statistical models that estimate the relationship between landscape covariates and mean, minimum, and maximum river temperatures.

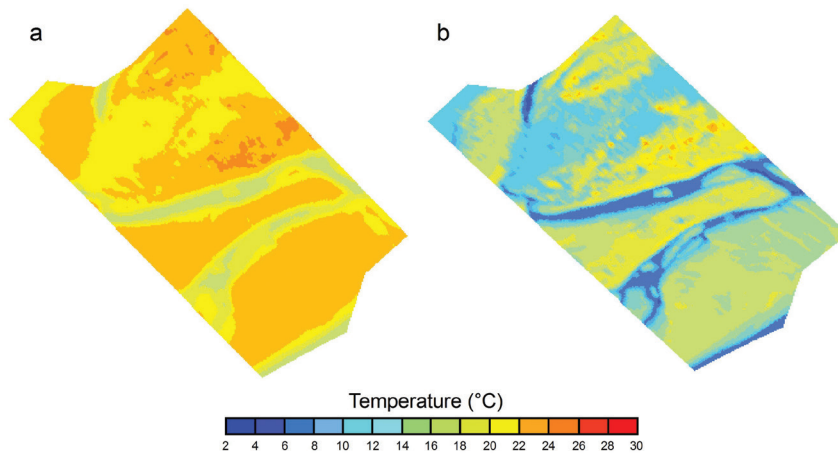


Figure 3. Thermal heterogeneity in river floodplains. Spatial patterns of (a) average daily surface temperature and (b) diel temperature range across the floodplain of the Tagliamento River in northeastern Italy. The average daily temperature across the floodplain was 16.6°C–24.7°C, and the diel temperature range was 4.9°C–24.4°C. Modified from Tonolla and colleagues (2010). Abbreviation: °C, degrees Celsius.

Wavelet decomposition (Steel et al. 2007, 2016) and Fourier analysis (Maheu et al. 2016a) provide mathematical methods for extracting and modeling variability over time; the resulting parameters can then be compared across locations or modeled over space.

A need for refined terminology. Envisioning moment-to-moment and meter-to-meter changes in water temperature is often hampered by imprecise terminology. The term water temperature implies a value or a state such as 3.2°C and has its roots in the fairly simple ways we began measuring water temperature—one person, one place, and one thermometer at a time. Thus, the term *water temperature* is a description of a single value, anchored in space and time. For example, “the water temperature was 6.7°C in the center of the pool at river km 26, at 16:00 on 24 August 2015.” To refer to the time series of data that describes water temperature in one place over time, we suggest relying on the commonly used term *thermal regime*. When spatial variation is added to the picture, we describe water temperature patterns fluctuating over time and varying on the river network (supplemental materials 1, 2, and 3) as a *thermal landscape*.

Thermal complexity has traditionally been summarized through the use of metrics such as mean or maximum temperatures; however, aquatic organisms experience far more than means and maxima. They live in microclimates, distributed over space and varying in time (Ward and Stanford 1982). Examination of data from the Sauk River floodplain, Washington, United States (figure 1), reveals that the mean of all values within a time series of temperature measurements captures only a part of the important signal in the data and, furthermore, that the mean over the floodplain would capture little if any of the important information about the spatial distribution of thermal habitats. Mean temperatures

are clearly important descriptors of the thermal landscape, but they describe only one aspect of the biologically and ecologically relevant information. The proliferation of fine-scale water-temperature data in the last decade now provides the opportunity to calculate summary statistics, such as variability within a time window, mean daily range, variability in extremes, or longitudinal thermal profiles, that describe temporal fluctuations and spatial diversity in water temperature (Fullerton et al. 2015, Steel et al. 2016, Tsang et al. 2016).

In exploring the potential impacts of climate change, Garcia and colleagues (2014) described how alternative dimensions of climate change may be summarized by metrics that each have particular implications for biodiversity and other ecological phenomena. Similarly, it is challenging to identify and quantify the

aspects, or facets, of the thermal landscape that are biologically and ecologically relevant. Poff and colleagues (1997) introduced the concept of a *natural flow regime* to capture the magnitude, frequency, duration, timing, and rate of change of the natural dynamics of riverine flows. Thermal regimes share these same components, which are distributed on river networks. Unlike flow in natural systems, which primarily accumulates downstream and has indirect impacts on biota through its effects on physical habitat, water temperature may increase or decrease as it moves downstream (Fullerton et al. 2015) and has direct effects on fundamental levels of biological reactions.

We define a *facet* of the thermal landscape as a particular spatial or temporal element of interest within a thermal landscape. Every component of the thermal regime, such as magnitude, duration, or frequency, has potential ecological consequences (table 1). For example, the facet of the thermal regime most closely related to mayfly emergence phenology is temperature experienced after egg deposition (Li et al. 2011). To capture this facet, we define a mathematical metric such as “number days after 20 July until 1075 degree-days are accumulated.” An analysis focused on the juvenile life stage of stream-rearing salmonids might require information about sudden increases in temperature that trigger juvenile migration from mainstems to cooler tributaries. Such a facet could be captured with “day of the year at which daily range first exceeds 5°C” or perhaps “day at which maximum daily temperature first exceeds 20°C.” Because the exact threshold or the exact time frame linking temperature and biological response is often unknown, multiple mathematical formulations, such as metrics, may be used to capture a particular facet. The best metric to be used in any analysis will depend on the question being considered and therefore the facet of interest (table 1). In addition, the specific metric with the

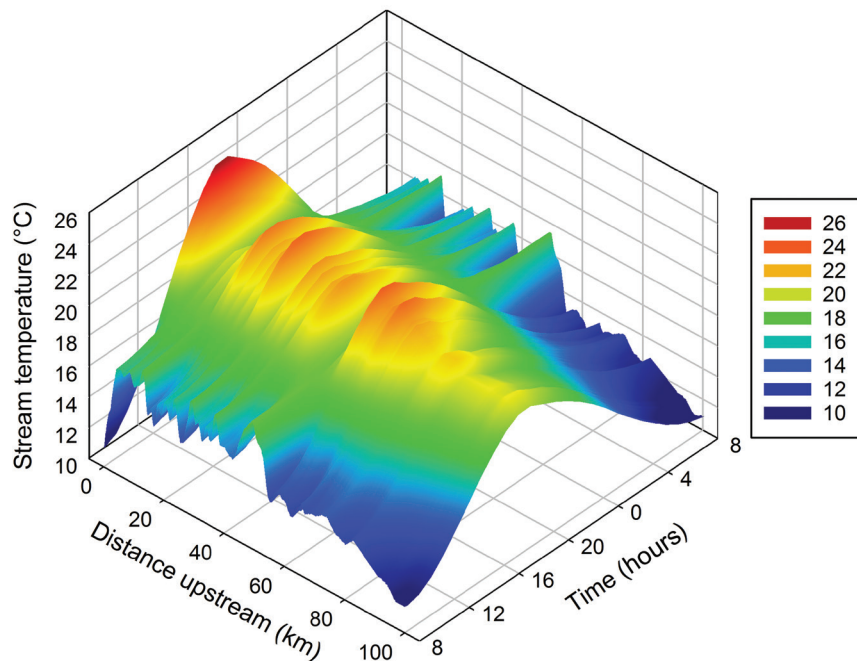


Figure 4. Stream-temperature estimates, based on a combination of thermal infrared data and stationary loggers, for approximately 100 kilometers (km) of the main stem of Big Hole River, Montana, United States, for a 24-hour time period beginning at 8:00, 20 July 2008. Spatial heterogeneity is greatest at daily maxima and minima. Modified from Vatland and colleagues (2015). Abbreviation: °C, degrees Celsius.

best correspondence to biological phenomena or human actions across a range of investigations will help researchers understand exactly which facet of the thermal landscape matters to a specific species or how the thermal landscape may respond to future climates and human actions.

The spatial distribution of facets on the stream network may be stable over time or may vary daily or seasonally. For example, on the Snoqualmie River, Washington, United States, gradients of mean temperatures were very similar in summer and winter, but gradients in temperature variability were reversed in the two seasons (figure 5; Steel et al. 2016). Downstream areas that are relatively warmer in summer have relatively low variability compared with upstream areas. In winter, these same areas are still relatively warmer but are more variable than the upstream reaches. We can describe this and similar phenomena as facets distributed on the stream network in configurations that shift over time. Thermal habitats may be arranged in spatial configurations that are adequate for one life stage (e.g., juvenile salmonid moving between feeding areas during summer) but not for another (e.g., adult salmonids migrating upstream during autumn). When considering lateral variability in water-temperature patterns across even one small floodplain, similar phenomena can be observed. In box 1, we use 8 years of data collected every 30 minutes across a natural floodplain of the Sauk River, Washington, United States, to explore seasonal

shifts in correlation between multiple facets of the thermal regime.

Emerging understanding

New data, models, and conceptual frameworks are providing insights into the biological implications of both temporal and spatial variability in water temperature patterns as well as illuminating ways in which humans have altered and are continuing to alter thermal landscapes.

The biological importance of thermal variability in time. Temperature regulates metabolism in aquatic biota, determining growth, phenology, and survival and ultimately driving food webs and community structure in aquatic ecosystems (Caissie 2006, Webb et al. 2008). Individual reactions to temperature are often summarized by thermal performance curves; however, these are typically defined under static laboratory conditions and may not be indicative of how organisms are likely to respond to natural or altered patterns of thermal variability (Dowd et al. 2015).

Evidence is mounting that biological and ecological reactions to thermally fluctuating environments will differ from

expectations based on mean temperature alone (Vasseur et al. 2014). Given that enzymatic reactions to temperature are generally nonlinear (Brown et al. 2004) and that temperature performance curves for most species are also nonlinear (Vasseur et al. 2014), variation that is symmetric about the mean generates disproportionate effects of relatively cooler times and relatively warm times. This phenomenon is well understood in statistics and captured using Jensen's inequality (Ruel and Ayres 1999). *Jensen's inequality* ensures that the mean outcome of a nonlinear reaction that occurs at multiple temperature values will not be equal to the value of the outcome of that same nonlinear reaction occurring at the mean temperature. Pioneering work in terrestrial ecology is demonstrating such effects. For example, Estay and colleagues (2011) showed that flour beetles (*Tribolium confusum*) exposed to increased thermal variability have a reduced maximum reproductive rate.

Experimental evidence has also demonstrated that seasonal shifts in temperature as well as smaller daily fluctuations in rivers do have consequences beyond those predicted from mean temperatures alone or from degree-day models. Conventional degree-day models assume that organisms respond to accumulation of temperature units in a predictable pattern, regardless of how those temperature units are delivered; however, Steel and colleagues (2012) found that altered variance alone (with relatively little

Table 1. The five main components of thermal regimes, examples of some presumed or documented facets of biological or ecological importance, and example metrics to capture each facet.

Components of a thermal regime	Facet of biological or ecological importance	Example metric
Magnitude	Differences in mean temperature across river systems contribute to determining which species are present and which are absent	Daily mean temperature in summer
	The mortality of fish, amphibians, and invertebrates occurs above lethal thresholds	Mean of the 7-day maximum in August
	Reduced metabolic rate leads to reduced growth rates	Mean daily minimum temperature from April to October
	Accumulation of degree-days drives egg development and emergence timing	Accumulation of degree-days between 15 September and 15 March
Frequency	Species-specific differences in response to high temperatures provide preferential advantages to particular species	Number of days over 20°C during the hydrologic year
	Reduction in growth rate from low temperatures may influence individual fitness	Number of days below 0°C after 1 March
Duration	Accumulated stress may trigger migration and other major life-history transitions	Longest number of days with mean daily temperatures above 15°C
	The local distribution of predators and prey is partially regulated by individual small movements to maximize growth potential	Total number of days in a year with mean daily temperature below 5°C
	Pathogens may require long periods of warm, stable temperatures	Maximum number of consecutive days with mean daily temperature above 5°C and daily range below 2°C
Rate of change	Fast temperature shifts may cause individual stress, increasing susceptibility to disease	Mean diurnal temperature range in summer
	Rate of warming may alter developmental stage at emergence and/or shift timing of emergence	Variability in thermal regime at timescales between 1 day and 1 year as quantified by wavelet coefficients
	The competitive advantage of one species over another may be determined by conditions in both summer and winter	Difference between mean temperature in August and mean temperature in February
Timing	Seasonal thermal patterns determine whether emergence occurs before, after, or during high-flow events	Julian date at which a particular number of degree-days has been accumulated
	Seasonal thermal patterns can determine reproductive timing	Number of days after maximum flow at which temperatures first exceed a particular threshold
	Organisms may have evolved a reduced metabolic demand during parts of the annual cycle when fewer food resources were available	Julian date at which the lowest 30-day minimum temperature begins

change to the daily mean temperature) could lead to a difference in emergence timing of nearly a week in streams with winter temperatures averaging 3°C. Additional observations of the influence of fluctuations in water temperature on phenology have been made across a wide range of aquatic species (table 2). Fluctuating water temperature regimes may alter growth patterns, reproductive rates, disease resistance, and community structure in aquatic environments (table 2).

The impacts of thermal variability may ripple through food webs. Increases in variability are understood to destabilize aquatic communities through reduced predictability (Waples et al. 2009); reductions in natural patterns in variability may also have negative consequences (table 2). Vinson (2001) observed differences in response to altered patterns of water release over a dam between a macroinvertebrate community that benefited from a tributary providing a naturally variable thermal regime and a community that did not. Other facets of the thermal regime may also play a role in structuring aquatic communities. Li and colleagues (2011) found asynchronous emergence of male and female aquatic insects under warmer conditions. Fish assemblages

across European rivers are correlated not only with the mean temperature of the warmest quarter of the year but also with the maximum temperature of the warmest month (Pletterbauer et al. 2014). Given the strong link between water temperature and phenology, there is even the potential for thermal regimes to contribute to evolution in salmonids (Angilletta et al. 2008). Dams can shift the seasonal timing of warmer and cooler waters, potentially inducing fish emergence just before high flows when survival would be low. These changes create the potential for increased genetic fitness of early spawning salmon or of rapid development from egg to emerging fry (Angilletta et al. 2008, Crozier and Hutchings 2014).

The biological importance of thermal diversity in space. Intricate spatial patterns in water temperature within reaches (Torgersen et al. 1999, 2012), across floodplains (Tonolla et al. 2010), on stream networks (Isaak et al. 2015), and across watersheds (Fullerton et al. 2015, Woltemade 2016) define thermally diverse natural river systems across space. The spatial complexity of geomorphic, hydrologic, and

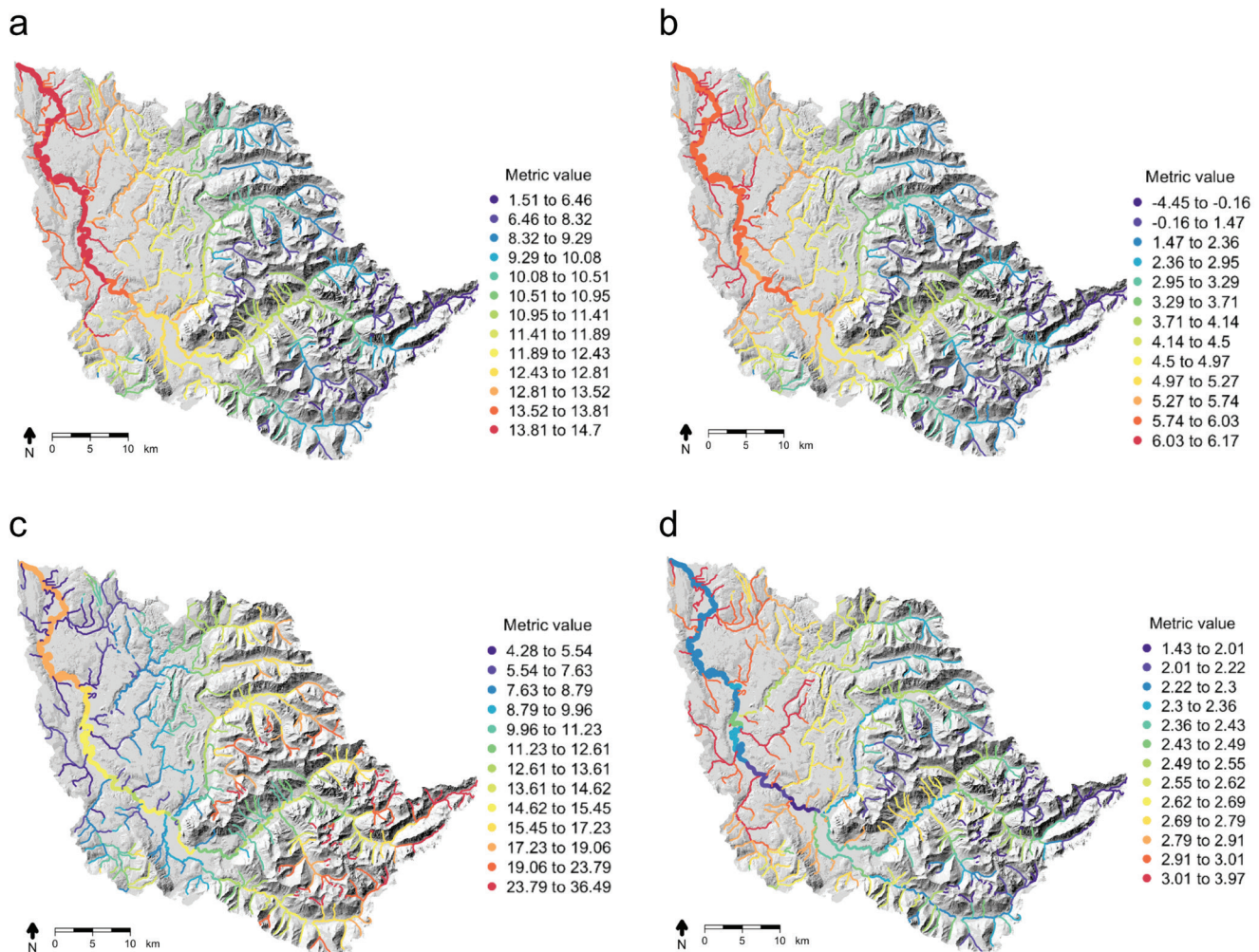


Figure 5. The modeled mean temperature (a and b) and thermal variance (c and d) over summer (a and c) and winter (b and d) across the Snoqualmie River watershed in western Washington, United States. The modeled temperatures are from a spatial stream-network model (Peterson et al. 2013) that included three covariates (elevation, mean annual flow, and percentage of commercial land use), used a tail-up exponential moving-average spatial-correlation structure, and applied a streamflow-based spatial weighting scheme. (modified from Steel et al. 2016). Panels describe stability and instability in spatial distribution of thermal metrics across seasons: (a) mean temperature in summer, (b) mean temperature in winter, (c) temperature variance in summer, and (d) temperature variance in winter. Abbreviation: km, kilometers.

riparian features in natural riverine landscapes promotes a highly varied thermal network that provides aquatic organisms with options for moving among thermal habitats in order to maximize growth, reproduction, and survival. This spatial thermal diversity influences species interactions at population, subpopulation, and individual levels. Exploring microbial respiration, the foundation of aquatic ecosystems, Jankowski and colleagues (2014) determined that community respiration was controlled by stream temperature and that spatial variation in how watersheds sequester and release carbon across the Wood River basin, Alaska, United States, was therefore related to geomorphic differences across watersheds. They note that their work considered only differences in mean temperature across treatments and

suggest that a more complex experimental design could be used to capture more realistic thermal regimes.

Spatial heterogeneity across thermal networks results in a patchwork of aquatic ecosystem properties and comprises the range of conditions to which species have adapted in the absence of humans (McCullough et al. 2009). In Europe, the concept of fish zones—that is, areas of a watershed in which particular fish assemblages are expected—is a well-established concept used to describe predictable shifts in aquatic communities across thermal gradients (Matulla et al. 2007). Fish and other aquatic organisms use spatial thermal diversity to maximize growth and reproduction by moving among cold and warm environments (Armstrong et al. 2013, Brewitt and Danner 2014). Spatial diversity in

Box 1. Shifting correlations between temperature metrics by season, Sauk River, Washington, United States.

One simple way to describe the spatiotemporal complexity of thermal landscapes is to measure water temperature at multiple locations over time and observe correlations between metrics describing those thermal regimes. We measured water temperature every 30 minutes over years and across multiple channels of a relatively undisturbed floodplain on the Sauk River, Washington, United States. If we explore, for example, the relationship between average weekly average temperature (AWAT), a commonly used metric for describing mean temperature, and maximum weekly average temperature (MWAT), a commonly used metric for describing the maximum in summer (May–September), we see that the mean and maximum are highly positively correlated ($r = .87$) in summer. A similar pattern is observed in winter (November–March; $r = .85$; figure 6). However, relationships between average temperature and other metrics of thermal diversity shift across seasons. AWAT is weakly positively correlated with total variance of all observations (VAR) in summer ($r = .27$) but weakly negatively correlated with VAR in winter ($r = -.37$). Relationships between maximum temperatures and other aspects of the thermal regime also shift by season. VAR and the average daily range (AvgRg) are positively correlated with maximums in summer ($r = .65$), but these same measures are not correlated at all in winter ($r = -.1$ and 0). In other words, data on maximum temperatures can provide good estimates of variability in thermal regimes in summer, but this same summary of the data provides relatively little predictive power or understanding of thermal variability in winter. We conclude that relationships between metrics, and therefore facets, are not stationary over time. No one metric can capture all the biologically relevant information about a thermal regime.

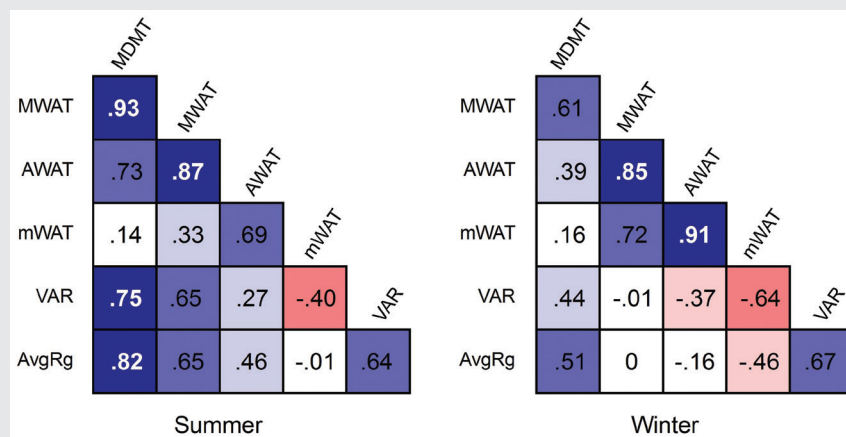


Figure 6. The correlations among six metrics of thermal diversity for summer (1 May–30 September) and winter (1 November–30 March): maximum daily maximum temperature (MDMT), maximum weekly average temperature (MWAT), average weekly average temperature (AWAT), minimum weekly average temperature (mWAT), total variance of all observations (VAR), and average daily range (AvgRg). Replicate observations of each metric included up to seven seasons of data at up to 16 reaches ($n = 106$) within one unmanaged and free-flowing 2-kilometer-long floodplain of the Sauk River, Washington, United States.

thermal regimes can lead to spatial diversity in the phenology of spawn timing in salmonids (Lisi et al. 2013), as well as spatial variation in the phenology of emergence timing for aquatic insects, because sufficient degree days for emergence are accumulated at different times throughout the thermal network. Such spatial patterns in the availability of aquatic food resources may lead to improved foraging opportunities for dependent terrestrial predators such as gulls and bears (Schindler et al. 2013).

Spatial diversity also provides patches of cooler or warmer water that can act as thermal refuges, which are important for survival when temperatures exceed upper or lower

tolerances (Torgersen et al. 1999). The use of cold water habitats as refuge during thermally stressful conditions has been well documented (Brewitt and Danner 2014, Keefer et al. 2015). With the recent public focus on increasingly stressful summertime water temperature in streams (Johnson K 2015), natural-resource management agencies in the United States have been grappling with how to define, measure, and conserve connectivity among thermally suitable habitats for species of conservation or economic concern. The functional value of thermally suitable habitat patches depends on whether they are adequately connected in time, on multiple biological factors (e.g., species, life stage, and predators), and

Table 2. Biological and ecological impacts of thermal variability across a range of response types, organisms, and life stages, with examples of specific studies.

Response type	Organism	Life stage	Examples of specific studies
Phenology	Midge <i>Chironomid</i>	Emergence	Diel patterns of emergence linked to diel fluctuations in temperature (Ward and Stanford 1982)
	Amphibians <i>Hynobius tokyoensis</i> ; <i>Rana ornativentris</i> ; <i>Rhacophorus arboreus</i>	Breeding	Earlier breeding with increasing mean monthly temperature in month directly preceding breeding season (Kusano and Inoue 2008)
	Yakima River hatchery Chinook salmon <i>Oncorhynchus tshawytscha</i>	Eggs and fry	Emerged later and more developed with unnatural daily and seasonal variability; emerged having accumulated fewer degree-days with natural daily and seasonal variability as opposed to more stable thermal regimes with similar average temperatures (Steel et al. 2012)
Growth	Mosquito <i>Anopheles quadrimaculatus</i> Say	Immature	Increased developmental speed with fluctuating temperatures; degree of increased developmental speed depended on pattern of fluctuations (Huffaker 1944)
	Water boatman <i>Sigara alternata</i>	Eggs; adults	Development rates linked to diel fluctuations (Sweeney and Schnack 1977)
	Snake River fall Chinook salmon <i>Oncorhynchus tshawytscha</i>	Juvenile	Reduced growth with fluctuating temperatures (Geist et al. 2010)
Disease susceptibility	Amphibians	All	Some aspects of immunity to disease in amphibians are suppressed at low temperatures and others are likely stable or even enhanced at low temperatures; unclear how variability in temperature regimes influences immunocompetence in amphibians (Blaustein et al. 2010)
Community Composition	Macroinvertebrates	All	Loss of taxon richness with reduced thermal variability (Vinson et al. 2001)

on the surrounding physical environment (e.g., dissolved oxygen, availability of food, and cover). Reductions in thermal diversity over space can lead to reduced opportunities for aquatic species to complete local migrations to favorable habitats and the loss of thermal refuges necessary for survival during thermal extremes (Ebersole et al. 2003).

Human alteration of thermal landscapes. Human actions and a changing climate have and will continue to increase mean water temperatures (Hester and Doyle 2011) and the likelihood of extreme warm events (Markovic et al. 2013, Kurylyk et al. 2014, Orr et al. 2015). The types of human activities that alter water temperature patterns are numerous (figure 7). Globally, few rivers remain untamed and unmanaged (Dynesius and Nilsson 1994), and, as more fine-scale data become available, it is clear that the impact of such human activities on thermal landscapes extends well beyond increasing means and maximums.

Major challenges to understanding the full range of human influence on riverine thermal landscapes are that activities can both exaggerate or dampen spatial and temporal variation and that changes might occur for one facet and not another. Often, these changes are challenging to assess because natural patterns were not documented. Land conversion (box 2), upland forest harvest (box 2), riparian forest harvest (Johnson SL 2004), water withdrawals, impoundment, urbanization (Somers et al. 2013, Hathaway et al. 2016), and channelization each influence spatial and temporal variability in water temperature. Dams, for example, have likely altered many facets of the thermal landscape at a range of

temporal scales (Steel and Lange 2007, Olden and Naiman 2010) and in particular seasons or time windows (Maheu et al. 2016b). Maheu and colleagues (2016b) found that small- and medium-sized storage dams in eastern Canada increased winter temperature variability as compared with reference sites. In a study of urbanized watersheds in Australia and the United States (Hathaway et al. 2016), urbanization influenced thermal variability, but that effect varied with catchment size. In addition, in a shading experiment, Johnson (SL 2004) found that maximum temperatures were reduced with experimental shade whereas means and minimums were less affected. Clearly, changes may occur in one facet and not in others (e.g., box 2). We might, for example, observe that a particular activity increases mean temperature only during the warmest months or only in downstream reaches, leads to no change in mean temperature but an increase in diel range during a particular life stage, or leads to a decrease in mean temperature with a reduction in spatial heterogeneity across habitat units. Any of these effects would be missed or misrepresented if data were collected at one time or place or at coarse spatiotemporal scales or if fine-scale data were summarized only as daily or reach means. New data and tools therefore play a key role in identifying the facets of the thermal landscape most closely tied to a particular human activity or suite of activities, improving our ability to measure the influence of human development and to mitigate the most deleterious effects.

Climate change is shifting thermal variability at multiple timescales (Kaushal et al. 2010) as well as across space. The impacts of these changes in spatiotemporal variability

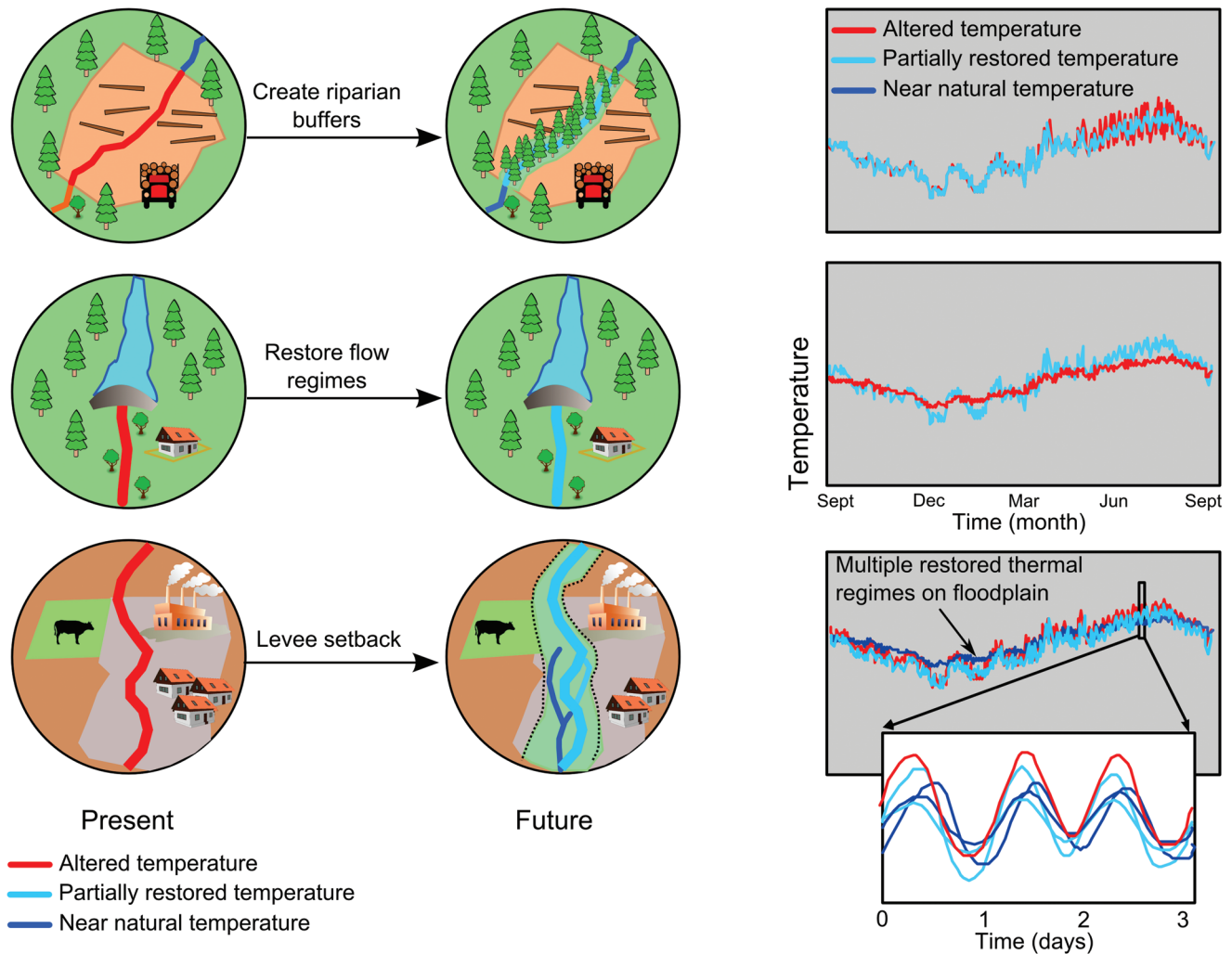


Figure 7. The left column describes common anthropogenic alterations to thermal regimes, including logging or other riparian vegetation removal that increases diurnal temperature range and summer maxima, dams that dampen both seasonal and daily variation, and loss of floodplain habitats, which decreases reach-scale spatial variation. The center column describes a suite of coordinated restoration actions across an entire watershed with the potential to restore key elements of natural thermal regimes, including natural seasonal cycles, daily variation, watershed-scale patterns, and small-scale thermal refuges. Restoration actions include managing riparian buffers to promote shade, partially restoring thermal regimes below dams by restoring key environmental flow attributes, and restoring floodplain connectivity to recreate spatial variation in temperatures among the main channel and floodplain channels. The right column contrasts natural, altered, and partially restored thermal regimes in headwaters, midreaches, and downstream reaches as may be expected given the anthropogenic alterations and restoration actions depicted to the left.

on fish and other ectotherms are predicted to be as big as or bigger than those of increasing mean temperatures (Paaijmans et al. 2013, Vasseur et al. 2014). For example, although river and groundwater temperatures have both warmed (Kaushal et al. 2010), the pattern has not been consistent over space. Warming has occurred in some seasons but not others (Isaak et al. 2012) and in some streams but not others (Arismendi et al. 2012). In a study of streams in Pennsylvania, United States, thermal sensitivity to warming air temperatures also varied over space (Kelleher et al. 2012), and in a long-term study of Austrian rivers, increases

in mean temperature were observed for streams draining lakes and sites on the mainstem Danube River, whereas little or no change in mean temperature was observed on smaller streams fed by glacier and snow melt (Webb and Nobilis 1995). Many temporal facets of the thermal landscape with strong ties to aquatic biota are also likely to change in the future. In the Elbe and Danube Rivers, a phase shift of almost 2 weeks, an increase in the number of days with maximum river temperatures over 25°C, and an increase in the duration of periods thought to cause heat stress to fish are all predicted (Markovic et al. 2013). Some of the most

Box 2. Correlations between human development, landscapes, and thermal regimes in the Willamette River basin, Oregon, United States.

Is there evidence that human development or other landscape features influence variability in water temperature at particular timescales? We used wavelet decomposition, a method for partitioning a time series of data to estimate variability that occurs independently at each of several timescales, to assess correlations between landscape predictors and variability in water temperature across the Willamette River basin, Oregon, United States. Temperature data were obtained from US Geological Survey gages across the basin for all available years. The longest available time series that maximized both the number of sites with daily water-temperature data ($n = 12$) and the length of a near-continuous time record (fewer than 5 days missing) was 11 April 1976 to 4 February 1977. Wavelet decomposition was performed on each time series at timescales ranging from 1 to 32 days, with higher values of wavelet coefficient variance indicating more variability at a particular timescale. The area upstream of each gage was delineated using a geographic information system; land cover and geology, hydrologic regime, and climate were summarized across the watershed. Simple linear regressions were built to describe how well log-transformed wavelet coefficient variances for each scale could be estimated from the landscape-scale covariates. Models were fit independently for each landscape scale covariate and at each temporal scale.

We identified some fairly strong relationships between water-temperature variability and landscape predictors (figure 8); more interestingly, the strength of these relationships depended on whether we were considering temperature fluctuations at daily versus weekly or monthly timescales. The percentage of the watershed that was forested, the percentage of the watershed with rain-on-snow-dominated hydrology, and the maximum air temperature, for example, were strongly correlated with monthly variance in water temperature but only weakly correlated with water temperature at shorter temporal scales. The percentages of agriculture, urban, sandstone geology, and floodplain in the watershed were most strongly correlated with water temperature at 1- and 2-day timescales, although each variable also had a strong relationship with water temperature at monthly timescales (figure 8). Our results suggest that human actions, such as forest harvest or urbanization, which are understood to affect mean and maximum temperatures, also influence other facets of the thermal regime but to different degrees depending on timescale and other factors.

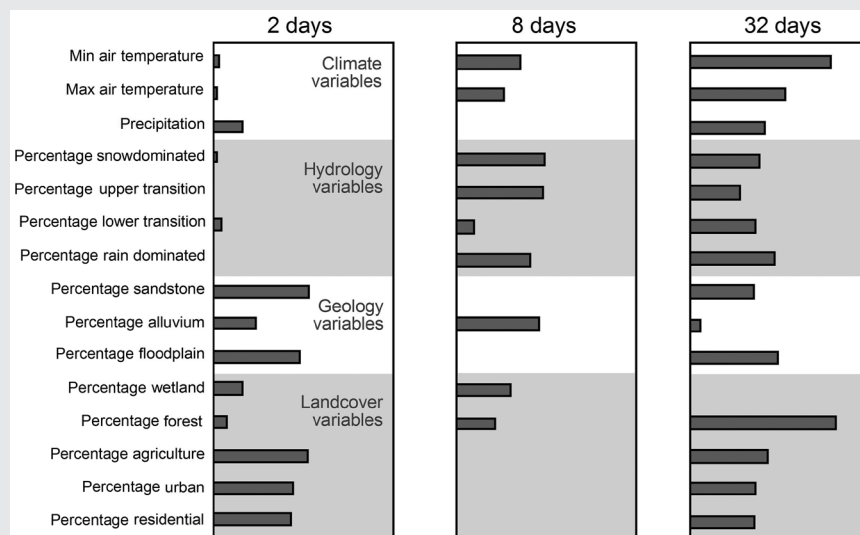


Figure 8. The R-squared values for each independent simple linear regression of landscape-scale predictors on log-transformed wavelet coefficient variances of water temperature within the Willamette River basin, Oregon, United States.

dramatic signals of warming temperatures have occurred for minimum temperatures. In the Pacific Northwest in the United States, where salmonid eggs are incubating during winter, there have been fewer and less dramatic cold spells, with a concurrent reduction in daily range and thermal variability (Arismendi et al. 2013).

Many regions of the globe are not as well studied. The combination of rapid development and climate change in developing or recently developed areas generates risks of habitat loss, biodiversity loss, and reductions in food security; however, the lack of baseline data on environmental conditions, species distributions, and physiological

vulnerabilities makes predictions of changes in riverine thermal regimes and the biological impacts of those changes challenging, if not impossible (Williams et al. 2016). As climate models that can reproduce precipitation, solar radiation, and other hydroclimatological variables become available (e.g., Oguntunde et al. 2016), researchers will need to explore the predicted impacts of climate change on riverine thermal regimes across a wider range of ecological systems and consider the consequences of shifting patterns of thermal variability on inland fisheries globally.

Needs and opportunities

An enriched understanding of the ecological value of temperature variation over time and space provides an opportunity to fine-tune management actions for the conservation of riverine ecosystems. Actions to improve the management of thermal landscapes may range from shifts in how we communicate water-temperature patterns to answering emerging research questions, improving current monitoring programs, protecting and restoring the processes that lead to thermal complexity, and revising regulatory definitions of what constitutes a healthy river.

Communicating the importance of thermal variability and diversity. Conservation of aquatic resources can be improved by simple shifts in communication. Although scientists have measured “thermal regimes” for decades, we often use the short-cut term “water temperature” when speaking with generalist audiences, and we rely on examples of lethal thresholds or relationships between growth and mean temperature to convey the importance of temperature in regulating aquatic ecosystems. We can improve communication by being more explicit about metrics and indicators that are best suited to answering particular questions (table 1; Helmuth et al. 2014). In addition, images as simple as a line graph of a messy time series (e.g., figure 1) or as complicated as high-resolution thermal infrared images (e.g., figure 2) and videos (e.g., videos S1–S3) can convey the fluctuations over time and patchiness over space that characterize natural thermal regimes to students, managers, conservation groups, policymakers, and the general public. To articulate our emerging understanding of thermal complexity, we can use terms such as thermal variability and diversity, thermal regimes on river networks, and thermal landscapes.

Linking human impacts to thermal landscapes and thermal landscapes to biotic responses. Fine-scale data and models of spatiotemporal complexity in thermal landscapes have opened the door to exciting research opportunities. We need to better understand the drivers of complexity in thermal landscapes across multiple temporal and spatial scales, particularly in under-studied regions of the world. A second need is to more fully decipher the biological and ecological consequences of thermal variability by identifying links between facets of the thermal regime, particularly those that are rapidly changing, and specific biological responses. Research

on temporal variability might determine how particular facets of thermal regimes promote or constrain phenological diversity within species of interest or their prey. Research on spatial variability might focus on predicting where patches of cooler water are most likely to be found across varied ecosystems and how their configuration might influence species. Development of appropriate conservation strategies depends on accurate understanding of the potential range of ecological response to future changes in the thermal landscape. For example, how might predicted changes in thermal landscapes shift the balance between native and nonnative species? The third research need is to untangle relationships between anthropogenic actions and particular facets of the thermal landscape (e.g., figure 7). Without this understanding, we may unknowingly continue to degrade (or fail to restore) essential functions of riverine ecosystems.

Redesigning and improving water-temperature monitoring programs. Monitoring programs can provide comprehensive, fine-scale data sets to model and understand the thermal landscape and through which thermal variation, as it is experienced by individual organisms, can be estimated (*sensu* Dowd et al. 2015, Woods et al. 2015). Arrays of water-temperature loggers across river networks have been installed for a wide range of temperate rivers, and efforts to compile these data into publicly accessible databases have been successful (e.g., www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html); however, data are often collected at daily scales, summarized as daily means, maximums, and minimums or, even more simply, compiled as average weekly or monthly temperatures. Moreover, many monitoring stations are only active in the summer. The USGS provides publicly available water-temperature data at a subset of their flow gaging stations; these data may span an impressively long time period, but observations are frequently available only as daily summaries and at one mainstem location per river system. Data measured across a range of upstream tributaries are also necessary to capture spatial pattern, but tributary data can be challenging to collect because of limited access on private lands, rugged terrain, and remote locations.

Sensors are generally inexpensive to purchase and install, but a significant investment of time is required to maintain monitoring arrays during low-flow and high-flow conditions, as well as to clean (Sowder and Steel 2012) and archive temporally and spatially explicit data. Research is needed on the design of efficient monitoring systems for river networks, including the arrangement of monitoring arrays, data architecture, data-cleaning methods, and data-sharing protocols. Although there have been impressive recent developments in statistical methods to model phenomena on river networks, tools that can capture both spatial and temporal variability simultaneously are still needed; perhaps new tools will be able to synthesize not only disparate sources of data (Dodds et al. 2012) but also disparate types and scales of data. For example, to understand the spatial distribution of temperature across habitats and over time, continuous

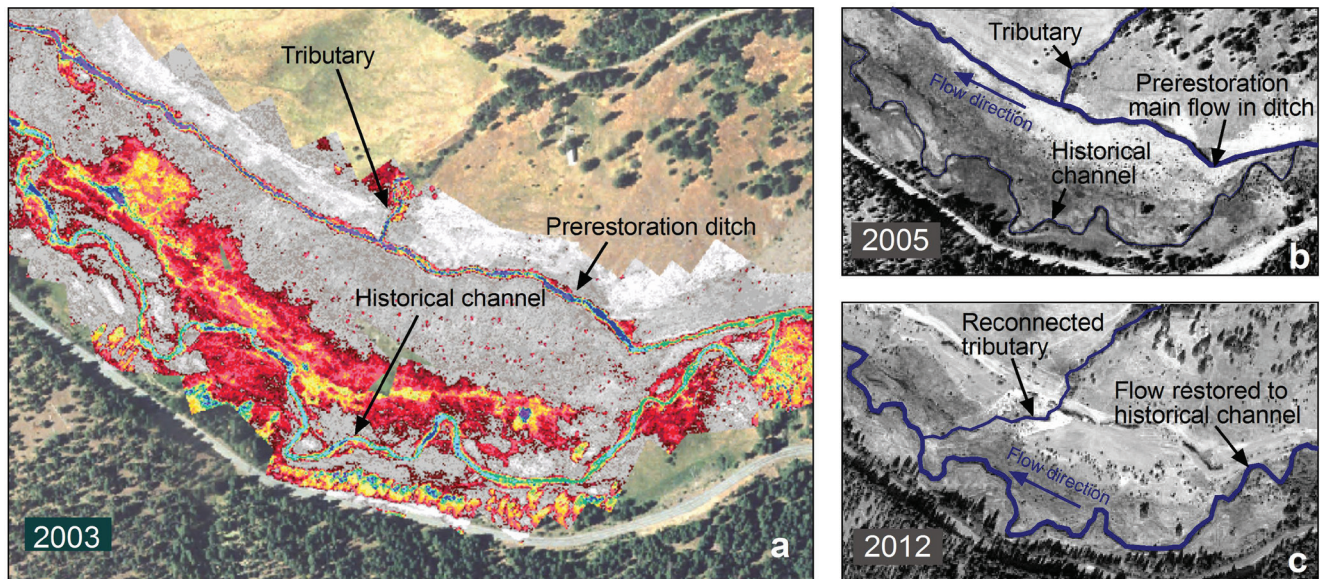


Figure 9. Floodplain restoration in the Oxbow Conservation Area of the Middle Fork John Day River, Oregon, United States, incorporated aerial thermal infrared imagery (a) and digital elevation models derived from LiDAR to guide channel placement in relation to subsurface-flow patterns. To create thermal diversity and cold-water refuges for aquatic biota, a cold tributary was reconnected to the floodplain and historical main channel; flow was redirected from an artificial channel (b) and restored to the historical stream channel (c) (Brian Cochran, Confederated Tribes of the Warm Springs Indian Reservation of Oregon, personal communication, 19 September 2011; Oxbow Conservation Area, Middle Fork John Day River Dredge Mining Restoration Project). Modified from Torgersen and colleagues (2012).

spatial monitoring could be combined with existing arrays of sensors at fixed locations.

Deploying in-stream sensors for an entire year (Arismendi et al. 2013), selecting sites that cover the range of environmental characteristics that are likely to influence facets of most interest (e.g., Jackson et al. 2016), archiving hourly or daily information in long-term data sets, installing temperature loggers in remote tributaries, and synthesis across disparate data types are some of the ways in which monitoring programs might be improved to better assess thermal landscapes. Increased empirical data will continue to reduce our reliance on modeled predictions, enable faster detection of anthropogenic change, and refine our conceptual model of thermal landscapes.

Protecting and restoring thermal landscapes. We can shape the future of thermal complexity in rivers through restoration actions that restore driving processes, ameliorate future effects of climate change and development, maintain connectivity, and increase resilience of riverine ecosystems (Beechie et al. 2013, Kurylyk et al. 2014). Supporting the natural pathways of water, wood, and sediment from tributaries to mainstem reaches will simultaneously create thermal diversity, surface-water and groundwater connections, and natural patterns of daily and seasonal temperature fluctuations. We propose that protection and restoration be focused on a few key aspects of water-temperature regimes. Without losing sight of the importance of mean temperature or the

risks of extreme temperatures, managers may also want to consider preserving or restoring natural (a) seasonal cycles in water temperatures, (b) daily variation in water temperature, (c) network-scale longitudinal patterns of water temperature, and (d) small-scale thermal refuges.

Stream restoration to create thermal diversity is still in the experimental stages but is increasingly being considered by water-resources managers (figure 9; Kurylyk et al. 2014). Although there are many restoration actions that affect the thermal landscape in particular ways (table 3), we describe in more detail three example actions to address altered variability in thermal regimes: restoring riparian areas, promoting natural flow regimes, and restoring connectivity. Restoring riparian shade generally reduces stream temperatures locally and also tends to reduce diel variation. Over-restoration through increased riparian plantings at a catchment scale has even been considered for the protection of global biodiversity hotspots where projected riverine thermal regimes will be intolerable and movement of endemic aquatic species is geographically constrained (Davies 2010). Restorative management of flows or of the temperature of water released from reservoirs can reduce stream temperatures and restore both diel extremes and seasonal patterns. Removal of dams or other migration barriers can not only restore flow and thermal regimes downstream of the dam but may also restore migratory pathways that allow fishes and other organisms to access a wider array of thermal regimes upstream

Table 3. Example effects of restoration actions on thermal landscapes.

Restoration action	Process effect	Change to spatial diversity	Change to temporal diversity
Remove bank stabilization or levees	Increase hyporheic exchange, floodplain connectivity, and habitat complexity	Increase spatial diversity and availability of thermal refuges	Increase diversity of thermal regimes
Riparian restoration	Increase shade, bank stability, and habitat complexity	Decrease patchiness in both mean and extreme temperatures	Local decreases in diurnal range
Dam removal	Restore natural flow and sediment regime; restore fish access to cooler temperature regimes at higher elevations	Increase availability of thermal refuges as sediment accumulates and hyporheic exchange is restored	Restore natural seasonal and diurnal variation downstream of dam site
Reduce water withdrawals	Increase stream flows particularly during the summer growing season	Increase off-channel habitats and thermal refuges	Decrease mean and maximum temperatures; decrease daily variability
Wood jam additions	Increase number of deep pools	Potential increase in thermal refuges or increase in spatial diversity of temperatures	Local decreases in diurnal range
Restore beaver dams or install beaver dam analogs	Increase beaver dams and associated pools; increase development of side channels and habitat complexity	Potential increase in thermal refuges, and spatial diversity of temperatures	Increases or decreases in thermal variability; reduce maximums

(Waples et al. 2009). Restoring lateral connectivity between a river and its floodplain (e.g., through levee removal) increases thermal diversity at the reach scale, both spatially and temporally (Tonolla et al. 2010). Where channels are incised into alluvial fills, re-aggrading the incised channel is expected to restore the alluvial aquifer, increase summer stream flows, and decrease summer temperatures (Beechie et al. 2010). Each of these types of restoration actions can contribute to restoring thermal diversity at small spatial scales, but conserving and restoring thermal regimes at the basin scale require a coordinated suite of restoration actions across a watershed (figure 7).

Managing for thermal complexity. Envisioning and embracing complexity require that we recognize our lack of understanding and identify solutions that are robust to that uncertainty (Ruel and Ayres 1999). Currently, the management of stream temperature tends to be driven by thresholds and standards that are based on mean and maximum temperatures; however, managers and decision-makers are recognizing that thermal diversity is needed to support healthy aquatic ecosystems. Across terrestrial systems, thermal variability is increasingly considered in assessments of climate impacts (Morelli et al. 2016). Aquatic systems are likely to benefit from similar approaches. For example, Isaak and colleagues (2015) provided regional predictions of future thermal landscapes based on August mean temperatures, and this approach could be expanded to provide regional-scale predictions of other facets of the thermal regime or even of uncertainty in future thermal regimes. The spatial distribution of variability likely differs from that of means and maxima; Detenbeck and colleagues (2016) created SSNMs of multiple facets of stream temperature across New England and were able to create strong models of growing season means and medians but were not able to explain as much of the spatial variation in diel fluctuations or in timing of maximum temperatures.

Management of rivers improved through an understanding and appreciation of their natural flow dynamics (Poff et al. 1997). The future of thermal diversity also depends, in part, on recognizing the role of temperature variability over both space and time in structuring healthy river systems that support fish and other organisms. The idea of managing for thermal complexity is not new. Poole and colleagues (2004) called for regime-based regulatory standards that (a) describe a desirable distribution of water temperatures over space and time, (b) can be applied at the watershed scale, and (c) account for interannual variation. Over the past decade, the daunting scientific and management challenges of designing and implementing such standards have not been met. A process-oriented approach to restoring thermal diversity (Ward et al. 2001) may ultimately achieve the aims of regime-based standards without limiting ourselves to one set of metrics by which to chart progress. Most importantly, maintaining a vision of thermal landscapes as a spatial mosaic of water temperatures, with each component fluctuating somewhat independently over time (videos S1–S3), can help scientists and managers guide the future of riverine ecosystems.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

References cited

- Angilletta MJ Jr, Steel EA, Bartz KK, Kingsolver JG, Scheuerell MD, Beckman BR, Crozier LG. 2008. Big dams and salmon evolution: Changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* 1: 286–289.
- Arismendi I, Johnson SL, Dunham JB, Haggerty R, Hockman-Wert D. 2012. The paradox of cooling streams in a warming world: Regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* 39 (art. L10401).
- Arismendi I, Johnson SL, Dunham JB, Haggerty R. 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. *Freshwater Biology* 58: 880–894.
- Armstrong JB, Schindler DE, Bentley KT, Brooks GT, Ruff CP, Torgersen CE. 2013. Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94: 2066–2075.
- Beechie TJ, Sear DA, Olden JD, Pess GR, Buffington JM, Moir H, Roni P, Pollock MM. 2010. Process-based principles for restoring river ecosystems. *BioScience* 60: 209–222.
- Beechie T, et al. 2013. Restoring salmon habitat for a changing climate. *River Research and Applications* 29: 939–960.
- Blaustein AR, Walls SC, Bancroft BA, Lawler JJ, Searle CL, Gervasi SS. 2010. Direct and indirect effects of climate change on amphibian populations. *Diversity* 2: 281–313.
- Brewitt KS, Danner EM. 2014. Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. *Ecosphere* 5 (art. 92).
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 130–137.
- Caissie D. 2006. The thermal regime of rivers: A review. *Freshwater Biology* 51: 1389–1406.
- Cardenas MB, Doering M, Rivas DS, Galdeano C, Neilson BT, Robinson CT. 2014. Analysis of the temperature dynamics of a proglacial river using time-lapse thermal imaging and energy balance modeling. *Journal of Hydrology* 519: 1963–1973.
- Crozier LG, Hutchings JA. 2014. Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* 7: 68–87.
- Davies PM. 2010. Climate change implications for river restoration in global diversity hotspots. *Restoration Ecology* 18: 261–268.
- Detenbeck NE, Morrison AC, Abele RW, Kopp DA. 2016. Spatial statistical network models for stream and river temperature in New England, USA. *Water Resources Research* 52: 6018–6040.
- Dodds WK, et al. 2012. Surprises and insights from long-term aquatic data sets and experiments. *BioScience* 62: 709–721.
- Dowd WW, King FA, Denny MW. 2015. Thermal variation, thermal extremes and the physiological performance of individuals. *Journal of Experimental Biology* 218: 1956–1967.
- Dugdale SJ. 2016. A practitioner's guide to thermal infrared remote sensing of rivers and streams: Recent advances, precautions and considerations. *WIREs Water* 3: 251–268.
- Dugdale SJ, Bergeron NE, 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.
- Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753–762.
- Ebersole JL, Liss WJ, Frissell CA. 2003. Cold water patches in warm streams: Physicochemical characteristics and the influence of shading. *Journal of the American Water Resources Association* 39: 355–367.
- Estay SA, Clavijo-Baquet S, Lima M, Bozinovic F. 2011. Beyond average: An experimental test of temperature variability on the population dynamics of *Tribolium confusum*. *Population Ecology* 53: 53–58.
- Fullerton AH, Torgersen CE, Lawler JJ, Faux RN, Steel EA, Beechie TJ, Ebersole JL, Leibowitz SG. 2015. Rethinking the longitudinal stream temperature paradigm: Region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. *Hydrological Processes* 29: 4719–4737.
- Garcia, RA, Cabeza M, Rahbek C, Araújo MB. 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* 344 (art. 1247579).
- Geist D, Deng Z, Mueller R, Brink S, Chandler J. 2010. Survival and growth of juvenile Snake River fall Chinook salmon exposed to constant and fluctuating temperatures. *Transactions of the American Fisheries Society* 139: 92–107.
- Hathaway JM, Winston RJ, Brown RA, Hunt WF, McCarthy DT. 2016. Temperature dynamics of stormwater runoff in Australia and the USA. *Science of the Total Environment* 559: 141–150.
- Helmuth B, Russell BD, Connell SD, Dong Y, Harley CD, Lima FP, Sará G, Williams GA, Mieszkowska N. 2014. Beyond long-term averages: Making biological sense of a rapidly changing world. *Climate Change Responses* 1: 10–20.
- Hester ET, Doyle MW. 2011. Human impacts to river temperature and their effects on biological processes: A quantitative synthesis. *Journal of the American Water Resources Association* 47: 571–587.
- Huffaker CB. 1944. The temperature relations of the immature stages of the malarial mosquito, *Anopheles quadrimaculatus* Say, with a comparison of the developmental power of constant and variable temperatures in insect metabolism. *Annals of the Entomological Society of America* 37: 1–27.
- Isaak DJ, Wollrab S, Horan D, Chandler G. 2012. Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Climate Change* 113: 499–524.
- Isaak DJ, Young MK, Nagel DE, Horan DL, Groce MC. 2015. The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Climate Change Biology* 21: 2540–2553.
- Jackson FL, Malcolm IA, Hannah DM. 2016. A novel approach for designing large-scale river temperature monitoring networks. *Hydrology Research* 47: 569–590.
- Jackson FL, Hannah DM, Fryer RJ, Millar CP, Malcolm IA. 2017. Development of spatial regression models for predicting summer river temperatures from landscape characteristics: Implications for land and fisheries management. *Hydrological Processes* 31: 1225–1238.
- Jankowski K, Schindler DE, Lisi PJ. 2014. Temperature sensitivity of community respiration rates in streams is associated with watershed geomorphic features. *Ecology* 95: 2707–2714.
- Johnson K. 2015. Finding refuge for salmon, cold water preferred. *New York Times*. (11 April 2017; www.nytimes.com/2015/12/12/us/finding-refuge-for-salmon-cold-water-preferred.html?_r=1)
- Johnson SL. 2004. Factors influencing stream temperatures in small streams: Substrate effects and a shading experiment. *Canadian Journal of Fisheries and Aquatic Management* 61: 913–923.
- Kaushal SS, Likens GE, Jaworski NA, Pace ML, Sides AM, Seekell D, Belt KT, Secor DH, Wingate RL. 2010. Rising stream and river temperatures in the United States. *Frontiers of Ecology and the Environment* 8: 461–466.
- Keefer ML, Clabough TS, Jepson MA, Naughton GP, Blubaugh TJ, Joosten DC, Caudill CC. 2015. Thermal exposure of adult Chinook salmon in the Willamette River basin. *Journal of Thermal Biology* 48: 11–20.

- Kelleher C, Wagener T, Gooseff M, McGlynn B, McGuire K, Marshall L. 2012. Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes* 26: 771–785.
- Kurylyk BL, MacQuarrie KTB, Linnansaari T, Cunjak RA, Curry RA. 2014. Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). *Ecohydrology* 8: 1095–1108.
- Kusano T, Inoue M. 2008. Long-term trends toward earlier breeding of Japanese amphibians. *Journal of Herpetology* 42: 608–614.
- Leach JA, Olson DH, Anderson PD, Eskelson BNI. 2016. Spatial and seasonal variability of forested headwater stream temperatures in western Oregon, USA. *Aquatic Sciences* 1–17.
- Letcher BH, Hocking DJ, O'Neil K, Whiteley AR, Nislow KH, O'Donnell MJ. 2016. A hierarchical model of daily stream temperature using air–water temperature synchronization, autocorrelation, and time lags. *PeerJ* 4 (art. e1727).
- Li JL, Johnson SL, Sobota JB. 2011. Three responses to small changes in stream temperature by autumn-emerging aquatic insects. *Journal of the North American Benthological Society* 30: 474–484.
- Lisi PJ, Schindler DE, Bentley KT, Pess GR. 2013. Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. *Geomorphology* 185: 78–86.
- Maheu A, Poff NL, St-Hilaire A. 2016a. A classification of stream water temperature regimes in the conterminous USA. *River Research and Applications* 32: 896–906.
- Maheu A, St-Hilaire A, Caissie D, El-Jabi N. 2016b. Understanding the thermal regime of rivers influenced by small and medium size dams in Eastern Canada. *River Research and Applications* 32: 2032–2044.
- Markovic D, Scharfenberger U, Schmutz S, Pletterbauer F, Wolter C. 2013. Variability and alterations of water temperatures across the Elbe and Danube River Basins. *Climatic Change* 119: 375–389.
- Matulla C, Schmutz S, Melcher A, Gerersdorfer T, Haas P. 2007. Assessing the impact of a downscaled climate change simulation on the fish fauna in an Inner-Alpine River. *International Journal of Biometeorology* 52: 127–137.
- McCullough DA, et al. 2009. Research in thermal biology: Burning questions for coldwater stream fishes. *Reviews in Fisheries Science* 17: 90–115.
- McNysset K, Volk C, Jordan C. 2015. Developing an effective model for predicting spatially and temporally continuous stream temperatures from remotely sensed land surface temperatures. *Water* 7: 6827–6846.
- Morelli TL, et al. 2016. Managing climate change refugia for climate adaptation. *PLOS ONE* 11 (art. e0159909).
- Oguntunde PG, Babatunde JA, Lischeid G. 2016. A numerical modelling study of the hydroclimatology of the Niger River Basin, West Africa. *Hydrological Sciences Journal* 61: 94–106.
- Olden JD, Naiman RJ. 2010. Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater integrity. *Freshwater Biology* 55: 86–107.
- Orr HG, et al. 2015. Detecting changing river temperatures in England and Wales. *Hydrological Processes* 29: 752–766.
- Paaajmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, Murdock CC, Thomas MB. 2013. Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology* 19: 2373–2380.
- Peterson EE, et al. 2013. Modelling dendritic ecological networks in space: An integrated network perspective. *Ecology Letters* 16: 707–719.
- Pike A, Danner E, Boughton D, Melton F, Nemani R, Rajagopalan B, Lindley S. 2013. Forecasting river temperatures in real time using a stochastic dynamics approach. *Water Resources Research* 49: 5168–5182.
- Pletterbauer F, Melcher AH, Ferreira T, Schmutz S. 2014. Impact of climate change on the structure of fish assemblages in European rivers. *Hydrobiologia* 744: 235–254.
- Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. *BioScience* 47: 769–784.
- Poole GC, et al. 2004. The case for regime-based water quality standards. *BioScience* 54: 155–161.
- Ruel JJ, Ayres MP. 1999. Jensen's inequality predicts effects of environmental variation. *Trends in Ecology and Evolution* 14: 361–366.
- Schindler DE, Armstrong JB, Bentley KT, Jankowski KJ, Lisi PJ, Payne LX. 2013. Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters* 9 (art. 20130048).
- Somers KA, Bernhardt ES, Grace JB, Hassett BA, Sudduth EB, Wang S, Urban DL. 2013. Streams in the urban heat island: Spatial and temporal variability in temperature. *Freshwater Science* 32: 309–326.
- Sowder C, Steel EA. 2012. A note on the collection and cleaning of water temperature data. *Water* 4: 597–606.
- Steel EA, Lange IA. 2007. Using wavelet analysis to detect changes in water temperature regimes at multiple scales: Effects of multi-purpose dams in the Willamette River basin. *River Research and Applications* 23: 351–359.
- Steel EA, Tillotson A, Larsen DA, Fullerton AH, Denton KP, Beckman BR. 2012. Beyond the mean: The role of variability in predicting ecological impacts of stream temperature. *Ecospheres* 3 (art. 104).
- Steel EA, Sowder C, Peterson EE. 2016. Spatial and temporal variation of water temperature regimes on the Snoqualmie River network. *Journal of the American Water Resources Association* 52: 769–787.
- Sweeney BW, Schnack JA. 1977. Development, growth and metabolism of *Sigara alternata* (Say) (Hemiptera: Corixidae) in fluctuating thermal environments. *Ecology* 58: 265–277.
- Tonolla D, Acuña V, Uehlinger U, Frank T, Tockner K. 2010. Thermal heterogeneity in river floodplains. *Ecosystems* 13: 727–740.
- Torgersen CE, Price DM, Li HW, McIntosh BA. 1999. Multiscale thermal refugia and stream habitat associations of Chinook salmon in Northeastern Oregon. *Ecological Applications* 9: 301–319.
- Torgersen CE, Ebersole JL, Keenan DM. 2012. Primer for Identifying Cold-Water Refuges to Protect and Restore Thermal Diversity in Riverine Landscapes. US Environmental Protection Agency. Report no. EPA 910-C-12-001. (10 April 2017; www3.epa.gov/region10/pdf/water/torgersen_et_al_2012_cold_water_refuges.pdf)
- Tsang YP, Infante DM, Stewart J, Wang L, Tingly RW III, Thornbrugh D, Cooper AR, Daniel WM. 2016. StreamThermal: A software package for calculating thermal metrics from stream temperature data. *Fisheries* 41: 548–554.
- Turschwell MP, Peterson EE, Balcombe SR, Sheldon F. 2016. To aggregate or not? Capturing the spatio-temporal complexity of the thermal regime. *Ecological Indicators* 67: 39–48.
- Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, McCann KS, Savage V, Tunney TD, O'Connor MI. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B* 281 (art. 20132612).
- Vatland SJ, Gresswell RE, Poole GC. 2015. Quantifying stream thermal regimes at management-pertinent scales: Combining thermal infrared and stationary stream temperature data in a novel modeling framework. *Water Resources Research* 51: 31–46.
- Vinson MR. 2001. Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecological Applications* 11: 711–730.
- Waples RS, Beechie T, Pess GR. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? *Ecology and Society* 14 (art. 3).
- Ward JV, Stanford JA. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27: 97–117.
- Ward JV, Tockner K, Uehlinger U, Malard F. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research and Management* 17: 311–323.
- Wawrzyniak V, Piégay H, Allemand P, Vaudor L, Grandjean P. 2013. Prediction of water temperature heterogeneity of braided rivers using very high resolution thermal infrared (TIR) images. *International Journal of Remote Sensing* 34: 4812–4831.

- Webb BW, Nobilis F. 1995. Long term water temperature trends in Austrian rivers. *Hydrological Sciences Journal* 40: 83–96.
 - Webb BD, Clack PD, Walling DE. 2003. Water–air temperature relationships in a Devon river system and the role of flow. *Hydrological Processes* 17: 3069–3084.
 - Webb BW, Hannah DM, Moore RD, Brown LE, Nobilis F. 2008. Recent advances in stream and river temperature research. *Hydrological Processes* 22: 902–918.
 - Westhoff MC, Savenije HH, Luxemburg WM, Stelling GS, Van de Giesen NC, Selker JS, Pfister L, Uhlenbrook S. 2007. A distributed stream temperature model using high resolution temperature observations. *Hydrology and Earth System Sciences* 11: 1469–1480.
 - Williams GA, Helmuth B, Russell BD, Dong YW, Thiagarajan V, Seuront L. 2016. Meeting the climate change challenge: Pressing issues in southern China and SE Asian coastal ecosystems. *Regional Studies in Marine Science* 8: 373–381.
 - Woltemade CJ. 2016. Stream temperature spatial variability reflects geomorphology, hydrology, and microclimate: Navarro River watershed, California. *The Professional Geographer* 1–14.
 - Woods HA, Dillon ME, Pincebourde S. 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology* 54: 86–97.
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