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MODELING USA STREAM TEMPERATURES FOR STREAM BIODIVERSITY AND CLIMATE CHANGE ASSESSMENTS

by

Ryan A. Hill

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Watershed Science

Approved:

Charles P. Hawkins Major Professor	D. Richard Cutler Committee Member
David G. Tarboton Committee Member	Sarah E. Null Committee Member
Jiming Jin Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2013

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ABSTRACT

Modeling USA Stream Temperatures for Stream Biodiversity and Climate Change Assessments

by

Ryan A. Hill, Doctor of Philosophy

Utah State University, 2013

Major Professor: Dr. Charles P. Hawkins
Department: Watershed Sciences

Stream temperature (ST) is a primary determinant of individual stream species distributions and community composition. Moreover, thermal modifications associated with urbanization, agriculture, reservoirs, and climate change can significantly alter stream ecosystem structure and function. Despite its importance, we lack ST measurements for the vast majority of USA streams. To effectively manage these important systems, we need to understand how STs vary geographically, what the natural (reference) thermal condition of altered streams was, and how STs will respond to climate change. Empirical ST models, if calibrated with physically meaningful predictors, could provide this information. My dissertation objectives were to: (1) develop empirical models that predict reference- and nonreference-condition STs for the conterminous USA, (2) assess how well modeled STs represent measured STs for predicting stream biotic communities, and (3) predict potential climate-related alterations to STs. For objective 1, I used random forest modeling with environmental data from several thousand US Geological Survey sites to model geographic variation in nonreference mean summer, mean winter, and mean annual STs. I used these models

to identify thresholds of watershed alteration below which there were negligible effects on ST. With these reference-condition sites, I then built ST models to predict summer, winter, and annual STs that should occur in the absence of human-related alteration (r^2 = 0.87, 0.89, 0.95, respectively). To meet objective 2, I compared how well modeled and measured ST predicted stream benthic invertebrate composition across 92 streams. I also compared predicted and measured STs for estimating taxon-specific thermal optima. Modeled and measured STs performed equally well in both predicting invertebrate composition and estimating taxon-specific thermal optima (r^2 between observation and model-derived optima = 0.97). For objective 3, I first showed that predicted and measured ST responded similarly to historical variation in air temperatures. I then used downscaled climate projections to predict that summer, winter, and annual STs will warm by 1.6 °C - 1.7 °C on average by 2099. Finally, I used additional modeling to identify initial stream and watershed conditions (i.e., low heat loss rates and small base-flow index) most strongly associated with ST vulnerability to climate change.

(167 pages)

PUBLIC ABSTRACT

Modeling USA Stream Temperatures for Stream Biodiversity and Climate Change Assessments

by

Ryan A. Hill

Stream temperature in one of the most biologically important aspects of water quality, but we lack temperature information for the vast majority of streams within the USA. Stream temperature can be influenced by several types of landscape and waterway alteration including upstream urbanization, agriculture, and reservoir releases. Stream temperatures are also expected to be affected by climate change over the next century. We need to know how stream temperatures vary naturally, how they are influenced by human activity, and how they will respond to climate changes to effectively manage stream ecosystems. I used data from several thousand streams within the conterminous USA to build models that predict mean summer, mean winter, and mean annual stream temperature. These models predict temperatures at unmeasured streams as a function of both natural features and upstream watershed alteration. I then used these models to identify those streams with minimal thermal modification and built models to predict natural stream temperatures. These models were both accurate and precise. I then used these models to explore the degree to which watershed alteration affects stream temperatures.

To be useful, stream temperature models must represent the thermal environments of streams in a biologically realistic way. I therefore compared how well modeled and measured summer stream temperatures predicted stream invertebrate

distributions across 92 streams within the USA. Modeled and measured stream temperatures performed identically and were the most important predictors associated with the distributions of stream invertebrate species. Predicted and measure stream temperatures also produced very similar estimates of temperature preference for individual stream species.

There is great concern that climate change will alter stream temperatures over the next century. I assessed how well my models could predict climate-related alterations to stream temperature by examining how predicted and measured changes in stream temperature responded to changes in air temperature between the 1970s and the present. The response of predicted stream temperatures to climate variation was similar to that of observed stream temperatures. I then used climate projections to predict potential shifts in stream temperature by the end of the 21st century. My models predicted that stream temperatures will warm by about 1.7°C, on average by 2099.

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Ryan A. Hill

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CHAPTER 1

INTRODUCTION

Temperature is a fundamental characteristic of all ecosystems that influences both ecological structure and function (Brown et al. 2004). Most organisms that live in streams and rivers are ectothermic, meaning their internal temperatures, and hence metabolisms, are dictated by their external thermal environment (Vannote and Sweeney 1980). Stream temperature (ST) determines the distributions of individual species and structures whole community composition (Hawkins et al. 1997, Haidekker and Herring 2008) through its influence on development, growth, size, phenology, reproduction and fecundity, and mortality (Vannote and Sweeney 1980, Ward and Stanford 1982). Thus, accurately quantifying geographic variation in ST is critical for predicting and understanding macro-ecological patterns in stream biodiversity. Despite the biological importance of ST, the vast majority of streams within the conterminous USA lack temperature measurements. In addition, the thermal conditions of many streams with temperature data have been altered by human activity, such as urbanization, agriculture, and reservoir storage and release. The general lack of temperature records at most streams, coupled with the thermal alteration that has occurred at many streams, makes it difficult to understand and assess what the natural thermal state of streams should be in the absence of human-related alteration, i.e., the thermal reference condition (Stoddard et al. 2006). Stream temperatures are also expected to respond to climate changes over the next century. To improve assessment and management of these systems we need the ability to quantify and predict current reference-condition temperatures of streams and predict stream-specific responses of ST to climate change. Models that predict site-specific reference-condition ST could provide this ability. In chapter 2, I develop models for predicting mean summer, mean winter, and mean

annual STs across a broad range of environmental conditions for the conterminous USA. In chapter 3, I assess how ecologically realistic modeled STs are relative to measured STs for predicting the stream benthic invertebrate assemblage composition of 92 reference-condition streams. Finally, in chapter 4, I use the ST models to estimate potential climate-related alterations in ST by the end of the 21st century and explore why some streams will be more vulnerable to climate change than others. Here, I briefly provide background and rationale for each chapter.

Many approaches exist for modeling ST and these approaches range greatly in their complexity, physical realism, temporal and spatial scales, and purpose. Deterministic models predict ST by accounting for heat exchange processes across the stream surface and bed (Caissie 2006). Due to this physical realism, deterministic models can be used to explore management scenarios for mitigating ST alteration (Null et al. 2010). Deterministic models differ in terms of the complexity of heat transport mechanisms that are used and the numbers and types of environmental parameters that are required for model development. However, deterministic models are generally data and labor intensive to develop, limiting their use in regional surveys of thermal condition where numerous streams must be assessed. Empirical ST models have been developed as an alternative to deterministic models and include both single-site and multi-site models. Single-site models usually relate measured STs at a site to air temperatures from a nearby weather station through statistical techniques (e.g., Johnson 1971, Mohseni et al. 1998). Single-site models are typically parameterized only to air temperatures (see van Vliet et al. [2011] for a recent exception) and do not include contextual information about the stream environment that would allow for prediction to new, unmeasured sites. Multi-site models relate STs observed at several sites to the specific stream and watershed features that occur at these sites, such as air

temperature, hydrology, topography, and riparian vegetation. These multi-site models are used to model spatial differences in ST (e.g., Isaak et al. 2010, Wehrley et al. 2006, 2009). If calibrated with physically meaningful predictors and across a broad range of environmental conditions, multi-site empirical model should allow STs to be predicted at new, unmeasured streams. In addition, ST models calibrated with data from sites with minimal upstream alteration could predict reference-condition STs at sites that are suspected of being thermally altered. For these reasons, I used multi-site empirical models in chapter 2.

Predicted STs can potentially improve biological assessments of streams. Many bioassessment approaches rely on multi-taxon niche models that predict what the stream assemblage composition would be under reference conditions. For such assessments, measured STs are inappropriate for predicting reference-condition assemblage composition because STs are also sensitive to human-caused alterations. Instead, most multi- and single-taxon niche models have traditionally relied on surrogates of reference ST, such as latitude, elevation, watershed area (e.g., Hawkins 2006), and air temperature (e.g., Hawkins et al. 2010) to represent the thermal environments of streams. However, these surrogates may not accurately capture geographic variation in ST. In addition, several of these ST surrogates can be associated with other stream features, such as watershed area and latitude, thereby reducing the interpretability of the niche models. To be useful in bioassessments, modeled STs must emulate both the performance and the behavior of measured STs in niche models. Chapter 3 describes both a test of the performance of predicted STs in a multi-taxon niche model and an assessment of how well predicted ST can be used to estimate the thermal optima of stream benthic invertebrates.

Climate change is expected to alter STs over the next century. Understanding why and where some streams will be more vulnerable to climate change than others will help focus future research and mitigation efforts. Numerous approaches have been used to study the potential effects of climate change on STs (e.g., Mohseni et al. 1999, Isaak et al. 2010, Null et al. 2013). However, these approaches have either been limited in their geographic scope or have not provided environmental context to understand why some streams will be more responsive to climate-related alterations than others. Chapter 4 describes an evaluation of the ST models for predicting climate-related alterations based on historical data. In addition, I used downscaled climate projections to predict USA-wide changes in ST by the end of the 21st century. Finally, I used additional modeling to explore the stream and watershed features that are most strongly associated with stream-specific thermal vulnerability to climate change.

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CHAPTER 2

PREDICTING THERMAL REFERENCE CONDITION FOR USA STREAMS AND RIVERS*

Abstract

Temperature is a primary driver of the structure and function of stream ecosystems. However, the lack of stream temperature (ST) data for the vast majority of streams and rivers severely compromises our ability to describe patterns of thermal variation among streams, test hypotheses regarding the effects of temperature on macroecological patterns, and assess the effects of altered STs on ecological resources. Our goal was to develop empirical models that could: 1) quantify the effects of stream and watershed alteration (SWA) on STs, and 2) accurately and precisely predict natural (i.e., reference condition) STs in conterminous USA streams and rivers. We modeled 3 ecologically important elements of the thermal regime: mean summer, mean winter, and mean annual ST. To build reference condition models (RCMs), we used daily mean ST data obtained from several thousand US Geological Survey temperature sites distributed across the conterminous USA and iteratively modeled ST with Random Forests to identify sites in reference condition. We first created a set of dirty models (DMs) that related STs to both natural factors (e.g., climate, watershed area, topography) and measures of SWA, i.e., reservoirs, urbanization, and agriculture. The 3 models performed well (r^2 = 0.84 – 0.94, residual mean square error [RMSE] = 1.2 °C – 2.0 °C). For each DM, we used partial dependence plots to identify SWA thresholds below

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* Coauthored by Charles P. Hawkins and Daren M. Carlisle. Reproduced by permission of Society for Freshwater Science (*Hill et al.* 2013).

which response in ST was minimal. We then used data from just the sites with upstream SWA below these thresholds to build RCMs with only natural factors as predictors (r^2 = 0.87 – 0.95, RMSE = 1.1 °C – 1.9 °C). Use of only reference-quality sites caused RCMs to suffer modest loss of predictor space and spatial coverage, but this loss was associated with parts of ST response curves that were flat and, therefore, not responsive to further variation in predictor space. We then compared predictions made with the RCMs to predictions made with the DMs with SWA set to 0. For most DMs, setting SWAs to 0 resulted in biased estimates of thermal reference condition.

Introduction

Quantifying the thermal regime may be key to understanding the structure and function of all ecosystems (Brown et al. 2004). In lotic ecosystems, spatial and temporal variation in stream temperatures (STs) (see Table 2-1 for definitions of acronyms used in this paper) affects the distributions of individual species (Vannote and Sweeney 1980) and, hence, geographic variation in entire communities (Hawkins et al. 1997). Life-history patterns, individual growth and production, and ecosystem metabolism are also temperature dependent (Benke et al. 1988, Acuña et al. 2008). As a consequence, any natural or human-induced change in thermal regime probably will affect stream ecosystem structure and function.

Because of their ecological importance, STs are extensively monitored by local, state, and federal agencies (Haag and Luce 2008), and millions of dollars are spent annually in thermal remediation efforts (Wu et al. 2003, Seedang et al. 2008). However, determining whether the thermal condition of a stream has been altered requires that we compare observed STs to those expected under natural conditions (Hawkins et al. 2010). To make such assessments in the absence of historical data, reference-condition

ST (RCST) must be predicted. Useful RCST predictive models should account for the effects of naturally occurring stream and watershed features on water temperatures. Alternatively, if reference condition streams are rare or unavailable, predictive models must account for the effects of human-caused stream or watershed alteration (SWA) on STs in a way that natural STs can be inferred.

The natural and anthropogenic factors that can affect STs are well known and vary spatially and temporally within and among watersheds (Ward 1985, Poole and Berman 2001, Allan 2004, Caissie 2006, Webb et al. 2008). Incoming solar radiation and its attenuation by streamside shading, incoming and outgoing long-wave radiation,

Table 2-1. Definition of acronyms used in this paper.

Acronym	Definition
BFI	Base-flow index
CFD	Cumulative frequency distribution
DM	Dirty model
E	Expected
LOWESS	Locally weighted regression and smoothing scatterplots
MAST	Mean annual stream temperature
MSE	Mean squared error
MSST	Mean summer stream temperature
MWST	Mean winter stream temperature
NID	National Inventory of Dams
NLCD	National Land Cover Dataset
NSE	Nash–Sutcliffe efficiency coefficient
O	Observed
PBIAS	% bias
PDP	Partial dependence plot
RCM	Reference-condition model
RCST	Reference-condition stream temperature
RF	Random Forest
RMSE	Root mean squared error
RMSE/SD	Model RMSE/standard deviation of observed stream temperatures
ST	Stream temperature
SWA	Stream and watershed alteration
USGS	US Geological Survey

evaporative cooling, and the stream surface area available on which these heat-exchange processes occur all play critical roles in determining STs. Other important factors include spatial variation in groundwater inputs and local climatic conditions, such as air temperature and precipitation. Human activities that affect STs include removal of streamside vegetation (Brown 1970, Bartholow 2000, Hagen et al. 2006, McTammany et al. 2007), dam operations, such as hypolimnetic vs epilimnetic release (Sinokrot et al. 1995, Preece and Jones 2002, Lessard and Hayes 2003, Olden and Naiman 2010, Risley et al. 2010), power generation and release of wastewater effluent (Stefan and Chau 1976, Kinouchi et al. 2007), runoff from urbanized areas (Klein 1979, Kinouchi et al. 2007, Nelson and Palmer 2007, Kaushal et al. 2010), and agricultural irrigation extraction and return flows.

A variety of models have been developed to predict STs. Most published ST models can be classified as single-site physical, single-site empirical, or multisite empirical models (see Hawkins et al. 2010). Both single-site physical and empirical models have limitations for use in regional ST assessments because they are parameterized for individual stream reaches or watersheds, and therefore, predictions at new, unmeasured locations probably would be inaccurate. In addition, application of single-site physical models to assess many streams in a large region would be cost and time prohibitive because they require measurement and parameterization of heat-exchange processes at each reach (Edinger et al. 1968, Brown 1969, Theurer et al. 1984, Morin et al. 1987, Caissie et al. 2007). Single-site empirical models require long-term time-series measurements of stream and air temperatures that are related through regression (Cluis 1972, Mohseni et al. 1998, van Vliet et al. 2011, Kelleher et al. 2012) or other empirical techniques (Chenard and Caissie 2008), and such data are available for few streams.

Multisite, empirical models hold the best potential for use in regional assessments. These models can make predictions at unmeasured locations (Hawkins et al. 2010), are often based on easily obtained geographical information system (GIS) predictors, and do not require long ST records. These models relate STs observed at multiple sites to local stream and watershed attributes, such as air temperature, watershed area, channel slope, elevation, and latitude (Miyake and Takeuchi 1951, Vannote and Sweeney 1980, Donato 2002, Risley et al. 2003, Jones et al. 2006, Wehrly et al. 2006, Isaak et al. 2010, McKenna et al. 2010). Such models should be able to predict RCSTs at new locations if they are developed with data from reference-condition sites. These models often use predictor variables, such as elevation and latitude, that are known to be correlated with ST but are not necessarily causative. These models typically have been focused on summer STs (Werhly et al. 2009). However, Allan and Castillo (2007) noted that streams with similar summer STs can have different overall thermal regimes resulting from differences in winter STs, which could have substantial ecological effects (Haidekker and Hering 2008), and suggested characterizing the thermal regime to capture these differences.

When predicting RCST, models ideally would be based on data collected at sites in thermal reference condition. However, the number of reference-quality sites present in a region may be limited, and these sites may not represent the full range of naturally occurring environments that need to be assessed. This issue is especially problematic in regions with substantial SWA (Kilgour and Standfield 2006). However, if the effects of SWA can be accounted for in models (Soranno et al. 2011), it is theoretically possible to predict RCST by setting SWA to 0 (e.g., Baker et al. 2005). Such an approach would maximize the range of natural conditions (environmental space) to which models apply and should result in more robust models than those derived from data collected only at

reference-quality sites. However, we do not yet know if such models adequately account for the effects of SWAs and, thus, produce unbiased estimates of RCST. Our general goal was to develop spatially explicit empirical models to predict reference-condition mean summer, mean winter, and mean annual STs (MSST, MWST, and MAST, respectively) at unmeasured locations across the conterminous USA. Our specific objectives were to: 1) develop models that included both natural factors and measures of SWA as predictor variables (henceforth dirty models [DM] because they contain the full range of SWA values), 2) use these initial DMs to identify stream reaches in thermal reference condition, 3) build reference-condition models (RCMs) with data from just those streams in thermal reference condition, and 4) compare general performance of both DMs and RCMs and determine if DMs provided similar estimates of RCST as RCMs when SWAs were set to 0 in the DMs.

Methods

Overview of RCM development

We used an iterative process to identify US Geological Survey (USGS) temperature sites in reference condition to develop models of RCST. We used an extensive database of STs to first build DMs that empirically related estimates of MSST, MWST, and MAST to spatial variation in natural factors and SWA. We then examined the relationship between STs and each of the SWAs to identify thresholds in SWA below which STs showed little or no association with SWAs. We used these thresholds to identify sites in thermal reference condition. Next, we built RCMs with data from just those sites identified as being in thermal reference condition. Last, to examine whether RCSTs can be predicted with DMs, we compared predictions made by setting SWA to 0 in DMs and predictions from RCMs with known RCSTs.

ST data

The USGS provided daily mean ST measurements for 3714 sites distributed across the conterminous USA (Fig. 2-1). A long period of record was available for some sites (e.g., 30 y), but we chose to analyze data from a 10-y period that spanned 1999 to 2008 to match years for which we had reliable land use information (agriculture and urbanization). Daily records were often not continuous within or across the years of record at all sites, but this 10-y analysis window contained 2,766,369 daily records. We screened for and removed outliers from the data by visually examining plots of daily mean STs vs year, month, and calendar day for each USGS site to identify observations

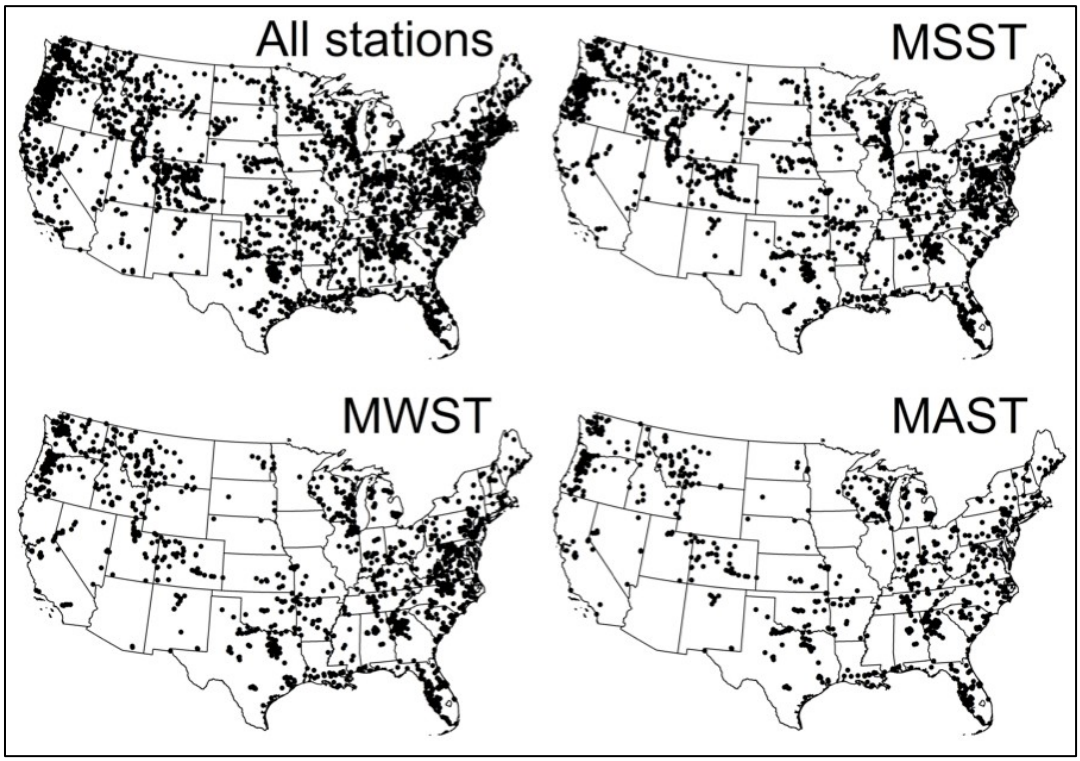

Fig. 2-1. Distribution of US Geological Survey sites with temperature data in the conterminous USA, and sites for which mean summer (MSST), winter (MWST), and annual (MAST) stream temperatures were calculated.

that were the result of instrument malfunctions, did not fit typical seasonal patterns of STs in the conterminous USA, or had values outside those generally expected within the conterminous USA (–0.1°C ≤ ST ≤ 35°C). We retained winter ST values as low as –0.1°C because streams can become super-cooled to this temperature when air temperatures are <0°C for several days (Martin 1981), and this value is within the reported range of accuracy of USGS temperature measurements (Wilde 2006). After quality-control screening, we excluded 98 sites from further analyses. We used the retained data to calculate MSST (July and August), MWST (January and February), and MAST for each site–year combination. We required that a monthly record used in analyses have recorded temperatures for ≥⅔ its days. After these data manipulations, each USGS site had from 1 to 10 y of site–year observations. We randomly selected 1 site–year observation from each site for modeling (Table 2-2). For the 10-y analysis window, we identified 2136 MSST, 1580 MWST, and 996 MAST observations for modeling (Fig. 2-1).

Natural predictor variables

We used the Multi-Watershed Delineation Tool (Chinnayakanahalli et al. 2006) to delineate the upstream watershed boundaries for each site from 30-m USGS digital elevation models. For each predictor, we calculated the mean values within a watershed,

Table 2-2. Summary statistics for mean summer (MSST), winter (MWST), and annual (MAST) stream temperature data

Model	Sites	Minimum °C	Maximum °C	Mean °C
MSST	2136	4.5	33.7	21.3
MWST	1580	–0.1	23.4	5.6
MAST	996	3.2	26	13.8

the mean values within a 100-m-wide riparian buffer within the watershed, and the point-level measurement at the site (Appendix A; available online from: http://dx.doi.org/10.1899/12-009.1.s1). The natural predictors included incoming solar radiation (Kumar et al. 1997), streamside vegetation height and density (Rollins and Frame 2006), Parameter-elevation Regressions on Independent Slopes Model (PRISM) air temperature and precipitation (Daly et al. 2008), dominant surficial geology type and % watershed in each geology type (Reed and Bush 2001), soil characteristics, such as permeability, water table depth, and bulk density (Wolock 1997), watershed shape and area, elevation range, channel slope, runoff (McCabe and Wolock 2010), base-flow index (BFI) (Wolock 2003), a stream flow-stability index (Appendix A), the enhanced vegetation index (Huete et al. 2002), and the % area of each watershed in lake and wetland land cover (Homer et al. 2007) (see Appendix A for details). We based the selection of these potential predictors on an extensive literature review of the physical processes and stream and watershed characteristics previously shown to be important in either empirical or deterministic models. Solar radiation was computationally intensive to estimate for each watershed, so we tested the predictive value of this factor in a preliminary analysis of data obtained from 22 states west of the Mississippi River before developing models for the entire conterminous USA. Including solar radiation estimates failed to improve the western USA models, so we excluded solar radiation as a potential predictor for the conterminous USA models (see *Excluded Predictors* in Discussion). We did all spatial analyses with ArcGIS 9.3.1 Spatial Analyst (Environmental Systems Research Institute, Redlands, California). We also used the method published by Isaak et al. (2010) and applied inverse-distance weighting schemes to watershed and riparian-buffer averages for several predictors to place greater emphasis on values of the predictor that were spatially closer to each ST site. We used the weighting,

$$w_i = e^{-\left(\frac{D_f}{D_e}\right)}, \qquad [1]$$

where D_f represents the flow distance from any upstream pixel to the ST site and D_e represents an e-folding distance, i.e., the distance over which the weight decreases exponentially. We averaged the inversely weighted upstream pixels within the watershed or riparian buffer.

Indices of SWA

Reservoirs.—Release of water impounded by large, hypolimnetic-release dams results in cooler summer and warmer winter STs than in unregulated streams (Ward 1963, 1985). We used the georeferenced National Inventory of Dams (NID) (USACE 2006) to quantify the presence and size of dams and associated reservoirs in each watershed. The NID provides dam attributes, such as year of construction, structural height, and volume of each reservoir. However, examination of the NID revealed errors in the geographic locations of many dams. Important attributes, such as the year of completion and dam height, were incomplete for many records. In addition, some critical features, such as reservoir volume, were repeated in the database if a reservoir had multiple dikes or locks. Therefore, we screened 53,041 NID records to ensure they represented unique dam structures and had complete and accurate records of year of completion and reservoir volume (Appendix B; available online from: http://dx.doi.org/10.1899/12-009.1.s2).

Dam height may be a better indicator of hypo- vs epilimnetic release, but we had to characterize reservoirs within each watershed by the total, mean, and maximum volumes of water they impounded. We used reservoir volume because numerous NID records lacked dam height information and, therefore, could not be used to model STs. For each dam in each watershed, we applied the exponentially decaying inverse-

distance weighting with D_e = 50, 100, 150, and 200 km to account for the downstream attenuation of reservoir effects in our models. These distances were based on literature values (Preece and Jones 2002) and our own examination of sites below large reservoirs in which we found that thermal effects of reservoirs decreased exponentially with distance downstream and sometimes extended to ~75 to 150 km. In addition, we normalized these values by the watershed areas above each temperature site. We did these calculations only if a dam was constructed before the year temperatures were recorded at a site, e.g., a dam completed in 2005 was not counted for a ST recorded in 2000.

Agriculture and urbanization.—We estimated the total and percentage of each watershed in agricultural (row crop) and urban land uses (medium and high intensities) from the 2001 (version 2.0) and 2006 National Land Cover Dataset (NLCD) (Homer et al. 2007; http://www.mrlc.gov/). We matched ST data from 1999 to 2003 and 2004 to 2008 with the 2001 and 2006 NLCD layers, respectively, to ensure the estimated SWA was within 2 y of their respective temperature measurements. We also estimated the total area of riparian buffers composed of agricultural and urban land uses with the area of each land use pixel inversely weighted with D_e = 1, 4, 15, and 25 km above the ST sites. We normalized riparian estimates of each SWA by upstream watershed area.

Modeling approach

Random forests.—We used Random Forest modeling (RF) (Breiman 2001) to empirically model STs. RF is a nonparametric, nonlinear modeling technique based on the well-known classification and regression tree algorithm. However, an RF model is produced by building hundreds of regression trees from randomized subsets of the data, and predictions to new sites are simply the average of the predictions made by all trees

in the resulting forest (see Cutler et al. 2007). We used the *randomForest* (Liaw and Wiener 2002) function in the R statistical software package (version 2.15.1; R Development Core Team, Vienna, Austria) to fit our models.

RF has been increasingly used in diverse natural-science applications, including meteorology (Holden et al. 2011), hydrology (Ordoyne and Friedl 2008), geomorphology (Francke et al. 2008, Snelder et al. 2011), ecology (Cutler et al. 2007, Peters et al. 2007, Chinnayakanahalli et al. 2011), and water-quality monitoring (Carlisle et al. 2009, 2010, Catherine et al. 2010). RF has generally superior predictive performance when compared with other modeling techniques (Prasad et al. 2006, Banfield et al. 2007, Cutler et al. 2007, Peters et al. 2007), and the RF algorithm is easy to understand conceptually (Cutler et al. 2007). RF models make no assumptions about normality of data and are resistant to over-fitting and multicollinearity of predictor variables (Breiman 2001). In addition, spatial and temporal autocorrelations in the data do not affect RF predictions to new samples (Karpievitch et al. 2009). RF produces validation statistics by calculating the mean squared error (MSE) and pseudo-R^2 from the randomized subsets of data that are withheld (out-of-bag samples) during model development.

Variable selection.—We sought to produce RF models that were both interpretable and parsimonious in terms of the number of predictor variables used. However, little guidance exists for variable selection with RF (Genuer et al. 2010). Therefore, we selected predictors that maximized the physical interpretability of the model, reduced redundancy among predictor variables, and maximized model performance. We developed the RF models by iteratively adding predictors that produced the greatest improvement in the RF performance metrics, were physically interpretable, and had low correlation with other predictors. We stopped the selection

processes when additional predictors failed to decrease the square root of the MSE by ~0.1 °C or were redundant with predictors already in the model.

Model performances.—We compared observed STs with their out-of-bag predictions to calculate several model-performance metrics (Moriasi et al. 2007): the Nash–Sutcliffe coefficient of model efficiency (NSE), % bias (PBIAS), and root mean squared error (RMSE) normalized by the observed standard deviation (RMSE/SD). NSE measures the total residual error relative to the total variance within the data. Models that perform well and have little bias have NSE values that are similar to the squared correlation coefficient (r^2), but NSE is more sensitive to deviation from the 1:1 line. We report both NSE and r^2. PBIAS estimates the tendency of a model to over predict (PBIAS < 0) or under predict (PBIAS > 0). RMSE measures the absolute error associated with each model and is in the units for which predictions are made (°C), whereas RMSE/SD allows comparison between models. Smaller values of RMSE and RMSE/SD indicate better model performance. In addition, we plotted observed vs predicted STs and visually examined the plots for outliers and biases.

Reference-site identification

To identify reference-quality sites, we used partial dependence plots (PDPsb) (Hastie et al. 2001) to examine associations between ST and measures of SWA. A PDP is a plot of the average of the response variable (ST) vs a predictor variable and accounts for the effects of other predictor variables within the model (Hastie et al. 2001). We visually selected thresholds for each SWA below which the response in ST was minimized, while maximizing the number of sites retained for modeling.

Two important considerations are the range of natural conditions within which each model can be applied and whether environmental space was lost through

reference-site selection. To compare the predictor space associated with the RCMs and DMs, we plotted the cumulative frequency distribution (CFD) of each natural predictor used in each model. In addition, we overlaid these plots onto the CFDs of each predictor for all USGS sites with available ST data. Although probably not representative of all environments within the conterminous USA, the CFD plots of each predictor at all USGS ST sites encompass a large range of conditions. Thus, they allow comparison between the predictor space of each model and the predictor space of all ST sites in the conterminous USA. When we observed a difference between the RCM and DM in a predictor's CFD, we noted the point beyond which the reference-condition and dirty predictors did not overlap. We then examined the response of ST in the PDP beyond that point to determine how the RCMs might be affected by the lost predictor space. In addition, we compared maps of reference and nonreference site locations to identify regions where reference-site selection resulted in geographic underrepresentation.

RCMs vs DMs

We examined whether the DMs could be used to predict RCSTs by comparing SWA-zeroed predictions with RCM predictions and observed RCSTs. To make the SWA-zeroed predictions, we used a leave-one-out procedure that removed 1 site from the data, developed a DM on remaining sites, and predicted reference-condition ST at the withheld site by setting its SWA to 0. This procedure was repeated for each site across the full range of SWAs, i.e., true reference to the highest levels of alteration. The out-of-bag predictions can be obtained directly from the RF models, but also we used the leave-one-out procedure in the RCMs to ensure comparability of predictions made with the DMs and RCMs. At nonreference sites, we simply applied the RCMs because these sites were not used in model development.

Environmental and ecological assessments are often conducted by comparing observed (O) conditions to those expected (E) in the absence of human alteration, computed as the deviation of E from O (e.g., O – E). For an assessment to be effective, O – E should be near 0 when sites are in reference condition and should depart measurably from 0 at thermally altered sites. We first compared RCM and SWA-zeroed DM predictions made at reference-condition sites to assess whether biases were present in RCMs or DMs when predicting to sites of known thermal condition. To estimate biases in predictions, we calculated the mean O – E at reference condition sites for both RCMs and SWA-zeroed DMs. We also quantified the precision of predictions as the standard deviation of O – E values at known reference sites. To assess if the relationship between O – E and SWA depended on whether RCMs or SWA-zeroed DMs were used to predict E, we isolated the effects of each SWA by selecting sites that failed the reference screening for the particular SWA of interest, but passed the reference screening for the other SWAs (e.g., failed agriculture but passed the dam and urbanization screens). We then plotted O – E values against the full range of each SWA and fit locally weighted regression and smoothing scatterplots (LOWESS) lines to the data (Cleveland 1979). We plotted a vertical line at the point for each SWA that we had previously defined as the boundary between reference and nonreference conditions. For streams to the left of the boundary, i.e., streams in reference condition, LOWESS lines should be near O – E = 0. As SWA increases, the LOWESS lines should deviate from O – E = 0. A LOWESS trend above O – E = 0 represents warming and below 0 represents cooling in response to a particular SWA. If predictions made by setting SWA to 0 perform similarly to predictions from RCMs, the LOWESS lines of the 2 models should show similar trends and overlap with each other. We log(x)-transformed all SWA measures to aid in interpretation of the plots.

Results

DMs

Mean summer stream temperature (MSST).—Nine predictors were selected to model MSSTs (Fig. 2-2, Appendix Table C; available online from: http://dx.doi.org/10.1899/12-009.1.s3), including 6 natural predictors (Fig. 2-3) and 3 measures of SWA (Fig. 2-4). MSSTs warmed with increasing values of 5 predictors: mean summer air temperature, watershed area, soil bulk density, and 2 measures of SWA: % watershed in agricultural and urban land uses (henceforth agriculture and urban indices, respectively). Factors negatively associated with MSST, in rank order of importance, were BFI, maximum upstream reservoir volume (inversely weighted by an D_e = 50 km and normalized by watershed area; reservoir index), average channel slopes within the watershed, and elevation ranges within watersheds (Figures 2-3, 2-4).

Mean winter stream temperature (MWST).—As in the MSST model, mean winter air temperature was the most important predictor of MWSTs (Figures 2-2, 2-3). In addition to air temperature, 5 natural predictors (Fig. 2-3) and 3 measures of SWA (Fig. 2-4) were selected to model MWSTs (Fig. 2-2, Appendix Table C). Two measures of SWA (the reservoir and urban indices) were positively associated with MWSTs, whereas the agricultural index was negatively associated with MWSTs (Fig. 2-4). Compared with the MSST model, the direction of the relationships between MWST and the agricultural and reservoir indices were reversed (cf. MSST and MWST PDPs in Fig. 2-4). Slightly warmer MWSTs were associated with higher values of soil and geologic permeability (Fig. 2-3). These factors may be associated with the amount of shallow and deep groundwater flow within the watershed. Cooler MWSTs were associated with greater elevation range and steeper average channel slopes within the watershed. PDPs for

watershed area and geologic permeability showed little response in MWSTs but both contributed to the overall performance of the model. Most watersheds with large areas were associated with slightly cooler MWSTs. Warmer MWST values occurred at the largest watershed areas, but the scarcity of data for large watersheds limited the reliability of trend lines in this part of the PDP (Fig. 2-3) (Hastie et al. 2001).

Mean annual stream temperature (MAST).—The predictor variables (Fig. 2-2, Appendix Table C) selected for the MAST model and the directions of their relationships with MAST were very similar to those observed for the MSST model (cf. MSST and MAST; Figures 2-2, 2-3, 2-4). However, the order and relative magnitude of associations between MAST and its predictors differed. For example, the urban and agriculture indices were the 3rd and 4th most important predictors in the MAST model, whereas these predictors were ranked lower for the MSST model (cf. MSST and MAST; Fig. 2-2). In contrast, the reservoir index was ranked higher for the MSST model, compared with the MAST model (Fig. 2-2). Mean annual air temperatures, watershed area, and the urban and agricultural indices were positively associated with MASTs (Figures 2-3, 2-4). Increasing values of BFI, elevation range, average stream slopes within the watershed, long-term precipitation, and the reservoir index were all associated with cooler MASTs (Figures 2-3, 2-4).

Reference-site selection and models

We used conservative thresholds to select reference-condition sites (e.g., ≤ 1% agriculture and urbanization within the MSST watersheds). Applying the SWA thresholds (Fig. 2-4) to identify reference-condition sites for each model period identified 570 MSST, 481 MWST, and 273 MAST sites. The same natural predictors that were selected in the DMs were selected in the RCMs. The direction and pattern of ST

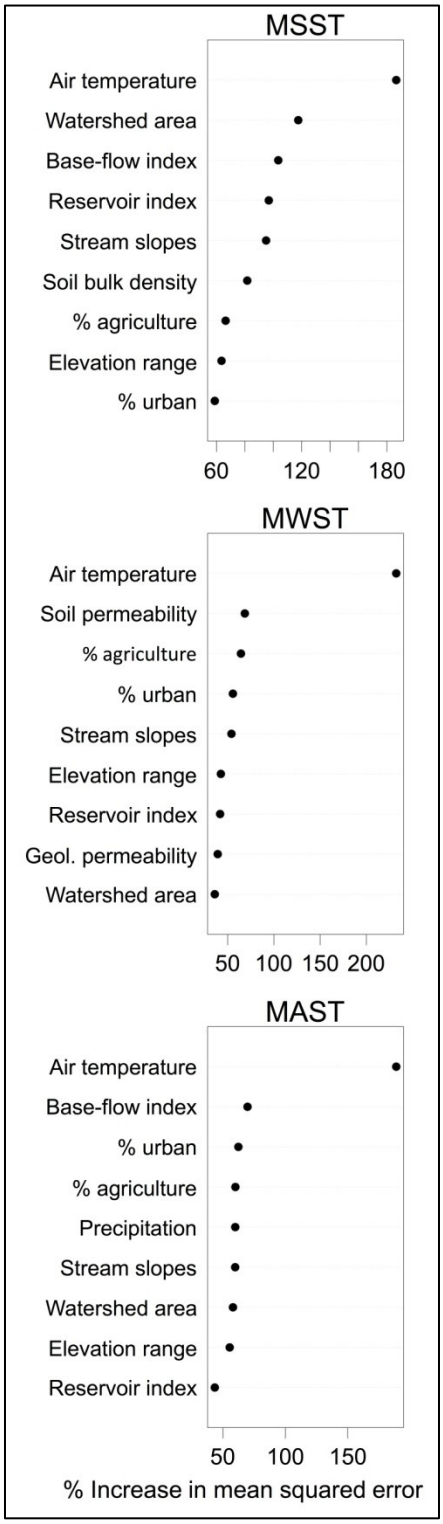

Fig. 2-2. Ranked importance (% increase in mean square error) of the predictor variables for the mean summer (MSST), winter (MWST), and annual (MAST) stream temperature models.

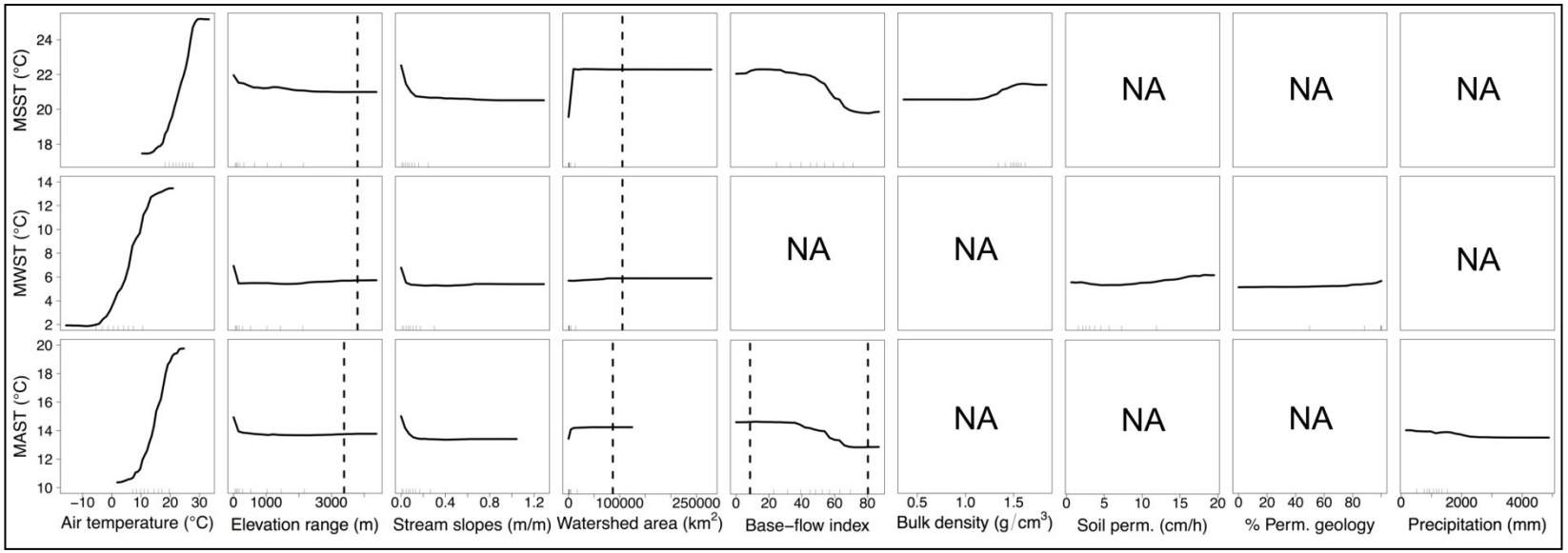

Figure 2-3. Partial dependence plots showing how stream temperature responded to the individual natural predictors selected for the mean summer (MSST), winter (MWST), and annual (MAST) stream temperature dirty models. The vertical dashed lines represent the extremes of values observed at reference sites, if different from observations used in dirty models. NA = not applicable.

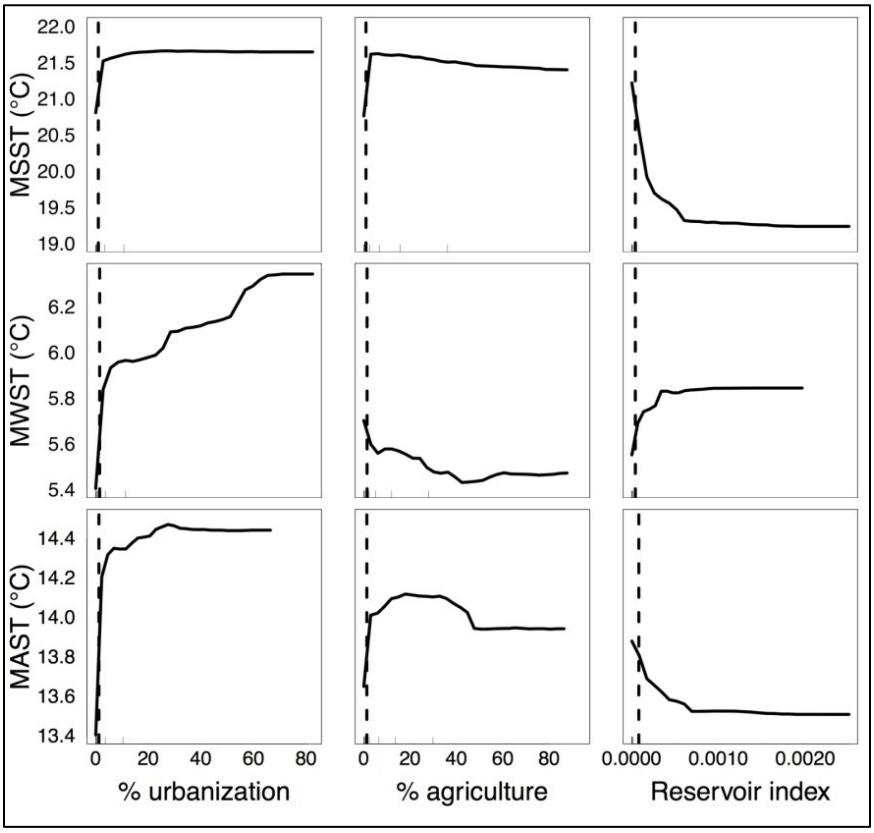

Fig. 2-4. Partial dependence plots showing how mean summer (MSST), winter (MWST), and annual (MAST) stream temperature responded to individual measures of stream and watershed alteration. The vertical dashed lines represent values of alteration below which we considered US Geological Survey stream temperature sites to be in thermal reference condition.

responses to the natural predictors were very similar in the RCMs and DMs and the RCM. PDPs are not shown here.

Reference screening decreased the geographic representativeness of the data, especially in Midwestern states where agriculture is ubiquitous (cf. Figures 2-1 and 2-5). Despite the loss of geographic coverage of the reference data sets, CFD plots for the predictor variables showed that most of the predictor space was retained (cf. RCM, DM, and all USGS ST site CFD plots in Appendix D; available online from: http://dx.doi.org/10.1899/12-009.1.s4), except for the largest watershed areas and

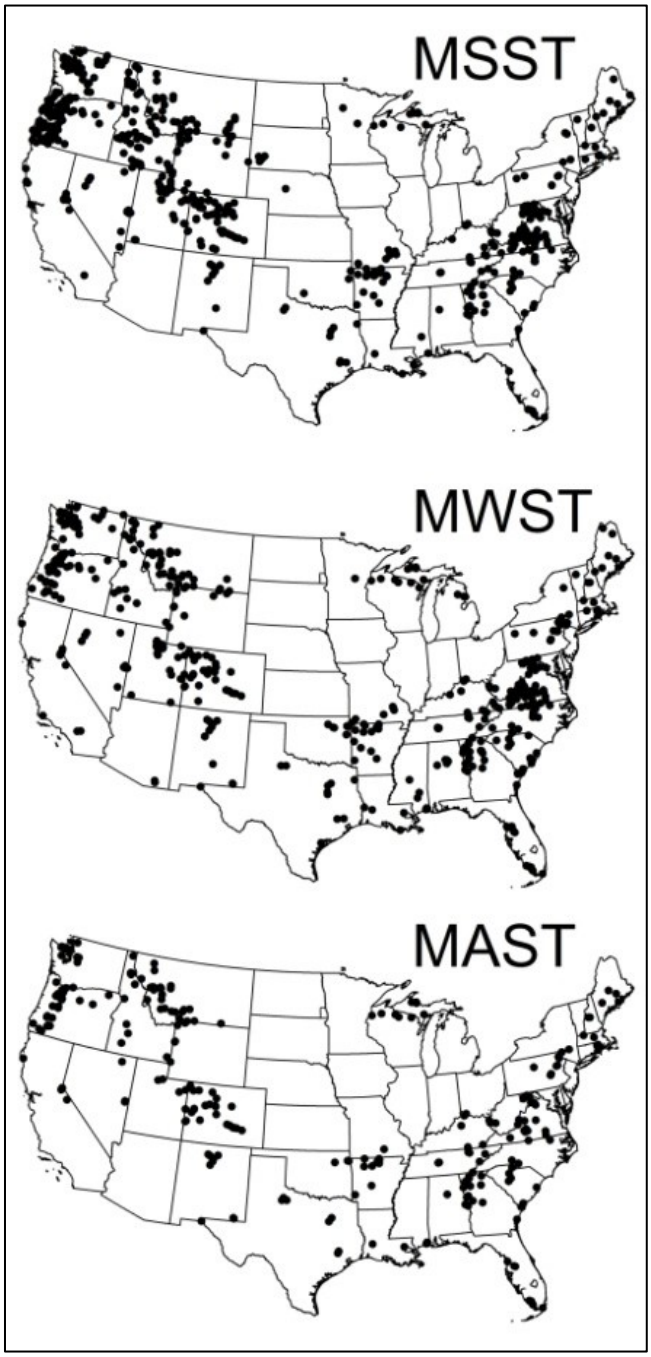

Fig. 2-5. Distribution of US Geological Survey sites with temperature data within the conterminous USA, and sites for which mean summer (MSST), winter (MWST), and annual (MAST) stream temperatures were used to develop the reference condition models.

elevation ranges (Fig. 2-6). The largest watersheds were not geographically concentrated, but the largest elevation ranges were concentrated in the Rocky and Appalachian mountains. The reference MAST data set lost additional predictor space at the lowest and highest values of BFI (Fig. 2-6). Sites with the lowest BFI values were spatially concentrated in the Southwestern and Central Plains States, such as Arizona, New Mexico, Texas, Oklahoma, Kansas, and Missouri. Sites with the highest BFI values occurred in the Rocky Mountains and northern Michigan. For most predictors, both the reference-condition and SWA-influenced sites covered the same range of predictor

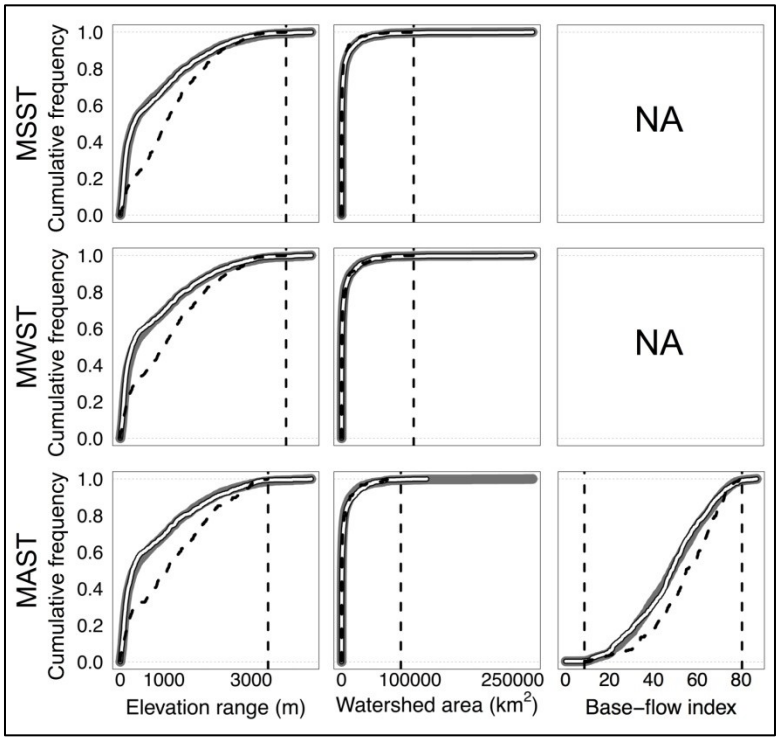

Fig. 2-6. Cumulative frequency distribution (CFD) plots of natural predictors that had truncated ranges (vertical black dashed lines) in the reference-condition models (black dashed) compared with dirty models (solid white) for mean summer (MSST), winter (MWST), and annual (MAST) stream temperatures. Solid grey lines represent the CFDs of all available US Geological Survey stream temperature sites.

values as the full set of USGS temperature sites. Only the highest stream slopes and largest watershed areas were not included in our models. However, the DM PDPs showed that STs were probably not sensitive to increased values of these predictors (see vertical lines in Fig. 2-3), i.e., response scope was similar in both RCMs and DMs.

Model performances

Both the DMs and RCMs explained a large proportion of the variance in STs (r^2 values = 0.84—0.95, Table 2-3). The performance metrics and observed-vs-predicted plots were similar between the DMs and RCMs (Table 2-3), and only the DM observed-vs-predicted plots are presented here (Fig. 2-7). PBIAS values ranged between –0.7 (slight over-prediction of MWST RCM) and 0.07 (slight under-prediction of MSST RCM). These PBIAS values indicate little bias in the models and were well below the values Moriasi et al. (2007) suggested as indicative of good performance for stream characteristics modeled at monthly time steps with simulation models (i.e., stream flow PBIAS < ±10, sediment PBIAS < ±15, and N and P PBIAS < ±25). The PBIAS values

Table 2-3. The squared correlation coefficient (r^2), Nash–Sutcliffe coefficient (NSE), % bias (PBIAS), root mean squared error (RMSE), and RMSE/observed standard deviation (RMSE/SD) for the mean summer (MSST), winter (MWST), and annual (MAST) stream temperature models.

Model	r^2	NSE	PBIAS	RMSE (°C)	RMSE/SD
DM					
MSST	0.84	0.84	0.07	2.0	0.40
MWST	0.92	0.92	–0.42	1.4	0.28
MAST	0.94	0.94	–0.05	1.2	0.25
RCM					
MSST	0.87	0.87	0.07	1.9	0.36
MWST	0.89	0.88	–0.70	1.4	0.34
MAST	0.95	0.95	–0.06	1.1	0.23

associated with both the RCM and DM for MAST models were very small (–0.06 and –0.05, respectively), and observed and predicted values were in good agreement (Fig. 2-7). The NSE and RMSE/SD values also indicated good model performance based on values suggested by Moriasi et al. (2007) (i.e., NSE ≥ 0.75 and RMSE/SD ≤ 0.5; Table 2-3). The MWST RCMs and DMs had absolute RMSE values of 1.4°C. The MAST and MSST RMSE values for the RCM was slightly lower than that for the DM (MAST = 1.1 vs 1.2°C, MSST = 1.9 vs 2.0°C).

Predicting reference-condition ST with DMs

When applied to sites in reference condition, the SWA-zeroed DMs produced biased predictions of MSST and MAST (cf. LOWESS lines in Fig. 2-8; mean O – E values in Table 2-4). In contrast, the RCMs predictions were unbiased. The MSST RCM was also more precise than the MSST DM (Table 2-4). The biases produced by the SWA-zeroed MSST and MAST DMs carried over to predictions made at nonreference sites (plotted to the right of the vertical dashed lines in Fig. 2-8). For nonreference sites, the DMs overestimated the effects of urbanization and agriculture relative to the RCMs. Conversely, the DMs underestimated cooling at nonreference sites below reservoirs. For MWST, DM and RCM predictions agreed well (Fig. 2-8). Both the DM and RCM slightly overestimated MWST at reference-condition sites (LOWESS lines below 0), but these biases were small (mean O – E in Table 2-4).

The O – E LOWESS trends were consistent with the PDP plots (cf. Figures 2-4 and 2-8). The MSST and MAST models showed warming in response to increasing values of agriculture within the watershed and cooling in association with the reservoir index. In contrast, the winter model showed the reverse relationship with these

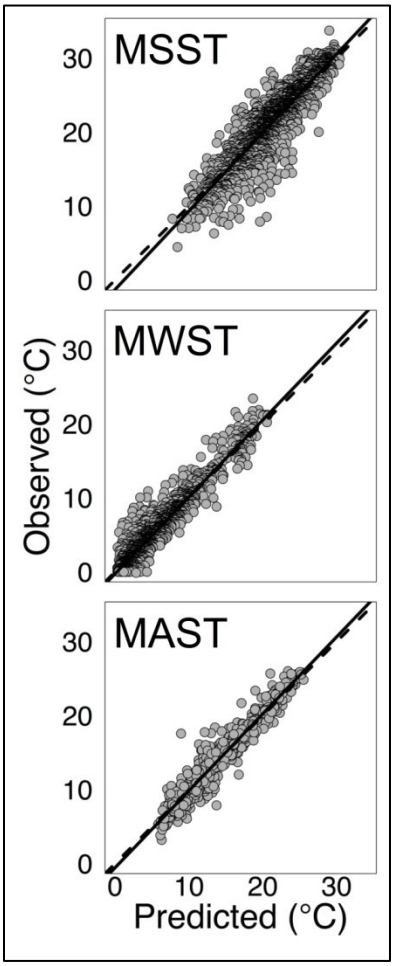

Fig. 2-7. Observed vs predicted mean summer (MSST), winter (MWST), and annual (MAST) stream temperatures with the least-squares fitted lines (dashes) and 1:1 lines (solid).

measures of SWA. All models displayed warming associated with greater urbanization within the watershed. In addition, most of the O – E LOWESS lines began to deviate from 0 at SWA values that were lower than the thresholds we used to define reference condition (vertical dashed lines in Fig. 2-8), implying a response in ST to SWA below the thresholds used to select reference-condition sites.

Table 2-4. Mean and standard deviation (SD) of mean summer (MSST), winter (MWST), and annual (MAST) stream temperature differences between observed (O) conditions and those expected (E) in the absence of human alteration (O – E) for dirty models (DM) and reference condition models (RCM).

Model	Mean O – E	SD O – E
DM		
MSST	0.67	2.2
MWST	–0.07	1.4
MAST	0.42	1.1
RCM		
MSST	0.02	2.0
MWST	–0.04	1.4
MAST	–0.002	1.1

Discussion

Assessments of our models suggest they accurately and precisely estimate STs across a large geographic extent with varied environments, but several factors must be considered. First, our models must be placed in context with other published empirical ST models. A favorable comparison of the performance of our models with that of other published models should provide additional confidence in their potential use for: 1) assessing the thermal conditions of USA streams, 2) providing a mechanistic understanding of macroecological patterns in streams and rivers, and 3) exploring historical and future responses of streams to climate change. In addition, we can gain insight into the relative influence of certain landscape features on STs by comparing the selected and excluded predictors of published empirical models that were developed at different geographic scales. Last, we briefly consider the use of DMs and RCMs to infer RCST and the implications of our findings for hindcasting of water-quality variables.

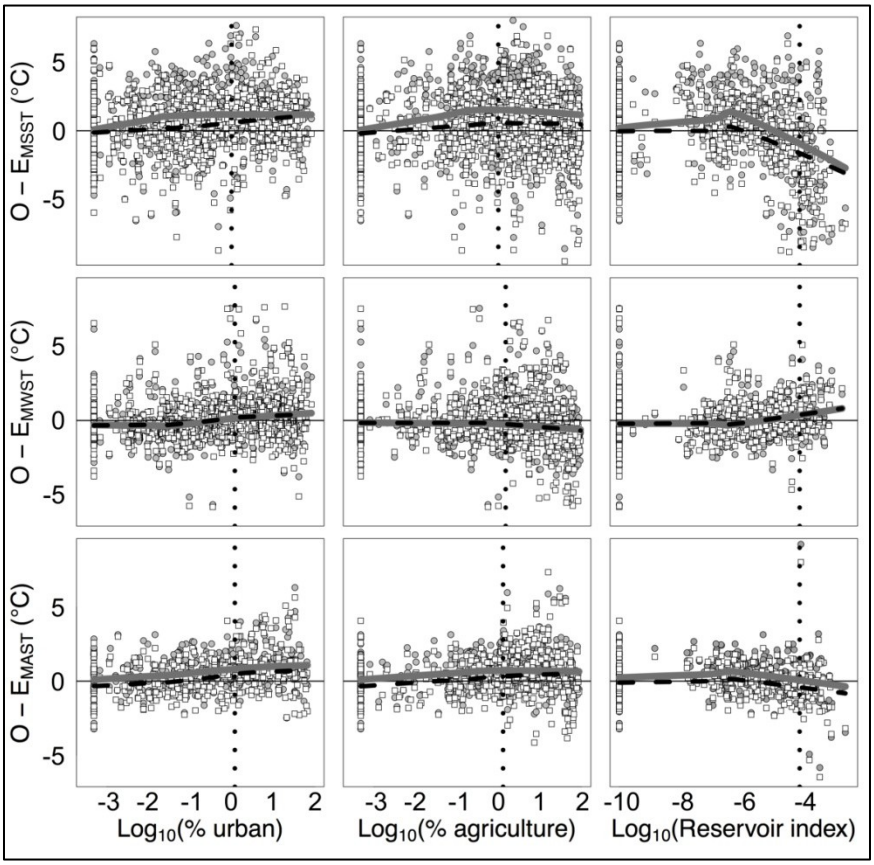

Fig. 2-8. Bias in model predictions of mean summer (MSST), winter (MWST), and annual (MAST) stream temperatures as a function of urbanization, agriculture, and reservoir alteration. Bias is measured as the difference between observed (O) and expected (E) reference-condition stream temperatures. Expected values for MSST, MWST, and MAST were derived from both reference-condition models (dashed line) and dirty models (solid grey line) for which stream and watershed alterations were set to 0. Vertical dashed lines represent thresholds used to define reference condition for each stream or watershed alteration measure.

Model performance

Spatially explicit models that relate landscape features to stream characteristics, such as STs, are gaining popularity (Wang et al. 2006), but most previous work has not reported performance statistics that would allow objective comparison with our models. Isaak et al. (2010) modeled summer STs (15 July–15 September) with data from 780 ST sites within the Boise River, Idaho. Based on leave-one-out cross validation, they

reported an RMSE of 0.74°C and an SD of observed STs of 2.7°C, resulting in an RMSE/SD of 0.27. This value is smaller than the RMSE/SD values of our MSST models but similar to those of our MWST and MAST models (Table 2-3). Wehrly et al. (2006) modeled mean July STs in lower Michigan, and reported an SD of residual errors of 1.9°C. However, Wehrly et al. (2006) did not report the SD of observed STs. To compare the performance of their model with ours, we used their reported range of observed July STs (9.2–26.7°C) to calculate a normalized SD of residual errors of 11%, which is higher than our normalized SD of residual errors of 7% for MSST. These values suggest similar or better performance of our models but at a spatial scale several orders of magnitude larger than was used in the 2 previous studies. Our models are an important advance in characterizing regional variation in STs, especially given the spatial scale at which they can be applied.

Model applications

Assessments of the ecological condition of streams are routinely conducted in the USA and elsewhere, and researchers have expended substantial effort on developing statistical tools to objectively assess the biological condition of streams (reviewed by Hawkins et al. 2010). Similar approaches could be applied with the models presented here to assess the thermal condition of streams. We used natural landscape predictors that allow accurate predictions of STs at unmeasured locations, and these site-specific predictions of reference-condition STs can be used as benchmarks to infer whether an assessed stream reach is thermally impaired. Furthermore, ST models could be used in support of ecological assessments because ST is a major determinant of the distribution of aquatic species within a landscape (Vannote and Sweeney 1980, Haidekker and Hering 2008). Many ecological assessments compare observed biota

with the biota predicted to occur under reference environmental conditions (Moss et al. 1987, Hawkins et al. 2000, Simpson and Norris 2000). The species distribution models used to predict reference-condition biota typically use surrogates of natural ST, such as latitude, elevation, or drainage area. These surrogates are imperfect predictors of thermal reference conditions in streams. Inclusion of well predicted STs in species distribution models such as River InVertebrate Prediction and Classification System (RIVPACS; Moss et al. 1987, Hawkins 2000) should improve the precision and accuracy of ecological assessments and their interpretation. In addition, conducting a thermal assessment in conjunction with a biological assessment should aid in diagnosing whether altered temperature is a likely cause of observed biological impairment.

ST models will be essential tools in establishing a more comprehensive understanding of ST changes that have already occurred and probably will occur in response to climate warming. For example, Isaak et al. (2010) used a multisite empirical model in the Boise River basin, Idaho, to account for variation in observed STs between 1993 and 2006. They found that the effects of climate change on thermal habitats depend on landscape context and that the loss of available Bull Trout (*Salvelinus confluentus*) thermal habitat was greatest in headwater streams. However, most empirical studies of the potential effects of climate change on STs were based on empirical stream–air temperature relationships at individual sites (e.g., Mohseni et al. 1999, 2003) and, thus, the landscape context associated with differing vulnerabilities of STs to predicted changes in climate could not be considered. Empirical models derived from data that cover the range of conditions found within a region of interest will have much greater utility in assessing the potential region-specific effects of climate change on STs and identifying individual streams and regions that may be especially vulnerable to climate change.

Excluded predictors

Those predictors that were excluded from the models during calibration were as notable as the predictors that were selected. We expected estimates of solar radiation to be strongly associated with variation in STs among sites, especially in summer. However, solar radiation was not a significant predictor in any model. When we included solar radiation in the pilot western USA MSST model, RMSE decreased by only <0.1°C. If we substituted solar radiation for air temperature, MSST and MWST RMSEs increased by 17% and 80%, respectively. The observed lack of strong association between ST and solar radiation may have been the result of inaccurate estimates of solar radiation striking each stream. However, Wehrly et al. (2006) also noted a weak association between STs and solar radiation in a multisite empirical model of STs in Michigan. Conversely, Isaak et al. (2010) found that radiation was an important predictor of STs in the Boise River basin, Idaho. Whether solar radiation is an important predictor of STs in empirical models may be related to the scales at which models are developed, the effects of cloud cover on solar radiation (not measured in this analysis), and the spatial variability of radiation relative to other predictors within the model. Wehrly et al. (2006) suggested that studies in which solar radiation is a good predictor of STs are generally conducted in single watersheds where other environmental predictors vary little relative to canopy cover and, thus, the solar radiation striking the stream. In short, at large spatial scales, air temperature may integrate the multiple heat-exchange processes that influence ST.

We also included several short- and long-term measures of precipitation as potential predictors (Appendix A) and expected them to be strong predictors of STs because of their relationship with stream flow. However, long-term precipitation was only

moderately important as a predictor in the MAST model. Additional research may be needed to better characterize precipitation (e.g., timing of precipitation events) for predicting MSST and MWST or to conclude that precipitation is a weak predictor of STs at a large geographic scale. Last, in contrast to the observation of Wehrly et al. (2009), who found that mean July STs in Michigan were positively related to the amount of upstream lentic waterbodies, lakes and wetlands were not selected in any of the models. The importance of lentic waterbodies to July STs in Michigan and Wisconsin may reflect the prominence of this landscape feature in these States and its role in influencing STs at that scale relative to the conterminous USA

RCMs vs DMs

Stream assessments must be precise and unbiased to be useful. If a management goal were to maintain or restore naturally occurring thermal reference conditions, on average the SWA-zeroed MSST and MAST O – E models would underprotect (Type I error) sites with upstream reservoirs and overprotect (Type II error) sites with urban and agricultural land uses within the watersheds. For these thermal attributes, the RCMs would provide more accurate and defensible assessments. However, for MWST, use of either the RCM or the DM would allow reasonably precise and unbiased assessments. These results have important implications for hindcasting of historical conditions. The DMs we developed included both reference and nonreference sites and, therefore, did not extrapolate beyond the range of the data. However, even with the benefit of a full spectrum of SWA information, the MSST and MAST DMs produced biased predictions of reference-condition ST. Models calibrated without data from sites in reference condition would have to extrapolate predictions of thermal

reference conditions, which would almost certainly result in larger biases than observed in our DMs.

Our analyses also illustrate a specific challenge associated with establishing reference-condition expectations from a network of reference sites that vary in their quality (i.e., the amount of SWA potentially affecting them). The most liberal land-cover thresholds we defined were 1.5% of the watershed in agriculture or urbanization in the MWST models. The MSST and MAST thresholds were more conservative (agriculture and urban indices ≤ 1% in MSST watersheds, and ≤ 1.2 and 1.3%, respectively in MAST watersheds). Yet several of the RCM O – E LOWESS lines showed systematic deviation from 0 in response to these SWAs below these thresholds (Fig. 2-8). The deviations were small enough for urbanization and agriculture that use of the thresholds we selected would not seriously compromise predictions of true RCSTs. However, the deviations in O – E values associated with the reservoir index were larger, a result implying that we should consider adjusting the reservoir threshold when selecting reference sites. For example, if the reference-condition threshold were adjusted to a $\log_{10}$(reservoir index) value of –5, biases in the O – E values at reference sites could be minimized (Fig. 2-8). However, doing so would reduce the MAST reference observations from 273 to 224 for the conterminous USA and further reduce the spatial and environmental representativeness of the model. The addition of nonUSGS ST sites could increase the number and environmental representativeness of reference-condition sites (e.g., http://greatnorthernlcc.org/technical/stream-temp-maps). However, additional reference-quality streams are not likely to be identified in regions with nearly ubiquitous SWA, such as agriculture in the Midwestern USA (Fig. 2-5). Selecting sites that are “reference enough,” while maintaining a sufficient number of sites to be representative of the environments within a region, is a major challenge in all environmental assessments.

The inability of the SWA-zeroed MSST and MAST DMs to produce unbiased O – E values could be caused by the coarseness of the SWA measures, such as the reservoir index. First, because of incomplete NID records, we were forced to use reservoir volumes as a predictor. Reservoir volume is only weakly associated with reservoir depth within the NID (r^2 = 0.27), and the temperature of the water released by a dam is a function of the depth at which it is released (Bonnet et al. 2000, Lindim et al. 2011). The addition of information to the NID that specifies the depth or type of water release (e.g., hypolimnetic or epilimnetic) might improve the accuracy of our models. Alternatively, correcting and completing NID structure-height information could improve results because this attribute is probably better correlated with the likelihood of thermal stratification in reservoirs than volume and, thus, the temperature of released water. Second, we expended considerable effort to screen 53,041 NID records, but errors still exist within the data. We noted several outliers within the calibration data sets while developing the models. These outliers often were associated with inaccurate reservoir location information, and correction improved predictions. However, missing or inaccurate information may not always result in obvious outliers, but rather noise within the models. Additional screening of the NID could improve confidence in predictions.

Concluding remarks

Our RCMs accurately and precisely predicted reference STs at unmeasured streams across a broad range of environments in the conterminous USA. We think these models represent a significant step towards a more comprehensive assessment of the environmental and ecological conditions of USA rivers and streams. Thermal assessments would complement previous and ongoing assessments of the biological (Paulsen et al. 2008) and hydrologic condition (Carlisle et al. 2009) of the USA streams

and rivers. In addition, these models provide a tool for understanding how specific SWAs have affected STs and how other alterations, such as climate change, might further alter them in the future.

To our knowledge, no investigators have compared RCM predictions and DM hindcasting of reference condition. Relative to RCMs, the DMs produced biased estimates of reference-condition STs. These predictions potentially could be improved with better land use information that accounts for more specific alterations, such as reservoir-release temperatures, wastewater treatment facilities in urban areas, irrigation withdrawals, and return flows associated with agricultural and mining activities. However, these types of data are not readily available everywhere and will take time to develop. Unless a high degree of confidence exists that the available measures of SWA account for nearly all of the thermal alteration that occurs at different sites, we recommend caution in using DMs to predict reference-condition water quality.

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CHAPTER 3

USING MODELED STREAM TEMPERATURES TO PREDICT MACRO-SPATIAL PATTERNS OF STREAM INVERTEBRATE BIODIVERSITY *

Abstract

Stream temperature (ST) is a primary determinant of the spatial distribution of stream biota, but we cannot fully evaluate its importance because we lack ST data for most streams. Past research often relied on surrogates of ST such as elevation, latitude, watershed area, and air temperature to examine biota-temperature relationships. However, these surrogates may not accurately represent differences among sites in the thermal environments biota experience. Moreover, use of ST surrogates could potentially confound interpretations of biota-temperature relationships due to the covariation with other environmental features. In the absence of measured ST data, modeled STs could improve our ability to both predict patterns of stream biodiversity and interpret the relative importance of different mechanisms that influence local and regional biodiversity. To test this hypothesis, we built 4 multi-taxon niche models (MTNM) with invertebrate and environmental data from 92 reference-quality streams. These models differed in the type of temperature data used as predictors: (MTNM1) three geographic surrogates of temperature that are often used together (elevation, latitude, and watershed area), (MTNM2) air temperature, (MTNM3) predicted STs, and (MTNM4) measured STs. Predicted STs were obtained from a USA-wide model we previously developed from 569 reference-quality sites with local climate and watershed features as predictors (e.g., air temperature and topography). We assessed the

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* Coauthored by Charles P. Hawkins.

precision of each niche model as the standard deviation (SD) of the ratio of observed-to-expected (O/E) taxa richness values at each site. MTNM3 and MTNM4 were the most precise niche models (O/E SD = 0.15 for both) and explained 71% of the possible range in O/E SD values (replicate-sampling SD = 0.13 and null model SD = 0.20). MTNM2 (O/E SD = 0.17) and MTNM1 (O/E SD = 0.18) were less precise (43% and 29% of possible SD range, respectively). Plots of taxon-specific, predicted capture probabilities against predicted and measured STs were very similar, indicating that modeled STs mirrored measured STs in predicting individual taxa. Estimates of taxon-specific thermal optima derived from predicted and measured STs were also similar (regression r^2 = 0.97, slope = 1.09), which also indicated ecologically relevant thermal environments were well characterized by modeled STs. We conclude that modeled STs can be used to improve our understanding of stream biodiversity patterns and predict the effects of human-caused thermal alterations on stream biodiversity, such as those associated with land use and climate change.

Introduction

The spatial and temporal distributions of many ectothermic organisms are strongly associated with temperature variation (Brown 2004, Pörtner et al. 2006). These patterns are especially strong for streams (Vannote and Sweeney 1980, Ward and Stanford 1982). The strong associations between assemblage composition and stream temperature (ST) (Schlosser 1990, Hawkins et al. 1997, Wehrly et al. 2003, Haidekker and Hering 2008, Chinnayakanahalli 2011) imply that stream ectotherms have evolved to partition thermal gradients and that temperature is a primary environmental filter (Tonn et al. 1990, Poff 1997, Liebold 1995) that strongly influences local community assembly and maintenance. If this thermal niche view of stream communities is correct,

accurately predicting spatial and temporal variation in the distribution of stream species will depend on how well we characterize ecologically relevant aspects of the thermal environments of streams. Such predictions of community composition are a critical element of stream ecosystem management including the assessment of biodiversity status (e.g., Joy and Death 2002, Hawkins 2006) and the establishment of conservation and restoration goals (Minns et al. 1996, Lake et al. 2007). However, we lack spatially and temporally appropriate temperature records for the vast majority of stream reaches in the USA. Moreover, information regarding naturally occurring STs is especially lacking, because watershed alterations (e.g., urbanization and reservoirs) have transformed the thermal regimes of many streams and rivers (Poole and Berman 2001, Chapter 2).

Most previous biota-temperature analyses used surrogates of ST because of the paucity of direct and ecologically meaningful temperature measurements (e.g., continuous measures of ST over weeks to months as compared with spot temperature measurements). These surrogates typically included elevation, latitude, and watershed area (e.g., Vannote and Sweeney 1980, Moss et al. 1987, Rahel and Nibbelink 1999, Hawkins et al. 2000, Joy and Death 2002, Hawkins 2006), but air temperatures have also been used recently (e.g., Hawkins et al. 2010a, Domisch et al. 2013). However, surrogates of ST may not accurately depict stream thermal environments or their spatial variation because local controls on ST can vary greatly in environmentally heterogeneous regions, such as the western USA. For example, for the conterminous USA latitude is associated with 38% of the variation in mean summer STs, but only 11% of the variation in ST in western US streams (unpublished data). Moreover, surrogates such as latitude and watershed area may covary with other environmental features, such as streamflow, confounding interpretations of biota-environment relationships. Models

that accurately predict reference-condition ST across a broad range of environmental conditions could eliminate the need for surrogates when characterizing the thermal environments of streams. Doing so could provide biologically meaningful interpretations of the distribution of taxa across landscapes and help set site-specific expectations of stream biodiversity (Boon 2000).

Our main objective was to evaluate how well modeled ST represented measured ST for (1) predicting stream benthic invertebrate composition and (2) estimating taxon-specific responses to temperature. We addressed this objective in the context of how well various ST surrogates performed. Specifically, we compared the performance of four multi-taxon niche models (MTNM) (Moss et al. 1987, Hawkins et al. 2000) that used the following thermal variables as predictors: elevation, latitude, and watershed area (MTNM1); air temperature (MTNM2); model predicted STs (MTNM3), and directly measured STs (MTNM4). These four niche models represent a progression from coarse surrogates of ST to direct measurements. We expected the performance of the models to progressively improve with the precision of MTNM1 to be < than that of MTNM2 and so forth.

Modeled environmental conditions can provide biologically-relevant characterizations of the environment for predicting species distributions (e.g., hydrology in Jähnig et al. 2012). However, linking models may also propagate and compound errors that could reduce the accuracy and interpretability of predictions. We assessed the potential significance of this issue by examining responses of individual stream taxa to both predicted and measured ST to determine if taxa were responding to predicted ST in a realistic manner. Similar and unbiased responses in stream taxa would indicate that modeled STs can represent biologically relevant thermal conditions and can be substituted for measured STs when either direct measurements are unavailable or when

predictions based on naturally occurring, reference condition temperatures (Hawkins et al. 2010b) are needed.

Methods

General approach

We used benthic invertebrate sample data collected from across the conterminous USA to build the four MTNMs. The United States Geological Survey (USGS) collected these samples from streams at which STs were continuously recorded. Each MTNM was calibrated with one of the four sets of thermal variables that represented the progression from coarse geographic surrogates to directly measured ST. We then compared the performance of these models for predicting the taxonomic composition of streams. We also graphically and statistically compared taxon-specific capture probabilities produced by MTNM3 and MTNM4. Finally, we compared taxon-specific thermal optima derived from both predicted and measured STs.

Stream benthic invertebrate samples and ST predictions

The USGS provided information on benthic invertebrate samples from 481 sites that were sampled as part of the National Water-Quality Assessment Program. These data were collected between 1999 and 2007 and invertebrates were identified to the finest taxonomic resolution possible (usually genus or species) (see Moulton et al. 2000 for USGS benthic invertebrate sampling and identification procedures). Because species-level identifications were inconsistent across samples, species counts were aggregated to genus. Likewise, a handful of closely related genera were also aggregated (e.g., *Cricotopus* and *Orthocladius* of the Dipteran subfamily Orthocladiinae).

We used the rrarefy function in the vegan package (R Statistical Software) to randomly resample the original benthic invertebrate count data to 300 individuals to reduce the influence of across-site variation in abundance on comparisons of composition and richness (Vinson and Hawkins 1996, Gotelli and Colwell 2001). These count data were then converted to taxon presences and absences at each site.

We used benthic macroinvertebrate data collected from reference-quality sites for all analyses in this paper. We identified those sites that we considered to be in near-natural thermal and biological reference condition by applying the screening criteria of Chapter 2 to the amount of land use (National Land Cover Dataset, Homer et al. 2007; http://www.mrlc.gov/) and the volume of reservoirs occurring in each watershed (National Inventory of Dams, USACE 2009). We considered streams with ≤1% upstream urbanization and row-crop agriculture and with total reservoir volumes per watershed area $\leq 4 \times 10^{-5}$ km^3/km^2 to be in reference condition (see Chapter 2).

We characterized summer thermal environments at each site in four ways. The coarsest representation of ST consisted of elevation, latitude, and watershed area, which were obtained from digital elevation models. The second characterization consisted of mean summer air temperatures for the year each biological sample was collected. These data were obtained from the PRISM climate dataset (Daly et al. 2008). The third characterization consisted of predicted mean summer ST for the year that each biological sample was collected. Predicted mean summer ST was obtained by applying a random forest (Breiman 2001) ST model (Chapter 2) to each site. This model was developed from continuous ST data that the USGS collected at 569 reference-quality sites within the conterminous USA (see Chapter 2 for details of model development). The model used stream and watershed information (PRISM air temperature, base-flow index, topography, geology, and soils information) as predictors of ST. Model evaluation

showed that the root mean squared error (RMSE) of predictions was 1.9 °C across an observed temperature range of 5 °C – 30 °C. Of the reference-condition USGS sites with stream benthic invertebrate data, 63 had been used to calibrate the ST model. For those 63 sites, we used the random forest out-of-bag predictions of ST when developing MTNM3. Out-of-bag predictions are made by bootstrapping data and are regarded as a reasonable approximation of predictions made to an independent dataset (Cutler et al. 2007). The fourth characterization of the thermal environment consisted of measured summer STs that were provided by the USGS. We chose to use summer (July-August) stream and air temperatures in our analyses because temperatures during this period likely impose an upper thermal limit for many stream taxa.

Multi-taxa niche models

We developed four RIVPACS-type (River InVertebrate Prediction and Classification System) (Moss et al. 1987) MTNMs from benthic invertebrate data collected from the reference-condition sites. These models differed in how the thermal environment was characterized. MTNMs are constructed in five steps (Hawkins et al. 2000). First, differences in taxonomic composition (Sørensen dissimilarities) were calculated for all pairwise combinations of reference sites (vegan package, R Statistical Software). Second, we applied unweighted pair-group method with arithmetic mean flexible-β clustering (cluster package, R Statistical Software) to the dissimilarity matrix to identify groups of taxonomically similar sites. Based on visual inspection of the cluster diagram, we identified seven stream classes to use in modeling. We then developed four random forest (Breiman 2001) models to predict the probability of each site belonging to each of the seven classes as a function of its environmental setting. Each model used one of the four ways to characterize ST. We also included other stream and watershed

features that were not strongly related (i.e., |r| < 0.7) to either measured ST or any of the surrogates as additional candidate predictors. Non-thermal predictors included long-term PRISM precipitation (annual totals, maximums, minimums) (Daly et al. 2008), base-flow index (Wolock 2003), soil characteristics (Wolock 1997), and geologic types (Reed and Bush 2001) within each watershed. The fourth step consisted of predicting taxon-specific capture probabilities (p_i) at each site by weighting the frequencies of each taxon's occurrence within each group by the predicted probabilities of class membership (Moss et al. 1987):

$$p_i = \sum_{j=1}^{m} p_j \, c_{j,i}, \tag{1}$$

where p_j is the probability of a site belonging to class j of m total classes, and $c_{j,i}$ is the proportion of sites in class j that contain taxon i. Finally, these taxon-specific capture probabilities were summed for taxa with capture probabilities ≥ 0.5 to estimate the expected (E) taxa composition and richness at each site. We used $p_i \geq 0.5$ because we were mainly interested in modeling variation among sites in core (locally common) taxa and because restricting models to taxa with $p_i \geq 0.5$ usually results in greater model precision (Van Sickle et al. 2007).

We assessed model agreement with observation as the ratios of observed taxa richness (O) to the expected (E) taxa richness predicted by each MTNM (i.e., O/E ratio). Across reference-condition sites, the standard deviation (SD) of O/E values measures the precision of MTNMs (by definition O/E at a reference site is 1.0). To develop each model, we first set the temperature variables as the default starting predictors. We then used a forward selection procedure to identify a second, non-thermal, predictor variable that most improved model precision (i.e., minimized the SD of O/E values). We added additional predictors until negligible improvement in precision was detected based on

out-of-bag observations. The precision of each model was evaluated in the context of the O/E SD produced by both a null model and a model whose O/E SD is only associated with variation among replicate benthic invertebrate samples at a site (Van Sickle et al. 2005). The SD of a null model sets the lower limit (worst case) in niche model performance by assuming a taxon has the same probability of occurring at any site, and hence the expected composition and richness (E) are identical at all sites. In contrast, the O/E SD due only to variation among replicate samples sets the upper limit (best case) in model precision that can theoretically be achieved by a perfect niche model, given the variation associated with benthic invertebrate sampling (Van Sickle et al. 2005). We calculated the percent of the range (PctRange) between the best- and worst-case scenarios that each model explained:

$$PctRange = (100)\left(\frac{O/E_{SD(NULL)} - O/E_{SD}}{O/E_{SD(NULL)} - O/E_{SD(RS)}}\right), \quad (2)$$

where $O/E_{SD(NULL)}$, O/E_{SD}, and $O/E_{SD(RS)}$ are the O/E SDs of the null model, the model being tested, and replicate-sampling model, respectively. In addition, we report the model-specific O/E SD values, mean O/E values, and the additional predictors that were selected for each model.

Response of stream taxa to measured and predicted STs

We evaluated how well predicted STs matched measured STs for predicting taxon-specific probabilities of capture with graphical and regression techniques. We first graphically assessed how well modeled STs matched measured STs in predicting site-specific capture probabilities by plotting the taxon-specific MTNM3 and MTNM4-derived p_i values against predicted and measured STs, respectively. We excluded taxa with <20 observed occurrences across sites or that were identified to a coarser taxonomic

resolution than family. For each taxon, we next regressed MTNM4 p_i values on MTNM3 p_i values to evaluate how closely (r^2 and slopes) taxon-specific predictions from the two models matched. Slopes that are significantly different from 1 imply that the two models are biased estimators of one another.

We also evaluated the use the ST model in estimating thermal optima of stream taxa by comparing MTNM3-derived optima with MTNM4-derived optima. To estimate thermal optima we calculated the weighted averages of both predicted and measured ST observed at sites with the site-specific relative abundances of each taxon as weights (ter Braak and Barendregt 1986). This approach is commonly used by paleolimnologists to infer historical thermal environments by applying thermal optima estimated for extant taxa to taxa counts retrieved from sediment cores. This approach can sometimes produce biased estimates of thermal environments (Yuan 2005), but we used it here simply to test the relative agreement between thermal optima derived from predicted and measured STs. We used simple linear regression to examine agreement between modeled and measured ST-derived thermal optima.

Results

Reference-condition data

Stream sites varied greatly in terms of both taxonomic composition and thermal environments. Taxonomic aggregation resulted in 227 genera and 27 families (spanning 17 orders) that were used in modeling (Table 3-1). A few higher-order taxa (four phyla and two classes) were also included in the MTNMs (Table 3-1). Of the 481 USGS sites with stream benthic invertebrate data, 92 met our criteria for being in reference-condition (Fig. 3-1). Reference-condition sites spanned the conterminous USA, but were sparse in

the upper Midwest where agriculture is nearly ubiquitous (Fig. 3-1). Benthic invertebrate sites represented a large range of thermal conditions and streams sizes (Table 3-2). Measured mean summer STs ranged from 10.6 °C – 28.5 °C across reference sites. This range was slightly larger than was predicted by the ST model (12.3 °C – 27.4 °C), indicating slight over and under prediction at the lower and upper ends of the temperature gradient, respectively. However, average predicted

Table 3-1. List of taxa found at reference sites and used to develop multi-taxon niche models. Other taxonomic ranks included in the models were Oligochaeta, Arachnida, Nemertea, Nemata, Platyhelminthes, and Porifera.

Order	Family	Genus
Amphipoda	0	3
Arhynchobdellida	1	0
Basommatophora	2	5
Coleoptera	2	31
Decapoda	3	0
Diptera	7	78
Ephemeroptera	2	35
Hemiptera	1	2
Isopoda	0	2
Megaloptera	0	3
Mesogastropoda	1	4
Odonata	2	6
Paleoheterodonta	0	1
Plecoptera	4	16
Rhynchobdellida	0	1
Trichoptera	0	40
Veneroida	2	0

and measured temperatures were very similar (19.7 °C and 19.6 °C, respectively), and the RMSE for both measured and predicted ST at the 92 reference sites was 1.9 °C –

the same as was observed during ST model calibration (Chapter 2). Mean summer air temperatures had a similar range as ST (13.3 °C – 27.7 °C).

Niche model performances

Distinct geographic and thermal patterns were associated with the seven benthic invertebrate clusters (Figs. 3-1 and 3-2). Geographic separation between biological clusters was more distinct in eastern than western USA streams (Fig. 3-1). Predicted and measured ST varied in a similar way among the seven biological clusters, and ST discriminated several clusters from one another (Fig. 3-2). Clusters with substantial thermal overlap were often separated by large geographic distances but also differed in terms of other predictor variables. For example, clusters 1 and 3 had similar thermal environments (Figs. 3-2) but differed in terms of precipitation (not shown here).

The MTNMs that used predicted and measured ST (MTNM3, MTNM4) both accounted for 71% of the possible range in O/E SD (Table 3-3), and ST was the best predictor of taxonomic composition in both models. Indeed, removal of ST from either model reduced PctRange from 71% to 29%. MTNM1 (elevation, latitude, and watershed area) and MTNM2 (mean summer air temperature) explained 29% and 43% of this range, respectively. All models slightly underestimated observed sample richness (cf. mean O/E values in Table 3-3); a consequence of the use of p_i values > 0 and the relatively small number of reference sites used in the RIVPACS models (Yuan 2006). MTNM3 and MTNM4 were similar in model performance, but the models differed in terms of the non-thermal predictors that were selected. In addition to predicted ST, MTNM3 used total long-term annual precipitation (mm), number of days with measurable

Fig. 3-1. Distribution of 92 reference-condition USGS streams with benthic invertebrate samples. Symbols represent biological clusters.

Table 3-2. Summary statistics for predicted (P-) and measured (M-) mean summer stream temperature (MSST), mean summer air temperature (MSAT), elevation (Elev), latitude (Lat), and watershed area (WA) at reference-condition sites. Annual precipitation (AnnPrcp) and day of the year (DOY) benthic invertebrate were sampled are also included in this table.

	P-MSST (°C)	M-MSST (°C)	MSAT (°C)	Elev. (m)	Lat. (deg.)	WA (km^2)	AnnPrcp (mm)	DOY (day)
Mean	19.7	19.6	22.3	649	39.87	600	1077	204
Min.	12.3	10.6	13.3	13	30.70	5	348	106
Max.	27.4	28.5	27.7	2440	47.57	10189	3070	287

precipitation during the driest month each year, base-flow index, and the % of the upstream watershed composed of quaternary geology. In contrast, MTNM4 used 6 predictors in addition to measured ST, including the day of year that invertebrate samples were collected, minimum and long-term total annual precipitation (mm), % of the watershed composed of granitic geology, average depth to water table (m), and soil bulk density (grams/cm^3) within the watershed. The best model achieved with air

temperature (MTNM2) included total precipitation during the driest month (mm), days with measurable precipitation during the wettest month of the year, average depth to the water table (m), and % of the watershed composed of sedimentary geology. MTNM1 included total number of days per year with measureable precipitation and total annual precipitation (mm).

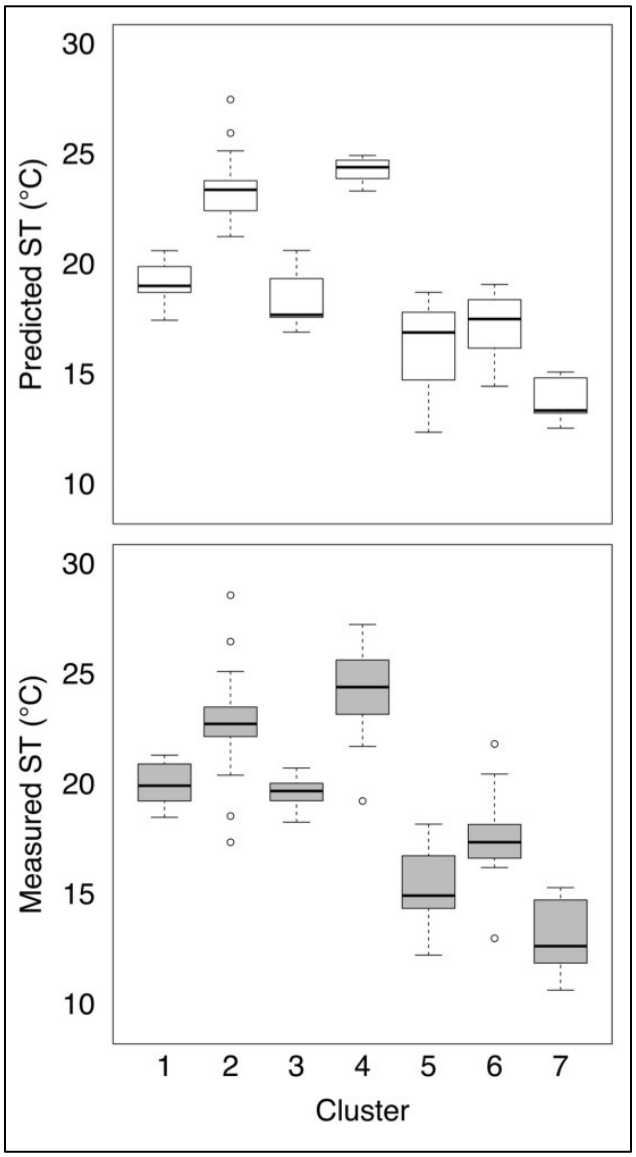

Fig. 3-2. Boxplots of predicted and measured stream temperature (ST) versus the 7 biological clusters derived from benthic invertebrate distributions.

Taxon-specific responses to measured and predicted STs

Use of measured and predicted STs resulted in similar taxon-specific associations with temperature. Of the 56 taxa observed at ≥20 sites, predicted capture probabilities varied markedly in relation to both predicted and measured ST (see Fig. 3-3 for examples and Appendix A for plots of all 56 taxa). Capture probabilities often exhibited monotonic increasing, monotonic decreasing, or unimodal responses to variation in ST (Fig. 3-3). Although patterns derived from MTNM3 and MTNM4 were usually very similar to one another, patterns did differ for a few taxa (e.g., the Coleopteran genus *Psephenus* as illustrated in Fig. 3-3). The average r^2-value for the regression of MTNM4- on MTNM3-derived predicted capture probabilities was 0.85 (range: 0.73 – 0.95). Despite this general agreement, 29 of the 56 MTNM4 on MTNM3 regression slopes were statistically different from 1 ($p < 0.05$; genera with slopes different from 1 are marked with an asterisk in plots of each regression in Appendix B). The mean slope for the statistically different regressions was 0.86, indicating that the MTNM3 model either under predicted

Table 3-3. Performance statistics of multi-taxon niche models based on predicted (P-) and measured (M-) mean summer stream temperature (MSST), mean summer air temperature (MSAT), and elevation, latitude, and drainage area (ELWA). The standard deviation (SD) of observed-to-expected (O/E) taxonomic richness measures niche model precisions. Unbiased models should have mean O/E values close to 1. The table also includes the % of the range (PctRange) each model captures between a null model SD (worst case) and a theoretical replicate-sample model SD (best case). Null and replicate-sample SDs were 0.20 and 0.13, respectively.

Base model	O/E_{SD}	Mean O/E	PctRange
P-MSST	0.15	1.05	71
M-MSST	0.15	1.05	71
MSAT	0.17	1.03	43
ELWA	0.18	1.03	29

high capture probabilities or over predicted low capture probabilities relative to the MTNM4 model. Finally, there was a high degree of correspondence between taxon-specific thermal optima derived from relative abundance-weighted averages based on predicted and measured ST (Fig. 3-4) (r^2 = 0.97, slope = 1.09).

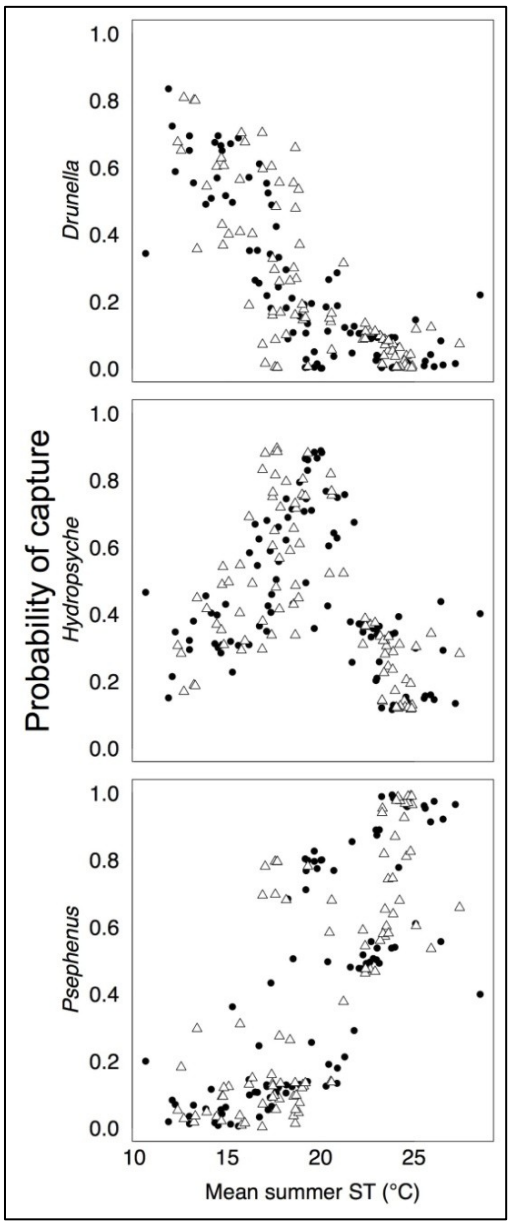

Fig. 3-3. Response of the predicted capture probabilities of 3 benthic invertebrate genera versus predicted (white triangles) and measured (black circles) stream temperature (ST).

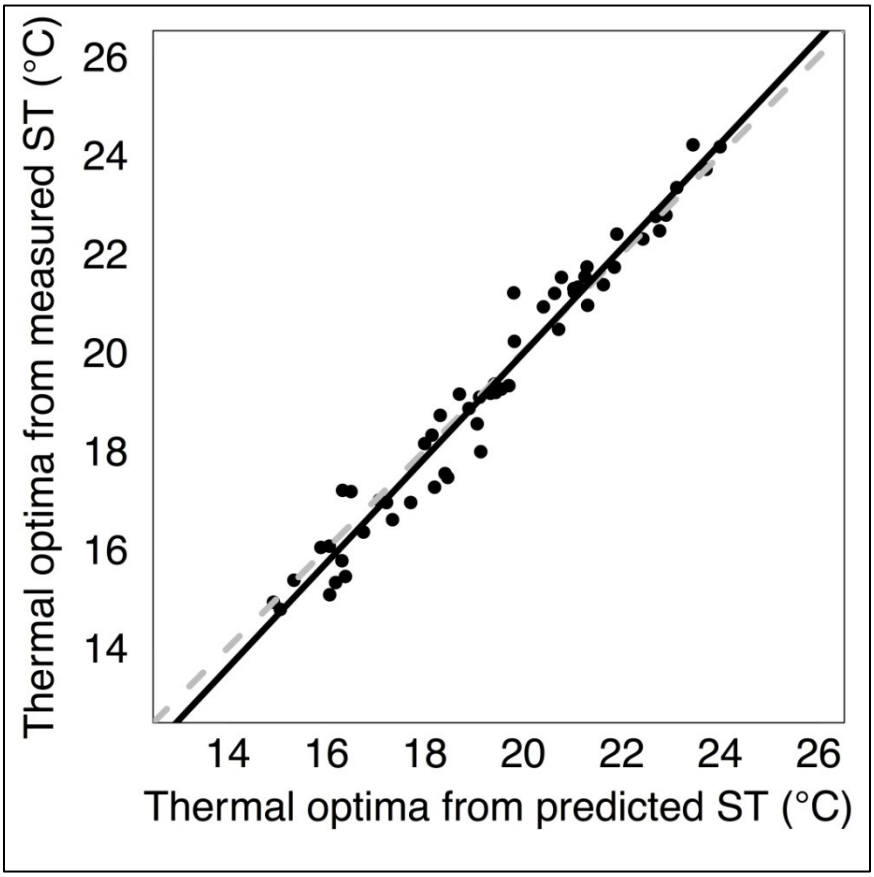

Fig. 3-4. Regression of thermal optima derived for 56 benthic invertebrate taxa from predicted and measured stream temperature (ST). Regression r^2 = 0.97 and slope (black line) = 1.09. The grey dashed line represents the 1:1 line.

Discussion

Our results show that modeled ST can accurately represent ecologically relevant thermal environments when measurements are unavailable or when reference-condition temperatures are required. Indeed, predicted STs surpassed our expectations for predicting the composition of stream benthic invertebrates and for estimating taxon-specific thermal optima. However, several factors must be considered when applying these ST models for use in ecological studies. Here, we provide context for considering under what conditions predicted STs might be used and their potential limitations. We

consider potential reasons for observed differences between selected predictors in MTNM3 and MTNM4 and the implications of these differences. In addition, we discuss potential applications of ST models for helping understand and manage stream ecosystems. Finally, we conclude by considering how ST models can help improve prediction and interpretation of species thermal niches.

The unexpectedly strong performance of predicted STs was probably due to (1) the close agreement between predicted and measured ST (Chapter 2) and (2) the strength of responses to temperature by stream communities. Our ST model was driven primarily by air temperature, but the inclusion of additional variables that can influence local ST (Poole and Berman 2001) and the use of random forest models to account for nonlinearities between ST and predictor variables (Cutler et al. 2007) allowed us to more fully characterize thermal differences among sites than was possible with ST surrogates. The general importance of ST in structuring stream communities is illustrated by the fact that use of relatively coarse ST surrogates, such as air temperature, can reveal thermal related patterns in the distribution (Rahel and Nibbelink 1999) and composition (Domisch et al. 2013) of stream species. Modeled STs were precise and unbiased enough to predict both the composition of stream taxa and taxon-specific thermal optima as precisely as observed STs over the range of observed STs (17.9 °C). If the range of thermal conditions among sites is small, it is unlikely that either predicted or observed temperatures would strongly discriminate biological differences among sites. However, additional work is needed to determine the minimum differences in ST that produce a detectable biological response. This information would allow us to assess if our ST models are sufficiently precise to characterize ecologically important thermal conditions among streams or if more precise temperature models are needed. In addition, the temporal resolution of our ST model (July-August) limits its use for studying effects of

shorter-term (daily or weekly) thermal variation on stream biota. Enhancing the temporal resolution of our ST model is theoretically possible but is practically limited by the temporal resolution of the PRISM climate data (monthly) that largely drives the ST model. Relatively few studies have attempted to identify the thermal parameters (e.g., mean temperature, peak temperature) most strongly associated with variation in benthic invertebrate assemblage composition (Haidekker and Hering 2008). Such information is needed to guide future ecologically-based, ST modeling.

We cannot fully explain why MTNM3 and MTNM4 differed in the non-thermal predictors that were selected. From a prediction context, these differences do not appear to be important, e.g., relationships between taxon-specific capture probabilities and predicted and measured STs were similar (Fig. 3-3). In addition, estimates of thermal optima (Fig. 3-4) derived from the two models were similar. Given that we used an empirical model to predict STs, we suspect that the differences in the non-thermal predictors used in the two niche models are associated with the degree to which these variables are truly statistically independent of stream temperature. Slight differences in correlations between the non-thermal predictors and the two thermal variables could result in different variables being selected in the two niche models.

Modeled STs have the potential to advance both understanding and management of stream ecosystems in at least three ways. First, an important advantage of using predicted STs in niche models is that interpretability was greatly improved relative to that of temperature surrogates. This increased interpretability was evident in both the p_i-modeled ST relationships and the estimates of thermal optima. Neither surrogate of ST used in MTNM1 nor MTNM2 could be used to derive actual taxon-specific ST optima. Thus, our results suggest that ST models are capable of both improving the precision of stream species niche models and improving the interpretation

of temperature-dependent relationships. Second, modeled STs can be used to characterize the natural thermal environments of thousands of streams within the conterminous USA that lack temperature records. Such predictions could greatly enhance the analysis and interpretation of large biological data sets that have been compiled over the last 2 decades. For example, the Western Center for Monitoring and Assessment of Freshwater Ecosystems (www.cnr.usu.edu/wmc) and the National Aquatic Monitoring Center (www.usu.edu/buglab) jointly maintain a database of more than 30,000 benthic invertebrate samples collected from thousands of sites in the western USA. However, little-to-no temperature information is available for most of these sites. Other databases of this nature exist at a national scale, such as those based on the USEPA's National Aquatic Resource Surveys and the USGS's National Water Quality Assessment (NAWQA) program. Application of ST models to sites in these databases could (1) refine our understanding of the extent to which local and regional stream macroinvertebrate biodiversity is influenced by temperature, (2) allow statistically robust estimates of thermal preferences for hundreds of stream invertebrate taxa, and (3) guide development of biologically-relevant temperature criteria for streams and rivers. Moreover, by coupling niche models to ST models, we can predict patterns of biodiversity in entire stream networks across large regions to better understand macro-spatial patterns in biodiversity. Third, the effects of climate change on stream ecosystem will present a major challenge to water resource managers. Managers will need to understand and detangle climate-related alterations in ST from those already imposed by other human-caused watershed and channel alterations. ST models could provide an important tool for predicting the region- and site-specific vulnerability of ST to climate change, understanding likely biological response to those changes (through coupling

with niche models), and focusing mitigation where such efforts are most likely to succeed.

Characterizing and predicting thermal niches is increasingly important for understanding stream biodiversity and human-caused alterations to this diversity. Several steps can be taken to improve the characterization of species-specific thermal niches. We need to first identify the best approach for modeling thermal niches from field samples. The multi-taxon models used here are attractive because they predict both taxonomic composition and taxon-specific capture probabilities with a single model. In addition, community-level models may both account for species interactions and improve predictions of rare species (Ferrier and Guison 2006, Bonthoux et al. 2013). However, single-taxon niche models can be tailored to individual species and may provide better species-specific niche predictions for core species. Second, we need to broaden the range of thermal conditions over which niche models are developed. For example, field data often fail to cover the full breadth of thermal conditions over which many taxa occur. Statistically modeled thermal niches based on these data often exhibit monotonic increasing or decreasing responses to ST (e.g., *Drunella* and *Psephenus* in Fig. 3-3, see also Yuan 2004), which are unlikely to fully represent the thermal niches of most ectotherms (Pörtner et al. 2006). Large-scale application of ST models could provide a broader thermal window for characterizing and modeling the thermal niches of many species. Finally, the degree to which thermal niches derived from field data can be interpreted in terms of physiological responses of species to temperature needs to be experimentally validated. Such validation would increase confidence in interpreting the mechanistic foundations underlying model predictions and hence our confidence in their application. The role that temperature plays in structuring and maintaining stream biodiversity will be best understood through integration of both natural and laboratory

experiments, i.e., each approach provides validation and interpretation to the other (Pörtner et al. 2006). Improved understanding, quantification, and validation of thermal niches will be important for moving towards mechanistic-based predictions in community ecology.

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CHAPTER 4

PREDICTING THERMAL VULNERABILITY OF STREAM AND RIVER ECOSYSTEMS TO CLIMATE CHANGE*

Abstract

We used predictive models of mean summer, mean winter, and mean annual stream temperature (ST) to assess the vulnerability of USA streams to thermal alteration associated with climate change (CC). Models were calibrated with recent (1999-2008) data from several hundred US Geological Survey ST sites in the conterminous USA. The models used air temperature (AT) and watershed features (e.g., watershed area and slope) as predictors. To assess how well models predicted climate-related changes in STs (ΔST), we compared observed and predicted ΔSTs for each site. For these comparisons, we subtracted the earliest observed ST record (1972-1998) at each site from observations used for calibration. We calculated predicted ΔSTs in the same way. Analysis of covariance showed that observed and predicted ΔST responded similarly to changes in AT. When applied to spatially-downscaled climate model projections of AT (A2 emission scenario) for the end of the 21st century (2090-2099), the ST models predicted nationally-averaged ST warming of ~1.6 °C. STs were most responsive to CC in the Cascade, Rocky, and Appalachian Mountains and least responsive to CC in the south-eastern USA. We used random forest models to identify those stream features most strongly associated with both observed (1972-1998 vs 1999-2008) and predicted future (2000-2010 vs 2090-2099) changes in summer, winter, and annual STs. Several consistent relationships emerged across the models. Larger ΔSTs were generally

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* Coauthored by Charles P. Hawkins and Jiming Jin.

associated with warmer future ATs (increase in magnitude of exposure), greater AT changes (change in exposure), and larger watershed areas. Smaller ΔSTs were predicted for streams with high initial rates of heat loss associated with long-wave radiation and evaporation and relatively greater groundwater contributions (measured as the base-flow index). These models provide important insight into the potential extent of ST warming within the conterminous USA and why some streams will likely be more vulnerable to CC than others.

Introduction

Climate change (CC) is projected to have profound effects on stream ecosystems (Buisson et al., 2008; Chessman, 2009; Woodward et al., 2010; Domisch et al., 2011, 2013). However, forecasting the effects CC will have on specific stream ecosystems will require that we first understand how the thermal environments of individual streams will respond to CC. Developing this understanding will require that we better characterize how local climates will change at individual streams and how local stream features and processes will interact with these local changes in climate to affect stream temperatures (STs).

Both changes in heat input and the channel and watershed attributes that influence heat fluxes within streams determine the vulnerability of streams to thermal alteration. In general, climate is a good surrogate of overall stream heat budgets as evidenced by the strong spatial and temporal association between ST and air temperature (AT) (Stefan and Preud'homme, 1993; Mohseni et al., 1998, 1999, 2003; Pilgrim et al., 1998). STs are therefore expected to parallel future changes in climate. Indeed, numerous studies of historical records from around the world confirm that STs have generally followed AT trends over the last century (Webb, 1996; Langan et al.,

2001; Hari et al., 2006; Durance and Ormerod, 2007, 2009; Webb and Nobilis, 2007; Pekarova et al., 2008; Bonacci et al., 2008; Chessman, 2009; Kaushal et al., 2010; Isaak et al., 2010, 2011; Elliott and Elliott, 2010; Kvambekk et al., 2010). However, these studies were based on relatively few streams and short periods of record, making it difficult to generalize from them regarding (1) the potential future extent of ST warming within the conterminous USA, (2) where the most and least vulnerable streams are, and (3) why some streams are more vulnerable to CC than others.

A major challenge in estimating how climates will change for individual streams is that general circulation model (GCM) forecasts are too spatially coarse to adequately characterize local changes in climate. GCMs are computationally intensive to develop and are therefore often produced with spatial resolutions of ~150 km at the latitude of the continental USA - an area equivalent to the US state of New Jersey. At such coarse spatial resolutions, these global models cannot account for important surface processes, such as those associated with complex topography, to provide realistic local estimations of CC. Most previous CC-ST studies have either used GCM projections for which single values represent CC across large, topographically heterogeneous regions (e.g., Mohseni et al., 1999, 2003) or assumed stepwise shifts in AT (e.g., +2 °C to +6 °C) to examine ST responsiveness to a range of potential future climates (e.g., van Vliet et al., 2011; Null et al., 2013). However, we need finer resolved climate information to understand how exposure of individual streams to atmospheric-related forcings will be altered by CC to make better site and region-specific ST projections (Flint and Flint, 2012). Climate projections can be spatially refined through statistical (Hijmans et al., 2005) and dynamical (Jin et al., 2011) downscaling, or a hybrid of both approaches (Chu et al., 2008; Meija et al., 2012) to improve characterization of local climates (see review of downscaling approaches by Fowler et al., 2007).

The degree to which STs at individual streams respond to CC depends on a balance between heat gains and losses. In general, streams that experience greater climate warming should be more susceptible to ST warming. However, the initial, pre-CC, thermal state of a stream should influence the amount of additional heat it can assimilate. Warmer streams experience greater heat loss due to evaporation and long-wave radiation, which are the dominant non-advective heat losses from streams (Caissie, 2006; Webb et al., 2008). As streams progressively warm, these losses can eventually match heat gains thereby limiting the warmest temperature a stream can achieve (Mohseni and Stefan, 1999; Mohseni et al., 2002). To understand and forecast ST vulnerability we must understand the relative influence of both exposure to climate warming and heat loss, and how both processes may vary geographically.

Numerous approaches have been employed to examine the potential response and vulnerability of STs to CC. Mohseni et al. (1999, 2003) developed logistic ST-AT regression models for hundreds of streams across the continental USA to predict potential shifts in fish thermal habitats in association with CC (Mohseni et al. 2003), but this approach did not provide insight into why some streams are more vulnerable to CC than others. Recently, van Vliet et al. (2011) built on the approach of Mohseni et al. (1999, 2003) by including discharge as a covariate with AT in logistic regression models of ST for streams located around the world. Incorporating discharge improved the regression models, and perturbing flows by -20%, -40%, and +20% exacerbated or moderated the predicted effects of AT shifts on STs by an average of +0.3 °C, +0.8 °C, and -0.2 °C, respectively. Kelleher et al. (2012) developed individual logistic ST-AT regression models for 57 streams in Pennsylvania, USA. They then used multiple-linear regression to identify stream and watershed features associated with the slopes of the individual logistic curves, which indicate differences in the responsiveness of ST to

changes in AT. Streams with greater base-flow index values were less responsive to AT variability, whereas streams with Strahler stream order > 3 were more responsive. Isaak et al. (2010) used spatial regression to account for the effects of climate variation and fire regime on STs over a 13-year period within the Boise River, Idaho. ST warming was most strongly related to AT warming, but was also greatest in watersheds where fires had also occurred (Isaak et al., 2010). Recently, Isaak and Rieman (2013) used ST-elevation lapse rates, long-term climatic warming rates, and simple trigonometric relationships to further estimate that ST isotherms within the Boise River shifted by 1.5-43 km in stream length during the 20th century and could shift an additional 5-143 km by ~2050. Others have used deterministic models to examine the responsiveness of STs to CC (e.g., Stefan and Sinokrot, 1993; Morrison et al., 2002; Gooseff et al., 2005; Null et al., 2013). For example, Null et al. (2013) used coupled mesoscale deterministic ST and hydrologic models to examine the effects of hypothetical +2 °C, +4°C, and +6 °C AT change scenarios in the Sierra Nevada Mountains, California. STs were responsive to alterations in runoff volume and timing associated with precipitation shifting from rainfall to snowfall. Deterministic models provide important insight regarding the processes that drive observed trends in ST (Arismendi et al., 2012) and allow for testing of stream-specific management scenarios designed to mitigate CC effects (Null et al., 2013). However, if calibrated appropriately with physically meaningful predictors, empirical models of ST vulnerability could: (1) identify streams and regions that may be especially susceptible to CC, and (2) identify stream and watershed features associated with this vulnerability. Doing so at the scale of the Nation could result in an important tool for focusing and improving research and mitigation efforts within the USA.

Our primary objective was to estimate future effects of CC on the thermal condition of streams within the conterminous USA. In addition, we sought to determine

the stream and watershed features that were most strongly associated with climate-related ST vulnerability. To address these objectives, we first determined if three previously developed empirical models (Chapter 2) could adequately predict the effects of CC on mean summer, winter, and annual STs within the conterminous USA. We evaluated three specific aspects of these ST models for predicting CC effects on ST: (1) how faithfully did the models predict past climate-related changes in ST (henceforth ΔST), (2) did the models predict past STs with enough precision to detect climate related ΔSTs, and (3) over what geographic range within the conterminous USA could these predictions be made with confidence. After model evaluation, we then estimated ΔSTs over a 100-year analysis window by applying downscaled climate predictions made for the beginning (2001-2010) and end (2090-2099) of the 21st century to the ST models. Finally, we developed additional empirical models to identify those stream and watershed features most strongly associated with ST vulnerability.

Materials and Methods

Reference condition ST models

For this study, we used random forest models (Breiman, 2001) that we previously developed to predict mean summer (July-August), mean winter (January-February), and mean annual STs under recent climate conditions (1999-2008) (see Chapter 2 for details). We used the randomForest (Liaw and Wiener, 2002) library in the R statistical software (version 2.15.1, R Development Core Team) to develop the models. Random forest is a non-linear, non-parametric modeling technique that can capture important interactions between predictors and is insensitive to over-fitting and correlated predictors (Breiman, 2001; Cutler et al., 2007). We developed the models with United States Geologic Survey (USGS) data from 569 summer, 480 winter, and 273 annual ST sites

that had minimal human-caused stream and watershed alteration, i.e., reference condition (Stoddard et al., 2006). These sites were distributed across the conterminous USA and represented a large range of physical environments and river sizes (e.g., watershed areas of 0.5-100,000 km^2). However, reference-condition sites were sparse in regions that are dominated by agricultural land use. We used single years of ST record because very few USGS sites have long-term temperature data for modeling. When a site had >1 year of record, we randomly selected one record from 1999-2008 for analysis. We matched specific years of ST and PRISM climate AT data (Daly et al., 2008) to incorporate both spatial and annual variation in STs and ATs when modeling. We included spatial stream and watershed features as predictors, such as drainage area, base-flow index (Wolock 2003), soil and geologic permeability (Wolock 1997, Reed and Bush 2001), and channel slope to provide environmental context and improve both performance and interpretation of the models (see Chapter 2 for details of predictor derivations). The models explained a large proportion of the observed variance in STs (summer r^2 = 0.87, winter r^2 = 0.89, annual r^2 = 0.95), were unbiased, and had root mean squared errors (RMSE) of 1.9 °C (summer), 1.4 °C (winter), and 1.1 °C (annual) (Chapter 2). Notably, PRISM AT was the best predictor in each ST model.

Assessing the ST models for predicting effects of CC on streams

To evaluate how well our models could predict the effects of CC on STs at individual stream sites, we compared observed and predicted changes in historical ST. If predicted and observed ΔSTs behave similarly in response to AT shifts, the models may be useful for assessing the potential effect of future CC on STs. We used the earliest ST data (1972-1998) for which we could calculate mean summer, mean winter, and mean annual STs based on the same data sufficiency requirements applied in Chapter 2.

These requirements resulted in 133 summer, 127 winter, and 92 annual ST sites with data prior to 1999. If a site had multiple years of ST record, we selected the earliest available year. We then matched the selected site-year ST records with the corresponding site-year PRISM AT climate data and applied the ST models to predict historical STs. The mean annual ST model used both AT and precipitation as predictor variables. To examine the effects of AT variability in isolation and in tandem with precipitation variability, we made two sets of historical mean annual ST predictions: (1) with AT changes only (i.e., precipitation kept at calibration values), and (2) with both AT and precipitation changes.

We calculated the differences between observed current (O_{curr}) and observed historical (O_{hist}) STs:

$$\Delta ST_O = ST_{O_{curr}} - ST_{O_{hist}} \quad (1)$$

and predicted current (P_{curr}) and predicted historical (P_{hist}) STs:

$$\Delta ST_P = ST_{P_{curr}} - ST_{P_{hist}}. \quad (2)$$

We then regressed ΔST_O and ΔST_P on changes in PRISM AT (AT_{curr} - AT_{hist}) for the same sites over the years for which we had ST data. We used analysis of covariance (ANCOVA) with alpha = 0.05 to test for differences in the regression slopes and intercepts of ΔST_O and ΔST_P as functions of ΔAT. ANCOVA first tests for differences in the slopes of two regression lines. Similar slopes would indicate that ΔST_O and ΔST_P behave similarly in response to ΔAT. If slopes are statistically identical, ANCOVA then tests for differences in the regression intercepts. Different regression intercepts would indicate systematic bias (consistent over- or underprediction) in the ΔST_P response to ΔAT, relative to ΔST_O. Finally, ANCOVA also tests whether the slopes of the two regressions lines are different from 0. If the ΔST-ΔAT regression slope is different from

0, it suggests that the precision of the ST predictions is sufficient to detect climate-related ST variability.

Assessing the geographic scope of ST models under climatic conditions

Random forests are a tree-based modeling technique (Breiman, 2001), and therefore cannot extrapolate beyond the data used to develop them. Attempts to extrapolate with predictor values higher or lower than those used to develop the models result in flat response curves above and below these predictor values, respectively. We therefore quantified the proportion of the conterminous USA that was predicted to have AT values outside of the experience of our random forest ST models by the end of the 21st century (2090-2099). These regions do not necessarily represent AT environments that are novel to the conterminous USA, but rather places where the model cannot be applied with confidence to make ST projections. We removed any USGS ST sites that fell within these pixels from further analyses of CC-related changes in ST. In addition, we present maps of these regions.

Future climate and ST projections

We used 10-yr mean AT values to represent the climate expected for a typical year at both the beginning and end of this century. These AT values were derived from hybrid-downscaled (i.e., dynamically and statistically) climate predictions. We first used the Weather Research and Forecasting (http://wrf-model.org/index.php) regional climate model to dynamically downscale the Community Climate System Model (CCSM3) (Collins et al., 2006) simulations under the A2 emission scenario from a resolution of ~150 km to 50 km for the conterminous USA (see Jin et al. 2011 for methods). The downscaled model was developed with CCSM3 output from 1949-2000, and 50-km projections were produced for 2001-2010 (henceforth 2000s) and 2090-2099 (henceforth

2090s). These 50-km climate grids were then statistically downscaled to 4 km by creating regression relationships between the 50-km pixels and each of the 4-km PRISM pixel within them. We then applied the regression relationships to the area within each 50-km climate pixel that corresponded with each 4-km PRISM pixel to produce spatially downscaled and bias-corrected monthly climate projections. These downscaled climate projections were then temporally averaged to create national-level summer, winter, and annual 10-yr AT means for the 2000s and 2090s. We considered these decadal AT means to represent the most likely climate condition experienced by streams for any given year during each decade. We then applied these 10-yr AT means to each ST model to predict mean summer, mean winter, and mean annual STs at the beginning and end of the 21st century. To evaluate the use of the downscaled AT projections in the ST models, we compared summer, winter and annual ST predictions made with the downscaled 10-yr AT means for the 2000s with predictions made with decade-averaged PRISM ATs for the same period. Predictions made with the downscaled climate grids closely matched those made with PRISM climate data (all r^2-values ≥ 0.98), indicating that the downscaled climate projections did not introduce additional bias or error to the ST predictions. We subtracted the ST predictions made for the 2000s from ST predictions made for the 2090s to estimate future climate-related changes in summer, winter, and annual STs:

$$\Delta ST_{fut} = ST_{P_{2090s}} - ST_{P_{2000s}}. \quad (3)$$

We calculated nationally-averaged future ΔSTs and mapped site-specific changes to explore spatial patterns in ST vulnerability to CC.

Predicting ST vulnerability to CC

We used random forest modeling to identify those stream and watershed features most strongly associated with predicted ΔST. We developed two sets of models based on two datasets of estimated ΔST. The first dataset included measured historical ΔST (i.e., ΔST_O in Equation 1) based on the 133 summer, 127 winter, and 92 annual ST sites with data prior to 1999 that were used for model evaluation. The second dataset included predicted future ΔSTs (ΔST_{fut} in Equation 3) from all USGS sites that were used to calibrate the original ST models (569 summer, 480 winter, and 273 annual sites) and were also predicted to be within the experience of the ST model at the end of the 21st century. The first dataset (ΔST_O) was smaller, but consisted of measured ST values. In contrast, the second dataset (ΔST_{fut}) had greater sample sizes and ranges of environmental conditions, but consisted of predicted ST values. For each set of models, we related summer, winter, and annual ΔSTs (six models in total) to watershed size, base-flow index (Wolock 2003), soil characteristics (Wolock 1997), % of geologic types within the watershed (Reed and Bush 2001), channel and watershed slopes, and the presence and size of lakes and wetlands within the watershed (Homer et al. 2007). In addition, we included both future AT and changes in AT expected at each site to represent the potential future exposure to climatic forcings that influence ST and changes in exposure from initial conditions, respectively.

For each ΔST model, we estimated the potential evaporative heat loss and long wave radiation emitted by each stream at the beginning of each model period. For example, we estimated these energy losses during the 2000s to represent the initial thermal states of the streams to predict ΔSTs by the end of the 21st century. We estimated potential evaporative heat loss from empirical relationships between vapor pressure and ST and PRISM dew point temperature (Chapra 1997):

$$VPD = 4.59e^{\frac{17.27ST}{237+ST}} - 4.59e^{\frac{17.27DPT}{237+DPT}}, \quad (4)$$

where VPD is the vapor pressure deficit (kPa) at the air-water interface, and ST and DPT are the measured stream and PRISM air dew point temperatures (°C) at each site. We used the Stefan-Boltzmann law to approximate differences in long wave radiation among sites based on the initial ST as:

$$LWR = \varepsilon\varphi(ST + 273)^4, \quad (5)$$

where LWR is the long wave radiation emitted by a stream (Wm^{-2}), ε is the emissivity of water (~0.97), and φ is the Stefan-Boltzmann constant (5.67×10^{-8} $Wm^{-2}K^{-4}$).

We used a forward selection procedure to identify the predictor variables most strongly associated with each measure of ΔST. We first identified the single predictor that explained the greatest proportion of variation in ΔST (random forest pseudo r-squared). We sequentially added additional predictors to the model if they both improved the random forest pseudo r-squared by about ≥5 points and had moderately low correlations ($r \leq |0.60|$) with predictors already within the model to minimize redundancy between predictors. For each selected predictor, we then created a partial dependence plot (Hastie et al. 2001) to interpret its association with ΔST. Partial dependence plots are sensitive to the overall means of the response variables and can therefore be difficult to compare. To facilitate comparisons between the observed historical ΔST and predicted future ΔST models, we standardized ΔSTs in both to have means = 0 and standard deviations = 1 (i.e., z-scores). Random forests also produce a ranked list of the importance each predictor has in explaining variation in ΔST, which we provide for each model.

Results

ST models for CC studies

The slopes for the regressions of ΔST_O and ΔST_P on ΔAT were not significantly different from each other for summer, winter, or annual STs (Table 4-1). However, the regression intercepts of ΔST_P on ΔAT for each model were different from the ΔST_O intercepts, and under predicted the average responses of summer, winter, and annual ΔST to ΔAT by 0.49 °C, 0.26 °C, and 0.50 °C respectively (Table 4-1). Estimates of CC-related effects on STs will therefore likely be conservative. Although the variance explained in each model was low (Table 4-2), ΔSTs in all models were positively and statistically significantly associated with ΔATs (Table 4-1), indicating that model precision was sufficient to detect climate-related ΔST. For mean annual ST, the regressions produced by varying ATs only and both ATs and precipitation were essentially identical, indicating that including precipitation as a predictor did not improve the accuracy or precision of the ΔST estimates (Table 4-1). We therefore used AT-only predictions of mean annual STs in subsequent analyses.

Geographic scope of ST models under past and future climatic conditions

Most predicted future thermal climatic conditions were represented by the data used to calibrate the ST models (i.e., ≥95% of predicted future ATs were within the experience of all models). The climate models predicted summer and annual AT environments that were novel to the ST models in southern California, Nevada, Arizona, and Texas. Additional future novel winter and annual AT environments were predicted to occur in southern Florida (Fig. 4-1). Very few ST sites that were used to calibrate the ST models were predicted to have novel AT conditions by the 2090s: 4 summer

Table 4-1. Analysis of covariance (ANCOVA) of observed and predicted (OvsP) changes in mean summer, mean winter, and mean annual stream temperatures versus observed changes in air temperature (ΔAT). ANCOVA first checks for statistically significant differences in slopes ($p < 0.05$) between observed and predicted STs (significant ΔAT x OvsP interactions) (bold p-values). If none is found, it then checks for significant differences in regression intercepts, i.e., adjusted means (OvsP). Where differences in intercepts are detected, the parameter estimate of OvsP represents the bias associated with predicted ΔST (p-values marked with "*"). Statistically significant relationships were also observed between ΔAT and ΔST in each model (underlined p-values).

Model	Param. Estimate	Std Error	t	p-value
Summer-				
Test for difference in slopes				
Intercept	0.58	0.11	5.50	<0.001
ΔAT	0.42	0.07	6.10	<u><0.001</u>
OvsP	-0.55	0.15	-3.71	<0.001
ΔAT x OvsP	0.11	0.10	1.19	**0.237**
Test for difference in means				
Intercept	0.55	0.10	5.37	<0.001
ΔAT	0.47	0.05	9.78	<u><0.001</u>
OvsP	-0.49*	0.14	-3.52	**<0.001**
Winter-				
Test for difference in slopes				
Intercept	0.15	0.07	2.24	0.026
ΔAT	0.28	0.03	10.10	<u><0.001</u>
OvsP	-0.25	0.09	-2.63	0.009
ΔAT x OvsP	-0.02	0.04	-0.52	**0.602**
Test for difference in means				
Intercept	0.16	0.07	2.33	0.020
ΔAT	0.28	0.02	13.78	<u><0.001</u>
OvsP	-0.26*	0.09	-2.77	**0.006**
Annual (AT-only)-				
Test for difference in slopes				
Intercept	0.48	0.07	6.70	<0.001
ΔAT	0.44	0.06	6.86	<u><0.001</u>
OvsP	-0.47	0.10	-4.68	<0.001
ΔAT x OvsP	-0.05	0.09	-0.52	**0.601**
Test for difference in means				
Intercept	0.49	0.06	7.55	<0.001
ΔAT	0.42	0.05	9.19	<u><0.001</u>
OvsP	-0.50*	0.08	-6.04	**<0.001**

Table 4-1. Continued.

Model	Param. Estimate	Std Error	t	p-value
Annual (AT + precipitation)-				
Test for difference in slopes				
Intercept	0.48	0.07	6.66	<0.001
ΔAT	0.44	0.06	6.82	<0.001
OvsP	-0.46	0.10	-4.51	<0.001
ΔAT x OvsP	-0.08	0.09	-0.83	**0.409**
Test for difference in means				
Intercept	0.50	0.07	7.63	<0.001
ΔAT	0.40	0.05	8.83	<0.001
OvsP	-0.50*	0.08	-6.03	**<0.001**

Table 4-2. Coefficients of determination (r^2 values) between historical changes in observed (ΔST_O) and predicted (ΔST_P) stream temperature and observed air temperature (ΔAT).

Model	ΔST_O	ΔST_P
Summer	0.15	0.53
Winter	0.36	0.57
Annual	0.26	0.43

(southern Nevada and coastal South Carolina and Georgia), 8 winter (southern Florida), and 10 annual sites (Florida) (sites identified with “Xs” in Fig. 4-1). The removal of these sites resulted in 565 summer, 472 winter, and 263 annual sites that we used to make ST projections to the 2090s.

Climate and ST projections

ATs at study sites were projected to warm by 3.0°C to 3.3 °C on average over the next century. In response to these changes, the ST models predicted average warming of 1.7 °C for summer STs, 1.7 °C for winter STs, and 1.6 °C for mean annual STs (Table 4-2). However, values of future ΔSTs varied greatly among individual sites

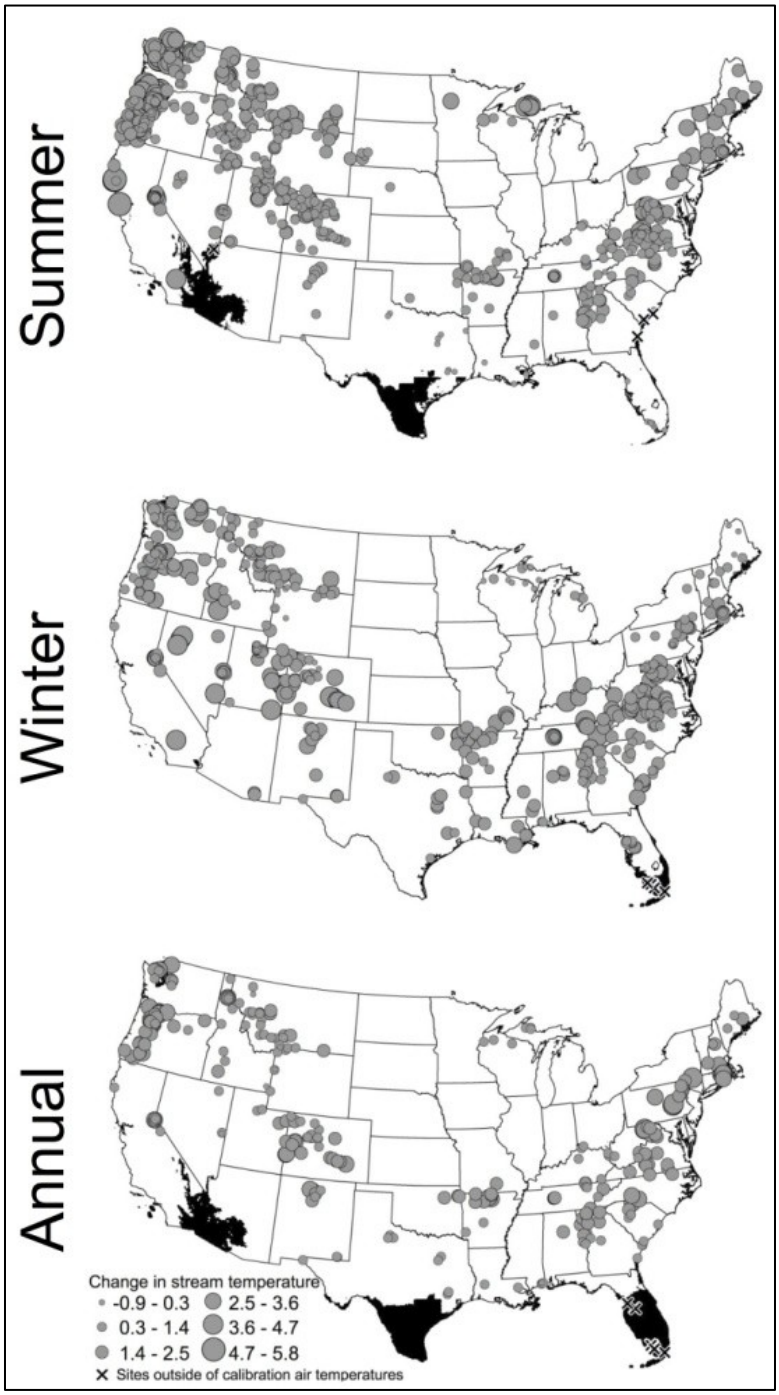

Fig. 4-1. Predicted changes in summer, winter, and annual stream temperatures (ST) between the 2000s and the 2090s. Black zones and Xs represent regions and USGS ST sites with predicted future air temperatures beyond the range of PRISM climate data used to develop the original ST models.

(summer ΔST = -0.1 °C to +5.9 °C, winter ΔST = -0.9 °C to +4.4 °C, and annual ΔST = 0 °C to +4.3 °C). The models predicted the greatest summer and annual ST warming in the Pacific Northwest and the Northern Appalachian Mountains with some of the most severe warming predicted for summer STs (Fig. 4-1). For example, the summer ST model predicted average warming of 2.8 °C for streams in the Cascade Mountains of Oregon, but 20% of those sites (23/113 sites) were predicted to experience warming ≥4 °C. Relative to the Cascade Mountains, Southeastern Rocky Mountain and Southern Appalachian Mountain streams generally had smaller predicted changes in summer ST. The winter ST model predicted near ubiquitous warming throughout most of the conterminous USA, but winter warming was predicted to be less severe in the Northeastern States (e.g., Maine and Vermont), northern Michigan, and Wisconsin (Fig. 4-1). The ST models predicted that for each 1 °C rise in AT, STs will warm by 0.5 °C to 0.6 °C over the next century.

Vulnerability of STs to CC

We identified several consistent stream and watershed features associated with ΔST for both model eras (historical and future) and for all model periods (summer, winter, and annual) (Fig. 4-2). The direction of association for these features was also similar across models of ΔST (Fig. 4-3). Historical and future ΔSTs were positively associated with greater ΔAT, whereas ΔST was always negatively associated with initial long wave radiation and vapor pressure deficit at study sites (Fig. 4-3). ΔST_O (historical ΔST) showed a consistent positive association with PRISM ATs in the 2000s (grey with black dashed lines in Fig. 4-3). However, the association between ΔST_{fut} and predicted ATs for the 2090s was unimodal in all plots (black lines in the AT_{fut} plots in Fig. 4-3) and was the only relationship that was not generally consistent between time periods.

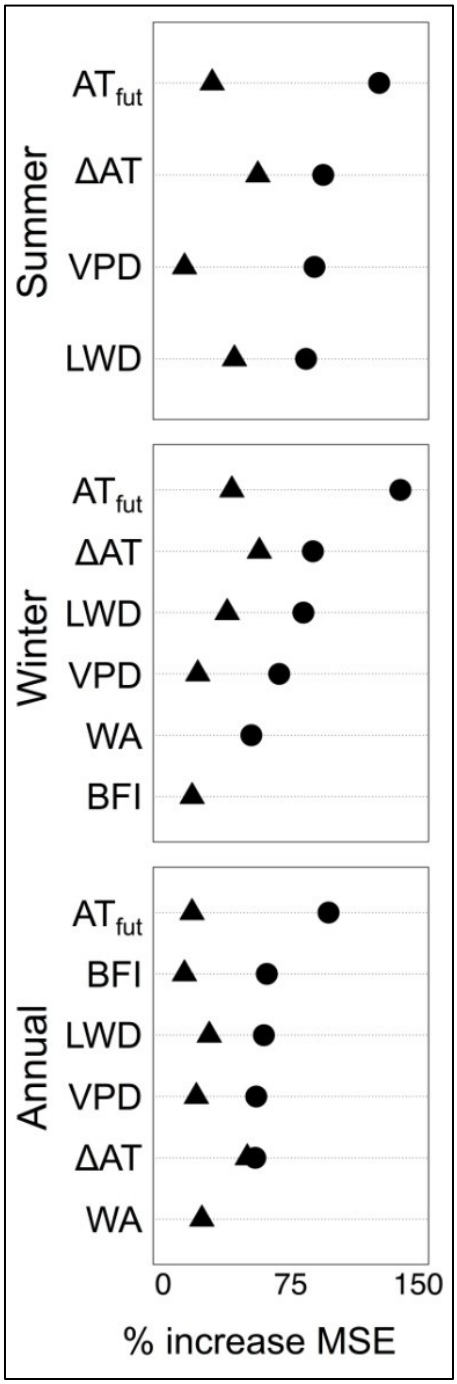

Fig. 4-2. Ranked importance (% increase in mean squared error of the model when the predictor is not included) of the predictor variables for historical (triangles) and future (circles) stream temperature vulnerability models. Abbreviations in figure: ΔAT = change in historical PRISM or predicted future air temperature from current (2000s) conditions, AT_{fut} = future air temperature observed (PRISM in 2000s) or predicted (2090s) to occur relative to the initial time period used to develop the ST vulnerability measures, LWR = initial long-wave radiation, VPD = initial vapor pressure deficit at the air-water interface of each stream, WA = watershed area, BFI = base-flow index.

ΔST had positive associations with increasing base-flow index values and negative associations with increasing watershed area, but these factors were not selected in all models (e.g., summer in Fig. 4-3) or time periods (cf. watershed area in winter and annual plots in Figs 4-2 and 4-3). However, the associations between ΔST and base-flow index and watershed area were consistent across models and time periods for which they were selected. ATs at the end of each model period were the most important predictor in all models of ΔST_{fut}. In contrast, ΔAT was the most important predictor in all ΔST_{O} models, but was also the 2nd most important predictor in summer and winter ΔST_{fut} models (Fig. 4-2). Although ΔAT was the least important predictor for annual ΔST_{fut}, the difference in the importance of ΔAT compared with the second ranked predictor (base-flow index) was small (Fig. 4-2). With the exception of base-flow index in the annual ΔST_{fut} model, both base-flow index and watershed area generally had small or no importance in predicting ΔST (Figs 4-2 and 4-3). The ΔST_{fut} models had higher random forest pseudo r-squared values (0.70 – 0.79) than the ΔST_{O} models (0.25 – 0.37) (Table 4-3), which may simply reflect differences in the range of STs in the two models or the use of predicted and observed ΔSTs in the respective models.

Discussion

This study provided new insight regarding how CC is likely to affect STs over the 21st century at the scale of the conterminous USA. Not surprisingly, new questions also emerged from our study. Below, we address the following general questions. How consistent are our results with previous studies of CC effects on ST? What challenges will differences in ST vulnerability pose to aquatic resource managers? How can we better target future research on CC-related ST effects and mitigation given the differences in ST vulnerability we observed?

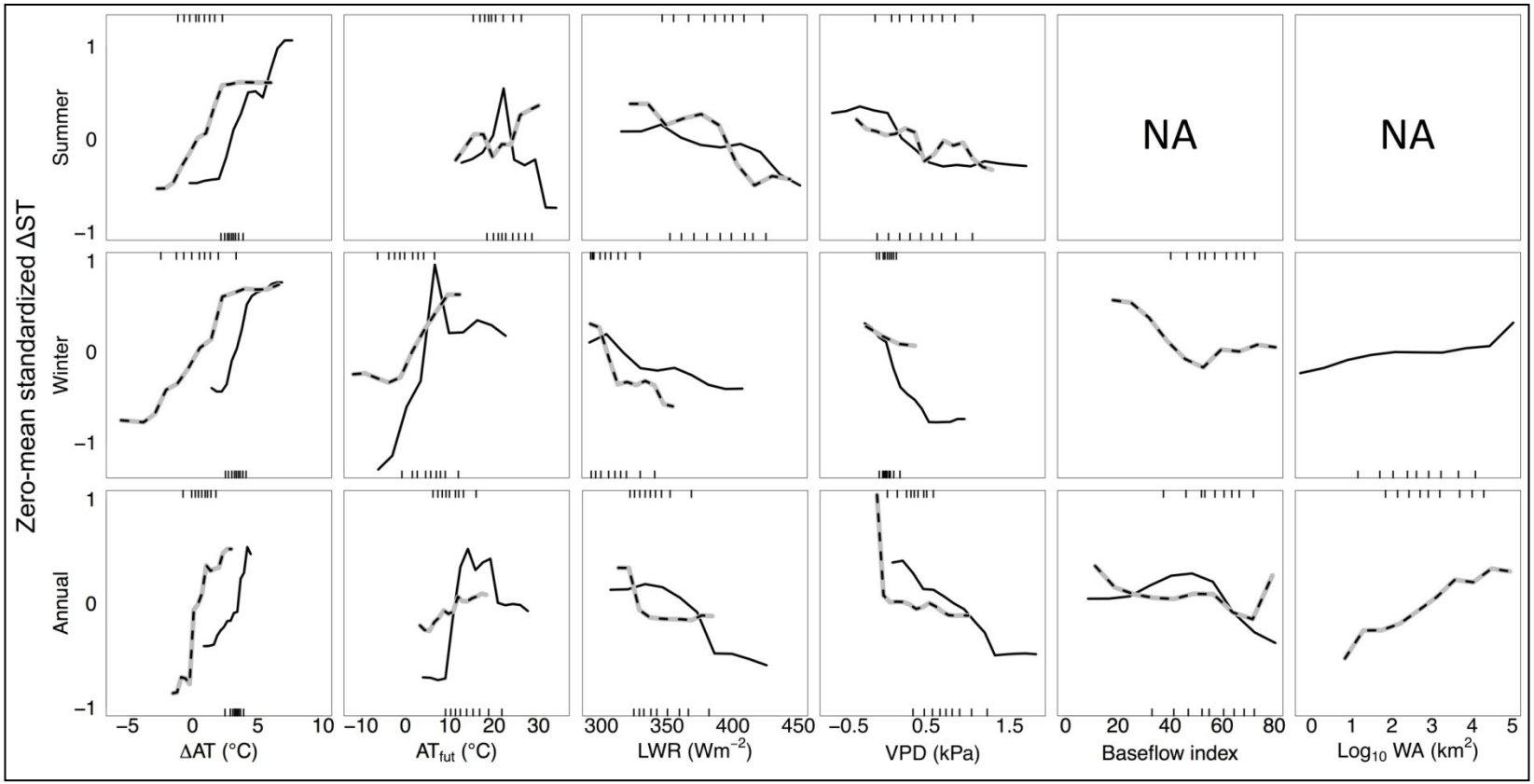

Fig. 4-3. Partial dependence plots showing the relationship between historical (grey with black dash) and predicted future (black) stream temperature (ST) vulnerability and predictor variables. See Equations 1 and 4 for the definitions of ST vulnerability used here) ST vulnerability values were standardized to have mean = 0 and standard deviation = 1. Additional abbreviations in figure: ΔAT = change in historical PRISM or predicted future air temperature from current (2000s) conditions, AT_{fut} = future air temperature observed (PRISM in 2000s) or predicted (2090s) to occur relative to the initial time period used to develop the ST vulnerability measures, LWR = initial long-wave radiation, VPD = initial vapor pressure deficit at the air-water interface of each stream, WA = watershed area.

Table 4-3. Nationally-average changes in projected air temperatures (ΔAT) and stream temperature (ΔST) at USGS reference sites from 2000 to 2090.

Model	Sites	ΔAT (°C)	ΔST (°C)	ΔST/ΔAT
Summer	565	+3.0	+1.7	0.57
Winter	472	+3.3	+1.7	0.52
Annual	263	+3.2	+1.6	0.50

Numerous studies have used various techniques to examine the effects of CC on STs, including observational, empirical, and deterministic approaches. Consistency of our results with other studies would lend support to the changes in ST that we predicted. For example, Kaushal et al. (2010) observed long-term mean annual ST warming rates of 0.009 – 0.077 °C yr^{-1} in individual streams that were distributed across the conterminous USA. Our models predicted that 74% of the USGS ST sites used in our study will have warming rates within this range during the 21st century. Isaak et al. (2010) estimated mean summer ST (15 July to 15 September) warming between 0.06 – 1.71 °C from 1993 to 2006 at 780 sites within the Boise River, Idaho. When applied to USGS ST sites within and near the Boise River, our summer ST model predicted warming of 0.95 – 3.0 °C; a similar to slightly greater amount predicted by Isaak et al. (2010) for many sites. Finally, the deterministic model developed by Null et al. (2013) predicted a 0.8 °C increase in mean annual ST (range = 0.6 °C – 0.95 °C) for every 1 °C rise in mean annual AT for streams within the Sierra Nevada Mountains, California. For USGS ST sites within the Sierra Nevada mountains, our ST models predicted average increases in mean summer STs of 0.65 °C and mean annual STs of 0.5 °C per 1 °C increase in summer and annual ATs, respectively, over the 21st century. These comparisons show that our model predictions are generally consistent with other studies that used observational or either empirical or deterministic modeling approaches to

examine the effects of CC on ST. This consistency among studies provides support that the variability in ST vulnerability predicted by our models is realistic and plausible.

The effects of CC on STs will pose serious challenges for freshwater resource managers. For example, 2 °C to 5 °C changes in ST can have substantial effects on stream biota and ecosystems (Sweeney, 1993; Hawkins et al., 1997; Durance and Ormerod, 2007; Haidekker and Hering, 2008; Chessman, 2009), and our models predicted that about one-third of the summer, winter, and annual ST sites will change by ≥2 °C by the end of the century. Moreover, the CC related changes in ST we predicted here are similar to or greater than ST alterations associated with stream and watershed alterations such as water regulation and land use changes. For example, Chapter 2 showed that sites in watersheds with urban development were thermally altered by +0.6 °C to +0.9 °C on average. In other words, our analyses indicate that over the 21st century, summer STs could be influenced by CC more than they have been affected to date by other human-related alterations, such as urbanization, agriculture, and water regulation. Unlike other sources of human-caused alteration that are isolated to specific watersheds, CC will affect both pristine and altered streams alike. However, for the vast majority of streams, climate-related changes in ST will not occur in isolation from other forms of human-related alteration, and our projections do not account for these potential interactions. It will be a major challenge to untangle CC caused changes in ST from that caused by other human-related activities when designing mitigation strategies.

When designing mitigation strategies, it will be increasingly important to understand both that some streams will likely be more thermally vulnerable to CC than others and why such differences occur. Our models of ΔST vulnerability identified several factors that may exacerbate or moderate ST responsiveness to CC that may help us understand and predict how streams will respond in the future. Of the factors

that increased ST vulnerability, the consistent and strong importance of ΔAT underscores the need for unbiased, appropriately resolved, climate predictions for understanding how the response of individual streams to changing atmospheric conditions will vary spatially. Likewise, it will be important to clarify how ST vulnerability is affected by future AT exposure. The unimodal responses of ΔST_{fut} to ATs at the end of the model period that we observed (Fig. 4-3) may be a consequence of the s-shaped ST-AT relationship described by the ST models we used to make the future ST forecasts (Chapter 2). This s-shaped relationship between ST and AT implies that upper STs may be constrained by the amount of evaporative heat loss occurring at warm stream temperatures (Mohseni at al., 2002). Our models also indicated that ST vulnerability increases with watershed area. Kelleher et al. (2012) observed a similar positive correlation between ST responsiveness and stream order, which the authors attributed to greater correspondence between STs and ATs in larger rivers caused by the accrual of heat through non-advective processes at the water surface. Brown (1970) noted that ST responsiveness in logged watersheds was a function of the water surface area-discharge ratio, with larger ratios resulting in more responsive streams. The surface area-discharge ratio is generally positively correlated with watershed area (Leopold et al., 1964), hence we should expect that STs would more closely approach ATs as the surface area over which heat exchange occurs increases relative to water volume.

Our results also show that the current thermal state of a stream can significantly affect its vulnerability to CC. The critical role of vapor pressure deficit and long wave radiation in affecting ST vulnerability was well illustrated in Cascade Mountain streams of Oregon and Washington (Fig. 4-1). These streams were especially responsive to projected CC and had the coolest summer STs and lowest vapor pressure deficits in the USGS ST dataset. Cold water streams will therefore likely experience the most

substantial changes in ST in response to CC, and research should target developing approaches to mitigate the effects of CC on these streams. In the ST vulnerability models, we treated vapor pressure deficit as a fixed factor, but its components – air and water vapor pressures – will also likely be affected by CC. In the future, we will need to improve our understanding of how air and water vapor pressures will change under future climate regimes and interact to determine ST vulnerability. Simulations derived from deterministic models should be especially useful in this regard.

Our models indicated that groundwater inputs, as measured by base-flow index, influences ST vulnerability. Base flow is the contribution of groundwater to stream flow relative to other sources, such as runoff. Groundwater temperatures are generally constant throughout the year and are approximately mean annual AT (Schmidt et al., 2006). The constancy of groundwater flow and temperature is an important buffer to the heat exchange processes that occur at the stream surface (Kelleher et al., 2012). We treated the base-flow index as a fixed variable within the vulnerability models, an assumption that may be robust over moderate time scales. However, the factors that influence base flow (e.g., soils characteristics, precipitation, and evapotranspiration) will likely change over the next century (Singh, 1968). Groundwater temperatures will also likely warm over the long term in response to warmer ATs and thus reduce the apparent effectiveness of groundwater inputs as a buffer to CC. Nonetheless, maintaining groundwater flow to streams may be an important strategy for mitigating climate related thermal alterations because of the responsiveness of ST alteration to the volume of stream flow (Brown, 1970). To further improve predictions of ST vulnerability, we need to understand how CC will affect groundwater flow and temperature (Loaiciga, 2009), and thus influence long-term patterns of ST.

Concluding remarks

We predicted substantial ST warming by the end of the 21st century. However, our own evaluations of the ST models suggested that these predictions could be conservative by up to 0.5 °C on average. In addition, recent work suggests that CO_2 emissions may be accelerating beyond the A2 emissions scenario used in this study (Raupach et al., 2007). Thus, our future ST predictions may also not be fully capturing the true extent of warming that streams may experience. Despite these potential shortcomings, our models of ST change and vulnerability provide important insight and context on CC effects on STs at a near-continental scale that can help guide future research.

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CHAPTER 5

CONCLUSION

My dissertation provides insight and practical tools that should advance our understanding and management of stream ecosystems in several ways. First, my dissertation advances our knowledge of and ability to predict stream thermal environments across a broad range of environmental conditions. Second, the stream temperature (ST) models I developed are a potentially powerful tool for understanding the role ST plays in structuring local stream biological communities and maintaining macro-scale patterns of stream biodiversity. Third, these models provided important insight into the vulnerability of stream ecosystems to climate change and the ability to predict these changes.

The models I developed in chapter 1 provide important insight into human-related alterations of ST and what constitutes thermal reference quality in streams. The selection of reference-quality sites through the use of “dirty” models implied that surprisingly small amounts of watershed alteration were associated with thermal alterations. The subsequent removal of nonreference-condition sites substantially reduced the number of sites for modeling, and implies that the vast majority of streams and rivers within the conterminous USA are thermally altered to some extent. The dirty models also provided insight regarding our ability to infer reference condition by modeling out the effects of watershed alterations on ST. Ideally, the descriptors of watershed alteration (i.e., the urban, agriculture, and reservoir indices) would account for thermal alterations in a way that allows hindcasting of thermal reference conditions. However, the biased predictions of reference-condition STs produced by the dirty models indicate that the alteration indices need to be refined to fully account for the

effects of these alterations. In addition, these results imply that, whenever possible, reference-quality sites should be used to set environmental benchmarks (Hawkins et al. 2010).

The models of reference-condition ST should improve assessments of both the thermal and biological conditions of streams. Although reference site selection resulted in a greatly reduced dataset for modeling, these sites covered a broad range of river sizes and environmental settings and model evaluations indicated that the models were both accurate and precise. Large-scale application of these models could quantify the natural thermal environments of thousands of streams that currently lack measurements. These reference-condition ST predictions could also provide benchmarks against which streams that are suspected of being thermally altered can be compared. Finally, I showed that the use of predicted reference condition STs in multi-taxon niche models improved model precision and interpretability and the use of predicted STs should translate to more precise and interpretable biological assessments.

Modeled STs could potentially improve our understanding of how species partition thermal environments of streams and how this partitioning produces macro-scale patterns of stream biodiversity. The use of ST surrogates is common in biota-temperature studies (e.g., Larson and Olden 2012) but is also problematic. For example, the relationship between air temperature and water temperature is nonlinear and imprecise, hence biota-air temperature relationships must be interpreted carefully. Other surrogates, such as latitude, elevation, and watershed area often covary with other environmental features that confound interpretation of observed relationships with stream biota. I showed that model predicted STs can represent biologically-relevant thermal environments and that the responses of species to predicted ST is realistic relative to measured ST. In short, the ST models I developed move us closer to being

able to interpret field-based observations of ecological phenomena in terms of physiological responses of species to their thermal environments. Coupling field-based, ecological models that use ST predictions with laboratory experiments that more precisely quantify physiological responses of species to temperature will provide powerful insight into the mechanisms structuring stream communities.

In chapter 4, the ST models implied that streams in the USA will vary greatly in their vulnerability to climate change. This vulnerability was positively associated with the degree of predicted climate warming. However, the initial thermal conditions of streams and groundwater inputs will also likely play important roles in determining the degree of warming that streams will experience. Coldwater, mountainous streams were predicted to be the most vulnerable. In contrast, streams in the southeastern USA were predicted to be less vulnerable. These findings have important implications for focusing research and mitigation efforts most effectively.

The ST models have numerous applications that are yet to be explored. I showed that they can adequately characterize STs for biota-temperature studies and can predict climate-related changes in ST. Additionally, a thermal assessment of streams could be developed and compared directly to biological assessments to help diagnose sources of biological impairment. Such an assessment could help in development of biologically-based, site-specific ST criteria. In addition, climate-related changes in ST could be linked to species thermal niche models to understand how the distributions of species will respond to climate change. Finally, these models could be expanded to predict a range of ST variables (e.g., mean ST for each month, annual ST range, cumulative degree days) that may be more relevant for quantifying thermal environments during critical life stages of stream organisms (e.g., Sweeney and Vannote 1986) and understanding the effects of intra-annual variations in ST (e.g., Brown 1999) on stream species.

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APPENDICES

Appendix A. Calculation of natural predictor variables

We briefly describe the calculation of natural predictor variables used to model stream temperatures (STs). Each section states the scale at which the predictor variable was calculated (i.e., point, 100-m riparian buffer, or watershed), and whether an inverse-distance weight was applied.

Climate

We used the 4-km-resolution PRISM air and precipitation datasets (Daly et al. 2008, http://prism.oregonstate.edu) to characterize the climatic conditions at each station and within each watershed. The PRISM climate grids cover the conterminous USA and are derived through a unique interpolation method that accounts for the physiographic setting of each climate station. These data are available for download at monthly and annual time steps, and we created summer and winter air temperature grids by averaging the July–August and January–February grids for each year. Each year's summer, winter, and annual air temperatures were then associated with the respective season and year of ST data from each station (i.e., point-level measurement). We estimated site-level and watershed-averaged total precipitation for summer, winter, the standard 12 mo (January–December), and the 12 mo preceding summer ($June_{x-1}$ to May_x) of each year, where x is the year of ST record. We also calculated the 30-y average of total precipitation for each watershed (1971–2000).

Geology and soils

Both the amount and flow rate of water through a watershed are influenced by the underlying geology and soils via permeability, storage capacity, and subsurface water depth. These factors can affect the ratio of surface to subsurface stream flow (i.e.,

base flow), and thus STs (O'Driscoll and DeWalle 2006, Tague et al. 2007). We calculated the % composition of each geology class (mafic–ultramafic, quaternary, gneiss, granitic, sedimentary, and volcanic) within each watershed, and the geology class at each ST station, from a simplified version of the Generalized Geologic Map of the Conterminous United States (Reed and Bush 2001). We used the State Soil Geographic database (STATSGO) (Wolock 1997) to summarize the soil characteristics as both watershed-averaged and point-level measurements of available water capacity (volume of water available/volume of soil), permeability (cm/h), soil bulk density (g/cm^3), and depth to water table (m).

Hydrology

We characterized both the volume of the stream flow and the proportion of stream flow composed of groundwater and surface flow. Stream flow determines the mass of water within channels and, thus, the thermal inertia of streams. Groundwater generally emerges near the regional mean annual air temperature, and the relative amount of ground water to other types of stream flow helps buffer heat-exchange processes that affect STs. We used a raster of the 30-y average annual runoff, calculated at the scale of 8-digit US Geological Survey (USGS) Hydrologic Unit Codes (HUCs) for the conterminous USA (McCabe and Wolock 2010) to estimate average stream flow in each watershed. We averaged the long-term runoff raster values within each ST watershed to generate these estimates. We characterized the relative amounts of ground water from 2 measured stream-flow characteristics because we could not measure groundwater inputs directly. The baseflow index (BFI) estimates the % stream flow that is composed of ground water relative to event flow. The USGS generated a 1-km-resolution grid of base flows derived by interpolating calculated base flows at 19,000

USGS stream-flow gauging stations distributed across the conterminous USA (Wolock 2003). To estimate a stream's base flow we averaged all pixels of the interpolated grid within each watershed as suggested by Wolock (2003). We also derived an index of the hydrologic stability (HSTAB) of stream flows defined as $\min_{x_i}/\max_{x_i}$, where x_i is the mean monthly discharge (m^3/s) for month *i* for the period of record ($x_i \geq 12$ mo) at ~10,000 USGS gauging stations across the western USA. These values were then interpolated with an inverse-distance-squared weighting of values from the 12 closest USGS flow stations within 100 km to create a grid of HSTAB for the western USA. We then calculated watershed-averaged and point-level HSTAB for each ST station. Values of HSTAB close to 1 indicate a minimum monthly flow that is similar to the maximum monthly flow and, thus, more stable flow. HSTAB values <1 indicate small minimum monthly flows relative to maximum monthly flows and, therefore, large potential variation in discharge during the period of record. Stable discharges may imply greater groundwater contributions and therefore cooler streams in the summer and warmer streams in the winter.

Solar radiation

We used an Environmental Systems Research Institute (ESRI) Arc Macro Language script (http://www.wsl.ch/staff/niklaus.zimmermann/programs/aml1_2.html) based on Kumar et al. (1997) and 30-m digital elevation models (DEMs) to estimate the average daily clear-sky shortwave radiation striking the surface of each stream (W/m^2) during the 3 modeling periods (summer, winter, and annual). We multiplied the solar radiation grids by the area of each channel segment (i.e., estimated channel width multiplied by the flow distance between 2 tributaries) to calculate the total radiation (W) striking the channels within each watershed. We followed the method published by

Quigley (1981) to adjust the estimates of bare-ground shortwave radiation based on the average height of the vegetation (USDA LANDFIRE Dataset; Rollins and Frame 2006) within 100 m of the channels, the average compass flow direction, latitude, and the estimated channel width of each channel segment. In addition to the average upstream radiation striking all channels, we calculated the average radiation striking only those stream segments that made up 10%, 25%, 50%, 75%, and 90% of the total drainage area above each ST station, i.e., the fraction of the stream network closest to the outlet. Thus, averages were calculated for shorter distances in small watersheds and longer distances in large watersheds, i.e., proportional to the watershed area. This weighting scheme scaled the length of river over which averages were calculated to the size of each station's watershed and is based on the concept that smaller streams are affected by heat-transfer processes over a shorter distance than larger rivers because of their smaller masses (Brown 1969, Caissie 2006, Poole and Berman 2001). In addition to the total radiation striking the stream surface, we normalized these values by each station's watershed area.

Watershed and channel topography/morphology

We calculated the total contributing area above each temperature station, watershed shape, elevation range, and channel slope. Watershed area is a surrogate for river size (volume and surface area (Leopold et al. 1964) and, thus, exposure time to heat-exchange processes. We calculated shape factor (i.e., rounded vs elongated) as the ratio of the watershed area (m^2) to the square of the mean flow length (m^2) to the watershed's outlet. A rounded watershed (i.e., larger ratios) delivers water to the outlet of the stream faster than an elongated watershed (Snyder 1938), which implies the water in a rounded watershed is exposed for less time to heat-exchange processes and,

thus, should produce cooler temperatures in summer and warmer temperatures in winter. We estimated 2 measures of channel slope: local slope at the ST station and the average of all channel slopes in the watershed. Steeper channel slopes result in faster movement of water from headwaters to outlets and, therefore, should result in less time for streams to either warm or cool over a unit length, potentially resulting in cooler summer and warmer winter STs. We estimated local slope from the National Hydrography Dataset Plus (NHD). To estimate average channel slope, we used the ArcGIS hydrologic tools to define flow direction, flow accumulation, flow length, and stream channels from DEMs. We calculated channel slope for each DEM-derived stream-channel segment as the change in elevation between 2 tributaries divided by the segment length. We then used these estimates of segment slope to calculate watershed-average channel slope. We also used e-folding distances of 1 and 4 km to create 2 weighted averages of stream-segment slopes.

Enhanced vegetation index

We used the enhanced vegetation index (EVI) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data at 500-m pixel resolution (Huete et al. 2002) to characterize average monthly vegetation cover between 2000 and 2009. EVI may be associated with regional patterns of hillslope and streamside shading that could decrease the transfer of shortwave radiation to watersheds and channels. We calculated seasonal (summer and winter) and annual averages from the monthly average grids. For each temperature station, we calculated the point-level and watershed-averaged EVI for the 2 seasons and the annual mean.

Lakes and wetlands

Wehrly et al. (2006) found that the proportion of watershed areas composed of lakes and wetlands was positively related to mean July STs in Michigan, USA. Slow moving, lentic water is exposed to heat-exchange processes for longer periods of time. Thus, wetlands should influence STs. We calculated the total area (km^2) and proportion of each watershed composed of the Open Water land cover class within the National Land Cover Dataset (NLCD).

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Appendix B. Quality screening of National Inventory of Dam records

We screened 53,041 records from the National Inventory of Dams (NID) to ensure the quality of the data for predicting the effects of reservoirs on stream temperatures. Here, we briefly describe this screening process. Examination of the NID revealed that reservoirs often had associated locks, dikes, or canals, and each was represented as a unique record within the NID. Thus, the reported volume of a reservoir with 2 dikes would be triple-counted when calculating an upstream reservoir index for a US Geological Survey temperature site. To remove duplicated reservoir volumes from the database, we first deleted any records with the words *dyke*, *dike*, *canal*, or *lock* in the structure name. We desired to use permanent reservoirs in the stream temperature (ST) models that could, at a minimum, be detected with satellite imagery. To achieve this, we spatially joined the National Hydrography Dataset Plus (NHDPlus; Simley and Carswell 2009) water bodies polygon file and the National Land Cover Dataset (NLCD) (Homer et al. 2007; http://www.mrlc.gov/) Open Water land-cover class because we noted that some waterbodies within the NHDPlus were very small or ephemeral (i.e., not visible in Google Earth®). This layer was then spatially joined to the NID to provide a table with the volume of each reservoir (NID), reservoir surface areas from both NHDPlus and NLCD, and the distance of each dam to the nearest reservoir (NHDPlus and NLCD). Where available, the table also included the NHDPlus waterbody and dam names. We then examined this table to identify inconsistencies, such as disagreement between a reservoir volume and surface area, very large distances between a dam and its associated reservoir, and multiple NID records spatially joined to a single reservoir. When we observed inconsistencies, we examined reservoirs in Google Earth and inspected the NID, NHDPlus, and NLCD layers in ArcGIS (version 9.3.1, Environmental

Systems Research Institute, Redlands, California). Where possible, we corrected errors in the spatial location of dams. Small reservoirs (i.e., <100 acre-feet) that were a significant distance from a water body were ignored and removed from the NID.

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Appendix C. Table of potential predictor variables

This table contains a short description of the natural and stream-watershed alteration geographic information system (GIS) predictor variables that we calculated for each station and associated upstream channel network or watershed boundary. The column *Predictor description* contains a brief explanation of what each predictor variable measures. Appendix A and the main body, respectively, contain more detailed descriptions of the natural and watershed-alteration predictors and their data sources, calculation methods, and justifications (including citations) for testing these predictors for inclusion in the stream temperature models. *Measurement level* specifies the scale at which the predictor was measured, i.e., whether the predictor was measured at the station, within the upstream channel network, or the entire watershed. For several predictors, we tested weighting schemes to determine whether emphasis on certain stream characteristics closer to the temperature station could produce better estimates of stream temperature. The type of weighting scheme and the weights used are specified in the column labeled *Weighting distance*. See the main text for a description of e-folding distances and Appendix A for a description of the weighting system used in calculating the solar radiation predictors. The final 3 columns specify whether the predictor variable was retained for the final summer, winter, or annual stream temperature models. If a weight was used, the distance is specified in the columns (e.g., 1 km).

Table C. Table describing the predictor variables tested for use in the mean summer stream temperature (MSST), mean winter stream temperature (MWST), and mean annual stream temperature (MAST) models, the scale at which each was measured (e.g., point vs watershed), whether a weighting scheme was used in the calculation, and whether the predictor was selected for a model, including the weight if used. See Appendix S1 for additional details of variable calculations, data sources, and justifications for use. USGS = US Geological Survey, DEM = digital elevation model, ag = agriculture, NLCD = National Land Cover Dataset.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Natural predictors							
Climate	TmeanPt	PRISM mean daily summer, winter, or annual air temperature	Point		X	X	X
Climate	PrcpSmrWs	PRISM total summer precipitation during year of stream temperature measurement	Watershed				
Climate	PrecipWs12m	PRISM total annual (January–December) precipitation during year of stream temperature measurement	Watershed				
Climate	PrcPt	PRISM total summer, winter, or annual precipitation during year of stream temperature measurement	Point				

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Climate	PrecipPYWs	PRISM total annual precipitation during the year previous to stream temperature measurement					
Climate	PrecipLTWs	PRISM long-term average total precipitation (1971–2000)	Watershed				X
Geology	MAFUL, QTRNRY, GNEISS, GRANITIC, SDMNTRY, VOLCANIC	% of watershed in geology classes: mafic–ultramafic, quaternary, gneiss, granitic, sedimentary, volcanic	Watershed				
Geology	DOM_GEOL	Dominant geology class (defined above) within each watershed	Watershed				
Geology	QtSdVol	Total % watershed composed of quaternary, sedimentary, or volcanic geology classes	Watershed			X	
Hydrology	RunoffAve	USGS annual total runoff	Watershed				
Hydrology	BFI_WS	USGS base-flow index	Watershed		X	X	X
Hydrology	HSTAB	Ratio of minimum monthly flow to maximum monthly flow	Watershed				

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Soils	AWC_WS, PERM_WS, BD_WS, WTDP_WS	STATSGO available water capacity, permeability, soil bulk density, depth to water table	Point, Watershed		X (BD)	X (PERM)	
Solar radiation	SolRad100	DEM-estimated total summer, winter, or annual solar radiation striking all	Watershed				
Solar radiation	SolRad100-ByWs	DEM-estimated total summer, winter, or annual solar radiation striking all stream channels normalized	Watershed				
Solar radiation	SolRad10, ...25, ...50, …75, ….90	Weighted DEM-estimated total summer, winter, or annual solar radiation striking stream channels	Stream network	Streams that made up 10, 25, 50, 75, 90% of basin			
Solar radiation	SolRad10ByWs, ...25ByWs, ...50ByWs, …75ByWs, ….90ByWs	Weighted DEM-estimated total summer, winter, annual solar radiation striking stream channels normalized by watershed area	Stream network	Streams that made up 10, 25, 50, 75, 90% of basin			

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Topo-morphology	SQ_KM	Total upstream watershed area	Watershed		X	X	X
Topo-morphology	ElvRnge	Range of elevation values within watershed	Watershed		X		X
Topo-morphology	SHAPE	Ratio of watershed area to the square of the mean watershed flow length to watershed outlet	Watershed				
Topo-morphology	NHDSlope	National Hydrography Dataset channel slope at stream temperature station	Point				
Topo-morphology	SlpStr_Ws	DEM-estimated slope of channels upstream of stream temperature station	Stream network		X	X	X
Topo-morphology	slp1km, slp4km	Weighted DEM-estimated slope of channels upstream of stream temperature station	Stream network				
Vegetation	EVI	Watershed averaged enhanced vegetation index	Watershed				
Water bodies	OWSqKm, OWByWs	Total area of NLCD "Open Water" cover class, OWSqKm normalized by watershed area	Watershed				

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Watershed alterations							
Land cover	urbSqKm	Total watershed area composed of urban land use	Watershed				
Land cover	UrbSqKm-ByWs	% of watershed area composed of urban land use	Watershed		X	X	X
Land cover	urb1Km, urb4km, urb15km, urb25km	Total area composed of urban land use within 100-m buffer of stream channel	Stream network	1, 4, 15, 25-km e-folding			
Land cover	urb1KmByWs, urb4kmByWs, urb15kmByWs, urb25kmByWs	Total area composed of urban land use within 100-m buffer of stream channel normalized by watershed area	Stream network	1, 4, 15, 25-km e-folding			
Land cover	agSqKm	Total watershed area composed of ag land use, proportion of watershed area composed of ag land use	Watershed				
Land cover	agSqKmByWs	% of watershed area composed of ag land use	Watershed		X	X	X
Land cover	ag1Km, ag4km, ag15km, ag25km	Total area composed of ag land use within 100-m buffer of stream channel	Stream network	1, 4, 15, 25-km e-folding			

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Land cover	ag1KmByWs, ag4kmByWs, ag15kmByWs, ag25kmByWs	Total area composed of ag land use within 100-m buffer of stream channel normalized by watershed	Stream network	1, 4, 15, 25-km e-folding			
Reservoirs	AvgOfDamVol	Average of reservoir volumes within watershed	Watershed				
Reservoirs	SumOfDamVol	Sum of reservoir volumes within watershed	Watershed				
Reservoirs	MaxOfDamVol	Maximum of reservoir volumes within watershed	Watershed				
Reservoirs	AvgOfDamVol ByWs	Average of reservoir volumes within watershed normalized by watershed	Watershed				
Reservoirs	SumOfDamVol ByWs	Sum of reservoir volumes within watershed normalized by watershed area	Watershed				
Reservoirs	MaxOfDamVol ByWs	Maximum of reservoir volumes within watershed normalized by watershed area	Watershed				

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Reservoirs	AvgOfDamVolWt50, ...100, ...150, ...200	Average of weighted reservoir volumes within watershed	Watershed	50, 100, 150, 200-km e-folding			
Reservoirs	SumOfDamVolWt50, ...100, ...150, ...200	Sum of weighted reservoir volumes within watershed	Watershed		X	X	X
Reservoirs	MaxOfDamVolWt50, ...100, ...150, ...200	Maximum weighted reservoir volume within watershed	Watershed		X		X
Reservoirs	AvgOfDamVolWt-50ByWs, ...100ByWs, ...150ByWs, ...200ByWs	Average of weighted reservoir volumes within watershed normalized by watershed area	Watershed				
Reservoirs	SumOfDamVolWt-50ByWs, ...100ByWs, ...150ByWs, ...200ByWs	Sum of weighted reservoir volumes within watershed normalized by watershed area	Point				

Table C. Continued.

Predictor category	Predictor name	Predictor descriptors	Measurement level	Weighting distance	MSST model	MWST model	MAST model
Reservoirs	MaxOfDamVolWt-50ByWs, ...100ByWs, ...150ByWs,	Maximum weighted reservoir volume within watershed normalized by watershed area	Stream network		X	X	X

Appendix D. Cumulative distribution function plots of all natural predictor variables used in the mean summer stream temperature, mean winter stream temperature, and mean annual stream temperature models

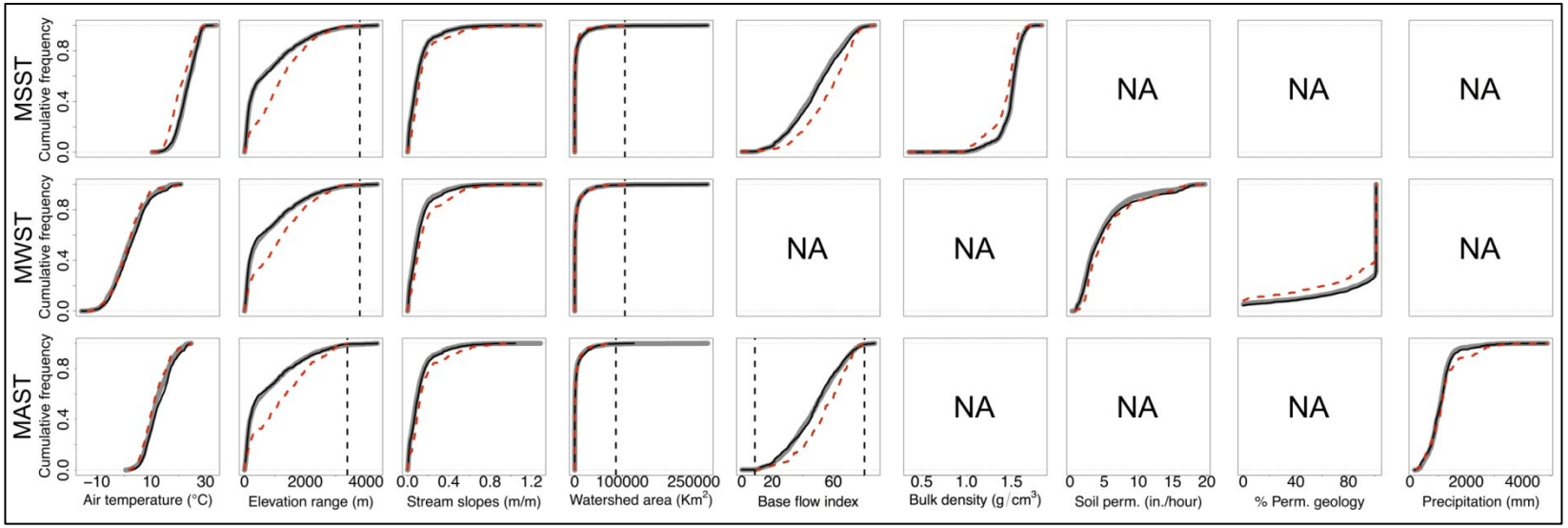


Figure D. Cumulative distribution function (CDF) plots of all natural predictor variables used in the mean summer stream temperature (MSST), mean winter stream temperature (MWST), and mean annual stream temperature (MAST) models. CDFs of the reference condition model (RCM) predictors are plotted with red dashed lines, dirty model (DM) RCM predictors in solid black, and all US Geological Survey stream temperature stations in solid grey. The vertical black dashed lines represent the point where the range of the RCM predictors fails to overlap with the DM predictors.

Appendix E. Response of the predicted capture probabilities of benthic invertebrate taxa versus predicted and measured stream temperature

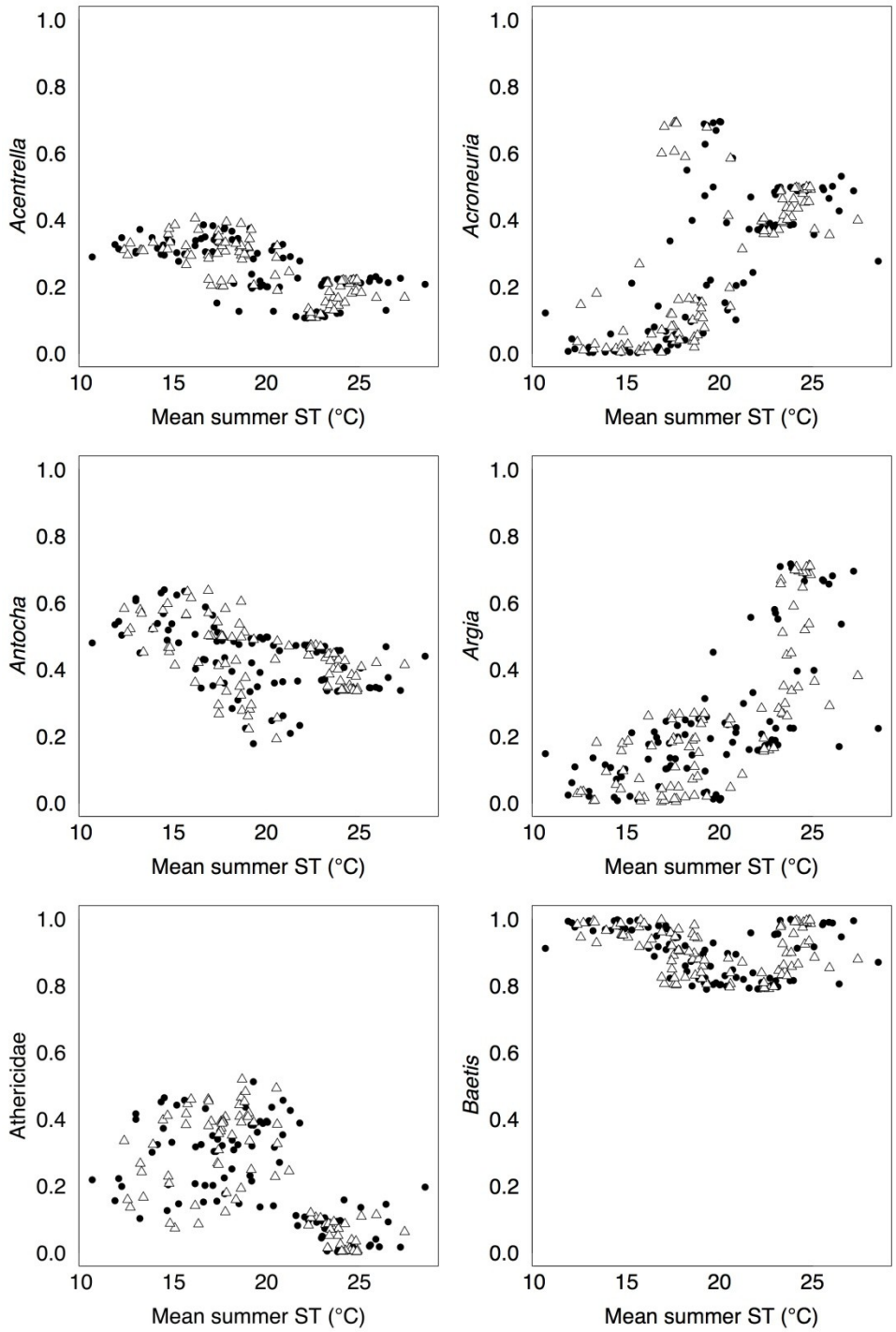


Figure E. Response of predicted capture probabilities of benthic invertebrate taxa versus predicted (white triangles) and measured (black circles) stream temperature (ST).

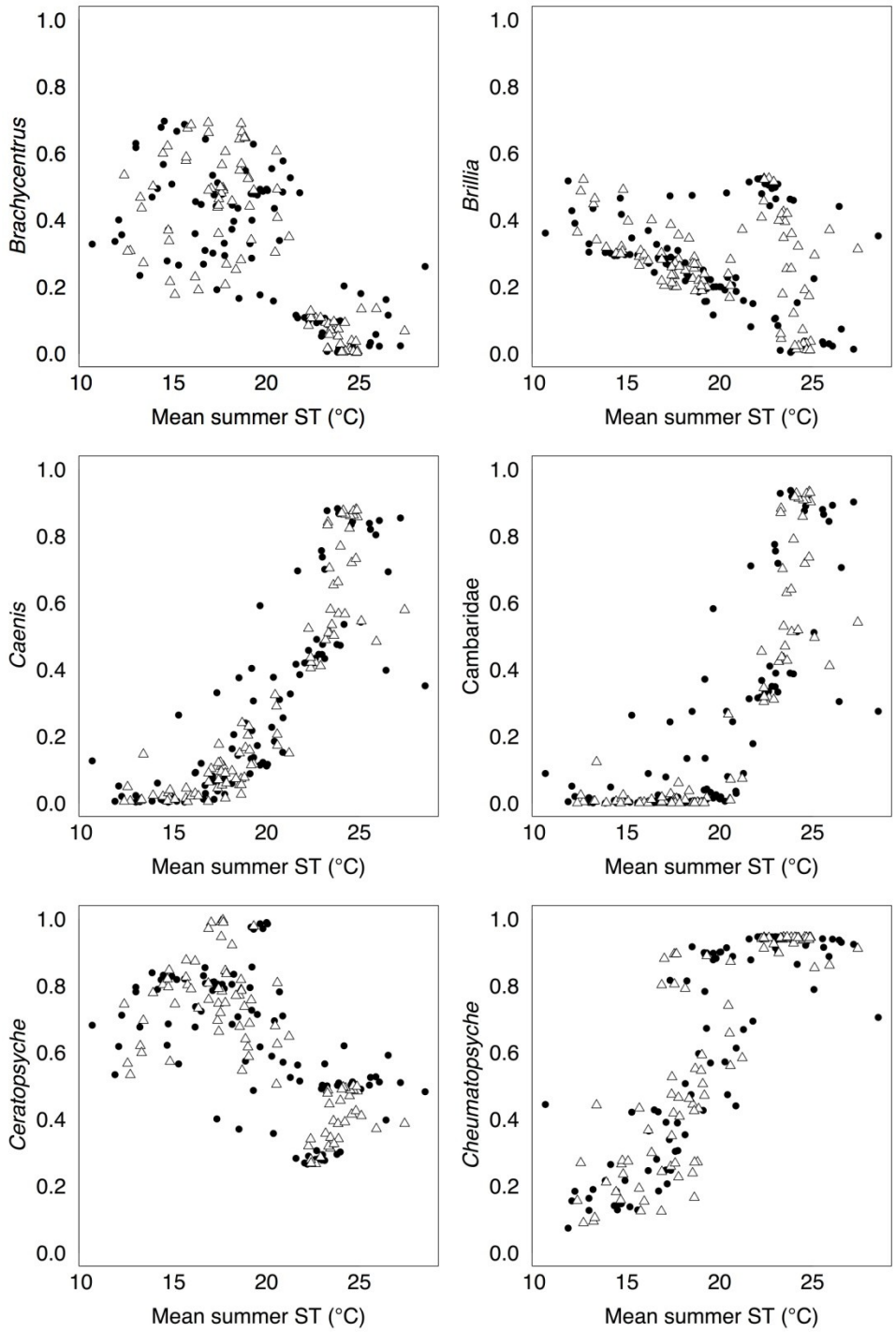


Figure E. Continued.

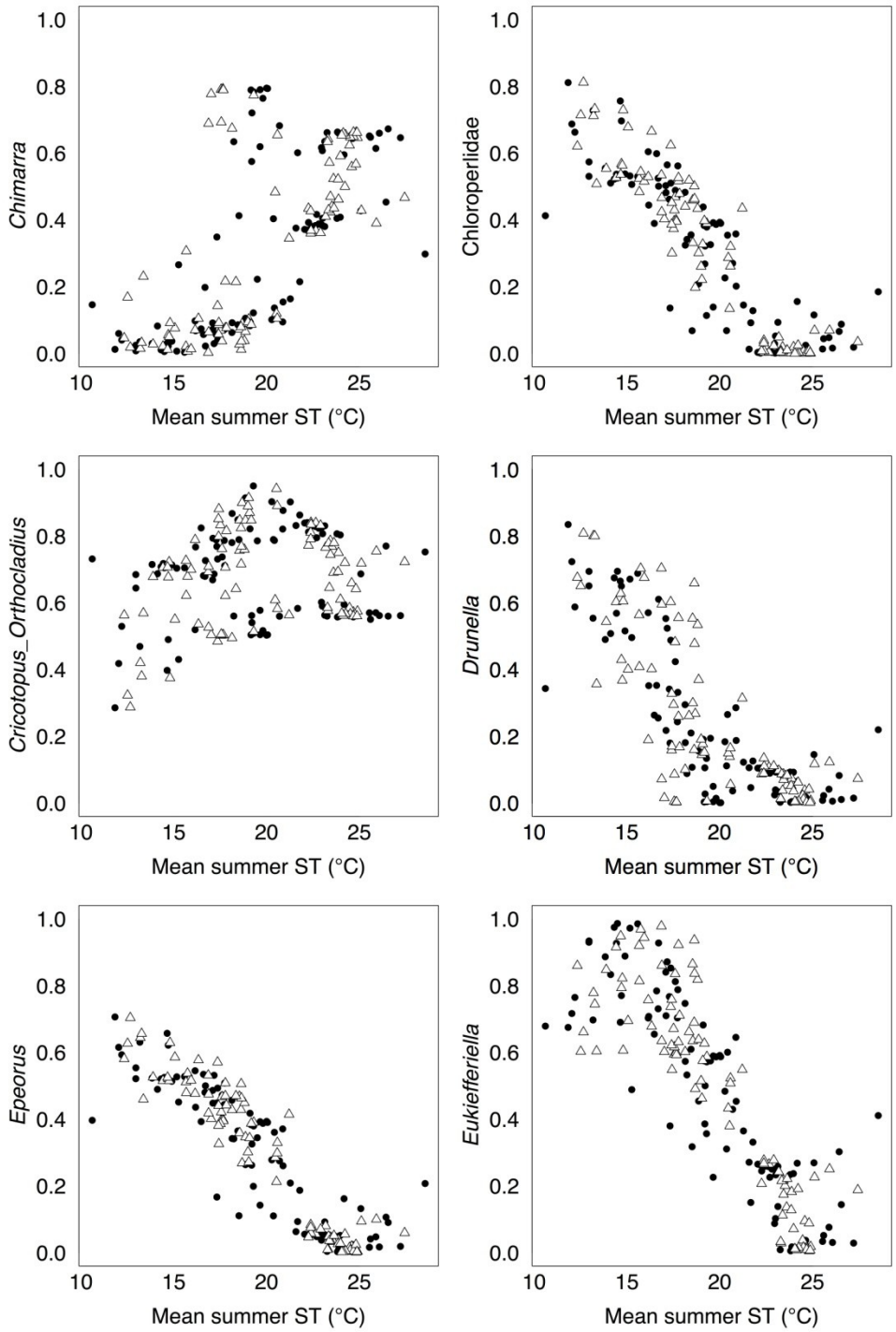


Figure E. Continued.

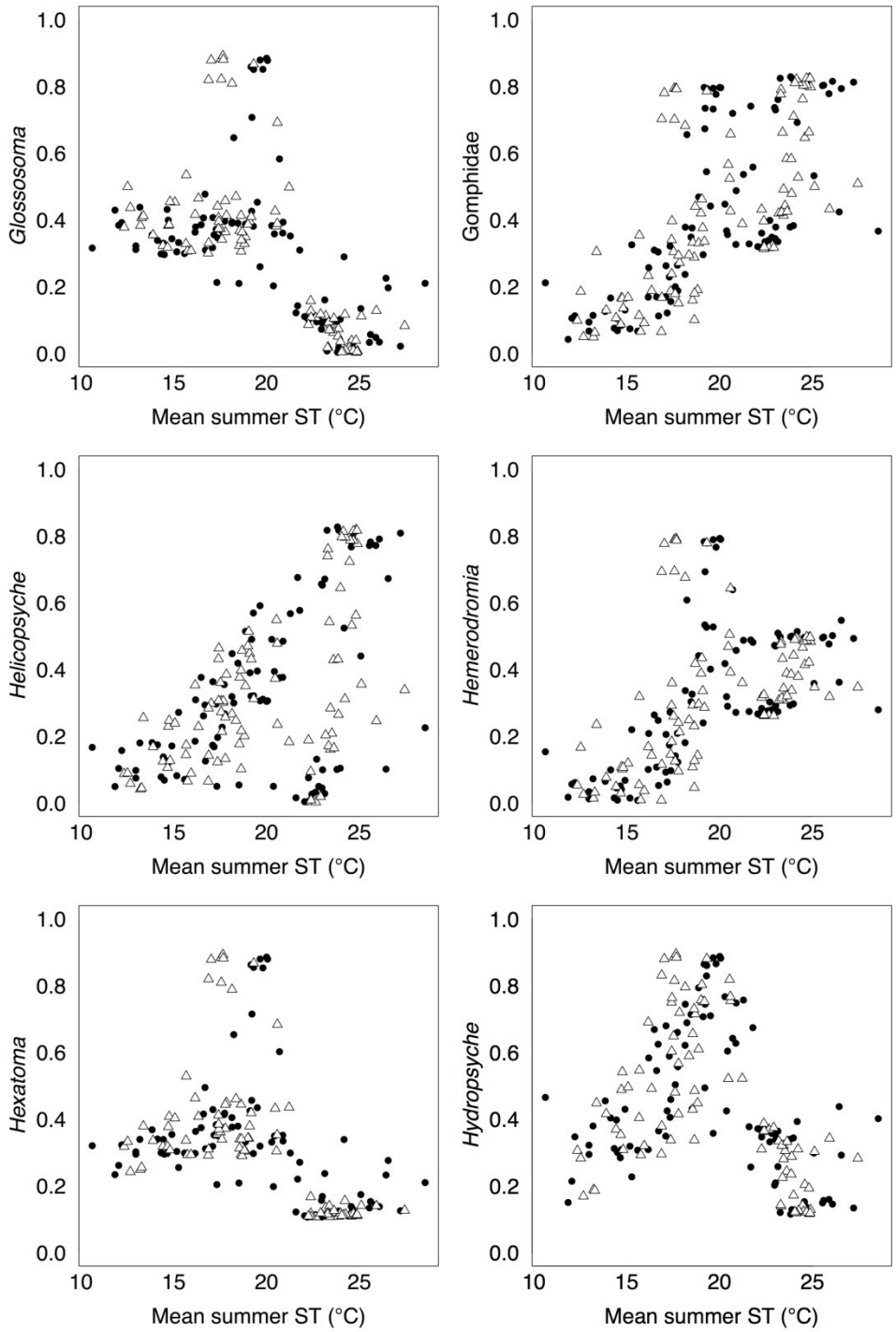


Figure E. Continued.

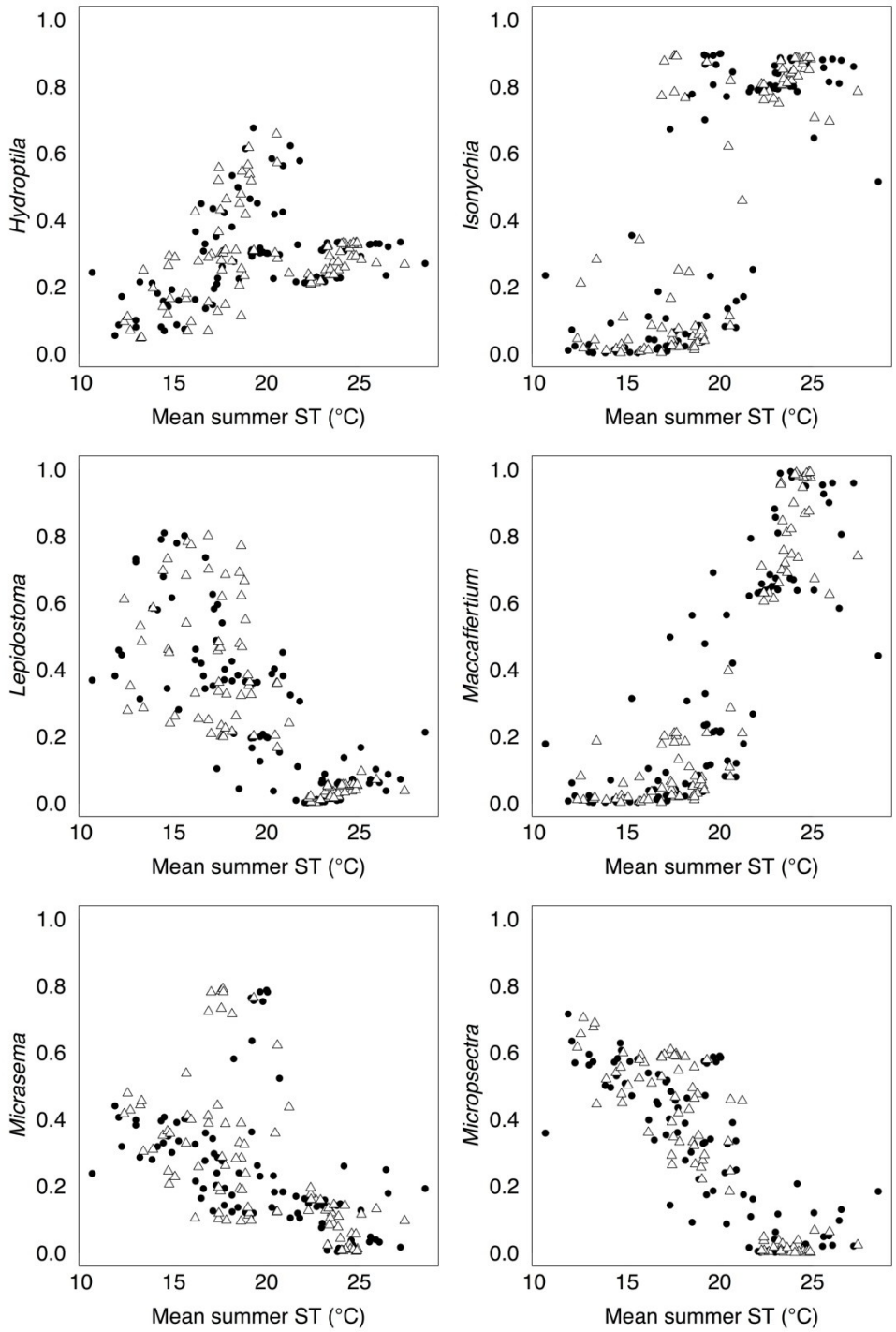


Figure E. Continued.

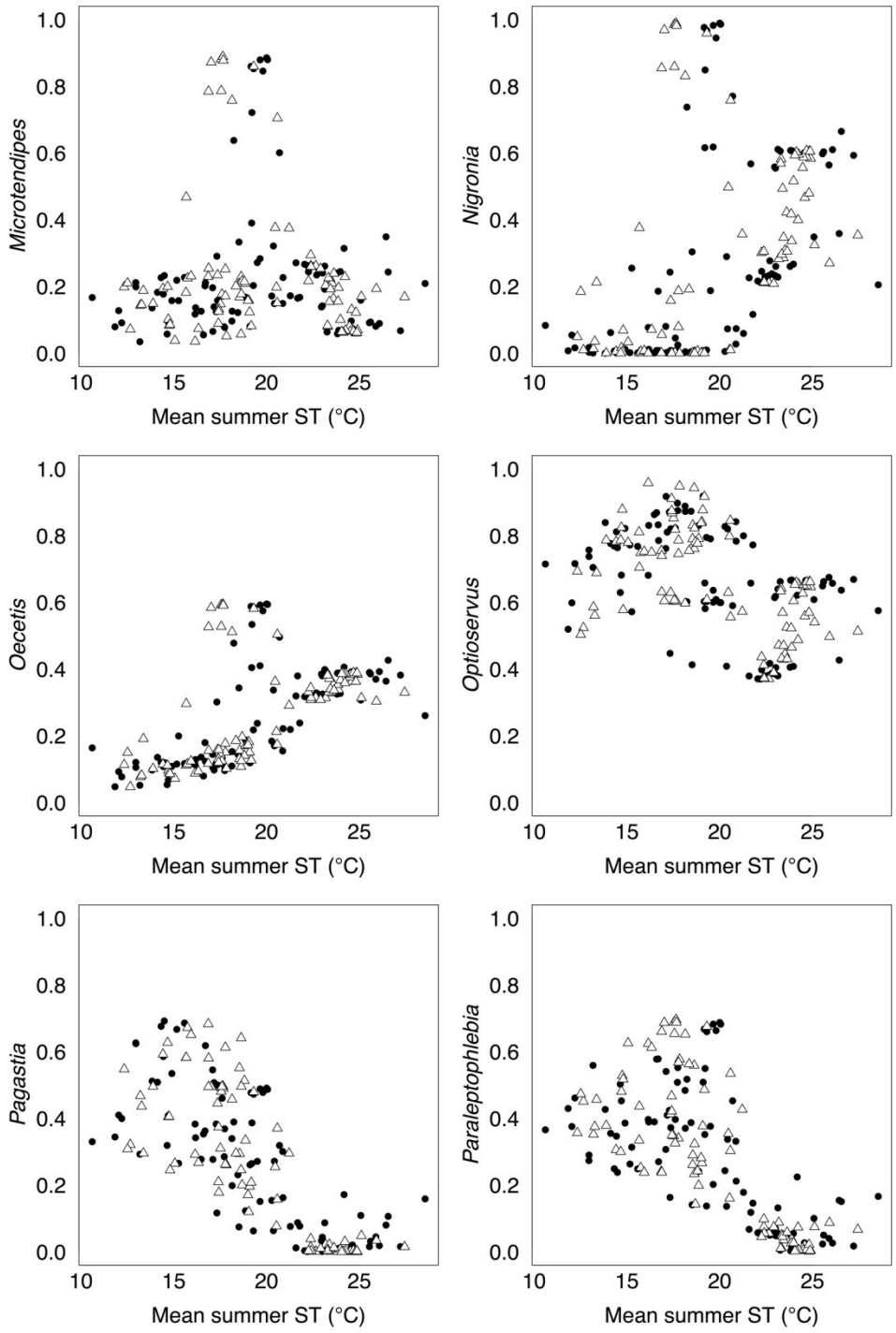
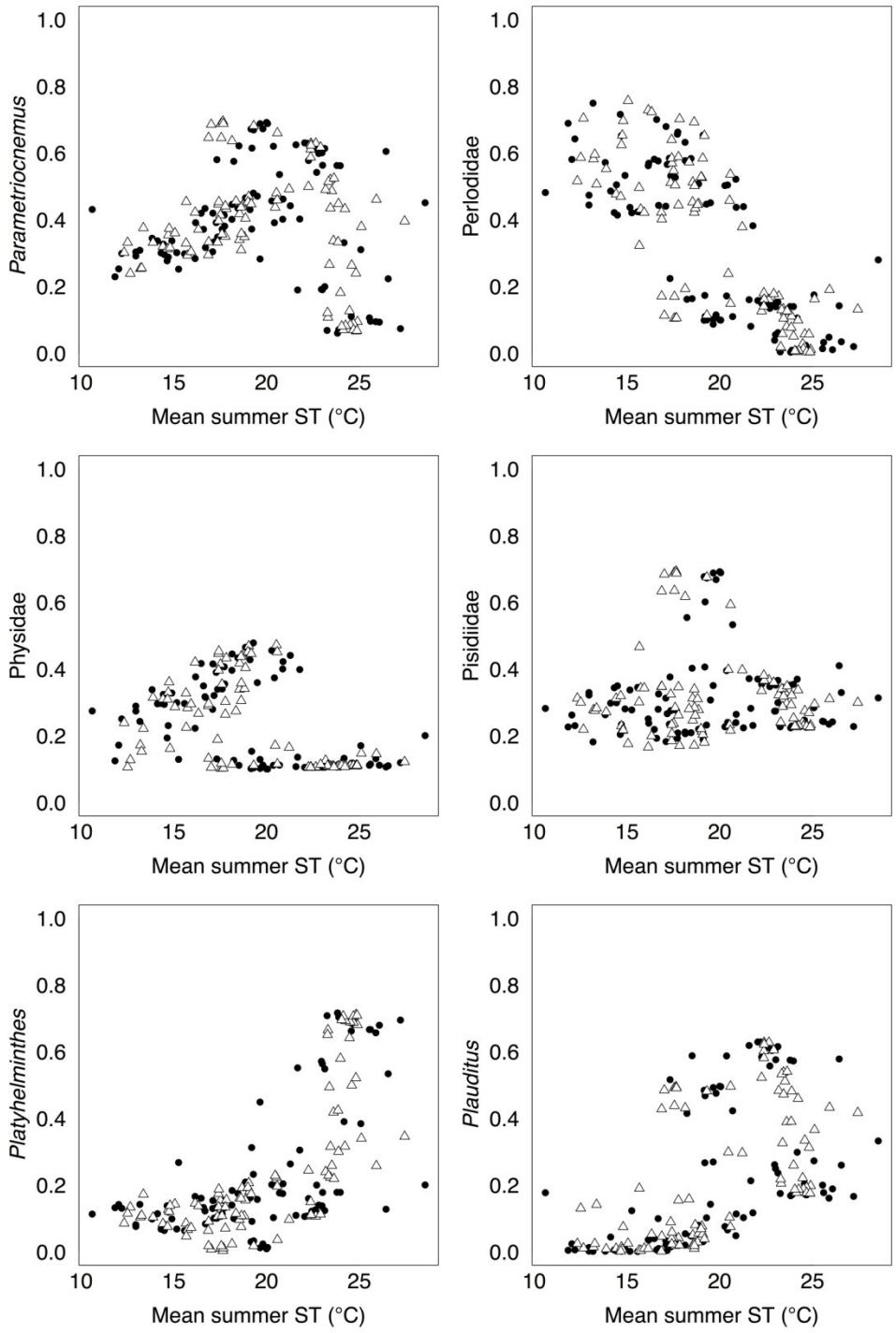


Figure E. Continued.



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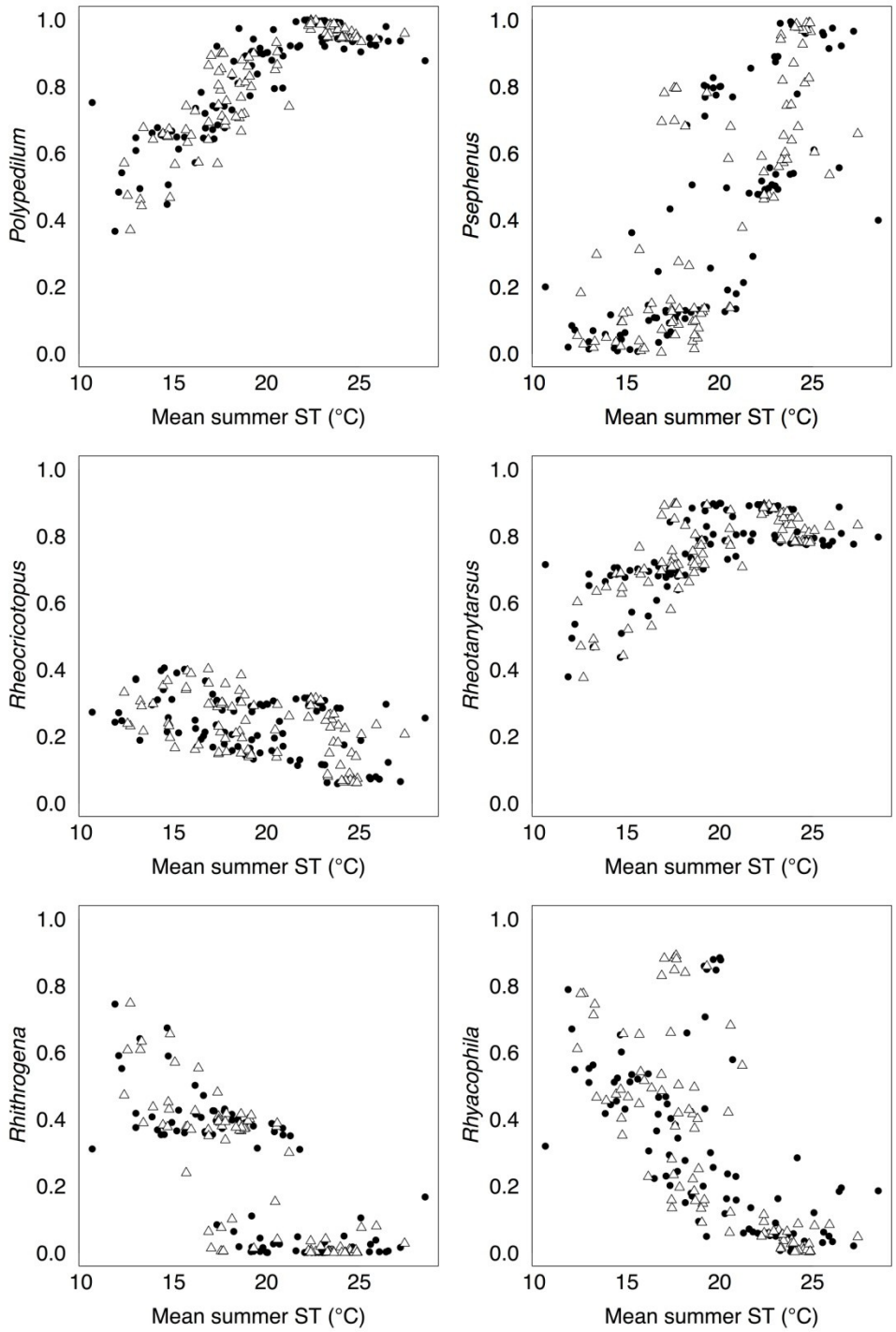
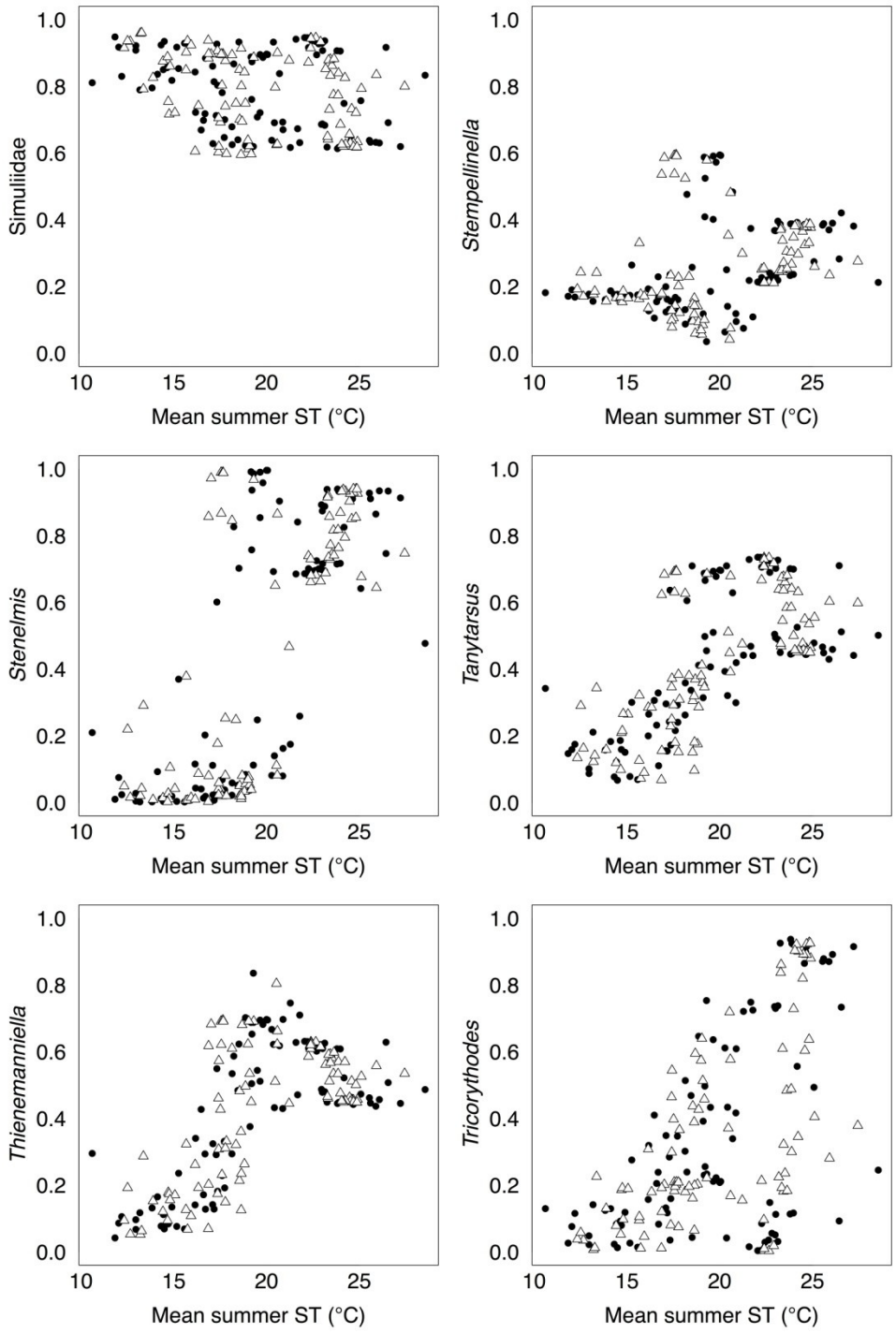


Figure E. Continued.



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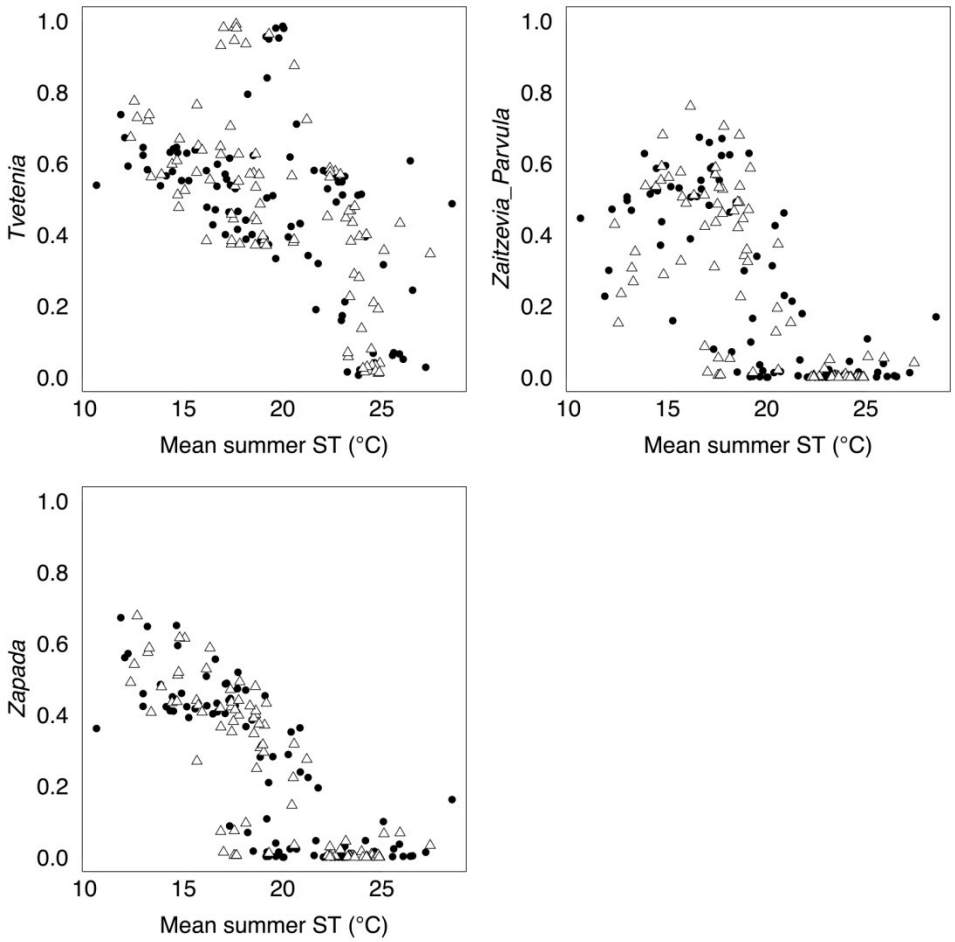

Figure E. Continued.

Appendix F. Taxon-specific relationships between predicted capture probabilities based on measured predicted stream temperatures

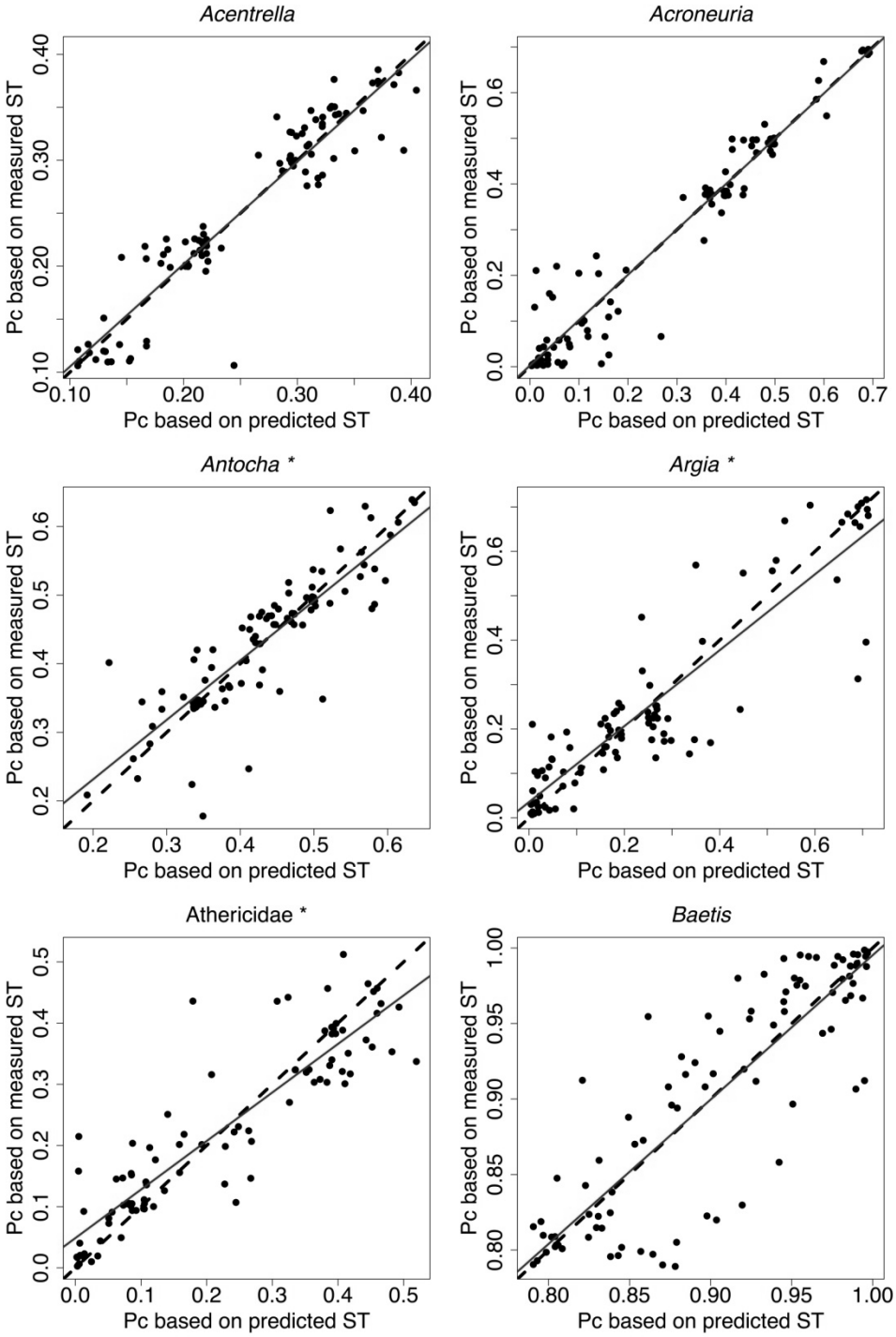

Figure F. Taxon-specific relationships (grey solid lines) between predicted capture probabilities (Pc) based on measured and predicted stream temperatures (ST). Taxa with regression slopes that are statistically different from 1 are marked with asterisks.

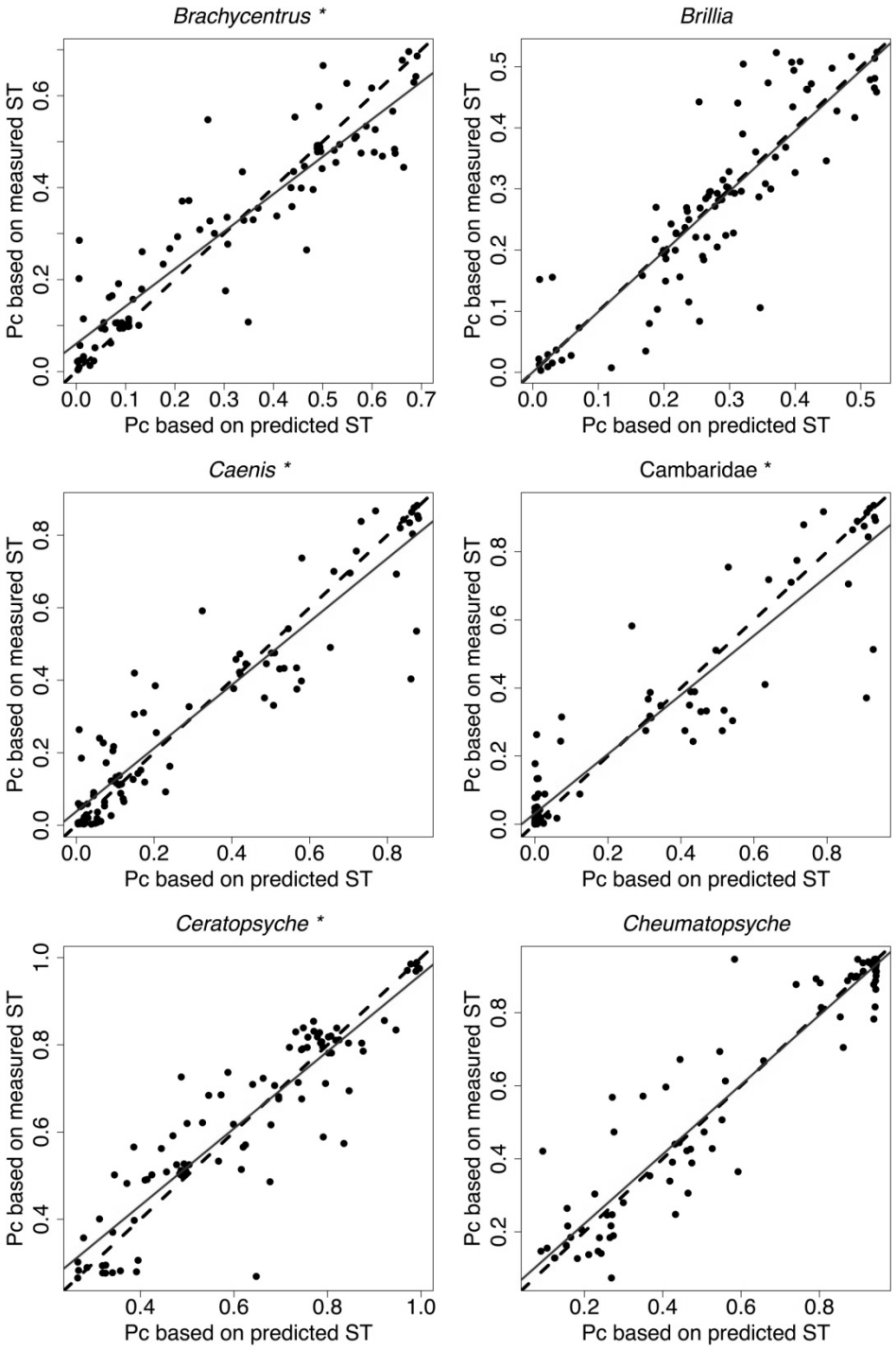

Figure F. Continued.

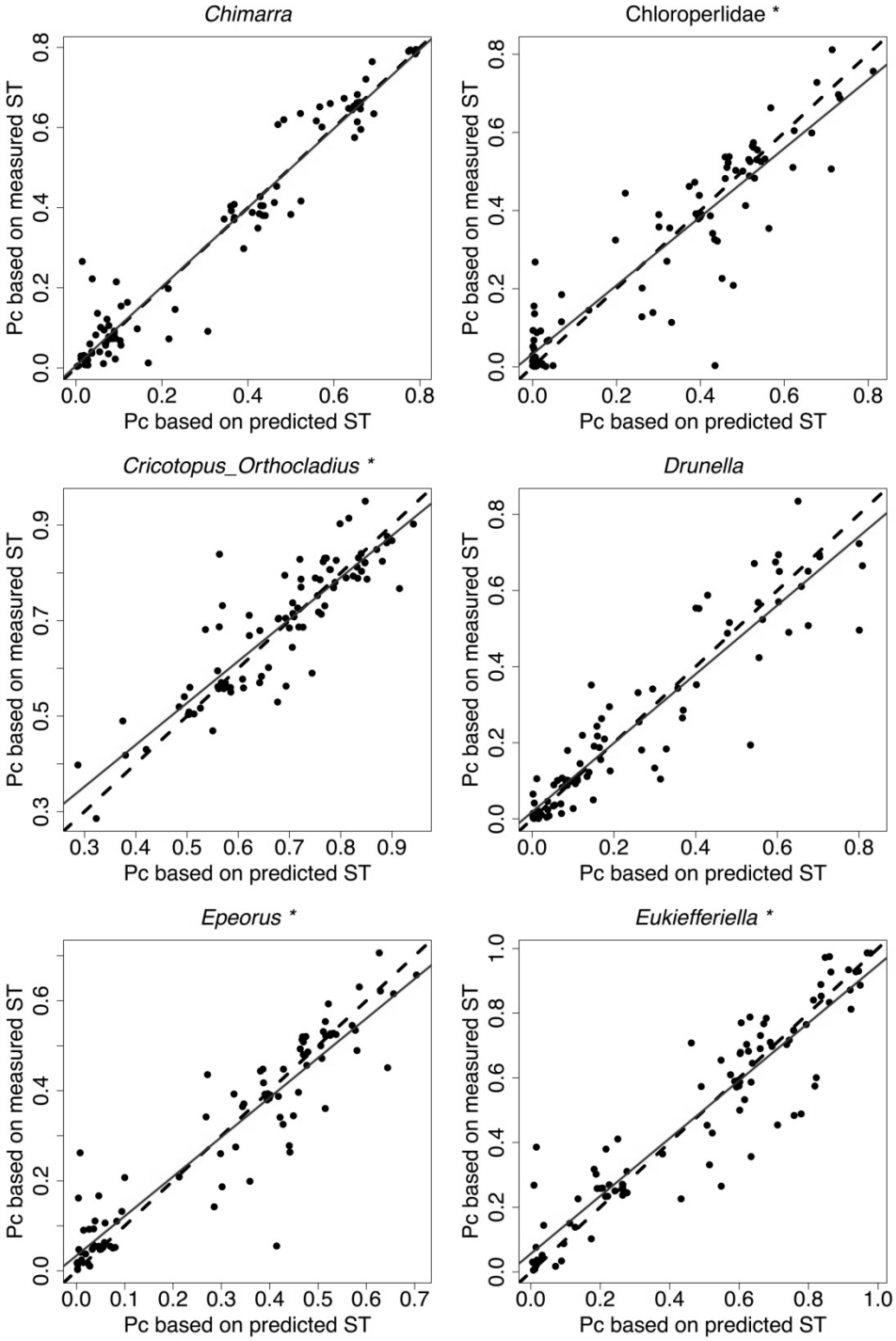

Figure F. Continued.

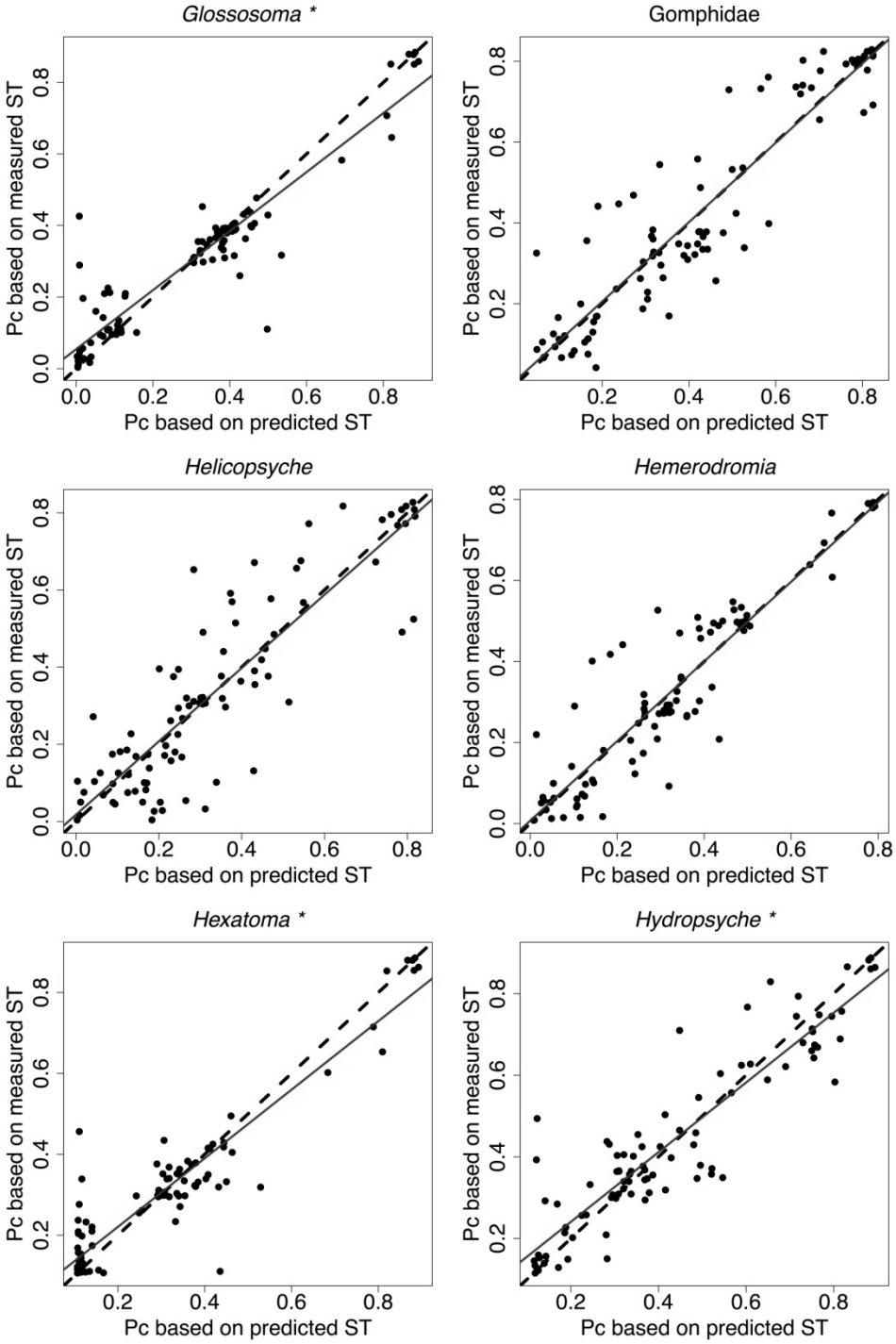

Figure F. Continued.

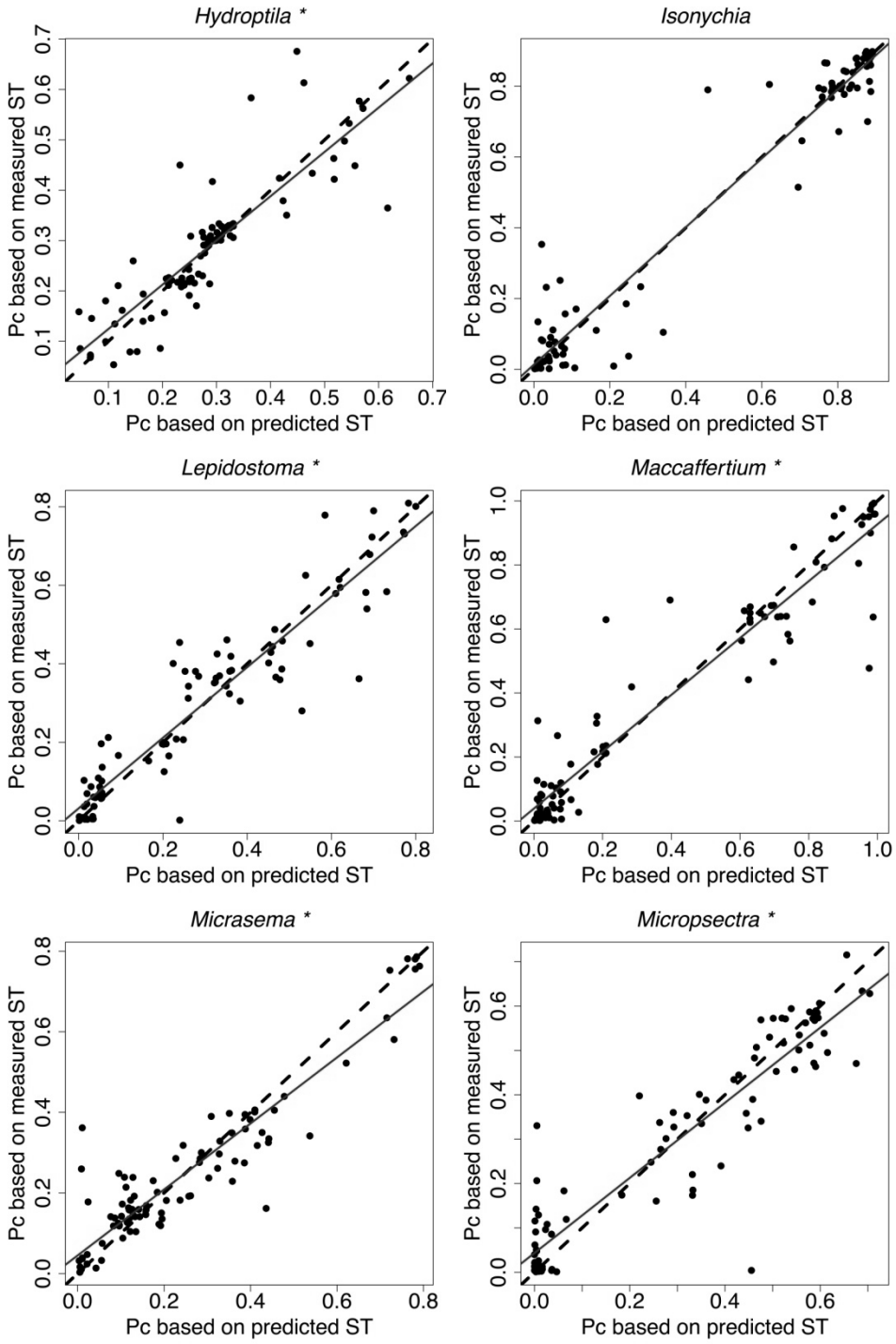

Figure F. Continued.

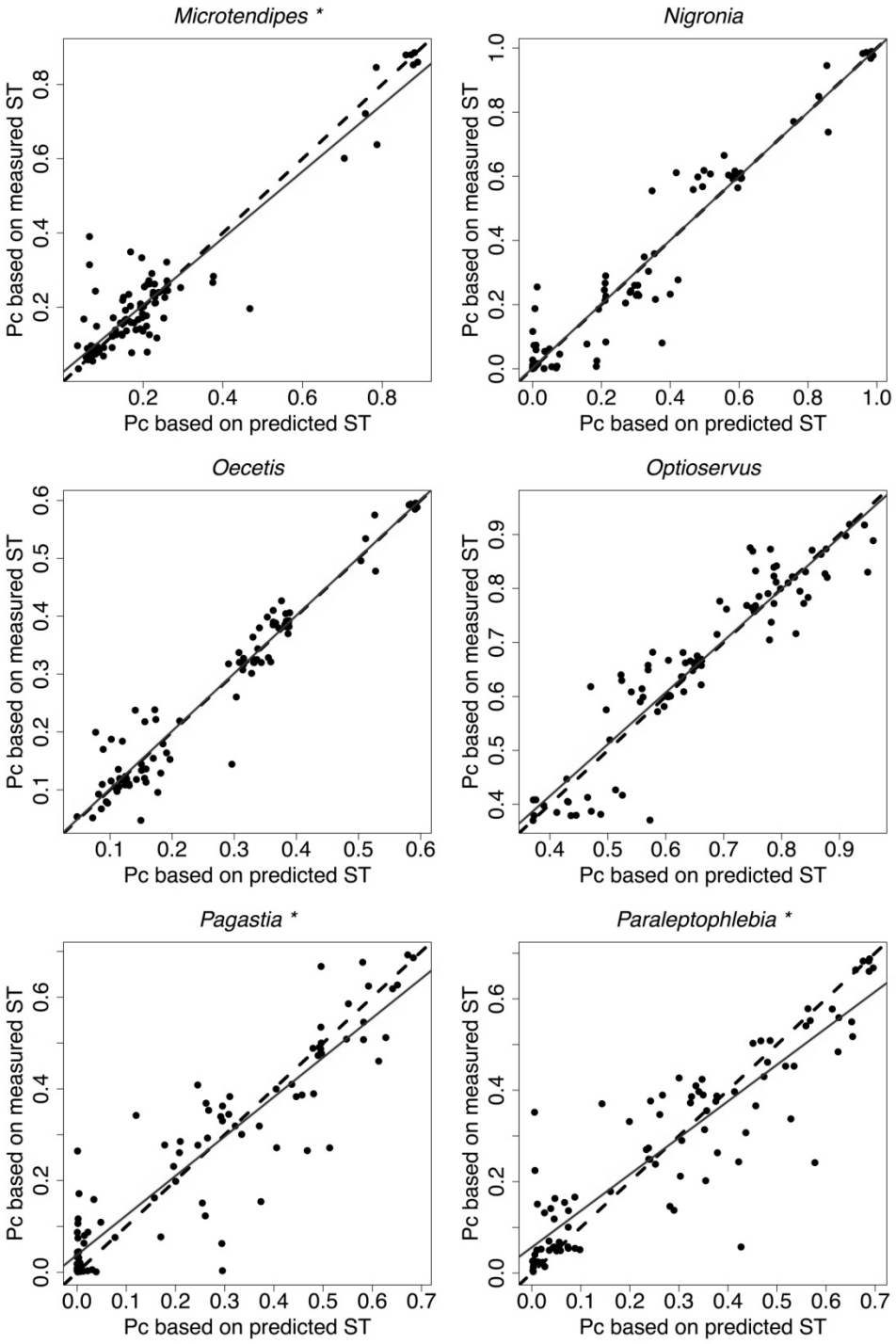

Figure F. Continued.

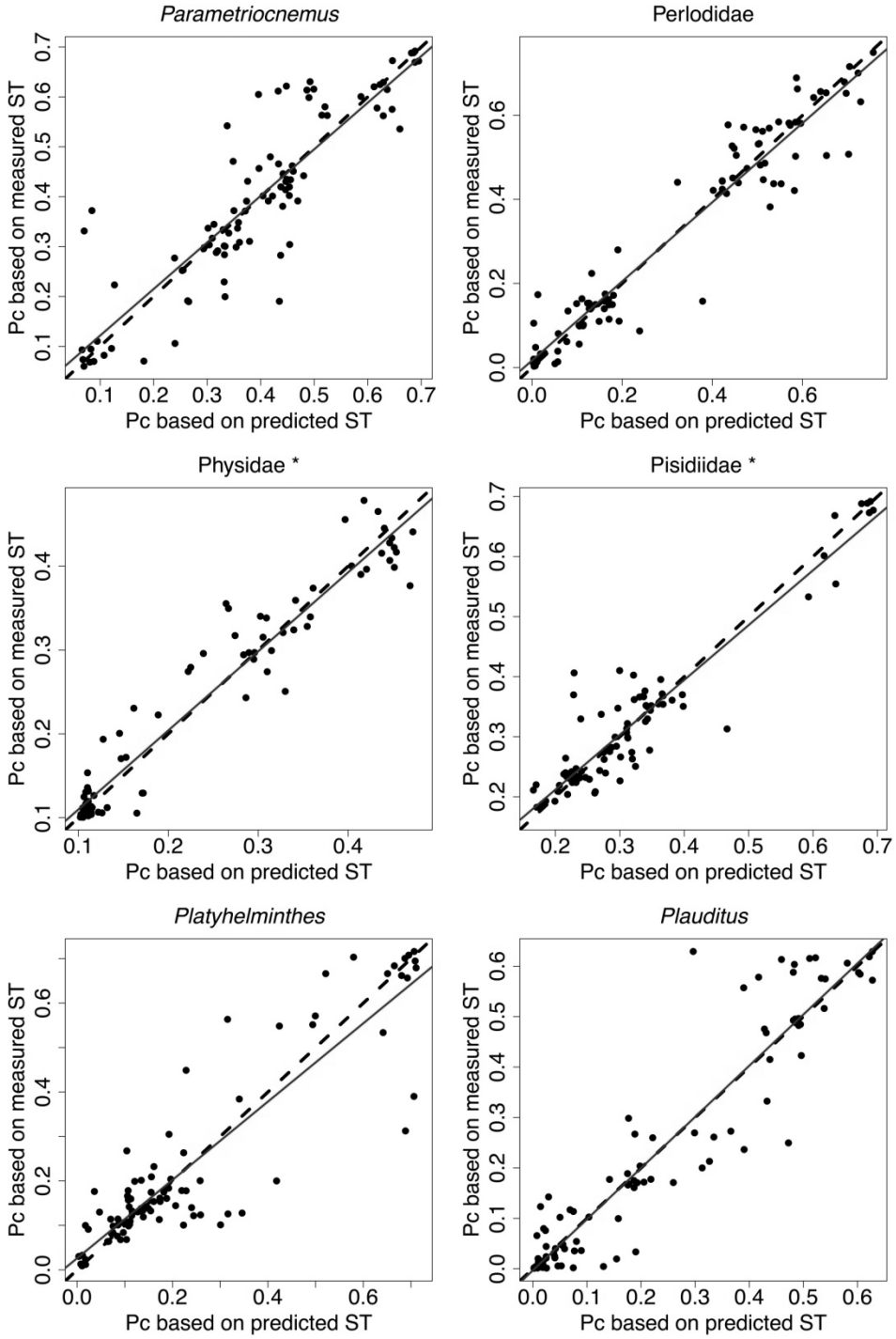

Figure F. Continued.

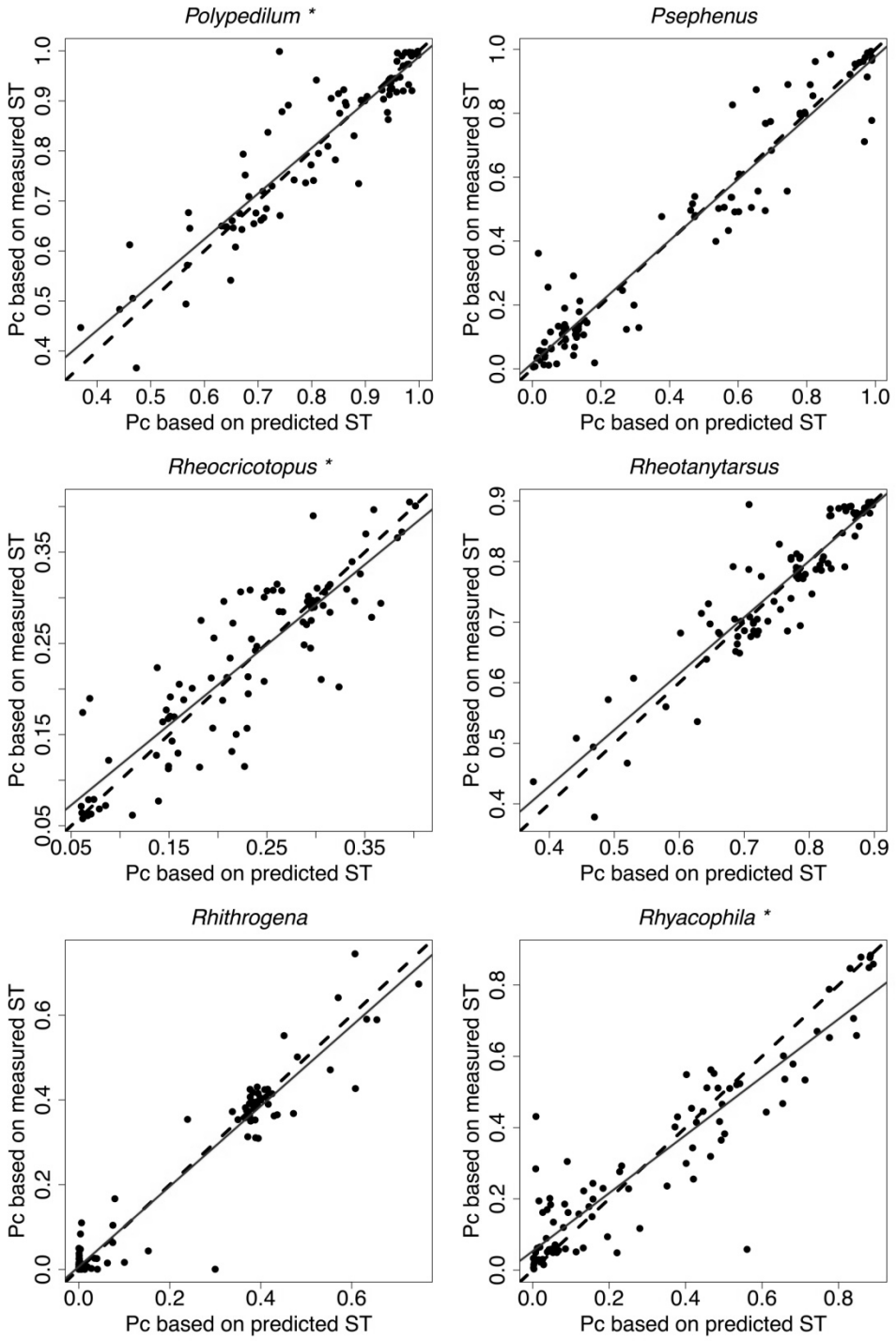

Figure F. Continued.

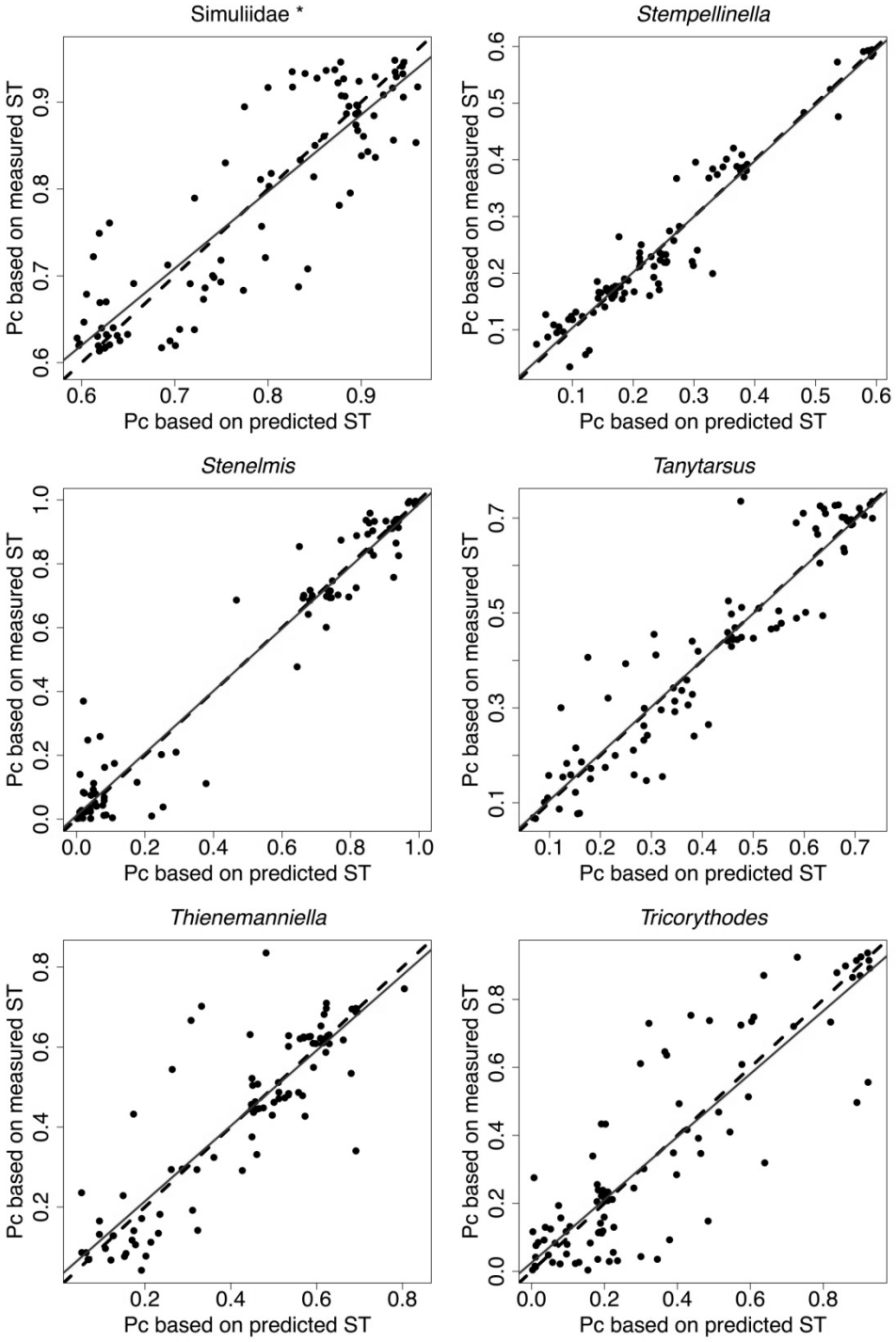

Figure F. Continued.

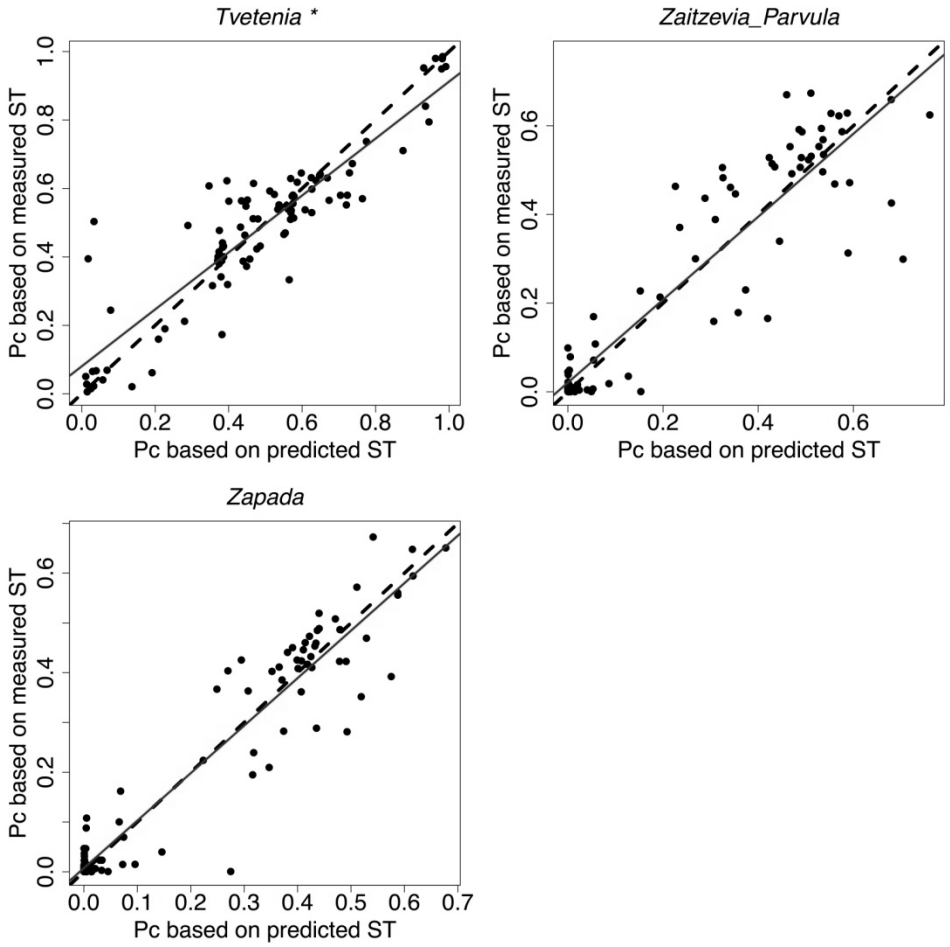

Figure F. Continued.

Appendix G. Permission-to-Reprint Letters

From: Ryan Hill [mailto:ryan.hill@usu.edu]
Sent: Tuesday, April 23, 2013 1:30 PM
To: Pamela Silver
Subject: Permission to reprint article in dissertation

Dear Pam,
I am preparing my dissertation and wish to request permission to reprint, as a chapter in my dissertation, an article that was recently published in *Freshwater Science*. The article in question is:

Hill, R. A., C. P. Hawkins, and D. M. Carlisle. 2013. Predicting thermal reference condition for USA streams and rivers. Freshwater Science 32: 39-55.

Please note that USU sends dissertations to Bell & Howell Dissertation Services to be made available for reproduction.

I will include an acknowledgement to the article on the first page of the chapter, as shown above. Copyright and permission information (i.e., your response) will be included in a special appendix. Please indicate if you would prefer a different acknowledgement. I have inquired and an email from you is sufficient to indicate your approval of this request. Please indicate if you charge a reprint fee for use of an article by the author.

Thank you,
Ryan

From: PAMELASILVER<psb3@psu.edu>
Subject: RE:Permissiontoreprintarticleindissertation
Date: April 23, 2013 11:42:11 AM MDT **To:** 'Ryan Hill' <ryan.hill@usu.edu>

Hi Ryan – you have my permission to use the article as described and the acknowledgement you propose is fine. I am not sure what you mean by a reprint fee to use the article, but there is no charge to use it in your dissertation. Pam

Appendix G. Continued

From: **Ryan Hill <ryan.hill@usu.edu>**
Subject: Permission-to-use letter
Date: May 2, 2013 4:43:07 PM MDT
To: Daren M Carlisle <dcarlisle@usgs.gov>

Daren,

I am preparing my dissertation for submission to the USU graduate school. I must obtain permission-to-use letters from coauthors on dissertation chapters that were not signatories to the title page. I have inquired and an email from you would be sufficient to indicate your permission to print, as a chapter in my dissertation, our paper titled:

Hill, R. A., C. P. Hawkins, and D. M. Carlisle. 2013. Predicting thermal reference condition for USA streams and rivers. Freshwater Science 32: 39-55.

Thanks,
Ryan

From: **Daren M Carlisle <dcarlisle@usgs.gov>**
Subject: Re: Permission-to-use letter
Date: May 2, 2013 4:35:28 PM MDT
To: Ryan Hill <ryan.hill@usu.edu>

Permission granted.

CURRICULUM VITAE

Ryan A. Hill
April 2013

Department of Watershed Sciences
Western Center for Monitoring and Assessment of Freshwater Ecosystems
College of Natural Resources
Logan, Utah 84322-5210
Utah State University
Phone: 435.770.0906, Email: ryan.hill@usu.edu
http://www.researcherid.com/rid/I-3206-2012

Research Interests:

- Stream Ecology
- Climate Change
- Stream temperature / Geomorphology
- Bioassessment / Environmental modeling / Statistics
- Geospatial Analyses / Geographic Information Systems (GIS)

Education:

Ph.D. –	Utah State University, Logan. Watershed Science (Ecology emphasis). May 2013.
B.S. –	Utah State University, Logan. Major: Environmental Studies. Minor: Portuguese. 2001.

Professional Experience:

Senior Research Associate (2006 – Present)	Utah State University – Western Center for Monitoring and Assessment of Freshwater Ecosystems: Development of large-scale models of stream temperature, hydrology, and stream benthic invertebrate distributions as part of USEPA and USGS funded projects. Development and generation of watershed and stream reach-level descriptors within a GIS in support of more than 10 state and national aquatic bioassessments.
Research Assistant (2002 – 2006)	Utah State University – Department of Watershed Sciences: US EPA STAR (Science Towards Achieving Results) funded research to develop an automated process for rapid delineation of many watershed boundaries and development of GIS-based predictors of stream invertebrate assemblages for bioassessments.

Publications:

Journal Articles

Hill, R.A., C.P. Hawkins, and D.M Carlisle. 2013. Predicting thermal reference conditions for USA streams and rivers. Freshwater Science 32: 39-55.

Chinnayakanahalli, K. J., C.P. Hawkins, D.G. Tarboton, and **R.A. Hill**. 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.

Hawkins, C.P., J.R. Olson, and **R.A. Hill**. 2010. The reference condition: predicting benchmarks for ecological and water-quality assessments. Journal of the North American Benthological Society 29: 312-343.

Manuals

Chinnayakanahalli, K., **Hill, R.A**., Olson, J.R., Kroeber, C., Tarboton, D.G., and C.P. Hawkins. 2006. The multi-watershed delineation tool: GIS software in support of regional watershed analyses, users manual. Department of Civil and Environmental Engineering and Department of Aquatic, Watershed, & Earth Resources, Utah State University.

Presentations:

Hill, R.A. and C.P. Hawkins. 2013. Modeled stream temperature matched observed temperature in predicting stream invertebrate community composition. Annual meeting of the Society for Freshwater Science, Jacksonville, FL.

Hill, R.A. and C.P. Hawkins. 2012. Predicting differential vulnerabilities of stream and river temperatures to climate change. Annual meeting of the American Geophysical Union, San Francisco, CA.

Hill, R.A. and C.P. Hawkins. 2012. Predicting the vulnerability of stream and river temperatures to climate change. Annual meeting of the Society for Freshwater Science, Louisville, KY.

Hill, R.A. and C.P. Hawkins. 2011. Effects of natural and altered catchment attributes on stream temperatures of the western USA. Annual Meeting of the North American Benthological Society, Providence, RI.

Hill, R.A. and C.P. Hawkins. 2010. Establishing Thermal Reference Condition: Development of Stream Temperature Models in Support of Biological Monitoring and Assessment in the Western USA. National Water Quality Monitoring Conference, Denver, CO.

Hill, R.A. and C.P. Hawkins. 2009. Establishing Thermal Reference Condition: Development of Stream Temperature Models in Support of Biological Monitoring and Assessment in the Western USA. Northwest Biological Assessment Workgroup, McCall, ID.

Hawkins, C.P., N.K. Burbank, **R.A. Hill**, and J.R. Olson. 2009. The nature and consequences of systematic prediction errors in ecological assessments — or why it is inappropriate to be concerned about mice when there are tigers abroad. Annual Meeting of the North American Benthological Society, Grand Rapids, MI.

Hill, R.A., Hawkins, C.P. and N. Burbank. 2008. Establishing thermal reference condition for streams: A critical need for assessing the effects of altered climate, riparian cover, and hydrology on stream temperatures and biota. Annual Meeting of the North American Benthological Society, Salt Lake City, UT.

Hill. R.A. and C.P. Hawkins. 2005. Spatially explicit mapping of potential benthic invertebrate assemblage classes with GIS. Annual Meeting of the North American Benthological Society, New Orleans, LA.

Rollins, S.L., R.J. Stevenson, C.P. Hawkins, K.M. Manoylov, J.R. Olson, and **R.A. Hill**. 2005. Predicting Diatom Assemblages in Minimally-Impacted Streams Using a New Hybrid Modeling Approach. Annual Meeting of the North American Benthological Society, New Orleans, LA.

Hill, R.A. and C.P. Hawkins. 2004. Valley width as a predictor of streambed sediment size in the western United States. Annual Meeting of the North American Benthological Society, Vancouver, BC.

Hill, R.A. and C.P. Hawkins. 2003. Correlations between valley width and sediment size distribution: A GIS-based approach to characterizing physical stream structure. Annual Meeting of the North American Benthological Society, Athens, GA.

Posters:

Olson, J.R., Hawkins, C.P. and **R.A. Hill**. 2009. Deriving continuous measurements of stream environmental gradients from categorical geologic maps. Annual Meeting of the US Regional International Association for Landscape Ecology.

Burbank, N., Hawkins, C.P. and **R.A. Hill**. 2008. A comparison of two recently developed ecological niche modeling programs: Predicting the distributions of 18 fish species in Colorado streams. Annual Meeting of the North American Benthological Society, Salt Lake City, UT.

Hill, R.A., Chinnayakanahalli, K., Olson, J.R., Hawkins, C.P. and D.G. Tarboton. 2007. Rapidwatershed delineation and characterization with the Multi-Watershed Delineation tool: GIS software in support of regional watershed analyses. Annual Meeting of the North American Benthological Society, Columbia, SC.

Chinnayakanahalli, K., Tarboton, D.G., Olson, J.R., **Hill, R.A.** and C. Kroeber. 2006. A Tool to Delineate Watersheds and River Networks for Multiple Sites Spread over Large Digital Elevation Models. Hydrology Days, Colorado State University, Fort Collins, CO.

Teaching Experience:

Teaching Assistant (Fall 2000)	Utah State University – Department of Geography: Geographic Information Systems (GEOG 4930).

Awards:

Best Oral Presentation On An Applied Research Topic (2003) – Annual Meeting of the North American Benthological Society, Athens, GA.

Additional Experience/Interests/Skills:

Ad Hoc referee for the journal Ecology, backpacking, whitewater rafting, cooking, travel, functional in Spanish, fluent in Portuguese