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Title: Probabilistic measures of climate change vulnerability, adaptation action benefits, and related uncertainty from maximum temperature metric selection

Running head: Max temperature metric selection uncertainty

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Abstract

Predictions of the projected changes in species distribution models and potential adaptation action benefits can help guide conservation actions. There is substantial uncertainty in projecting species distributions into an unknown future, however, which can undermine confidence in predictions or misdirect conservation actions if not properly considered. Recent studies have shown that the selection of alternative climate metrics describing very different climatic aspects (e.g., mean air temperature vs. mean precipitation) can be a substantial source of projection uncertainty. It is unclear, however, how much projection uncertainty might stem from selecting among highly correlated, ecologically similar climate metrics (e.g., maximum temperature in July, maximum 30-day temperature) describing the same climatic aspect (e.g., maximum temperatures) that is known to limit a species' distribution. It is also unclear how projection uncertainty might propagate into predictions of the potential benefits of adaptation actions that might lessen climate change effects. We provide probabilistic measures of climate change vulnerability, adaptation action benefits, and related uncertainty stemming from the selection of four maximum temperature metrics for brook trout (*Salvelinus fontinalis*), a cold-water salmonid of conservation concern in the eastern U.S. Projected losses in suitable stream length varied by as much as 20% among alternative maximum temperature metrics for mid-century climate projections, which was similar to variation among three climate models. Similarly, the regional average predicted increase in brook trout occurrence probability under an adaptation action scenario of full riparian forest restoration varied by as much as 0.2 among metrics. Our use of Bayesian inference provides probabilistic measures of vulnerability and adaptation action benefits for individual stream reaches that properly address statistical uncertainty and can

help guide conservation actions. Our study demonstrates that even relatively small differences in the definitions of climate metrics can result in very different projections and reveal high uncertainty in predicted climate change effects.

Introduction

The effects of climate change are evident in contemporary range shifts for many species (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006), and even more widespread shifts are expected to occur in the future (Xenopoulos et al., 2005; Thuiller et al., 2008; Urban et al., 2012). Species distribution models (SDMs), based on correlative relationships between species distributions, climate metrics and other environmental predictors, are the most commonly used approach to predict distribution changes in response to climate change scenarios (Guisan & Thuiller, 2005; Botkin et al., 2007; Elith & Leathwick, 2009a). Predicted changes provide a view of potential futures that can help guide conservation actions, such as protecting areas predicted to be less vulnerable to climate change (Loyola et al., 2013). SDMs can also further guide conservation by predicting the potential benefits of specific adaptation actions taken to lessen climate change effects, such as habitat restoration (Renton et al., 2012; Beechie et al., 2013; Justice et al., 2017). Given their potential to guide conservation and management actions, it is important to understand the limitations of and uncertainty in SDM-based predictions of potential climate change effects and adaptation action effects.

The uncertainty inherent in predictions of future species distributions, which we refer to as projection uncertainty, can be better understood by comparing multiple SDM-based predictions of projected species distributions. Many studies have shown that differences in projections of predicted outcomes for a species under climate change can be very high (e.g., Thuiller, 2004; Watling et al., 2015), which may undermine confidence in predictions of climate change effects if not properly understood. Projection uncertainty may also result in very different predictions of the potential benefits of adaptation actions, resulting in uncertainty about which actions may be best for species conservation in specific habitats.

The major components of projection uncertainty include scenario uncertainty (e.g., alternative IPCC scenarios), model uncertainty (e.g., alternative climate models, SDM methods, or predictor variables), and parameter uncertainty (Thuiller, 2004; Yoe, 2011; Watling et al., 2015). Several studies have focused on how the selection of alternative climate metrics can lead to very different species distribution predictions under current conditions and future projections of climate change (Synes & Osborne, 2011; Braunisch et al., 2013; Pliscoff et al., 2014; Watling et al., 2015). Predictor selection, including climate metrics, is one of the most difficult aspects of SDM development because predictors are often highly correlated and it is difficult to identify which predictor, if any, best characterizes climatic and other controls on a species' current distribution given available information (Elith & Leathwick, 2009a; Austin & Van Niel, 2011; Bucklin et al., 2015). Braunisch et al. (2013) found that distributions predicted using four alternative climate metrics were very similar under current conditions, but that differences under climate change were quite high due to divergence in predicted changes among the four climate metrics. Others have also found that climate metric selection could be a comparably large component of projection uncertainty (Synes & Osborne, 2011; Pliscoff et al., 2014), although it may be lower than from other sources (Watling et al., 2015).

The metrics compared in previous studies described different climatic aspects (e.g., total precipitation in May-July vs. mean temperature in May-July), which were selected presumably because such data are readily available through online databases (e.g., worldclim.org) or because there was insufficient ecological knowledge to help guide metric selection (e.g., Braunisch et al. 2013). Even when knowledge of a species' physiological constraints clearly points to the importance of a specific aspect of the climatic regime for model development, a number of very similar metrics may describe the same climatic aspect. Many organisms are physiologically limited by maximum temperatures, for example, but a large number of plausible metrics describing maximum temperatures can be identified (e.g., mean temperature in the warmest month, maximum thirty-day mean temperature, or maximum seven-day mean temperature). Laboratory studies of cold-water fish species demonstrate that multiple maximum temperature metrics can limit survival, with thermal maxima increasing as exposure time decreases (Beitinger et al., 2000). Similarly, field investigations have also demonstrated that different metrics describing maximum water temperature for different time windows can all adequately describe the observed distribution of cold-water fish species (Wehrly et al., 2007). Given that such metrics describe similar ecological processes and are often very highly correlated, modeled relationships, predictive performance and current predicted distributions are likely to be nearly indiscernible. However, if the degree of projected change varies among a group of climate metrics, divergent projections of species distributions are likely (Braunisch et al., 2013).

Projection uncertainty from metric selection and other sources may also propagate into SDM-based predictions of the potential benefits of adaptation actions, which may make associated decisions more difficult. In comparison to the large number of studies predicting climate change effects, relatively few studies have predicted the potential for adaptation actions to benefit species conservation by lessening climate change effects (Battin et al., 2007; Renton et al., 2012; Beechie et al., 2013; Justice et al., 2017). This is surprising because such predictions can help conservation practitioners focus resources on location-specific actions that might limit climate change effects. Predicted effects of management actions are also a requirement for adaptive management, which may greatly benefit conservation efforts under climate change due to its focus on better decision making through uncertainty reduction (Nichols et al., 2011). To our knowledge, no studies have quantified projection uncertainty in predicted benefits of adaptation actions for species conservation.

River and stream ecosystems are especially vulnerable to air temperature increases and changes in precipitation patterns (Ficke et al., 2007; Van Vliet et al., 2013), but riparian restoration may be an effective adaptation action for limiting changes (Seavy et al. 2009). Because of this high vulnerability, widespread changes in species distributions are expected (Xenopoulos et al., 2005), especially for species that are physiologically limited to a relatively narrow temperature window. Many cold-water fish species are especially susceptible to warming because suitable temperatures often occur only in headwaters and there is no option to migrate further upstream to seek colder areas. Rising air temperatures are predicted to result in widespread losses in distributions and increasingly fragmented habitat of cold-water fish species (Rahel et al., 1996; Roberts et al., 2013), although some streams may warm slowly relative to air temperatures and remain suitable (Isaak et al. 2016). Some studies have already demonstrated observed declines in survival, population abundance, hybridization, and distribution shifts for cold-water species (Isaak et al., 2012; Bassar et al., 2016). Restoring riparian vegetation, especially in forested areas, may help to lessen climate change effects by shading streams from solar radiation and heat exchange (Battin et al., 2007; Bond et al., 2015; Justice et al., 2017). Justice et al. (2017) demonstrated that riparian restoration may result in substantial water temperature reductions and increases in Chinook salmon populations in comparison to current conditions, even under scenarios of substantial warming. Given that riparian ecosystems can also provide benefits for water quality, flood control, and wildlife species, riparian restoration may prove to be a very useful adaptation action to help lessen climate change effects on river and terrestrial ecosystems (Seavy et al. 2009).

In this paper, we quantify projection uncertainty in predicted distribution changes and potential adaptation action benefits for brook trout *Salvelinus fontinalis*, a cold-water fish species native to eastern North America that is a conservation priority throughout much of its range. We predict climate change effects on brook trout occurrence using four ecologically similar metrics describing maximum water temperature and compare related projection uncertainty with that resulting from three alternative climate models. We also quantify metric- and model-based projection uncertainty in probabilistic estimates of vulnerability and the potential benefits of riparian forest restoration for lessening climate change effects on individual stream reaches. In the process, we describe novel measures for quantifying projection uncertainty in a Bayesian framework based on the amount of overlap in posterior distributions, which more accurately accounts for uncertainty in predictions. Finally, we discuss implications for selecting among ecologically similar climate metrics and provide guidance for quantifying and communicating uncertainty in the potential benefits of adaptation actions under climate change.

Materials and Methods

Study Species and Region

The brook trout is a socially, economically and ecologically important cold-water fish species native to eastern North America. Brook trout are physiologically limited to habitats with suitably cold-water temperatures, which is one of the primary determinants of where they are distributed (MacCrimmon & Campbell, 1969). Laboratory studies have determined that brook trout can survive if water temperatures do not exceed approximately 24-25 °C for longer than one week (McCormick et al., 1972) or 29-30 °C for any period (Lee and Rinne, 1980). Wehrly et al. (2007) similarly showed that brook trout are rare when maximum weekly mean temperatures exceed 23 °C based on field observations, but that temperature metrics summarized for different time periods (e.g., maximum 3-day, maximum 14-day) may also limit the distribution at different temperatures. Due to this physiological constraint, widespread losses of habitat and brook trout populations are likely to occur because of warming water temperatures in the southern portion of the species native range in the eastern United States (Meisner 1990; Flebbe 2006). Prior studies did not link predictions of climate change effects on the brook trout distribution to specific stream reaches, which somewhat limits their utility for guiding management and conservation actions.

The study region included the native range of brook trout in the eastern U.S. as defined by the Eastern Brook Trout Joint Venture (http://easternbrooktrout.org/), a collaboration of partners focused on brook trout conservation (see inset in Figure 2; Hudy et al., 2008). The region represents approximately 30% of the worldwide native range of brook trout and 70% of its range in the U.S. (Hudy et al., 2008). We chose this region out of an interest in providing predictions of potential climate change effects on brook trout to help support conservation and research decisions of the EBTJV and member states. Our predictions were based upon a base map of 195,134 stream reaches (National Hydrography Dataset Plus Version 1.0; accessed from http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php, access date March 2010) that had all available predictor variables for all time steps. The included stream reaches had an average length and local catchment area of approximately 7 km and 2.5 km^2, respectively. The use of individual stream reaches enabled us to provide predictions of climate change effects for specific stream reaches, which can help prioritize areas based on vulnerability or the potential to benefit from riparian restoration.

Climate Data and Models

We calculated the average daily temperature from the 10 nearest climate stations from the National Climate Data Center (NCDC; http://www.ncdc.noaa.gov/, accessed March 2010) to describe air temperatures for a given stream reach (see DeWeber and Wagner 2014 for details). Mean air temperatures for a given stream reach were used to predict water temperatures under baseline and future scenarios as described under *Water Temperature and Brook Trout Models*. We calculated baseline air temperatures as a five-year average centered on 1997 for each of the 184 days from April 1 through October 31. We centered the baseline period on 1997 because it was the closest historical time period to the land cover and fish sampling data for which climate model projections were available (see Hostetler et al. 2011). We obtained projected air temperatures from regional downscaled climate models (approximately 15 km spatial resolution): ECHAM5, GENMOM, and GFDL (Hostetler et al. 2011). We used projections from the A2 scenario of the Intergovernmental Panel on Climate Change (IPCC) AR4 report, which provided a near upper bound to future emissions (IPCC, 2008; Hostetler et al., 2011). These models provide a contrast in projected temperature increases over North America in response to CO_2 doubling, with 2-3 °C for GENMOM, 2-4 °C for ECHAM5, and 3-5 °C for GFDL (Hostetler et al., 2011). Although there are newer IPCC scenarios and updated climate models, we chose these projections because they provided a range of air temperature projections at a daily spatial resolution that were required to contrast differences among metrics (described further below). Similar to empirical data, we calculated baseline and future mean daily air temperatures based on 5-year averages centered on 1997, 2042, 2062 and 2087 for the ECHAM5 and GENMOM models; GFDL only had projections for 1997, 2042 and 2062. For each time step, we attributed the modeled mean daily air temperature of the model grid cell to the NCDC site that was located within that grid cell. Simply calculating changes between modeled future air temperature and current empirical air temperature could bias projections of change because models do not perfectly represent current conditions. Instead, we used the delta approach described by Hay et al. (2000), wherein we added the projected changes from each model (future – 1997) to empirical baseline averages so that future changes reflect projected air temperature increases.

Water Temperature and Brook Trout Models

We developed a neural network ensemble model for mean daily water temperatures (hereinafter water temperature model) throughout the study region (DeWeber & Wagner, 2014) and used predicted water temperatures with other landscape attributes to develop a hierarchical logistic regression model of brook trout occurrence (hereinafter brook trout model; DeWeber & Wagner, 2015a). We briefly describe these models here and refer the reader to DeWeber and Wagner (2014, 2015a) for further details.

The water temperature model (DeWeber & Wagner, 2014) had reasonable accuracy at a total of 1,080 stream reaches throughout the region based on root mean square error (RMSE ~ 2.0°C) and low bias (percent bias = 2%). In order of importance, predictors included current day mean air temperature, prior 7-day mean air temperature, network area, network forest cover, network mean aspect, and riparian forest cover within the local catchment. We used the 30 m 2001 National Land Cover Dataset (Homer et al. 2004) to describe land cover conditions and the 30 m National Elevation Dataset to derive aspect (see DeWeber & Wagner, 2014 for details). We utilized the model to predict mean daily water temperatures for baseline and future projected air temperatures for each of the time steps and climate models mentioned above. We then calculated four ecologically similar water temperature metrics used to characterize maximum water temperatures and identify suitable brook trout habitat: mean seasonal water temperature (MnSeason); mean July water temperature (MnJuly); and the maximum 7-day (Max7) and 30-day (Max30) moving averages. We chose these metrics because prior studies have shown that the distribution of brook trout and other closely related fish species can be predicted by temperatures summarized for 7-day and 30-day periods (Wehrly et al., 2007; Roberts et al. 2013), the warmest month (Rahel et al. 1996; Iaak et al., 2016), and throughout the season (Al-Chokhachy et al. 2013).

We developed hierarchical logistic regression models to predict the probability of brook trout occurrence using one of the four water temperature metrics describing baseline conditions and relevant predictors. DeWeber and Wagner (2015a) describes the brook trout model in detail for a single metric, Max30. We developed models with two levels, allowing the intercept and the effects of covariates at the stream reach (habitat unit) scale to vary among ecological drainage units (EDUs; Higgins et al. 2005). Brook trout probability of occurrence in stream reaches decreased sharply as Max30 increased, and intercepts were also lower in EDUs with warmer average Max30. Additional covariates included negative effects of developed and agricultural land covers in the local catchment and a positive effect of soil permeability. Soil permeability had a nominal spatial resolution of 1:250,000 (Schwarz and Alexander 1995), which was used to calculate the average within each local catchment. Model accuracy was reasonable based on area under the receiver operating curve (AUC = 0.7).

To estimate projection uncertainty resulting from alternative climate metrics, we developed similar models to those described above but substituted Max30 with the alternative metrics: Max7, MnSeason, and MnJuly. The effects of other landscape covariates did not change when alternative climate metrics were included. We refer to these models as the Max 7, Max 30, July and Season models throughout the manuscript. We used Bayesian inference to estimate parameters as described in DeWeber and Wagner (2015a), except that in this study we saved fewer draws (1,000 instead of 5,000) from posterior distributions for each parameter to make comparing posterior distributions less computationally demanding. Models converged quickly with values of the potential scale reduction factor (Gelman and Rubin 1992) less than 1.1 for all parameters.

Quantifying Projection Uncertainty

We calculated Spearman's rank correlations (ρ) between pairs of water temperature metrics for the baseline and future projections as a measure of similarity among metrics. We also calculated ρ between predicted changes in pairs of metrics to measure the degree of concordance in projected metric changes for each climate model and time step. Low ρ in predicted metric changes means that some metrics are likely to change more than others, which could result in greater projection uncertainty (Braunisch et al., 2013).

To estimate projection uncertainty, we calculated dissimilarity among metrics and models as the lack of overlap in posterior distributions of predictions for each stream reach. Comparing posterior distributions provides a more robust way to compare predictions than simply comparing mean estimates because statistical uncertainty is included. We first converted each distribution into a relative frequency histogram with bins of width 0.01 (equal to the precision of predictions) ranging from 0 to 1 for each distribution. We then calculated dissimilarity $D_{r,}$ for a given stream reach *r* as one minus the sum of the minimum relative frequency from the two distributions for each bin *b*: $D_r = 1 - \sum_1^B \min(freq1_b, freq2_b)$. We have included an example of dissimilarity between two hypothetical posterior distributions in Figure 1. Dissimilarity equals 1 if there is no overlap in distributions and 0 if distributions are identical. We calculated D_r and its mean across all stream reaches ($D_{\bullet}$) for pairs of metrics M_1 and M_2 for the baseline scenario ($D_{\bullet base,M1xM2}$), for pairs of metrics for a given time step *t* and climate model *C* ($D_{\bullet t,C,M1xM2}$), and for pairs of climate models for a given time step and metric ($D_{\bullet t,M,C1xC2}$). We also calculated the mean among all pairs of metric comparisons for a given time step and model ($D_{\bullet tC}$) and among all pairs of climate model comparisons ($D_{\bullet tM}$) for a given time step *t* and metric as estimates of average prediction variability, respectively. We used the ratio of $D_{\bullet tM}$ / $D_{\bullet tC}$ in our study to compare projection uncertainty among metrics and climate models for each time step.

Quantifying Climate Change Effects

We also wanted to understand how prediction variability among metrics and models might result in differences in the predicted negative effects of climate change on brook trout. Since our study region includes only the southern portion of the brook trout native range where warm temperatures are often limiting, we considered only negative effects on occurrence probability to be likely because of warming. We used two metrics to measure negative effects of climate change on brook trout: 1) decline probability for each stream reach and 2) changes in total suitable stream length. Decline probability is a measure of vulnerability of brook trout to climate change for each stream reach and provides a useful way to compare vulnerability among stream reaches. We calculated decline probability as the proportion of the 90% credible interval of posterior samples from each future prediction (i.e., a given future time step and model) of brook trout occurrence that was less than the 90% credible interval from the baseline posterior distribution for each metric. We also calculated differences in decline probability among metrics and models for a given time step to provide an additional means of quantifying projection uncertainty.

The total suitable stream length was the total length of stream reaches with a mean probability greater than or equal to 0.46 for each metric, model and time step combination. We selected the 0.46 threshold because it was equal to the prevalence of the training dataset, which balances false positives and negatives (Liu et al. 2005). We recognize that threshold selection is context dependent and that other thresholds would produce different estimates (see DeWeber and Wagner, 2015a for a more thorough discussion in relation to brook trout), but we use a single threshold here simply to help communicate projection variability. Changes in total suitable stream length represent potential climate change driven changes in suitable habitat amount throughout the study region.

Quantifying Riparian Restoration Benefits

We developed a simple scenario to predict the potential for riparian forest restoration to lessen climate change effects on brook trout throughout the region (riparian restoration scenario). In the riparian scenario, we changed the actual riparian forest cover calculated from the 2001 National Land Cover Dataset (Homer et al., 2004) to be fully forested (100%) for all stream reaches. The baseline riparian forest cover averaged 56.7% and ranged from 0 to 100% (see map in Figure S1). Note that streams with a high proportion of baseline riparian forest would receive little or no benefit from the riparian restoration scenario. We then predicted daily water temperatures using 100% riparian forest, calculated the four water temperature metrics, and predicted the probability of occurrence for all four metrics under the riparian restoration scenario for the baseline and projected climate change air temperatures.

We calculated the potential benefit of riparian forest restoration as the probability that occurrence probability was higher under the riparian restoration scenario than under baseline riparian scenario with the same climate conditions (benefit probability). Specifically, we quantified benefit probability as the proportion of the 90% credible interval of posterior samples from the riparian restoration scenario that was above the 90% credible interval of the baseline riparian scenario using the same metric, time step and model. Benefit probability provides a stream reach specific measure of the potential benefits of riparian forest restoration, and we compared the mean regional benefit probability among models and metrics to quantify projection uncertainty. We also calculated decline probability and total suitable stream length for the riparian restoration scenario and compared these to the same measures from the baseline riparian scenario to quantify a net benefit of riparian restoration for lessening climate change effects.

Results

Correlations among metrics under baseline conditions were very high (ρ ≥ 0.97), and SDMs with different metrics performed very similarly (AUC=0.78-0.81). The total baseline suitable stream length varied among metrics by less than 4,700 km or 3% (Table 1), and spatial patterns in predictions of mean occurrence probability were very similar (Figure S2). Based on similar predictive performance and knowledge of brook trout physiology, all of the metrics appear equally important for limiting the distribution of brook trout and a change in any may result in distribution shifts. As expected, the temperature considered suitable decreased as the number of days summarized by a climate metric increased. For example, when all other predictors were held at their median values, the probability of occurrence was very low (<0.05) when MnSeason approached 20 °C but not until Max7 approached 24 °C (Figure S3). Mean metric dissimilarity for the baseline ranged from 0.13 to 0.27 (mean = 0.2) and was higher for pairs that included MnSeason (Table 2). This indicates that although metrics had nearly identical model performance and baseline mean predictions, there were some underlying differences in posterior distributions of predictions not reflected in the mean.

Similar to the baseline, correlations among metrics for a given future time step and climate model were consistently high (>0.91). Correlations among projected changes in metrics for a given climate model and time step were often much lower, however, suggesting that metrics were projected to diverge in the future (Table S1). Correlations between changes in Max7 and Max30 were relatively high (ρ ≥ 0.44), whereas any correlations including MnSeason or MnJuly were highly variable. For example, the correlation among changes in MnJuly and Max7 was -0.34 for GFDL in 2062, but was 0.9 for ECHAM5 in 2062. The magnitude of projected air and water temperature changes generally decreased in order of Max7, Max30, MnSeason, and MnJuly.

Metric dissimilarity among predictions for future selected time steps and climate models was often much higher than for the baseline but was highly variable, ranging from 0.1 to 0.57 (Table 2). Metric dissimilarity was generally greatest for the intermediate time steps 2042 (mean = 0.28) and 2062 (mean =0.32), but was even lower than the baseline in 2087 (mean = 0.18). Similar to metric dissimilarity, model dissimilarity varied widely depending upon the time step, models compared, and metric (Table 3). Model dissimilarity was slightly higher on average than metric dissimilarity in 2042 (mean = 0.35) and 2062 (mean = 0.32), and was much higher in 2087 (mean = 0.66). The ratio of mean model dissimilarity to metric dissimilarity was 1.25 in 2042, 1.03 in 2062, and 3.64 in 2087. Model dissimilarity was much higher in 2087 because only highly divergent projections from ECHAM5 and GENMOM were available. Model dissimilarity between ECHAM5 and GFDL, which had relatively similar projected air temperature increases, was relatively low and decreased from 2042 to 2062 for all metrics. In contrast, projected temperature increases from GENMOM were lower and there was thus greater dissimilarity that increased with each future time step.

Decline probability varied considerably depending upon the metric used in the intermediate 2042 and 2062 time steps (Table 4). For example, mean decline probability for GFDL in 2062 was 0.92 with Max7 but was only 0.54 with MnJuly. Maps of decline probability for Max7 and MnJuly in 2062 clearly show that decline probability varied greatly throughout the region (Figure 2) and among individual stream reaches (Figure 3). Decline probability was almost always higher in the southern portion of the range, while its variation was often greater in the north (Figure 2). Decline probability was generally lowest when MnJuly was used, while it was highest when Max7 or MnSeason was used (Table 4). Mean decline probability increased with projected warmer air temperatures, and declines were substantially greater for ECHAM5 and GFDL than for GENMOM for all time steps (Table 4). The mean decline probability for ECHAM5 in 2087 was predicted to be very high (0.98) and did not vary among metrics, as substantial warming for all metrics resulted in similar reductions. In contrast, mean decline probability for GENMOM 2087 was lower and had some variation, ranging from 0.7 to 0.8 among metrics.

Losses in suitable stream length generally reflected the patterns in decline probability, but there were some differences since a high decline probability did not always coincide with a drop from above to below the threshold used to define suitable habitat. Predicted losses of suitable stream length varied among metrics in 2042 and 2062, and losses were lower with MnJuly than with other metrics (Table 1). For example, predicted losses were 84.6% when Max7 was used but only 64.9% when MnJuly was used with GFDL in 2062 (Table 1). Projected losses of suitable stream length in 2087 were very high and similar across all metrics (range = 94.0-98.3%) for ECHAM5, but were much lower and similar (range = 62.0-66.7%) for GENMOM.

Riparian Restoration Benefits

Substantial increases in occurrence probability were predicted under the riparian restoration scenario for baseline and climate change conditions. The mean benefit probability under baseline climate conditions was 0.41-0.48 (mean = 0.45; Table 5), and an additional 67.2-71.5 Km of stream length were predicted to be suitable (Table S2). Mean benefit probability under projected conditions in 2042 was relatively high and varied relatively little across models or metrics (range = 0.35-0.46, Table 5). Projection uncertainty in benefit probability stemming from metrics was greatest in 2062, with the mean ranging from 0.22 to 0.36 for ECHAM5 and from 0.2 to 0.4 for GFDL (Table 5). Maps comparing mean benefit probability for GFDL in 2062 illustrate the magnitude of projection uncertainty in potential benefit probability that may result from selection among similar climate metrics (Figure 4). Mean benefit probability had relatively little projection uncertainty among metrics in 2087, and was much lower for ECHAM5 (range = 0.12-0.2) than for GENMOM (range = 0.3-0.37).

The predicted increases in occurrence probability under the riparian restoration scenario translated into substantial reductions of climate change effects compared to baseline riparian conditions, especially in intermediate time steps. Mean decline probability was reduced by more than 0.3 under the riparian restoration scenario for many metric, models and time steps, but reductions varied greatly among metrics and models (Table S3). Reductions in mean decline probability were lower (<0.1) and varied very little for the conditions with the highest (ECHAM5 in 2087) and lowest (GENMOM in 2042) projected air temperature increases. Losses of suitable habitat were predicted to be reduced by more than 50 Km in 2042 and 30 Km in 2062 will riparian restoration for almost all combinations of metrics and models (Table S2). Riparian restoration was predicted to reduce habitat losses by 15.9-22.1 Km even under the warmest future conditions (ECHAM5 in 2087). In general, predicted reductions in losses of suitable stream length under riparian restoration did not vary greatly among metrics (< 13.4 Km) for a given model and time step (Table S2).

Discussion

We found that projections of climate change effects on brook trout and potential benefits of riparian restoration varied among four ecologically similar maximum water temperature metrics, especially for mid-century climate projections. Projected losses in suitable stream length varied by up to 30 Km (out of 150 Km of baseline suitable habitat) for mid-century climate projections, which was similar to variation among climate models. Similarly, the regional average predicted increase in brook trout occurrence probability resulting from full riparian restoration under a climate change scenario varied by as much as 0.2. Among metrics, variation in projected effects was very low compared to much higher variation between two climate models with different air temperature increases for near end-of-century climate projections. Similar to assessments for most taxonomic groups, most studies of climate change effects on brook trout (Meisner, 1990; Flebbe et al., 2006) and other cold-water fish (e.g., Wenger et al., 2011; Logez et al., 2012) have included only a single climate metric, which may ignore significant projection uncertainty and could result in biased projections. Previous studies have shown that selection among climate metrics describing different climatic aspects (e.g., maximum temperature, total precipitation) can be a large source of projection uncertainty in climate change effects on species distribution (Synes & Osborne, 2011; Braunisch et al., 2013; Pliscoff et al., 2014), but it was unclear how much projection variation could be expected among very similar metrics describing the same climatic aspect. Our study demonstrates that even relatively small differences in the definitions of climate metrics can result in very different projections, revealing high projection uncertainty. We predicted that using mean temperatures in the warmest month, July, could underestimate climate change effects on brook trout compared to similar metrics such as the maximum 30-day average. Although it is common practice to use temperature or precipitation in the warmest or driest month or other defined period, it may be more prudent to use metrics that are not tied to a defined time period (e.g., maximum and minimum moving averages) since greater changes may occur outside of pre-defined periods.

Our use of Bayesian inference enabled us to quantify probabilistic measures of projection uncertainty, vulnerability, and benefits of adaptation actions while properly accounting for statistical uncertainty in model predictions. Many studies focused on projection uncertainty have compared predicted species occurrence maps (e.g., (Araújo et al., 2005; Dormann et al., 2008; Braunisch et al., 2013), which relies upon the potentially problematic selection of an occurrence threshold (Fielding & Bell, 1997; Liu et al., 2005), ignores statistical uncertainty inherent in model-based predictions, and only provides region wide uncertainty estimates. Fewer have compared predicted values of mean probability or suitability (Syphard & Franklin, 2009; Brandt et al., 2017), which also ignores statistical uncertainty. While these studies produce valid comparisons of occurrence and mean estimates, they do not provide any estimate of the probability or magnitude of a difference in projections for each habitat unit or the region as a whole. By comparing posterior distributions, we were able to quantify the magnitude of projection uncertainty between pairs of metrics and models for each stream reach, which avoided the use of occurrence thresholds and accounted for statistical uncertainty. In addition, we were able to calculate the probabilities of negative and positive change resulting from climate change and adaptation actions for individual habitat units. Additional measures that are focused on specific questions or conservation actions can also be quantified through posterior distributions (e.g., the probability that a given adaptation action maintains suitable habitat; the mean difference in the expected benefit between two adaptation actions). It is important to note that we did not consider the full range of statistical uncertainty because we only used mean estimates from climate change and water temperature models, ignoring the uncertainty in those predictions and in predictor variables. Propagating uncertainty through all models would help to provide a more complete estimate of projection uncertainty (Araújo and New 2007).

We projected between 64% and 98% of suitable habitat for brook trout in the eastern U.S. could be lost near the end of the century due to warming air temperatures from climate change, which is similar to widespread negative effects predicted in prior studies (Meisner, 1990; Flebbe et al., 2006). We predicted greater losses in the southern portion of the study region, where brook trout populations are often already limited to highly fragmented headwaters and further losses would likely result in local extirpations. Substantial losses of habitat were also predicted further north in areas with relatively intact brook trout populations (Hudy et al. 2008), which could result in habitat fragmentation and the potential loss of life history diversity (e.g., potadromy) as larger streams become thermally unsuitable. Although there are fewer studies documenting observed shifts, Bassar et al. (2016) recently demonstrated that warming temperatures reduced survival and ultimately abundance of brook trout populations. Widespread losses of brook trout could have negative effects on ecosystems due to the loss of a top predator (Baum and Worm 2009). Population reductions and losses could also have negative socioeconomic effects through loss of an iconic species and lost angling opportunities for the only native cold-water game fish in much of the eastern U.S. (DeWeber & Wagner, 2015b). In addition, projected losses of cold-water habitat would likely result in widespread changes in ecosystems that could be exacerbated by losses in stream protection, as many states in the region (e.g., Pennsylvania) afford greater water quality protection to streams with brook trout and other trout species. We also predicted that full riparian restoration could increase suitable habitat under baseline climate conditions and help mitigate the effects of climate change for many stream reaches, although these benefits varied among stream reaches. Predictions of vulnerability and benefit probability can help identify stream reaches where climate change is less likely to result in extirpation or where riparian restoration may have small (large) benefits within a greater decision framework. We were unable to account for some important factors that may determine the response of brook trout to climate change, including groundwater and thermal refuges (Snyder et al., 2015), interactions with other species (Wagner et al., 2013; Hitt et al., 2016), dispersal, and interactions with human land use (Wagner and Midway 2014). We also caution that our estimates of the potential benefit of riparian restoration are based on an unrealistic scenario of fully forested riparian forests in all stream reaches, which we used to demonstrate its quantification and variability. Our model estimates provide information for understanding potential climate change effects and riparian restoration benefits, but local knowledge and additional information could greatly improve their utilization for guiding management and conservation of cold-water habitat and brook trout.

The variability in projections among climate metrics reveals uncertainty in climate change effects, and the manner in which this uncertainty is considered depends upon the objectives of the study or decision makers. One approach is to be precautionary and select the metric predicted to have the greatest negative effects. We think that this may be reasonable because based on similar model performance and ecological knowledge, we are very confident that substantial warming in any of the maximum temperature metrics used could greatly reduce brook trout habitat suitability. If the purpose of a future study is to predict the greatest potential changes and multiple similar metrics are available, it may be prudent to select the metric with the greatest projected changes during model development. A second and less precautionary approach would be to average predictions from all four metrics to create ensemble predictions that balance predicted effects, an approach that has been suggested for dealing with uncertainty in climate change effects (Araújo & New, 2007). Some studies have demonstrated that predictions from models with multiple metrics (Braunisch et al., 2013) or ensembles of predictions from multiple models (Araújo et al., 2005) provided more accurate estimates of observed species range shifts. If model-averaged estimates are employed, we propose that it would be prudent to utilize model weights that are updated through future monitoring of changes in climate metrics and species responses in an adaptive management framework (Nichols et al., 2011; Conroy & Peterson, 2012). A third approach would be to determine if any metric has a stronger association with brook trout distribution changes between multiple periods with temperature differences. We did not have data from multiple time-periods to conduct such an analysis, but this could be accomplished through analysis of historic data or future monitoring. Perhaps most importantly, if managers will be prioritizing monitoring or conservation efforts, it could be very beneficial to use a structured decision making approach (Conroy & Peterson, 2012) to first determine if and how projection uncertainty would actually alter decisions (e.g., where to restore riparian forests).

We think that linking projection uncertainty to decision making is an especially important area for future global change research, as it could help identify what sources of uncertainty actually matter for decisions focused on conservation and restoration.

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Table 1 Length of stream (Km) predicted to be suitable for brook trout for a given time step (Year), climate model and water temperature metric. Water temperature metrics included maximum 7 day mean (Max7), maximum 30 day mean (Max30), mean July (MnJuly) and mean April through October warm season (MnSeason) temperatures. Projected conditions were not available for the GFDL climate model in 2087, so no predictions are available (NA).

Year	Model	Max7	Max30	MnJuly	MnSeason
1997	Baseline	149.4	148.7	149.8	145.1
2042	ECHAM5	81.8	90.2	101.8	86.8
	GFDL	72.3	70.4	80.4	70.3
	GENMOM	126.7	127.6	136.9	124.7
2062	ECHAM5	31.7	33.5	47.9	43.1
	GFDL	23.0	35.9	52.6	38.9
	GENMOM	67.5	65.5	81.8	78.4
2087	ECHAM5	2.5	2.8	5.4	8.6
	GFDL	NA	NA	NA	NA
	GENMOM	51.1	49.5	56.9	52.3

Table 2 Mean regional metric dissimilarity between pairs of brook trout occurrence predictions made using pairs of water temperature metrics for the baseline and each given climate model and time step (Year). Dissimilarity was calculated as one minus the overlap in posterior distributions, and is equal to 0 for identical distributions and 1 if distributions do not overlap (see text and Figure 1 for further details). Water temperature metrics include maximum 7 day mean (Max7), maximum 30 day mean (Max30), mean July (MnJuly) and mean April through October warm season (MnSeason). Projected conditions were not available for the GFDL climate model in 2087, so no predictions or dissimilarity measures are available (NA).

Year	Model	Max07-Max30	Max07-MnJuly	Max07-MnSeason	Max30-MnJuly	Max30-MnSeason	MnJuly-MnSeason
1997	Baseline	0.13	0.15	0.27	0.13	0.26	0.26
2042	ECHMAM5	0.24	0.4	0.28	0.28	0.33	0.42
	GFDL	0.16	0.22	0.35	0.25	0.26	0.42
	GENMOM	0.16	0.27	0.28	0.21	0.24	0.29
2062	ECHAM5	0.18	0.44	0.24	0.33	0.23	0.31
	GFDL	0.39	0.57	0.37	0.37	0.31	0.55
	GENMOM	0.14	0.29	0.24	0.33	0.28	0.21
2087	ECHAM5	0.1	0.18	0.2	0.17	0.2	0.22
	GFDL	NA	NA	NA	NA	NA	NA
	GENMOM	0.15	0.17	0.19	0.18	0.16	0.24

Table 3 Average dissimilarity between pairs of brook trout occurrence predictions made using projections from pairs of climate models for a given water temperature metric (Metric) and time step (Year). Dissimilarity was calculated as one minus the overlap in posterior distributions, and is equal to 0 for identical distributions and 1 if distributions do not overlap (see text for further details). Projected conditions were not available for the GFDL climate model in 2087, so no predictions or dissimilarity measures are available (NA).

Year	Metric	ECHAM5-GFDL	ECHAM5-GENMOM	GFDL-GENMOM
2042	Max07	0.25	0.43	0.39
	Max30	0.26	0.32	0.46
	MnJuly	0.23	0.24	0.4
	MnSsn	0.22	0.43	0.57
2062	Max07	0.35	0.46	0.48
	Max30	0.23	0.31	0.23
	MnJuly	0.29	0.32	0.18
	MnSsn	0.1	0.48	0.53
2087	Max07	NA	0.64	NA
	Max30	NA	0.65	NA
	MnJuly	NA	0.65	NA
	MnSsn	NA	0.68	NA

Table 4 Mean probability of decline from the baseline and climate change scenarios for a given time step (Year), climate model (Model) and water temperature metric. Water temperature metrics included maximum 7 day mean (Max7), maximum 30 day mean (Max30), mean July (MnJuly) and mean April through October warm season (MnSeason) temperatures. Projected conditions were not available for the GFDL climate model in 2087, so no predictions are available (NA).

Year	Model	Max07	Max30	MnJuly	MnSeason
2042	ECHAM5	0.48	0.34	0.14	0.48
	GFDL	0.42	0.52	0.30	0.66
	GENMOM	0.09	0.09	0.06	0.08
2062	ECHAM5	0.92	0.90	0.73	0.88
	GFDL	0.92	0.81	0.54	0.90
	GENMOM	0.68	0.75	0.49	0.57
2087	ECHAM5	0.98	0.98	0.98	0.98
	GFDL	NA	NA	NA	NA
	GENMOM	0.74	0.77	0.70	0.80

Table 5 Mean predicted benefit probability of full riparian restoration from the current riparian conditions for a given time step (Year), climate model (Model) and water temperature metric. Projected conditions were not available for the GFDL climate model in 2087, so no predictions are available. Water temperature metrics include maximum 7 day mean (Max7), maximum 30 day mean (Max30), mean July (MnJuly) and mean April through October warm season (MnSeason). Projected conditions were not available for the GFDL climate model in 2087, so no predictions are available (NA).

Year	Model	Max07	Max30	MnJuly	MnSeason
1997	Baseline	0.41	0.46	0.48	0.46
2042	ECHAM5	0.40	0.35	0.42	0.45
	GFDL	0.38	0.40	0.45	0.38
	GENMOM	0.46	0.45	0.40	0.44
2062	ECHAM5	0.36	0.31	0.22	0.28
	GFDL	0.31	0.20	0.33	0.40
	GENMOM	0.34	0.39	0.40	0.31
2087	ECHAM5	0.15	0.20	0.18	0.12
	GFDL	NA	NA	NA	NA
	GENMOM	0.30	0.34	0.37	0.36

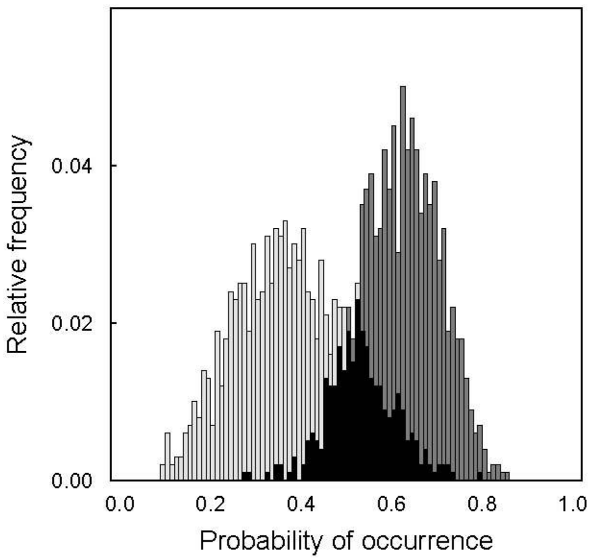
Fig. 1 The dissimilarity of two posterior distributions was calculated as the lack of overlap (non-black regions) between two posterior predictive distributions and was used as a measure of prediction similarity. Dissimilarity was 0.69 in this example, which reflects the relatively large difference between the two distributions.

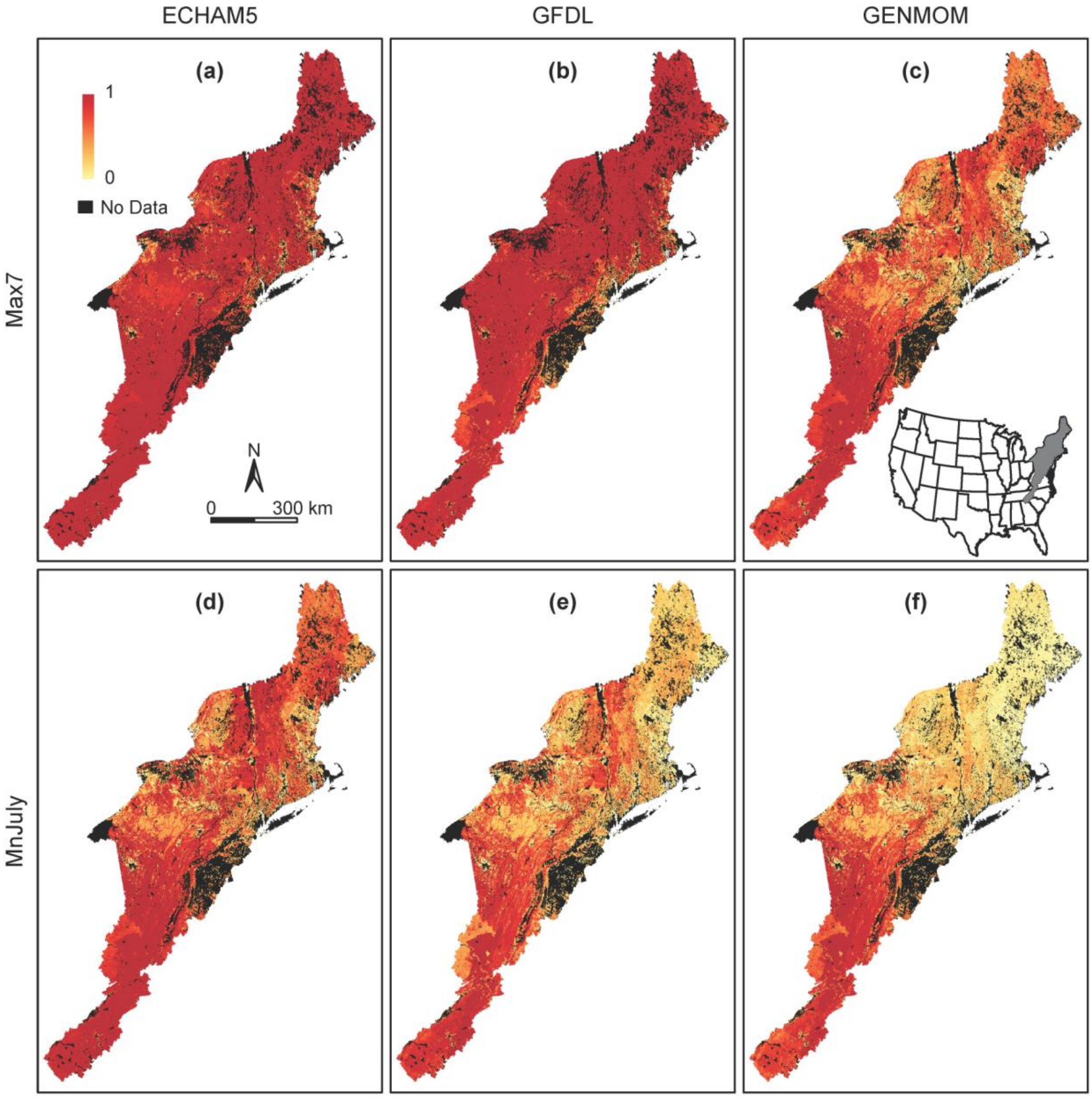
Fig. 2 Maps of the predicted decline probability in brook trout occurrence probability for the 2062 time step demonstrate projection uncertainty among the three climate models and two metrics (MnJuly and Max7). Water temperature metrics compared include maximum 7 day mean (Max7) and mean July (MnJuly) temperatures. The inset map in the top right panel shows the location of the study region relative to the contiguous United States. No data reflects reaches where predictions were unavailable or where a decline was impossible because baseline occurrence probability was equal to 0.

Fig. 3 Maps of the predicted decline probability in brook trout occurrence probability for individual stream reaches in the Penns Creek watershed (Pennsylvania, USA) for the 2062 time step demonstrate projection uncertainty among two climate models (ECHAM5 and GENMOM) and two metrics (MnJuly and Max7). Water temperature metrics compared include maximum 7 day mean (Max7) and mean July (MnJuly) temperatures. The ‘X’ in the inset map (upper left corner) shows the location of Penns Creek watershed relative to the study region.

Fig. 4 Maps of the predicted benefit probability of full riparian restoration from the current riparian conditions in brook trout occurrence probability for the 2062 time step and GFDL climate model demonstrate projection uncertainty among the four metrics. Water temperature metrics include maximum 7 day mean (Max7), maximum 30 day mean (Max30), mean July

(MnJuly) and mean April through October warm season (MnSeason) summarized from predicted daily mean water temperatures. No data represents reaches where predictions were not made due to a lack of predictors.




ECHAM5
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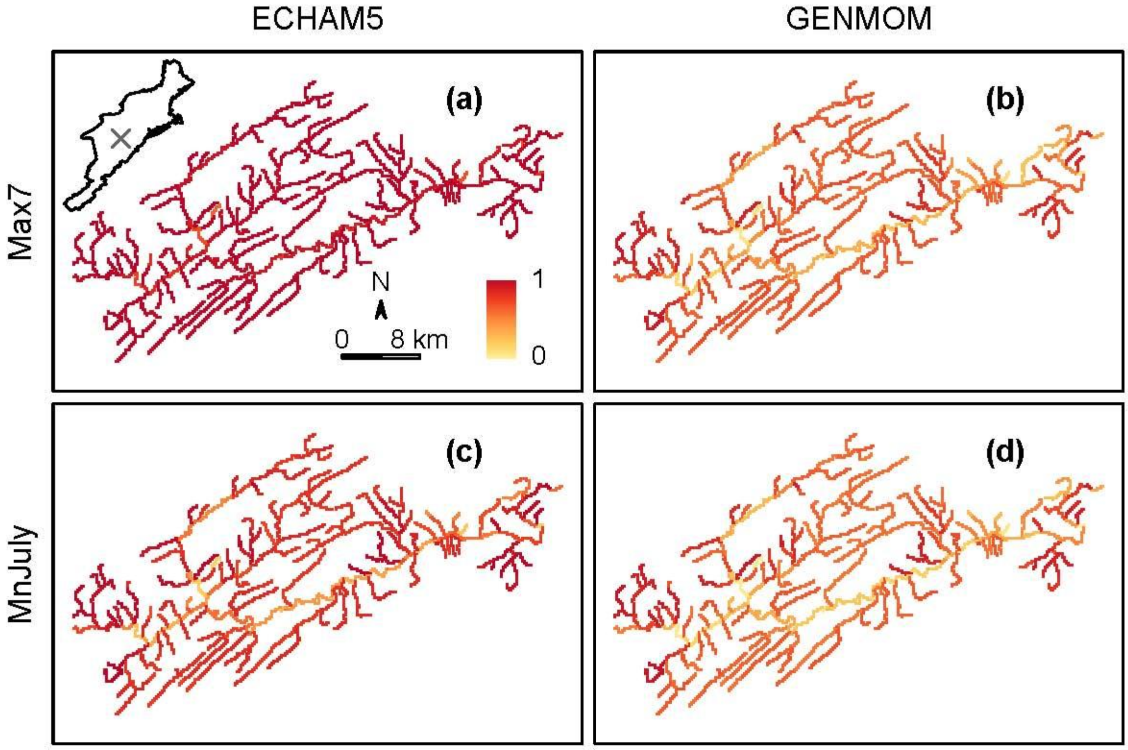
ECHAM5
GENMOM
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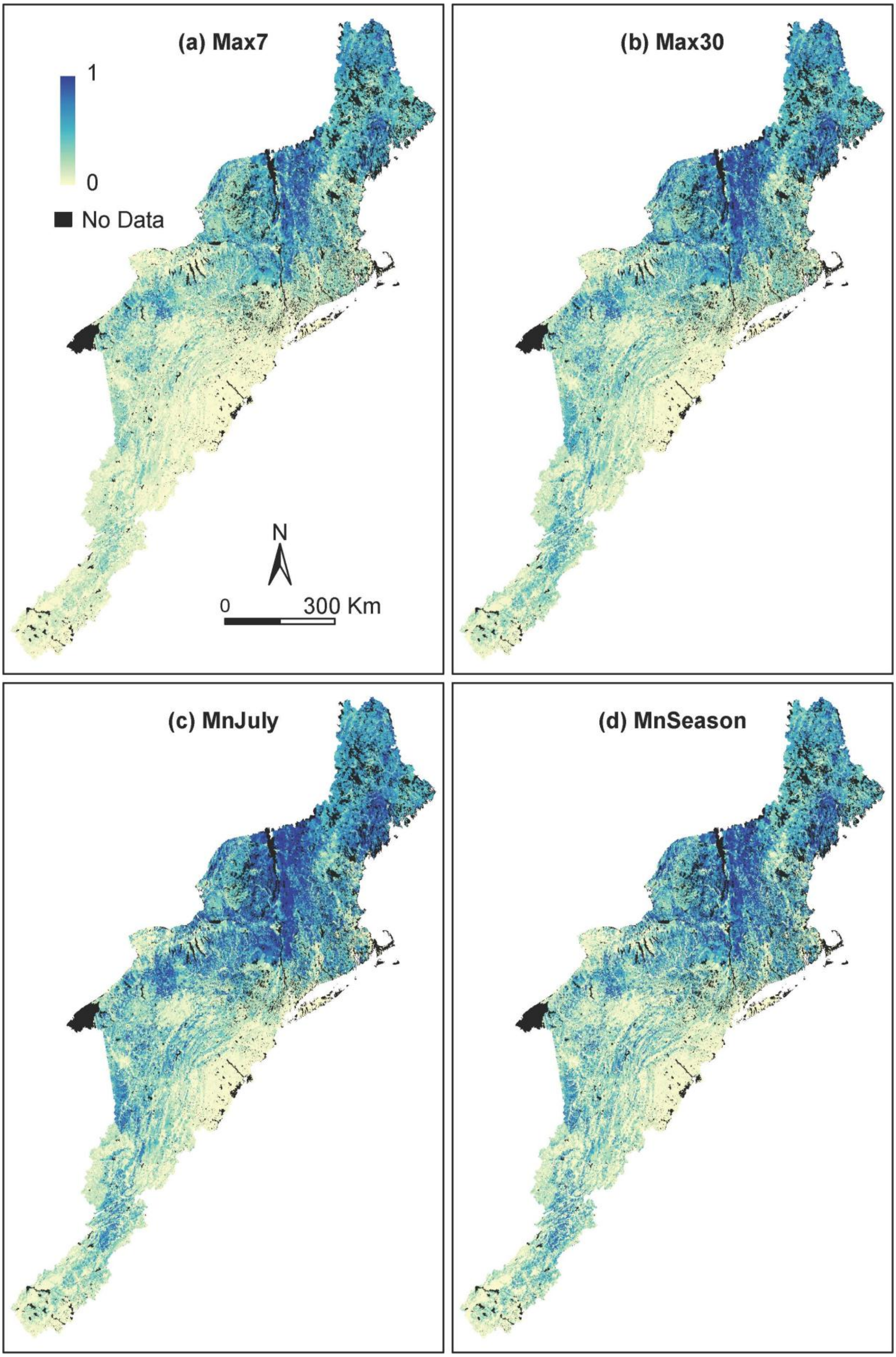
1
0


(a) Max7
1
0
No Data
N
0
300 Km
(b) Max30
(c) MnJuly
(d) MnSeason