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ARTICLE

Predicting Brook Trout Occurrence in Stream Reaches throughout their Native Range in the Eastern United States

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Abstract
The Brook Trout *Salvelinus fontinalis* is an important species of conservation concern in the eastern USA. We developed a model to predict Brook Trout population status within individual stream reaches throughout the species' native range in the eastern USA. We utilized hierarchical logistic regression with Bayesian estimation to predict Brook Trout occurrence probability, and we allowed slopes and intercepts to vary among ecological drainage units (EDUs). Model performance was similar for 7,327 training samples and 1,832 validation samples based on the area under the receiver operating curve (∼0.78) and Cohen's kappa statistic (0.44). Predicted water temperature had a strong negative effect on Brook Trout occurrence probability at the stream reach scale and was also negatively associated with the EDU average probability of Brook Trout occurrence (i.e., EDU-specific intercepts). The effect of soil permeability was positive but decreased as EDU mean soil permeability increased. Brook Trout were less likely to occur in stream reaches surrounded by agricultural or developed land cover, and an interaction suggested that agricultural land cover also resulted in an increased sensitivity to water temperature. Our model provides a further understanding of how Brook Trout are shaped by habitat characteristics in the region and yields maps of stream-reach-scale predictions, which together can be used to support ongoing conservation and management efforts. These decision support tools can be used to identify the extent of potentially suitable habitat, estimate historic habitat losses, and prioritize conservation efforts by selecting suitable stream reaches for a given action. Future work could extend the model to account for additional landscape or habitat characteristics, include biotic interactions, or estimate potential Brook Trout responses to climate and land use changes.

The Brook Trout *Salvelinus fontinalis* is an economically, socially, and ecologically important species of conservation concern throughout its native range in the eastern United States. Brook Trout have relatively narrow habitat requirements, but they were historically widespread in areas where cold water, access to suitable spawning substrates, and instream cover were available. Largely as a result of anthropogenic habitat changes, Brook Trout have been extirpated from 28% of subwatersheds in their native range within the eastern USA and have been greatly reduced (>50% of populations lost) in an additional 35% of subwatersheds (Hudy et al. 2008). A number of activities and stressors have negatively affected Brook Trout, including historical deforestation and contemporary land use changes (Hudy et al. 2008; Stranko et al. 2008), acid deposition (Schofield 1976; Haines and Johnson 1982), population fragmentation (Letcher et al. 2007; Whiteley et al. 2013), and the introduction of nonnative species (Larson and Moore 1985; Wagner et al. 2013). Further land cover changes related to urbanization, forestry, and relatively new factors (e.g., natural gas exploration) are likely to

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result in continued losses of Brook Trout locally (Moglen et al. 2003; Stranko et al. 2008; Steen et al. 2010; Weltman-Fahs and Taylor 2013), while alterations in water temperature, streamflow, and related habitat characteristics driven by climate change are expected to result in widespread losses throughout much of the region (Meisner 1990; Clark et al. 2001; Flebbe et al. 2006).

In response to concerns about the future of Brook Trout in the eastern United States, federal, state, and conservation stakeholders formed the Eastern Brook Trout Joint Venture (EBTJV) and provided a baseline assessment to summarize existing knowledge on the status of Brook Trout populations (Hudy et al. 2008). This assessment provided a regionwide overview of Brook Trout population status in subwatersheds and identified landscape attributes that were related to population status, providing a valuable guide for transboundary management and conservation efforts. However, subwatershed status from the assessment cannot be used to elucidate the effects of stressors that act locally or to infer the status of individual populations, as there are many unique stream reaches within a subwatershed and each may represent a unique resident Brook Trout population (Castric et al. 2001; Kanno et al. 2011). Although an assessment of Brook Trout population status within individual stream reaches would provide more valuable information, there are insufficient data and knowledge throughout this large region (Hudy et al. 2008). In such cases, a regional overview of potential population status in stream reaches can be gained by predicting occurrence or abundance using species distribution models (SDMs).

Species distribution models have been developed using a wide range of methods to accurately predict distributions and guide management decisions for diverse taxa (see Elith and Leathwick 2009 for a review), including Brook Trout (Wenger et al. 2011; Al-Chokhachy et al. 2013) and several other salmonid species (Isaak et al. 2010; Wenger et al. 2011; Ruesch et al. 2012) throughout large regions in the western United States. For example, models predicting the distribution of Bull Trout *Salvelinus confluentus* and Cutthroat Trout *Oncorhynchus clarkii* have been used to predict potential distributions resulting from climate changes and nonnative species and thus to help prioritize conservation actions (Peterson et al. 2013). Although there are many SDMs of varying complexity and spatial extent for predicting Brook Trout occurrence and abundance in the eastern United States (Meisner 1990; Flebbe et al. 2006; McKenna and Johnson 2011; Wagner et al. 2013, 2014), none of those SDMs was developed to obtain predictions at the stream reach scale throughout the entire EBTJV region.

Here, we describe the first effort to predict the status of Brook Trout populations within individual stream reaches throughout the species' native range in the eastern United States. We developed a Bayesian hierarchical logistic regression model to predict the probability of Brook Trout occurrence based on predicted water temperature and a set of ecologically relevant landscape attributes. The estimated effects of predicted water temperature and landscape attributes, occurrence predictions, and uncertainty estimates provide useful information that can be used to help coordinate conservation and management activities throughout the region at multiple scales.

METHODS

Study region.—The study region included the native range of Brook Trout in the eastern USA as defined by the EBTJV and represents approximately 30% of the worldwide native range of Brook Trout and 70% of its U.S. range (Figure 1; Hudy et al. 2008). Because the EBTJV region was originally defined based on subwatershed boundaries, we modified the EBTJV region slightly to include all streams from the National Hydrography Dataset Plus version 1.0 (NHDPlus; USEPA and

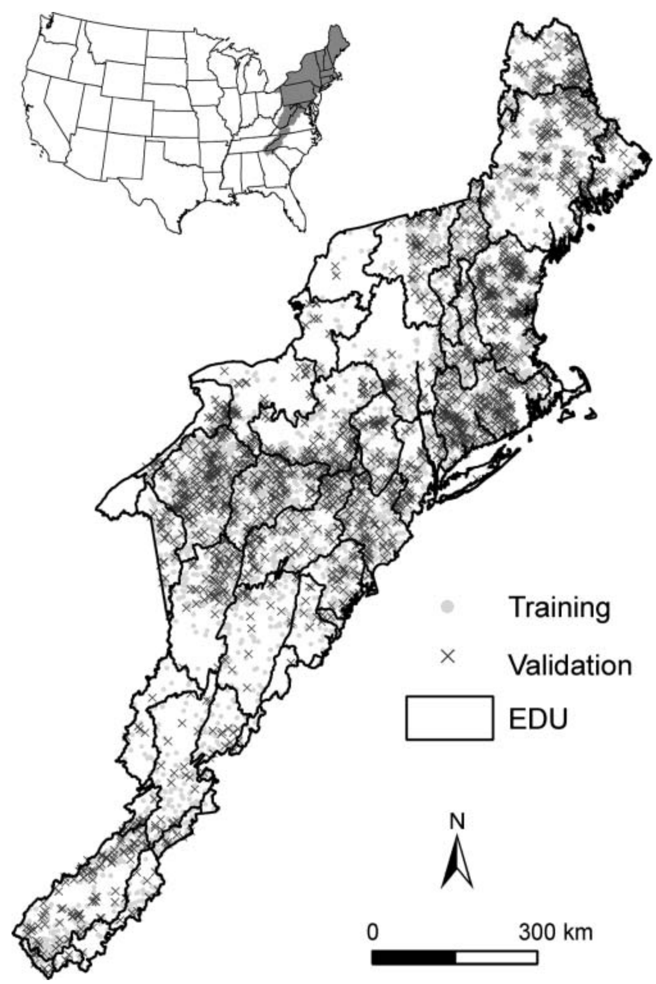

FIGURE 1. Study region, ecological drainage unit (EDU) boundaries, and locations of stream sites used for model training and model validation. The inset shows the location of the study region within the conterminous USA.

USGS 2005) for which the local catchments were at least 90% within the study region boundary. In total, there are 239,350 NHDPlus stream reaches in the region, but only 195,134 of the stream reaches were topologically connected and had all available predictor variables in the base map upon which our model was based. The study region roughly corresponds to the historic range of Brook Trout, which are limited to streams with suitably cold water temperatures (Meisner 1990) that are typically found at higher elevations (>200 m; Flebbe et al. 2006) in the southern portion of the region but are found at nearly all elevations at higher latitudes. Brown Trout *Salmo trutta* and Rainbow Trout *O. mykiss* have been introduced widely and have established populations in various portions of the region. The predominant land cover in the region is second-growth forest, but several urban centers support a large human population, agricultural land use is widespread in lower elevations, and forest management is common throughout much of the range.

Fish data.—We compiled fish sampling records from throughout the region in the winter of 2013 through direct contact with state agencies and by downloading data directly from the Multistate Aquatic Resources Information System (MARIS) website (www.marisdata.org/). We linked sampling locations to the nearest NHDPlus stream segment within 150 m, removing those that were farther away from any stream segment. Our ideal data set would have only included samples collected via electrofishing that targeted all species, but this was not entirely feasible since the compiled data sets originated from a variety of sampling programs with various objectives and sampling gear was not always reported. Thus, when sampling gear was recorded, we included only samples collected by electrofishing methods (i.e., backpack, barge, or boat electrofishing); when sampling gear was not recorded, we included all samples because agency communications suggested that electrofishing was the primary gear used. We removed any samples that targeted black basses *Micropterus* spp., percids, or esocids because Brook Trout might not have been recorded if captured.

For each sample, we recorded the occurrence of Brook Trout and attributed all samples to the nearest NHDPlus stream reach. We selected samples that were collected between May and October from 1991 to 2011, which span the year of satellite image collection for the 2001 National Land Cover Dataset that we used to represent land cover in our analysis (see below). Sampling month was not available for data from Tennessee, but we included all samples since stream surveys are most often conducted in the summer months during low-flow periods. When multiple samples were available for a given NHDPlus stream reach, we selected the most recent sample collected within the reach.

Water temperature and landform predictors.—Water temperature is a key determinant of habitat suitability for Brook Trout both globally (MacCrimmon and Campbell 1969) and locally (e.g., Martin and Petty 2009), but there are insufficient data available to use measured water temperature to characterize thermal habitat regionally. Although air temperature, elevation, and latitude have been used as surrogates of water temperature in previous efforts, water temperature represents a more direct link to stream habitat, and predicted water temperatures have provided more accurate predictions than surrogate variables for Brook Trout in the western USA (Al-Chokhachy et al. 2013). For this reason, we used predicted water temperatures from a neural network ensemble model that we developed to predict mean daily water temperatures throughout the study region (DeWeber and Wagner 2014). We briefly describe the model here, and we refer the reader to our previous paper (DeWeber and Wagner 2014) for further details. The neural network ensemble model predicted water temperature for a total of 1,080 stream reaches throughout the region with good accuracy based on root mean square error (RMSE $\sim$ 1.9°C) and low bias (percent bias < ±2%). In order of importance, predictors included current-day mean air temperature, prior 7-d mean air temperature, network area, network forest cover, network mean aspect, network mean base flow index, and riparian forest cover within the local catchment.

We modified the water temperature model slightly to help ensure that the model would generalize well to the large number of stream reaches in the region. First, we removed network mean base flow index because sensitivity analysis plots showed irregular effects on water temperature that could bias predictions for some stream reaches (see Figure 6 in DeWeber and Wagner 2014). Model performance was not negatively affected by the removal of this predictor (i.e., RMSE remained unchanged). Second, we retrained the model using all available water temperature observations because the large amount of data that were withheld for validation during the original model development provided information that could inform regional predictions. The modified model had similar performance (RMSE = 2.0°C; percent bias = 0.02%) and predictor effects nearly identical to those of the original model (DeWeber and Wagner 2014). We utilized the modified model to predict mean daily water temperatures that were representative of current conditions by using a 5-year average (centered on 1997) of observed mean daily air temperature for each day during May–October. We then calculated five water temperature metrics for describing the thermal suitability of river habitat for Brook Trout: mean seasonal water temperature; mean July water temperature; and maximum 7-, 14-, and 30-d moving averages. Because all five thermal metrics were highly correlated for the 1997 average conditions, hereafter we only describe the models that were developed using the maximum 30-d moving average (Max30Temp).

A large suite of landscape attributes and human disturbance metrics summarized within the local catchment (i.e., the local, reach-level catchment containing the site) and network catchment (i.e., all upstream reach-level catchments, including the local catchment) of each stream reach was available to describe fish habitat, as detailed by Esselman et al. (2011).

From this suite, we selected three ecologically relevant landscape attributes that were relatively independent from each other and from Max30Temp: mean soil permeability (mm/h), agricultural land cover (%), and developed land cover (%). Mean soil permeability was included as a metric of soil size, and we expected higher permeability (i.e., coarser soils) to represent more suitable habitat for Brook Trout given ecological characteristics (Argent and Flebbe 1999; Sweka and Hartman 2001). Because the local and network measures of these three landscape attributes were highly correlated ($|r| > 0.70$), the measure that was most correlated with Brook Trout occurrence was selected for inclusion in the model (Table 1). We did not include any landscape attributes that were previously used to predict water temperature because any potential effects on Brook Trout were at least partially accounted for by predicted water temperature, and their inclusion could confound modeled relationships. We also did not consider elevation, latitude, or other attributes that would primarily be surrogates of climate or water temperature because their inclusion could confound the effects of water temperature (Stanton et al. 2012).

Next, the NHDPlus stream reaches were assigned to ecological drainage units (EDUs), and several EDU-level attributes (model covariates) were calculated, including the mean of predicted seasonal (May–October) water temperature; mean soil permeability; and percentages of forest, agricultural, and urban land cover. We chose to stratify the study region by using EDUs because they are watershed-based units that are designed to have similar habitats and freshwater assemblages due to common zoogeographic, physiographic, and climatic characteristics (Higgins et al. 2005). We calculated EDU-level covariates to account for any cross-scale interactions, which occur if the effects of local Brook Trout occurrence predictors vary spatially as a result of interactions with driving factors that operate at a larger spatial scale (Soranno et al. 2014). The EDU attributes were summarized from the reach-level predictors; the exception was the land cover percentages, which were calculated as the areal percent covered by each land cover type in an EDU. For clarity, we refer to stream reach attributes as "predictors" and EDU attributes as "covariates" throughout this paper. Prior to model development, we standardized all predictors and covariates by subtracting the mean and dividing by the SD from the population of all stream reaches or EDUs in the region. We then randomly selected 20% of the observations from each EDU for model validation.

Model development.—We used hierarchical logistic regression models because they have been shown to generalize to new locations (Wenger and Olden 2012), they account explicitly for hierarchical data structure, and they can accommodate spatial autocorrelation that may exist in ecological data sets (Wagner et al. 2006). The first level (reach level) of our model predicted the probability of Brook Trout occurrence in individual stream reaches based on stream reach predictors (Table 1). The general reach-level formula was

$$\text{logit}(p_i) = \alpha_j + \beta_{1j}X_{ij} + bX_{ij}Q_{ij},$$

where p_i is the probability of Brook Trout occurrence, α_j is the intercept, β_{1j} is the estimated effect of reach-level predictor X_{ij}, and b is the estimated interaction between reach-level predictors X_{ij} and Q_{ij} for the jth EDU and ith stream reach. Without covariates, the EDU-specific intercepts and slopes are modeled at the EDU level as

$$\begin{pmatrix} \alpha_j \\ \beta_{1j} \end{pmatrix} \sim N\left(\begin{pmatrix} \mu_\alpha \\ \mu_{\beta_1} \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_{\beta_1} \\ \rho\sigma_\alpha\sigma_{\beta_1} & \sigma_{\beta_1}^2 \end{pmatrix} \right),$$

where σ_α^2 and $\sigma_{\beta_1}^2$ are variance estimates and ρ is the correlation between group-specific intercepts and slopes. We did not account for imperfect detection in our model because adequate data do not exist. Detection probability can vary in relation to stream size, presence of nonnative species, sampling gear, and water chemistry (Hense et al. 2010; Wagner et al. 2013), and this variation could affect model inferences and predictions (Royale and Dorazio 2009). Nevertheless, we are confident in the accuracy of most recorded absences because detection probability for Brook Trout was generally high across a

TABLE 1. Stream-reach-level and ecological drainage unit (EDU)-level attributes that were tested as candidate predictor variables in hierarchical logistic regression models for predicting Brook Trout occurrence.

Attribute	Level	Units	Source	Spatial resolution	Land cover code
Max30Temp (maximum 30-d moving average temperature)	Reach	°C	Predicted water temperature[a]	Reach	
Network soil permeability	Reach	mm/h	Schwarz and Alexander 1995	1:250,000	NA
Local developed land	Reach	% cover	Homer et al. 2004	30-m grid	21 + 22 + 23 + 24
Network agriculture	Reach	% cover	Homer et al. 2004	30-m grid	81 + 82
Forest cover	EDU	% cover	Homer et al. 2004	30-m grid	41 + 42 + 43
Mean water temperature	EDU	°C	Predicted water temperature[a]	30-m grid	NA
Mean soil permeability	EDU	mm/h	Schwarz and Alexander 1995	1:250,000	NA

[a]Predicted water temperature was based on a model described by DeWeber and Wagner (2014).

variety of streams with similar sampling variation in Pennsylvania (>0.90; Wagner et al. 2013).

The EDU level of the model allowed intercepts and slopes to vary among EDUs to help account for potential variation in the average probability of occurrence and the effects of reach-level covariates on Brook Trout occurrence throughout the region. We also modeled this among-EDU variation using the aforementioned EDU-level covariates to determine whether and how intercepts and slopes varied among EDUs as a function of landscape attributes. With covariates, the EDU level of the model became

$$\begin{pmatrix} \alpha_j \\ \beta_{1j} \end{pmatrix} \sim N\left(\begin{pmatrix} \gamma_0^{\alpha} + \gamma_1^{\alpha} Z_j \\ \gamma_0^{\beta_1} + \gamma_1^{\beta_1} Z_j \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha}^2 & \rho\sigma_{\alpha}\sigma_{\beta_1} \\ \rho\sigma_{\alpha}\sigma_{\beta_1} & \sigma_{\beta_1}^2 \end{pmatrix} \right),$$

where γ_0^{α} is the intercept and γ_1^{α} is the estimated slope for the EDU-level covariate Z_j; $\gamma_0^{\beta_1}$ is the intercept and $\gamma_1^{\beta_1}$ is the estimated effect of EDU-level covariate Z_j; and σ_{α}^2 and $\sigma_{\beta_1}^2$ are conditional variance estimates. The model can be extended to include p reach-level predictors and k EDU-level covariates by adding β_{pj} and $\gamma_k^{\beta_p}$ parameters.

Although this hierarchical approach has several advantages, model selection is not straightforward, largely because of the difficulty in determining the effective number of parameters estimated. As a result, information criteria (e.g., deviance information criterion) cannot be used to effectively compare models or determine weights for model averaging (Bolker et al. 2009). For this reason, we used a sequential forward selection approach to first select reach-level predictors and then EDU-level covariates to include as described below (Model Selection). All models were fitted in a Bayesian framework in the program JAGS (Plummer 2011) using the R2Jags package (Su and Yajima 2013) in the R statistical environment (R Development Core Team 2014). Diffuse priors were used for all parameters. For model selection, we kept every third draw from three chains for a total of 30,000 draws from the posterior distribution after discarding the first 10,000 iterations from each chain. We examined trace plots and verified that the scale reduction factor was close to 1.0 to ensure that the chains converged. We included reach-level predictors and EDU-level covariates in the final model if the 90% credible intervals did not include 0.

Model selection.—We first selected reach-level predictors to include in the model because our primary interest was to predict Brook Trout occurrence in stream reaches throughout the region. Before selecting predictors, we fitted preliminary models with a single reach-level predictor, allowing effects to vary among EDUs, to determine whether the inclusion of multiple reach-level predictors greatly changed parameter estimates, which could signify problems resulting from collinearity. Because all four reach-level predictors had important effects on Brook Trout and because collinearity effects were not evident, we included all four reach-level predictors throughout model development. Lastly, we selected interactions among reach-level predictors by sequentially adding each two-way interaction to the model and retaining those that differed from 0 (as determined by 90% credible intervals that did not overlap 0). Two-way interactions between reach-level predictors were not allowed to vary among EDUs. After selecting reach-level predictors, we calculated the degree to which intercepts and slopes varied among EDUs to determine whether the variation was substantial and could potentially be explained by EDU-level covariates. We considered variation to be substantial whenever EDU-specific slopes and intercepts differed from the grand mean intercept or slope (as determined by nonoverlapping 90% credible intervals) for at least 10% of the EDUs.

After identifying parameters with substantial variation, we used forward selection to sequentially test each potential EDU-level covariate, retaining those that differed from 0. If multiple EDU-level covariates were selected for a varying intercept or slope, we used backward stepwise selection to test the effects of all covariates plus two-way interactions, sequentially removing those that most overlapped 0. We then visually inspected predicted relationships to ensure that the included covariate effects could be interpreted clearly and were not simply the result of outliers or confounding relationships. We tested all of the covariates in this manner until we obtained the final habitat model where the 90% credible intervals for the effects of all reach-level predictors and EDU-level covariates differed from 0.

Model performance and output.—Due to computational limitations, we could not use 30,000 posterior draws for estimating Brook Trout occurrence probability at over 190,000 stream reaches. Therefore, we retrained the final selected model using 5,000 draws from the posterior distribution to estimate model parameters. All parameter posterior means estimated from 5,000 draws varied by less than 1.6% from those estimated from 30,000 draws, and parameter density plots suggested good convergence. For all stream reaches in the region, we then predicted occurrence probability for each of the 5,000 posterior draws and calculated the posterior mean and SD of the occurrence probability for each stream reach. We mapped both of these measures throughout the region to show the spatial distribution of Brook Trout occurrence predictions and related uncertainty. Because results were difficult to display in vector format, we produced maps in a raster format with a spatial resolution of approximately 200 m.

We then calculated the area under the receiver operating curve (AUC) and plotted classification accuracy across different probability thresholds (ROCR package in R; Sing et al. 2005). The AUC is a useful and standard measure of model performance (Hanley and McNeil 1982) but does not provide information regarding error rates whenever one or more thresholds are used to determine occurrence. However, binary classification (i.e., present or absent) of continuous probabilities are often required, either explicitly or implicitly, for conservation and management purposes. Therefore, model performance for a series of threshold-based classification strategies was estimated based on balancing or minimizing the rates of errors of omission or commission to categorize predictions. For each of these thresholds, we calculated the classification accuracy, sensitivity, specificity, and Cohen's kappa statistic (Cohen 1960; Allouche et al. 2006). Threshold 1 was selected to ensure that Brook Trout were predicted to be present at 90% of sites where they actually occurred (i.e., sensitivity = 0.90); this represents a low threshold that could be employed when false negatives have large costs and when overprediction of the occupied habitat is acceptable. We considered threshold 1 to estimate the potential distribution of Brook Trout where habitat may be suitable. Threshold 2 was equal to prevalence in the training data set, which produces near-optimal classification accuracy and could be used when false positives and false negatives have equal costs (Liu et al. 2005). We considered threshold 2 to identify suitable habitat where Brook Trout are likely to be present. Lastly, threshold 3 was selected to ensure that Brook Trout were predicted to be absent at 90% of sites where they were actually absent (i.e., specificity = 0.90). We considered threshold 3 to identify highly suitable habitat where Brook Trout are very likely to be present; this threshold might be used when false positives have a high cost.

To better understand errors and visualize potential biases, we also calculated two metrics of measurement error to determine how well the habitat model predicted occurrence at individual stream reaches. The first metric, which we refer to as mean deviation, was the average difference between the observation (Brook Trout not detected = 0; Brook Trout detected = 1) and the mean predicted probability of occurrence. For the second metric, we classified occurrence using threshold 2 (probability = prevalence) for each of the 5,000 posterior draws, and we calculated the proportion of incorrect classifications. We mapped these two error metrics throughout the region to identify potential spatial biases in predicted distributions.

RESULTS

There was a total of 9,159 stream reaches with fish samples spanning the study region, but sampling and prevalence were uneven across the 42 EDUs (Figure 1; Table 2). One EDU (southern Lake Erie; Figure 1) did not have any samples and was therefore excluded from model development and predictions. Brook Trout were present at 3,361 (45.6%) of the 7,327 stream reaches used for model fitting and were present at 842 (45.9%) of the remaining 1,832 samples used for model validation. The distributions of reach-level predictors were similar among the training data set, the validation data set, and the population of stream reaches throughout the region.

The reach level of the final model included the effects of all four predictors plus an interaction between Max30Temp and network agriculture (Table 3). The primary determinant of Brook Trout occurrence was Max30Temp, which had a strong negative effect. For example, the mean Brook Trout occurrence probability was always high (>0.60) when Max30Temp was below 16°C, and the mean occurrence probability was always low (<0.20) when Max30Temp was above 22°C. The interaction between Max30Temp and network agriculture revealed that the effect of Max30Temp was greater when agricultural land cover was high (Figure 2). The positive effect of network soil permeability and the negative effects of network agriculture and local developed land cover were weaker than that of Max30Temp but were still important for predicting Brook Trout occurrence (Figure 3).

The EDU level of the model included substantial variation in the intercepts and slopes (i.e., at least 10% of EDU-specific intercepts and slopes differed from the grand mean intercept or slope) for the effects of Max30Temp, network soil permeability, and network agriculture but not for the effect of developed land cover. Intercepts were negatively correlated with EDU mean seasonal water temperature, and the network soil permeability slope was negatively correlated with EDU mean soil permeability (Table 3; Figure 4). Although variation was evident in the slopes for Max30Temp and network agriculture (Figure 5), no EDU covariates were able to clearly explain variation in either of these slopes. Lastly, the slope for local developed land cover was relatively constant among EDUs (Figure 5).

The model was able to predict Brook Trout occurrence much better than chance for the training data set (mean AUC = 0.79; SD = 0.01) and validation data set (mean AUC = 0.78; SD = 0.01). The three thresholds chosen to correspond to a 10% false-negative rate, training data prevalence, and a 10% false-positive rate were 0.19, 0.46, and 0.67, respectively. Classification accuracy, Cohen's kappa, and number of stream reaches where Brook Trout are predicted to occur are shown in Table 4 for the three thresholds. As expected, overall accuracy and kappa were highest for threshold 2 (probability ≥ 0.46), and tradeoffs in accuracy, specificity, and sensitivity were evident for the lower and higher thresholds. Mean occurrence probability was generally higher in the northern portion of the study region and at higher elevations (Figure 6), whereas the SD of occurrence probability showed no clear spatial patterns (Figure 7). Much of the region was identified as potential habitat (probability ≥ 0.19), but highly suitable habitat (i.e., probability ≥ 0.68) had a very limited geographic extent situated primarily in the northern portion of the range (Figure 7). Maps of mean occurrence probability for a portion of the Penns Creek watershed in central Pennsylvania, illustrate the detail (spatial resolution) of predictions and the

TABLE 2. Descriptions of ecological drainage units (EDU), including the name of each EDU, number of samples (*N*), prevalence of Brook Trout (prevalence), mean water temperature (temp, °C; SD in parentheses), forest land cover (%), and mean soil permeability (mm/h; SD in parentheses). The EDU numbers are reference numbers and correspond to numbers along the *x*-axis in Figure 5.

EDU no.	EDU name	*N*	Prevalence	Temp	Forest	Soil
1	Alleghany Mountain tributaries	316	0.37	16.1 (1.5)	71.1	68.9 (53.3)
2	Apalachicola River–Piedmont	8	0.00	17.8 (1.5)	74.7	53.3 (17.8)
3	Cape Cod	13	0.31	16.8 (1.1)	39.2	218.4 (137.2)
4	Coosa River	38	0.00	17.3 (1.1)	88.2	50.8 (22.9)
5	Eastern Lake Erie	148	0.09	16.0 (1.5)	40.7	45.7 (50.8)
6	Eastern Chesapeake Bay	7	0.00	17.7 (1.1)	29.3	55.9 (20.3)
7	Glaciated Ohio River tributaries	103	0.02	16.5 (1.6)	49.9	50.8 (33.0)
8	Lake Champlain	230	0.41	15.1 (1.5)	66.4	81.3 (68.6)
9	Long Island	3	0.00	18.0 (1.3)	19.2	182.9 (152.4)
10	Lower Connecticut River	986	0.44	16.3 (1.4)	57.2	129.5 (81.3)
11	Lower Delaware River	399	0.34	17.1 (1.6)	41.1	61.0 (43.2)
12	Lower Hudson River	210	0.29	17.1 (1.6)	47.5	73.7 (61.0)
13	Lower Potomac River	16	0.00	18.0 (1.5)	42.4	68.6 (43.2)
14	Lower St. Croix River–downeast Maine coastal	202	0.60	14.5 (1.1)	69.0	99.1 (81.3)
15	Lower Susquehanna River	165	0.05	17.8 (1.5)	26.4	48.3 (22.9)
16	Middle Connecticut River	211	0.71	15.3 (1.4)	76.5	114.3 (66.0)
17	Middle Potomac River	34	0.00	17.7 (1.5)	32.0	58.4 (17.8)
18	Middle Susquehanna River–Juniata River	507	0.47	16.8 (1.7)	60.8	96.5 (48.3)
19	New River	112	0.10	16.1 (1.5)	73.0	83.8 (38.1)
20	Northeast Lake Ontario	42	0.43	15.5 (1.5)	48.5	101.6 (109.2)
21	Northwest Adirondacks	12	0.42	15.2 (1.4)	65.0	121.9 (109.2)
22	Penobscot–Kennebec– Androscoggin rivers	730	0.56	14.5 (1.4)	72.1	76.2 (70.0)
23	Saco–Merrimack–Charles rivers	836	0.52	15.3 (1.5)	64.1	165.1 (94.0)
24	Southern Alleghany Plateau	26	0.04	16.7 (1.5)	87.8	76.2 (40.6)
25	Southern Lake Ontario	168	0.29	16.0 (1.5)	30.5	43.2 (45.7)
26	Tennessee River–Blue Ridge	458	0.15	16.9 (1.5)	77.9	81.3 (50.8)
27	Tennessee River–Ridge and Valley	58	0.36	16.6 (1.5)	65.7	71.1 (35.6)
28	Upper Alleghany River	892	0.54	15.5 (1.6)	68.0	73.7 (45.7)
29	Upper Connecticut River	228	0.79	14.4 (1.2)	84.5	91.4 (55.9)
30	Upper Delaware River	227	0.52	15.6 (1.5)	78.1	53.3 (53.3)
31	Upper Hudson River	181	0.40	15.4 (1.4)	61.6	76.2 (71.1)
32	Upper James River	49	0.08	16.9 (1.6)	81.8	99.1 (40.6)
33	Upper Pee Dee River	38	0.13	16.4 (1.2)	70.2	55.9 (53.3)
34	Upper Potomac River–upper Shenandoah River	125	0.20	17.0 (1.7)	64.6	104.1 (45.7)
35	Upper Rappahannock River and middle James River	12	0.25	17.5 (1.5)	67.4	71.1 (27.9)
36	Upper Roanoke River	8	0.13	16.9 (1.3)	76.3	91.4 (86.4)
37	Upper Santee River	40	0.00	16.6 (1.5)	75.5	53.3 (20.3)
38	Upper Savannah River	8	0.00	17.3 (1.4)	78.7	50.8 (12.7)
39	Upper St. John River–Aroostook River	350	0.77	13.7 (1.1)	70.8	38.1 (25.4)
40	Upper Susquehanna River	421	0.52	15.8 (1.5)	59.0	48.3 (38.1)
41	West Branch Susquehanna River	542	0.79	15.6 (1.6)	77.5	91.4 (40.6)
NA	Southern Lake Erie	0	NA	16.2 (1.4)	38.2	35.6 (35.6)

general spatial pattern of probabilities decreasing in a downstream direction throughout river networks (Figure 8). We did not observe any clear spatial biases in predictions based on visual inspection of the maps of mean deviation (see Figure A.1) or the proportion of incorrect classifications.

DISCUSSION

This study provides an SDM for predicting Brook Trout occurrence based on habitat suitability throughout the entire EBTJV region at the individual stream reach scale. Predictions of occurrence probability and knowledge of relationships with

TABLE 3. Reach-level predictors and ecological drainage unit (EDU)-level covariates included in the final hierarchical logistic regression model used to predict Brook Trout occurrence; estimated posterior mean, SD, and 90% credible interval (CI) are presented for each parameter.

Parameter	Attribute	Mean	SD	90% CI
	Reach level			
γ_0^a	Intercept	−1.02	0.22	−1.39, −0.67
μ_{β_1}	Max30Temp (maximum 30-d moving average temperature)	−1.15	0.12	−1.33, −1.15
$\gamma_0^{\beta_2}$	Network soil permeability	0.23	0.12	0.04, 0.23
$\mu_{\beta 3}$	Network agriculture	−0.59	0.15	−0.83, −0.36
$\mu_{\beta 4}$	Local developed land	−0.33	0.11	−0.52, −0.15
b	Max30Temp × network agriculture	−0.18	0.08	−0.32, −0.05
σ_a^2	Intercept variation	1.1	0.18	0.84, 1.40
$\sigma_{\beta_1}^2$	Max30Temp slope variation	0.43	0.08	0.31, 0.58
$\sigma_{\beta 2}^2$	Network soil permeability slope variation	0.48	0.09	0.35, 0.64
$\sigma_{\beta 3}^2$	Network agriculture slope variation	0.61	0.13	0.44, 0.83
$\sigma_{\beta 4}^2$	Local developed cover slope variation	0.38	0.08	0.28, 0.51
	EDU level			
γ_α^1	EDU temperature	−0.67	0.22	−1.04, −0.32
$\gamma_1^{\beta_2}$	EDU soil permeability	−0.32	0.12	−0.53, −0.12

habitat descriptors, in combination with estimates of uncertainty, provide valuable information that can be used to help guide ongoing transboundary management and conservation activities. Similar SDMs that have been developed at the stream reach scale for native and nonnative salmonids (including Brook Trout) in the western USA have proven useful for predicting species distributions, estimating historic habitat losses, understanding biotic and environmental determinants of species distributions, and identifying potential climate change effects (Isaak et al. 2010; Wenger et al. 2011; Ruesch et al. 2012; Al-Chokhachy et al. 2013).

The EBTJV's assessment of Brook Trout population status in subwatersheds was based upon empirical observations and expert knowledge (Hudy et al. 2008) and is the only region-wide "ground-truth" with which we can compare our model predictions. Despite differences in spatial scale, methods, and objectives, the mean probability summarized within the subwatersheds used for the EBTJV showed close relationships to subwatershed population status. Focusing on only the subwatersheds where sufficient data were available to assign population status in the EBTJV assessment, the mean occurrence probability was 0.22, 0.37, 0.45, and 0.57 in subwatersheds with extirpated, greatly reduced, reduced, and intact populations, respectively. Although such comparisons are limited due to differences in spatial scale and methodology, the positive association lends additional support to our model predictions. These comparisons further demonstrate the benefit of using SDMs in such a large region because predictions are available for almost all stream reaches in the region, whereas population status at the relatively coarse subwatershed scale was unknown in much of the region due to insufficient data (Hudy et al. 2008).

The most important determinant of Brook Trout occurrence probability was predicted water temperature, as would be expected based on physiology (e.g., Lee and Rinne 1980; De Staso and Rahel 1994), field observations (Barton et al. 1985; Picard et al. 2003), previous modeling efforts (Wehrly et al. 2007; Stranko et al. 2008; Martin and Petty 2009), and assumptions used in prior climate change studies (Meisner 1990; Clark et al. 2001; Flebbe et al. 2006). Earlier modeling efforts to predict Brook Trout occurrence throughout large portions of the study region accounted for temperature effects by including surrogate variables, such as elevation or latitude (Meisner 1990; Flebbe et al. 2006). Predicted water temperatures offered a more direct link to Brook Trout and also simplified model development because a number of potential predictors were partially accounted for by predicted water temperature (e.g., elevation, latitude, and watershed area). A further benefit is that the difference between predicted and observed water temperatures in a stream reach can be compared by users to determine the reliability of Brook Trout predictions.

We included soil permeability as a metric of soil structure, and we found a positive association between Brook Trout and coarse soils (i.e., higher permeability), which was expected because fine soils can negatively affect feeding and reproduction by covering eggs or impeding groundwater exchanges (Argent and Flebbe 1999; Sweka and Hartman 2001). Similarly, negative effects of agricultural land cover and developed land cover have been found in prior studies (e.g., Hudy et al.

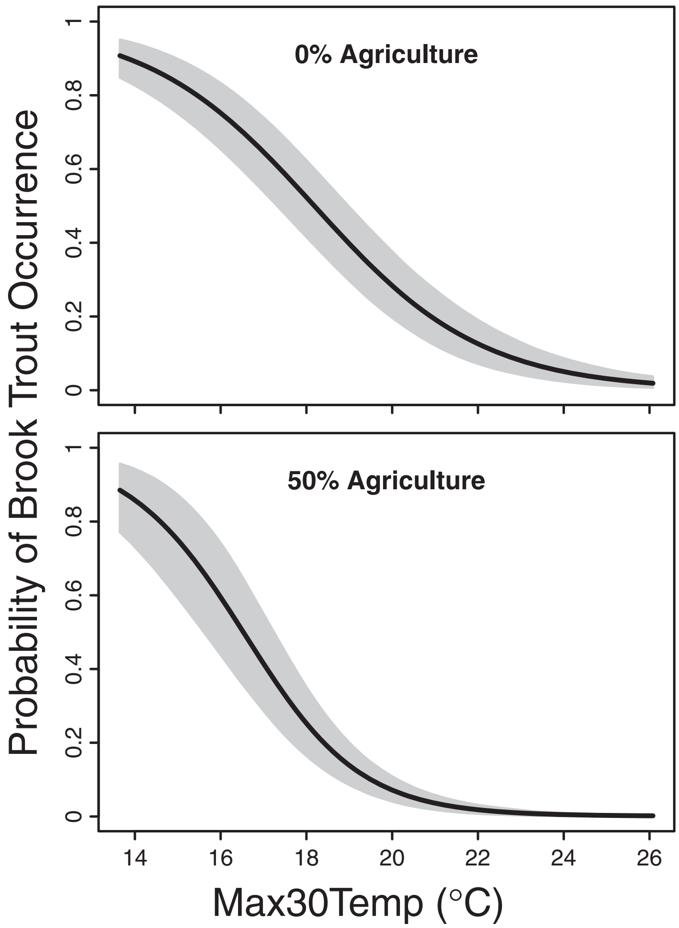

FIGURE 2. Effects of maximum 30-d mean water temperature (Max30-Temp) on Brook Trout occurrence probability at low (0%) and high (50%) levels of agricultural land cover (black line = predicted posterior mean effect; gray shaded area = 90% credible region).

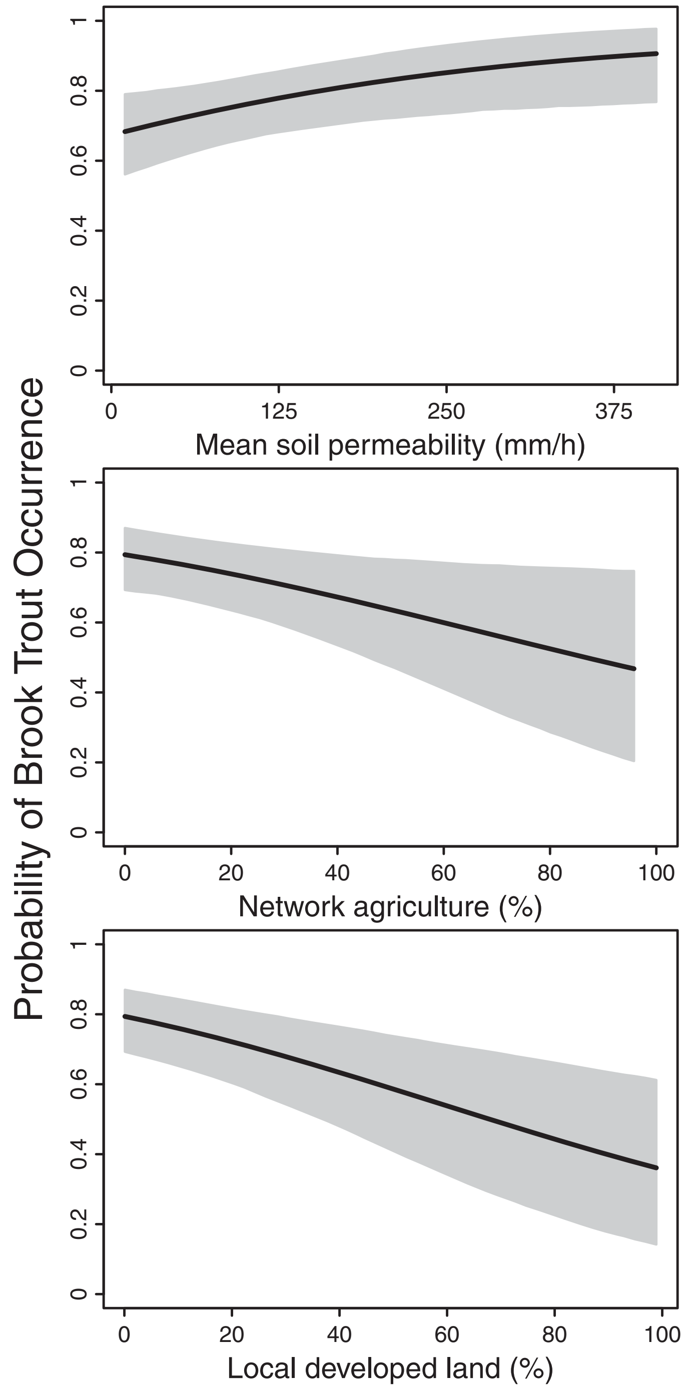

FIGURE 3. Brook Trout occurrence probability as a function of network soil permeability, network agriculture, and local developed land cover (black line = predicted posterior mean effect; gray shaded area = 90% credible region).

2008; Stranko et al. 2008) and reflect the many negative instream habitat alterations that can occur as a result of human activity in the surrounding watershed (Allan 2004). For example, Stranko et al. (2008) identified Brook Trout population reductions and extirpations resulting from development in Maryland (Stranko et al. 2008), and Hudy et al. (2008) identified agricultural land cover as a major determinant of Brook Trout population status in subwatersheds. We also found that the effect of agricultural land cover was greater in areas with warmer water temperatures. This interaction has important implications for climate and land use changes, indicating a greater vulnerability of altered landscapes to increases in water temperature, as was suggested for western U.S. landscapes affected by wildfire (Isaak et al. 2010).

We identified substantial variation in the EDU-level average probability of occurrence (i.e., varying intercepts) and in three varying slopes that was partially explained by EDU-level attributes. We were not surprised to find lower intercepts for EDUs with higher average water temperature given the strong negative effect of water temperature at the reach level. Nevertheless, this relationship could potentially be used to set realistic expectations for the proportion of habitat occupied by Brook Trout based on average water temperature in EDUs or other regions of interest. The negative effect of EDU mean soil permeability on the soil permeability slope shows the

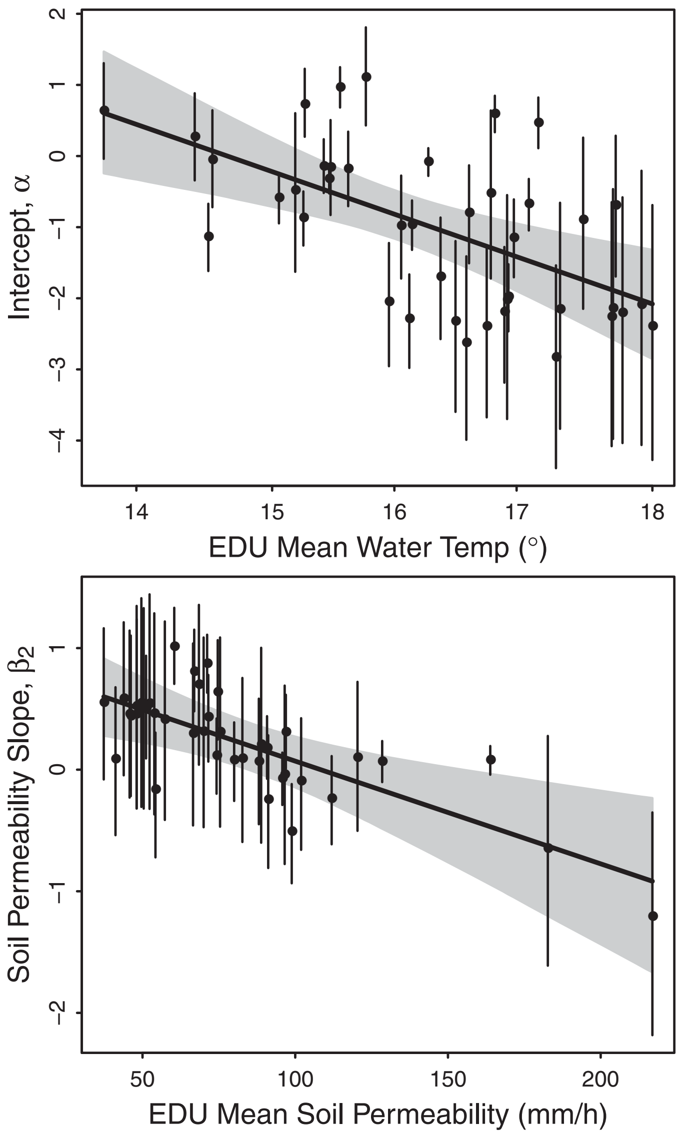

FIGURE 4. Effect of ecological drainage unit (EDU) mean temperature on intercepts (logit-scaled EDU mean Brook Trout occurrence probability); and effect of EDU mean soil permeability on the reach-level soil permeability slope (black line = predicted posterior mean effect; gray shaded area = 90% credible region; points with vertical lines = EDU-specific posterior mean parameter estimates ± 90% credible intervals).

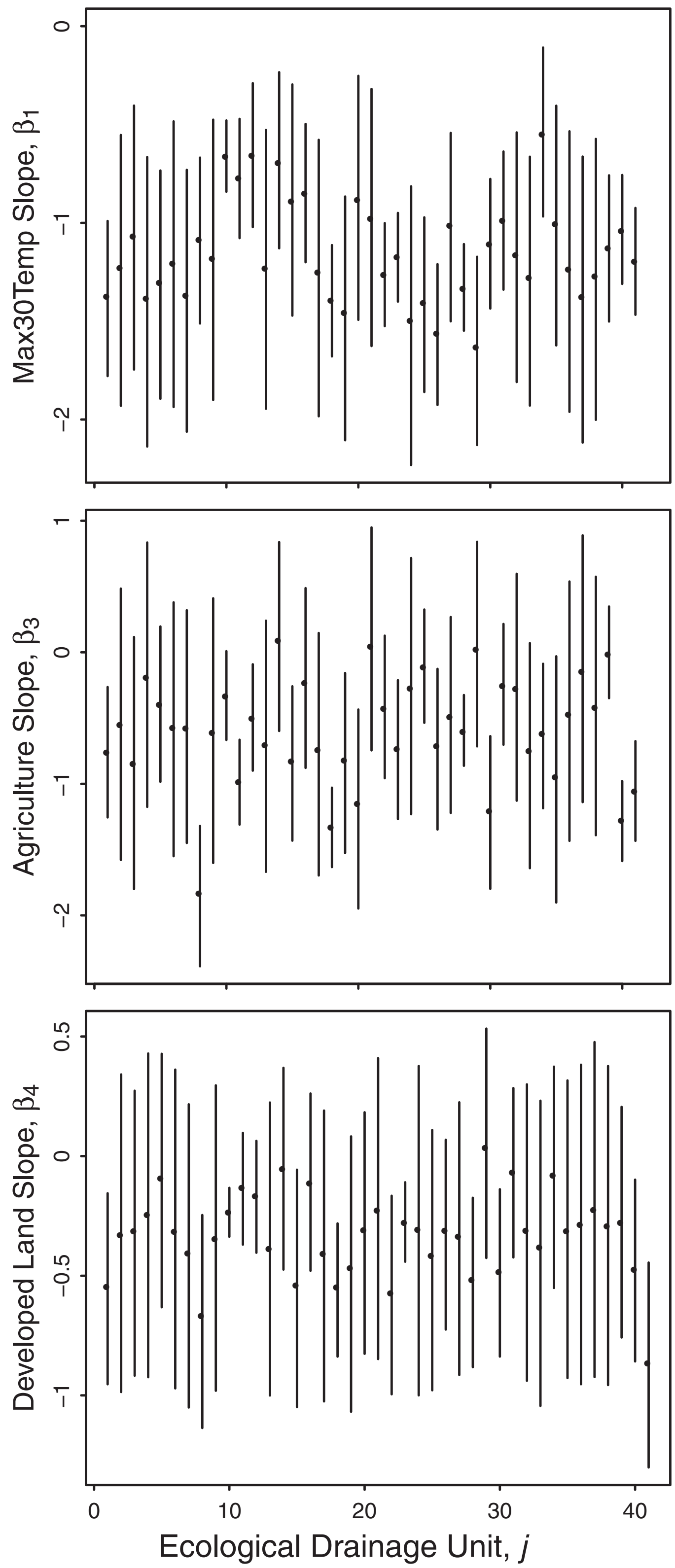

FIGURE 5. Variation in the reach-level slopes for maximum 30-d mean water temperature (Max30Temp), agriculture, and developed land cover among ecological drainage units (EDUs; points with vertical lines = posterior means ± 90% credible intervals).

importance of landscape attributes in the greater surrounding region and demonstrates a cross-scale interaction (Soranno et al. 2014). In this case, the positive effects of network soil permeability were greater in EDUs with lower mean soil permeability. This is presumably because EDUs with higher soil permeability have suitable soils in most catchments, such that further increases in network soil permeability do not provide additional benefits for Brook Trout.

The study region and the factors determining Brook Trout population status are complex, and we recognize that our model does not account for many landscape attributes (e.g.,

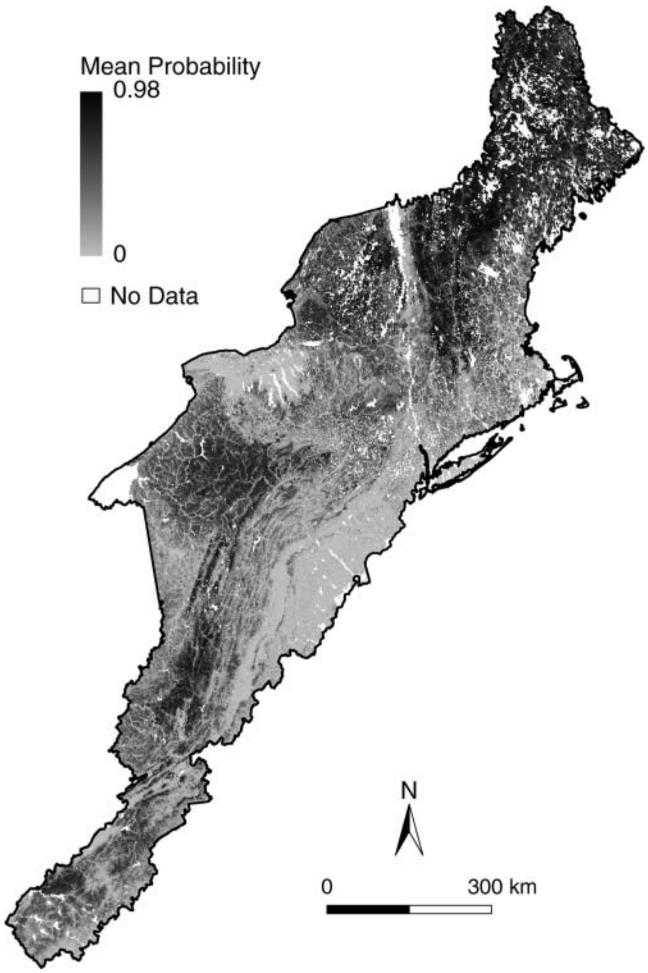

FIGURE 6. Map of mean predicted Brook Trout occurrence probability throughout the study region. White areas with no data did not have predictions because they were not true stream reaches or because the predictor variables were missing.

impervious surfaces), stressors (e.g., acid mine drainage), biotic interactions (e.g., nonnative Brown Trout), or infrastructure (e.g., dams and culverts) that might have negative effects. The data set did not differentiate between stocked and wild fish, which could skew predictions in favor of slightly warmer stream reaches in areas with greater human presence, where Brook Trout may be stocked but where habitat is unsuitable for supporting self-sustaining populations. We also recognize that nonnative salmonids (e.g., Brown Trout and Rainbow Trout) may have important effects (e.g., Wagner et al. 2013), but we did not include these effects because we were interested in identifying suitable habitat where Brook Trout may potentially occur irrespective of biotic interactions. In addition, the lack of occurrence data and stocking records for these salmonid species across the region makes it difficult to conduct a regional assessment of their effects. A separate, carefully designed analysis that is focused solely on nonnative species would likely be necessary to accurately estimate these effects. Finally, predicted water temperature and occurrence probability are based upon an idealized stream network that does not account for the effects of dams and other water infrastructure, and this could produce overestimates in areas where thermal and other habitat alterations have occurred. In areas where additional factors may render habitat suitable or unsuitable, model predictions are likely to be underestimates or overestimates. Since we are unable to

TABLE 4. Comparison of overall classification accuracy, sensitivity, specificity, Cohen's kappa statistic, and the number of stream reaches in the study region identified as occupied by Brook Trout ($N_{occupied}$) among three probability thresholds.

Threshold	Accuracy	Sensitivity	Specificity	Kappa	$N_{occupied}$
0.17	0.68	0.90	0.50	0.38	129,328
0.46	0.72	0.66	0.78	0.44	61,977
0.68	0.68	0.42	0.90	0.33	25,867

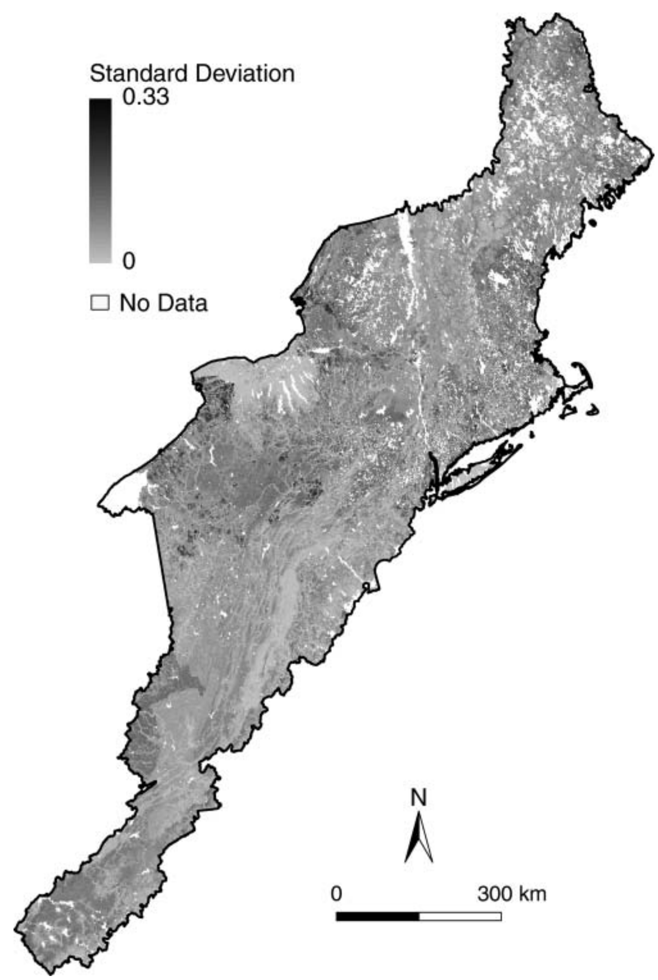

FIGURE 7. Map of the SD of predicted Brook Trout occurrence probability, showing uncertainty in predictions throughout the region. White areas with no data did not have predictions because they were not true stream reaches or because the predictor variables were missing.

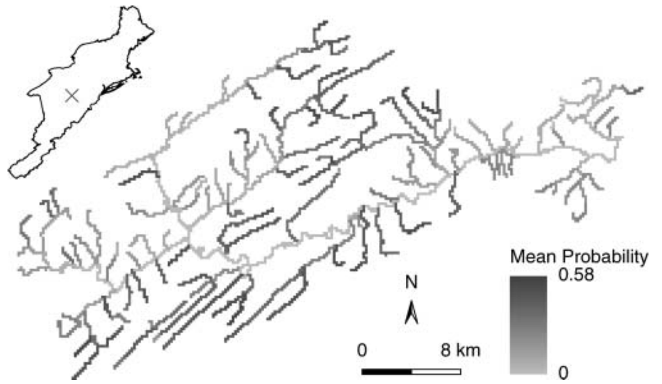

FIGURE 8. Map of mean predicted Brook Trout occurrence probability for the Penns Creek watershed in central Pennsylvania. The × symbol in the inset map shows the location of Penns Creek relative to the study region.

account for many factors that may be important locally, our predictions are probably most suitable for addressing management objectives across large spatial extents (i.e., regionwide or multiple states) unless combined with local knowledge.

Model inferences and predictions could also be biased as a result of our inability to account for imperfect detection. In general, we do not expect these biases to be large because detection probability for Brook Trout is generally high (∼0.90; Wagner et al. 2013). Nevertheless, a failure to account for imperfect detection in sampling could result in underestimation of the extent of occurrence, especially in habitats where detection probability is lower (Royale and Dorazio 2009). Since detection probability for Brook Trout and other fishes can be lower in streams with greater habitat volume or lower-density populations (Hense et al. 2010; Wagner et al. 2013), it is possible that occurrence probability is systematically underestimated in stream reaches that are larger or that have densities limited by biotic interactions or habitat quality.

Despite these possible limitations, our model can be used to compare stream reaches for their potential to support self-sustaining Brook Trout populations throughout the species' native range in the eastern USA. Because higher occurrence probabilities should be representative of higher habitat suitability as long as extraneous factors are not limiting, stream reaches can be prioritized for a given action. For example, in recent years, several states in the EBTJV region have used targeted sampling to document the presence of Brook Trout in previously unassessed waters to gain a better understanding of Brook Trout distribution. Predicted occurrence probabilities and prediction uncertainties can be used to guide such sampling efforts by identifying stream reaches where Brook Trout are more likely to occur or where greater uncertainty exists. Although model performance was reasonable, we welcome efforts to improve the utility of the model for addressing specific objectives by incorporating imperfect detection, predicting abundance or density, including interannual variability through dynamic modeling, or incorporating biotic interactions.

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REFERENCES

Al-Chokhachy, R., S. J. Wenger, D. J. Isaak, and J. L. Kershner. 2013. Characterizing the thermal suitability of instream habitat for salmonids: a cautionary example from the Rocky Mountains. Transactions of the American Fisheries Society 142:793–801.

Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics 35:257–284.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Argent, D. G., and P. A. Flebbe. 1999. Fine sediment effects on Brook Trout eggs in laboratory streams. Fisheries Research 39:253–262.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario, Canada, streams. North American Journal of Fisheries Management 5:364–378.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Castric, V., F. Bonney, and L. Bernatchez. 2001. Landscape structure and hierarchical genetic diversity in the Brook Charr, *Salvelinus fontinalis*. Evolution 55:1016–1028.

Clark, M. E., K. A. Rose, D. A. Levine, and W. W. Hargrove. 2001. Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. Ecological Applications 11:161–178.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20:37–46.

De Staso, J., and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River Cutthroat Trout and Brook Trout in a laboratory stream. Transactions of the American Fisheries Society 123:289–297.

DeWeber, J. T., and T. Wagner. 2014. A regional neural network ensemble for predicting mean daily river water temperature. Journal of Hydrology 517:187–200.

Elith, J., and J. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology 40:677–697.

Esselman, P. C., D. M. Infante, L. Wang, D. Wu, A. R. Cooper, and W. W. Taylor. 2011. An index of cumulative disturbance to river fish habitats of the conterminous United States from landscape anthropogenic activities. Ecological Restoration 29:133–151.

Flebbe, P. A., L. D. Roghair, and J. L. Bruggink. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Transactions of the American Fisheries Society 135:1371–1382.

Haines, T. A., and R. E. Johnson. 1982. Acid rain/fisheries: proceedings of an international symposium on acidic precipitation and fishery impacts in northeastern North America. American Fisheries Society, Northeast Division, Bethesda, Maryland.

Hanley, J., and B. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36.

Hense, Z., R. W. Martin, and J. T. Petty. 2010. Electrofishing capture efficiencies for common stream fish species to support watershed-scale studies in the central Appalachians. North American Journal of Fisheries Management 4:1041–1050.

Higgins, J. V., M. T. Bryer, M. L. Khoury, and T. W. Fitzhugh. 2005. A freshwater classification approach for biodiversity conservation planning. Conservation Biology 19:432–445.

Homer, C., C. Q. Huang, L. M. Yang, B. Wylie, and M. Coan. 2004. Development of a 2001 National Land-Cover Database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the eastern United States. North American Journal of Fisheries Management 28:1069–1085.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20:1350–1371.

Kanno, Y., J. Vokoun, and B. Letcher. 2011. Fine-scale population structure and riverscape genetics of Brook Trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. Molecular Ecology 20:3711–3729.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic Rainbow Trout into stream populations of native Brook Trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195–203.

Lee, R. M., and J. N. Rinne. 1980. Critical thermal maxima of five trout species in the southwestern United States. Transactions of the American Fisheries Society 109:632–635.

Letcher, B. H., K. H. Nislow, J. A. Coombs, M. J. O'Donnell, and T. L. Dubreuil. 2007. Population response to habitat fragmentation in a stream-dwelling Brook Trout population. PLoS ONE [online serial] 2:e1139.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of Brook Trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 26:1699–1725.

Martin, R. W., and J. T. Petty. 2009. Local stream temperature and drainage network topology interact to influence the distribution of Smallmouth Bass and Brook Trout in a central Appalachian watershed. Journal of Freshwater Ecology 24:497–508.

McKenna, J. E., and J. H. Johnson. 2011. Landscape models of Brook Trout abundance and distribution in lotic habitat with field validation. North American Journal of Fisheries Management 31:742–756.

Meisner, J. D. 1990. Effect of climatic warming on the southern margins of the native range of Brook Trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 47:1065–1070.

Moglen, G. E., K. C. Nelson, M. A. Palmer, J. E. Pizzuto, C. E. Rogers, and M. I. Hejazi. 2003. Hydro-ecologic responses to land use in small urbanizing watersheds within the Chesapeake Bay watershed. Pages 41–60 in R. DeFries, G. Asner, and R. Houghton, editors. Ecosystems and Land Use Change. American Geophysical Union, Washington, D.C.

Peterson, D. P., S. J. Wenger, B. E. Rieman, and D. J. Isaak. 2013. Linking climate change and fish conservation efforts using spatially explicit decision support tools. Fisheries 38:112–127.

Picard, C. R., M. A. Bozek, and W. T. Momot. 2003. Effectiveness of using summer thermal indices to classify and protect Brook Trout streams in northern Ontario. North American Journal of Fisheries Management 23:206–215.

Plummer, M. 2011. JAGS version 3.3.0 user manual. Available: http://iweb.dl.sourceforge.net/project/mcmc-jags/Manuals/3.x/jags_user_manual.pdf. (May 2014).

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Royale, J. A., and R. M. Dorazio. 2009. Modeling occupancy and occurrence probability. Pages 83–125 in J. A. Royale and R. M. Dorazio, editors. Hierarchical modeling and inference in ecology. Academic Press, San Diego, California.

Ruesch, A. S., C. E. Torgersen, J. J. Lawler, J. D. Olden, E. E. Peterson, C. J. Volk, and D. J. Lawrence. 2012. Projected climate-induced habitat loss for salmonids in the John Day River network, Oregon, USA. Conservation Biology 26:873–882.

Schofield, C. L. 1976. Acid precipitation: effects on fish. Ambio 5:228–230.

Schwarz, G. E., and R. B. Alexander. 1995. Soils data for the conterminous United States derived from the NRCS State Soil Geographic (STATSGO) data base. U.S. Geological Survey Open File Report 95-449. Available: http://water.usgs.gov/lookup/getspatial?ussoils. (May 2014).

Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21:3940–3941.

Soranno, P. A., K. S. Cheruvelil, E. G. Bissell, M. T. Bremigan, J. A. Downing, C. E. Fergus, C. T. Filstrup, E. N. Henry, N. R. Lottig, E. H. Stanley, C. A. Stow, P. Tan, T. Wagner, and K. E. Webster. 2014. Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. Frontiers in Ecology and the Environment 12:65–73.

Stanton, J. C., R. G. Pearson, N. Horning, P. Ersts, and H. Reşit Akçakaya. 2012. Combining static and dynamic variables in species distribution models under climate change. Methods in Ecology and Evolution 3:349–357.

Steen, P. J., M. J. Wiley, and J. S. Schaeffer. 2010. Predicting future changes in Muskegon River watershed fish distributions under future land cover alteration and climate change scenarios. Transactions of the American Fisheries Society 139:396–412.

Stranko, S. A., R. H. Hilderbrand, R. P. Morgan, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook Trout declines with land cover and temperature changes in Maryland. North American Journal of Fisheries Management 28:1223–1232.

Su, Y., and M. Yajima. 2013. R2jags: a package for running jags from R. R package version 0.03-11. Available: http://CRAN.R-project.org/package=R2jags.(May 2014).

Sweka, J. A., and K. J. Hartman. 2001. Influence of turbidity on Brook Trout reactive distance and foraging success. Transactions of the American Fisheries Society 130:138–146.

USEPA (U.S. Environmental Protection Agency) and USGS (U.S. Geological Survey). 2005. National Hydrography Dataset Plus, version 1.0. Available: http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php. (May 2014).

Wagner, T., J. T. Deweber, J. Detar, D. Kristine, and J. A. Sweka. 2014. Spatial and temporal dynamics in Brook Trout density: implications for population monitoring. North American Journal of Fisheries Management 34:258–269.

Wagner, T., J. T. Deweber, J. Detar, and J. A. Sweka. 2013. Landscape-scale evaluation of asymmetric interactions between Brown Trout and Brook Trout using two-species occupancy models. Transactions of the American Fisheries Society 142:353–361.

Wagner, T., D. B. Hayes, and M. T. Bremigan. 2006. Accounting for multilevel data structures in fisheries data using mixed models. Fisheries 31:180–187.

Wehrly, K. E., L. Z. Wang, and M. Mitro. 2007. Field-based estimates of thermal tolerance limits for trout: incorporating exposure time and temperature fluctuation. Transactions of the American Fisheries Society 136:365–374.

Weltman-Fahs, M., and J. M. Taylor. 2013. Hydraulic fracturing and Brook Trout habitat in the Marcellus Shale region: potential impacts and research needs. Fisheries 38:4–15.

Wenger, S. J., D. J. Isaak, J. B. Dunham, and K. D. Fausch. 2011. Role of climate and invasive species in structuring trout distributions in the interior Columbia River basin, USA. Canadian Journal of Fisheries and Aquatic Sciences 68:988–1008.

Wenger, S. J., and J. D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3:260–267.

Whiteley, A. R., J. A. Coombs, M. Hudy, Z. Robinson, A. R. Colton, K. H. Nislow, and B. H. Letcher. 2013. Fragmentation and patch size shape genetic structure of Brook Trout populations. Canadian Journal of Fisheries and Aquatic Sciences 70:678–688.

APPENDIX: MEAN DEVIATION IN BROOK TROUT OCCURRENCE

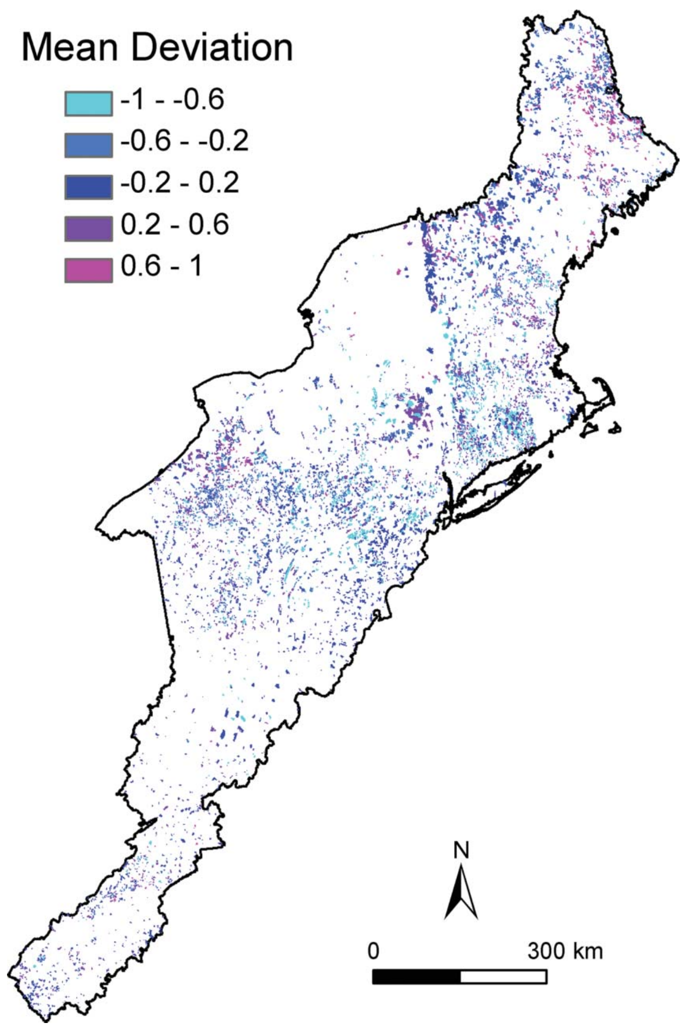

FIGURE A.1 Map of the mean deviation between predicted Brook Trout occurrence probability (from 5,000 posterior draws) and observed occurrence (presence/absence). Positive values represent stream reaches where predictions were overestimates on average, and negative values represent stream reaches where predictions were underestimates on average. [Figure available online in color.]