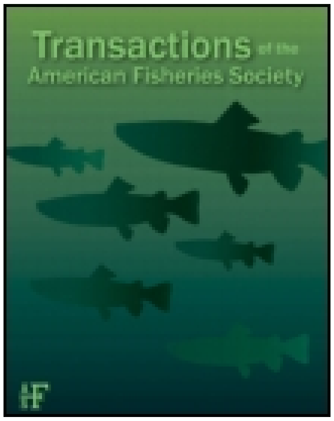

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Environmental Factors Affecting Brook Trout Occurrence in Headwater Stream Segments

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ARTICLE

Environmental Factors Affecting Brook Trout Occurrence in Headwater Stream Segments

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Abstract
We analyzed the associations of catchment-scale and riparian-scale environmental factors with occurrence of Brook Trout *Salvelinus fontinalis* in Connecticut headwater stream segments with catchment areas of <15 km^2. A hierarchical Bayesian approach was applied to a statewide stream survey data set, in which Brook Trout detection probability was incorporated and statistical significance of environmental covariates was based on 95% credible intervals of estimated coefficients that did not overlap a value of zero. Forested land at the catchment scale was the most important covariate affecting Brook Trout occurrence; i.e., heavily forested catchments with corresponding low levels of developed and impervious land area were more likely to be occupied by Brook Trout. Coarse surficial geology (an indicator of groundwater potential) and stream slope had significantly positive effects on occurrence, whereas herbaceous plant cover and wetland and open water area had significantly negative effects. Catchment-scale and riparian-scale covariates were highly correlated in many instances, and no riparian-scale covariate was retained in the final model. Detection probability of Brook Trout at the stream-segment scale was high (mean, 0.85). Our model had a high predictive ability, and the mean value of receiver operating characteristic area under the curve was 0.80 across 100 leave-some-out iterations. The fine spatial grain of this study identified patches of suitable stream habitat for Brook Trout in Connecticut, particularly in the northwestern part. Our analysis revealed a more optimistic status of Brook Trout in Connecticut than did a coarser-grained analysis across the USA.

With land use and climate change threatening persistence of stream fish, fish–habitat relationships at a broad spatial extent (e.g., state, region) need to be understood to inform management and conservation decisions. For these models to be useful for resource managers, the spatial grain of analysis needs to be broad enough to allow for a meaningful comparison across space (e.g., habitat prioritization), but it also needs to be fine enough to capture heterogeneity in environmental and habitat conditions that solicit variable biological responses. Stream networks are composed of linear habitat segments, in which tributary confluences may characterize a sharp change in environmental conditions (Benda et al. 2004; Kiffney et al. 2006). Accordingly, biological patterns and processes differ within a stream network (Grant et al. 2007; Letcher et al. 2007), and stream segments (i.e.,

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confluence to confluence) serve as a useful spatial grain for analysis of fish–habitat relationship.

Fish–habitat relationships are also increasingly analyzed by accounting for imperfect detection of organisms. Hierarchical models encompass a broad range of statistical techniques, but a group of models that explicitly considers ecological processes and detection errors has become widely used in recent years (e.g., MacKenzie et al. 2002, 2003; Royle 2004). These approaches make use of additional information available on detection probabilities of individuals or a species. Models have been successfully applied to stream fish to understand species occupancy patterns (Wenger et al. 2008; Falke et al. 2012).

Rigorous approaches to defining fish–habitat relationships are much needed for species occupying stream headwaters. Headwater streams are the most common lotic habitat type by number and total length in the USA (Allan and Castillo 2007), and their small drainage size makes them highly sensitive to land use change and other anthropogenic activities. Headwater streams are located at the terminus of the dendritic stream network, where species richness is lower and colonization may play a less important role in fish population and assemblage dynamics than in larger-order streams (Brown et al. 2011). Concurrently, local habitat conditions can be more important in structuring populations and assemblages in headwater streams than in larger streams (Brown and Swan 2010). Habitat modeling of a headwater species is therefore an important tool in fish conservation.

Brook Trout *Salvelinus fontinalis* are native to the eastern USA, and their populations are primarily found in small headwater streams, except in the northern part of their range, where they also occur in larger streams and lakes. Brook Trout populations have declined throughout their native range (Hudy et al. 2008), and they continue to face various threats including land-cover change (Stranko et al. 2008), groundwater extraction (Waco and Taylor 2010), natural gas development (Weltman-Fahs and Taylor 2013), and introduced trout species (Hoxmeier and Dieterman 2013). Climate change will further impact this coldwater species (Eaton and Scheller 1996; Lyons et al. 2010). At the same time, Brook Trout populations can persist in small isolated habitats <1 km in length (Letcher et al. 2007; Kanno et al. 2011), and their population size often recovers quickly due to early maturation and high fecundity (Letcher et al. 2007; Öhlund et al. 2008). This indicates that small headwater streams will be a primary long-term habitat for Brook Trout in much of their U.S. range and that identifying characteristics of these streams that sustain Brook Trout is a key conservation goal.

We examined Brook Trout occurrences in small headwater streams (<15 km^2) in Connecticut, as related to environmental conditions at catchment and riparian spatial scales. We used a Bayesian hierarchical approach to identify a group of environmental covariates that affected Brook Trout occurrence by accounting for imperfect detection. Model performance and predictive ability were assessed by using receiver operating characteristic area under the curve (AUC) and leave-some-out simulations. Environmental factors associated with Brook Trout occurrence have been studied previously at a coarser spatial grain—i.e., subwatershed level (mean catchment area = 89.7 km^2)—across the USA rangewide scale (Hudy et al. 2008). In our study, we examined Brook Trout occurrence at a finer spatial grain—i.e., stream segment (mean catchment area = 6.5 km^2, range of 1–15 km^2)—focused on a single state, Connecticut.

METHODS

Our goal was to assess Brook Trout occurrence in Connecticut headwaters at the stream-segment scale, defined as a stream section ranging from one confluence to another on the 1:24,000-scale, National Hydrography Dataset (NHD) flowlines. Brook Trout occurrence at the segment scale was the response variable in our models. Predictor variables included a set of GIS-derived data at two spatial scales: catchment and riparian.

We restricted our analysis to catchments that ranged 1–15 km^2 in entire upstream area to address our goal of examining spatial variation among headwater streams. The lower threshold was set so as not to include the smallest catchments in which flow intermittency could be a major limiting factor for Brook Trout persistence. The upper threshold represented the catchment size recommended by Kanno et al. (2010) for application of a coldwater index of biotic integrity in Connecticut; Brook Trout occurrence and abundance were low when catchment size exceeded 15 km^2.

Environmental Data

We characterized environmental conditions from the lowermost point of each stream segment towards all contributing area upstream at the catchment scale, and to the beginning of a headwater stream along the NHD flowlines at the "riparian" scale. Catchments were delineated based on a 10-m Digital Elevation Model, which was reconditioned with the 1:24,000-scale, U.S. Geological Survey high-resolution NHD using ArcGIS 10.1 and ArcHydro 10.1 software (ESRI, Redlands, California). We set 1 km^2 as the minimum threshold of the catchment size when delineating catchments in ArcHydro software. Riparian areas were defined as those areas located ±50 m along the entire upstream stream network based on the high-resolution NHD. Thus, the riparian area was a subset of the catchment.

A suite of environmental data were characterized at the catchment and riparian scales (Table 1). Topographical features (e.g., slope) and land cover (e.g., forest) have been associated with Brook Trout populations in previous studies (Stranko et al. 2008; Kanno et al. 2010; Waco and Taylor 2010; McKenna and Johnson 2011). We also included a geological variable, percent sandy and gravelly (denoted, "coarse_cat"), as an indicator of groundwater potential (Cervione et al. 1982), groundwater having been identified as important thermal resources for Brook Trout (Curry and Noakes 1995; Borwick et al. 2006). Catchment-scale covariates were denoted with the suffix "_cat" and riparian-scale covariates with the suffix "_rip" hereafter (Table 1).

We also characterized spatial variation in air temperature and precipitation among catchments (Table 1). These climate variables exert a major effect on lotic thermal and flow regimes, and they will also be affected greatly by climate change (Hayhoe et al. 2007). We characterized the mean values of daily minimum and maximum air temperature and total precipitation for all catchments in 1981–2010 using the PRISM data set (http://prism.oregonstate.edu).

At the completion of GIS data analysis, we compiled environmental data for a total of 4,804 headwater catchments (1–15 km^2) in Connecticut. Of those catchments, fish survey data were available for 413 catchments.

Fish Data

We used a stream fish survey data set collected by the Connecticut Department of Energy and Environmental Protection between 1999 and 2012. A standardized protocol was used during this period. Fish surveys were conducted across the state, 93% occurring between June and August (range, May–October). Fish were collected primarily during base-flow conditions to maximize capture efficiency. Fish were collected by a crew of 4–8 people using pulsed DC backpack electrofishers (Model L-24, Smith-Root, Vancouver, Washington, or Coffelt Model BP-4, Coffelt Manufacturing, Flagstaff, Arizona). Sample reach lengths were determined by targeting 15–30 times the mean stream width to characterize fish community composition (Dauwalter and Pert 2003; Reynolds et al. 2003). This protocol typically included a mix of riffle, run, and pool habitat types represented at a stream reach. Single-pass

TABLE 1. Summary of environmental data at catchment-scale and riparian-scales that were used as explanatory variables in submodels of Brook Trout occurrence in Connecticut. Median and percentiles are based on 413 stream segments sampled for Brook Trout.

Abbreviation	Variable	Median	Percentile: 2.5– 97.5	Data resolution (m)	Source
	Catchment-scale covariates				
fore_cat	Percent forested land within a catchment	79	2–95	30	NLCD[b]
herb_cat	Percent herbaceous plant cover within a catchment	1	0–5	30	NLCD[b]
agri_cat	Percent agricultural land within a catchment	5	0–31	30	NLCD[b]
devlop_cat	Percent developed land within a catchment	8	2–80	30	NLCD[b]
imperv_cat	Percent impervious land within a catchment	1	0–26	30	NLCD[b]
wetl_cat	Percent wetland within a catchment	3	0–16	30	NLCD[b]
opnwtr_cat	Percent lentic and lotic area within a catchment	1	0–8	30	NLCD[b]
slope_cat	Mean slope (%) of a catchment	5	2–9	30	NED[c]
coarse_cat	Percent surficial geological materials that are sandy and gravelly within a catchment	4	0–34	10	gSSURGO[d]
cross_cat	Number of road crossings per catchment area in km[b]	2.1	0.5–6.2	30	NLCD[b]
tmin	Mean of daily minimum temperature in 1981–2010 (°C)	3.8	2.2–5.8	800	PRISM[a]
tmax	Mean of daily maximum temperature in 1981–2010 (°C)	15.1	13.2–16.1	800	PRISM
prcp	Mean of total yearly precipitation in 1981–2010 (mm)	1,262	1,157–1,340	800	PRISM
	Riparian-scale covariates				
fore_rip	Percent forested land within a riparian buffer	79	31–97	30	NLCD[b]
herb_rip	Percent herbaceous plant cover within a riparian buffer	1	0–10	30	NLCD
agri_rip	Percent agricultural land within a riparian buffer	3	0–29	30	NLCD
devlop_rip	Percent developed land within a riparian buffer	8	1–66	30	NLCD
imperv_rip	Percent impervious land within a riparian buffer	1	0–17	30	NLCD
slope_rip	Mean slope (%) of a riparian buffer	4	2–7	30	NED[c]
coarse_rip	Percent surficial geological materials that are sandy and gravelly within a riparian buffer	7	0–37	10	gSSURGO[d]

[a]PRISM: PRISM Climate Group (http://prism.oregonstate.edu).
[b]NLCD: National Land Cover Database (http://mrlc.gov/nlcd2006.php).
[c]NED: National Elevation Dataset (http://ned.usgs.gov).
[d]gSSURGO: Gridded Soil Survey Geographic Database (www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/home/?cid=nrcs142p2_053628).

electrofishing was conducted, and all fish were returned to the stream after species identification and abundance enumeration.

A total of 719 surveys were available from 559 unique sites in 413 catchments (some catchments contained multiple sites). A majority of sites (443 sites or 79%) were visited once between 1999 and 2012, but other sites were revisited 2–6 times. These multiple-visit data to the same stream segment were used to account for imperfect detection. The data set distinguished wild from stocked Brook Trout, and our statistical analysis used only wild Brook Trout records.

Statistical Analysis

Model description.—We analyzed Brook Trout occurrences at the segment scale using a Bayesian hierarchical approach. It was composed of an ecological submodel that related environmental covariates to Brook Trout occurrence and a detection submodel that accounted for imperfect detection. First, the ecological submodel was specified using the logistic regression,

$$\begin{aligned} &z_i \sim \text{Bernoulli}(\text{psi}_i)\\ &\text{logit}(\text{psi}_i) = a_{j[i]} + \beta_1 X_1 + \ldots + \beta_n X_n \\ &a_j \sim \text{Normal}(u, \sigma^2), \end{aligned} \tag{1}$$

where z_i is the true but imperfectly observed state of Brook Trout occurrence at stream segment i ($z_i = 1$ for true presence, $z_i = 0$ for true absence), psi$_i$ denotes probability of occurrence, α_j denotes an intercept term that varies among 10-digit hydrologic unite code (HUC10) basins having a mean of u and a variance of σ^2 across HUC basins, X denotes n environmental covariates, and β denotes the effect size of n covariates on occurrence probability (i.e., slopes). We used a random effect for the intercept term because our preliminary analysis had identified that spatial autocorrelation in model residuals was present in a simple logistic regression approach (data not shown). This analytical approach has become common among fish occupancy studies (e.g., Wenger et al. 2013). Forty-nine HUC10 basins existed in our study area.

Second, we modeled imperfect detection using multiple visits to a subset of segments during the study period (1999–2012). We assumed that the state of occurrence remained constant during this recent survey period. We also assumed that detection probability in this study would be high because Brook Trout are not numerically rare where the species occurs, and trout presence is defined as detecting at least one individual during a survey. Additionally, electrofishing techniques in headwater streams are highly effective for detecting the presence of salmonids (Wagner et al. 2013). However, detection was probably not determined perfectly, especially because a majority (79%) of survey sites were visited only once, multiple visits to a segment typically represented a set of surveys conducted at different local sites. The survey design in our data set was not originally intended for inference on detection probability, but we considered that auxiliary data on detection available in a state stream fish survey data set should be utilized maximally. We assumed that the number of visits with Brook Trout observed (k_i) from the total number of visits (N_i) to segment i followed a binomial distribution, given that Brook Trout were present at the segment ($z_i = 1$):

$$k_i \sim \text{Binomial}(N_{i,}, z_i \times p_i), \tag{2}$$

where p_i denotes detection probability of Brook Trout at segment i. We further modeled that detection probability would be affected by catchment area:

$$\text{logit}(p_i) = \gamma_0 + \gamma_1 \times (\text{catchment\_area}_i). \tag{3}$$

Electrofishing efficiency is typically affected by stream size (Falke et al. 2010; McCargo and Peterson 2010). Given the lack of stream flow data at stream segments, catchment area was used as a surrogate of stream size in our analysis.

Model development.—We used the model above (equations 1–3) to select a subset of environmental covariates that were influential in Brook Trout occurrence. First, we examined correlation among environmental covariates (Table 1) and deleted one covariate when a pair of covariates were highly correlated with each other (Pearson's product-moment correlation coefficient: $|r| > 0.6$). Covariate values were highly correlated with each other at the catchment and riparian scales (r ranged from 0.61 to 0.91). To reduce correlation of the same covariates between the two spatial scales, the riparian-scale covariate was recalculated as $\Delta X = X_{\text{riparian}} - X_{\text{catchment}}$, where X_{riparian} is a value of environmental covariate X at the riparian scale and $X_{\text{catchment}}$ is a value of X at the catchment scale (Zuur et al. 2009). Although this approach limits our abilities to infer the effect of riparian-scale covariates on Brook Trout occurrence, the retention of catchment-scale covariates is reasonable because a vast majority of previous studies linking stream fish occurrence to GIS-derived environmental data have emphasized catchment-scale data (Hudy et al. 2008; Wenger et al. 2008; Wagner et al. 2013); fewer studies documenting the importance of riparian-scale environmental heterogeneity (e.g., Tormos et al. 2014).

We used all retained covariates as main effects in the ecological submodel. In addition, we included interactive effects between catchment-scale forest cover (fore_cat) and each of the other covariates in this global model. We focused on forest cover because (1) it has been identified as an important driver of Brook Trout occurrence in other studies (Hudy et al. 2008; Wagner et al. 2013), (2) it was the most important covariate (i.e., largest effect size) in our own analysis, and (3) considering all potential interactive effects among the large number of environmental covariates, it would not be ecologically interpretable. Prior to analysis, each covariate was standardized by subtracting its mean value and dividing by its standard deviation. Percent forest, percent agriculture, percent wetland, percent open water, and percent coarse geology were logit-transformed prior to standardization because data were skewed. Covariates were considered not statistically significant when the 95% credible interval (CI) overlapped with a value of zero. Nonsignificant covariates were dropped from the global model and we ran the final analysis with significant covariates only ("final model" hereafter).

Model validation.—The final model was assessed for goodness of fit and predictive ability. We fit the final model to 75% of randomly selected segments in our data and used its regression coefficients to make predictions for the remaining 25% of the observations. This procedure was repeated 100 times. For each iteration, predictive performance was assessed using the area under the curve (AUC) of the receiver operating characteristics. The values of AUC range from 0 and 1, values closer to 1 indicating higher predictive performance. In hierarchical models that account for imperfect detection, the AUC is a measure of the ability to correctly predict locations in which a species occurs (Zipkin et al. 2012). The AUC values were calculated using the R package ROCR (Sing et al. 2005), and uncertainties in AUC values were quantified across 100 iterations.

Analysis of models.—We analyzed our models using Markov-chain Monte Carlo (MCMC) methods in JAGS (Plummer 2012) called from Program R (R Development Core Team 2014) with the rjags package. Uninformative priors were used throughout, including Jeffery's priors (mean = 0, SD = 1.643) for the intercept and slope terms on the logit scale. Posterior distributions of model parameters were estimated by taking every fifth sample from 5,000 iterations for each of three chains after discarding 5,000 burn-in iterations. Model convergence was confirmed by ensuring that plots of the MCMC chains achieved good mixture, as well as by examining the R-hat statistic. This statistic compares variance within and between chains, and models are considered to have converged when the value is <1.1 for all model parameters (Gelman and Hill 2007). The R-hat values were <1.02 for all parameters in our models.

RESULTS

A total of five covariates (Table 1) were removed from analysis due to high Pearson r values ($|r| > 0.6$; Table 2). At the catchment scale, forested land was correlated with developed ($r = -0.91$) and impervious ($r = -0.86$) land, and only forested land was retained in the global model. We also deleted mean daily maximum temperature due to its correlation with mean daily minimum temperature ($r = 0.80$). At the riparian scale, developed ($r = -0.85$) and impervious ($r = -0.80$) land were removed because they were again correlated with forested land at the riparian scale.

The global model included 10 catchment-scale covariates (Table 1; fore_cat, herb_cat, agri_cat, wetl_cat, opnwtr_cat, slope_cat, coarse_cat, cross_cat, tmin, prcp), five riparian-scale covariates (fore_rip, herb_rip, agri_rip, slope_rip, coarse_rip), and 14 interaction terms (catchment-scale forest versus each covariate; Table 2). Of these covariates, six catchment-scale covariates had a statistically significant effect on Brook Trout occurrence (fore_cat, herb_cat, wetl_cat, opnwtr_cat, slope_cat, coarse_cat). No riparian-scale covariates or interaction terms had a significant effect. In the detection submodel, catchment area did not affect detection probability of Brook Trout. It was removed and the final model was an intercept-only model with a constant detection probability across stream segments, such that $k_i \sim \text{Binomial}(N_{i,}, z_i{*}p)*$. Notice the lack of indexing for detection probability (p) by segment i.

Accordingly, the final model included the six catchment-level covariates in the ecological submodel and a detection

TABLE 2. Summary of Connecticut environmental data characterized at catchment and riparian scales that were used as explanatory variables in Brook Trout occurrence (ecological) submodels.

Abbreviation	Deleted due to correlation	Deleted during model selection[a]	Retained in the final model
Catchment scale			
fore_cat			yes
herb_cat			yes
agri_cat		yes	
devlop_cat	yes		
imperv_cat	yes		
wetl_cat			yes
opnwtr_cat			yes
slope_cat			yes
coarse_cat			yes
cross_cat		yes	
tmin		yes	
tmax	yes		
prcp		yes	
Riparian scale			
fore_rip		yes	
herb_rip		yes	
agri_rip		yes	
devlop_rip	yes		
imperv_rip	yes		
slope_rip		yes	
coarse_rip		yes	

[a]The global model also included interaction terms with catchment-scale forest cover (fore_cat) and each remaining covariate. None of interaction terms were statistically significant.

submodel with constant detection probability (Table 3). The detection probability of Brook Trout occurrence at the segment scale was high with a mean of 0.85 (95% CI: 0.80–0.89; Table 3). Forested land had the greatest effect (i.e., slope coefficient) on Brook Trout occurrence in Connecticut (Table 3; Figure 1). For example, the probability of Brook Trout occurrence decreased from 0.87 to 0.80, when catchment forest cover decreased by 10% from 79% (the median value across all delineated surveyed catchments) to 69%, while fixing all other covariates at their mean values (Figure 1). Herbaceous plant cover, wetland, and open water had negative effects on Brook Trout occurrence, whereas forested land, coarse surficial geology, and slope had positive effects. Mean Brook Trout occurrence differed among HUC basins, with a mean of 1.81 (95% CI: 1.16–2.84) and a standard deviation value of 0.93 (95% CI: 0.22–2.00) on the logit scale (Table 3).

The final model demonstrated a high predictive ability. The mean AUC value was 0.80 (range: 0.71–0.91) across 100 iterations in which 75% of observations were used for model calibration and the remaining 25% of observations were used for prediction. Predicted occurrences of Brook Trout closely followed land use patterns in Connecticut (Figure 2). Brook Trout were not likely to occur (< 0.3 probability) in the southwestern and middle-central parts of Connecticut, where human population densities are the highest in the state. The northwestern part of the state harbored a large concentration of stream segments with high Brook Trout occurrences (>0.7 probability).

TABLE 3. Parameter estimates from the final model to predict Brook Trout occurrence in Connecticut. All values are on the logit scale, except that the intercept of detection probability is on the natural scale (i.e., true detection probability).

Parameters	Posterior mean values (95% CI)
Occurrence probability	
Intercept	
Mean among HUC basins	1.81 (1.16, 2.84)
SD	0.93 (0.22, 2.00)
Slopes	
fore_cat	1.18 (0.63, 1.88)
herb_cat	−0.60 (−1.05, −0.22)
wetl_cat	−0.88 (−1.55, −0.33)
opnwtr_cat	−0.72 (−1.18, −0.32)
slope_cat	0.92 (0.28, 1.69)
coarse_cat	0.71 (0.34, 1.15)
Detection probability	
Intercept	0.85 (0.80, 0.89)

DISCUSSION

The fine spatial grain of our study revealed a different status assessment of Brook Trout distribution from a previous broader-grain study. Hudy et al. (2008) assessed Brook Trout distribution status across the eastern USA range (Georgia in the south to Maine in the north) at the subwatershed scale, in which the mean catchment area of subwatersheds was

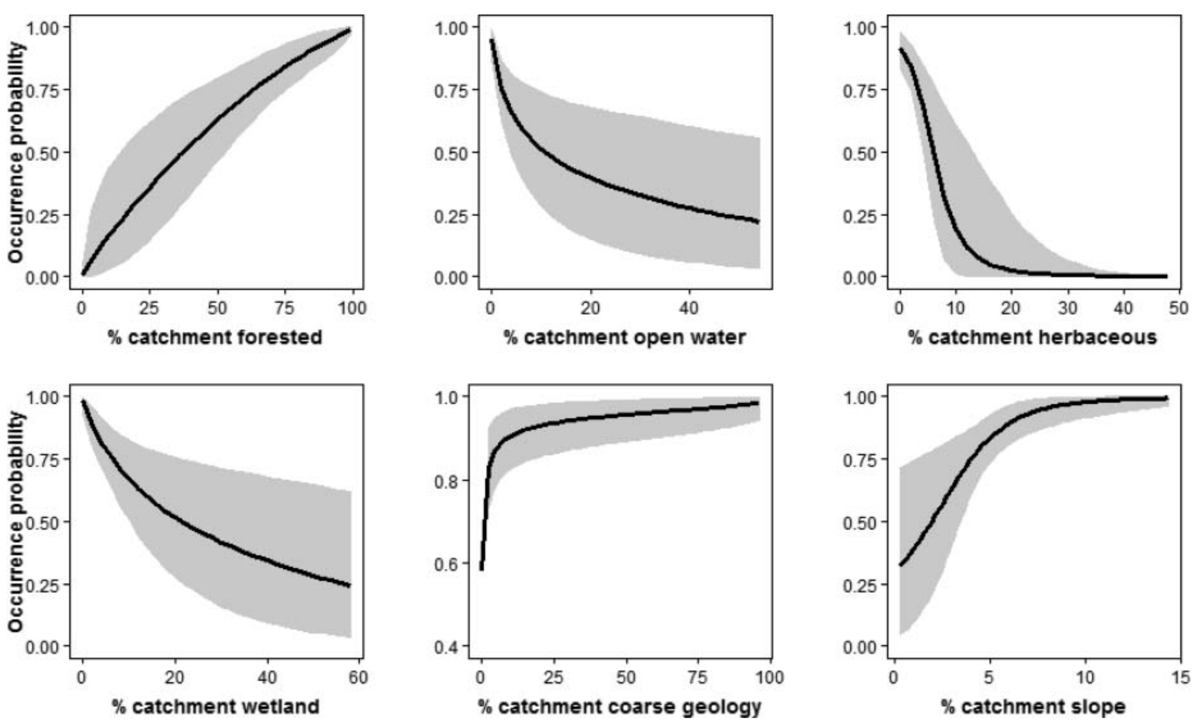

FIGURE 1. Effects of six catchment-scale covariates on Brook Trout occurrence probability in the final model. The black line indicates the posterior mean and the grey shade indicates 95% credible region. Covariates are described in Table 1, and all other covariates were held at their mean values.

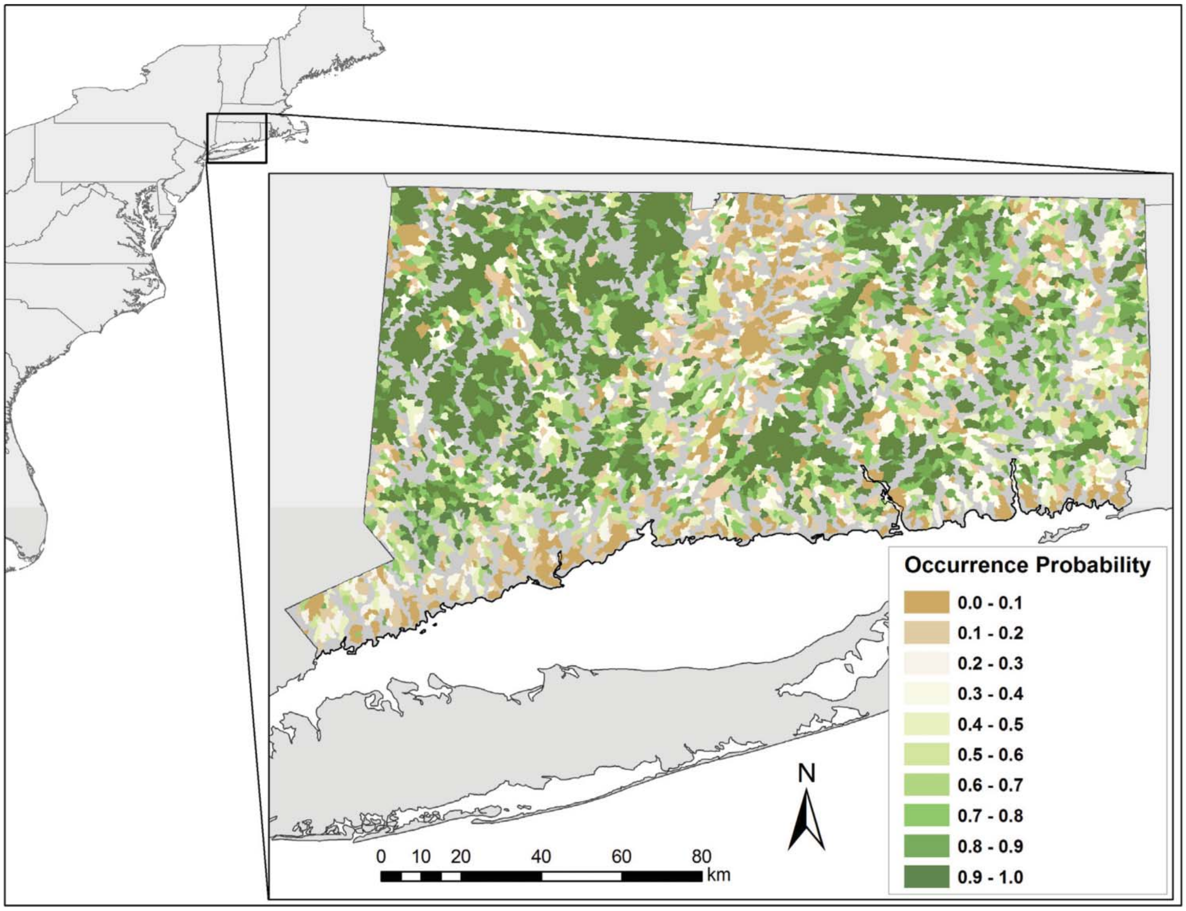

FIGURE 2. Map of Connecticut showing mean predicted occurrence probabilities of Brook Trout for each stream segment based on the final Bayesian hierarchical model. Land areas locally draining to each segment are colored for visual clarification. [Figure available online in color.]

89.7 km^2. Hudy et al. (2008) reported a bleaker status of Brook Trout in Connecticut: extirpation from 10% of historical subwatersheds and >50% reduction in their habitat in 72% of subwatersheds. In contrast, our study focused on stream segments with catchment areas of 1–15 km^2, and we identified many stream segments with high probabilities (>0.7) of Brook Trout occurrence, particularly in the northwestern region of Connecticut. In fact, Brook Trout were recorded at 260 out of 413 stream segments from which data were available in this study. Although these two studies are not directly comparable and the historical range of Brook Trout has indeed been reduced in the mostly suburban–urban landscape of Connecticut, we stress the importance of spatial grain of investigation on fish status assessments. The fine spatial grain was required because Brook Trout populations can persist in small, isolated headwater habitats (Letcher et al. 2007; Kanno et al. 2011), and landuse and environmental characteristics differed at the fine spatial scale in Connecticut. We also note that the identification of stream segments using ArcHydro software made possible a more detailed and finer delineation of upstream catchments than the NHDPlus data set based on the 1:100,000 resolution NHD flowlines used in the Hudy et al. (2008).

Of the statistically significant catchment-scale covariates, forested land was the most important covariate affecting occurrences of Brook Trout in Connecticut headwater streams. Previous studies similarly indicated that Brook Trout occurrence and abundance have been positively related to forested land (McKenna and Johnson 2011; Wagner et al. 2013) and negatively related to impervious cover (Stranko et al. 2008) and agricultural land (Wagner et al. 2013). In our analysis, slope had the second greatest effect on Brook Trout occurrences, and percent wetland and open water (lentic and lotic habitat) had negative effects on Brook Trout occurrence. We suspect that the effects of these covariates indicate that Brook Trout are less likely to be present in catchments that are characterized with low-elevation relief (i.e., flat landscape), or manmade reservoirs and impoundments. Coarse surficial geology was another covariate that has not been typically recognized as a predictor of Brook Trout occurrence. Base-flow level was positively correlated with coarse-grained stratified drift, and this geological feature is an indicator of groundwater potential in Connecticut streams (Cervione et al. 1982). The proportion of stratified drift within a catchment has been associated with fish assemblage composition in coolwater streams in the state (Kanno and Vokoun 2010). The discovery of some unexpected covariates as important predictors of Brook Trout occurrence may be partly due to the fine spatial grain of our analysis. The results reinforce the concept that Brook Trout populations persist in high-gradient and groundwater-fed streams in forested catchments.

Climate change is widely recognized as a major threat to coldwater species, and weather patterns have been associated with temporal population dynamics of Brook Trout in previous studies (Xu et al. 2010; Kanno et al., in press). However, we did not find evidence that air temperature and precipitation affected Brook Trout occurrence in Connecticut. This finding can be attributed to at least two reasons. First, the spatial extent of the study was confined to Connecticut, the third smallest state in the USA (land area of approximately 12,500 km^2). Our study region covered a small subset of the native range of Brook Trout, and we suspect that climate variables will exert greater influence on Brook Trout distribution at a larger spatial extent. Second, we considered air temperature as a surrogate for stream temperature and precipitation as a surrogate for stream flow, but this assumption may not hold true. In particular, air temperature may not have been a good surrogate for stream temperature at the fine spatial grain. Recent studies have shown that stream temperature profiles of Brook Trout streams can vary greatly within a region or catchment due to groundwater and riparian effects (Kanno et al. 2014; Trumbo et al. 2014). Understanding the fine-grain spatial heterogeneity in stream temperature at a broad spatial extent is challenging, but it will hold a key in predicting stream fish distributions under current and future environmental conditions.

We also did not detect influence of riparian-scale covariates on Brook Trout occurrence. Riparian areas mediate sediment transport, maintain physical habitat structure, control channel complexity, and provide allochthonous energy input (Pusey and Arthington 2003; Richardson et al. 2010). Benefits of riparian areas to Brook Trout may include cooling of stream temperature by shading (Gaffield et al. 2005), greater habitat diversity from large woody debris (Sweka and Hartman 2006), and expanded food sources from terrestrial insects that fall into water (Wilson et al. 2014). Riparian-scale land characteristics have been identified as important drivers of stream fish populations and assemblages in some studies (Lorion and Kennedy 2009; Marzin et al. 2013), but other studies concluded that catchment-scale characteristics were more important than riparian-scale characteristics for stream fish assemblages (Roy et al. 2007) or that riparian characteristics did not affect stream fish assemblage (Fischer et al. 2010). In our study, correlation of covariates between catchment and riparian scales (Pearson's r = 0.61–0.91) limited our ability to make strong inferences on the relationship between riparian corridors and Brook Trout occurrence, and we modeled the residual effect of riparian-scale covariates after accounting for the catchment-scale effect. The lack of any riparian-scale covariate in our final model may indicate that catchment characteristics overwhelm riparian-scale influence or the quality of riparian-scale characteristics used in this study (e.g., NLCD) was not detailed enough to discern ecologically important influence at this spatial scale. Future studies are warranted to examine the effect of riparian areas on Brook Trout using environmental data with higher precision, such as light detection and ranging data.

Detection probability of Brook Trout at a stream segment was high (0.85). This result was expected because Brook Trout are not numerically rare at local sites where they occur and the fine-grain delineation of stream segments resulted in relatively small and homogeneous habitats within segments where Brook Trout distribution was not patchy. At the local site scale, Wagner et al. (2013) reported a 99% detection probability for allopatric Brook Trout populations in Pennsylvania. We originally included catchment size as a covariate affecting detection probability, but its effect was not statistically significant and thus removed in the final model. This result may be due to the narrow range of catchment size we selected (1–15 km^2) and efficiency of Brook Trout capture in small streams. Quantifying detection probability has become increasingly popular in stream fish occupancy studies of hard-to-detect species (Wenger et al. 2008; Falke et al. 2012), and a strength of our analytical approach was to incorporate detection probability based on stream-fish survey data routinely collected by state fisheries agencies. However, the high detection probability also indicates that historical stream fish data collected by federal and state agencies can be reliably used, at least for locally common species with high detection probability, to examine spatial or temporal patterns of distribution. Utilizing these various data sources is particularly important for Brook Trout, for which landscape-level conservation is needed and is being pursued in its native range (e.g., Eastern Brook Trout Joint Venture project).

In conclusion, Brook Trout populations in Connecticut were more likely to be found in high-gradient forested catchments with geological features that were associated with high groundwater potential. The fine-grain spatial analysis revealed that a good portion of the state still harbors stream segments that are highly suitable for Brook Trout. Hierarchical analytical approaches similar to ours will foster clear thinking and understanding of ecological and sampling hierarchies inherent in stream fish research and will be useful for many other species.

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