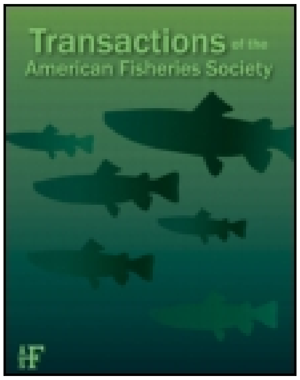

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Ranking Site Vulnerability to Increasing Temperatures in Southern Appalachian Brook Trout Streams in Virginia: An Exposure-Sensitivity Approach

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ARTICLE

Ranking Site Vulnerability to Increasing Temperatures in Southern Appalachian Brook Trout Streams in Virginia: An Exposure-Sensitivity Approach

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Abstract

Models based on simple air temperature–water temperature relationships have been useful in highlighting potential threats to coldwater-dependent species such as Brook Trout *Salvelinus fontinalis* by predicting major losses of habitat and substantial reductions in geographic distribution. However, spatial variability in the relationship between changes in air temperature to changes in water temperature complicates predictions. We directly measured paired summer air and water temperatures over 2 years in a stratified representative sample of watersheds (<1–274 km^2) supporting wild Brook Trout throughout Virginia near the southern edge of the species distribution. We used the temperature data to rank streams in terms of two important components of habitat vulnerability: sensitivity (predicted change in water temperature per unit increase in air temperature) and exposure (predicted frequency, magnitude, and duration of threshold water temperatures). Across all sites, sensitivity was substantially lower (median sensitivity = 0.35°C) than the 0.80°C assumed in some previous models. Median sensitivity across all sites did not differ between the 2 years

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of the study. In contrast, median exposure was considerably greater in 2010 (a particularly warm summer) than in 2009, but exposure ranks of habitat patches were highly consistent. Variation in sensitivity and exposure among habitat patches was influenced by landscape metrics (percent forested riparian corridor, patch area, and elevation), but considerable unexplained variation in sensitivity and exposure among sites was likely due to local-scale differences in the extent of groundwater influence. Overall, our direct measurement approach identified significantly more Brook Trout habitat patches with low sensitivity and low exposure that may persist under warming air temperatures than did previous large-scale models. Our sensitivity and exposure classification should provide a useful general framework for managers in making investment decisions for protecting and restoring Brook Trout habitat.

Climate change is viewed as one of the most important stressors of fish populations (Flebbe 1994). Although, to date, no known Brook Trout *Salvelinus fontinalis* populations have been documented as extirpated due to the effects of climate change (Hudy et al. 2008), several studies have predicted that air temperature increases will dramatically reduce the current range of Brook Trout in the eastern United States (Meisner 1990; Flebbe 1994; Flebbe et al. 2006). While useful in highlighting the potential long-term threat from increases in air temperature, uncertainty associated with assumptions about air–stream temperature relationships (i.e., predicted air temperatures [Daly et al. 1994, 2002; PRISM 2007] and predicted water temperature responses) makes predictions of the persistence of Brook Trout habitat problematic (Johnson 2003). Existing models of changes in coldwater species distribution generally assume simple relationships between fluctuations in air temperature and subsequent response of water temperature (Meisner 1990; Flebbe 1994; Keleher and Rahel 1996; Clark et al. 2001; Rieman et al. 2007; Williams et al. 2009). For example, a model by Flebbe et al. (2006) predicted that Brook Trout would be essentially extirpated from the southern part of their range within the next century. Their model assumed a linear relationship between air and water temperature (i.e., 1°C air temperature change = 0.8°C water temperature change). Predictions of habitat loss based on models that assume a simple positive direct relationship between air and water temperature across all habitats are likely to be overly pessimistic. Some Brook Trout habitats may persist even under the most extreme climate change scenarios due to localized landscape conditions because stream temperature may vary, not only as a function of air temperature, but also as a function of factors associated with habitat, geomorphology, and climate.

Variation in the relationship between air and water temperature can be quantified (Cluis 1972; Pilgrim et al. 1998; Mohseni and Stefan 1999; Isaak and Hubert 2001) and effectively used by managers to rank the vulnerability of individual Brook Trout populations to various climate change scenarios. Identifying resistant coldwater habitats is an important step in prioritizing the restoration and conservation work of the Eastern Brook Trout Joint Venture (EBTJV) (EBTJV 2006). Our pilot studies and earlier research (Fink 2008) suggest that the relationship between air and water temperature is (1) highly variable at the current Virginia Brook Trout population scale (mean area, <30 km^2), and (2) influenced by local conditions and their interactions (i.e., elevation, aspect, topography, shading, riparian cover, latitude, longitude, insolation, and groundwater sources). The influence of these characteristics at localized scales appears to play an important role in stream thermal stability that is not well accounted for in more general models (Meisner 1990; Pilgrim et al. 1998; Moore et al. 2005; Wehrly et al. 2007; Fink 2008).

In this study, we extended our previous work by measuring paired summer air and water temperatures in current Brook Trout habitats throughout the state of Virginia over two summers in 2009 and 2010. We used these data to calculate two important aspects of potential stress related to the likelihood of summer water temperatures exceeding Brook Trout thermal limits. The measures we used are similar to those used to assess vulnerability of an ecosystem to climate change through sensitivity to changes, exposure to changes, and the ability or capacity of the system to adapt to changes (McCarthy et al. 2001; Solomon et al. 2007). Although possibly interpreted in this manner, our view is more closely related to hazard and risk assessment. We used habitat *sensitivity* to describe the extent to which water temperature increases with unit change in air temperature. Habitat *exposure* describes the average frequency, duration, and magnitude of episodes where stream temperatures currently exceed critical temperatures. We then used these metrics to classify Brook Trout habitats with respect to risk and assess the factors accounting for differences in these metrics among habitat patches. Our overall goal was to develop a robust, logistically feasible framework for prioritizing coldwater fish conservation and restoration in the context of climate change, using measures and metrics that can be easily adopted by fisheries managers.

METHODS

Study area and sample unit delineation and selection.—This project includes all habitats with naturally reproducing populations of Brook Trout within the state of Virginia. Brook Trout presence–absence data from the EBTJV (Mohn and Bugas 1980; EBTJV 2006; Hudy et al. 2008) were overlaid on catchments from the National Hydrography Dataset Plus (NHD+) (USGS 2008) to produce a data set of catchments currently occupied by Brook Trout. Contiguous catchments containing Brook Trout were then dissolved into individual watersheds or habitat "patches." Each patch was presumed to be isolated (genetically and reproductively) from other patches. A total of 272 patches were found in Virginia. Candidate landscape metrics

TABLE 1. Candidate landscape metrics summarized for each patch or watershed above each centroid (sample areas = patch or centroid watershed). Metrics followed by an asterisk (*) were used in the cluster analysis to obtain the strata for subsampling; NA = not applicable.

Metric	Units	Source
Area: sample watershed area	km^2	Derived
Riparian: sample riparian area	ha	Derived (100 m buffer NHD+)
Solar_ann: total annual solar gain sample watershed area	kWh	Fu and Rich (1999)
Solar_ann_corr: total annual solar gain in sample riparian area*	kWh	Fu and Rich (1999)
Solar_ann_mean_corr: mean solar gain (July 1–September 30) in riparian sample area (100 m buffer) corrected for the percentage of canopy cover	kWh/30 m pixel	Fu and Rich (1999)
Elev: sample point elevation*	m	PRISM (2007)
Maxtemp: sample point 30-year mean maximum air temperature*	°C	PRISM (2007)
Mean_BFI_Corr: % groundwater (base flow index) in sample riparian watershed*	% of riparian	Wolock (2003)
Canopy: mean canopy cover in sample watershed 30 m pixel	% of patch	USGS (2009)
Canopy_Corr: mean canopy cover in sample riparian watershed area	% of riparian	USGS (2009)
Forest: % forest area in sample watershed*	% of patch	USGS (2009)
Forest_Corr: % forest in sample riparian watershed area	% of riparian	USGS (2009)
NLCD: land use area by category in sample watershed	ha and% of patch	USGS (2009)
NLCD_Corr: land use area by category in sample riparian watershed	ha and% of patch	USGS (2009)
GEOL: geology type and category in sample watershed	NA	DMME (2008)

hypothesized to be important to potential air temperature and water temperature relationships were summarized in a GIS for both the watershed area above the pour point and the watershed area above the patch centroid (Table 1). These included metrics associated with basin characteristics (watershed area, watershed elevation), land use (percent forest and riparian canopy cover), and hydrology (base flow index [BFI]). In addition we calculated two metrics that are directly associated with exposure to solar radiation: Solar Gain, which is jointly determined by watershed aspect, elevation, and topography, and Corrected Solar Gain, which accounts for shading by riparian forest canopy. The pour point is the intersection of the NHD+ stream segment and the most downstream catchment boundary occupied by Brook Trout. The centroid location of the Brook Trout habitat patch was determined by a GIS algorithm and then "snapped" to the nearest stream channel.

Patches were selected for sampling based on a stratified sampling approach with strata selected based on cluster analysis of selected GIS variables (see, for example, Dolman 1990). Our goal was to sample paired air and water temperatures at sites representing the range of landscape conditions in which Brook Trout currently occur in the state. The GIS exercise resulted in over 50 potential landscape variables. The set of variables was first reduced by eliminating variables that were highly correlated or were primarily zero (e.g., percent mining) resulting in a set of five cluster variables (see Table 1 for variables used in the cluster analysis). The five variables were used in a hierarchical cluster analysis (Ward's method, SAS 2000) to cluster the 272 patches into nine strata. We then selected 50 patches from the nine strata with sample size roughly proportional to strata size. In each selected patch we placed two pairs (air and water) of thermographs, one at the patch pour point and one at the centroid, for a total of 100 thermographs.

The resulting data for air and water temperature consisted of temperature measurements at every 30 min or 48 measurements per day. The overall dates and time period varied slightly for different sites because devices were placed in the site or removed from the site on different dates. The data from each site was reduced to standardize the period of sampling and to form daily metrics. Although there are many possible temperature metrics, we focused on daily maximum water temperature (*DMAXW*) and daily maximum air temperature (*DMAXA*) for the critical summer and early fall period for this study because (1) increases in *DMAXA* (and presumed increases in water temperature) have the highest probability of occurrence in various climate change scenarios (Solomon et al. 2007), (2) *DMAXW* metrics for presence and absence of naturally reproducing populations of Brook Trout are known (Stoneman and Jones 1996; Picard et al. 2003; Wehrly et al. 2003, 2007; Huff et al. 2005), and (3) water temperatures in excess of physiological tolerance provide a clear stress threshold for Brook Trout populations.

Sampling protocol.—Paired (air and water) thermographs (HOBO Watertemp Pro v2; accuracy, 0.2°C; drift, <0.1 annually: Onset Computer Corporation 2009) were placed at the pour point and centroid of each sampled patch. All thermographs were set to record every 30 min (Dunham et al. 2005; Huff et al. 2005) from July 1 through September 30 (Stoneman and Jones 1996), thus encompassing the primary period when water temperatures begin to be stressful (>17°C) or potentially lethal (>23°C) for Brook Trout in Virginia. This period may, of course, change with climate changes; however, for this study the period represents a reasonable range for temporal sampling.

Thermographs were calibrated before and after deployment following methods summarized in Dunham et al. (2005). Because of the possibility that stream channels may run dry during summer low-flow periods, thermographs used to record water temperatures were placed near maximum residual pool depths (Lisle 1987) when possible. A shield was used to reduce direct ultraviolet-light contact with air temperature thermographs (Dunham et al. 2005; Trumbo et al. 2012) and water temperature thermographs were placed in stream under boulders or wood to shield them from direct sunlight.

We screened the raw air and water temperature series to identify outliers and other oddities such as thermograph malfunctions, launch and recording interval errors, or potential dry stream beds. Scatterplots of water and air temperature were drawn to evaluate the relationships and look for irregularities in the daily maximum values. Index plots of lagged 1-d differences were also used to identify oddities (rapid change) in temperature and potentially dry streams.

Estimating sensitivity and exposure.—Two important concepts in the evaluation of risk to temperature change are sensitivity and exposure. Sensitivity of stream water temperature is a measure of the degree to which a change in air temperature changes the water temperature. Sensitivity is defined here as the change in water temperature associated with a 1°C change in air temperature. Sensitivity may be measured as a characteristic of a model (i.e., slope in linear regression model) that relates air and water temperature; however, our examination of individual sites clearly demonstrated that the functional relationship was often nonlinear and did not have a consistent shape across all sites. Linear models fit some, but not all, of the data at the sites. Although some types of global nonlinear models (S-shaped or logistic) fit air–water temperature relationships reasonably well when using year-round data (Mohseni and Stefan 1999), we found such models were a poor fit for our data. There are two reasons for this; our data were summer only, and the measurements were at a much finer interval using air and water temperature recording devices placed in a close proximity to each other. Our data were much more sensitive to local characteristics that depended on the geophysical aspects of the individual sites as well as temperature-specific variations within each site. These effects are often hard to capture using the usual logistic regression models. Other types of parametric nonlinear models seem to share the same difficulty, as confirmed by our investigation. To deal with the local nature of the data and varying shape of the relationships, a nonparametric regression using kernel smoothing was used (Simonoff 1996; Bowman and Azzalini 1997). Kernel regression estimates the conditional expectation of a (dependent) variable based on other (independent) variables. The calculation involves selection of a symmetric kernel function (we use a Gaussian function) and a bandwidth (with the Gaussian kernel the bandwidth is equivalent to the standard deviation). The kernel function and bandwidth determine how much influence neighboring observations have on the estimated curve. Due to the physical nature of the air–water temperature coupling, models relating water temperature to air temperature are expected to have a monotone increasing relationship. The smoothing parameter was selected to achieve a relatively stiff fit to the data.

To calculate an overall measure of sensitivity, a local slope was calculated from the fitted nonparametric models by first calculating predicted values for water temperature over a range from 21°C to 30°C in air temperature using an interval of 0.1°C. Slopes were then calculated for each interval as the change in predicted water temperature divided by 0.1. The time interval for calculating the local slope (0.1) was chosen to produce an accurate measure of average or median slope, given the curvature of some nonparametric regression fits. Larger intervals were considered but did not always give good estimates of the average or median slope. The air temperature range (21–30°C) provided a large number of local slopes for each site and represented the middle to upper range of air temperatures where the water sensitivity is highly relevant to the survival of the Brook Trout population. Although temperatures exceeded 30°C, this was not common and we found the estimates were less variable when the limit was set to 30°C rather than a higher value. The median of the local slopes over the range of air temperature at the site was used to estimate overall sensitivity of the particular site.

Exposure to stress associated with increased water temperature was characterized through three measures: frequency, duration, and magnitude. Although any of these measures could be used to indicate exposure, all three measures were computed, scaled to be in the interval (0, 1), and then averaged to produce an overall measure. To be precise our approach was as follows. Consider a time interval from t_0 to t_1 with N daily measurements in the interval. The data used for calculating exposure and sensitivity consists of pairs of daily maximum temperatures, $(DMAXW_t, DMAXWA_t)$, for times $t = t_0, \ldots\ t_1$. The three components of exposure were measured relative to a threshold temperature, T_c. A range of critical temperatures was used as a literature search did not result in a consensus concerning a critical temperature.

The relative or *scaled frequency* of exposure $(R(T_c)_s)$ is the proportion of days the $DMAXW$ exceeds T_c over the time period of interest. Mathematically, $R(T_c)_s = \frac{1}{N}\sum_{t=t_0}^{t_1} I(DMAXW_t > T_c)$. Here $I(x)$ is the indicator function, i.e. $I(x) = 1$ if x is true and zero otherwise. N is the number of days in the time period.

The *duration* of exposure (D) was calculated as the maximum number of consecutive days when $DMAXW$ exceeded T_c. In general, there were periods when the maximum temperature rose to about the threshold temperature then fell below it. The first step in the calculation is to divide the overall interval (t_0, t_1) into r consecutive subintervals where for each interval water temperature is below T_c then rises above the critical temperature, then falls below T_c. Note that r will possibly be different for each site. Let t_{i0} and t_{i1} be the times associated with interval i ($i = 1, 2, \ldots ,r$). Then we define the duration associated with critical temperature T_c as the maximum over the subintervals; i.e. $D(T_c) = \max_i \sum_{t=t_{i0}}^{t_{i1}} I(DMAXW_t > T_c)$. The *scaled duration* is $D(T_c)_s = \frac{1}{N} \max_i [\sum_{t=t_{i0}}^{t_{i1}} I(DMAXW_t > T_c)]$. This formula scales the maximum number of consecutive days above the critical temperature by the maximum possible number of days the temperature could exceed T_c.

The *magnitude* of exposure for day t, associated with a threshold value T_c, is the positive amount that the maximum daily water temperature ($DMAXW_t$) exceeds T_c, i.e., $M_t(T_c) = (DMAXW_t - T_c)_+$. Note that $(.)_+$ results in zero if the value in parenthesis is negative and the value otherwise. The value was then scaled by dividing by the potential range in temperature relative to T_c, using a maximum value of 30°C, i.e.,

$$M_t(T_c)_s = \left[\frac{(DMAXW_t - T_c)_+}{30 - T_c} \right].$$

A further refinement is needed to prevent the values from possibly exceeding 1.0. If the *DMAXW* at time t exceeds 30°C, $M_t(T_c)_s$ is set to 1. Thus the *scaled magnitude* for the entire period is defined as the maximum of the scaled values for each time over the interval of interest, i.e., $M(T_c)_s = \max_t [\min(M_t(T_c)_s, 1)] = \max_t [\min(\frac{(DMAXW_t - T_c)_+}{30 - T_c}, 1)]$.

The scaling of the magnitude, duration, and frequency results in three measures that are in the interval (0, 1). To form an overall measure, the three measures of exposure were combined into a single value by averaging the measures for each site (i.e., the exposure is given by $E(T_c) = [R(T_c)_s + D(T_c)_s + M(T_c)_s]/3$). Although the measures are conceptually different, the calculated measures suggested a high degree of similarity. We found that the correlations between pairs of measures were greater than 0.8 and pairwise plots were relatively linear. Also the principal component analysis of the measures resulted in a single eigenvalue that accounted for most of the variation and weights that were roughly equal for the three metrics. These facts justify averaging to combine the three measures as a single measure of the exposure to water temperature stress.

Analysis of the data could be undertaken for each value of the critical temperature, T_c; however, this would require a specific value that was deemed critical. We did not find strong support in the literature for a single critical value. Instead of using a single critical temperature, an exposure profile was obtained for each site by varying T_c. To calculate an overall measure of exposure for a site, exposure was calculated for threshold water temperatures that encompassed stressful to lethal water temperature conditions (17–23°C) for Brook Trout using incremental steps of 0.1°C. These values were then averaged to produce an overall measure that was within the interval (0, 1). The range was selected to provide an indication of sites at risk as these sites will have values close to 1.0 for most values of *T*. Also, the streams with consistently lower temperature will have values closer to 0.0, which helped in ranking those sites with little current exposure to harmful *DMAXW* temperatures.

Estimates of sensitivity and exposure were graphically displayed and compared across 2009 and 2010. The display for 2009 was divided into four categories based on exposure greater or less than the median exposure (resulting in two groups: HE and LE) and sensitivity greater or less than the median sensitivity (resulting in two groups: HS and LS). The median was used to split the 2009 data into two equal-sized groups for comparison with the 2010 data. Also, evaluation of the 2009 exposures indicated that this corresponded roughly to a threshold temperature of 21°C (i.e., 75% of the profile plots had an exposure value below the overall median exposure at 21°C). Bootstrap confidence intervals were used to determine the uncertainty associated with the medians and hence identify sites that might have low classification certainty. The same values were used to categorize values in the plot of the 2010 data, thus allowing for evaluation of change in categories between years. Although we did not specifically define sites in the LE/LS category to be resistant, we expect these sites to be the relevant ones to focus on for further evaluation. Sites in the bootstrap interval represent those where there is high uncertainty about the classification. To further evaluate whether site exposure and sensitivity ranks were consistent across years, we used calculated Spearman correlation ranks between 2009 and 2010 values. Finally, parametric (paired t-test) and nonparametric (Wilcoxon signed rank test) paired tests were used to test for differences in median sensitivity and exposure between years across sites.

Exposure and sensitivity values were related to landscape and other variables using correlation and regression methods. Model-averaged regression methods (Burnham and Anderson 2002; Lukacs et al. 2010) were used to relate the components of vulnerability to landscape and other variables, and the resulting models were used to predict the risk to Brook Trout for 272 sites in Virginia. To develop models, the independent variable set was first reduced by removing variables that were highly correlated with other variables. Although some evidence exists indicating that model averaging is useful when variables are moderately correlated (Freckleton 2011), we chose to remove some variables as our interest is prediction rather than explanation and we were concerned about inflated prediction variance. A correlation of 0.9 was used as a cutoff and the approach resulted in a set of seven variables (Table 2). To reduce the effect of colinearity on the intercept, the independent variables were first standardized to have a mean of zero and variance of one. We fit all possible (128) regression models and calculated regression weights based on the corrected Akaike information criterion (AIC). For model m_j, the corrected AIC (*AICC*) is given by

$$AICC_j = -2 \log L\left(\hat{\beta}_j, \hat{\sigma}_j^2 | m_j, data\right) + 2k + \frac{2k(k+1)}{n-k-1},$$

where $L(\hat{\beta}_j, \hat{\sigma}_j^2 | m_j, data)$ is the likelihood calculated using the parameter estimates $\hat{\beta}_j$ and $\hat{\sigma}_j^2$, k is the number of parameters (i.e., k was set to the number of variables in the model plus 1 for the intercept and 1 for the variance) and n the number of

TABLE 2. Kendall correlations (τ) between vulnerability metrics and landscape variables. *P*-value and sample size are given below each correlation.

Variable	Average exposure, 2009	Average exposure, 2010	Median sensitivity, 2009	Median sensitivity, 2010
Area	0.294	0.317	0.331	0.195
	<0.0001	<0.0001	<0.0001	0.0117
	83	78	83	78
Maximum temperature	0.358	0.374	0.045	−0.094
	<0.0001	<0.0001	0.5447	0.2253
	83	78	83	78
Elevation	−0.376	−0.370	−0.082	0.140
	<0.0001	<0.0001	0.2725	0.0700
	83	78	83	78
Forest Corr	−0.204	−0.155	−0.292	−0.252
	0.0065	0.0463	0.0001	0.0012
	82	77	82	77
Canopy	−0.154	−0.145	−0.292	−0.271
	0.0401	0.0599	<0.0001	0.0005
	83	78	83	78
Mean BFI Corr	−0.138	−0.084	−0.174	0.159
	0.0683	0.2849	0.0217	0.0416
	82	77	82	77
Solar annual mean Corr	−0.256	−0.226	−0.076	0.230
	0.0007	0.0037	0.3148	0.0030
	82	77	82	77

observations. Each model was assigned a weight $w_j = \frac{\exp(-\frac{1}{2}\Delta_j)}{\sum_{j=1}^{R}\exp(-\frac{1}{2}\Delta_j)}$, where $\Delta_j = AICC_j - \min(AICC)$ compares the *AICC* for the *j*th model with the best model, and *R* is the number of models. Parameter estimates were averaged, i.e., the estimate of parameter associated with the *i*th variable is $\bar{\hat{\beta}}_i = \sum_{j=1}^{R} w_j \hat{\beta}_{ij}$. The estimated variance was calculated using the unconditional variance estimate, $v\hat{a}r(\bar{\hat{\beta}}_i) = \sum_{j=1}^{R} w_j[v\hat{a}r(\hat{\beta}_{ij}|m_j) + (\hat{\beta}_{ij} - \bar{\hat{\beta}}_i)^2]$. If a parameter was not included in a model, the estimate and estimated model variance were assigned a value of zero. For each variable, the weighted average estimate and a 95% confidence limit was calculated. A t-score was calculated as the average estimate divided by the estimated SD and used to indicate overall variable importance. Models developed using the 2009 data were used to predict exposure and sensitivity for the 272 sites that had known Brook Trout populations. The predicted values were calculated for each of the 128 models and the weighted-average predicted values calculated and graphed to display predictions for the sites according to categories of risk. Calculations were made using SAS (SAS 2000) and R (R Development Core Team 2009). In addition, ANOVA was used to compare exposure and sensitivity groups on landscape and other variables.

RESULTS

Because of dry stream channels, lost, stolen, or damaged thermographs, and other quality control or assurance issues, only 83 sites in 2009 (45 pour points, 38 centroids) and 78 sites in 2010 (37 pour points, 41 centroids) provided useable matched data. Combining both years, 62 sites (32 pour points, 31 centroids) had useable matched data for the time period of July 23–September 15 in both years. This sample size and time period was used for the majority of the analyses. Note that results reported for specific sites have site numbers prefaced by a letter C, P, or S. The letter "C" indicates a centroid site, "P" indicates a pour-point site, and "S" indicates general reference to the site (e.g., S0033 is a general reference to site 33, while C0033 refers to the centroid location). Temperatures in 2010 (mean air, 20.95°C; mean water, 19.50°C) were generally higher than in 2009 (mean air, 19.22°C; mean water, 18.22°C). The average (over sites) of the maximum air temperature, *DMAXA*, (over dates) in 2009 was 29.70°C. In 2010, *DMAXA* increased by 3.60°C to 33.30°C.

The strength and form of the relationships between *DMAXA* and *DMAXW* varied considerably among sites and between years. This variability was well illustrated by air–water temperature relationships for two sites (C0026 and P0084) for the 2 years of the study (Figure 1). Kernel-smoothed estimates of the air–water relationship varied from near linear to somewhat nonlinear estimated curves. Curves from one year to the next were considerably different in this example. In 2009, for example, the kernel fit was nearly linear for C0026 but was curvilinear in 2010. Also the slope (i.e., sensitivity) did not change much from 2009 to 2010 for P0084 but changed considerably for C0026.

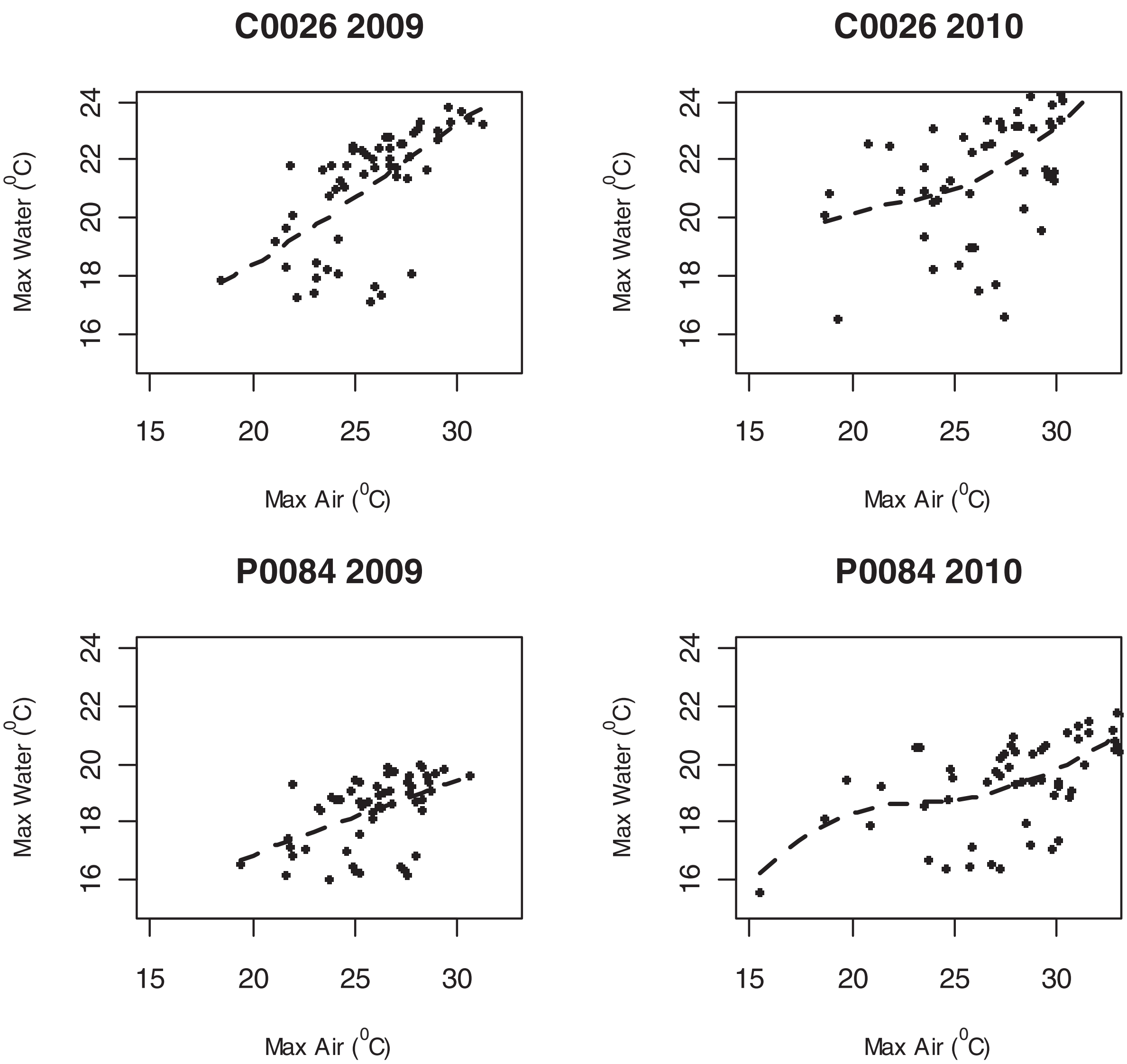

FIGURE 1. Relationship between daily maximum air temperature and daily maximum water temperature for two sites in 2009 and 2010. Kernel fit is given by the dashed line. Sites were chosen to display variation in the pattern of the kernel fits. For 2009 exposures were 0.54 and 0.27 and for 2010 were 0.64 and 0.29 for C0026 and P0084, respectively. For 2009 sensitivities were 0.49 and 0.26 and for 2010 were 0.30 and 0.27 for C0026 and P0084, respectively.

The data for 2010 for site C0026 shows more variation, and also in 2010 there were more dates with lower water temperatures for moderate to high air temperatures, resulting in shallower slopes over small intervals.

Sensitivity

The response of *DMAXW* to a 1°C increase in *DMAXA* had a median of 0.35°C among all sites and air temperature ranges in 2009. However, there was considerable variation in sensitivity, as a function of both temperature and site. For example, a 1°C increase in *DMAXA* from 16°C to 17°C averaged a 0.52°C increase in *DMAXW* but ranged from 0.13°C to 0.98°C depending on the sample site. A 1°C increase in *DMAXA* from 25°C to 26°C averaged (0.35°C) with a range of 0.10–0.82°C. While there was considerable variation within temperature range bins, median sensitivity tended to decrease at higher air temperatures. In 2010 (a much hotter and dryer year), the median sensitivity declined slightly to 0.31°C, but the between-year differences were not significant (paired t-test: $t = -1.090$, $P = 0.2765$; Wilcoxon signed-rank test: $S = -318$, $P = 0.0618$, $n = 70$). Site sensitivity ranks tended to be similar across the 2 years of the study, as evidenced by a significant positive correlation between 2009 and 2010 ranks. ($r = 0.51$, $P < 0.001$)

Exposure

Our exposure metrics also varied among sites and years. For example in 2009, at a threshold of 21°C, duration averaged 11.9 d (SD = 17.0; range, 0–55 d), frequency averaged

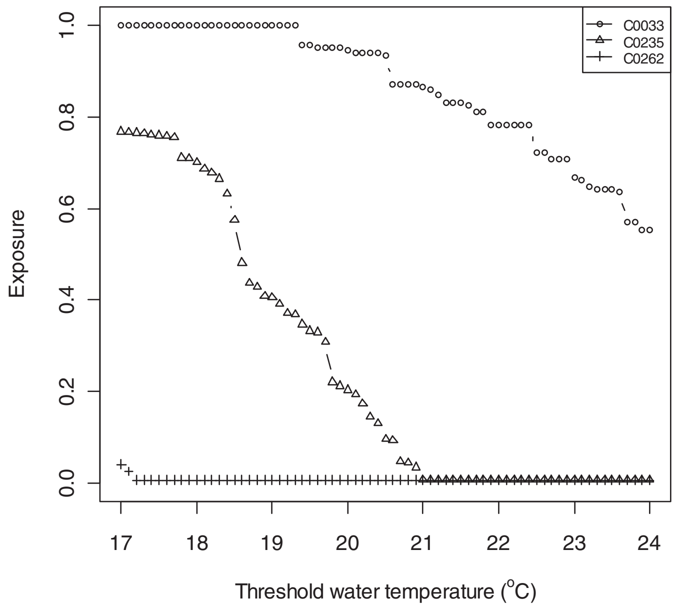

FIGURE 2. Exposure profiles for representative high (S033), medium (S0235), and low (S0262) exposure sites in 2009. Exposure scores integrate the frequency and duration of exposure for a given *DMAXW* (see text for detailed explanation of these metrics) and zero values indicate that a given *DMAXW* was never equaled or exceeded at the site.

29.1% (SD = 34.2%; range, 0.0–100.0%), and magnitude above 21°C averaged 1.84°C (SD = 2.46; range, 0.0–9.0°C). In 2010, a year when *DMAXA* was 3.5°C warmer, duration averaged 15.8 d (SD = 15.5; range, 0–55 d), frequency averaged 45.6% (SD = 31.5%; range, 0.0–100.0%), and magnitude above 21°C averaged 3.4°C (SD = 2.65°C; range, 0.00–9.0°C). As a result, the average exposure score (combination of duration, frequency, and magnitude) increased from 0.342 in 2009, to 0.489 in 2010. Exposure was significantly higher (paired t-test: $t = 11.24$, $P < 0.0001$; Wilcoxon signed-rank test: $S = 1{,}196$, $P < 0.0001$) in 2010 than 2009.

Profile plots for representative high (S0033), medium (S0235), and low (S0262) exposure sites illustrate some of the variability between sites (Figure 2). At site S0033, the water temperatures were high and thresholds below 19.5°C resulted in exposures of 1.0 indicating that *DMAXW* never dropped below the minimum threshold of 17°C in the summer, and there was high exposure (∼0.6) for at-or-above potentially lethal temperatures (24°C). In strong contrast, at site S0062, water temperature never exceeded 17.5°C and exposure was nearly zero for the temperature range of interest. However, in spite of considerable variation among year across sites and within years among sites, sites with relatively high or relatively low exposure in 2009 maintained their exposure ranks in 2010, as evidenced by a nearly complete correlation between 2009 and 2010 exposure values ($r = 0.94$, $P < 0.0001$)). Exposure was strongly correlated with sensitivity in 2009 ($r = 0.64$, $P < 0.0001$), but less so in 2010 ($r = 0.4$, $P < 0.004$).

Vulnerability Classifications and Determining Factors

Sensitivity and exposure scores for each site (both 2009 and 2010) were classified into one of four quadrants summarizing the different levels of high and low exposure and sensitivity (Figure 3). The classification cutoffs used were the median sensitivity and median exposure from 2009. In the case of exposure there is some biological justification for using the median, as roughly 50% of the profile plots have values above the median exposure at roughly 21°C in *DMAXW*, a water temperature value often used as a Brook Trout stress indicator. For most sites, exposure was greater in 2010 than in 2009, while sensitivity had both small increases and decreases (Figure 4). We used these classifications to represent predicted exposure and sensitivity for all 272 Brook Trout sites across Virginia (Figure 5).

Variation in exposure and sensitivity among sites was associated with landscape metrics (Table 2). Exposure in both years was positively correlated with watershed area and maximum air temperature, and negatively correlated with elevation and most of the solar insolation variables. The sensitivity measures were correlated negatively with percent forested riparian corridor and canopy cover, but weakly correlated with other metrics, with the exception of watershed area, which had a relatively strong positive correlation with sensitivity in 2009. Many of the correlations were consistent across years. Correspondingly, we found some support for models using landscape metrics to predict exposure and sensitivity (Table 3). In general, regression models for exposure had stronger relationships with the landscape variables than did the sensitivity models. The models for exposure were also consistent in 2009 and 2010 with the main difference being in the intercepts. Model-averaging results indicated that a variety of models gave similar results in terms of *AICC* and R^2 although there were some consistent variables (Table 3). Area and elevation dominated the exposure models, with forest corridor and canopy variables being moderately important. The best models (using *AICC*) had area, elevation, and forest corridor or canopy, and had R^2 values around 0.55. The models for sensitivity were not as strong as those for exposure and were dominated by area. The R^2 values were mostly below 0.45 in 2009 and 0.35 in 2010. Also, mean BFI tended to be important along with canopy and forest corridor. The solar variable was important to a lesser extent.

Model validation (using 2009 models to predict 2010 values) yielded mixed results. The exposure regression correctly classified 75% of the sites, and the sensitivity regression correctly classified 65% of the sites. When the categories were combined to produce the four classes defined in Figure 4, the correct prediction rate for the 2010 data based on the 2009 models was 46%. Predictions were good for the HE/HS group but poor for the HE/LS group, while other groups had small sample sizes. Kendall correlations indicated that the predictions for exposure tended to be reasonable ($\tau = 0.44$) for predicting the 2010 data using the 2009 model, but poor for sensitivity ($\tau = 0.17$). For exposure this suggests that the change from 2009 to 2010 was large but consistent. For sensitivity, the change was highly

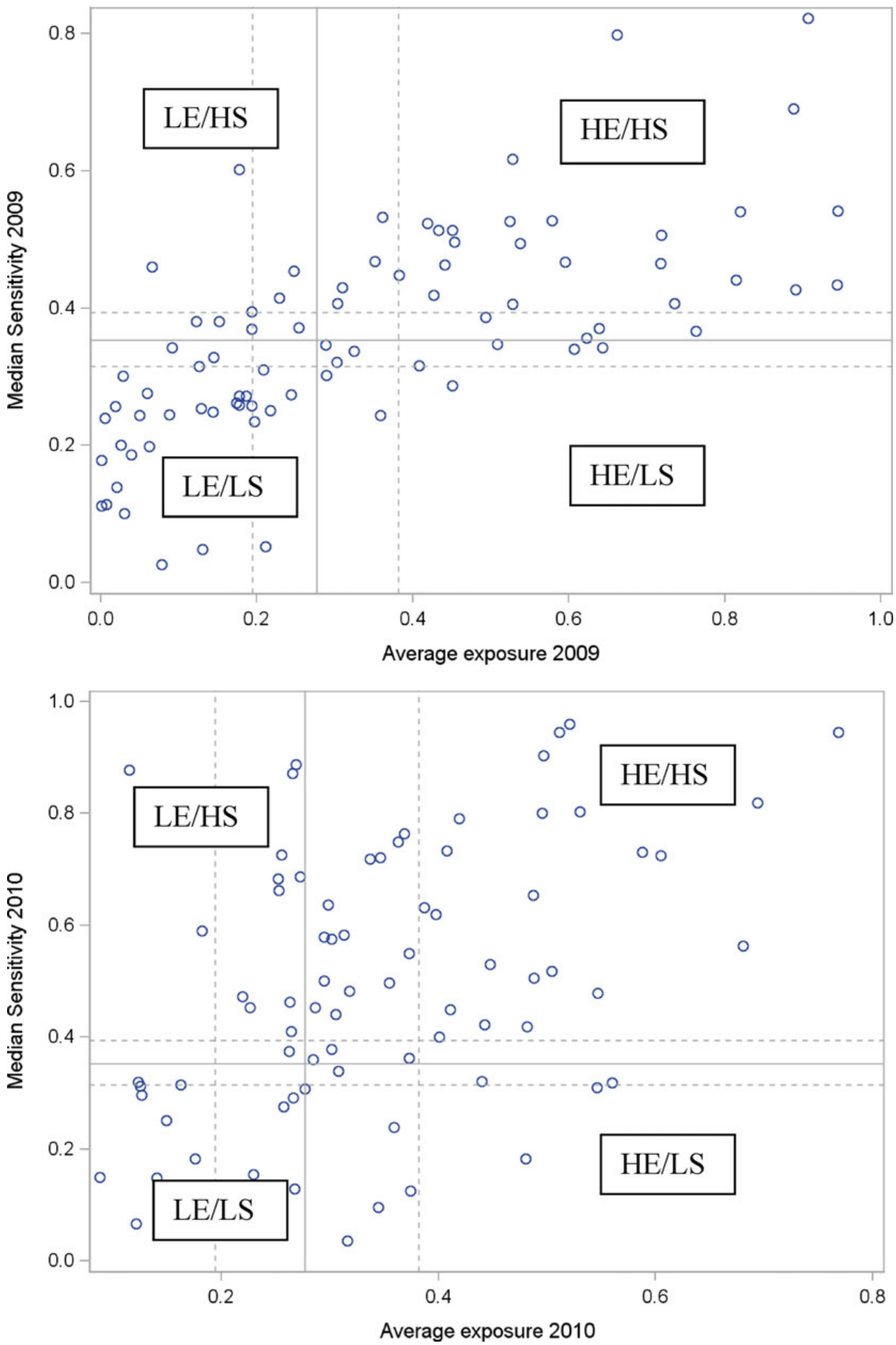

FIGURE 3. Plot of sensitivity and exposure for 2009 and 2010. Vertical and horizontal lines are at the median of values for 2009 along with upper and low bootstrap 95% confidence limits. HE/HS = high exposure–high sensitivity, HE/LS = high exposure–low sensitivity, LE/HS = low exposure–high sensitivity, LE/LS = low exposure–low sensitivity.

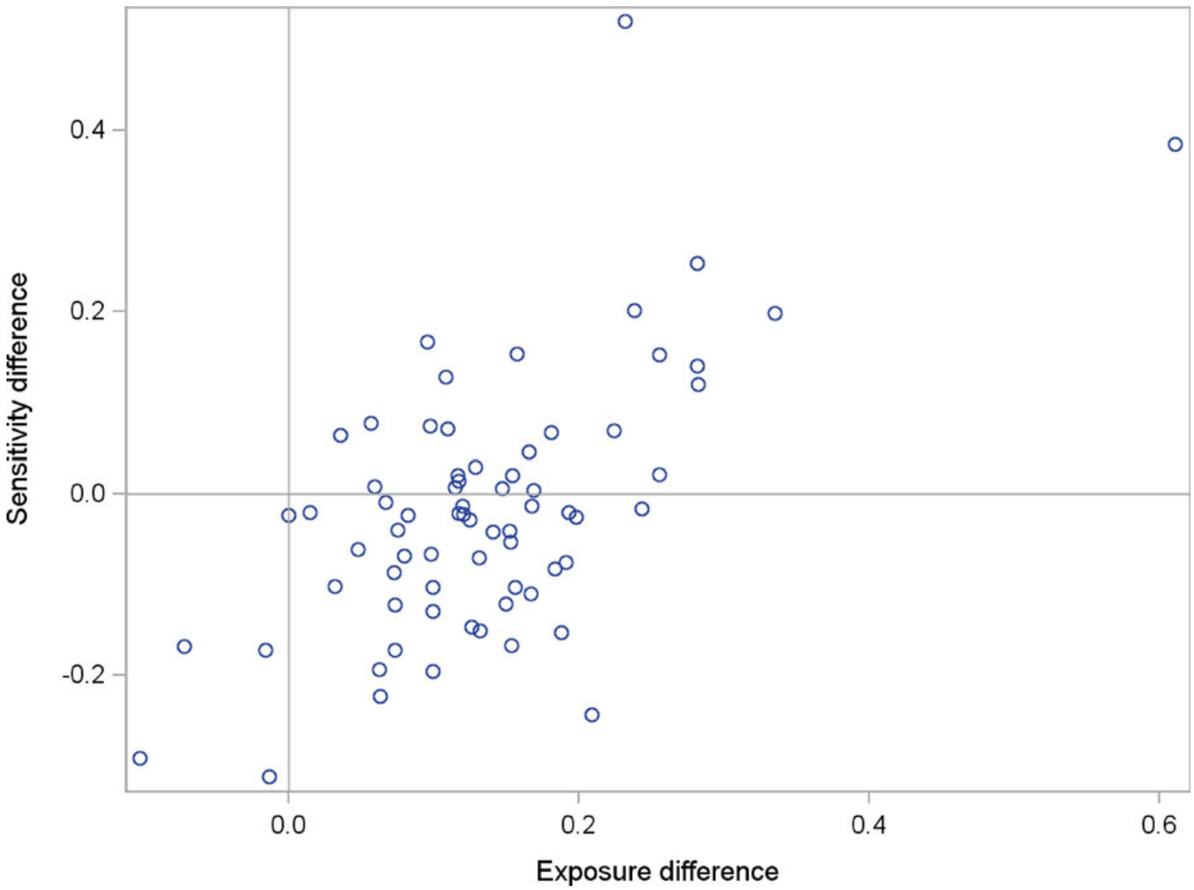

FIGURE 4. Differences (2010 values minus 2009 values) in sensitivity and exposure across the study sites. Data points to the right of the vertical line are sites with greater exposure in 2010, and data points above the horizontal line are sites with greater sensitivity in 2010.

variable, so that while the average did not change much, the numerical values did, indicating that the patterns for individual sites changed from year to year.

DISCUSSION

Direct measurements of paired summer air and water temperatures revealed substantial heterogeneity in thermal characteristics that are directly relevant to the potential persistence of Brook Trout and other coldwater-dependent species. In contrast to larger-scale models that assume simple relationships between air and water temperature, the direct measurement approach was able to identify Brook Trout habitats that are likely to be either relatively resistant (low sensitivity, low exposure) or particularly vulnerable (high sensitivity, high exposure) to temperature change (Figure 3). Further, we were able to identify some of the landscape and local-scale factors associated with among-site variation in vulnerability to increased air temperatures, although much of this variability remained unexplained. This information will aid management and conservation organizations to appropriately target their efforts to sites most likely to maintain suitable thermal habitat, as well as targeting habitat management efforts to increase temperature regime resilience in sensitive sites. More generally, this approach will, in combination with other determinants of resilience (e.g., habitat area, habitat connectivity, population size, and genetic diversity), yield more detailed predictions of the potential future distribution of Brook Trout in Virginia, and is applicable to habitats at the southern edge of the Brook Trout distribution. We also believe that this approach can help form the basis of a simple, cost-effective monitoring and assessment protocol for coldwater stream habitats.

Appropriate thermal habitat represents a primary constraint on the distribution and abundance of Brook Trout and other coldwater fishes (Rahel et al. 1996; Mohseni et al. 2003; Flebbe et al. 2006). Although climate change effects other than air temperature (e.g., rainfall, floods, droughts, changes in land cover, spawning times, invasive species) are important (Wenger et al. 2011), the low predictability of these metrics (both in magnitude and direction) at this time make it difficult for managers to incorporate this information into the decision-making process. Predictions of increasing air temperatures have the highest reliability (Solomon et al. 2007) and we believe that these increases pose the greatest threat to the current distribution of

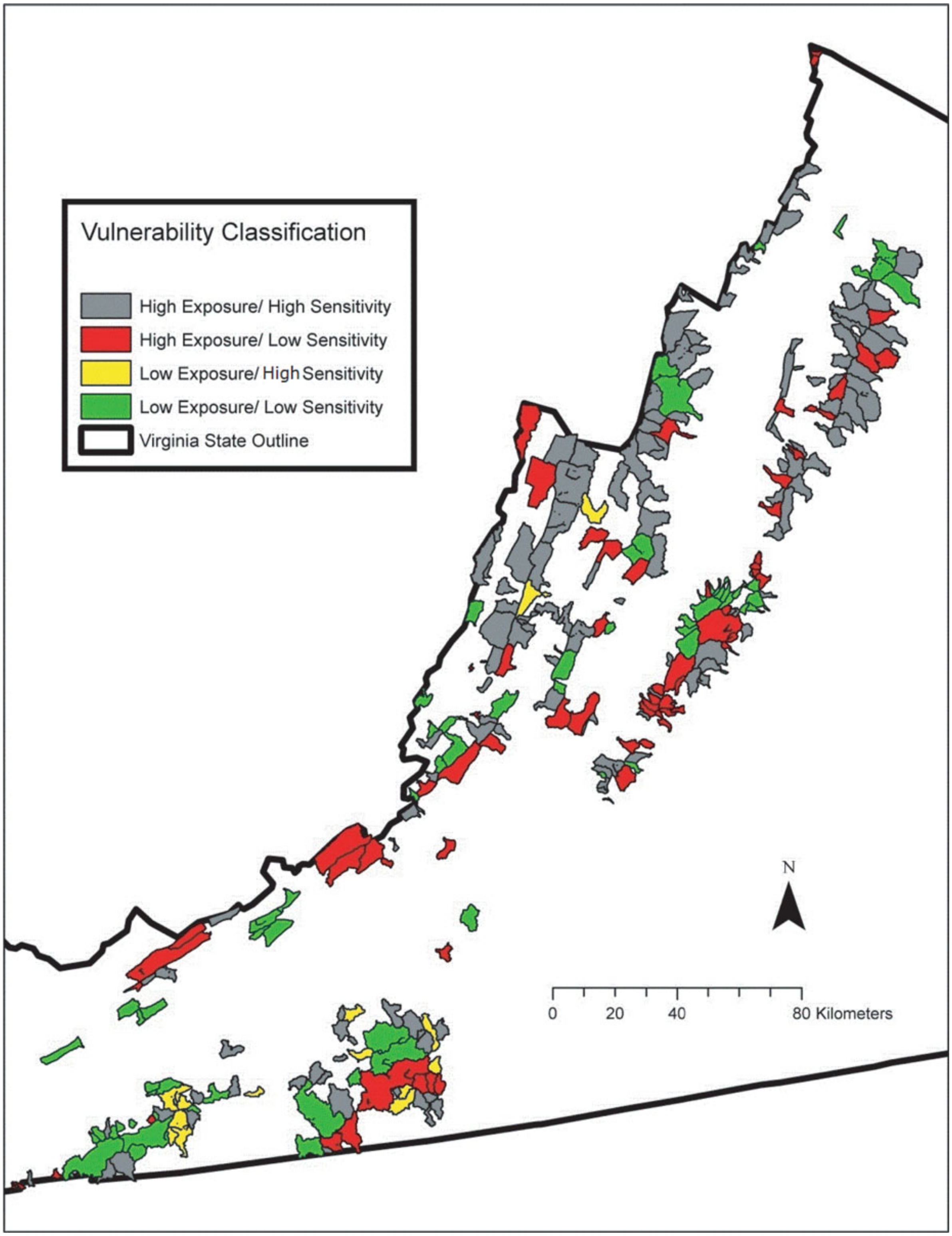

FIGURE 5. Predicted exposure–sensitivity categories for Brook Trout patches in Virginia. Gray = high exposure–high sensitivity, red = high exposure–low sensitivity sites, yellow = low exposure–high sensitivity, green = low exposure–low sensitivity sites.

TABLE 3. Summary of model averaging for exposure and sensitivity for 2009 and 2010. The estimate is the average weighted coefficient, lower and upper are the lower and upper 95% CI limits, and t-score is the average estimate divided by the SD. Three locations were removed to meet modeling assumptions.

Model term	Estimate	Variance	Lower	Upper	t-score
Exposure 2009					
Intercept	0.310	0.000	0.271	0.349	15.595
larea	0.098	0.000	0.055	0.141	4.480
Maxtemp	0.021	0.002	−0.068	0.110	0.467
Elev	−0.123	0.003	−0.229	−0.017	−2.282
Forest_Corr	−0.030	0.001	−0.099	0.038	−0.875
Canopy	−0.034	0.001	−0.102	0.035	−0.962
Mean_BFI_Corr	−0.003	0.000	−0.037	0.030	−0.201
Solar_ann_mean_Corr	0.008	0.001	−0.039	0.055	0.352
Exposure 2010					
Intercept	0.465	0.000	0.427	0.503	23.812
larea	0.091	0.000	0.047	0.134	4.104
Maxtemp	0.036	0.003	−0.070	0.142	0.671
Elev	−0.107	0.005	−0.240	0.027	−1.568
Forest_Corr	−0.026	0.001	−0.087	0.036	−0.824
Canopy	−0.026	0.001	−0.089	0.036	−0.830
Mean_BFI_Corr	−0.001	0.000	−0.029	0.027	−0.069
Solar_ann_mean_Corr	0.021	0.001	−0.044	0.087	0.638
Sensitivity 2009					
Intercept	0.340	0.000	0.315	0.366	26.116
larea	0.050	0.000	0.021	0.079	3.409
Maxtemp	0.002	0.000	−0.030	0.035	0.143
Elev	−0.001	0.000	−0.044	0.043	−0.036
Forest_Corr	−0.020	0.001	−0.072	0.031	−0.779
Canopy	−0.042	0.001	−0.095	0.011	−1.558
Mean_BFI_Corr	−0.032	0.000	−0.060	−0.004	−2.219
Solar_ann_mean_Corr	−0.001	0.000	−0.029	0.027	−0.067
Sensitivity 2010					
Intercept	0.338	0.000	0.311	0.364	24.663
larea	0.042	0.000	0.008	0.076	2.419
Maxtemp	0.015	0.001	−0.045	0.074	0.482
Elev	0.033	0.002	−0.047	0.112	0.806
Forest_Corr	−0.019	0.000	−0.062	0.023	−0.901
Canopy	−0.016	0.000	−0.057	0.026	−0.731
Mean_BFI_Corr	0.006	0.000	−0.019	0.031	0.488
Solar_ann_mean_Corr	0.017	0.001	−0.028	0.062	0.722

Brook Trout. While fish are influenced by multiple aspects of temperature regimes, we focused on maximum daily air and water temperature (*DMAXW*) as it represents a straightforward expression of potential thermal limits that is relatively easy to standardize across management and monitoring agencies. Further, we tested the use of a longer time interval (3-d maximum) and found no substantial improvements in model fits or changes in relative exposure and sensitivity among sites. Daily maximum air temperature fluctuations have the highest probability of occurrence in the event of a climate change scenario making *DMAXA* and *DMAXW* parameters useful in determining water temperature response to air temperature fluctuation. Using a threshold temperature approach for exposure also allows for evaluating a site and comparing sites based on a profile model. Our sensitivity and exposure metrics calculated using *DMAXA* and *DMAXW* provide a first-pass estimate of the likelihood of Brook Trout habitat persisting under a warming regional climate in Virginia. At the same time, we acknowledge that negative effects on population vital rates and population persistence are likely to begin at temperatures well below thermal distributional limits. In our study, daily maximum temperatures were strongly correlated with other aspects of the thermal regime (daily means and medians) suggesting that sites vulnerable to high maximum temperatures may also be vulnerable to sublethal effects. Finally, daily maxima are likely to be particularly important for southern populations of Brook Trout, which are currently distributed in small isolated patches with very low effective population sizes (Whiteley et al. 2013). In such small, fragmented populations, the loss of even a small number of individuals as a result of extreme temperatures may have significant consequences to population persistence.

Our sites varied considerably with respect to both the form and the strength of the relationship between daily maximum air and daily maximum water temperature. While logistic models have been suggested by previous studies (Mohseni and Stefan 1999), they proved to be largely inappropriate for our data, likely because our study was limited to the summer season. At the same time, linear models failed to adequately represent the air–water temperature relationship for many of our study sites. In the absence of detailed site-specific hydrologic information, nonlinear models provided the flexibility necessary to capture these empirical relationships across a wide range of sites, and consistently provided better fits to the data.

The summer of 2010 was markedly warmer than that of 2009 ($>2^\circ$C average air temperature, $>3.5^\circ$C *DMAXA*) and was associated with a larger percentage of our study sites experiencing higher levels of exposure to warm stream temperatures. Such interannual variation in weather conditions can give an early idea of the effects of a warming regional climate on the distribution and suitability of coldwater stream habitat. However, while overall exposure across sites differed between years, site rankings were highly consistent across years ($r = 0.94$). These results suggest that in a relatively few sampling years, habitat managers could obtain a fairly robust assessment of which sites are most likely to maintain appropriate thermal habitat under warm summer conditions. In contrast, while overall across-site sensitivity was not significantly different between years, site sensitivity ranks were substantially less consistent than exposure ranks (between-year correlation, $r = 0.5$). Hydrologic regime may have a strong influence on the air–water temperature relationship, and between-year differences in sensitivity within sites may reflect annual or seasonal hydrology. We were surprised to see the median sensitivity decrease in 2010. We hypothesize that in 2009 many sites had a much lower percentage of groundwater relative to surface water in the stream flow. In 2010, many sites were likely nearly 100% groundwater and very resistant to increases in air temperature (low sensitivity). Clearly additional investigation is required to better understand the factors associated with year-to-year variability in sensitivity and it may take additional monitoring (i.e., long-term data sets) to adequately estimate site-specific air–water temperature relationships. At the same time, longer time series of paired air–water temperatures across many sites may ultimately provide the most effective and relevant assessment of variation among sites in vulnerability to this aspect of regional climate change.

We had mixed success in predicting the exposure and sensitivity of Brook Trout habitats from GIS-based landscape and local-scale attributes. As expected, smaller, higher-elevation watersheds tended to be somewhat less sensitive and have lower exposure scores, reinforcing the potential importance of headwater habitats as thermal refugia. In addition, solar gain corrected for canopy cover appeared to significantly reduce sensitivity and exposure. This observation suggests that managers will be able to improve thermal habitat resilience by using GIS coverages to identify areas of low canopy cover and restore riparian shade. However, models failed to explain much of the variation in sensitivity and exposure among sites, had relatively low predictive power across years, and were much more successful in predicting some vulnerability categories (HE/HS) than others. For this reason, we underscore that our map of relative vulnerabilities based on predicted values (Figure 5) be considered an example of how this approach might work as opposed to an actual basis for prioritization, which we suggest should best be approached with direct measurement. Among-site differences in groundwater influence are likely responsible for a large part of this unexplained variation and it may be possible to account for this variation with long-term data sets. In contrast to the Upper Midwest ecoregion, where groundwater influence and thermal habitat suitability for coldwater species appears to be highly predictable from aspects of catchment geology that are readily obtainable (Wang et al. 2003), groundwater influence is much less predictable at the catchment scale (1–10 km^2) throughout most of the eastern range of Brook Trout. While our models utilized a relatively short-term, paired air–water temperature data set, long-term temperature data to accurately capture annual variability among years in metrics such as groundwater influence is important for model accuracy and relating site-specific responses to regional climate fluctuations. We therefore recommend direct site-specific measurements of sensitivity and exposure because the costs are generally low and decreasing (specifically the cost of thermographs and field time to launch the apparatus and download data). At the same time, we acknowledge that monitoring, assessment, and prioritization of coldwater habitats in the southern Appalachian region may benefit greatly from improvements in landscape-based models, which will in turn require a robust network of directly measured air and water temperatures.

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