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Article in *Wiley Interdisciplinary Reviews Water* · May 2014

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# Applications of spatial statistical network models to stream data

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Streams and rivers host a significant portion of Earth's biodiversity and provide important ecosystem services for human populations. Accurate information regarding the status and trends of stream resources is vital for their effective conservation and management. Most statistical techniques applied to data measured on stream networks were developed for terrestrial applications and are not optimized for streams. A new class of spatial statistical model, based on valid covariance structures for stream networks, can be used with many common types of stream data (e.g., water quality attributes, habitat conditions, biological surveys) through application of appropriate distributions (e.g., Gaussian, binomial, Poisson). The spatial statistical network models account for spatial autocorrelation (i.e., nonindependence) among measurements, which allows their application to databases with clustered measurement locations. Large amounts of stream data exist in many areas where spatial statistical analyses could be used to develop novel insights, improve predictions at unsampled sites, and aid in the design of efficient monitoring strategies at relatively low cost. We review the topic of spatial autocorrelation and its effects on statistical inference, demonstrate the use of spatial statistics with stream datasets relevant to common research and management questions, and discuss additional applications and development potential for spatial statistics on stream networks. Free software for implementing the spatial statistical network models has been developed that enables custom applications with many stream databases. © 2014 Wiley Periodicals, Inc.

## How to cite this article:

*WIREs Water* 2014. doi: 10.1002/wat2.1023

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## INTRODUCTION

Reliable scientific information is needed for streams and rivers because they host a disproportionate amount of the Earth's biodiversity<sup>1,2</sup> and provide important ecosystem services for human populations.<sup>3</sup>

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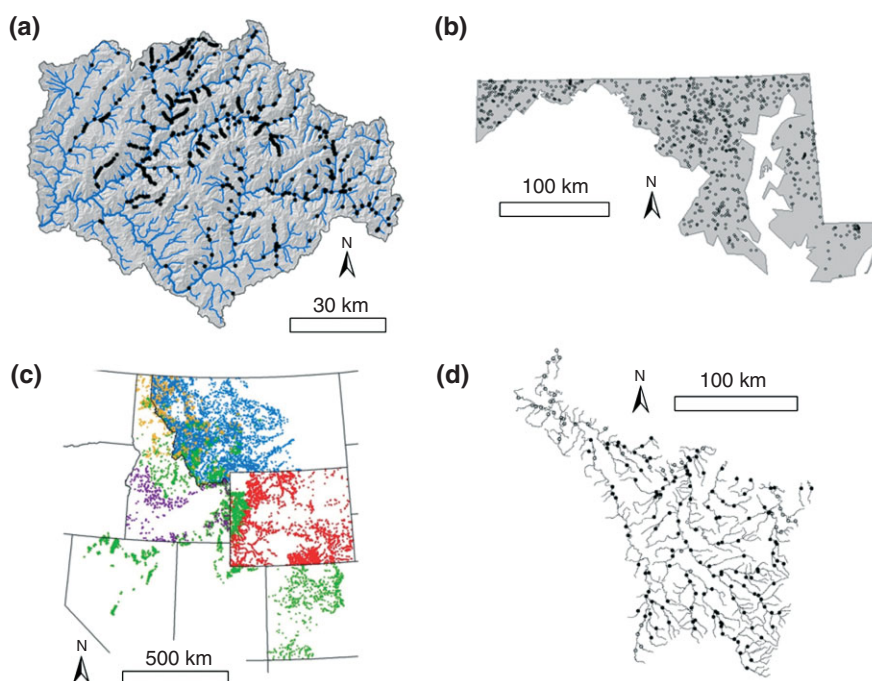
Conflict of interest: The authors have declared no conflicts of interest for this article.

That need will continue to grow as streams experience ongoing pressure from human development and climate change,<sup>4,5</sup> even as budgets for research, conservation, and management of aquatic resources remain limited. Doing more with less will be an ongoing theme, and developing better information for decision making is key to efficiency. One attractive option is simply developing new information from existing databases because it obviates the expenses associated with collecting new data. Advances in remote sensing, bioinformatics, computation, and data storage have dramatically increased the amount of stream data in recent decades<sup>6,7</sup> and large databases now exist in many areas that could be profitably mined (Figure 1). As data densities increase, however, measurement locations occur closer in space, the assumption in classical statistics of independence among observations may be violated, and poor parameter estimation and statistical inference could result.<sup>12</sup>

Classical statistical analyses were developed in the early 20th century to provide probabilistic inference on population parameters (e.g., means, totals, proportions) in study systems where the spatial arrangement of measurements was not important.<sup>13</sup> In field settings where spatial gradients sometimes caused parameter bias, stratified random sampling designs were developed to control for the nuisance variation caused by spatial effects.<sup>14</sup> It was later recognized

that space serves a vital role in structuring natural systems that is important to understand, which led to the development of spatial statistics and spatial ecology.<sup>15,16</sup> Spatial analyses accommodate, and often benefit from, nonindependence among observations and now provide an important inferential toolbox for research and management in terrestrial ecosystems.<sup>17</sup> The above considerations are equally relevant to data measured on stream networks,<sup>18</sup> but these systems have received much less attention than terrestrial systems. As a result, statistical techniques are usually developed for the latter and are only later adopted for use with streams. However, streams are fundamentally different from their terrestrial counterparts because they consist of directed networks that channel flows of energy, materials, and information through narrow corridors within terrestrial landscapes.<sup>19,20</sup> Statistical techniques need to account for those properties if they are to be optimized for stream data.

Theory for a generalizable class of spatial stream-network model (SSNM) has recently been developed on the basis of valid covariance structures for stream networks.<sup>21,22</sup> Those covariance structures account for the unique properties of stream networks such as a branching structure, directed flow, longitudinal connectivity, and abrupt changes near tributary confluences.<sup>23</sup> SSNMs can be used



**FIGURE 1** | Example databases with spatially clustered measurements that could be modeled using spatial statistical techniques. Stream temperature measurements from the Boise River in central Idaho (a; Source: Ref 8), water quality measurements across Maryland (b; Source: Ref 9), fish sampling locations across the western U.S. (c; modified Source: Ref 10), and (d) nitrate measurements from the Meuse River in France (Source: Ref 11).

with most types of stream survey data (e.g., water chemistries, habitat conditions, biological attributes) through application of several statistical distributions (e.g., Gaussian, binomial, Poisson). The use of SSNMs is growing<sup>8,9,11,24–29</sup> and free software has been developed that makes custom implementation of the models possible with many databases.<sup>30,31</sup> Because SSNMs have gone rapidly from theory to application, however, relatively few researchers are aware of their existence, and fewer yet have received formal training in their application or understand their potential. In areas where significant stream databases already exist, application of the spatial models may provide novel insights, increased predictive accuracy, better parameter estimates, and facilitate the development of new information at relatively low cost. In areas where less stream data exist, the SSNMs and associated simulation techniques can be used to develop sampling strategies that are optimized for different purposes on stream networks,<sup>32,33</sup> and which sometimes differ from current design recommendations that are influenced by a legacy of development for terrestrial systems.

In this paper, we briefly review the topic of spatial autocorrelation (i.e., nonindependence among observations) and its effect on statistical inference, and provide examples demonstrating how inference may be improved through application of the SSNMs to common datasets and research questions. The goal is not an in-depth treatment of any one topic but to provide interested readers with a sense of the possibilities and to identify resources for pursuing these possibilities in more detail. Unless otherwise noted, all subsequent analyses were performed using the SSN package<sup>31,34</sup> for R<sup>35</sup> and data preprocessing occurred in ArcGIS using two custom toolsets; STARS (Spatial Tools for the Analysis of River Systems)<sup>30</sup> and FLoWS (Functional Linkages of Watersheds and Streams).<sup>36</sup> Data and scripts for running similar analyses are contained in the SSN package and available at the SSN/STARS website.<sup>34</sup>

## WHAT IS SPATIAL AUTOCORRELATION AND WHY DOES IT MATTER?

Spatial autocorrelation is the tendency for measurements of an attribute to show a pattern of similarity relative to the distance separating them. Most frequently, closer measurements are more similar, which is referred to as positive autocorrelation. Mechanisms causing positive autocorrelation in streams could include local habitat similarities that result in high fish densities in adjacent pools<sup>37</sup> or turbulent stream flows

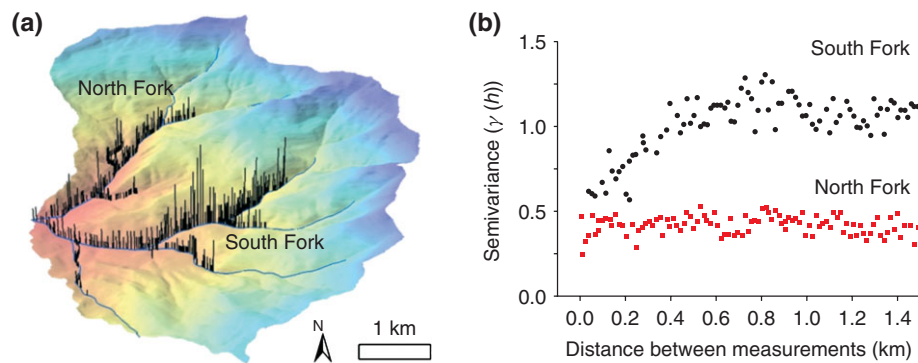
mixing water chemistries to create similar values over the span of several kilometers.<sup>25,26</sup> In fewer instances, negative autocorrelation occurs wherein greater dissimilarity exists among nearby measurements. A territorial fish, for example, excludes others from its immediate vicinity and causes negative spatial correlations at certain distances. Directly measuring or modeling the factors that cause those spatial patterns is desirable but often difficult or impossible, so methods that address spatial autocorrelation provide a useful means of estimation in many instances.

There are several ways to describe and visualize spatial autocorrelation<sup>17</sup> but the semivariance is one of the most common. Semivariance is the average variation between measurement values separated by some intervening distance<sup>38</sup> and has the following empirical estimator:

$$\gamma(h) = 0.5 \frac{1}{N(h)} \sum_{||x_i - x_j|| \in c(h)} [z(x_i) - z(x_j)]^2, \quad (1)$$

Where,  $\gamma(h)$  is the semivariance for distance lag  $h$ ,  $N(h)$  is the number of data pairs  $(x_i, x_j)$  separated by the distance  $h$ ,  $||x_i - x_j||$  is the distance between locations  $x_i$  and  $x_j$ ,  $c(h)$  is the interval around  $h$  (chosen to be mutually exclusive and exhaustive so that all distances  $h$  fall into one interval), and  $z(x_i)$  is the data value at location  $x_i$ . A plot of semivariance values relative to distance is called a semivariogram. When no spatial autocorrelation occurs in a set of measurements, a semivariogram shows no trend (Figure 2). If positive autocorrelation is present, however, the semivariance values are small near the origin and increase at greater distances.<sup>16</sup> When nonzero semivariances occur at the shortest distances, it represents spatial variation at resolutions smaller than the finest sampling grain and measurement errors, and is referred to as the ‘nugget effect’.<sup>18,38</sup> In some cases, semivariance values reach an asymptote—known as the ‘sill’, which represents the variance, or dissimilarity, in uncorrelated data. The distance where the sill is reached is called the ‘range’, and it indicates how quickly spatial autocorrelation decays with distance. At distances greater than the range, measurements are considered to be uncorrelated and no longer contain redundant information. Semivariograms developed for fish counts from two adjacent streams clearly show many of these characteristics, including the absence of spatial autocorrelation as indicated by the lack of a trend in one stream (Figure 2).<sup>19</sup>

Classical statistical techniques assume that each measurement is independent from others and contains non-redundant information. If measurements are spatially autocorrelated, however, then redundancy



**FIGURE 2** | Counts of cutthroat trout in habitat units along two forks of Hinkle Creek in western Oregon (a; Source: Ref 19). Semivariograms calculated from counts in the South Fork (black dots) show evidence of spatial autocorrelation, but there is no evidence of autocorrelation in the North Fork (b; red dots).

exists and the database contains less information than the number of measurements implies. Failure to account for this redundancy means that tests of statistical significance are too liberal and type I errors will occur more frequently than the specified  $\alpha$ -level because standard error estimates are artificially small.<sup>12,39</sup> Parameter estimates may also be biased because measurements are spatially clustered and over- or under-represent conditions in some areas. Because of the challenges that autocorrelation poses, classical experimental design techniques and environmental monitoring programs go to some length to randomize measurements and allocate samples in a spatially balanced manner.<sup>40</sup> But in many field studies, or where databases have been aggregated from multiple sources, site selection is not possible or is difficult to implement at scales large enough to minimize autocorrelation. A stream researcher may then either ignore spatial autocorrelation or dismiss it as unimportant, but this may discard important information about stream attributes and decrease the accuracy and validity of statistical inferences. A better choice is to use models that accommodate spatial autocorrelation.

## A COVARIANCE STRUCTURE FOR STREAM DATA

A spatial statistical model is simply an extension of the basic linear model that is commonly used in ecological studies. The linear model has the form  $y = \beta X + \epsilon$ , where the dimension of the response variable  $y$ , is an  $n \times 1$  vector, and where  $n$  represents the total number of observations. The relationship between the response variable and predictors is modeled through the design matrix  $X$  and parameters  $\beta$ . The linear model is considered nonspatial because one of its main assumptions is that the random errors,  $\epsilon$ , are

**TABLE 1** | Example Covariance Matrices for Nonspatial Statistical Model and Spatial Statistical Model

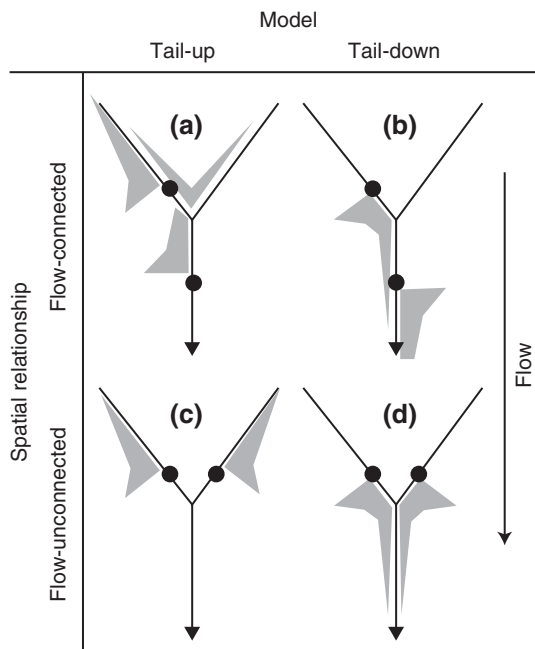
	Nonspatial Model Covariance			Spatial Model Covariance		
Site	1	2	3	1	2	3
1	$\sigma_{11}$	0	0	$\sigma_{11}$	$\sigma_{12}$	$\sigma_{13}$
2	0	$\sigma_{22}$	0	$\sigma_{21}$	$\sigma_{22}$	$\sigma_{23}$
3	0	0	$\sigma_{33}$	$\sigma_{31}$	$\sigma_{32}$	$\sigma_{33}$

The assumption in the nonspatial model is that measurements are independent and off-diagonal elements in the matrix are set to zero. A spatial statistical model makes no such assumption and instead estimates the covariance between pairs of measurements based on spatial distance relationships described with autocovariance functions.

independent, and so the variance of  $\epsilon$  ( $\text{var}(\epsilon)$ ) is equal to  $\sigma^2 \mathbf{I}$ , where  $\mathbf{I}$  is the  $n \times n$  identity matrix. In a spatial statistical model, the independence assumption is relaxed and values are allowed to be correlated, so  $\text{var}(\epsilon) = \Sigma$  (Table 1). The general formulation of the covariance matrix  $\Sigma$  has too many parameters to estimate, so the nugget, sill, and range parameters are estimated in an autocovariance function to describe the spatial relationships among elements in  $\Sigma$ . That provides a means of estimating the covariance between any two sets of locations and reduces the number of parameter estimates for  $\Sigma$  to 3 from  $n(n+1)/2$ .

In traditional spatial statistics, distance is measured in Euclidean space, which is the straight-line distance between two sites. When working with stream networks, however, it may be more appropriate to use along-channel distance to model autocovariance because movements of aquatic organisms and the transport of materials are often constrained to the network.<sup>19,20</sup> Along-channel distance can be treated symmetrically as the network distance between two sites<sup>19</sup> but depending on the type of data, important distinctions may exist between sites





**FIGURE 3** | Flow-connected (a and b) and flow-unconnected (c and d) spatial relationships on a stream network (Source: Ref 23). Moving-average functions for tail-up (a and c) and tail-down (b and d) relationships are shown in gray. Note that tail-up models restrict autocorrelation to flow-connected locations, whereas tail-down models permit correlation between flow-connected and flow-unconnected locations.

with flow-connected spatial relationships and those that are flow-unconnected. Sites are considered flow-connected if water from an upstream site flows past a downstream site (Figure 3(a) and (b)). Sites are considered flow-unconnected if some upstream movement would be required to facilitate a connection (Figure 3(c) and (d)). Flow-connected relationships may be useful for stream attributes characterized by passive downstream diffusion such as water chemistry, sediment, or temperature. Biological entities such as fish or macroinvertebrates that may move both downstream and upstream may be better represented by flow-unconnected relationships, or a combination of flow-unconnected and connected spatial relationships (discussed below).

Two classes of autocovariance functions have been developed to represent spatial relationships in streams; tail-up models and tail-down models.<sup>23,41</sup> The models are based on moving-average (MA) constructions and assume that the stream network is dendritic and not braided. In the tail-up models, the MA function points in the upstream direction and correlation is only permitted between flow-connected sites (Figure 3(a) and (c)). Spatial weights are used to split the tail-up MA function at confluences based on flow volume, watershed area, or other relevant

attributes, which allows tributary influences on downstream conditions to be accurately represented. In a tail-down model, the MA function points in the downstream direction and correlation is permitted between both flow-connected and flow-unconnected sites (Figure 3(b) and (d)). Several models may be used to represent tail-up or tail-down autocovariance functions, including the linear-with-sill, Mariah, exponential, Epanechnikov, and spherical models.<sup>11,41</sup> An autocovariance function can be chosen based on the properties of a stream attribute or using model selection techniques.<sup>11</sup> Spatial statistical models are generally robust against mis-specifying the autocovariance function<sup>42–44</sup> although the topic has not been directly addressed for SSNMs.

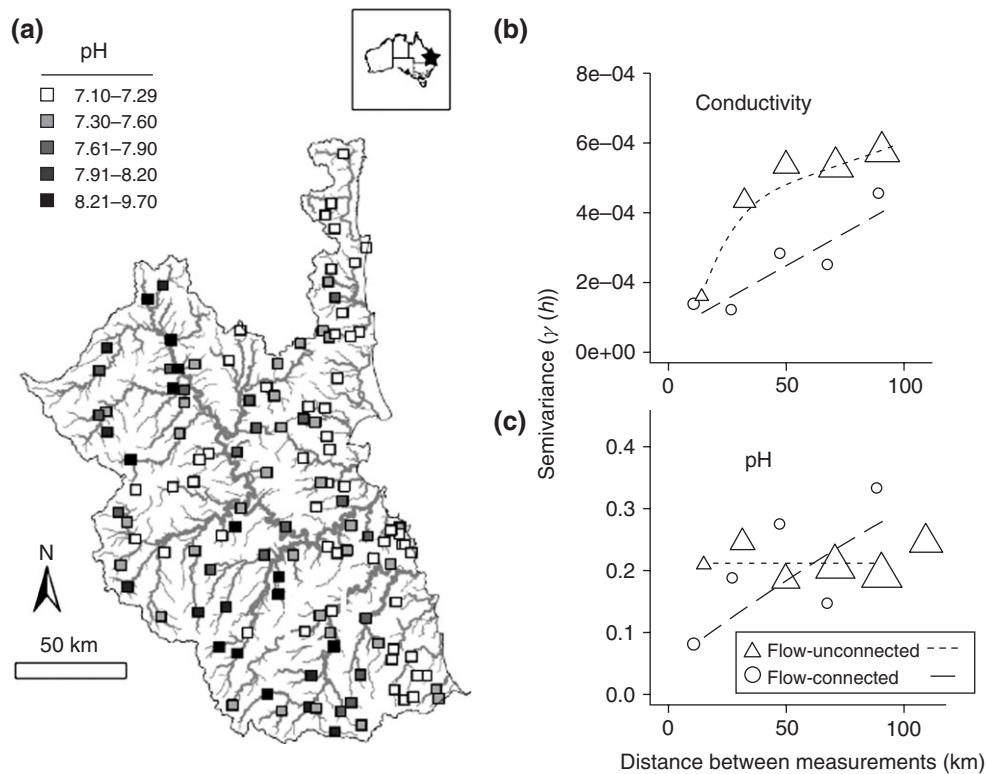
Autocovariance functions based on stream distance and network topology are useful in most instances, but spatial patterns in stream data can also be caused by linkages with the terrestrial landscape and atmosphere.<sup>20</sup> As a result, factors associated with climate, geology or landcover may be better represented by Euclidean distance and several functions are available for this.<sup>45</sup> Of particular note, autocovariance functions may be combined (e.g., flow-connected and Euclidean relationships) within a mixed model using a variance component approach that weights the contribution of each function to the overall variation.<sup>23,41</sup> That produces a flexible covariance structure which simultaneously accounts for many types of spatial relationships and avoids the need to choose a specific function.

## DESCRIPTION, ESTIMATION, AND PREDICTION ON STREAM NETWORKS

### The Torgegram: A Semivariogram for Data on Stream Networks

As described previously, the semivariogram is a useful tool for exploring and describing spatial patterns in data.<sup>46</sup> For example, counts of cutthroat trout (*Oncorhynchus clarki*) along two forks of Hinkle Creek in Oregon showed clear spatial patterns when described by semivariograms (Figure 2(b)). Cutthroat trout in the South Fork were correlated to a range of ~0.5 km and exhibited large overall spatial variation (large sill value). That contrasts to counts on the North Fork, which were less variable and had no clearly discernible range. Those patterns probably reflect some aspects of the habitats in the two forks, which could form the basis for more detailed investigations to understand the relevant processes.<sup>47</sup>

As useful as conventional semivariograms are, they may obscure important spatial relationships in



**FIGURE 4** | Torgegrams for electrical conductivity (b) and pH (c) developed from water quality measurements across a stream network in southeast Queensland, Australia (a) Symbol sizes are proportional to the number of data pairs averaged for each value. (Reprinted with permission from Ref 41. Copyright 2010 American Statistical Association)

streams due to differences in flow connectivity, so the Torgegram was developed specifically for visualizing spatial patterns in stream data.<sup>20,31</sup> A Torgegram splits semivariances into categories based on flow-connected and flow-unconnected relationships and plots these separately. Torgegrams for stream pH and electrical conductivity measurements across a network in southeast Queensland, Australia,<sup>41</sup> are shown in Figure 4. The Torgegrams were based on residuals from an SSNM that included several predictors and used a mixed-model autocovariance structure consisting of a tail-up exponential function and a tail-down linear-with-sill function. Conductivity showed increasing semivariances for both flow-connected and flow-unconnected sites (Figure 4(b)), which indicated that spatial autocorrelation occurred to distances of at least 100 km in this dataset (maximum value on the x-axis). The pH Torgegram showed a similar pattern for flow-connected sites but no spatial trend among flow-unconnected sites (Figure 4(c)). Those patterns suggest that important predictors affecting flow-connected relationships may have been missing from the regression model or that factors were operating at spatial extents larger than the stream network to create system-wide gradients. The lack of a spatial

trend in the pH residuals at flow-unconnected sites suggests that this water chemistry attribute exhibited different spatial properties than conductivity. It may also have been the case that a tail-up model, which restricts correlation to flow-connected sites, would have been more suitable than a tail-down model in this instance.

### Parameter Estimation and Significance Tests

A goal in many analyses [e.g., analysis of variance (ANOVA), analysis of covariance, regression] is parameter estimation wherein relationships are described between one or more predictor variables and a response variable such as fish or macroinvertebrate abundance, habitat conditions, or water quality. Multiple linear regression is commonly used for this purpose,<sup>48</sup> wherein elements in the parameter vector  $\beta$  from the linear model are estimated to describe how much a response variable changes relative to a 1-unit change in a predictor variable. An SSNM regression not only provides similar estimates but also accounts for spatial structure in residual errors using an autocovariance function and often improves parameter estimates.<sup>22,31</sup>

**TABLE 2** | Comparison of Parameter Estimates and Summary Statistics for Nonspatial and Spatial Multiple Regression Models Predicting Maximum Summer Stream Temperature across a 2500 km River Network in Central Idaho

Model	Predictor	<i>b</i> (SE)	<i>p</i> -value	<i>t</i>	<i>p</i>	AIC	<i>r</i> <sup>2</sup>	RMSPE (°C)
Nonspatial	Intercept	31.2 (0.918)	<i>p</i> < 0.01	34.1	6	3912	0.46	2.99
	Elevation (100 m)	−0.754 (0.0512)	<i>p</i> < 0.01	−14.7				
	Glacial valley (%)	−3.04 (0.574)	<i>p</i> < 0.01	−5.29				
	Valley bottom (%)	3.06 (0.631)	<i>p</i> < 0.01	4.85				
	Stream slope (%)	−6.62 (2.92)	<i>p</i> = 0.02	−2.27				
	Contributing area (100 km <sup>2</sup> )	0.124 (0.0048)	<i>p</i> = 0.01	2.58				
Spatial	Intercept	30.5 (1.69)	<i>p</i> < 0.01	18.0	13	3161	0.85	1.58
	Elevation (100 m)	−0.767 (0.0881)	<i>p</i> < 0.01	−8.70				
	Glacial valley (%)	−1.51 (0.797)	<i>p</i> = 0.06	−1.89				
	Valley bottom (%)	2.95 (0.645)	<i>p</i> < 0.01	4.58				
	Stream slope (%)	−0.0929 (3.57)	<i>p</i> = 0.98	−0.03				
	Contributing area (100 km <sup>2</sup> )	0.0495 (0.0864)	<i>p</i> = 0.57	0.57				

To illustrate how spatial autocorrelation may adversely affect parameter estimation, we compared results from nonspatial and SSNM regressions applied to a dataset consisting of 780 stream temperature measurements across a 2500 km river network (Figure 1(a)). The response variable was maximum summer stream temperature and predictor variables were elevation, stream slope, size of the upstream watershed, valley bottom width, and proportion of the watershed that was previously glaciated.<sup>8</sup> Parameter estimates were derived using maximum likelihood estimation. In the SSNM, a mixed-model autocovariance structure was used,<sup>41</sup> which consisted of exponential tail-up, exponential Euclidean, and linear-with-sill tail-down components.<sup>8</sup> Model results were compared using the spatial Akaike Information Criterion (AIC),<sup>49,50</sup> which penalizes for the number of parameters in the autocovariance function (seven in the mixed-model structure) along with parameters for the predictors. The *r*<sup>2</sup> and root mean square prediction error (RMSPE) based on observed temperatures and leave-one-out cross-validation predictions were also calculated.

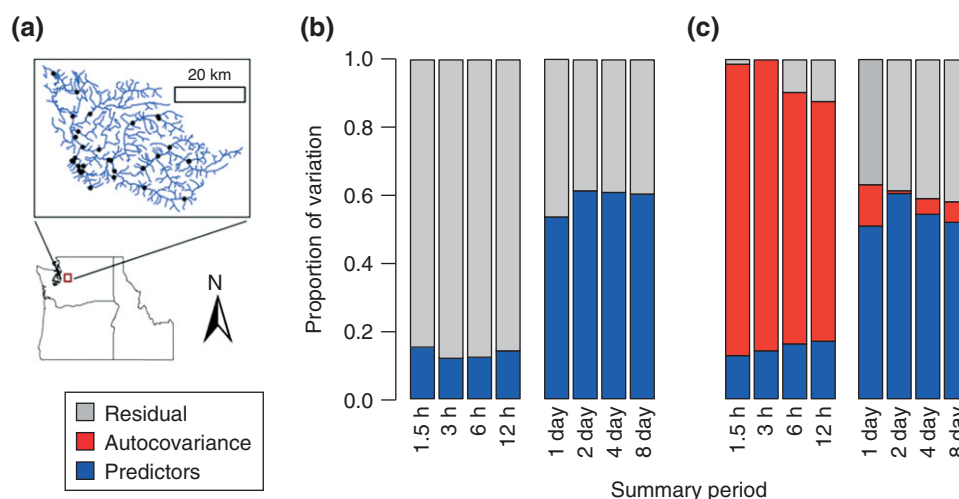
Results for the SSNM and nonspatial regression models provide several interesting contrasts (Table 2). First, parameter estimates for all predictor variables in the nonspatial regression model were statistically significant (*p*-value < 0.05). In the spatial model, however, only two of five predictors were significant, which suggested several type I errors (i.e., false detection of an effect) occurred in the nonspatial model. Second, the magnitude of the parameter estimates changed considerably for three of the predictors (glacial valley, stream slope, and contributing area),

suggesting the strong influence of values at measurement sites clustered within a subset of the network (Figure 1(a)). Third, measures of overall model performance indicated the SSNM was a clear improvement over the nonspatial model. The AIC value was 751 points lower for the spatial model (a difference of 2 AIC points is often used as indication of a better model),<sup>51</sup> despite inclusion of seven additional parameters in the autocovariance function. Predictive accuracy of the SSNM was also much better than the nonspatial model, in part because parameter estimates were more accurate, but mainly because useful spatial structure in the residuals was modeled by the autocovariance function. Differences between spatial and nonspatial regression model results would be smaller in databases with less spatial autocorrelation, but knowing the size of these differences is difficult without fitting both types of models.

### Variance Decomposition and Spatial Effects

Variance decomposition is used to allocate the total amount of variation associated with a response variable to different sources, which provides insight about the relative importance of key structuring processes.<sup>52</sup> Those sources may include predictor variables that represent spatial and temporal factors, interactions between these factors, and residual error. In traditional ANOVA settings, decomposition is done nonspatially by partitioning the sums of squares among the sources of variation included in the model (e.g., predictors and residual error). Decompositions using SSNMs are similar, but also represent spatial structure in model residuals using the autocovariance function.





**FIGURE 5** | Variance decomposition of stream temperature data from the Snoqualmie River in western Washington (a). Bargraphs show the proportion of total variation described by predictor variables, spatial structure modeled by the autocovariance function, and residual error for nonspatial regression models (b) and spatial regression models (c).

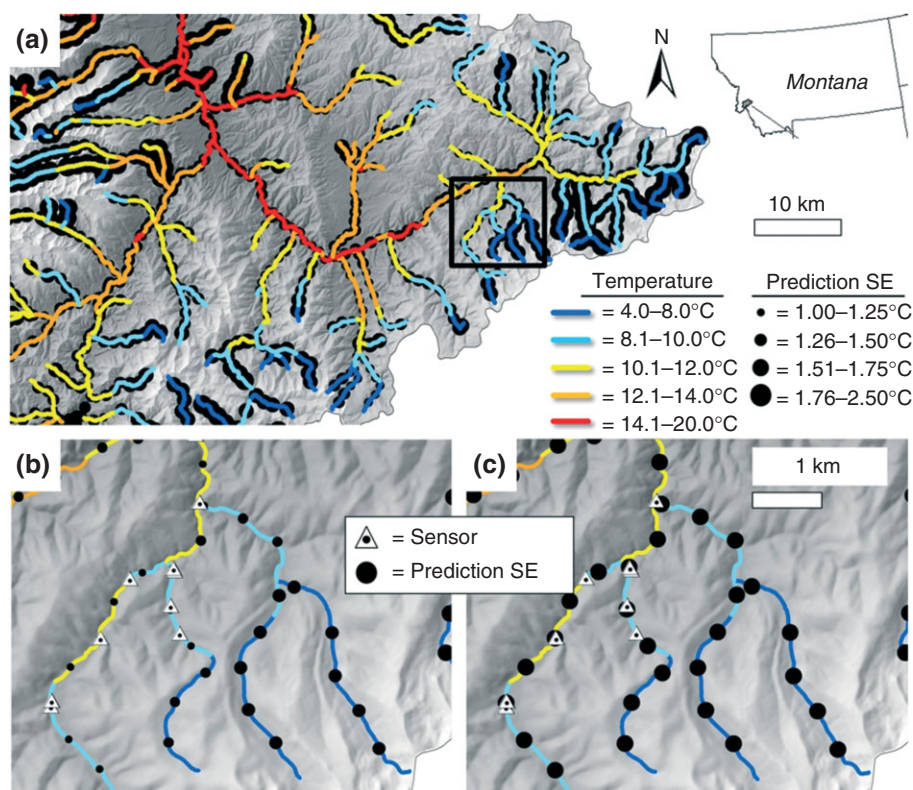
The contrast between nonspatial and spatial variance decompositions is illustrated using data from 30 temperature sensors that recorded measurements every 30 min over a 1-year period in the Snoqualmie River of western Washington (Figure 5). Wavelet analysis<sup>53</sup> was used to identify periodicities within the temperature records that were then used as logical summary periods. Accordingly, temperature measurements were summarized based on intra- (1.5, 3, 6, and 12 h) and inter-daily (1, 2, 4, and 8 days) periods. Nonspatial and SSNM regression models were used to predict these metrics from elevation, discharge, and percent commercial land use in a watershed. The SSNM used an exponential tail-up autocovariance function.

In the nonspatial regression models, the predictors explained only a small proportion of variation in intra-daily temperature summaries (12–15%), approximately half the variation in inter-daily summaries, and the remaining variation was allocated to residual error (Figure 5(b)). Spatial regressions for those same summaries, however, indicated that significant proportions of the residual variation could be spatially structured, especially with regards to intra-daily summaries (Figure 5(c)). Those results suggest that stream temperature patterns have a strong spatial component over short periods, but it becomes weaker over longer periods. More generally, this example highlights the importance of accounting for spatial effects beyond those directly attributable to predictor variables. Spatial effects may, or may not, be important but their exclusion could result in a very different view of the study system. Also worth noting is that the autocovariance structure

itself may be partitioned into tail-up, tail-down, and Euclidean components when a mixed model is used (see Appendix H in Ref 8).<sup>23</sup> Examining the relative contributions of the components could provide clues about mechanisms driving stream patterns or additional predictors to consider in future models.

### Predictions at Unsamped Locations

Stream and river networks comprise 100s to 10,000s of kilometers, so direct measurements for most attributes are too costly to obtain everywhere. An attractive feature of regression models is their utility for predicting a response variable at unsampled locations. Predictions are made by multiplying the model parameter estimates by the values of predictors at unsampled locations. If predictions are made at points placed systematically throughout a network, semi-continuous maps showing the status of a stream attribute can be developed. SSNMs make predictions similarly, but also use information from the autocovariance function to improve predictive accuracy near measurement sites. Those predictions are generated using the universal kriging equation,<sup>54</sup> which has two parts; a prediction based on the linear regression model and an adjustment for spatial autocorrelation. Thus, the model predictors set the mean process for an initial prediction, which is then adjusted based on any information that nearby measurements provide. Predictions may also be generated using ordinary kriging basely solely on values of the response variable, but this assumes that the average condition of the response variable remains constant across the study region. That assumption is often violated in



**FIGURE 6** | Kriged map of mean stream temperatures and prediction standard errors in the upper Bitterroot River of western Montana (a; Source: Ref 57). Box in panel a highlights the area shown in panels b and c. Note that standard errors vary in size relative to sensor measurement locations in the spatial model (b) but not in the nonspatial model (c).

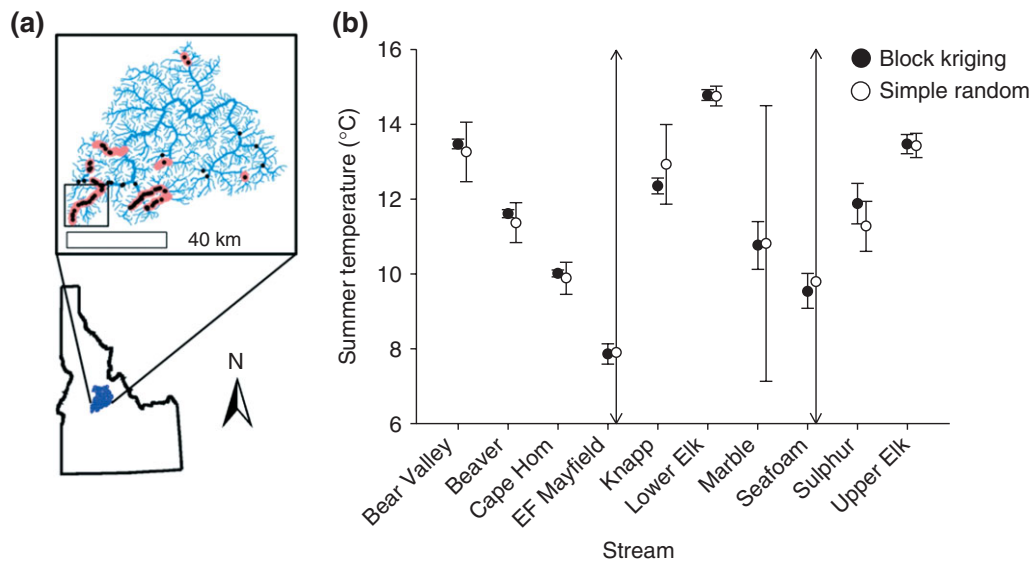
nature, which makes the predictions less accurate than those developed with universal kriging and predictor information.<sup>55,56</sup>

An example of a universal kriging map for a small network in western Montana is provided in Figure 6. The map was made by applying an SSNM to a large regional temperature database in the northwest United States and then generating predictions at 1-km intervals (more details are provided elsewhere<sup>57</sup>). The prediction map shows not only heterogeneous thermal conditions across the network, but also the expected pattern of colder temperatures in high-elevation streams trending to warmer conditions in low-elevation rivers. Researchers are usually most interested in the patterns associated with mean values at the prediction sites, but the spatial models also provide important information about the precision of these predictions. Note that the standard errors from the SSNM were small near measurement sites and increased as the distance to a measurement site increased (Figure 6(b)). That contrasted with predictions from a nonspatial regression model where the standard errors were homogenous regardless of network position (Figure 6(c)). Information about prediction precision is useful for understanding

model uncertainty, and for determining where new measurements could provide the most information. Strategically targeting an array of those measurements might also serve as the basis for monitoring designs that effectively accommodated existing data.

### Block-Kriging Estimates for Discrete Areas

It is often desirable to estimate totals and averages for stream attributes across an area (e.g., reach, segment, or network) and then to make comparisons among different areas. Those estimates may be obtained by using a spatial statistical technique called block kriging,<sup>54,58</sup> which the SSNMs now facilitate on stream networks.<sup>20,31</sup> To illustrate the technique, an SSNM was again fit to a set of temperature measurements and predictions were made at dense, 10-m intervals along sections of stream delimited by the upstream and downstream extent of measurements within individual streams (Figure 7). Block-kriging estimates of the mean temperature for each segment were then derived by integrating across the prediction sets.<sup>22,31</sup> Comparison of the block-kriging estimates to estimates based on simple random sampling (SRS), which used the observed measurements within



**FIGURE 7** | Stream temperature estimates based on block kriging and simple random sampling that were derived from measurements recorded across a river network in central Idaho (a). Red shading shows stream segments where mean temperatures were estimated (b). Error bars associated with estimates are 95% confidence intervals.

each stream, showed the former to be much more precise (Figure 7(b)). The gain in precision occurred because block-kriging estimates incorporated information from many prediction points and measurements along the segments, whereas the SRS estimates relied only on the few temperature measurements. Moreover, SRS estimates in two streams with single measurements had confidence intervals that were essentially infinite because variance calculations require at least two measurements.

Many powerful applications are enabled by block kriging on stream networks. For example, network-scale maps of water chemistry attributes could be queried to identify those areas that exceeded regulatory thresholds based on statistically defined thresholds.<sup>59,60</sup> Where those queries yielded estimates that were insufficiently precise, power analysis (discussed in the next section) and maps of prediction precision could be used to target new measurements and provide conclusive information. Block kriging could also be used to standardize and improve comparisons between reference and impacted sites<sup>61,62</sup> so that the magnitude and cause of differences in stream conditions were better understood. Used with count data for fish or other stream organisms, block kriging could provide estimates of population size for entire streams and river networks<sup>63</sup> analogous to similar estimates that are commonly available for wildlife populations in terrestrial settings.<sup>58,64</sup> That would provide biological information more commensurate with resource management decisions and the geographic scale of many populations, as opposed to the restricted scales

(i.e., 10s–100s m) of traditional stream population estimates.<sup>65,66</sup> Block-kriging estimates could also be developed from existing biological survey data<sup>10,67</sup> and would be far less labor intensive than existing techniques for censusing streams.<sup>37,68</sup>

### Power Analysis with Spatial Autocorrelation

Power analysis is an important tool for developing sampling designs and recommendations about sample sizes needed to achieve study objectives. Power analysis can also provide information about the likelihood that a type II error was committed (i.e., an effect existed but was not detected). Classical treatments of the subject for ecologists,<sup>69,70</sup> however, were done before the widespread availability of spatial statistical software and provide few insights regarding how spatial autocorrelation affects power. Using the temperature data from the previous block-kriging example, an SSNM was fit to these data using predictors that consisted of elevation and stream network (as a categorical effect) and a mixed-model autocovariance function (exponential tail-up, exponential tail-down, and Euclidean; Table 3). To calculate the minimum detectable effect size with a power of 0.80 (80% chance that a type II error would not be committed), conventional probability-based power methods assuming a normal distribution were used. A power curve was developed across a range of elevation parameters assumed to encompass the true value using the standard error of the elevation parameter (0.0064) and controlling the type I error rate at 5% by

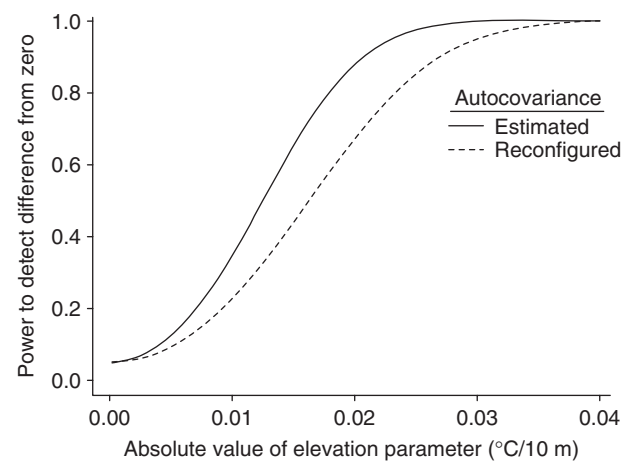
**TABLE 3** | Summary Statistics for a Spatial Stream-Network Model with a Mixed-Model Autocovariance Function Used to Predict Stream Temperature in a Power Analysis

Predictor	Autocovariance			
	Function	<i>b</i> (SE)	<i>p</i> -value	<i>t</i>
Intercept		64.5 (12.5)	<0.01	5.16
Elevation (°C/10 m)		−0.0254 (0.0064)	<0.01	−3.97
Stream network 1		—	NA	NA
Stream network 2		−0.767 (0.833)	0.363	−0.920
Autocovariance component				
Partial sill <sup>1</sup> (exponential model)	tail-up	1.85		
Range (km; exponential model)	tail-up	118		
Partial sill (exponential model)	tail-down	0.02		
Range (km; exponential model)	tail-down	65		
Partial sill (exponential model)	Euclidean	0.01		
Range (km; exponential model)	Euclidean	51		
Nugget		0.01		

<sup>1</sup>The partial sill is equal to the sill minus the nugget effect.

setting  $\alpha = 0.05$ . It was then assessed how power might change if a model with a different covariance structure was used. To do this, the partial sill parameters in the autocovariance function were switched between the tail-up and tail-down models to create a model dominated by the tail-down function (Table 3). The temperature model was then refit with the reconfigured autocovariance structure and the new standard error estimate for elevation (0.0083) used in the same set of power calculations described above.

Results suggest that achieving power of 0.80 required elevation parameters with absolute magnitudes  $\geq 0.0180^{\circ}\text{C}/10\text{ m}$  in the original model and  $\geq 0.0234^{\circ}\text{C}/10\text{ m}$  in the reconfigured model. The power curve for the reconfigured model was also shifted to the right of the original curve, which again demonstrated that the reconfigured model had

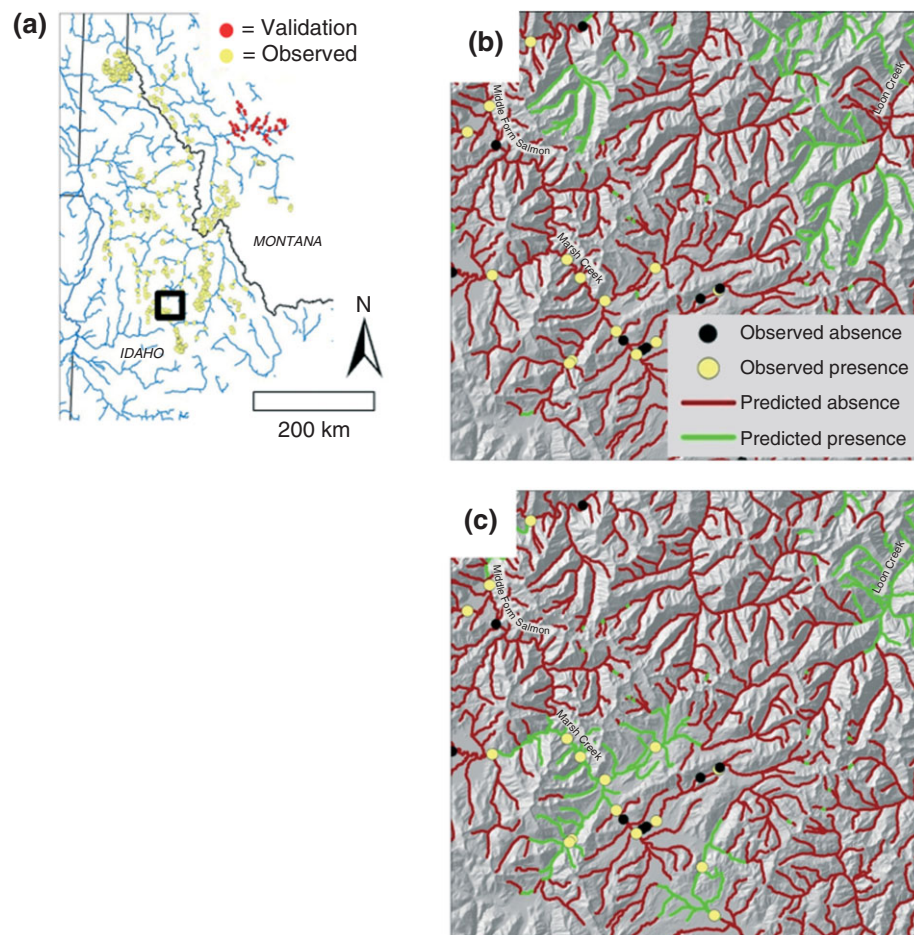
**FIGURE 8** | Power curves for elevation regression coefficient in a spatial stream-network model fit to temperature measurements using different autocovariance functions.

less power (Figure 8). This simple example demonstrates that spatial autocorrelation, and how it is described with an autocovariance function, affects power calculations and the probability of detecting certain effects. Many possibilities exist to explore this topic in more detail given a diversity of autocovariance functions<sup>11,41</sup> and convenience of making the calculations with the SSN software.<sup>31</sup> As autocovariance functions are described for more stream databases, consistencies might emerge for specific stream attributes (e.g., pH, temperature, fish density) and network types (e.g., mountain, coastal, desert) that could serve as a basis for generalizable forms of power analysis to inform the design of new studies.<sup>71</sup>

### Spatial Models for Non-Normal Data

Previous examples highlighted applications of the spatial models using continuous data and the Gaussian (i.e., normal) distribution. However, the SSNMs may also be applied to non-normal data such as counts (Poisson distribution) or occurrences (binomial distribution) through appropriate link functions.<sup>31</sup> Common types of count data for streams include the number of fish or macroinvertebrates within a sample area; whereas occurrence data consist of whether a species was present at a site or whether a regulatory threshold was exceeded. Application of the SSNMs to occurrence data is demonstrated with 961 stream sites surveyed for bull trout (*Salvelinus confluentus*) across Idaho and Montana (Figure 9).<sup>10</sup> Those data were fit with nonspatial and spatial logistic regression models; the latter used a mixed-model autocovariance structure. Both models used the same set of predictor variables (Table 4), which are described





**FIGURE 9** | Stream sites sampled for occurrence of bull trout in Idaho and Montana (a) that were used to develop a nonspatial logistic regression model (b) and a spatial logistic regression model (c) for predicting the distribution of this species. Box in panel a highlights the area shown in subsequent panels.

elsewhere.<sup>10</sup> The predictive accuracy of the models was assessed based on the area under the curve (AUC) of the receiver–operator characteristic calculated using leave-one-out cross-validation, and using an independent dataset of 65 sites.<sup>72</sup>

Similar to the results in the earlier section on parameter estimation, standard errors for the SSNM logistic regression model were larger due to autocorrelation among the fish survey sites (Table 4). The predictive performance was high for both models based on AUC characteristics but the SSNM performed better in both instances. In the cross-validation assessment, the spatial structure in the residuals made predictions near fish survey sites more accurate and improved the AUC from 0.791 to 0.908. The performance gain was less dramatic with the independent data because nearby sites were lacking but some improvement still occurred because parameter estimates in the spatial model were more accurate. When species distribution maps were made by applying a 0.5

probability cutoff to the model predictions, bull trout were predicted to occur in different areas within a subset of the network (Figure 9(b) and (c)).

## DISCUSSION

The concept of spatial autocorrelation is relevant to most types of data measured on stream networks and it may affect statistical inference from many databases. Spatial autocorrelation should no longer be ignored now that suitable statistical techniques and software are available. Quite the opposite, recognizing and embracing spatial autocorrelation present many exciting possibilities for developing new information about streams and their biota. Moreover, the common occurrence of autocorrelation in stream data at distances of 1–100 km<sup>9,18,37</sup> suggest that SSNMs will often be useful tools for describing and understanding spatial patterns throughout river networks.



**TABLE 4** | Comparison of Parameter Estimates and Summary Statistics for Nonspatial and Spatial Logistic Regression Models that Predict the Probability of Bull Trout Occurrence at 961 Sites across Idaho and Montana

Model	Predictors <sup>1</sup>	<i>b</i> (SE)	<i>p</i> -value	<i>t</i>	<i>p</i>	Cross-Validation AUC	Validation AUC
Nonspatial	Intercept	−0.87 (0.09)	<i>p</i> < 0.01	−9.02	5	0.791	0.702
	Wtemp	−0.97 (0.19)	<i>p</i> < 0.01	−5.17			
	W95	−1.99 (0.29)	<i>p</i> < 0.01	−7.34			
	Slope	−0.37 (0.17)	<i>p</i> = 0.09	−1.68			
	Vbdist	0.97 (0.15)	<i>p</i> < 0.01	6.21			
Spatial	Intercept	−0.23 (0.34)	<i>p</i> = 0.52	−0.63	12	0.908	0.734
	Wtemp	−1.06 (0.29)	<i>p</i> < 0.01	−3.73			
	W95	−0.85 (0.28)	<i>p</i> < 0.01	−2.93			
	Slope	−0.71 (0.17)	<i>p</i> < 0.01	−4.14			
	Vbdist	0.40 (0.23)	<i>p</i> = 0.097	1.66			

<sup>1</sup>Wtemp = mean summer air temperature in watershed associated with fish survey site; W95 = frequency of winter high flows; Slope = stream slope; Vbdist = distance between survey site and nearest unconfined valley bottom area.

Source: Ref 72.

That information could help fill an important information gap because it occurs at scales commensurate with those at which population dynamics occur and management decisions are made (e.g., within and among streams) regarding where to allocate conservation resources.<sup>73,74</sup> Accurate information for river networks also means that the SSNMs could provide a useful link between broad regional phenomena and local stream conditions. For example, two studies have already used the SSNMs to statistically downscale the effects of global climate change to stream thermal patterns.<sup>8,28</sup> The outputs from the stream models were sufficiently accurate that local managers familiar with the river basins rapidly adopted the information in decision making—a dynamic that was enhanced by the fact that the temperature measurements were obtained from aggregated databases contributed by the management community.<sup>57</sup> Maps of temperature predictions or other stream attributes could also stimulate better understanding of linkages between terrestrial and aquatic environments because stream information could then be co-registered with terrestrial conditions at any scale rather than being limited to areas where measurements occurred. Finally, accurate stream maps would enable a suite of derivative analyses<sup>6,20</sup> and the application of many powerful techniques from the field of spatial ecology that have seen limited use in stream research.<sup>75,76</sup>

The ability of SSNMs to accommodate nonindependence among measurements makes them powerful data mining tools and provides a strong incentive for database aggregation. There are 10,000s of stream measurements and biological surveys representing investments of tens of millions US\$<sup>10,67,77</sup> that could be examined to develop new information at relatively

low cost with spatial statistical techniques. If analyses were done in combination with nationally available geospatial hydrography data and stream reach predictors,<sup>78–80</sup> consistent status and trend assessments at national, regional, and local scales would be possible.<sup>57</sup> Such assessments are too often lacking for stream resources, are based on small numbers of measurements (e.g., 10s–100s of measurements), or provide coarse information relative to what is needed for local management and conservation decisions.<sup>5,81</sup> Developing information from aggregated databases presents issues related to differences in measurement techniques,<sup>66,82</sup> but large databases also provide users the flexibility to apply filters based on methodological criteria and still retain large samples for analysis. The yield of new information from aggregated databases makes those endeavors worthwhile and the broader context for analysis and inference that SSNMs and other data mining techniques provide should drive the standardization of measurement techniques over time.

Despite the many benefits and potential applications of SSNMs, they are not a panacea. Implementing the models is more complex than traditional statistical analyses and requires moderately advanced skills in geographic information systems and statistics, as well as familiarity with specialized software programs (ArcGIS and R). The spatial models are also more computationally demanding than nonspatial models because the covariance matrices are composed of  $n^2$  elements, which must be stored in memory and inverted during the modeling process. A database with 100 measurements, therefore, has a covariance matrix composed of 10,000 elements. We have used the SSNMs with 5000+ measurements

(matrices with 25,000,000 elements) but a single model fit for a dataset of this size required several hours on a modern desktop computer. Given the computational challenges as stream databases continue to grow, more efficient spatial routines like those based on fixed-rank kriging<sup>83</sup> may ultimately be needed. The spatial models also have larger minimum sample size requirements because of the additional parameters that are estimated for the autocovariance function. A simple function requires two or three parameters, but a full mixed-model autocovariance with tail-up, tail-down, and Euclidean components has seven parameters.<sup>41</sup> Those parameters are in addition to parameters for the predictors in an SSNM, so minimum sample sizes range from 50 to 100 measurements based on the general recommendation of 10 measurements for each parameter estimate.<sup>84</sup>

Current theory and SSNM applications provide a strong, but nascent, foundation on which much could be built. Direct analogues for most types of statistical analyses developed for terrestrial systems are now possible that would incorporate network structure. Particularly useful would be further generalizing model distributions to include multivariate responses and extreme values; as well as occupancy models that accommodate detection efficiency.<sup>85,86</sup> The SSNMs described here only account for spatial autocorrelation, but covariance structures that simultaneously address spatial and temporal autocorrelation<sup>87</sup> could be developed for streams. That would enable modeling of measurements recorded continuously across many sites as occurs often in water quality and temperature monitoring arrays.<sup>25,28</sup> Covariance structures could also be developed that accommodate nonstationarity<sup>88</sup> and spatial relationships that vary in different parts of networks (e.g., the range of autocorrelation could be longer in large streams than small streams).

Not surprisingly, spatial autocorrelation has important implications for designing aquatic monitoring programs.<sup>33</sup> Efficient sampling designs for spatial statistical models spread measurements along environmental gradients and include some spatial

clustering,<sup>32,71</sup> which contrasts with traditional sampling designs wherein measurements are randomly located and/or spatially balanced.<sup>40,89,90</sup> Moreover, inference from traditional sampling is based on the initial study design rather than an underlying model as is the case with spatial techniques.<sup>58,64</sup> An intriguing future possibility is hybrid sampling wherein traditional designs formed the core of a monitoring program but clusters of additional measurements were placed strategically so that the spatial autocovariance structure could be estimated. Hybrid designs would involve small additional costs but could diversify the information that a monitoring program provides by enabling both design- and model-based inferences.<sup>32,33</sup> The simulation function contained in the SSN software could be used to explore many sampling design issues in detail.<sup>31</sup>

## CONCLUSION

This paper was stimulated by past challenges we have experienced with the lack of appropriate statistical techniques for data on stream networks. Recent development of SSNMs provides novel opportunities to surmount many challenges but key impediments yet remain. At the time of this writing, spatial statistical courses for ecologists are taught at relatively few universities, and the unique issues that stream analyses present are addressed even more rarely. That is problematic given that streams, and many issues associated with their degradation, have inherently strong spatial dimensions that differ fundamentally from terrestrial systems. Our hope is that by highlighting new types of stream analyses and accompanying software tools, information development for these important ecosystems is accelerated so that streams are better understood, managed, and conserved. Readers interested in learning more about SSNM analysis of stream data, accessing the free software programs used for example analyses (STARS<sup>30</sup>; SSN package for R<sup>31</sup>), or downloading additional datasets are encouraged to visit the SSN/STARS website.<sup>34</sup>

## ACKNOWLEDGMENTS

This research was conducted as part of a Spatial Statistics for Streams working group supported by the National Center for Ecological Analysis and Synthesis (Project 12637), a Center funded by the National Science Foundation (Grant No EF-0553768), the University of California, Santa Barbara, and the State of California. Additional support was provided by NOAA's Alaska and Northwest Fisheries Science Centers, the U.S. Forest Service, Rocky Mountain Research Station, and the CSIRO Water for a Healthy Country Flagship. Two anonymous reviewers provided comments that improved the quality of the final manuscript. Any use of

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## REFERENCES

- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Leveque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, et al. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol Rev* 2006, 81:163–182. doi: 10.1017/S1464793105006950.
- Poff NL, Olden JD, Strayer DL. Climate change and freshwater fauna extinction risk. In: Hannah L, ed. *Saving a Million Species*. Washington: Island Press/Center for Resource Economics; 2012, 309–336.
- Vorosmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Liermann CR, et al. Global threats to human water security and river biodiversity. *Nature* 2010, 467:555–561. doi: 10.1038/Nature09440.
- Steel EA, Hughes RM, Fullerton AH, Schmutz S, Young JA, Fukushima M, Muhar S, Poppe M, Feist BE, Trautwein C. Are we meeting the challenges of landscape-scale riverine research? A review. *Living Rev Landsc Res* 2010, 4(1):1–60.
- Isaak DJ, Muhlfeld CC, Todd AS, Al-Chokhachy R, Roberts J, Kershner JL, Fausch KD, Hostetler SW. The past as prelude to the future for understanding 21st-century climate effects on Rocky Mountain trout. *Fisheries* 2012, 37:542–556. doi: 10.1080/03632415.2012.742808.
- Johnson LB, Host GE. Recent developments in landscape approaches for the study of aquatic ecosystems. *J N Am Benthol Soc* 2010, 29:41–66. doi: 10.1899/09-030.1.
- Porter JH, Hanson PC, Lin CC. Staying afloat in the sensor data deluge. *Trends Ecol Evol* 2012, 27:121–129. doi: 10.1016/j.tree.2011.11.009.
- Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, Parkes S, Chandler GL. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecol Appl* 2010, 20:1350–1371.
- Peterson EE, Merton AA, Theobald DM, Urquhart NS. Patterns of spatial autocorrelation in stream water chemistry. *Environ Monit Assess* 2006, 121:571–596. doi: 10.1007/s10661-005-9156-7.
- Wenger SJ, Isaak DJ, Dunham JB, Fausch KD, Luce CH, Neville HM, Rieman BE, Young MK, Nagel DE, Horan DL, et al. Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin. *Can J Fish Aquat Sci* 2011, 68:988–1008. doi: 10.1139/f2011-034.
- Garreta V, Monestiez P, Ver Hoef JM. Spatial modelling and prediction on river networks: up model, down model or hybrid? *Environmetrics* 2009, 21:439–456. doi: 10.1002/env.995.
- Legendre P. Spatial autocorrelation - trouble or new paradigm. *Ecology* 1993, 74:1659–1673. doi: 10.2307/1939924.
- Fisher RA. The arrangement of field experiments. *J Minist Agric G B* 1926, 33:503–515.
- Neyman J. On the two different aspects of the representative method: the method of stratified sampling and the method of purposive selection. *J R Stat Soc* 1934, 97:558–625. doi: 10.2307/2342192.
- Legendre P, Fortin MJ. Spatial pattern and ecological analysis. *Plant Ecol* 1989, 80:107–138. doi: 10.1007/Bf00048036.
- Ver Hoef JM, Cressie N, Fisher RN, Case TJ. Uncertainty and spatial linear models for ecological data. In: Hunsaker CT, Goodchild MF, Friedl MA, Case TJ, eds. *Spatial Uncertainty for Ecology: Implications for Remote Sensing and GIS Applications*. New York: Springer-Verlag; 2001, 214–237.
- Fortin MJ, Dale MR. *Spatial Analysis: A Guide for Ecologists*. Cambridge: Cambridge University Press; 2005.
- Cooper SD, Barmuta L, Sarnelle O, Kratz K, Diehl S. Quantifying spatial heterogeneity in streams. *J N Am Benthol Soc* 1997, 16:174–188. doi: 10.2307/1468250.
- Ganio LM, Torgersen CE, Gresswell RE. A geostatistical approach for describing spatial pattern in stream networks. *Front Ecol Environ* 2005, 3:138–144. doi: 10.1890/1540-9295(2005)003[0138:Agafds]2.0.Co;2.
- Peterson EE, Ver Hoef JM, Isaak DJ, Falke JA, Fortin MJ, Jordan CE, McNyset K, Monestiez P, Ruesch AS, Sengupta A, et al. Modelling dendritic ecological networks in space: an integrated network perspective. *Ecol Lett* 2013, 16:707–719. doi: 10.1111/Ele.12084.
- Cressie N, Frey J, Harch B, Smith M. Spatial prediction on a river network. *J Agric Biol Environ Stat* 2006, 11:127–150. doi: 10.1198/108571106x110649.
- Ver Hoef JM, Peterson E, Theobald D. Spatial statistical models that use flow and stream distance. *Environ Ecol Stat* 2006, 13:449–464. doi: 10.1007/s10651-006-0022-8.
- Peterson EE, Ver Hoef JM. A mixed-model moving-average approach to geostatistical modeling in stream networks. *Ecology* 2010, 91:644–651.
- Peterson EE, Urquhart NS. Predicting water quality impaired stream segments using landscape-scale data and a regional geostatistical model: a case study in Maryland. *Environ Monit Assess* 2006, 121:615–638. doi: 10.1007/s10661-005-9163-8.

25. Gardner KK, McGlynn BL. Seasonality in spatial variability and influence of land use/land cover and watershed characteristics on stream water nitrate concentrations in a developing watershed in the Rocky Mountain West. *Water Resour Res* 2009, 45:W08411. doi: 10.1029/2008wr007029.
26. Money ES, Carter GP, Serre ML. Using river distances in the space/time estimation of dissolved oxygen along two impaired river networks in New Jersey. *Water Res* 1948–1958, 2009:43. doi: 10.1016/j.watres.2009.01.034.
27. Money ES, Carter GP, Serre ML. Modern space/time geostatistics using river distances: data integration of turbidity and *E. coli* measurements to assess fecal contamination along the Raritan River in New Jersey. *Environ Sci Technol* 2009, 43:3736–3742. doi: 10.1021/Es803236j.
28. Ruesch AS, Torgersen CE, Lawler JJ, Olden JD, Peterson EE, Volk CJ, Lawrence DJ. Projected climate-induced habitat loss for salmonids in the John Day River network, Oregon, USA. *Conserv Biol* 2012, 26:873–882. doi: 10.1111/j.1523-1739.2012.01897.x.
29. Farrae DJ, Albeke SE, Pacifici K, Nibbelink NP, Peterson DL. Assessing the influence of habitat quality on movements of the endangered shortnose sturgeon. *Environ Biol Fish* 2013, doi: 10.1007/s10641-013-0170-2.
30. Peterson EE, Ver Hoef JM. STARS: An ArcGIS toolset used to calculate the spatial information needed to fit spatial statistical models to stream network data. *J Stat Softw* 2014, 56(2):1–17.
31. Ver Hoef JM, Peterson EE, Clifford D, Shah R. SSN: An R package for spatial statistical modeling on stream networks. *J Stat Softw* 2014, 56(3):1–45.
32. Zimmerman DL. Optimal network design for spatial prediction, covariance parameter estimation, and empirical prediction. *Environmetrics* 2006, 17:635–652. doi: 10.1002/Env.769.
33. Som NA, Monestiez P, Zimmerman DL, Ver Hoef JM, Peterson EE. Spatial sampling on streams: principles for inference on aquatic networks. *Environmetrics* (In Review).
34. Peterson EE, Ver Hoef JM, Isaak DJ. SSN/STARS: Tools for Spatial Statistical Modeling on Stream Networks. 2012. Available at: <http://www.fs.fed.us/rm/boise/AWAE/projects/SpatialStreamNetworks.shtml>. (Accessed February 22, 2014).
35. R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria; 2010. Available at: <http://www.Rproject.org/>. (Accessed February 22, 2014).
36. Theobald DM, Norman JB, Peterson E, Ferraz S, Wade A, Sherburne MR. Functional linkage of water basins and streams (FLoWS) v1 User's Guide: ArcGIS tools for network-based analysis of freshwater ecosystems. Natural Resource Ecology Lab, Colorado State University, Fort Collins, CO; 2006, 43.
37. Torgersen CE, Gresswell RE, Bateman DS. Pattern detection in stream networks: quantifying spatial variability in fish distribution. In: Nishida T, Kailola PJ, Hollingworth CE, eds. *GIS/Spatial Analyses in Fishery and Aquatic Sciences*, vol. 2. Saitama, Japan: Fishery–Aquatic GIS Research Group; 2004, 405–420.
38. Matheron G. Principles of geostatistics. *Econ Geol* 1963, 58:1246–1266.
39. Dale MRT, Fortin MJ. Spatial autocorrelation and statistical tests: some solutions. *J Agric Biol Environ Stat* 2009, 14:188–206. doi: 10.1198/jabes.2009.0012.
40. Stevens DL, Olsen AR. Spatially balanced sampling of natural resources. *J Am Stat Assoc* 2004, 99:262–278. doi: 10.1198/016214504000000250.
41. Ver Hoef JM, Peterson EE. A moving average approach for spatial statistical models of stream networks. *J Am Stat Assoc* 2010, 105:6–18. doi: 10.1198/jasa.2009.ap08248.
42. Putter H, Young GA. On the effect of covariance function estimation on the accuracy of kriging predictors. *Bernoulli* 2001, 7:421–438.
43. Ver Hoef JM, Temesgen H. A comparison of the spatial linear model to nearest neighbor (k-NN) methods for forestry applications. *PLoS One* 2013, 8:e59129. doi: 10.1371/journal.pone.0059129.
44. Stein ML. Asymptotically efficient prediction of a random field with a misspecified covariance function. *Ann Stat* 1988, 16:55–63.
45. Chiles J, Delfiner P. *Geostatistics: Modeling Spatial Uncertainty*. New York: John Wiley and Sons; 1999.
46. McGuire KJ, Torgersen CE, Likens GE, Buso DC, Lowe WH, Bailey SW. Network analysis reveals multi-scale controls on streamwater chemistry. *P Natl Acad Sci* (In Review).
47. Ettema CH, Wardle DA. Spatial soil ecology. *Trends Ecol Evol* 2002, 17:177–183. doi: 10.1016/S0169-5347(02)02496-5.
48. Fausch KD, Hawkes CL, Parsons MG. Models that predict standing crop of stream fish from habitat variables: 1950–85. Gen. Tech. Rep. PNW-GTR-213. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 1988; 52.
49. Akaike H. A new look at the statistical model identification. *IEEE Trans Automat Control* 1974, 19:716–722.
50. Hoeting JA, Davis RA, Merton AA, Thompson SE. Model selection for geostatistical models. *Ecol Appl* 2006, 16:87–98. doi: 10.1890/04-0576.
51. Burnham KP, Anderson DR. Multimodel inference: understanding AIC and BIC in model selection. *Sociol Method Res* 2004, 33:261–304.
52. Wiley MJ, Kohler SL, Seelbach PW. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. *Freshw Biol* 1997, 37:133–148. doi: 10.1046/j.1365-2427.1997.00152.x.



53. Percival DB, Walden A. *Wavelet Methods for Time Series Analysis*. Cambridge: Cambridge University Press; 2000.
54. Cressie N. *Statistics for Spatial Data*, Revised Edition. New York: John Wiley and Sons; 1993.
55. Phillips DL, Dolph J, Marks D. A comparison of geostatistical procedures for spatial-analysis of precipitation in mountainous terrain. *Agric Forest Meteorol* 1992, 58:119–141. doi: 10.1016/0168-1923(92)90114-J.
56. Qingmin M, Liu Z, Borders BE. Assessment of regression kriging for spatial interpolation—comparisons of seven GIS interpolation methods. *Cartogr Geogr Inf Sys* 2013, 40:28–39.
57. Isaak DJ, Wenger S, Peterson E, Ver Hoef JM, Hostetler S, Luce C, Dunham J, Kershner J, Roper B, Nagel D, et al. NorWeST: An interagency stream temperature database and model for the Northwest United States. U.S. Fish and Wildlife Service, Great Northern LCC Grant, 2011. Available at: [www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html](http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html). (Accessed February 22, 2014).
58. Ver Hoef JM. Sampling and geostatistics for spatial data. *Ecoscience* 2002, 9:152–161.
59. Birkeland S. EPA's TMDL program. *Ecol Law Q* 2001, 28:297–325.
60. Poole GC, Dunham JB, Keenan DM, Sauter ST, McCullough DA, Mebane C, Lockwood JC, Essig DA, Hicks MP, Sturdevant DJ, et al. The case for regime-based water quality standards. *Bioscience* 2004, 54:155–161. doi: 10.1641/0006-3568(2004)054[0155:Tcfwrq]2.0.Co;2.
61. Hawkins CP, Olson JR, Hill RA. The reference condition: predicting benchmarks for ecological and water-quality assessments. *J N Am Benthol Soc* 2010, 29:312–343. doi: 10.1899/09-092.1.
62. Kershner JL, Roper BB. An evaluation of management objectives used to assess stream habitat conditions on federal lands within the Interior Columbia Basin. *Fisheries* 2010, 35:269–278. doi: 10.1577/1548-8446-35.6.269.
63. High B, Meyer KA, Schill DJ, Mamer ERJ. Distribution, abundance, and population trends of bull trout in Idaho. *N Am J Fish Manage* 2008, 28:1687–1701. doi: 10.1577/m06-164.1.
64. Ver Hoef JM. Spatial methods for plot-based sampling of wildlife populations. *Environ Ecol Stat* 2008, 15:3–13.
65. Zippin C. An evaluation of the removal method of estimating animal populations. *Biometrics* 1956, 12:163–189. doi: 10.2307/3001759.
66. Peterson JT, Thurow RF, Guzevich JW. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. *Trans Am Fish Soc* 2004, 133:462–475. doi: 10.1577/03-044.
67. Comte L, Grenouillet G. Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* 2013, 36:1236–1246. doi: 10.1111/j.1600-0587.2013.00282.x.
68. Hankin DG, Reeves GH. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Can J Fish Aquat Sci* 1988, 45:834–844. doi: 10.1139/F88-101.
69. Peterman RM. Statistical power analysis can improve fisheries research and management. *Can J Fish Aquat Sci* 1990, 47:2–15. doi: 10.1139/F90-001.
70. Steidl RJ, Hayes JP, Schaubert E. Statistical power analysis in wildlife research. *J Wildl Manage* 1997, 61:270–279. doi: 10.2307/3802582.
71. Legendre P, Dale MRT, Fortin MJ, Gurevitch J, Hohn M, Myers D. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 2002, 25:601–615. doi: 10.1034/j.1600-0587.2002.250508.x.
72. Wenger SJ, Olden JD. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Method Ecol Evol* 2012, 3:260–267.
73. Rieman BE, Dunham JB. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecol Freshw Fish* 2000, 9:51–64. doi: 10.1034/j.1600-0633.2000.90106.x.
74. Fausch KD, Torgersen CE, Baxter CV, Li HW. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* 2002, 52:483–498. doi: 10.1641/0006-3568(2002)052[0483:Ltrbtg]2.0.Co;2.
75. Fortin MJ, James P, MacKenzie A, Melles SJ, Rayfield B. Spatial statistics, spatial regression, and graph theory in ecology. *Spatial Stat* 2012, 1:100–109.
76. Eros T, Olden JD, Schick RS, Schmera D, Fortin MJ. Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecol* 2012, 27:303–317. doi: 10.1007/s10980-011-9659-2.
77. Olson JR, Hawkins CP. Predicting natural base-flow stream water chemistry in the western United States. *Water Resour Res* 2012, 48:W02504. doi: 10.1029/2011wr011088.
78. Vogt J, Soille P, Colombo R, Paracchini ML, de Jager A. Development of a pan-European river and catchment database. In: *Digital Terrain Modelling*. Heidelberg: Springer Berlin; 2007, 121–144.
79. Cooter W, Rineer J, Bergenroth B. A nationally consistent NHDPlus framework for identifying interstate waters: implications for integrated assessments and interjurisdictional TMDLs. *Environ Manage* 2010, 46:510–524. doi: 10.1007/s00267-010-9526-y.
80. Wang LZ, Infante D, Esselman P, Cooper A, Wu DY, Taylor W, Beard D, Whelan G, Ostroff A. A hierarchical spatial framework and database for the National River Fish Habitat Condition Assessment. *Fisheries* 2011, 36:436–449. doi: 10.1080/03632415.2011.607075.



81. Wiens JA, Bachelet D. Matching the multiple scales of conservation with the multiple scales of climate change. *Conserv Biol* 2010, 24:51–62. doi: 10.1111/j.1523-1739.2009.01409.x.
82. Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM, Smith RI, Somerfield PJ, Watt AD. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol Evol* 2010, 25:574–582. doi: 10.1016/j.tree.2010.06.016.
83. Cressie N, Johannesson G. Fixed rank kriging for very large spatial data sets. *J R Stat Soc B* 2008, 70:209–226.
84. Van Belle G. *Statistical Rules of Thumb*, vol. 699. 2 ed. New York: John Wiley and Sons; 2011.
85. MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 2002, 83:2248–2255. doi: 10.2307/3072056.
86. Falke JA, Bailey LL, Fausch KD, Bestgen KR. Colonization and extinction in dynamic habitats: an occupancy approach for a Great Plains stream fish assemblage. *Ecology* 2012, 93:858–867.
87. Cressie N, Wikle CK. *Statistics for Spatio-Temporal Data*. Hoboken: John Wiley and Sons; 2011.
88. Sampson PD, Guttorp P. Nonparametric-estimation of nonstationary spatial covariance structure. *J Am Stat Assoc* 1992, 87:108–119. doi: 10.2307/2290458.
89. Herlihy AT, Larsen DP, Paulsen SG, Urquhart NS, Rosenbaum BJ. Designing a spatially balanced, randomized site selection process for regional stream surveys: The EMAP Mid-Atlantic Pilot Study. *Environ Monit Assess* 2000, 63:95–113. doi: 10.1023/A:1006482025347.
90. Courbois J-Y, Katz SL, Isaak DJ, Steel EA, Thurow RF, Wargo Rub AM, Olsen T, Jordan CE. Evaluating probability sampling strategies for estimating redd counts: an example with Chinook salmon (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci* 1814–1830, 2008:65. doi: 10.1139/f08-092.